Contextualizing chimpanzee research within the socioecological landscape of the Forestière region of the Republic of Guinea, Africa

Doctoral Thesis

by

Maegan Annette Fitzgerald

Wildlife Research Center

Kyoto University

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Chapter 1

General Introduction

Biodiversity is declining at an accelerating pace (Pimm et al. 2014). Much of this decline is attributed to increasing human demands for natural resources whereby our footprint far exceeds the earth's capacity to regenerate (Lin et al. 2018). Tropical forests harbor extremely high levels of biodiversity (Dirzo and Raven 2003; Gibson et al. 2011; Laurance et al. 2012). Due to human-driven land use changes, tropical forests are undergoing rapid loss, fragmentation, and modification (Gibson et al. 2011; Brockerhoff et al. 2017; Hansen et al. 2020). Studies have found that increased tree cover, both as part of forest canopy and agricultural landscapes, is correlated with increased levels of biodiversity (specifically species richness) and ecosystem function (Morris 2010; Mendenhall et al. 2016; Brockerhoff et al. 2017; Barrios et al. 2018) as well as human health (Johnson et al. 2013).

In 1995, the IUCN (International Union for Conservation of Nature) placed the *Pan troglodytes* taxon in the red list category of Endangered species. This listing included all four subspecies of chimpanzees: Western (*P.t. verus*), Central (*P.t. troglodytes*), Eastern (*P. t. schweinfurthii*), and Nigeria-Cameroon chimpanzee (*P.t. ellioti*). Since 1995, chimpanzee populations have continued to decline (Humle et al. 2016b). Western chimpanzee (*Pan troglodytes verus*) populations are estimated to have decreased by more than 80% from 1990 to 2014 (Kühl et al. 2017).

Similar quantifications of the decline in the other subspecies is yet to be done, but it is consistently reported that populations of all subspecies are decreasing (Oates et al. 2015; Maisels et al. 2016; Humle et al. 2016a; Plumptre et al. 2016). Given such a dramatic decline, western chimpanzees were uplisted to Critically Endangered (Humle et al. 2016a; Kühl et al. 2017). Thus, the western subspecies has the highest risk of extinction among chimpanzees. In 2019, the total western chimpanzee abundance was estimated to be 52,800 (95 % Confidence Interval: 17,577 – 96,564) (Heinicke et al. 2019). The geographic range of western chimpanzees spans across eight countries: Senegal, Guinea-Bissau, Mali, Republic of Guinea, Sierra Leone, Côte d'Ivoire, Liberia, and Ghana. Previously documented in Benin, Togo, and Burkina Faso, western chimpanzees are likely extirpated from these countries (Ginn et al. 2013; IUCN SSC Primate Specialist Group 2020). Their habitat covers a wide range of ecoregions, including West Sudanian savanna, Guinean forest-savanna mosaics, Guinean montane forests, Western Guinean lowland forests, and Eastern Guinean forests (Olson et al. 2001) (Fig. 1.1). The latter three ecoregions form part of the Upper Guinean Forest sub-region of the Guinean Forests of West Africa biodiversity hotspot (hereafter GFWA hotspot) (Fig. 1.1).

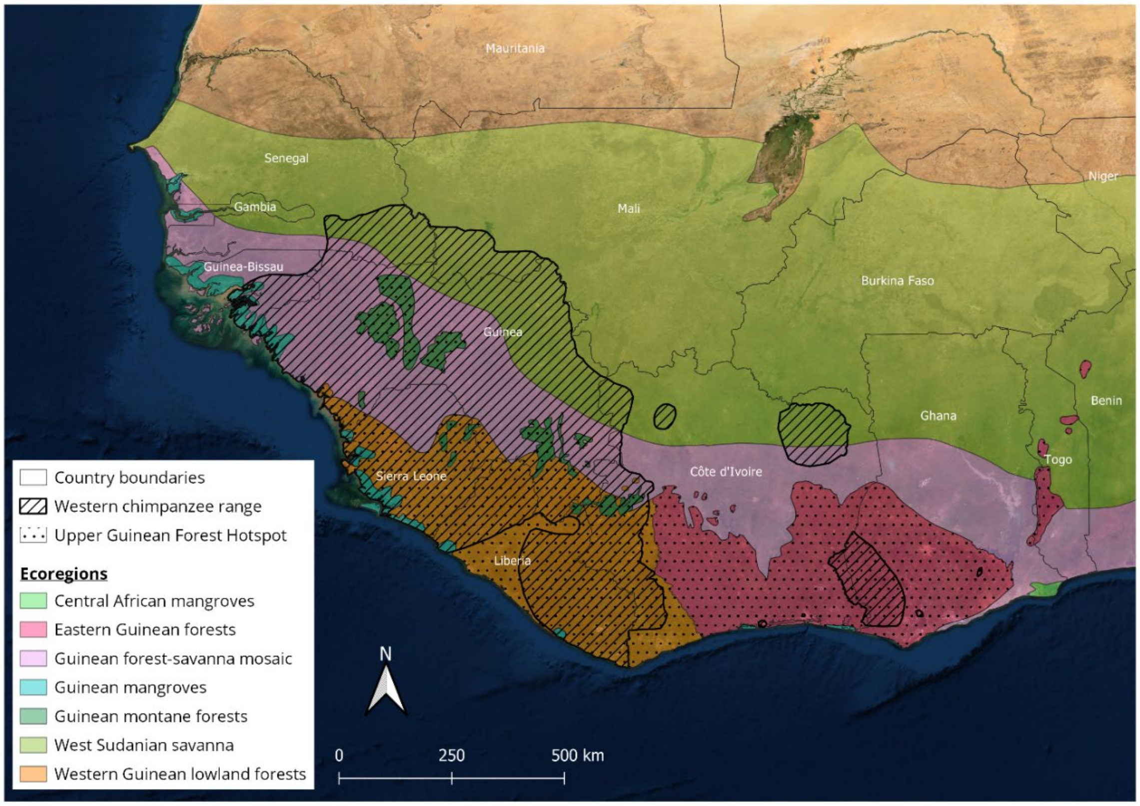


Fig. 1.1. The overlap of western chimpanzee range with terrestrial ecoregions and the Upper Guinean Forest hotspot. (Data sources for western chimpanzee range: (Humle et al. 2016b); country boundaries: Natural Earth @ naturalearthdata.com; Terrestrial ecoregions: (Olson et al. 2001); Upper Guinean Forest Hotspot: Mittermeier et al. 2004)

The GFWA hotspot stretches from southeast Guinea and Sierra Leone eastward to Cameroon and is divided in two sub-regions: Upper and Lower Guinean Forests (CEPF 2015). It has immense species diversity and high levels of endemism. Of the over 1,700 terrestrial animal species found there, more than 250 are endemic to the GFWA hotspot (CEPF 2015). Home to over a quarter of all the mammal species found in Africa, it is particularly notable for its high mammalian diversity, especially among primates (Mittermeier et al. 2004). The Republic of Guinea (hereafter Guinea) holds approximately

6% of the Upper Guinean Forest sub-region and is the north-westernmost edge of this hotspot (Fig. 1.1). It is also home to the largest remaining populations of the Critically Endangered western chimpanzees (Humle et al. 2016a; Heinicke et al. 2019).

Within Guinea, the majority of chimpanzees are concentrated in the Fouta Djallon area of La Moyenne-Guinée (approximately 17,700; Kühl et al., 2017), whereas the remaining chimpanzees are spread out across the country from Badiar in the northernmost of the country to the Nimba Mountains in the southeast (Heinicke et al. 2021). Not all of the locations where chimpanzee reside receive the same level of protection. For instance, the chimpanzee populations in the Nimba Mountains reside in an IUCN category I protected area (PA) that is part of both a UNESCO World Heritage Site (Mount Nimba Strict Nature Reserve) and a Biosphere Reserve. IUCN category 1 PAs are strictly protected and human use, impacts, and visitation are very limited (IUCN 2016). On the other hand, there are Classified Forests, such as Diécké, that are not explicitly listed under IUCN protected area categories, but have national management plans that confer some protection and limit the allowable activities within their borders (FAO 2010). It is estimated that there are 33,139 (95 % Confidence Interval: 8,796 – 68,203) chimpanzee in Guinea and that only 12% live in national parks or IUCN category I or II protected areas (Heinicke et al. 2019). The creation, support, and expansion of protected areas is considered fundamental to conserving chimpanzees (IUCN SSC Primate Specialist Group 2020) and overall biodiversity (CBD 2004; United Nations 2015).

The primary threats to western chimpanzees are habitat loss, disease, and hunting (IUCN SSC Primate Specialist Group 2020). Yet, how these threats are manifested and the social, political, and historical contexts behind these threats varies at the local and national levels. Likewise, the extent to which these threats affect chimpanzees varies by location. For example, cultural practices and religion can shape behaviors and attitudes towards chimpanzees. This, in turn, can influence the prevalence of hunting. In the Nimba Mountains of Guinea, although frequent signs of wildlife hunting are encountered, chimpanzees are likely not the intended target of hunting due to cultural beliefs by the Manon people living in the area (Kortlandt 1986). Such opportunistic hunting, like the setting of traps, can cause injuries to chimpanzees but this is not usually the intentions of such activities. Yet, such taboos are also not static in the face of changing cultures and dynamic ecological landscapes (Hicks et al. 2010; Hockings et al. 2012). In other areas of the western chimpanzee range, chimpanzees are hunted for medicinal purposes and cultural beliefs have more negative effects on chimpanzees (Kormos et al. 2003; IUCN SSC Primate Specialist Group 2020; Arcus Foundation 2021). Understanding these local distinctions in hunting is important when considering approaches to effective conservation.

Another example of the local, national and regional differences in specific threats can be found when assessing the drivers of habitat loss. For instance, agricultural expansion is a main driver of deforestation and therefore chimpanzee habitat loss in both Bossou, Guinea and the Bulindi area of Uganda. Yet what this agricultural expansion looks like and how it manifests itself is different between these two locations. In the Bulindi area (between the Budongo and Bugoma forest reserves), large-scale agriculture is driving deforestation (McLennan 2008). This has led to an increase in the area of agricultural land and comes on the back of a government push to reduce poverty through transitioning from subsistence to commercial agriculture (Arcus Foundation 2015). Such shifts do not typically lead to agricultural intensification (e.g. more production per unit of land), rather they lead to increases in the total farmed area (Arcus Foundation 2015). This resulted in the destruction of forested lands (and therefore chimpanzee habitat) in order to increase production and income. As habitat and the availability of wild food sources decreased, human-chimpanzee interactions increased (Arcus Foundation 2015). This has also led to decreased tolerance of chimpanzees, not only for fear of violent encounters, but also due to the greater economic losses incurred when chimpanzees damage valuable crops, like tobacco (McLennan and Hill 2012a).

In Bossou, the agricultural landscape is different but it also leads to habitat loss and intolerance of chimpanzees. Here, the chimpanzees live in a heavily impacted, anthropogenic landscape in which their core habitat is isolated to four hills (covering approximately 6 km^2) (Humle 2011). Surrounding these hills is a mosaic of secondary and riverine forests, cultivated fields, fallow areas, and coffee plantations (Bryson-Morrison et al. 2016). The cultivated fields are primarily small-scale subsistence agriculture, providing a mix of cultivars such as cassava (*Manihot esculenta*), rice (*Oryza* sp.), okra (*Zea mays*), and other fruits and vegetables (Bryson-Morrison et al. 2016). The coffee plantations are also small-scale, and beans are typically sold to neighboring communities and generate income (not purely subsistence farming). Similar to what occurred in the Bulindi area, human-chimpanzee interactions have increased and tolerance for chimpanzees has subsequently decreased (Hockings et al. 2012; Bryson-Morrison et al.

2016). Thus, despite the similar resulting phenomena, the specifics of what has caused habitat loss and changing perceptions of chimpanzees differ between sites. Likewise, the strategies to deal with these changes might also differ. The social, cultural, and political contexts that are threating the survival of chimpanzees are part of the human dimensions of the broader socioecological system, where people and nature are tightly coupled and interdependent (Bouamrane et al. 2016). Understanding the socioecological contexts in which chimpanzees exist is vital to the effectiveness of conservation actions (IPBES 2019).

In addition to studying the anthropogenic threats to chimpanzees' survival, it is vital to understand the behavior and ecology of chimpanzees in these socioecological systems. Knowledge of chimpanzee behaviors provides insights in to the ecological needs of chimpanzees. For instance, research on arboreal nesting in chimpanzees has shown that this behavior is found in all chimpanzee communities across all habitat types, including savanna–woodland mosaics (Badji et al. 2018), agricultural–swamp mosaics (Garriga et al. 2019), and primary forests (Koops et al. 2012b). Thus, trees, even those found in human-dominated and non-forest land cover types, such as savanna and woodland–shrubland mosaics, are critically important components of daily chimpanzee behavior. Buttress drumming is another chimpanzee behavior that is dependent upon trees, particularly large, buttressed trees that are often found in old-growth, primary forests. These are just two of many behaviors that demonstrate the reliance of chimpanzees on trees. Consequently, these insights into chimpanzee behavior, inform us that monitoring and protecting tree cover across habitat types is vital to protecting chimpanzees and their cultures.

This research focuses on two communities of chimpanzees in the Nimba Mountains, Guinea and the socioecological system in which they exist. These chimpanzee communities, hereafter Seringbara chimpanzees, inhabit an area of the mountains adjacent to the village of Seringbara, located about 6 km from Bossou (Koops 2011a) (Fig. 1.2). The Seringbara chimpanzees remain mostly unhabituated to humans as a result of the extremely rugged and mountainous terrain. Despite this, many years of research has provided extensive knowledge of Seringbara chimpanzees. For example, Koops et al. (2015) found that when Seringbara chimpanzees eat army ants (*Dorylus* sp.), they often eat one species more than expected (*D. nigricans*) and they selected for certain tool materials. They also used both tool sets (digging and dipping tools used sequentially) and composite tools (tree perches and digging/dipping tools used simultaneously) (Koops et al. 2015).

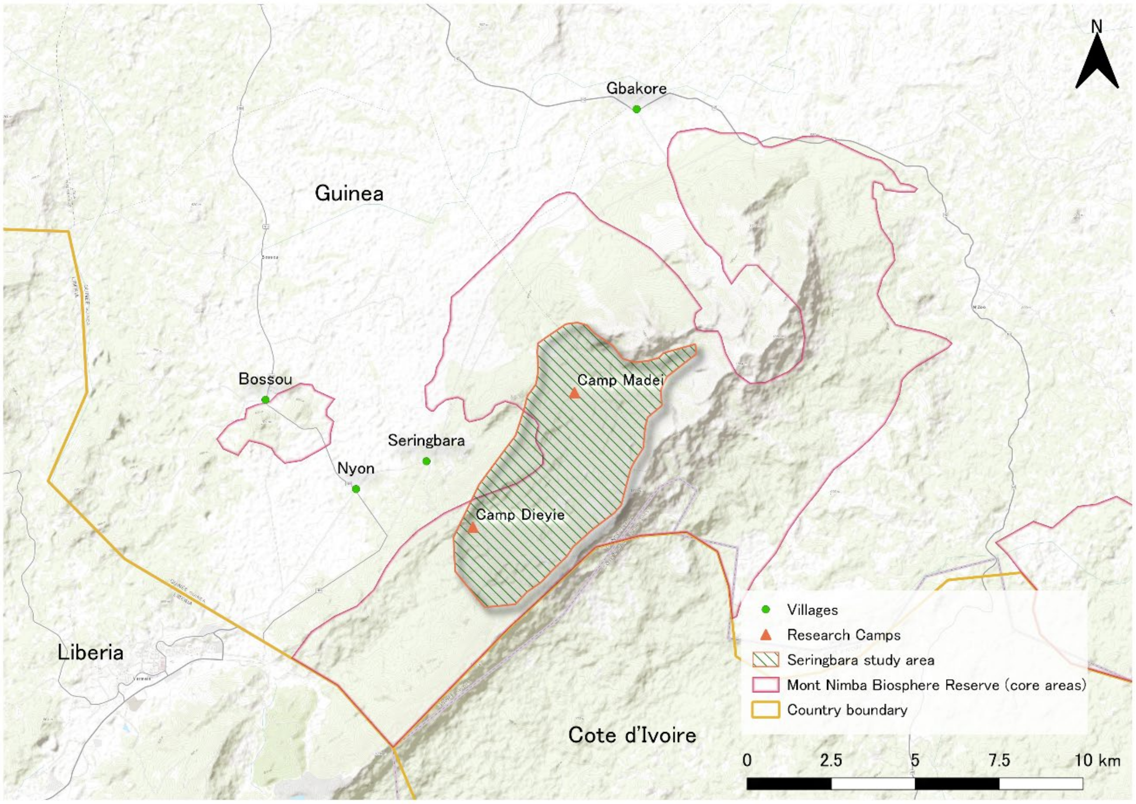


Fig. 1.2. Location of the Seringbara chimpanzee study area within the Nimba Mountains.

Research has also shown that the Seringbara chimpanzees prefer nesting at higher elevations and in primary forests (Koops et al. 2012a). They are also selective for large trees with dense canopy cover and they tend to avoid humidity by seasonally altering their within tree nesting height (Koops et al. 2012a). The Seringbara chimpanzees are also the only non-human apes to be documented habitually catching and eating freshwater crabs, termed crab-fishing (Koops et al. 2019). Additionally, knowledge of these chimpanzees has been obtained from motion-triggered cameras (camera traps). Van Leeuwan et al. (2020b) found that camera trap observations were suitable for measuring chimpanzee party size and composition. They also showed that fruit abundance and the presence of estrous females positively influenced party size in the Seringbara chimpanzees (van Leeuwen et al. 2020b). To effectively protect chimpanzees and their habitats, it is crucial to understand how chimpanzees perceive and respond to their environment. Further knowledge of the Seringbara chimpanzees' behavioral ecology will contribute to this understand and therefore their conservation.

This dissertation aims to contextualize chimpanzee studies within the larger socioecological landscape by integrating three studies. Chapter 2 investigates whether chimpanzees in the Nimba Mountains show selectivity in buttress drumming by comparing trees and buttresses used for drumming to those not used for drumming. This research provides a foundation for further assessing the cognitive underpinnings and functions of buttress drumming in wild chimpanzees and adds to the growing body of literature aiming to better understand chimpanzees in the Nimba mountains. It should be noted that the aim of the study was not to determine a single function of buttress drumming, but rather the study investigated the selectivity of trees and buttresses used by chimpanzees when drumming, which has never been analyzed before with respect to this particular behavior. The results tell us about one aspect of wild chimpanzees' perception and utilization of their environment.

In Chapter 3, chimpanzee behavioral data is used to evaluate how the spatial distribution of biophysical variables relates to the occurrence of chimpanzees in the Nimba Mountains. Specifically, Chapter 3 quantifies and maps the spatial distribution of biophysical variables within the study area using remotely sensed images, analyzes the importance of each biophysical variable in identifying suitable chimpanzee habitat, and employs species distribution modeling to identify areas most suitable for chimpanzees within the Nimba mountains and the surrounding landscape. This modeling effort tests the hypothesis that vegetation is one of the most important factors influencing the occurrence of great apes, including chimpanzees (Torres et al. 2010; Junker et al. 2012; Jantz et al. 2016). It also explores the importance of other biophysical variables, such as elevation, as they relate to the probability of Seringbara chimpanzee occurrence.

Chapter 4 is a remoting sensing based analysis of tree cover loss across the Guinée Forestière region of southeastern Guinea. The aim of this chapter is to contextualize areas of high biodiversity, including the Nimba Mountains, within the broader socioecological landscape of Guinée Forestière in order to better understand the threats to biodiversity, and therefore chimpanzees, and guide conservation. The specific objectives are to (1) use remotely sensed data to map and quantify tree cover loss across Guinée Forestière from 2000 to 2018 (2) estimate tree cover loss relative to PAs of high biodiversity, and (3) identify primary drivers of tree cover loss. Accuracy assessments are also carried out to ensure the robustness of the analyses.

By integrating chimpanzee behavioral data with remote sensing and modeling applications, this work not only contributes to a greater understanding of chimpanzee behavior and use of the landscape, but it situates this knowledge within the broader socioecological contexts in which chimpanzees exist. Specifically addressing the anthropogenic drivers of tree cover loss (part of the social system) that threaten the survival of not only chimpanzees, but biodiversity (the ecological system) across the

Forestière region of Guinea. This research provides knowledge needed for more effective and sustainable chimpanzee conservation in the Nimba landscape.

Chapter 2

To drum or not to drum: Selectivity in tree buttress drumming by chimpanzees (*Pan troglodytes verus*) in the Nimba Mountains, Guinea

2.1 Introduction

Wild chimpanzees have a fission-fusion social organization (Goodall 1968; Nishida 1968; Mitani et al. 2002; Aureli et al. 2008). Chimpanzees live in social groups called 'communities', which range in membership from 7 (Bossou, Guinea) to approximately 200 individuals (Ngogo, Kibale, Uganda; Langergraber et al. 2017). Within communities, chimpanzees form temporary sub-groups, or parties, of varying size depending on resource availability, mating opportunities, and predation pressures (Boesch 1991a; Chapman et al. 1995; Newton-Fisher et al. 2000; Anderson et al. 2002; Lehmann and Boesch 2004; Itoh and Nishida 2007). Chimpanzee party size, composition, and spatial distribution are thus constantly in flux. A vast repertoire of vocal and non-vocal forms of communication, ranging from pant-hoots and grunts to body gestures (Slocombe and Zuberbühler 2011; Hobaiter and Byrne 2017), allow chimpanzees to convey information in such a socially and spatially dynamic setting.

