Connectivity and conservation of Western Chimpanzee (*Pan troglodytes verus*) habitat in Liberia

Amy E. Frazier1 | Miroslav Honzák2 | Catherine Hudson1 | Rebecca Perlin1 | Alonzo Tohtsonie1 | Keith D. Gaddis3 | Celio de Sousa4,5 | Trond H. Larsen2 | Jessica Junker6 | Sylvain Nyandwi7 | Andrew B. Trgovac1

1Arizona State University, Tempe, AZ, USA
2Conservation International, Arlington, VA, USA
3NASA Headquarters, Washington, DC, USA
4NASA Goddard Space Flight Center, Greenbelt, MD, USA
5Universities Space Research Association, Columbia, MD, USA
6German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig Institute of Biology, Martin Luther University Halle-Wittenberg, Leipzig, Germany
7George Washington University, Washington, DC, USA

Correspondence
Amy E. Frazier, Arizona State University, Tempe, AZ, USA.
Email: amy.frazier@asu.edu

Funding information
This work was partially supported by a U.S. National Science Foundation grant to A.E.F. (HDR-1934759)

Editor: Trishna Dutta

Abstract

**Aim:** As part of the Gaborone Declaration for Sustainability in Africa, Liberia has pledged to include the value of nature in national decision making through natural capital accounting. Surveying species of concern, such as the western chimpanzee (*Pan troglodytes verus*), which was recently reclassified as “critically endangered” by the International Union for Conservation of Nature, and identifying protection priority areas are critical first steps towards achieving Liberia's goal to conserve 30% of its remaining forests and supporting the wave of conservation projects taking place in the country.

**Location:** Liberia, Africa.

**Methods:** We modelled western chimpanzee habitat suitability, focusing on determining relevant environmental predictors and the most appropriate scale for modelling species–habitat relationships. We built models at six resolutions (30–960 m) to identify scale domains where relationships remain constant. We include several habitat variables that have not been included in prior modelling efforts. We then used the suitability map as the conductance input into a connectivity analysis using Circuitscape.

**Results:** The amount of forest within 1–3 km was the most important predictor of chimpanzee occurrence. Variable ranks and importance shifted considerably between modelling scales, supporting the need for multiscale investigations, but scale domains were present. Several important corridors for chimpanzee habitat and movement overlap considerably with existing timber and palm oil concessions and overlap mining and rubber concessions to a lesser degree.

**Main conclusions:** The proportion of primary forest within 1–3 km is critically important for chimpanzee habitat. Ongoing conservation projects and efforts taking place in Liberia including the Good Growth Partnership and the Gaborone Declaration for Sustainability in Africa can utilize the spatial findings on connectivity provided by this study to inform future conservation decisions, particularly expanding exiting protected areas.
1 | INTRODUCTION

The chimpanzee (Pan troglodytes) is the closest living relative to humans (Ruvolo, 1997) and is on the International Union for Conservation of Nature (IUCN) Red List. The western chimpanzee subspecies (P. troglodytes verus), which occurs discontinuously in the forests of tropical West Africa, was recently reclassified as “Critically Endangered” (Humle et al., 2016; Kühl et al., 2017) after the population was reported to have reduced from about 175,000 individuals in 1990 to only 35,000 individuals in 2014 (Kühl et al., 2017). The population of western chimpanzees is estimated to have declined approximately 80% since 1990, and these declines are expected to continue into the future (Humle et al., 2016; Kühl et al., 2017). Liberia is thought to host the second largest—and most viable—population of western chimpanzees with some of the most suitable environmental conditions, including large blocks of continuous forest (Junker et al., 2012; Tweh et al., 2015). However, these forest blocks are largely unprotected (Freeman et al., 2019). Deforestation complicates conservation efforts because chimpanzee populations in Liberia and across West Africa are threatened by logging and wood harvesting, housing and urban development, forest clearing for agriculture, mining and other impacts such as hunting and poaching (Bene et al., 2013; Greengrass, 2011; Junker et al., 2012). Additionally, after more than 14 years of civil conflict and war that ended in 2003, Liberia has been rapidly losing prime chimpanzee habitat to development and extraction activities. Logging and mining interests have been extracting natural resources at alarming rates, often under the jurisdiction of Private Use Permits, which are subject to very few sustainability requirements and have led to more than 20,000 km² of forest being awarded to investors (MPEA, 2010; Tweh et al., 2015). Legal loopholes have opened almost half of Liberia’s remaining primary forest to potential access (Tweh et al., 2015).