Chimpanzees drum (hit) on tree buttresses, large above ground roots (Fig. 2.1), with hands and/or feet (hereafter buttress drumming) to produce acoustic signals (Reynolds and Reynolds 1965; Goodall 1968, 1986; see https://youtu.be/rUWncJMIaZY and https://youtu.be/U5BpFAL5GNo for drumming videos). These low-frequency drum sounds, that often times occur in sequence with pant hoot vocalizations, are presumed to play a role in long-distance communication between separated individuals and are often associated with travel (Boesch 1991b; Arcadi et al. 1998, 2004; Arcadi and Wallauer 2013; Babiszewska et al. 2015). Yet, the function of buttress drumming is not fully understood. In addition to long distance communication, it has also been referred to as a dominance display behavior (Goodall 1968, 1986; Nishida et al. 1999). Yet, the function of buttress drumming is not fully understood. In addition to long distance communication, it has also been referred to as a dominance display behavior (Goodall 1968, 1986; Nishida et al. 1999). Buttress drumming occurs in all studied wild chimpanzee populations and is considered a chimpanzee universal (McGrew 2013). As it is one of only a few forms of chimpanzee communication that depends upon a substrate to convey information (see also accumulative stone throwing, Kalan et al. 2019), buttress drumming in semi-habituated or unhabituated communities lends itself well to exploring behavioral selectivity in wild chimpanzee communication.

Selectivity is an attribute of goal-directed behavior, whereby an animal makes choices to achieve a particular outcome (Seed and Byrne 2010). Chimpanzees are renowned for their use of tools in various contexts and have been found to select tools with functional characteristics needed for a specific task. For instance, chimpanzees prefer to use specific plant species to make dipping tools when preying on aggressive army ants (Koops et al. 2015). Selectivity for tool material and tool characteristics is common across a wide range of chimpanzee tool use behaviors (termite fishing: Almeida-Warren et al. 2017; Sanz and Morgan 2007; nut cracking: Boesch et al. 2017; Carvalho et al. 2009; Sirianni et al. 2015; ant dipping: Koops et al. 2015; honey extraction: Boesch et al. 2009).

Tool selectivity is not limited to chimpanzees, but occurs in other primate species, as well as in other taxa. Bearded capuchin monkeys (*Cebus libidinosus*) select stones of certain material and weight to crack open nuts (Visalberghi et al. 2007, 2009; Schrauf et al. 2008). New Caledonian crows (*Corvus moneduloides*) choose specific plant species from which to make hooked stick tools (Klump et al. 2019). Moreover, selectivity extends beyond tool use to other types of behaviors. Chimpanzees, along with the other non-human great apes, make sleeping platforms, or nests, and exhibit preferences for specific tree species, tree characteristics, and nest sites in nest building (chimpanzees: Koops et al. 2012a; Sanz et al. 2007; Stanford and O'Malley 2008; gorillas: Mehlman and Doran 2002; bonobos: Mulavwa et al. 2010). By investigating if, and how, selectivity exists in a certain type of behavior, researchers are better able to elucidate the function or goal of that behavior.

Compared to other chimpanzee behaviors, drumming has been relatively understudied. A handful of studies have reported the acoustic characteristics and social factors affecting drumming behavior (Arcadi et al. 1998, 2004; Arcadi and Wallauer 2013; Babiszewska et al. 2015), but none so far have looked at the characteristics of the drumming tree itself. Related research has reported that chimpanzees at some study sites throw rocks at trees, referred to as accumulative stone throwing, or AST (Kühl et al. 2016). Kalan and colleagues (2019) measured the sound produced when a thrown rock impacts a tree. Impact sounds from AST trees were found to be more resonant than non-AST trees, a quality well-suited for propagating over long-distances. Hence, trees used in stone throwing have acoustic qualities suited for long-distance communication, one of the suspected functions of AST.

Here we investigate whether chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea, West Africa, show selectivity in buttress drumming. If buttress drumming is goal-directed, for example to communicate over long distances, we predict that chimpanzees will show preference for certain species and will select trees that are larger and have more buttresses Moreover, we hypothesize that used buttresses will have larger surface areas (i.e. more area upon which a chimpanzee can drum) and used buttresses will be thinner, as they are more pliant and conducive to producing resonant sounds when impacted (Kalan et al. 2019). Note that the aim of the study is to assess selectivity in chimpanzee buttress drumming, which would be present if the behavior is goal-directed. Results will not determine a single function of the behavior, nor will they eliminate any possible functions, such as long-distance communication, display, or any other function. The presence or absence of selectivity will allow us to make inferences about the function of buttress drumming.

2.2 Methods

2.2.1 Study site

The Mont Nimba Strict Nature Reserve (Mt. Nimba SNR) is classified as a UNESCO World Heritage Site in Danger (World Heritage Committee 2017). It encompasses most of the Nimba Mountain range in Guinea and much of the range in Côte d'Ivoire. The range, in its entirety, forms a natural border between Guinea, Côte d'Ivoire, and Liberia. Covering approximately 175 km^2, the reserve is dominated by wet, montane forests with diverse topographical features including rocky peaks, rough cliffs, steep river valleys, and high-altitude savannahs (Koops 2011b). The reserve is home to a variety of flora and fauna, including the Critically Endangered western chimpanzee (*P.t. verus*) (World Heritage Committee 2017).

The Seringbara study site (N07.634°, W08.425°), spanning about 30 km^2, is located on the Guinean side of the Mt. Nimba SNR (Fig. 1.2). The site is largely composed of dense, primary tropical forests, with elevation ranging from 595 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. 2012a).

We studied two communities of chimpanzees (i.e. Gahtoy and Tongbongbon), known as the Seringbara communities (Koops 2011b; van Leeuwen et al. 2020b). The Seringbara communities have been the focus of research and conservation efforts since 2003 (Koops 2011a) with intermittent ecological studies and surveys reaching back to 1996 (Matsuzawa and Yamakoshi 1996; Humle and Matsuzawa 2001, 2004). Despite the many years of study, the chimpanzees remain mostly unhabituated to humans as a result of the extremely rugged and mountainous terrain (Koops and Matsuzawa 2006; Koops 2011a).

2.2.2 Data collection

From January 2012 to April 2014 (27 months total), research teams surveyed the study area, collecting ecological and behavioral data on the Seringbara chimpanzee communities. Researchers maintained a nearly constant presence in the forest during this period, missing data collection for only 1–2 days a month. Data collection included tracking and observing chimpanzees, as well as monitoring a grid of motion-triggered camera traps. Although direct observations of drumming bouts were extremely rare, we were able to identify trees that were drummed on (hereafter drum trees) by the traces left on the buttresses, namely dirt residue and noticeable wearing of the buttress surface (Fig. 2.2). We validated our use of these traces to identify drum trees by placing motion-triggered camera traps (Bushnell Trophy Cam) at four suspected drum trees. At these trees, the place of drumming on the buttress was confirmed using motion-triggered camera videos. We therefore consider the occurrence of use traces on buttresses to be an accurate indication that chimpanzees drummed on a given tree and buttress.

We collected the following data for each drum tree (N = 24):

1. Tree species name.
2. Diameter at breast height, DBH (m), measured around the trunk above buttresses with a DBH tape measure (in some instances this was above breast height).
3. Number of individual buttresses per tree.

For each tree buttress, we collected the following data:

1. Surface area (m^2), measurements of the height and base length of a buttress were taken to calculate surface area of one buttress side. Measured with a tape measure. Although this measurement is not exact, it was standardized and provides an estimate of buttress surface area. In some cases, a buttress may have a smaller buttress protruding from it. If so, the smaller buttress

was measured as a separate buttress and its height was measured from the ground to the point of entry into the larger buttress. Additionally, buttresses that were too small to allow researchers to hit with an open palm (approximately 20 cm^2) were deemed unusable and neither measured nor recorded as a buttress.

2. Thickness (m), three measurements were taken with a tape measure along the ridge of the buttress (one near the top of the buttress, one near the middle, and one near the bottom) and then averaged. This was consistent across all measured trees.
3. Used for drumming or not (0/1). Hereafter referred to as used or unused buttresses.

For each drum tree, we set up a 20 m x 20 m vegetation plot with the drum tree at the center of the plot. Within these plots (N = 20), we recorded the species name, and DBH for all trees with a DBH ≥ 10 cm. If any of these trees had buttresses, but lacked evidence of drumming, they were measured as 'potential drum trees' and used as control trees (N = 51). We compared measurements of 'drum trees' to 'control trees' and 'used buttresses' to 'unused buttresses', as discussed below. Note that the number of plots (N = 20) does not equal the total number of drum trees (N = 24). The research project was paused in April 2014, due to the region's Ebola outbreak, and therefore some drum trees did not have vegetation plots.

2.2.3 Data analysis

We tested data for normality using the Shapiro-Wilk's test (Shapiro & Wilk, 1965). All data were non-normal so we used non-parametric statistical tests. All analyses were performed in R 4.0.3 (R Core Team, 2020) and Microsoft Excel (2016). We used Wilcoxon rank sum tests to compare DBH, and the number of buttresses between drum trees and control trees. We also used Wilcoxon rank sum tests to determine if there was a difference between the surface area and thickness of used buttresses compared to unused buttresses. A significance level of 0.05 was used for all tests.

To evaluate drumming tree species preference, we calculated Manly's α:

$$\alpha_i = \frac{r_i}{n_i} * \frac{1}{\Sigma(\frac{r_j}{n_j})}$$

where

α_i Manly's α for tree species *i*

r_i , r_j proportion of tree species *i* or *j* used for drumming (*i* and *j* = 1, 2, 3, …, *m*)

n_i , n_j proportion of tree species *i* or *j* available in the plot

m number of species available for drumming, established on the basis of plot data

This index allows us to assess chimpanzee preference for drumming tree species by taking into consideration a tree's usage for drumming given the prevalence, or availability, of different tree species. A Manly's α of 1/*m* is considered a neutral preference, whereas $\alpha > 1/m$ indicated a species is preferred and an $\alpha < 1/m$ indicated a species was not preferred. For further details on the use of Manly's α index to assess nest tree species preference, see

Brownlow et al., 2001, Furuichi & Hashimoto, 2004, Koops et al., 2012, and Mulavwa et al., 2010.

2.3 Results

Seringbara chimpanzees exhibit selectivity in buttress drumming. There was a significant difference (Wilcoxon rank sum test: W = 270.5, $P < 0.001$, Fig. 2.3A) in DBH between drum trees (N = 24, mean = 86 ± 35, median = 81) and control trees (N = 51, mean = 54 ± 25, median = 50). There was also a significant difference (Wilcoxon rank sum test: W = 207.5, $P < 0.001$, Fig. 2.3B) in the number of buttresses per tree between drum trees (N = 24, mean = 7 ± 4, median = 7) and control trees (N = 51, mean = 4 ± 2, median = 4).

We found a significant difference (Wilcoxon rank sum test: W = 3923, $P < 0.001$, Fig. 2.4A) between the surface area (m^2) of used (N = 40; mean = 4.34 ± 4.66, median = 2.67) and unused buttresses (N = 334; mean = 2.36 ± 2.87, median = 1.33). The thickness (cm) of used (N = 40; mean = 5.65 ± 2.74, median = 4.83) and unused buttresses (N = 334; mean = 7.61 ± 4.87, median = 6.33) was also significantly different (Wilcoxon rank sum test: W = 8413, $P = 0.0073$, Fig. 2.4B). Overall, drum trees had a larger diameter at breast height, and more buttresses than control trees and buttresses used for drumming were generally thinner and had a larger surface area than unused buttresses (Fig. 2.3 and 2.4, Table 2.1).

Additionally, chimpanzees showed preference for certain species of trees for drumming. In total, there were 100 identified trees species within the recorded vegetation plots. Only 36 species had buttresses and of those, 10 species were used for drumming. All buttressed tree species which were used for drumming were preferred (Manly's $\alpha > 0.028$) (see Table 2.2). We then assessed whether there was a significant difference between the dbh, number of buttresses, and surface areas of buttresses of preferred species compared to species that were not preferred. It is important to note that preference for a particular tree species does not equate to use of that species. For example, *P. bicolor* is a preferred species for drumming, but not all trees of this species are used for drumming (Table 2.2). There was a significant difference (Wilcoxon rank sum test: W = 513.5, $P = 0.045$, Fig. 2.5A) in DBH of preferred (N = 38; mean = 72.21± 35.47, median = 72.5) and non-preferred species (N = 37; mean = 55.97 ± 25.04, median = 55.0). There was also a significant difference (Wilcoxon rank sum test: W = 374, $P < 0.001$, Fig. 2.5B) in the number of buttresses per tree between preferred (N = 38, mean = 6 ± 4, median = 6) and non-preferred species (N = 37, mean = 4 ± 2, median = 4). The surface area (m^2) of buttresses on preferred species (N = 231; mean = 3.30 ± 3.61, median = 2.00) and buttresses on non-preferred (N = 143; mean = 1.4 ± 1.7, median = 0.94) was also significantly different (Wilcoxon rank sum test: W = 9555.5, $P < 0.001$, Fig. 2.5C).

2.4 Discussion

Our findings indicate that chimpanzees show selectivity in buttress drumming. This finding implies that drumming is not a random act, but rather goal-oriented and requiring knowledge of suitable trees and buttresses. In particular, the Seringbara chimpanzees prefer specific tree species and are selective for tree and buttress characteristics. A number of tree species were preferred both when comparing drum trees to all trees available, but also when comparing to buttressed trees only. Preferred species tended to have larger dbh, more buttresses, and buttresses with larger surface areas. Drum trees were found to have a larger DBH compared to nearby control trees (i.e. trees with buttresses not used for drumming). Likewise, drum trees had more buttresses than control trees. From these characteristics, we can generalize to say that chimpanzees prefer to use larger trees for drumming. This makes intuitive sense given that buttressed trees generally are larger than many non-buttressed trees and given that having more buttresses to choose from may increase the likelihood that a tree is drummed upon.

Additionally, Seringbara chimpanzees preferred tree buttresses with larger surface areas and thinner width. Although we did not measure acoustic properties of each buttress, such as stiffness or dampening capacity (Roohnia 2016), we predict that surface area and thickness are important factors influencing a buttress' acoustic (mechanical) properties and the sound signals it is capable of producing when struck. These two measures are further predicted to impact the propagation of the drum sound across a landscape and the extent to which information is communicated. This is analogous to how properties of the batter head and the shape of the shell determine the volume and therefore the sound produced by a snare or bass drum (Yamaha Corporation 2020). Future research will address exactly how tree and buttress characteristics impact the tree's acoustics and thereby sound propagation. A study on accumulative stone throwing (AST) by chimpanzees showed that AST trees appear to have acoustic properties that produce sounds better suited for long-distance communication, one of the suspected functions of AST (Kalan et al. 2019). A similar experimental approach could be taken for buttress drumming, although accurately reproducing a chimpanzee drum may be challenging. Nevertheless, chimpanzee selectivity for buttress surface area and thickness indicates that chimpanzees are selecting buttresses with certain qualities that impact sound production, which suggests that long-distance communication is indeed one function of this behavior.

Drumming has long been suggested to be a form of long distance communication and plays a role in information exchange between spatially separated individuals (Boesch 1991b; Arcadi et al. 1998, 2004; Arcadi and Wallauer 2013; Babiszewska et al. 2015). Yet, much of this is anecdotal and based on drums being low frequency sounds, similar to bass drums. No studies to date have quantitatively shown the extent to which chimpanzee drums propagate in a given landscape. The propagation of sound is dependent on many factors, such as ambient noise, atmospheric conditions, attenuation based on habitat or landscape characteristics, and the sound source (Waser and Waser 1977; Richards and Wiley 1980; Waser and Brown 1986; Brown and Waser 2017; Farina 2019). In this study, we focused on understanding aspects of the sound source and the behavioral selectivity exhibited in drumming. Our study provides a strong foundation for future research assessing the propagation of chimpanzee drum sounds across the landscape and thereby quantitatively addressing whether drumming is an effective long-distance communication modality relative to other forms of chimpanzee communication. Such research could start by investigating the potential selectivity of drumming sites and how location in a rugged, mountainous environment, like the Nimba mountains, impacts sound propagation. For example, future research could assess whether selected drumming sites are located along ridges, valleys, or slopes as this would alter the potential propagation of a drum across the landscape.

Studying and understanding the complex behavioral repertoire of chimpanzees provide insight into the chimpanzee mind. Selectivity in buttress drumming suggests this behavior is goal-directed and in particular the results indicate that one such goal is long-distance communication. Along with the short list of studies on buttress drumming (Boesch 1991b; Arcadi et al. 1998, 2004; Arcadi and Wallauer 2013; Babiszewska et al. 2015), our research provides a foundation for further assessing the cognitive underpinnings and functions of buttress drumming.

2.6 Figures

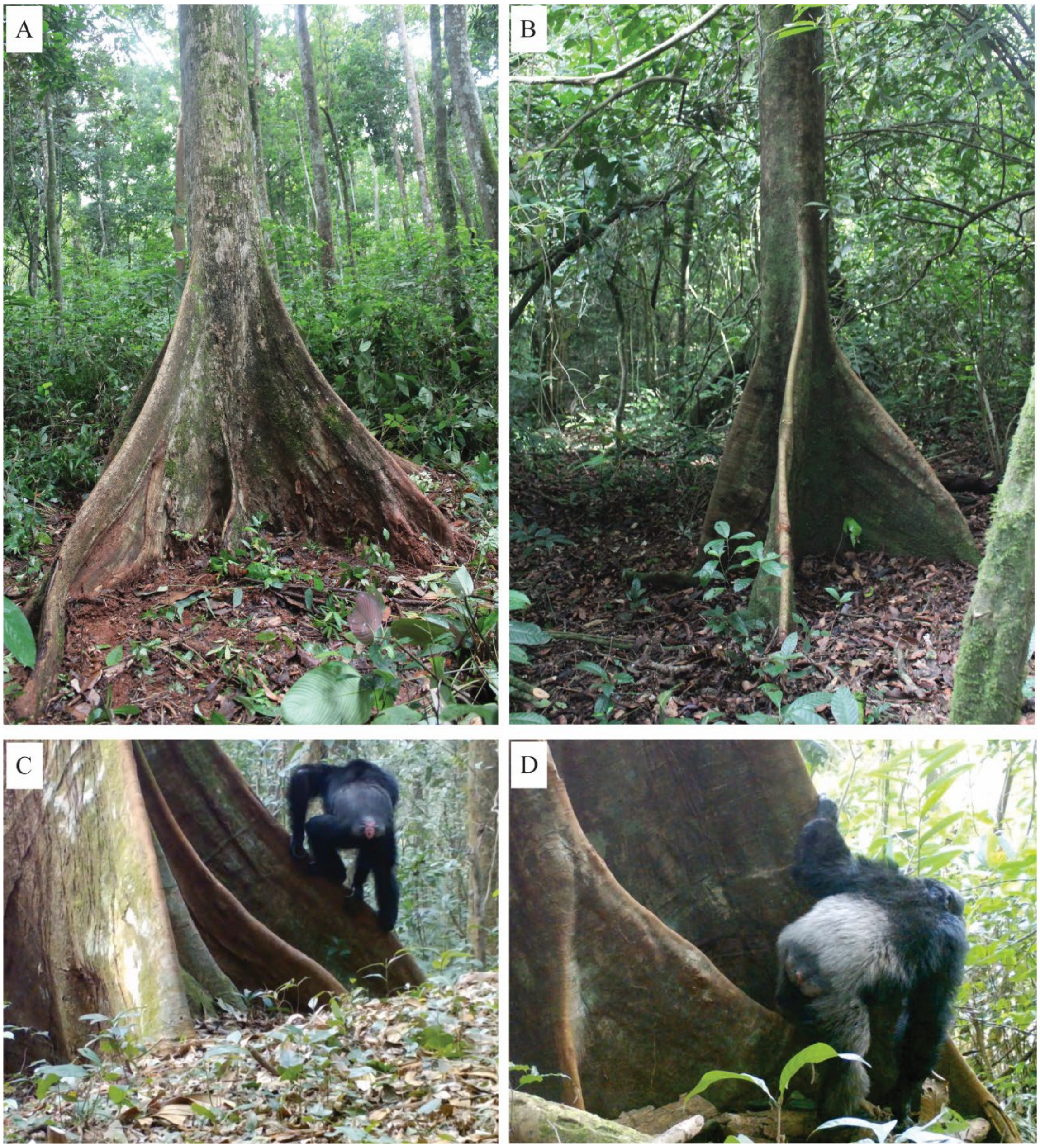


Fig. 2.1 Four buttressed trees in the Nimba Mountains, Guinea. The top two photos (A and B) are pictures of drum trees taken by the research team. The bottom photos (C and D) are still shots from motion-triggered

camera trap videos after chimpanzees drummed. (Photos © M. Fitzgerald) Visit https://youtu.be/rUWncJMIaZY and https://youtu.be/U5BpFAL5GNo for videos of C and D (respectively).

Fig. 2.2 Drumming traces (dirt residue and noticeable wearing of buttress surfaces) present on two drum trees.

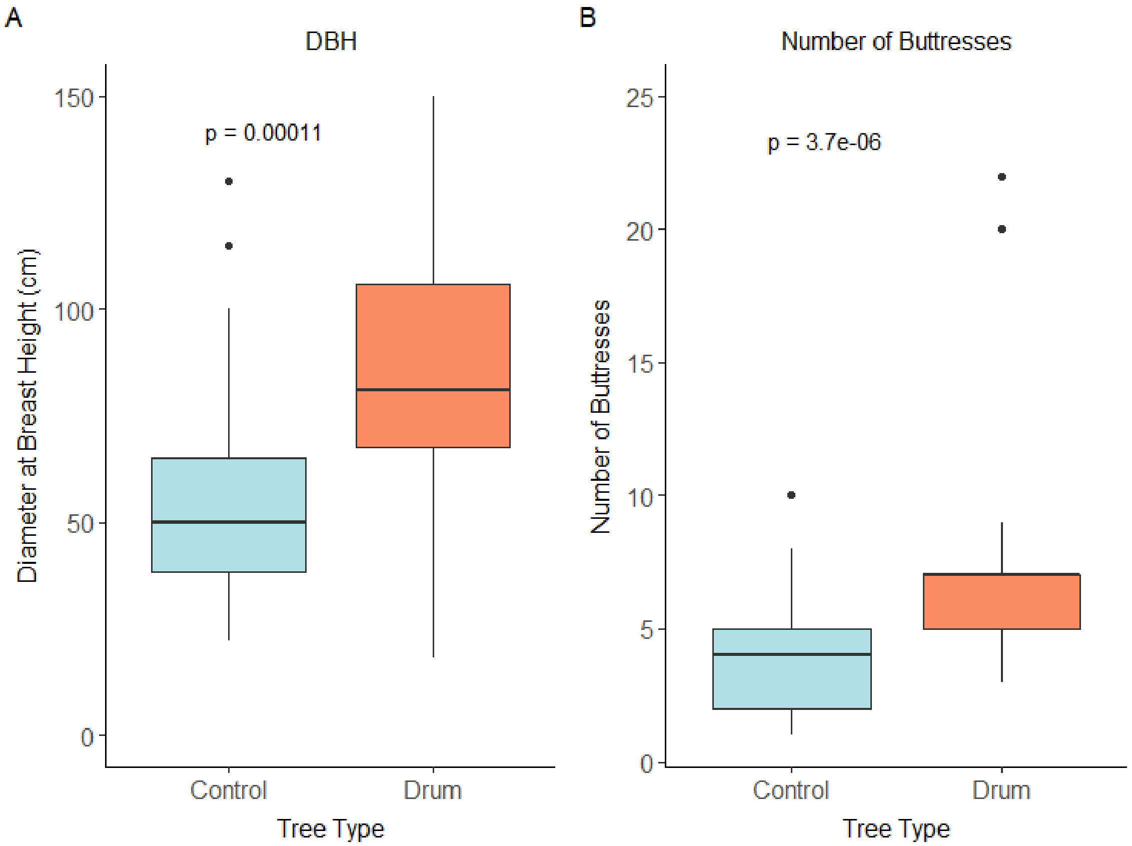


Fig. 2.3 Boxplots showing the diameter at breast height (A), and number of buttresses (B) for drum trees and control trees.

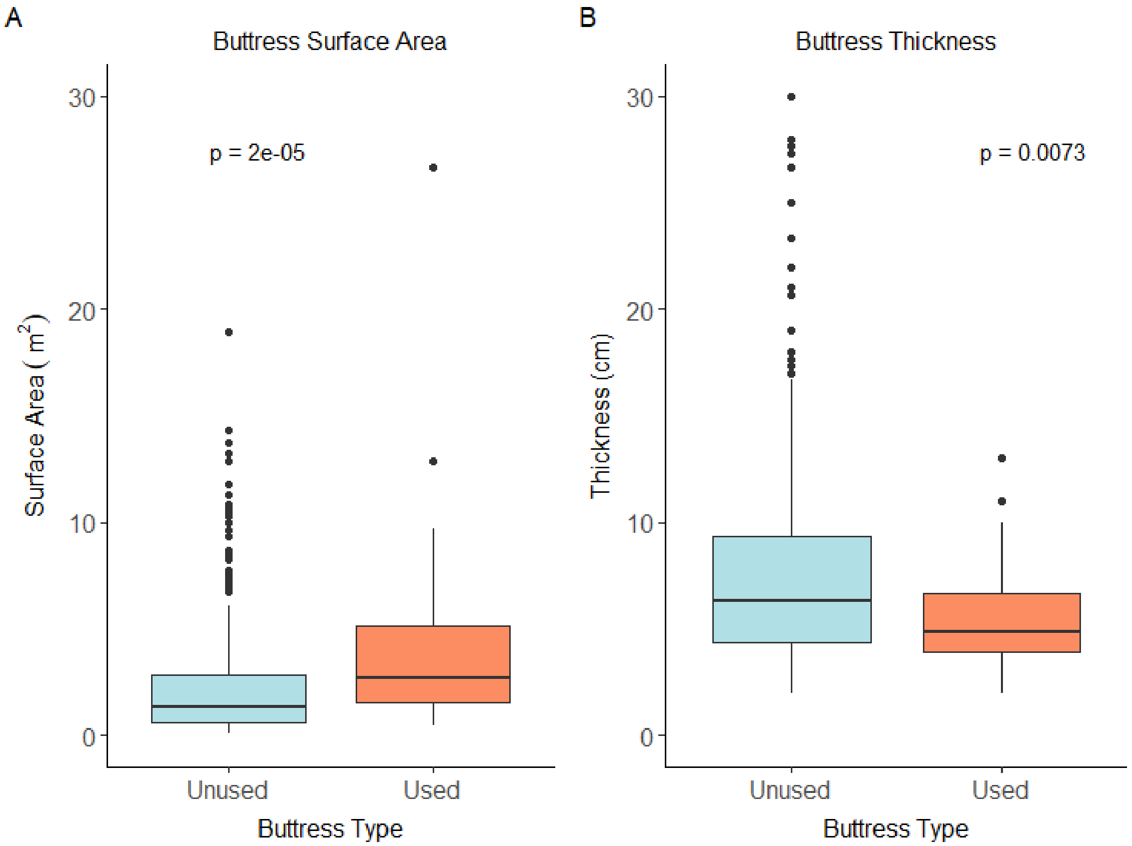


Fig. 2.4 Boxplots showing the surface area (A) and thickness (B) for buttresses used for drumming and buttresses not used for drumming.

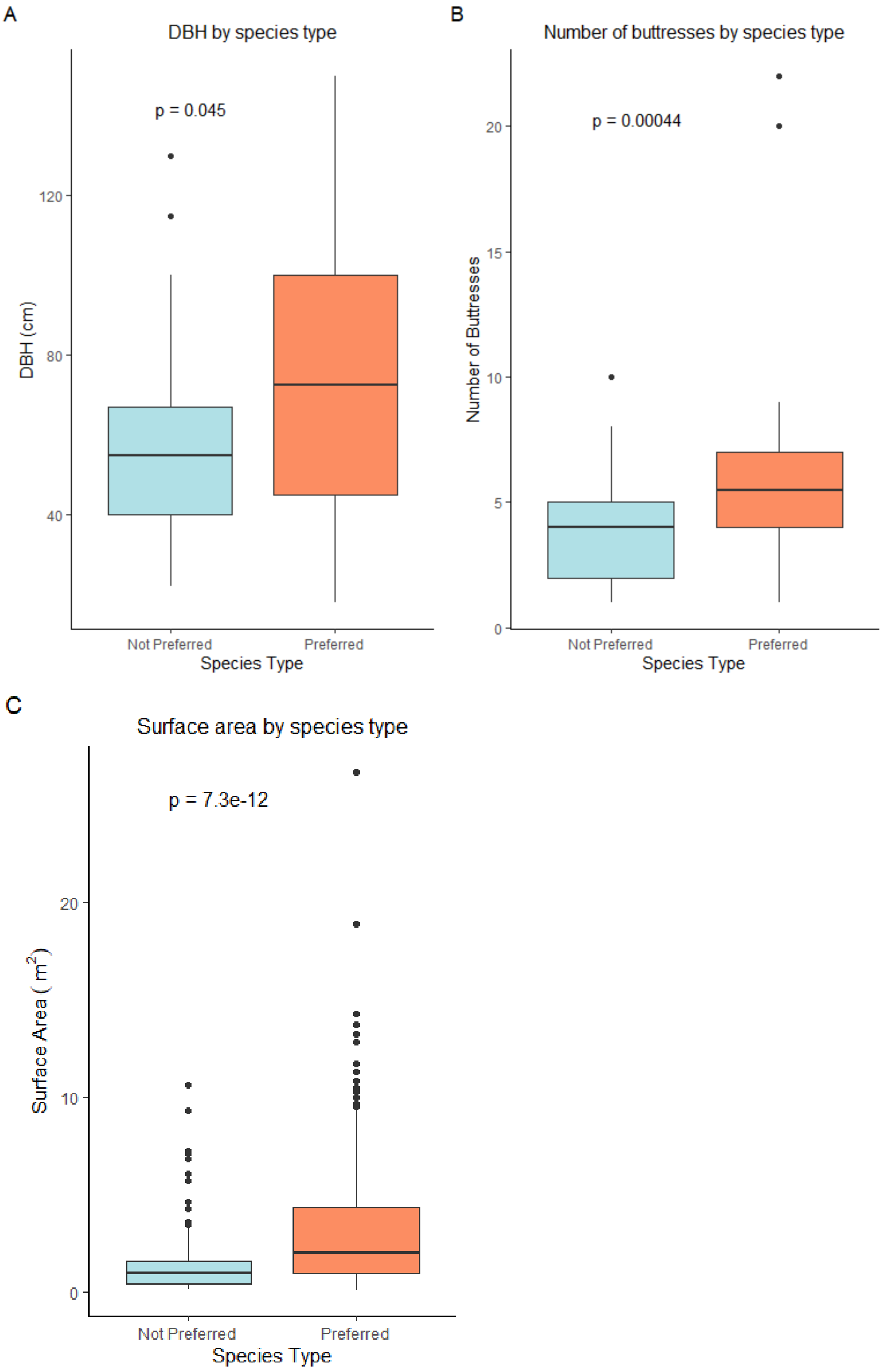

A
DBH by species type
p = 0.045
DBH (cm)
40
80
120
Not Preferred
Preferred
Species Type
B
Number of buttresses by species type
p = 0.00044
Number of Buttresses
0
5
10
15
20
Not Preferred
Preferred
Species Type
C
Surface area by species type
p = 7.3e-12
Surface Area (m^2)
0
10
20
Not Preferred
Preferred
Species Type

Fig. 2.5 Boxplots showing the DBH (A), number of buttresses (B), and buttress surface area (C) for species that were preferred and species that were not preferred. See Table 2.2 for a list of the preferred species.

2.7 Tables

Table 2.1 Summary statistics for tree and buttress characteristics

	Type	N	Mean (± SD)	Median	Max – Min
DBH (cm)	Control	51	54 (± 25)	50	22 – 130
	Drum	24	86 (± 35)	81	18 – 150
No. Buttresses	Control	51	4 (± 2)	4	1 – 10
	Drum	24	7 (± 4)	7	3 – 22
Surface area (m^2)	Unused	334	2.36 (± 2.87)	1.33	0.08 – 18.91
	Used	40	4.34 (± 4.66)	2.67	0.48 – 26.70
Thickness (cm)	Unused	334	7.61 (± 4.87)	6.33	2.0 – 30.0
	Used	40	5.65 (± 2.74)	4.83	2.0 – 13.0

Table 2.2 Tree species preference when comparing tree species used for drumming (N = 10) with all buttressed tree species (N = 36) recorded in vegetation plots. DT = drum tree.

Scientific name	**Family**	**Trees (*N*)**	**Trees (%)**	**DT (*N*)**	**DT (%)**	**Manly's α**	**Pref.**
Terminalia ivorensis	Combretaceae	1	1.37	0	0	0	-
Terminalia superba	Combretaceae	3	4.11	2	8.33	0.10	+
Piptadenia africana	Fabaceae	5	6.85	5	20.83	0.15	+

Chrysophyllum africanum	Sapotaceae	4	5.48	1	4.17	0.04	+
Grewia villosa	Tiliaceae	1	1.37	0	0	0	-
Pycnanthus angolensis	Myristiaceae	1	1.37	0	0	0	-
Amanoa bracteosa	Euphorbiaceae	1	1.37	0	0	0	-
Neolemonniera clitandrifolia	Sapotaceae	1	1.37	0	0	0	-
Heritiera utilis	Malvaceae	1	1.37	0	0	0	-
Pterocarpus santalinoides	Fabaceae	1	1.37	0	0	0	-
Trichoscypha chevalieri	Anacardiaceae	2	2.74	0	0	0	-
Morus mesozygia	Moraceae	1	1.37	0	0	0.00	-
Blighia welwitschii	Sapindaceae	2	2.74	0	0	0	-
Xylia evansii	Fabaceae	3	4.11	2	8.33	0.10	+
Klainedoxa gabonensis	Irvingiaceae	3	4.11	2	8.33	0.10	+
Newtonia aubrevillei	Fabaceae	1	1.37	0	0	0	-
Triplochiton scleroxylon	Malvaceae	1	1.37	1	4.17	0.15	+
Parinari excelsa	Chrysobalanaceae	1	1.37	0	0	0	-
Parkia bicolor	Fabaceae	10	13.70	6	25.00	0.09	+
Celtis adolfi friderici	Ulmaceae	1	1.37	0	0	0	-
Trichilia emdica	Meliaceae	4	5.48	0	0	0	-
Antiaris africana	Moraceae	1	1.37	0	0	0	-
Ituridendron bequaertii	Sapotaceae	1	1.37	0	0	0	-
Fagara sp.	Rutaceae	1	1.37	0	0	0	-
Ficus exasperata	Moraceae	1	1.37	0	0	0	-
Chidlowia sanguinea	Fabaceae	2	2.74	0	0	0	-
Samanea utilis	Fabaceae	1	1.37	0	0	0	-
Synsepalum afzelii	Sapotaceae	1	1.37	0	0	0	-

Sterculia tragacantha	Malvaceae	1	1.37	0	0	0	-
Claoxylon hexandrum	Euphorbiaceae	1	1.37	0	0	0	-
sp. unknown	unknown	1	1.37	0	0	0	-
Chrysophyllum perpulchrum	Sapotaceae	3	4.11	2	8.33	0.10	+
Chrysophyllum giganteum	Sapotaceae	4	5.48	1	4.17	0.04	+
Pouteria altissima	Sapotaceae	2	2.74	2	8.33	0.15	+
Alstonia congensis	Apocynaceae	1	1.37	0	0	0	-
Manilkara obovata	Sapotaceae	4	5.48	0	0	0	-

Manly's α = preference index for tree species. $m = 0.028$, thus Manly's α values > 0.028 are preferred (+) and values < 0.028 are not preferred (-). DT = Drum Tree.

Chapter 3

Modeling Habitat Suitability for Chimpanzees (*Pan troglodytes verus*) in the Greater Nimba Landscape, Guinea, West Africa

3.1 Introduction

In 1995, the IUCN (International Union for Conservation of Nature) placed the *Pan troglodytes* taxon in the red list category of Endangered species. This listing included all four subspecies of chimpanzees: Western (*P.t. verus*), Central (*P.t. troglodytes*), Eastern (*P. t. schweinfurthii*), and Nigeria-Cameroon chimpanzee (*P.t. ellioti*). Since 1995, populations have continued to decline (Humle et al. 2016b). The current estimate of the total population size of chimpanzees is approximately 200,000 individuals. This estimate indicates a 66% decline over a 30-year span (Kormos et al. 2003). Of the four subspecies, the western chimpanzee is the only subspecies listed as Critically Endangered (Humle et al. 2016a). Since 1990, the population size of western chimpanzees has declined approximately 80% (Kühl et al. 2017). The principal threats to western 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 (Kormos et al. 2003; Humle et al. 2016a). In recognition of the negative effects of habitat destruction and loss of biodiversity, protected areas (PAs) have historically been established in Guinea. 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 resides in these areas. The rest lives outside of PAs (Kormos et al. 2003).

Protected areas are impacted by 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 (approximately 1% of the reserve area) and 21.7 km^2 within a 10 km buffer zone around the reserve (Allan et al. 2017). Laurance et al. (2012) found that changes both within and outside PAs influence 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, threatening healthy, viable populations (Morin et al. 1994). Moreover, competition for land and resources leads to increases in human–chimpanzee interaction and conflict (McLennan and Hill 2012b; Hockings et al. 2015). For example, in Bossou, Guinea, where there are few forested areas, the chimpanzees rely heavily on cultivars (cassava, papaya, and bananas), terrestrial herbaceous vegetation (Zingeberaceae and Marantaceae families), and oil palm (*Elaeis guineensis*) during periods of fruit scarcity (Humle 2011). Many of these alternative food sources are in human settlements, so increased reliance accelerates human–chimpanzee conflict (Humle 2011). A decrease in forested areas due to human encroachment will result in an increase in the interaction of humans and chimpanzees.

To effectively protect chimpanzees and their habitats, it is important to understand how chimpanzees respond to their environment, so conservation 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) (also referred to as habitat suitability models, habitat models, ecological niche models, environmental niche models, etc.) are an informative way to evaluate the importance of environmental variables related to species distribution (Franklin 2009). Species distribution modeling provides a means for mapping chimpanzee habitat. The results of the modeling exercise can be used to guide reserve design, habitat management, and conservation planning. Species distribution models estimate conditions suitable for species survival by examining the relationships between species' occurrence and associated environmental conditions.

Here, we use direct and indirect evidence of chimpanzee occurrences from fieldwork, medium-resolution remote sensing data, and SDMs to evaluate how the spatial distribution of biophysical variables relates to the distribution of the Seringbara chimpanzee communities in the Mt. Nimba SNR. This modeling effort allows us to test the hypothesis that vegetation is one of the most important factors influencing the occurrence of great apes (Torres et al. 2010; Koops 2011a; Koops et al. 2012a, c; Junker et al. 2012; Jantz et al. 2016), specifically within the Seringbara chimpanzee communities. We will also explore the importance of other biophysical variables as they relate to the probability of Seringbara chimpanzee occurrence and compare our modeling results with relevant conservation efforts in the region. To do so, we will quantify and map the spatial distribution of biophysical variables within the study area using remotely sensed images, analyze the importance of each biophysical variable in modeling suitable chimpanzee habitat, and use SDMs to identify areas most suitable for chimpanzees within the Greater Nimba Landscape.

3.2 Methods

3.2.1 Study Site

The Mt. Nimba SNR is a UNESCO World Heritage Site in Danger (World Heritage Committee 2017). 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 km^2, 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 (Kormos et al. 2003; Koops 2011a; Avenard et al.). The reserve is home to a variety of flora and fauna, including the critically endangered endemic Mt. Nimba viviparous toad (*Nimbaphrynoides occidentalis*) and the Critically Endangered western chimpanzee (*P.t. verus*) (World Heritage Committee 2017).

The study site (N07.634°, W08.425°), spanning 30 km^2, is located on the Guinean side of the Nimba Mountains within the Mt. Nimba SNR (Fig. 1.2). 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 2011a). The elevation ranges from 595 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. 2012a, c, 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 2011a). Bossou is home to a community of (currently seven individuals) that have been the focus of research for over 30 years by the Kyoto University Primate Research Institute (KUPRI) (Matsuzawa and Humle 2011). The Mt. Nimba SNR and Bossou are separated by savannah that few chimpanzees traverse (Matsuzawa et al. 2011b). This study focuses on at least two communities of chimpanzees within the Mt. Nimba SNR, known as the Seringbara communities, that combined have an estimated total of 103 chimpanzees (Koops et al. *in prep*). The Seringbara communities have been the focus of habituation efforts since 2003 (Koops 2011a) and intermittent ecological studies and surveys since 1996 (Matsuzawa and Yamakoshi 1996; Humle and Matsuzawa 2001, 2004). The chimpanzees remain mostly unhabituated to humans (Koops and Matsuzawa 2006; Koops 2011a; Matsuzawa et al. 2011a).

3.2.2 Occurrence Data

Between January 2012 and April 2014, a team of research assistants collected data on chimpanzee behavior at the Seringbara study site on the Guinean side of the Mt. Nimba SNR. Research teams maintained a nearly constant presence in the forest during this period, only missing data collection for 1–2 days a month. Field days focused on tracking and directly observing chimpanzees to obtain data on ranging, grouping, diet, nest building, and tool use. Direct observations of wild chimpanzees can be difficult, 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.

Direct and indirect evidence of chimpanzee presences were recorded using handheld global positioning system (GPS) devices during daily tracking of the chimpanzees. Sampling effort within the study area was comprehensive, as we covered the whole study area when searching for chimpanzees by splitting into teams and exhaustively surveying the study area using opportunistic sampling. In total, 1385 occurrence points were recorded. Occurrence points were not evenly distributed throughout the study area due to the behavior of the chimpanzees and perhaps also 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. We used R 3.3.2 (Supplementary Appendix A) 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 (Fig. 3.1). Filtering to include only one occurrence point per cell did not influence our results because this study does not address the frequency nor magnitude of use by chimpanzees. Absence data were not available for this study. In addition, we chose to combine direct and various indirect types of evidence of occurrence for modeling, because (1) we wanted a robust sample size and classifying occurrences into behavior categories would drastically decrease sample size for the model and (2) it was unclear the behavior category for which we would attribute the feces occurrences, given that they can be found at feeding locations, along movement routes, at resting spots, as well as other locations of use (Supplementary Appendix A Table 1).