Through the Gaborone Declaration for Sustainability in Africa, Liberia has pledged to include the value of nature into national decision making through natural capital accounting. As part of these efforts, Liberia committed to conserving 30% of its remaining forests (about 1.5 million hectares) through protected forest areas networks, conservation corridors and national forests (Junker, Boesch, Freeman, et al., 2015; National Forestry Reform Law of 2006). Identifying land parcels to set aside as protected areas and prioritizing biodiversity is an essential first step in conservation (Jenkins et al., 2013). The Wild Chimpanzee Foundation, working in conjunction with the Liberia Forest Development Authority, has been instrumental in engaging local communities in the protection of new protected areas and drawing awareness to the issues surrounding their establishment (FPA, 2020). Thus, surveying species of concern, particularly chimpanzees, is critical to support ongoing conservation decision making in Liberia (Tweh et al., 2018). While general locations of some proposed protected areas within Liberia have been determined, the exact boundaries remain flexible. Therefore, an opportunity exists to incorporate habitat suitability and connectivity corridors for species of concern into the planning process. Furthermore, designing sustainable landscapes that expand the production of key agricultural commodities (e.g., palm oil) without incurring biodiversity losses, land conflicts, losses of ecosystem services and increasing greenhouse gas emissions are increasingly sought (UNDP, 2020). As Liberia is experiencing a wave of conservation projects and sustainability efforts, it is an opportune time to contribute scientific findings to guide these efforts.

Liberia’s commitment to preserving 30% of forests is foundational, but establishing isolated reserves is not sufficient for conserving biodiversity (Bonnin et al., 2020). Specific attention to protecting and enhancing connectivity is necessary to increase the resilience of conservation areas and networks (Rudnick et al., 2012). Habitat connectivity is a central tenet of conservation planning (Boitani et al., 2007; Jennings et al., 2020) and is key for population viability (Correa et al., 2016) because it allows for ecological processes such as dispersal, movement, gene flow, migrations and repopulation of areas (Gilbert-Norton et al., 2010; Rudnick et al., 2012). Connectivity also improves the chances that species will be able to adapt to changing climatic conditions (DeFries et al., 2005; Heller & Zavaleta, 2009; Krosby et al., 2010), which reduces extinction risks and minimizes the effects of environmental variability on small populations (Brown et al., 1977; Newmark, 1996).

Like other primate species, chimpanzees exhibit dispersal behaviour—a permanent movement of individuals from their natal group into neighbouring populations. Dispersal is one of the most important aspects of population dynamics and gene flow (Armitage et al., 2011; Waser & Jones, 1983), with clear linkages to habitat connectivity. The distance between habitat patches is particularly important in determining dispersal probability and success (Waser & Jones, 1983; Heino & Hanski, 2001). When dispersing individuals have to travel longer distances to reach new patches, it can negatively impact fitness and survival (Stamps et al., 2005). Conversely, remaining in their natal communities or dispersing less to more localized habitat patches can compromise genetic and evolutionary potential (Walker & Pusey, 2020). This can further impact long-term persistence and increase the risk of local extinctions. With deforestation occurring at high rates in the tropics (Hansen et al., 2013), chimpanzee movements are impeded by the fragmentation and loss of suitable habitat, which reduces dispersal potential and thus population viability (Bonnin et al., 2020).

In this study, we model the habitat suitability and connectivity of the western chimpanzee in Liberia, focusing on determining the most relevant environmental predictors and the most appropriate scale for modelling species–habitat relationships. In doing so, we first curate and test a set of environmental variables for parsimonious...
inclusion in the model, including several novel variables that capture habitat fragmentation that have not previously been included in chimpanzee suitability modelling. Next, we map suitable habitat for chimpanzees (*P. troglodytes verus*) in Liberia using MaxEnt (Phillips & Dudík, 2008) to determine the most important environmental indicators for suitable habitat and identify areas that may provide refuge. Lastly, using the habitat suitability information as an input representing ease of movement, we assess where important corridors of chimpanzee connectivity are located throughout the country using Circuitscape (McRae et al., 2008). We conclude with a discussion of the findings in the context of ongoing land management and conservation efforts in Liberia.

2 | METHODS

The methodology is a two-stage process whereby we first develop a species distribution model (SDM) to generate a habitat suitability map and then use that map as the input for a connectivity analysis. For the SDM approach, we follow the structured ODMAP reporting protocol (Zurell et al., 2020) with specific sections for Objective, Data, Modelling, Assessment, and Prediction.