3.2.3 Predictor Variables

Raster layers of predictor variables (Table 3.1) dealing with landscape structure and land cover, herein referred to as biophysical variables, were prepared at a 30 m spatial resolution. An initial set of 17 biophysical variables (Table 3.1) was assessed, as detailed below, before being narrowed down to 12 variables in the final model. Minimum distance, supervised classification of a Landsat 8 image, obtained during the study period (December 26, 2013), was developed in ENVI 5.0.2 to delineate five land-cover types: dense forest, mixed forest, bare ground, village, and savannah (Supplementary Appendix B). These five 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 comprised of tree species such as *Parinari excelsa*, *Parkia bicolor*, *Antiaris africana*, and *Aningeria altissima*. Mixed forests are mostly secondary, disturbed forests with less dense vegetation and less canopy cover. Tree species common in mixed forests include *Musanga cecropioides*, *Elaeis guineensis*, and *Uapaca sp*. 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%) in distinguishing between macrohabitats, 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) (Supplementary Appendix B). Because chimpanzees have sophisticated mental mapping capabilities (Boesch and Boesch 1984; Normand and Boesch 2009; Normand et al. 2009; Ban et al. 2014) and are able to perceive their surroundings at the level of individual trees and forest patches, vegetation indices were calculated to capture differences at microscales (Pintea et al. 2002; Torres et al. 2010). Landsat 8 imagery from six 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 from the near-infrared and red bands of a satellite image ((NIR – R)/(NIR + R)) (Campbell and Wynne 2011). In addition, we 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 four 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 et al. 2007, 2012a, c, 2013, 2015; Koops 2011c), as well as other non-human primates (Plumptre 2010; Torres et al. 2010;

Wich et al. 2012; Hickey et al. 2013; Gregory et al. 2014; Clee et al. 2015; Serckx et al. 2016), 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 2011c; 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., *P. excelsa*) (Koops 2011c). Moreover, the Seringbara chimpanzees prefer to nest at locations with lower humidity (Koops et al. 2012a, c). For example, they tend to nest at higher altitudes (above 1000 m) where relative humidity is low and avoided nesting in areas of high humidity (below 800 m) (Koops et al. 2012a, c). Therefore, the other biophysical variables included in the initial model were chosen for their ability to serve as proxies for these (i.e., climate, vegetation, and anthropogenic) factors (Franklin 2009).

The following variables were generated using ArcMap 10.2.2 (ESRI 2011) 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 3.1). The R script for calculating hierarchical slope position is found in Supplementary 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 m^2 cell from the nearest permanent river or stream.

We examined correlation between variables to reduce the effect of collinearity on interpreting Maxent results (Dormann et al. 2013; Rödder et al. 2013; Kumar et al. 2014). 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 (Estes et al. 2010; Dormann et al. 2013; Hickey et al. 2013).

3.2.4 Modeling Technique

To map suitable chimpanzee habitat and analyze biophysical variables contributing to suitability, we 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 (Phillips et al. 2006; Franklin 2009). Maxent performs well with presence-only data and frequently outperforms other SDM methods (Elith et al. 2006, 2011; Phillips and Dudík 2008; Wilson et al. 2013). The result is a best-fit model classifying locations in the study area according to probability of presence (0–1, 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 (Elith 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). Thus, a model with a high AUC has more discriminative power. A k-fold cross-validation procedure was replicated ten times to obtain a mean AUC value for the final model (Wich et al. 2012; Dormann et al. 2013; Kumar et al. 2014). Additionally, Maxent was used to generate response curves showing the relationship between each predictor variable and predicted probability of chimpanzee presence (i.e., predicted habitat suitability). Percent contribution and permutation importance were reported for each variable. Percent contribution is a measure of the amount of explained variance each variable contributes to the model. 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).

The model was projected beyond the study area to better assess habitat suitability for the Seringbara chimpanzees within the larger landscape. This geographically projected model is hereafter referred to as the final model. The extent, referred to as the Greater Nimba Landscape for this study, includes the majority of the Nimba Mountain range in Guinea, Liberia and Côte d'Ivoire, as well as the regions surrounding a few of the closest villages to the study site and an iron ore mining site (Fig. 3.2). The total area of the Greater Nimba Landscape is 992 km^2. By including these villages, namely Bossou, Seringbara, Nyon, and Zouguepo, 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 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. 2017). 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 procedure 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).

The final Maxent output is a gradient model classifying each pixel according to probability of presence or habitat suitability. In many cases, SDMs are converted to binary models, delineating suitable versus unsuitable habitat, which are used by conservationists and land managers (Escalante et al. 2013; Fourcade et al. 2014). 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, we 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 (Pearson et al. 2006; Escalante et al. 2013; Fourcade et al. 2014; Norris 2014). 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.

3.3 Results

3.3.1 Correlation analysis

The following 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 ($r = -0.72$) (Supplementary 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 3.1).

3.3.2 Gradient habitat suitability model

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 (Swets 1988; Pearce and Ferrier 2000; Araújo et al. 2005). The resulting map from the final model (Fig. 3.3) 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 3.2).

3.3.3 Variable response curves

The spatial distributions for the biophysical variables of highest importance were mapped and displayed above the corresponding response curves (Fig. 3.4). 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 (Fig. 3.4a). The response curve for elevation shows that probability of presence is highest between 800 and 1200 m (Fig. 3.5b). 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 and ridges (high HSP values) (Fig. 3.4c). For brightness, probability of chimpanzee presence peaks at an index value of 0.35 before declining sharply at higher brightness values (Fig. 3.4d). There is a negative relationship between DTR and probability of presence, with a sharp decline in probability of presence for areas farther than 500 m from a river (Fig. 3.4e). Response curves and maps for all other biophysical variables used in the final model can be found in Supplementary Appendix E.

3.3.4 Binary habitat suitability models

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) (Fig. 3.5a–c, respectively). Using a threshold allowed the amount of suitable versus unsuitable habitat to be delineated and quantified within the Greater Nimba Landscape (992 km2) (Table 3.3). 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) lends itself to a different interpretation of the Greater Nimba Landscape, as only 3% was classified as suitable habitat and 97% was unsuitable. Similarly, the 10% training presence threshold (0.33) delineated 7% of the Greater Nimba Landscape as suitable and 93% as unsuitable.

3.4 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 influences on habitat suitability for many different species. In this study, we 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 NDVI, elevation, hierarchical slope position, brightness, and distance to rivers contributed most to predicted habitat suitability (Table 3.2).

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 occurrence suggests that chimpanzees prefer forested areas with dense, healthy vegetation (Fig. 3.4a). A study by Koops et al. (2012a, b) showed that the Seringbara chimpanzees prefer 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., *P. excelsa*, *P. bicolor*, *A. africana*, and *A. altissima*) (Koops 2011c). This relation indicates that the habitat suitability model presented here is capturing important biological signals from the Seringbara chimpanzees' use of the landscape. Similar studies at other locations have also shown that vegetation influenced chimpanzee behavior (Torres et al. 2010; Jantz et al. 2016), as well as great ape behavior in general (Junker et al. 2012).

Elevation was the second most important biophysical variable in predicting habitat suitability for the Seringbara chimpanzees. The relationship between elevation and the probability of Seringbara chimpanzee occurrence is bell shaped (Fig. 3.4b). Increasing elevation up to 900 m is associated with increasing probability of occurrence. Above 900 m, increasing elevation is associated with decreasing probability of occurrence. Within the Greater Nimba Landscape, elevation serves as a good proxy for climate and vegetation, as well as anthropogenic disturbance. Unfortunately, there is not sufficient data on anthropogenic disturbance for the whole reserve, but based on personal observations, we noticed that many of 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. In addition, the protected status of the Nimba Mountains increases this effect because the mountains are within high elevation areas. Although protected status does not directly indicate a lack of anthropogenic disturbance, the Mt. Nimba Strict Nature Reserve is remote, hunting pressures tend to decrease with distance from villages, and illegal hunting is targeted at animals other than the Seringbara chimpanzees (pers. obs., Koops and Fitzgerald). Moreover, as elevation increases above 1200 m, the landscape is dominated by high altitude grasslands (Lamotte 1998), which may not provide ample resources for chimpanzees (Koops 2011c). Thus, resulting in the bell-shaped curve of the relationship between elevation and probability of Seringbara chimpanzee occurrence.

The HSP (a measure of topographic exposure) was the next most important variable in predicting chimpanzee presence. Topographic exposure is the degree to which a location is surrounded by high relief terrain. A high HSP value indicates that a location is not surrounded by areas of higher relief (i.e., exposed), such as a cliff face or ridge top. A low value indicates that the landscape is surrounded by high relief terrain (i.e., not exposed), such as valley bottoms and toe slopes. The relationship between topographic exposure and the probability of Seringbara chimpanzee occurrence is generally negative, where an increase in topographic exposure is associated with a decrease in the probability of occurrence (Fig. 3.4c). Thus, Seringbara chimpanzees are more likely to occur in less-exposed areas, such as mild slopes, not surrounded by high relief terrain. 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 (*Chiropotes sagulatus*) 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 behavior is yet to be explored for chimpanzees in the Greater Nimba Landscape. 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 (Cohen et al. 1995; Cohen and Goward 2004; Campbell and Wynne 2011). 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 (Fig. 3.4d). Other very similarly vegetated savannah regions have much higher brightness values. 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 (Koops 2011c; Hickey et al. 2013). In evaluating the distribution of the variable distance to river throughout the Greater Nimba Landscape (Fig. 3.4d), many of the places 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 slightly flatter and rivers are more dispersed. Riverine areas may also provide food resources not available elsewhere in the landscape (Koops pers. comm.).

The final habitat suitability 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 various threshold values (Fig. 3.5). A comparison of the three binary models also highlights the importance of carefully selecting a threshold value. In this study, the amount of suitable habitat within the landscape ranged for 3–42% (Table 3.3). This variation in amount of suitable habitat based on threshold values may result in very different conservation strategies and threshold selection should be carefully considered based on local knowledge, research, and specific conservation goals. 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 is useful for conservation practitioners (Liu et al. 2005; Escalante et al. 2013; Ferrer-Sánchez and Rodríguez-Estrella 2016). For example, Torres et al. (2010) delineated suitable from unsuitable chimpanzee habitat to assess changes in habitat suitability over time as well as temporal changes in the most important ecogeographical factors influencing chimpanzee habitat in Guinea-Bissau. Their results provide a basis for practitioners to adapt their strategies based on past changes as well as forecasted changes to chimpanzee habitat suitability.

Additionally, within the Nimba mountain range, high suitability areas are fragmented by terrain features such as high ridgelines and anthropogenic disturbances, such as the iron-ore mining concession in the NE region of the Nimba mountain range (Fig. 3.3). Thus, not only are the Seringbara chimpanzees isolated from other chimpanzee communities outside 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 hampers gene flow between groups and can lead to further decline in chimpanzee populations in the region.

Maintaining viable, healthy chimpanzee populations requires movement between communities, thus 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 utilized by chimpanzees in the savannah between the sites (Matsuzawa et al. 2011b). 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 from Bossou traveling 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 (e.g., use of unmanned aerial vehicles and satellite imagery) and modeling may prove useful for monitoring and expanding the corridor. In addition, as the vegetation in the corridor matures, its NDVI value will increase. NDVI was the most important biophysical variable in our model and increasing NDVI was related to increasing probability of occurrence. Our modeling effort supports the hypothesis that the corridor will increasingly provide more suitable habitat for chimpanzees as the vegetation within the corridor matures. Future plans for new corridors might additionally consider locations with low topographic exposure that are near rivers.

While 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 recognize the limitations of this study. Since 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 (Pearson et al. 2006; Elith et al. 2010; Zurell et al. 2012; Eger et al. 2017). 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 are better able to capture vegetation characteristics at a higher spatial resolution. Likewise, the model results could be improved by (1) additional surveys in the Greater Nimba Landscape beyond the study area used to create the model, (2) systematic data pertaining to anthropogenic disturbance, and (3) ground truthing of the variables used and results.

3.5 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) NDVI, elevation, hierarchical slope position, brightness, and distance to rivers had the greatest influence on habitat suitability for the Seringbara chimpanzees, (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.

3.7 Figures

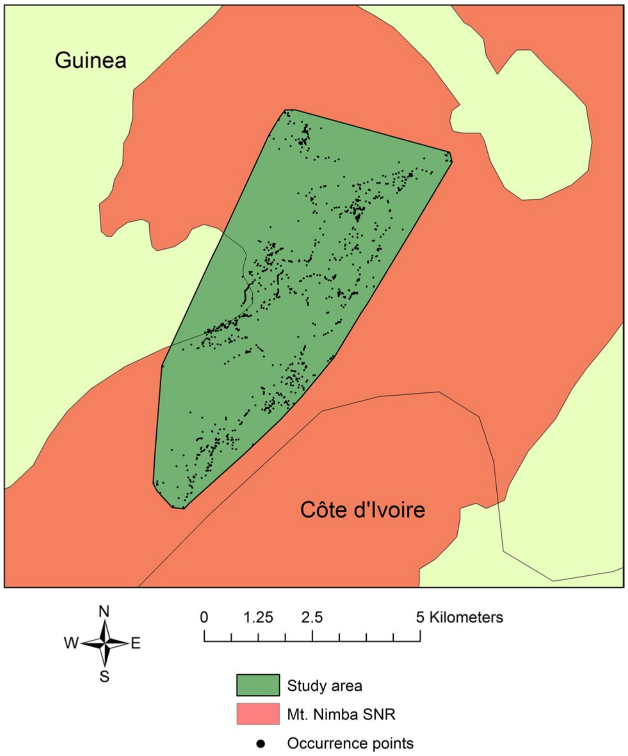


Fig. 3.1 Location of chimpanzee occurrence points used in the model ($N = 947$)

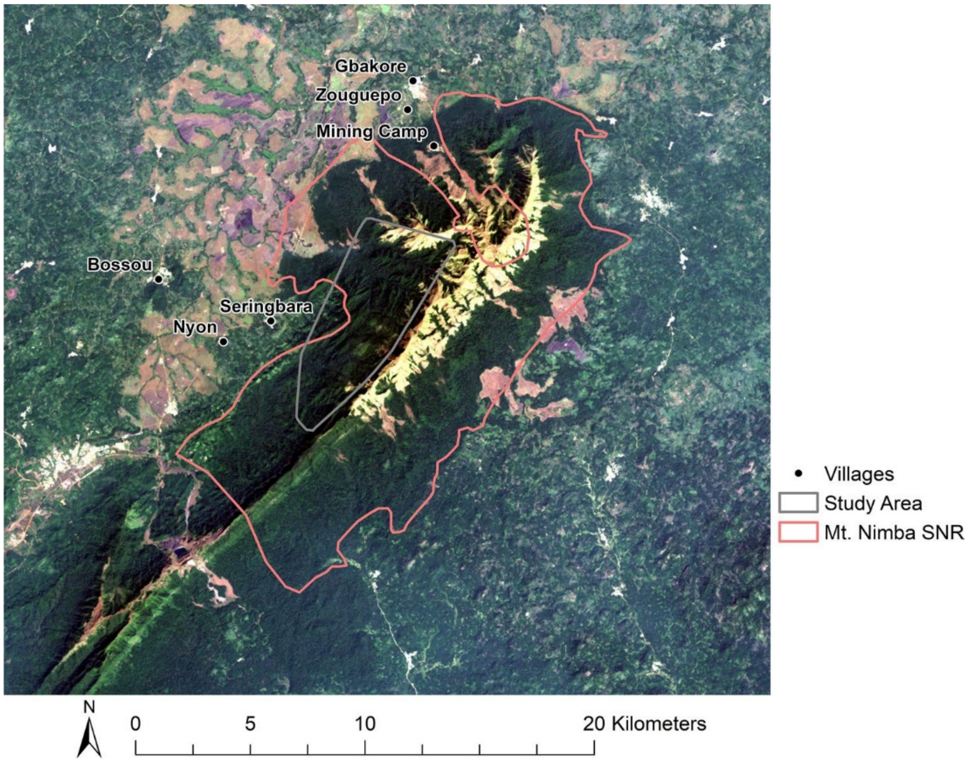


Fig. 3.2 Landsat 8 satellite image of the Greater Nimba Landscape

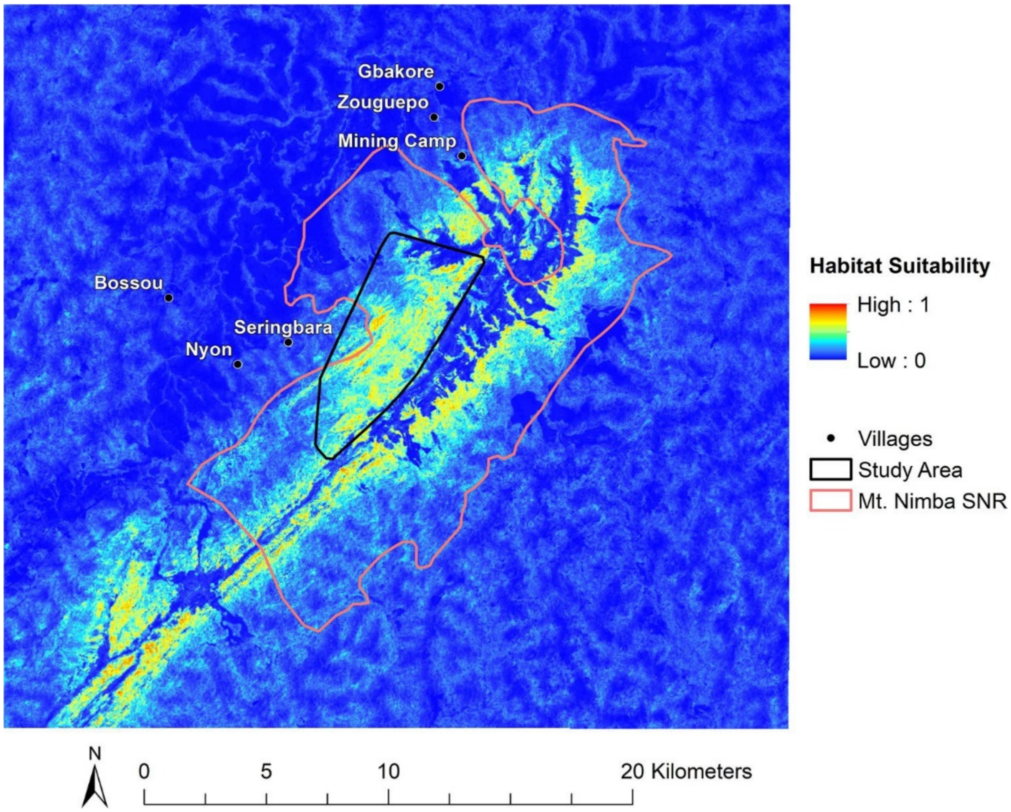
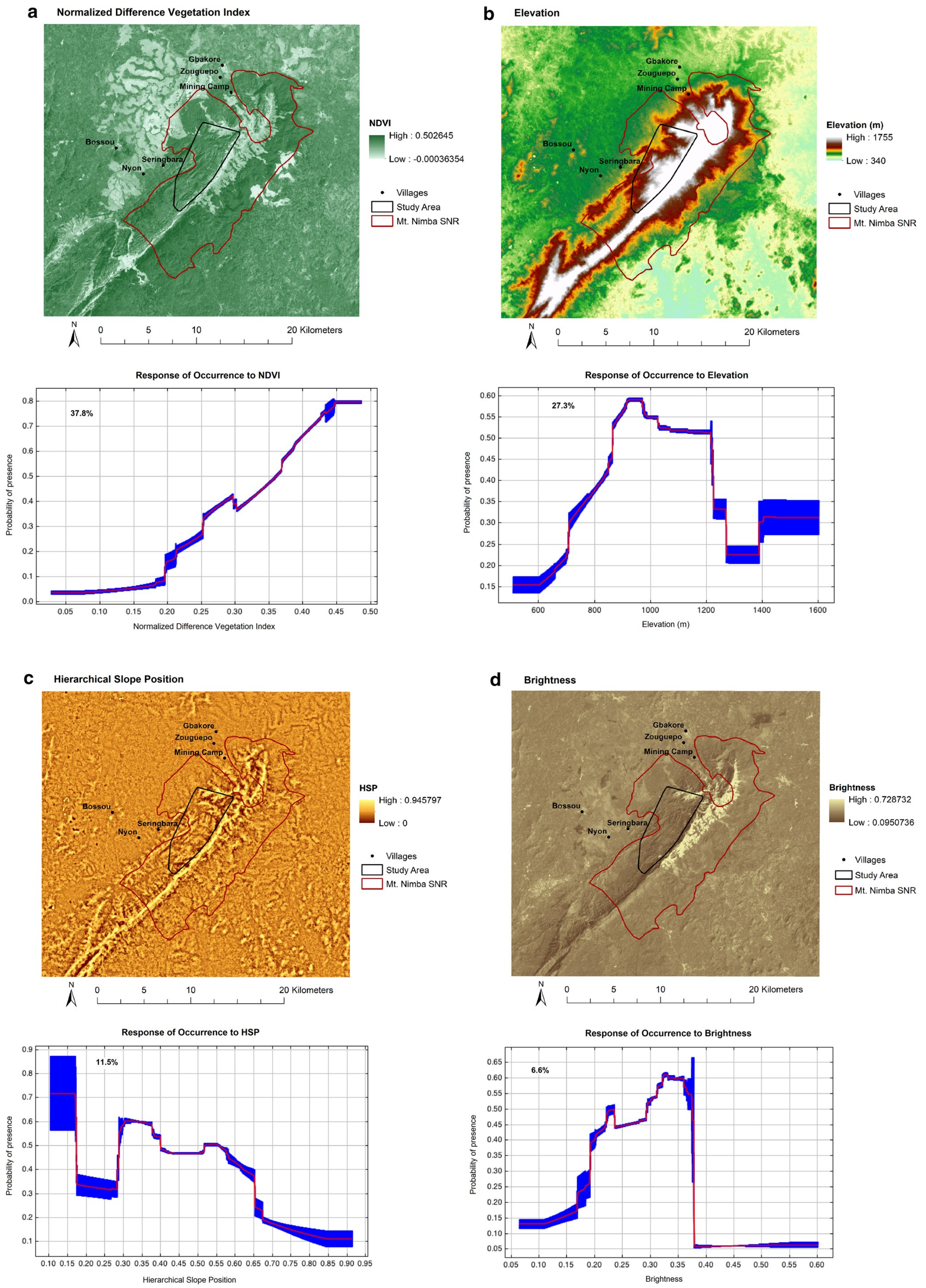


Fig. 3.3 Chimpanzee habitat suitability model showing the geographic distribution of suitable chimpanzee habitat throughout the Greater Nimba Landscape. This is a gradient model displaying habitat suitability on a scale from 0 (low suitability) to 1 (high suitability). This figure illustrates the importance of the Mt. Nimba SNR in providing habitat for chimpanzees within the Greater Nimba Landscape.



a
Normalized Difference Vegetation Index
Gbakore
Zouguepo
Mining Camp
Bossou
Seringbara
Nyon
NDVI
High : 0.502645
Low : -0.00036354
Villages
Study Area
Mt. Nimba SNR
N
0 5 10 20 Kilometers
Response of Occurrence to NDVI
37.8%
Probability of presence
Normalized Difference Vegetation Index
b
Elevation
Elevation (m)
High : 1755
Low : 340
Response of Occurrence to Elevation
27.3%
Elevation (m)
c
Hierarchical Slope Position
HSP
High : 0.945797
Low : 0
Response of Occurrence to HSP
11.5%
Hierarchical Slope Position
d
Brightness
Brightness
High : 0.728732
Low : 0.0950736
Response of Occurrence to Brightness
6.6%
Brightness

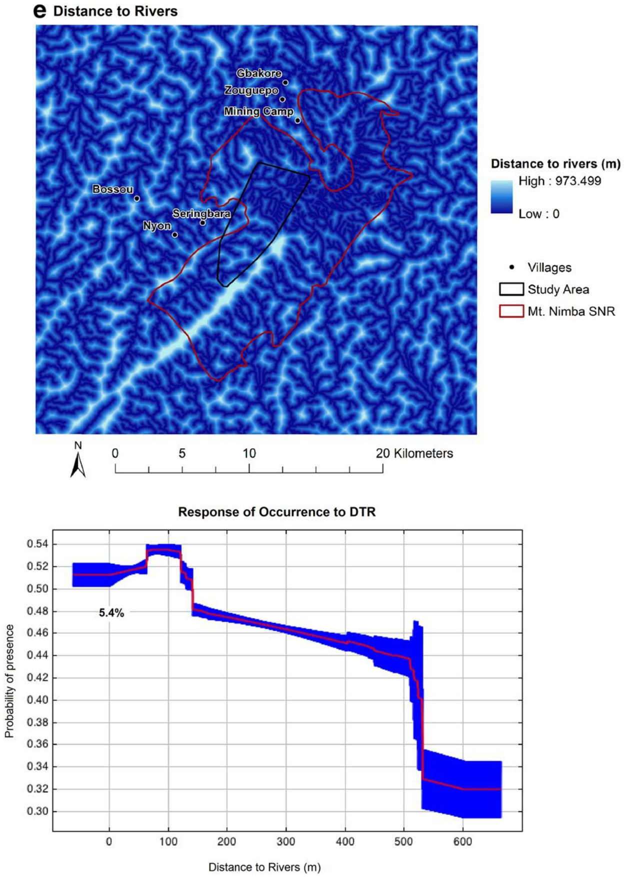


Fig. 3.4 (a-e) Plots of the response curves showing the dependence of probability of presence on a given biophysical variable. Each plot represents a Maxent model using only the corresponding variable. The plots are given for the five biophysical variables with highest per- mutation importance (percent 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.

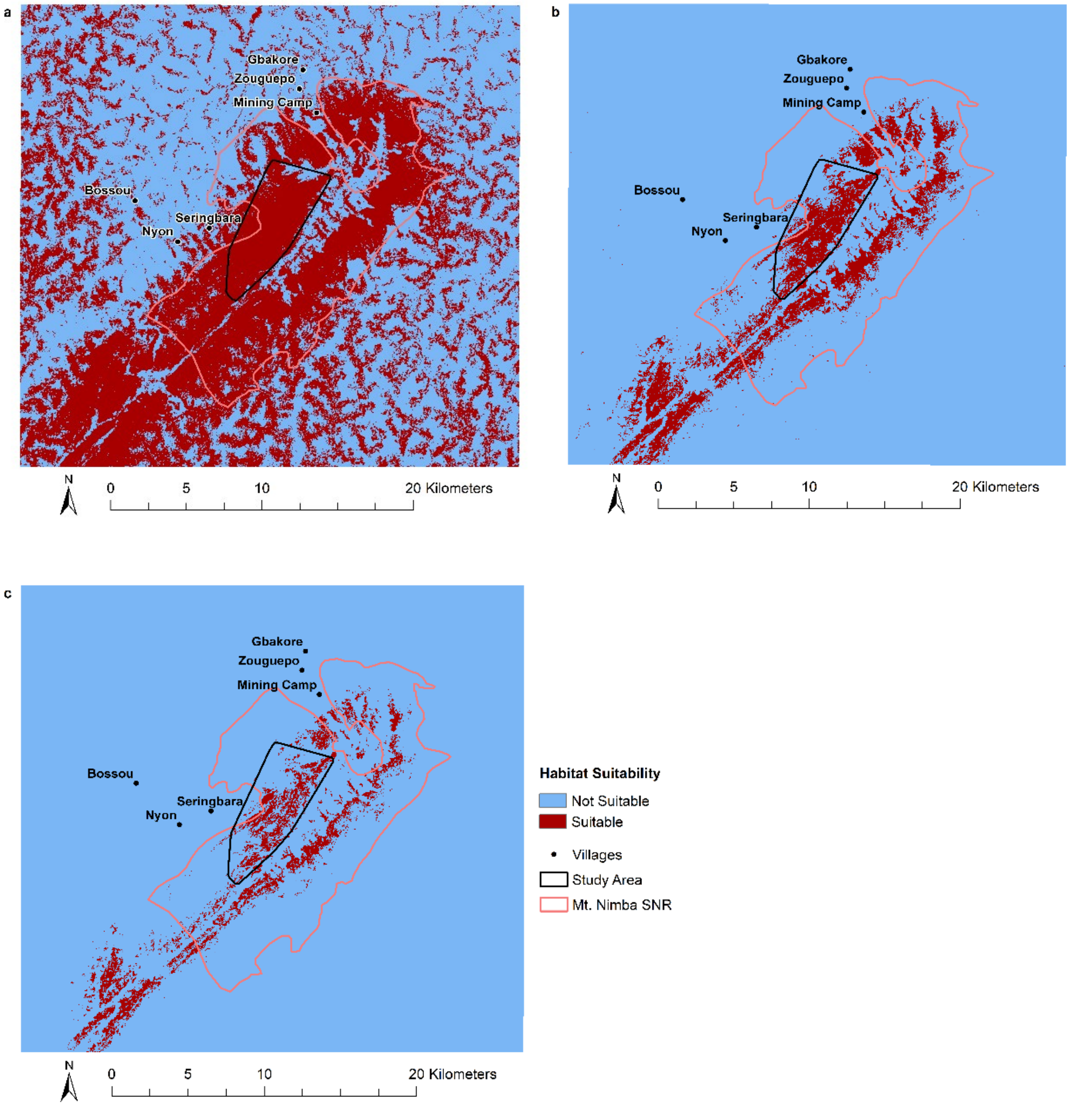


Fig. 3.5 Final model output showing the distribution of suitable chimpanzee habitat throughout the Greater Nimba Landscape as a series of binary models of three different threshold values: (a) minimum training presence, (b) 10% training presence, and (c) equal training sensitivity and specificity

3.8 Tables

Table 3.1 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 *)

Predictor Variable	Abbreviation	Units	Description	Source	Reference
Elevation*	elevation	Meters	Height above sea level	ASTER GDEM v.2	ArcMap 10.2.2
Aspect*	aspect	Degrees	Direction a slope faces	ASTER GDEM v.2	ArcMap 10.2.2
Slope	slope	Degrees	Steepness of a surface	ASTER GDEM v.2	ArcMap 10.2.2
Normalized Difference Vegetation Index*	NDVI	unitless	Index of relative biomass (average of 6 dates within study period)	Landsat 8	-
Greenness	greenness	unitless	Measure of photosynthetically active vegetation	Landsat 8	(Baig et al. 2014)
Wetness	wetness	unitless	Soil moisture content	Landsat 8	(Baig et al. 2014)
Brightness*	brightness	unitless	Soil brightness	Landsat 8	(Baig et al. 2014)
Land Cover Class	LCC	unitless	Categorization of land cover types	Landsat 8	-
Topographic Position Index	TPI	unitless	Difference between elevation at one point and the mean elevation around it	ASTER GDEM v.2	(Guisan et al. 1999; De Reu et al. 2013)
Integrated Moisture Index*	IMI	unitless	Estimate of soil moisture based on topography	ASTER GDEM v.2	(Iverson et al. 1997)
Heat load index*	HLI	unitless	Measurement of heat load considering steepness of slope and aspect	ASTER GDEM v.2	(McCune and Keon 2002)
Landform/slope curvature*	curvature	unitless	Index of concavity/convexity	ASTER GDEM v.2	(McNab 1989, 1993; Bolstad and Lillesand 1992)
Compound topographic index*	CTI	unitless	Steady state wetness index	ASTER GDEM v.2	(Gessler et al. 1995)
Surface relief*	relief	unitless	Measure of rugosity	ASTER GDEM v.2	(Pike and Wilson 1971)

Roughness*	roughness	unitless	Measure of surface roughness	ASTER GDEM v.2	Blaszczynski 1997; (Riley et al. 1999)
Hierarchical slope position*	HSP	unitless	Relative topographic exposure	ASTER GDEM v.2	(Murphy et al. 2010)
Distance to rivers*	DTR	Meters	Euclidean distance between a cell and nearest permanent river or stream	WorldView2 and DEM	ArcMap 10.2.2

Table 3.2 Permutation importance and percent contribution of each biophysical predictor variable used in creating the final habitat suitability model

Variable	Permutation importance	Percent Contribution
NDVI	37.8	45.4
elevation	27.3	27.4
HSP	11.5	8.9
brightness	6.6	4.5
DTR	5.4	4.4
aspect	2.8	1.2
HLI	1.9	1
CTI	1.8	0.6
IMI	1.7	3.6
roughness	1.6	2.2
curvature	1.1	0.6
relief	0.5	0.3

Table 3.3 The amount of area (km^2) within the Greater Nimba Landscape that was delineated as not suitable and suitable based on the assigned threshold value

	Minimum training presence: 0.08	10 percentile training presence: 0.33	Equal training sensitivity and specificity: 0.46
Not Suitable	580.38 (58%)	925.24 (93%)	957.62 (97%)
Suitable	411.87 (42%)	67.01 (7%)	34.63 (3%)

Chapter 4

Agriculture is the primary driver of tree cover loss across the Forestière region of the Republic of Guinea, Africa

4.1 Introduction

Biodiversity is declining at an accelerating pace (Pimm et al. 2014). Much of this decline is attributed to increasing human demands for natural resources whereby our footprint far exceeds the earth's capacity to regenerate (Lin et al. 2018). Declines in biodiversity can lead to an alteration of ecosystem structure and function, resulting in diminished capacity to provide ecosystem services to nature and humans (IPBES 2019, Morris 2010, Chapin III *et al* 2000, Isbell *et al* 2017). Such impacts, which can extend across large spatial scales, often negatively and disproportionately affect the poorest communities who rely on surrounding biodiversity and other ecosystem services for their livelihoods and human well-being (Roe et al. 2019). Thus, the conservation of biodiversity is not solely an environmental issue, but also one of social, economic, and ethical concern (IPBES 2019). Studies have found that increased tree cover, both as part of forest canopy and agricultural landscapes, is correlated with increased levels of species richness and ecosystem function (Morris 2010; Mendenhall et al. 2016; Brockerhoff et al. 2017; Barrios et al. 2018) as well as human health (Johnson et al. 2013).

Tropical forests harbor extremely high levels of biodiversity (Dirzo and Raven 2003; Gibson et al. 2011; Laurance et al. 2012). Additionally, they provide other important globally important ecosystem services, including climate regulation and carbon sequestration (Mitchard 2018; Sullivan et al. 2020). Due to human-driven land use change, however, tropical forests are undergoing rapid loss, fragmentation, and modification (Gibson et al. 2011; Brockerhoff et al. 2017; Hansen et al. 2020). Within tropical forests, protected areas are fundamental to conserving biodiversity, protecting ecosystem services, supporting livelihoods, and achieving the Sustainable Development Goals (CBD 2004; United Nations 2015). However, they are often vulnerable to human-driven land use change due to under-allocation of financial resources, low law-enforcement capacity, and lack of local stakeholder engagement for their protection (Watson et al. 2014; Oldekop et al. 2016; Geldmann et al. 2019). Knowing where land use changes are taking place, what is driving them, and to what extent the surrounding landscapes are changing, is essential to safeguarding the biodiversity and ecosystem services found in protected areas in tropical forest habitats. Hence, strategic efforts to monitor, restore, and protect tropical forest cover are critical to minimizing forest loss and the ecosystem services that they provide (Hansen et al. 2020). Remote sensing technologies allow for comprehensive spatial and temporal monitoring of forests and tree cover to enhance our understanding of particular threats to tropical forests and understand how those threats are evolving. Regular and systematic monitoring provides necessary data and information to support the formation of policies and management practices necessary for the restoration and protection of tropical forests (Mayaux et al. 2005; Romijn et al. 2015).

With the growth and increased accessibility of satellite-based remote sensing, systematic monitoring of ecological changes at global, regional, and local scales has become widespread. Remote sensing allows for controlled and frequent monitoring of the earth’s surface and provides datasets for a wide range of analyses, including tree cover loss and deforestation detection. However, despite the increasing reliability and robustness of remotely sensed data, these data are prone to certain limitations, such as cloud cover and low temporal or spatial resolution (Olofsson et al. 2014). Additionally, there are uncertainties associated with remotely sensed data analyses, such as classification errors. Often, these errors can prevent precise area calculations of changes that are necessary for monitoring at national and local levels (Olofsson et al. 2013; GFOI 2014). Thus, it is vital that data on tree cover changes are also supplemented with accuracy information so that users understand the data limitations and make more informed decisions. There are a number of well-establish methods for assessing the accuracy of change detection data derived from remote sensing, but a widely used and recommended method is stratified random sampling, a probability-based sampling design (Olofsson et al. 2014). Since it is almost always impossible or impractical to verify whether each classified pixel on a map is in agreement with the actual behavior on the ground, stratified random sampling is especially useful for accuracy assessment because it relies on just a subset of the region of interest to generate reference data in order to verify accuracy of the data, which makes the assessment more efficient. In addition, the sampling design’s statistically random generation of reference samples allows for unbiased assessments of map accuracy as well as area estimates and a host of other relevant thematic analyses like estimations of drivers of change (Tyukavina et al. 2017, 2018). Accompanied by accuracy assessments, remote sensing data have immense potential to greatly advance the efficient and systematic monitoring of tropical forest regions and contribute to more effective forest management and protection.

The Guinean Forests of West Africa is a global biodiversity hotspot (GFWA hotspot) that stretches from the Republic of Guinea and Sierra Leone eastward to Cameroon (CEPF 2015). It is estimated that these predominantly tropical and subtropical moist broadleaf forests once covered 624,000 km^2 (Mittermeier et al. 2004). The hotspot is divided into two sub-regions, 1) Upper and 2) Lower Guinean Forests, which are separated by a savannah zone called the Dahomey Gap that extends from eastern Ghana to Benin. The GFWA hotspot supports high levels of species richness and endemism. Of the over 1,700 terrestrial animal species found in this region, more than 250 are endemic to the GFWA hotspot (CEPF 2015). Home to over a quarter of all the mammal species found in Africa, the GFWA hotspot is particularly notable for its high mammalian diversity. Inside this hotspot, the Republic of Guinea (hereafter Guinea), contains lowland and montane forest zones that have some of the highest levels of terrestrial species richness found within the hotspot. The GFWA hotspot overlaps primarily with an area of Guinea known as the Forestière region of Guinea, or Guinée Forestière.

We analyzed tree cover loss in relation to locations of high biodiversity in order to better understand the threats to biodiversity and support and develop conservation actions within Guinée Forestière. To do so, we mapped and quantified tree cover loss occurring across Guinée Forestière from 2000 to 2018 using remotely sensed data (objective 1), estimated tree cover loss inside and outside of PAs of high biodiversity value (objective

2), and identified primary drivers of tree cover loss (objective 3). We also reported on the accuracy of our estimates to ensure the robustness of our analyses (objective 4).

4.2 Study Area

Guinea is a country of over 12.7 million people (World Bank 2019). Across Guinea, over 67% of Guineans live in rural areas and agriculture provides income for 57% of rural households (World Bank 2019). Smallholder agriculture is primarily an itinerant slash-and-burn practice for growing staple crops such as rice, cassava, yams, peanuts, coffee, and various other fruits and vegetables (Camara et al. 2009). Only 1.2% of Guineans have access to clean cooking fuels (non-solid fuels like ethanol or electricity) (Ritchie and Roser 2020). Thus, the majority of households use firewood and coal as energy sources (International Monetary Fund 2013). Human livelihoods in Guinea are reliant on the numerous ecosystem services provided by forests, including: timber for firewood and infrastructure, clean water, food and medicine derived from forest flora and fauna, micro-climate regulation, traditional sacred areas, and ecotourism opportunities (CEPF 2015).

Guinea is divided into four geographic regions (listed in order from west to east across Guinea): Guinée Maritime, Moyenne-Guinée, Haute-Guinée, and Guinée Forestière. This study focuses on Guinée Forestière, which covers approximately 17% (42,760 km^2) of Guinea's surface area (245,860 km^2). Despite its name, the region is not homogenously forested but is comprised of four ecoregions of varying amounts of forest cover and type: Guinean forest-savanna mosaic, Western Guinean lowland forests, Guinean montane forests, and West Sudanian savanna (Olson et al. 2001). Guinée Forestière exemplifies why the Upper Guinean Forests are a biodiversity hotspot, as it the home to at least 16 out of the 28 threatened terrestrial mammal species in Guinea (IUCN 2020). These species include pygmy hippopotamuses (*Choeropsis liberiensis*), western chimpanzees (*P. t. verus*), forest elephants (*Loxodonta cyclotis*), white-bellied pangolins (*Phataginus tricuspis*), and Nimba otter shrews (*Micropotamogale lamottei*).

We identified five protected areas (PAs) of high biodiversity importance for use in this analysis (hereafter high biodiversity areas or HBAs) (Fig. 4.1). The HBAs listed below were chosen because they are considered strongholds of the Upper Guinean Forests within Guinée Forestière (Van Rompaey et al. 2001) and span a variety of nationally and internationally-significant areas: (a) IUCN Category I - IV protected areas, (b) Classified Forests, (c) designated protected via international conventions (e.g. UNESCO Man and Biosphere reserves), and/or (d) Key Biodiversity Areas (KBAs) in Guinea identified by Brugiere and Kormos (2009). We considered Classified Forests as PAs for the purpose of this study. Classified Forests are not explicitly stated as part of a particular IUCN PA category, but they are typically areas of forests with management plans and limitations on activities allowed within their borders (FAO 2010). The five HBAs chosen for analysis in this study are described below.

1. The Mont Nimba Biosphere Reserve is an internationally recognized protected area designated by UNESCO as part of the Man and Biosphere Programme. This

site consists of three core areas (the Mount Nimba Strict Nature Reserve, Bossou Hills, and Déré Forest) covering a total of 253.6 km^2.

2. Massif du Ziama Biosphere Reserve is a nationally Classified Forest identified by Brugiere and Kormos (2009) that is also part of the Man and Biosphere Programme. It consists of a single core area covering 1159.1 km^2.
3. Diécké Forest is a nationally Classified Forest that was identified as a KBA by Brugiere and Kormos (2009). It covers 591.8 km^2.
4. Pic de Fon is a nationally Classified Forest and KBA that covers 320.9 km^2.
5. Mount Bero is a nationally Classified Forest and KBA that covers 274.6 km^2.

These five HBAs were used to stratify Guinée Forestière for use in the stratified random sampling design discussed below (section 4.3.2). Shapefiles of boundaries for these areas were compiled from UNEP-WCMC and IUCN (2019) and Biotope (2019).

4.3 Methods

The objectives for this study were completed in two stages: (1) annual tree cover mapping and change detection using Landsat time-series data (objective 1); and (2) sample analysis (objectives 2 – 4).

4.3.1 Landsat time-series tree cover loss mapping

We analyzed nineteen years (2000-2018) of Landsat satellite imagery available from the United States Geological Survey National Center for Earth Resources

Observation and Science (USGS EROS). Landsat images were processed using an automated method developed by Potapov et al. (2020) into a spatially and temporally consistent time-series dataset that served as input to the annual change detection model. The source Landsat image data represented top-of-atmosphere spectral reflectance affected by the variability of atmospheric conditions and cloud presence. First, we applied a set of per-pixel quality assessment models to exclude from further processing observations with high likelihoods of cloud or cloud shadow contamination. Second, we implemented a relative reflectance normalization using the global MODIS-derived surface reflectance as a normalization target to reduce the effects of atmospheric scattering and surface anisotropy. Finally, we transformed the cloud and shadow-free normalized surface reflectance data from individual Landsat images into a set of 16-day image composites to simplify the time-series analysis. To map annual tree cover loss, we used a set of 16-day composites from the current and three preceding years to calculate reflectance change metrics. These metrics represented a set of statistics derived from per-spectral band reflectance differences between observations of the current year with the average reflectance from three previous years for the same 16-day interval. Such feature space design allowed us to highlight inter-annual reflectance changes while ignoring the vegetation seasonality (Potapov et al., 2020).

We mapped annual tree cover loss using the approach developed by Potapov et al. (2019) (objective 1). Tree cover loss was mapped using a machine-learning decision tree model that we calibrated using tree cover and stable forest cover training areas throughout the region. The decision tree model was applied to a set of annual metrics resulting in a per-pixel change detection output map. We applied the same annual change detection model to map annual tree cover loss from the year 2000 to 2018. For repeated tree cover loss detections, we implemented a three-year delay before the repeated loss may be mapped to avoid double-counting of clearing events. Our annual change map for the last three years is similar to the global tree cover loss map (www.globalforestwatch.org). The new regionally calibrated annual forest change detection model has a better inter-annual consistency and better sensitivity to small-scale changes compared to the global product.

4.3.2 Sample analysis

The first step in the sample analysis was to select the sampling design. We employed stratified random sampling (Olofsson et al. 2014). We defined two strata within our area of interest inside Guinée Forestière (Table 4.1). Stratum 1 consisted of the area outside of the five HBAs defined above in section 2. Stratum 2 encompassed the area within the five HBAs. Samples (30m x 30m Landsat pixels) were selected randomly within each stratum. The allocation of samples across each strata is shown in Table 4.1. We compiled reference data for each sample that included temporal profiles of the normalized difference vegetation index (NDVI), normalized difference water index (NDWI), and short wave infrared reflectance (SWIR1) normalized surface reflectance; annual and bi-monthly averaged normalized surface reflectance image composites; and very high resolution (VHR) images from Google Earth. These data were accessible through a web-based interface and used during manual sample interpretation (described below).

The second step in the sample analysis was visual sample interpretation, or response design. For each sample we visually inspected and manually recorded whether tree cover loss was observed between years 2000 and 2018 (yes or no) and the driver of loss (Table 4.2). Based on this visual interpretation of samples, we assessed the accuracy of the annual tree cover loss map from Landsat time-series data (hereafter tree cover loss map data) (objective 4). We then estimated the per strata area of tree cover loss (objective 2). We also estimated the proximate drivers of tree cover loss across Guinée Forestière both within and outside of HBAs based on visual observations of the VHR imagery (objective 3). The methods used for estimating accuracy and area are based on the established approaches of Olofsson et al. (2013), Potapov et al. (2020); Stehman (2013, 2014) (objective 4).

4.4 Results

4.4.1 Map accuracy assessment

The tree cover loss map (Fig. 4.2) had an overall accuracy of 91.83% (SE=1.32%). The user's accuracy for tree cover loss was 88.32% (SE=3.25%), which reflects low commission error rates. In other words, the map had a low rate of false positives and correctly identified tree cover loss approximately 88% of the time. The producer's accuracy for tree cover loss was 78.35% (SE=3.92%), which reflects low omission rates. In other words, about 78% of the times when tree cover loss was identified in the manual sample interpretation, the map also classified the pixel as tree cover loss (i.e. low omission error rates).

4.4.2 Tree cover loss estimation and drivers of change

The sample-based estimate for total tree cover loss in Guinée Forestière between years 2000 and 2018 was 10,907 km^2 (SE = 889). This is approximately 25% of Guinée Forestière's total land area (42,760 km^2). Tree cover loss occurring within the HBAs was 364 km^2 (SE = 91) and tree cover loss occurring outside the HBAs was 10,543 km^2 (SE = 885). The primary identified drivers of loss, irrespective of strata, were activities associated with smallholder agriculture, logging, and human settlement (Table 4.3). Within the HBAs, tree cover loss was primarily attributed to logging and smallholder agriculture. Outside of these areas, loss was driven mostly by smallholder agriculture (Table 4.4). Note that there is an "unknown" category that accounts for large portions of tree cover loss. This category reflects areas where tree cover loss was identified during the sample analyses, but the exact proximate driver of loss was not identified. The area estimation (Tables 4.3 and 4.4) provides the following statistics for each driver: the estimated area (km^2) of tree cover loss and standard error (SE).

4.4.3 Annual tree cover loss

We analyzed tree cover loss annually for each HBA (stratum 2) and for the land area outside of HBAs (stratum 1) using a 3-year mean. Across all years, the Mont Nimba Biosphere Reserve had the highest amount of tree cover loss in relative to its land area

(Fig. 4.3a). Because this HBA consists of three core areas of varying PA classification, we disaggregated the results to show tree cover loss for each of the core areas (Fig. 4.3b). Tree cover loss occurring in the Déré Forest and Bossou Hills core areas contributed most to the total tree cover loss that occurred within the Mont Nimba Biosphere Reserve (Fig. 4.3b). However, the Mount Nimba Strict Nature Reserve (hereafter Mt. Nimba SNR), did not contribute as much to the total tree cover loss within that HBA. Mount Bero had the second highest amount of proportionate tree cover loss annually, with a large spike occurring between 2010 and 2015 (Fig. 4.3a).

4.5 Discussion

The tree cover loss data created for this study had an overall accuracy of 91.83%; SE=1.32%, which is considered high. When errors occurred, they occurred in the form of commission errors (false positives), found mostly in savanna areas. Omission errors (false negatives) occurred in areas where large trees were retained in new agricultural areas, which obscured the forest clearing. We estimated that the total tree cover loss in Guinée Forestière between years 2000 and 2018 was 10,907 km^2 (SE = 889), which consists of approximately 25% of the region's total land area. Of this total loss, 364 km^2 (SE = 91) of tree cover was lost within HBAs. This represents approximately 14% of the HBA land area and 0.9% of the total land area in Guinée Forestière.

Tree cover loss was not consistent across HBAs and did not appear to be related to PA classification. For example, Diecke Forest and Pic de Fon are Classified Forests which, on paper, receive the some of the lowest levels of protection among the types of PAs represented in this study. Yet, both of these HBAs had low percentages of tree cover loss relative to their areas (Fig. 4.3a). On the other hand, the Mont Nimba Biosphere Reserve had the highest percentage of tree cover loss (Fig. 4.3a) relative to its land area within Guinée Forestière. This site is part of UNESCO's Man and Biosphere Programme. Although Biosphere Reserves are not designated as part of a particular IUCN PA category, they consist of three core areas that are supposed to be strictly protected by the jurisdictions where they reside in order to ensure they best contribute to the conservation of species, ecosystems, and landscapes (UNESCO 2019). Those three core areas are: the Mt. Nimba SNR, Bossou Hills, and Déré Forest. Déré Forest is a Classified Forest and Mt. Nimba SNR is an IUCN Category 1a PA, the highest possible IUCN PA category. The Bossou Hills are neither a Classified Forest nor categorized as an IUCN PA. Overall, Déré Forest had more tree cover loss relative to its land area than the Bossou Hills (Fig. 4.3b). And despite its high level PA categorization, tree cover loss still occurred within the Mt. Nimba SNR (Fig. 4.3b). This indicates that PA status likely did not directly influence the amount of tree cover loss that occurred. Further research is needed to better understand the social and political factors that may impact the realized protection of these areas, such as resource allocation, local stakeholder engagement, and law-enforcement.

We found that smallholder agriculture (subsistence and cash crop farming) was the primary driver of tree cover loss across Guinée Forestière. This is not surprising given that agriculture, forestry, and fishing make up 24% of the country's GDP and agriculture alone provides income for over half of rural households in Guinea (World Bank 2019). Thus, it is also not unexpected that logging was also identified as a driver of tree cover loss both within and outside of HBAs. In Guinée Forestière, logging is likely an artisanal, as opposed to a large-scale commercial, operation. Apart from felling trees for building infrastructure and energy production, much of the artisanal logging is just the first step in slash and burn agricultural practices. If not already in place, more sustainable artisanal logging practices and more efficient use of wood as an energy source might go a long way toward protecting biodiversity and the structure and function of the ecosystems sustaining life in Guinée Forestière (Arcus Foundation 2014). Notably, large scale, industrial agriculture was not identified as a primary driver of tree cover loss in this region. There is potential for expansion of industrial agriculture across Guinée Forestière, as there have been a few industrial rubber and oil palm plantations located in this region in the past. For example, there are industrial oil palm and rubber plantations (Société Guinéenne de Palmier à huile et d'Hévéa (SOGUIPAH)) near the Diécké Forest (an HBA used in this study), but their development began prior to 2000 and therefore were not likely to have been a direct driver of tree cover loss during the time period analyzed. Apart from this, most of the agricultural activities in Guinée Forestière appear to function as subsistence and cash-crop farming on smaller scales.

We encountered several challenges throughout this study. One difficulty was the lack of consistent, freely available VHR imagery for use in the sample interpretation process. As a result, we needed to create an "unknown" category to capture drivers of tree cover loss for instances where loss was visually detected in the samples, but for where the imagery was either too coarse, obscured by cloud-cover and cloud shadow, or where the temporal resolution of available imagery was too low to visually identify the exact driver of loss. This “unknown” category allowed us to record the observed tree cover lost, but it did not provide details of what driver(s) directly caused the loss. In most cases, we were confident that the loss was anthropogenic, but we were unable to distinguish what type of human activities led to the observed tree cover loss.

We faced an additional challenge when interpreting the results. In this study, the sample-based approach for estimating the exact drivers of tree cover loss was not exhaustive of all possible drivers of tree cover loss. By stratifying and randomly sampling a portion of the overall area of interest, we are able to identify the most widespread proximate drivers, but were unable to identify drivers of tree cover loss that were not represented in the sampling effort. For instance, we know that between the years of 2000 and 2018, mining was a driver of tree cover loss within some of the identified HBAs. However, mining was never recorded as a driver of change during the sample interpretation process. In one case, the location of a sampled pixel was adjacent to an area that underwent deforestation due to mining, but since no tree cover loss took place within the sampled pixel, no driver was recorded (Fig. 4.4). This is an important caveat given that the world’s largest untapped iron-ore reserve is located within Pic de Fon (Simandou mountain range), an HBA used in this study. Although exploration began in the late 1990s and early 2000s, legal issues, corruption, and geographic remoteness have left it undeveloped. Mining, throughout all of its phases (exploration and evaluation, engineering and site selection, development, and operations), is an intensive process that both directly and indirectly impacts the environment (Arcus Foundation 2014). These impacts include deforestation and habitat loss, pollution, influxes of people for economic opportunities, and increased human access to once remote regions for hunting and logging (Arcus Foundation 2014; Sonter et al. 2018). Even though mining was not captured in the sample analysis as a proximate driver of tree cover loss, it likely has been an ultimate (indirect) driver even during the exploration, evaluation, engineering, and site selection phases. It is also likely to be a future driver of tree cover loss, both inside and adjacent to mining sites, once development and operations begin. Similar threats to biodiversity exist elsewhere in Guinée Forestière, namely in the Mont Nimba Biosphere Reserve (analyzed in this study), which has some of the largest reserves of iron-ore in the world. Together, these mining projects could have massive direct and indirect effects on biodiversity and the ecosystem services in the forests found at the Mont Nimba Biosphere Reserve and Pic de Fon.

4.6 Conclusions

This study analyzed tree cover loss across Guinée Forestière from 2000 to 2018. To our knowledge, this study is the first to quantify tree cover loss in West Africa using a regionally specific change detection model for a nineteen-year period of time (2000 to 2018). It is also the first to assess annual tree cover loss relative to protected areas of high biodiversity in Guinée Forestière. We found that tree cover loss occurred across 25% of Guinée Forestière’s land area. Results from the sample-based area estimates revealed that anthropogenic activities, especially smallholder agriculture, that result in tree cover loss pose serious threats to biodiversity within the Guinée Forestière landscape. The annual tree cover loss estimates showed that further research is needed to better understand the social and political factors impacting on-the-ground protection of the HBAs in this study. Our research also highlights important limitations to consider and address when using remote sensing to automate change detection across landscapes. We provided knowledge of tree cover dynamics that are needed for contextualizing biodiversity within the broader socioecological landscape and that are key to effective management and conservation. Preventing and mitigating the loss of biodiversity and ecosystem services will require a holistic approach based on robust monitoring and conservation activities that engages communities, governments, and scientists across many sectors.

4.7 Figures

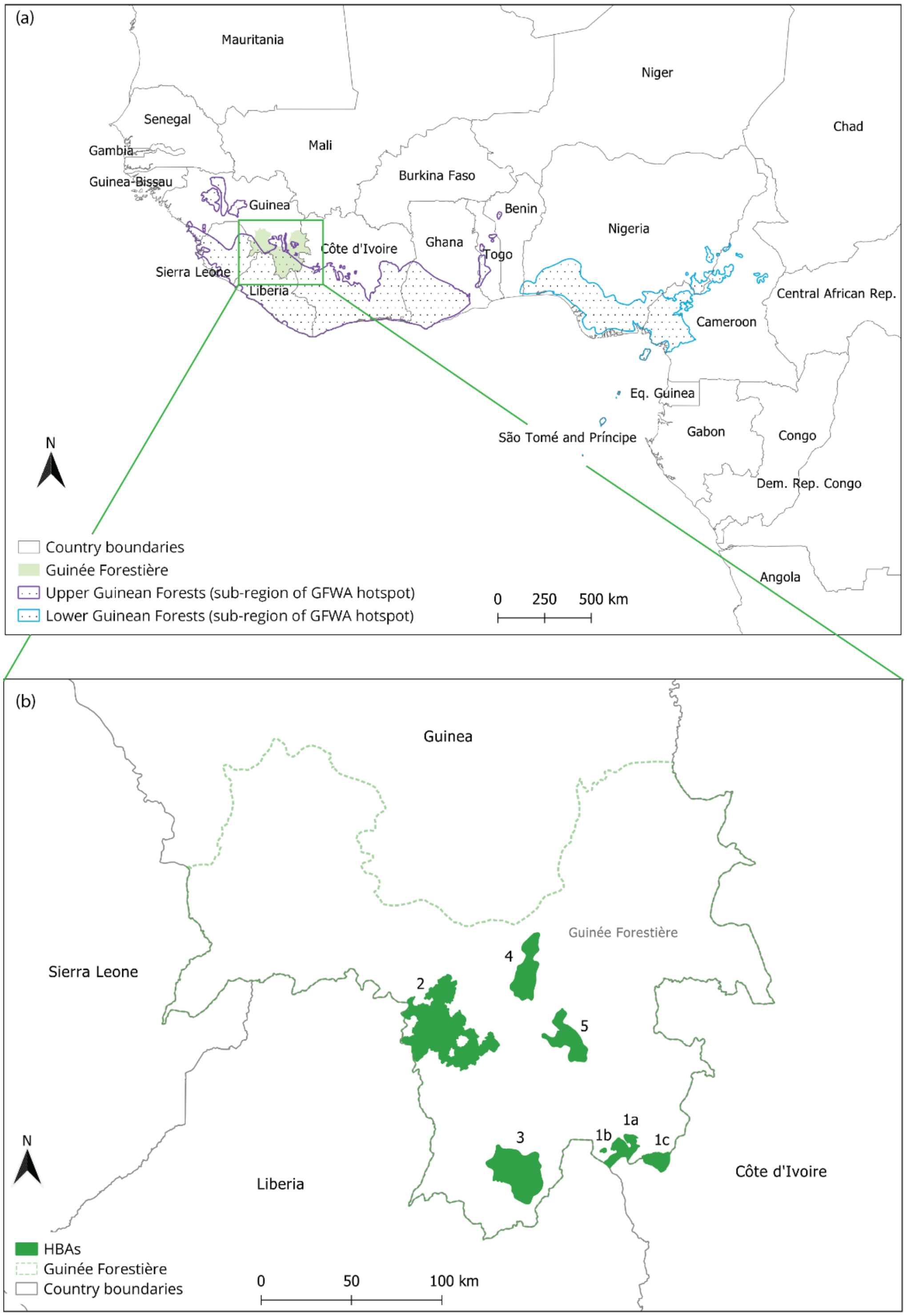

(a)
Mauritania
Niger
Chad
Senegal
Gambia
Mali
Guinea-Bissau
Burkina Faso
Guinea
Benin
Nigeria
Ghana
Côte d'Ivoire
Togo
Sierra Leone
Liberia
Central African Rep.
Cameroon
Eq. Guinea
São Tomé and Príncipe
Gabon
Congo
Dem. Rep. Congo
Angola
N
Country boundaries
Guinée Forestière
Upper Guinean Forests (sub-region of GFWA hotspot)
Lower Guinean Forests (sub-region of GFWA hotspot)
0 250 500 km
(b)
Guinea
Guinée Forestière
Sierra Leone
4
2
5
3
1b
1a
1c
Liberia
Côte d'Ivoire
N
HBAs
Guinée Forestière
Country boundaries
0 50 100 km

Fig. 4.1 Location of the Guinean Forests of West Africa (GFWA) hotspot (including Upper and Lower Guinean Forests sub-regions) (Figure 4.1a) along with the 5 HBAs (green polygons) within the study area (Guinée Forestière) (Figure 4.1b). The HBAs are labeled as: 1a = Mount Nimba Strict Nature Reserve core area of the Mont Nimba Biosphere Reserve; 1b = Bossou Hills core area of Mont Nimba Biosphere Reserve; 1c = Déré Forest core area of the Mont Nimba Biosphere Reserve; 2 = Massif du Ziama Biosphere Reserve; 3 = Diécké Forest; 4 = Pic de Fon; 5 = Mount Bero.

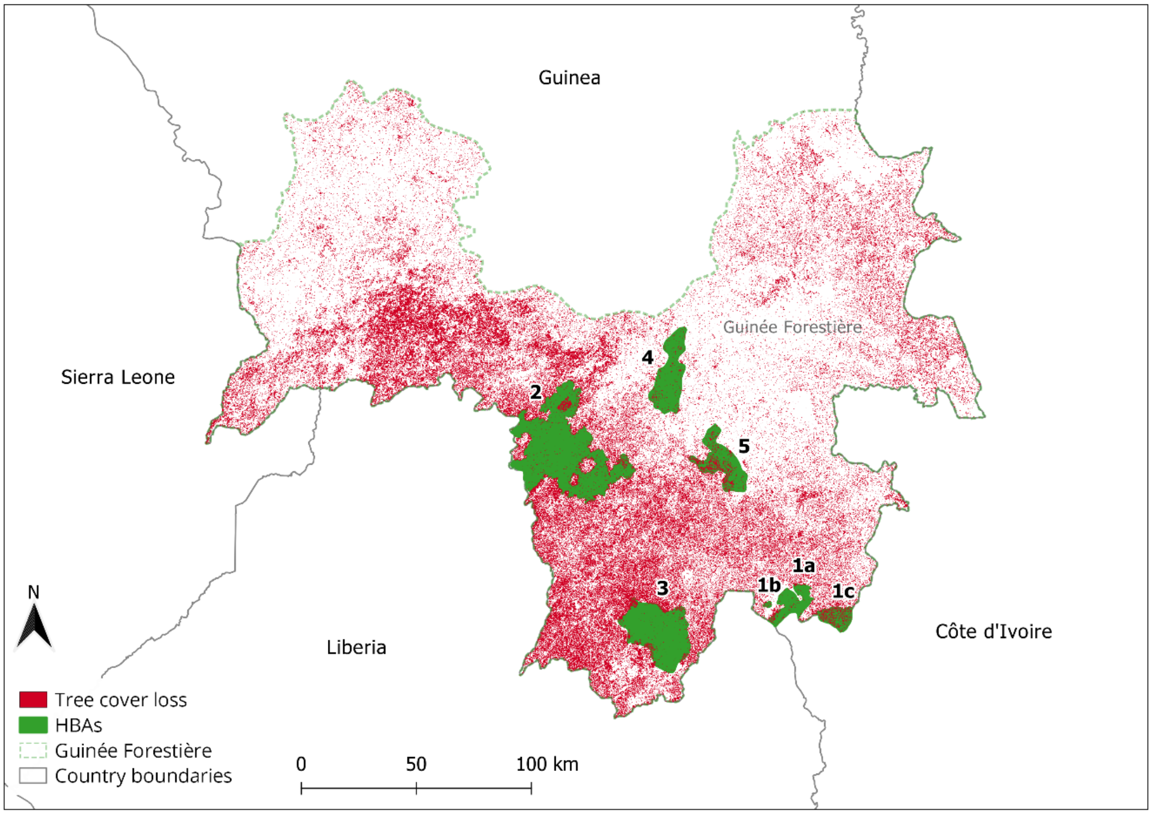


Fig. 4.2. Map of the tree cover loss that occurred across Guinée Forestière from 2000 to 2018.

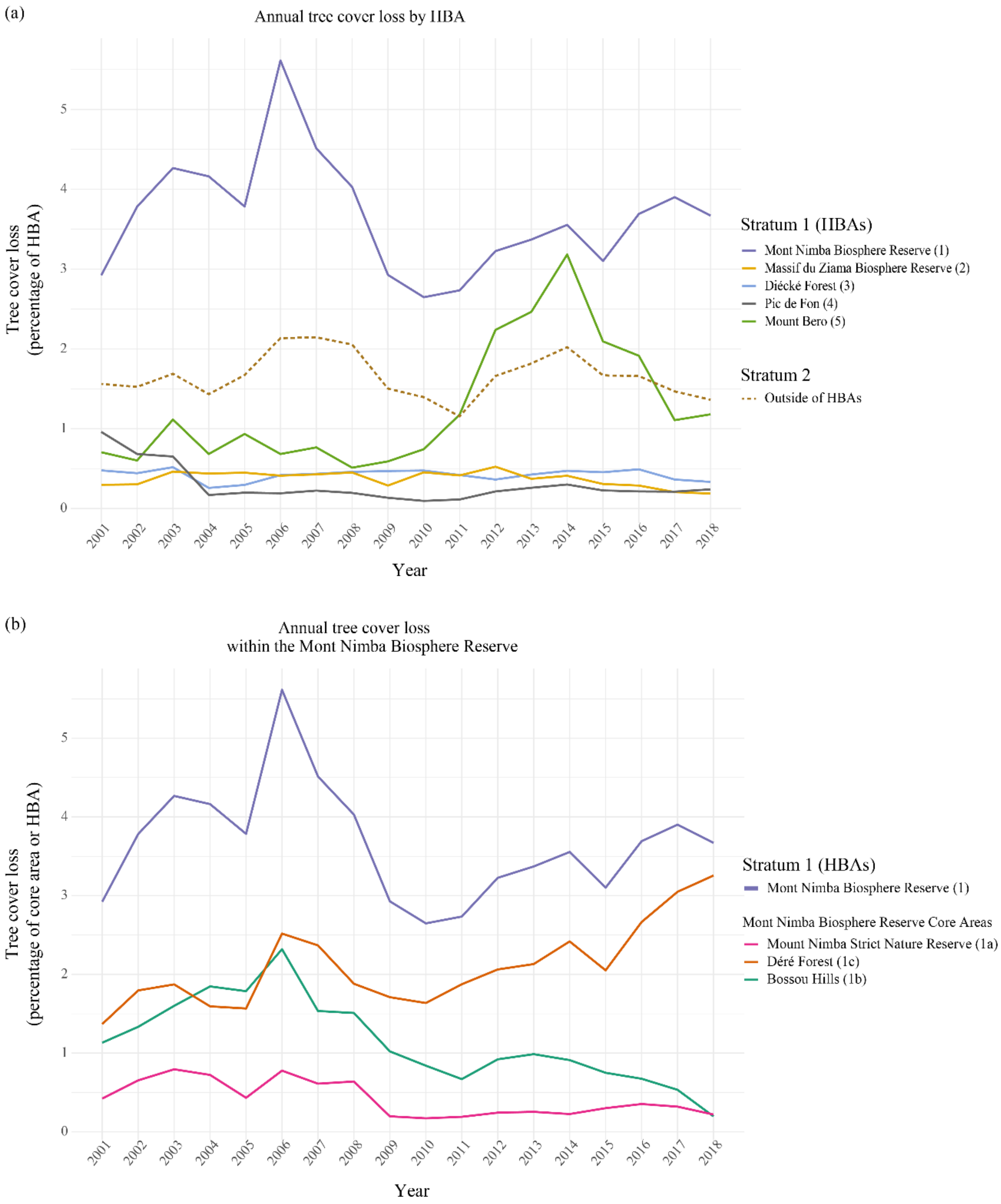


Fig. 4.3. Annual tree cover loss based on a 3-year mean. Loss is given as a percentage of the total area of each HBA (or in the case of graphs (b), percentage of either the HBA or core area). Graph (a) shows tree cover loss within each HBA and loss outside of HBAs across Guinée Forestière. Graph (b) depicts loss

specifically within the Mont Nimba Biosphere Reserve and its three core areas. Numbers in parentheses next to each HBA correspond to the labels used in the map of the study area (Fig. 4.1).

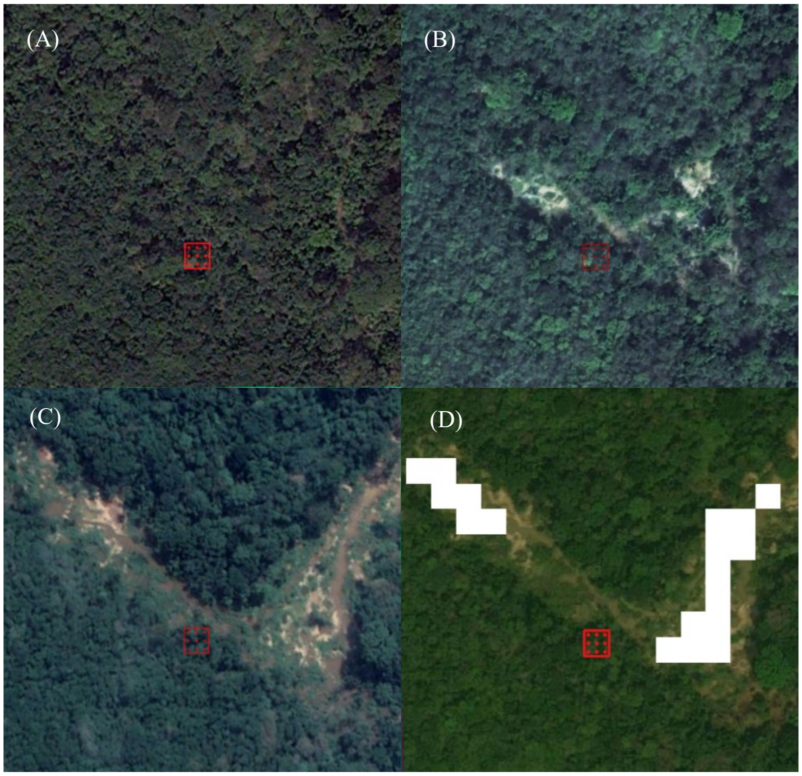


Fig. 4.4 Google Earth Imagery showing the sampled pixel (red square) and the area surrounding the sampled pixel. In this case, no change took place inside the sampled pixel as reflected in maps (A) through (D), but tree cover was lost in the surrounding area as shown in maps (B), (C), and (D). Image (A) shows baseline forest cover inside and outside of the sampled pixel in year 2011. Image (B) is from 2015 and shows forest cover within the sampled pixel and small forest clearings from nearby mining activity. Image (C) shows expansion of the forest clearings in 2019 due to mining in the areas surrounding the sampled pixel. Image (D) shows the sampled pixel and the superimposed pixels of detected loss (white) that were identified by the Landsat time series tree cover loss map between 2000 and 2018.

4.8 Tables

Table 4.1 Strata area and sampling sizes

Stratum	Area (km^2)	Pixel count	Sample size
1 (outside HBAs)	40160.6	52781552	400
2 (inside HBAs)	2602.0	3415081	100

Table 4.2 Drivers of tree cover loss and definitions used in this study.

Driver	Description
Logging	Forest clearings created by cutting down trees and without apparent agricultural or mining purposes
Smallholder Agriculture	Loss due to human use of land for subsistence or small scale cash crop farming
Mining	Clearings associated with mining activities (e.g. terraces, pits, and human-made ponds)
Settlement	Loss of tress from the creation or expansion of human settlements and building infrastructure
Road Infrastructure	Loss due to the expansion and creation of roads and associated road corridors
Industrial Agriculture	Loss due to large scale industrial agricultural activities
Unknown	Unable to discern driver of tree cover loss
None	No loss took place

Table 4.3 Drivers of tree cover loss across Guinée Forestière

Driver of loss	**Area (km^2)**	**SE (km^2)**
Smallholder Agriculture	6631	744
Unknown	4098	600

Logging	152	107
Settlement	26	26

Table 4.4 Drivers of tree cover loss by strata across Guinée Forestière

Stratum	Driver of loss	Area (km^2)	SE (km^2)
1 (outside HBAs)	Smallholder Agriculture	6527	742
	Unknown	3916	596
	Logging	100	100
2 (inside HBAs)	Unknown	182	67
	Smallholder Agriculture	104	51
	Logging	52	37
	Settlement	26	26

Chapter 5

General Discussion

This research provided additional knowledge of the behavioral ecology of the Seringbara chimpanzee communities in the Nimba Mountains. It also used knowledge of chimpanzee behavior to better understand the factors influencing their occurrence and habitat suitability within the Nimba landscape. Additionally, it investigated the socioecological dynamics and potential threats to biodiversity and chimpanzees in not only the Nimba Mountains, but across the entire Forestière region of Guinea.

Chimpanzees use an extensive repertoire of vocal and non-vocal forms of communication to convey information in a socially and spatially dynamic setting. They drum on tree buttresses with hands and/or feet producing low-frequency acoustic signals. Compared to other chimpanzee behaviors, drumming has been relatively understudied. A few studies have reported the acoustic characteristics and social factors affecting drumming behavior (Arcadi et al., 1998, 2004; Arcadi & Wallauer, 2013; Babiszewska et al., 2015), but none so far have looked at the characteristics of the drumming tree itself. Chapter 2, an analysis of the presence of selectivity in buttress drumming by the Seringbara chimpanzees in the Nimba Mountains, is the first such study. It compared trees and buttresses used for drumming to those not used for drumming and addressed two main hypotheses. First, if buttress drumming is goal-directed, namely to communicate over long distances, then chimpanzees would show preference for certain tree species and would select trees that are larger and have more buttresses. Second, used buttresses would have larger surface areas (i.e. more area upon which a chimpanzee can drum) and used buttresses would be thinner, as they are more pliant and conducive to producing resonant sounds when impacted (Kalan et al., 2019). The results indicate that chimpanzees are selective in drumming tree choice. Specifically, Seringbara chimpanzees prefer certain tree species, use trees that are larger, and select buttresses that are thinner and have greater surfaces areas. These findings imply that buttress drumming is not a random act, but rather goal-oriented and requiring knowledge of suitable trees and buttresses. Chapter 2 results also support long-distance communication as one probable function of buttress drumming based on selectivity for buttress characteristics likely to impact sound propagation. This research provides a foundation for further assessing the cognitive underpinnings and functions of buttress drumming in wild chimpanzees.

Resource management and conservation of endangered species requires an understanding of how species perceive and respond to their environments, so conservation efforts can focus on areas of highest importance for their long-term survival. Species distribution models (SDMs) are an informative way to evaluate the importance of environmental variables related to species distribution (Franklin 2009) and are an appropriate tool for identifying conservation areas of concern and importance. In Chapter 3, SDM was used to map and identify areas of suitable chimpanzee habitat within the Greater Nimba Landscape based on chimpanzee behavioral data and the spatial distribution of 12 biophysical variables within the study area. Additionally, this study explored the importance of these variables as they relate to the probability of Seringbara chimpanzee occurrence. The overall predictive performance of the model was 0.721. The most important variable in predicting chimpanzee habitat suitability was NDVI, which indicates the presence of photosynthetically active vegetation. The positive relationship between NDVI and probability of occurrence suggests that Seringbara chimpanzees prefer forested areas with dense, healthy vegetation. The final model also highlighted the isolation and fragmentation of chimpanzee habitat within the Greater Nimba Landscape. This is a major concern given that the viability of chimpanzee populations is dependent on gene flow between communities.

Chimpanzees are only one of many species whose populations are declining. Globally, biodiversity is declining an accelerating pace (Pimm et al. 2014). Much of this decline is attributed to increasing human demands for natural resources, to the extent that our footprint far exceeds the earth’s capacity to regenerate (Lin et al. 2018). Studies have found that increased tree cover, both as part of forest canopy and agricultural landscapes, is correlated with increased levels of species richness and ecosystem function (Morris 2010; Mendenhall et al. 2016; Brockerhoff et al. 2017; Barrios et al. 2018). In particular, tropical forests harbor extremely high levels of biodiversity (Dirzo and Raven 2003; Gibson et al. 2011; Laurance et al. 2012). But, due to human-driven land use changes, tropical forests are undergoing rapid loss, fragmentation, and modification (Gibson et al. 2011; Brockerhoff et al. 2017; Hansen et al. 2020). Comprehensive spatial and temporal monitoring can lead to a better understanding of the threats to tropical forests. It can provide the data and information to support the policies and management practices necessary for restoration and protection of tropical forests and all that they harbor, including chimpanzees (Mayaux et al. 2005; Romijn et al. 2015). Chapter 4 used remote sensing data to (1) map and quantify tree cover loss across Guinée Forestière from 2000 to 2018, (2) estimate tree cover loss relative to PAs of high biodiversity, and (3) identify primary drivers of tree cover loss. Results indicate that the total tree cover loss in Guinée Forestière between years 2000 and 2018 was 10,907 km^2 (SE = 8897), approximately 25% of the region's total land area. Of this total loss, 364 km^2 (SE = 91) of tree cover was lost within HBAs. This represents approximately 14% of the HBA land area and 0.9% of the total land area in Guinée Forestière. The primary driver of tree cover loss was smallholder agriculture. In addition, estimates of annual tree cover loss highlighted that tree cover loss was not consistent across HBAs and did not appear to be directly related to PA classification. Thus, further research is needed to better understand the social and political factors that may be impacting the realized protection of these HBAs, such as resource allocation, local stakeholder engagement, and law-enforcement. Chapter 4 provides knowledge of tree cover dynamics that are needed for contextualizing biodiversity within the broader socioecological landscape and key to effective management and conservation. It is also the first to quantify tree cover loss in West Africa using a regionally specific, change detection model for a nineteen-year period of time (2000 to 2018). It is also the first to assess annual tree cover loss relative to protected areas of high biodiversity in Guinée Forestière.

Chimpanzees are capable of living in a variety of environments, from human-modified landscapes to savanna–woodland mosaics (van Leeuwen et al. 2020a). Yet, even in human-dominated and non-forest land cover types, such as savanna and woodland–shrubland mosaics, trees form an important component of chimpanzee behavior. Nesting behavior is a prime example of the universal importance of trees for chimpanzees regardless of habitat type. All wild chimpanzees build nocturnal sleeping platforms. Typically these nests are constructed in the crowns of trees, although sometimes made on the ground (Fruth and Hohmann 1994; Koops et al. 2007). Arboreal nesting behavior is seen in chimpanzee communities across all habitat types, including savanna–woodland mosaics (Badji et al. 2018), agricultural–swamp mosaics (Garriga et al. 2019), and primary forests (Koops et al. 2012b). A complete loss of tree cover would make arboreal nesting impossible and critically impact chimpanzee behavior. Moreover, drumming behavior (Chapter 2) depends on trees. Further understanding of the propagation of chimpanzee drum sounds across the landscape is needed, but if drumming proves to be a significant long-distance communication modality relative to other forms of chimpanzee communication, the loss of trees, particularly large, buttressed trees, could impact the social and spatial dynamics of chimpanzees in the Nimba Mountains and elsewhere. Hence, monitoring of not only chimpanzee behavior, but of the surrounding socioecological dynamics that may lead to tree cover loss is important if chimpanzee conservation is to be effective.

Globally, landscapes are changing rapidly and these changes are most often attributed to anthropogenic causes (Curtis et al. 2018), as they were in this research (Chapter 4). It is known that human modified environments are able to provide habitat for chimpanzees, but the degree to which their behavioral flexibility (adaptability or plasticity) enables chimpanzees to survive long-term in human-dominated landscapes remains unknown (McLennan et al. 2017). If left unchecked, the behavioral flexibility of chimpanzees will continue to be tested as chimpanzee habitats are lost, modified, and fragmented. Thus, considerable attention needs to be paid to the human dimensions of conservation (Setchell et al. 2017). Not only are the causes of deforestation and tree cover loss driven by humans (Hansen et al. 2020), but such changes often result in increased interactions between humans and chimpanzees. The long-term sustainability of these interactions is not only dependent on chimpanzee adaptability but on the perception and response of humans to changing chimpanzee behaviors (McLennan et al. 2017). Thus, as Setchell et al. (2017) wrote, "conservation problems are at least as much about people as they are about animals."

This research also highlights the need to address what is driving chimpanzee habitat loss, primarily subsistence agriculture. The impacts that smallholder agricultural practices have had and are likely to continue having on chimpanzees and all biodiversity across Guinée Forestière are not small. If not already being done, communities in Guinée Forestière could explore ways to increase agricultural yield without further loss to natural resources and biodiversity, a process known as sustainable intensification (SI) (Garnett et al. 2013; Pretty and Bharucha 2014). Successful SI implementation will vary across localities, but focus should be placed on smallholder engagement and investing in and empowering the use of local knowledge to create innovative solutions to local agricultural challenges (Cook et al. 2015).

In addition to SI, which deals more with avoidance of loss, recommendations are also needed for when habitat loss has occurred and human–chimpanzee interactions increase. When chimpanzee habitat is lost, the conservation lens might shift from loss avoidance to that of ensuring that the resulting human–chimpanzee interactions are peaceful and mutually beneficial. In these situations, there is not a panacea for all communities. It is necessary to examine the economic, social, and cultural factors influencing human perceptions and responses to increased interactions with chimpanzees (Hill 2015; Hockings 2016). One action identified by the IUCN SSC Primate Specialist Group (2020) to assist with this, is culturally informed programs to raise public awareness of issues related to human–chimpanzee coexistence and laws protecting chimpanzees. Mitigating negative human–chimpanzee interactions must be an integrated part of conservation strategies that also address other concerns such as habitat loss, hunting, and disease (Hockings 2016).

If conservation is to be beneficial for chimpanzees and people, both must be understood and addressed as part of a dynamic socioecological system (Balasubramaniam et al. 2021). By combining chimpanzee behavioral data with information on their socioecological landscape, this research aims to provide knowledge and context that can lead to more effective conservation of chimpanzees in the Nimba Mountains and across all of Guinée Forestière. Given the threats to chimpanzees and the drivers of tree cover loss presented here, future research should focus on the social, cultural, and economic factors influencing the coexistence of humans and wildlife and work towards the sustainability of both across Guinée Forestière.

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Appendix A

R script – Spatial filtering (Chapter 3)

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=1385 occurrence points that were used to generate a model that was compared to models generated using other techniques for reducing sampling bias. Table 3.4 shows the breakdown of occurrence points categorized into different types of occurrence. 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.

```
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.

```
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 frame ###
occur_dups.spdf <- SpatialPointsDataFrame(125ords=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 Shapefle ###
write.csv(occur_prox30.spdf, “occur_prox40.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 Shapefle ###
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 Shapefle ###
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 3.5. 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 3.4 Breakdown of occurrence points (N = 1385) categorized into different types of occurrence

Type of occurrence	**Count**
Ant dipping sites	18
Chimpanzee sightings	130
Feces	814
Nests	308
Wadges	115

Table 3.5 Comparison of model results for different spatial filtering methods

Name	**Source**	**Function**	**Count**	**Maxent AUC**
occur_dups	R	!duplicated()	1386	0.753
dup_filter1_proj	R (csv) GIS (display xy)	gridSample()	947	0.721
occur_prox30	R	spatialFilter()	733	0.735
occur_prox40	R	spatialFilter()	645	0.73
occur_prox50	R	spatialFilter()	577	0.717

Appendix B

Land cover classification (Chapter 3)

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 (Fig. 3.7). 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 ArcMap10.2.2 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 Fig. 3.8.

Results

The unsupervised classification was unsuccessful and did not distinguish the spectral differences between all land cover classes, namely village and savanna (Fig. 3.9 and 3.10). 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 3.6 and 3.7). 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 3.8). Thus, the minimum distance classification method was chosen for use in the final model.

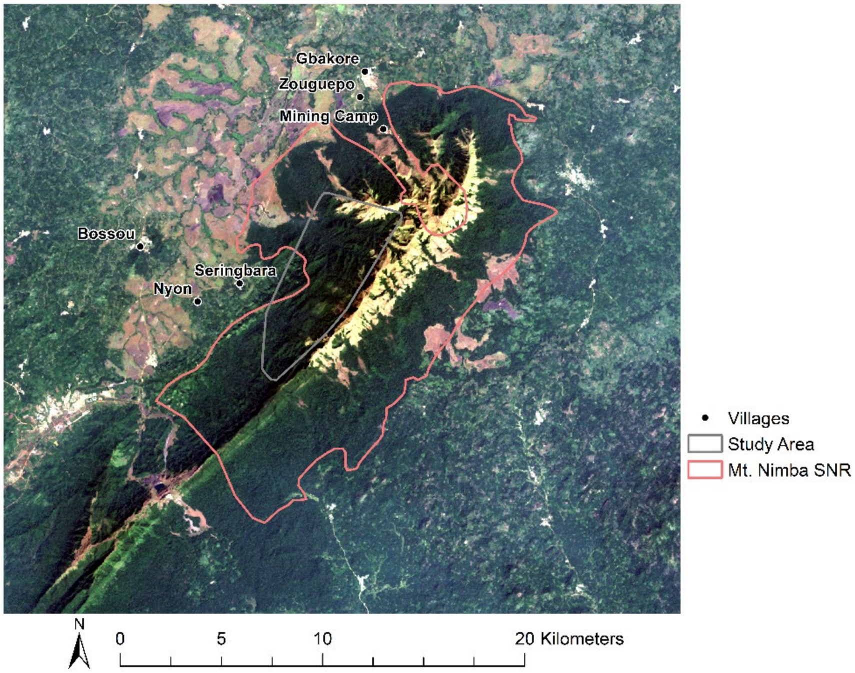
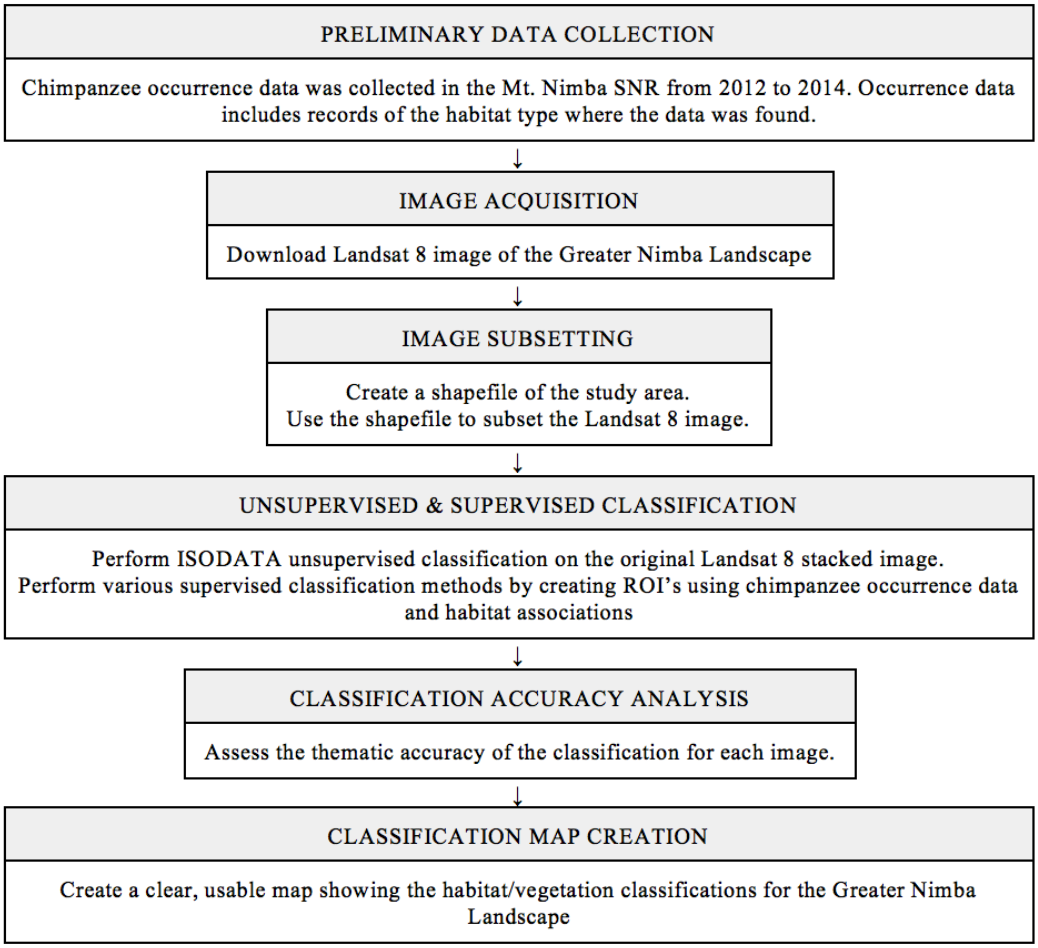


Fig. 3.7 Landsat 8 image of the Greater Nimba Landscape from December 26, 2013.



PRELIMINARY DATA COLLECTION

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

Fig. 3.8 Flowchart of methods for performing land cover classifications.

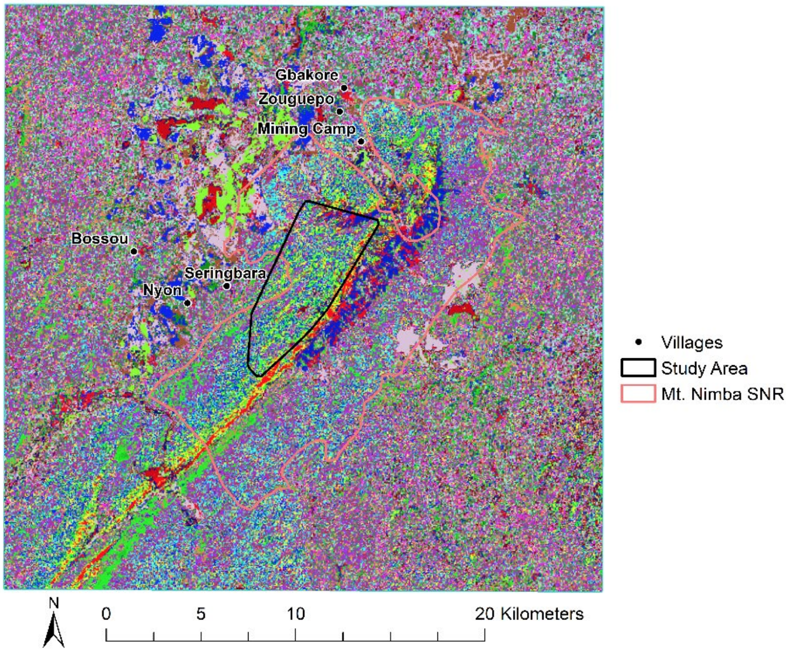


Fig. 3.9 The ISODATA unsupervised classification of the Greater Nimba Landscape.

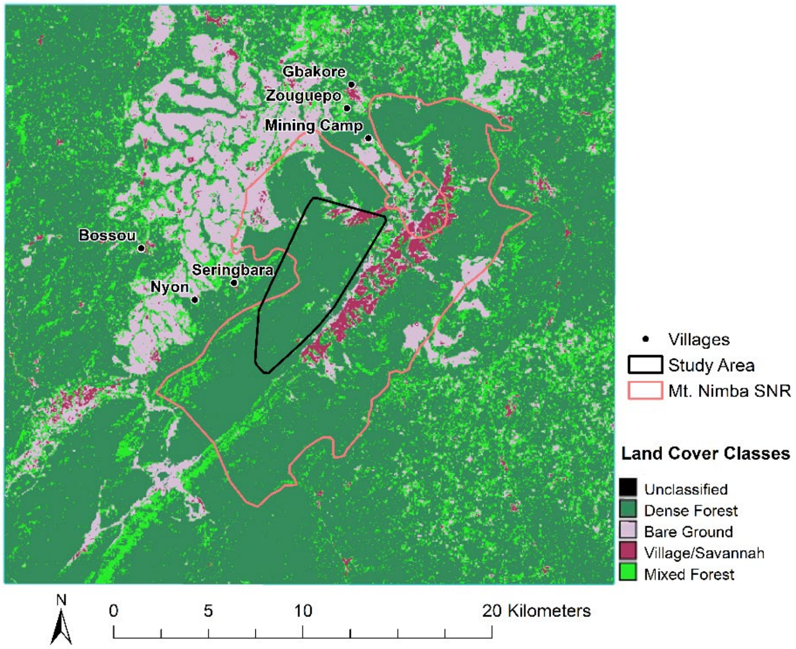


Fig. 3.10 The ISODATA unsupervised classification, conversion from spectral classes to five land cover classes for the Greater Nimba Landscape. The unsupervised classification was unsuccessful and did not distinguish the spectral differences between all land cover classes, namely village and savanna.

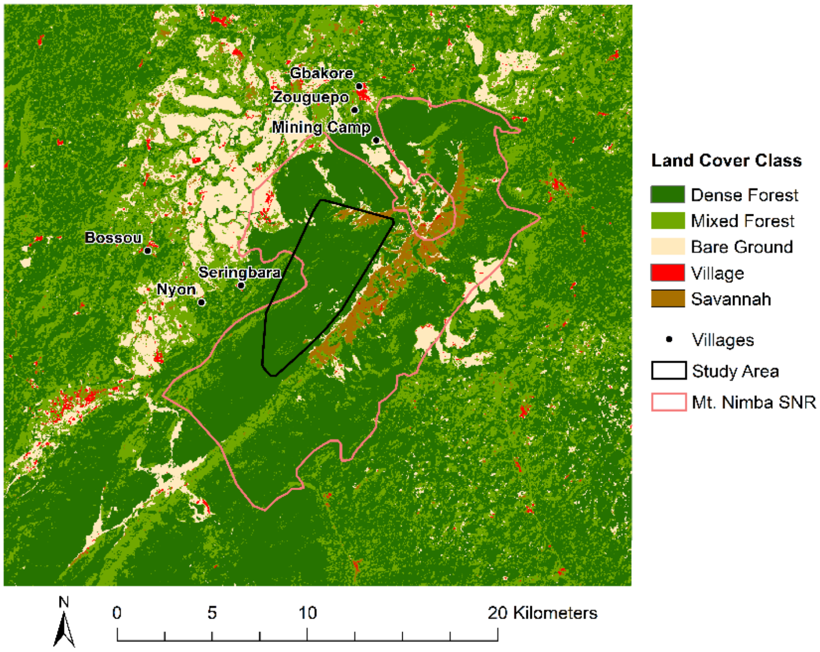


Fig. 3.11 Minimum distance supervised classification from the Greater Nimba Landscape. This classification method was chosen for the land cover class (LCC) variable. LCC was eventually removed from the model because it was highly correlated ($|r| > 0.7$) with wetness.

Table 3.6 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.

Class	Bare Ground	Savannah	Village	Dense Forest	Mixed Forest	Total
Bare Ground	96.79	0.96	3.4	0	0.76	19.68
Savannah	1.81	96.4	3.4	0	4.16	9.5
Village	1.31	2.16	93.2	0	0	3.19
Dense Forest	0	0	0	97.82	25.11	50.06
Mixed Forest	0.1	0.48	0	2.18	69.97	17.58
Total	100	100	100	100	100	100

Table 3.7 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.

Class	Bare Ground	Savannah	Village	Dense Forest	Mixed Forest	Total
Bare Ground	93.78	0	0	0	0	18.72
Savannah	0	97.84	0	0	0	8.18
Village	6.12	2.16	100	0.04	0.17	4.41
Dense Forest	0	0	0	99.6	31.64	52.4

Mixed Forest	0.1	0	0	0.36	68.19	16.29
Total	100	100	100	100	100	100

Table 3.8 Producer's and User's accuracy for the supervised minimum distance and maximum likelihood classifications for the Greater Nimba Landscape.

Producer's and User's Accuracy ***(Percent)***				
Class	**Producer (Min. Dist)**	**Producer (Max. Likeli.)**	**User (Min. Dist)**	**User (Max. Likeli.)**
Bare Ground	96.79	93.78	98.17	100
Savannah	96.4	97.84	84.81	100
Village	93.2	100	86.16	66.82
Dense Forest	97.82	99.6	88.15	85.74
Medium Forest	69.97	68.19	94.07	98.89

Table 3.9 Commission and omission errors for the supervised minimum distance and maximum likelihood classifications for the Greater Nimba Landscape.

Errors of Commission and Omission ***(Percent)***				
Class	**Commission (Min. Dist)**	**Commission (Max. Likeli.)**	**Omission (Min. Dist)**	**Omission (Max. Likeli.)**
Bare Ground	1.83	0	3.21	6.22
Savannah	15.19	0	3.6	2.16
Village	13.84	33.18	6.8	0
Dense Forest	11.85	14.26	2.18	0.4
Medium Forest	5.93	1.11	30.03	31.81

Appendix C

R script – HSP (Chapter 3)

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

```
### 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" untis are number of cells
#
```

```
# references
# Murphy M.A., J.S. Evans, and A.S. Storfer (2010) Quantify Bufo boreas connectivity
in Yellowstone National Park with landscape genetics. Ecology 91:252-261
#
# 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) {
              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

Correlation matrix (Chapter 3)

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 3.10 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.

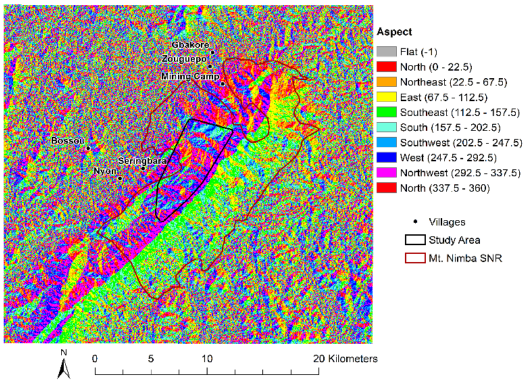
Variable	dtr	NDVI	brightnes	TPI	slope	rough	relief	IMI	HLI	curve	CTI	aspect	wetness	greennes	HSP	elevation
dtr																
NDVI	-0.07															
brightnes	-0.03	-0.06														
TPI	0.05	-0.02	-0.01													
slope	0.17	0.07	-0.09	0.01												
rough	0.15	-0.01	-0.04	0.00	0.85											
relief	0.04	-0.02	-0.01	0.37	0.00	0.00										
IMI	-0.07	-0.05	-0.25	-0.16	-0.05	-0.06	-0.04									
HLI	0.15	0.02	-0.11	0.00	0.62	0.52	0.00	-0.01								
curvature	0.05	-0.02	-0.01	1.00	0.01	0.00	0.37	-0.16	0.00							
CTI	-0.12	-0.02	0.03	-0.51	-0.45	-0.30	-0.13	0.41	-0.27	-0.51						
aspect	0.03	-0.11	-0.22	0.00	0.05	0.04	0.00	0.19	0.41	0.00	-0.02					
wetness	-0.06	0.74	-0.58	0.00	0.13	0.04	0.00	0.11	0.10	0.00	-0.05	0.05				
greennes	-0.07	0.91	0.07	-0.01	0.13	0.04	-0.01	-0.06	0.05	-0.01	-0.04	-0.12	0.74			
HSP	0.34	-0.12	0.02	0.54	0.08	0.08	0.25	-0.21	0.05	0.54	-0.42	0.00	-0.08	-0.09		
lcc	0.06	-0.56	0.55	0.00	0.01	0.08	0.00	-0.13	0.01	0.00	0.01	-0.08	-0.72	-0.47	0.06	
Elevation	0.16	-0.08	-0.07	0.05	0.56	0.53	0.04	0.05	0.39	0.05	-0.19	0.06	0.02	0.02	0.20	0.15

Appendix E

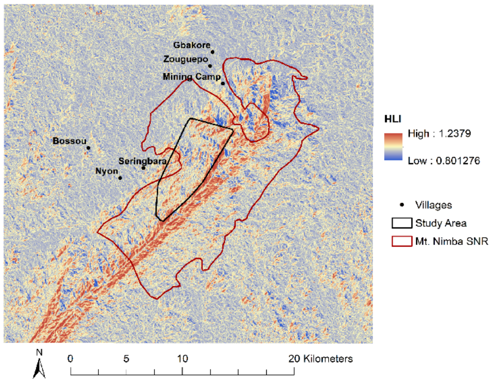
Response curves and maps of biophysical variables (Chapter 3)

The response curves and maps for the biophysical variables not discussed in detail in the main text are displayed below (Fig. 3.12). 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.

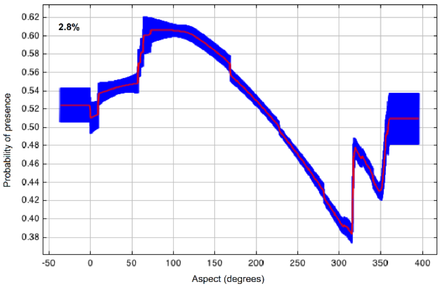
a. Aspect



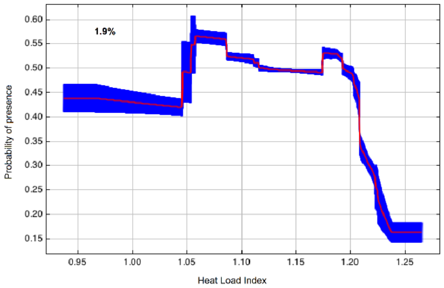
b. Heat Load Index



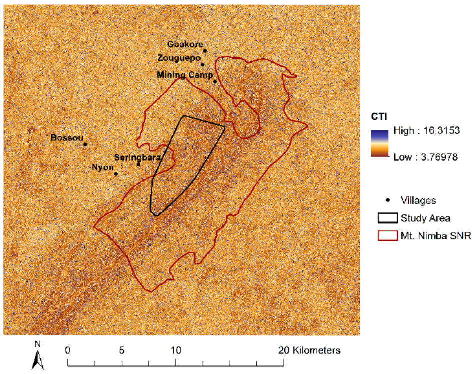
Response of Occurrence to Aspect



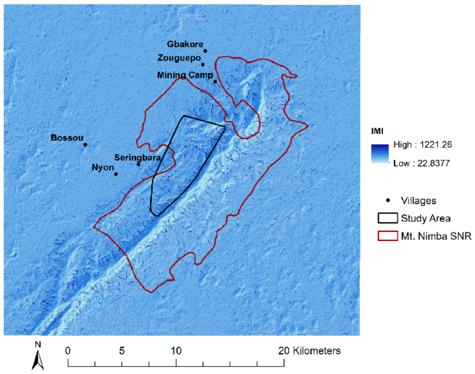
Response of Occurrence to HLI



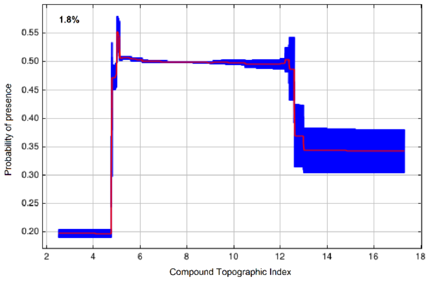
c. Compound Topographic Index



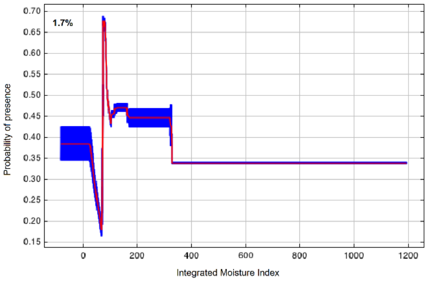
d. Integrated Moisture Index



Response of Occurrence to CTI



Response of Occurrence to IMI



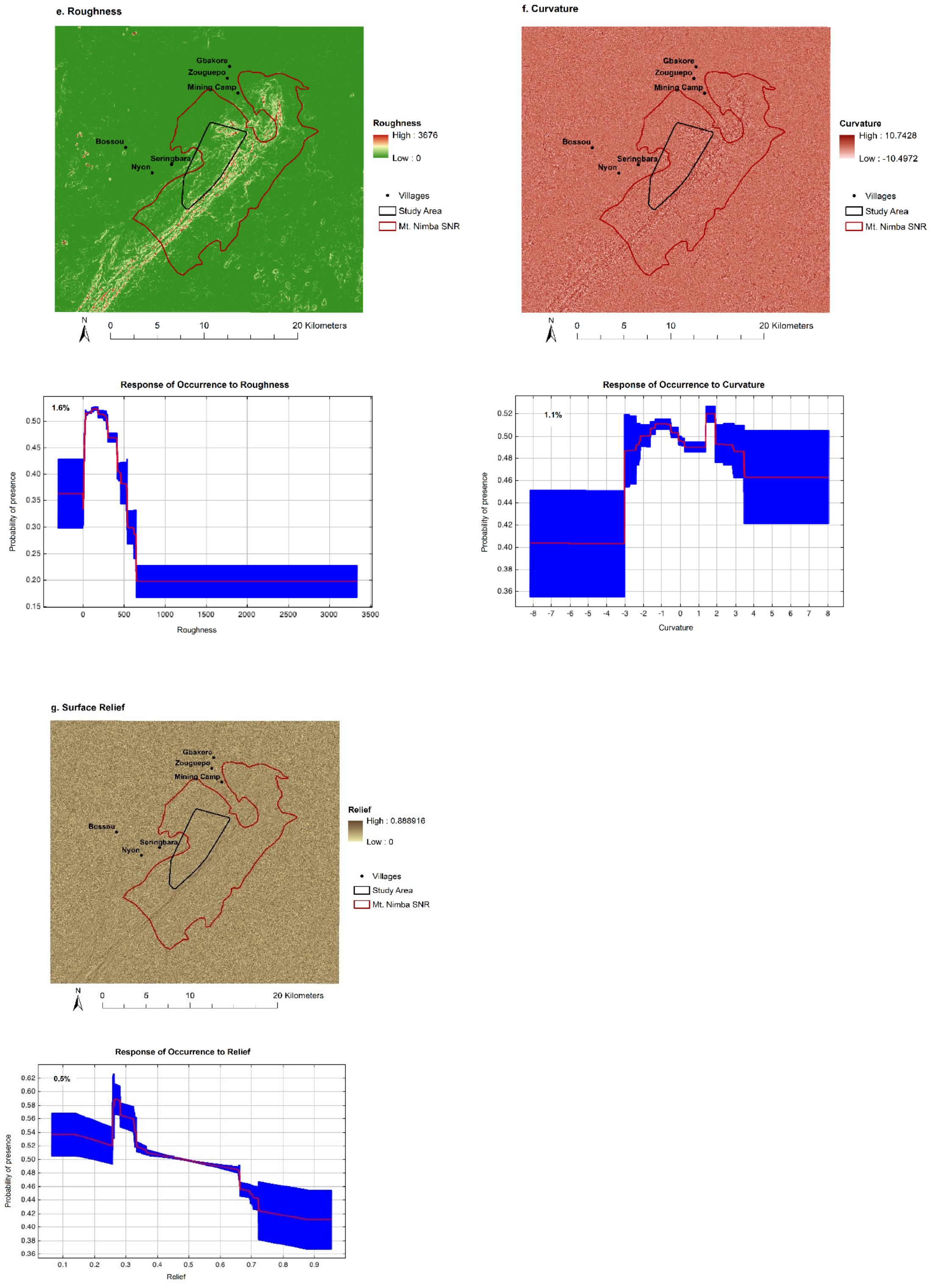


Fig. 3.12 Response curves and maps of the biophysical variables