2.1 | Overview and objective of species distribution modelling

The objective of the SDM is to map chimpanzee (*P. troglodytes verus*) habitat suitability in Liberia to permit an analysis of the connectivity of remaining habitat and relationships with known logging and concession areas. We place a specific focus on two aspects that are key for ensuring robust and accurate SDMs (Elith & Leathwick, 2009) (a) including appropriate and relevant environmental predictors, and (b) carefully considering scale. We use MaxEnt (Phillips et al., 2006), which is one of the most popular SDM softwares (Merow et al., 2013), has been found to outperform other types of SDMs (Elith et al., 2006, 2011; Phillips & Dudík, 2008; Wilson et al., 2017) and has been used for modelling great ape populations in Africa, including chimpanzees (Bonnin et al., 2020; Fitzgerald et al., 2018; Freeman et al., 2019; Junker et al., 2012).

2.1.1 | Location and spatial extent of the study area

Liberia is located on the West African coast, bordered by Guinea to the north, Cote d'Ivoire (Ivory Coast) to the east, Sierra Leone to the northwest and the Atlantic Ocean on the south and southwest (Figure 1). Geographically, the country is located between 4° and 9° N latitude and 7° and 12° W longitude and covers approximately 96,000 km² of land area (CIA World Fact Book, 2006). The residential population of Liberia was estimated around 4.5 million in 2015. The landscape is characterized by coastal plains along the south and southwest, with elevation increasing moving inland and to the northeast. There are low mountains along the Guinean border. Liberia is rich in natural resources including iron ore, timber, diamonds and gold (Ejigu, 2006). The climate is Tropical according to Koppen–Geiger with rain forest, monsoon and savanna subregions (Beck et al., 2018). Temperatures are hot and humid year round, with the rainy season occurring from May to October. Annual rainfall exceeds 5 m in some areas of the country. In 2003, 31% of the country was covered by forest, with almost 97% of that area being natural forest (FAO, 2003).

Liberia faces several challenges to conservation. Multiple endangered species are hunted and consumed as bushmeat including chimpanzees, elephants, pygmy hippopotamus, leopards, duikers and several types of monkeys. Shifting agricultural practices such as “slash-and-burn” along with illegal logging and resource extraction also contributes to deforestation of Liberia’s natural forests. Land rights have been a contentious issue during the postwar period, with confusion surrounding the rules fostering short-term extractive activities that resulted in widespread degradation of natural resources (Unruh, 2009).

2.1.2 | Multiscale species distribution modelling

Species–habitat relationships and connectivity are both scale dependent (Cushman et al., 2016; Mateo Sanchez et al., 2014), so it is critical to address scale explicitly in modelling studies. There is no single scale at which ecological patterns should be studied (Levin, 1992), and choice of modelling scale (i.e., resolution) can have profound impacts on model results, yet optimal scale is not always clear (Yang et al., 2020; Zarnetske et al., 2019). Humans tend to impose our own definitions of scale for modelling and often use the...
nominal spatial resolution at which data were captured, even when these scales may not be suitable for the phenomenon under investigation. Wu (2007) suggests ecological phenomena should be studied at their “characteristic scale”—the spatial and/or temporal scale at which the phenomenon principally operates—but identifying characteristic scales is difficult because they are not always apparent. As an alternative, relationships can be compared at several points along a scale spectrum to identify scale domains over which relationships do not change, or change only monotonically (Wiens, 1989). Proponents of hierarchy theory in landscape ecology (Urban et al., 1987) suggest identifying scale breaks through multiscale investigations to provide information on characteristic scales in the absence of other information (Wu, 1999).

Building on this theoretical background, we developed models at six observational scales and relied on changes in variable rank/importance of the models’ variables to provide information on where scale breaks/domains were occurring and guide decisions on the most appropriate scale for modelling. We resampled all variables (discussed below) to match the resolution and alignment of the finest resolution dataset (~30 m). This step not only prepared the data for MaxEnt but also provided a uniform baseline for aggregating data to multiple, coarser resolutions. The 30 m datasets were then aggregated to five coarser resolutions based on integer cell multiples of 2, 4, 8, 16 and 32. The final six datasets comprised resolutions of 30, 60, 120, 240, 480 and 960 m, which correspond to different levels of land cover heterogeneity on the ground (Figure 2). As the starting resolution was not quite 30 m (29.88 m), actual resolutions are slightly less than the integer values. All six resolutions for all models (detailed below) were used to create SDMs.

2.2 | Data for species distribution modelling

2.2.1 | Biodiversity occurrence data

Chimpanzee occurrence data were collected in Liberia between January 2011 and May 2012 through line transect surveys. Collection activities are detailed in Junker, Boesch, Mundry, et al. (2015) and Tweh et al. (2015). In short, systematically placed transects were surveyed on foot for evidence of chimpanzees, such as nests, droppings, and food scraps. In total, 428 chimpanzee occurrences were used, but as some observations were coincident or near each other, the effective number of points for modelling is reduced (Figure 1). At the 30-m scale, there were 283 observations, which is sufficient for presence-only modelling and well above the generally considered threshold of 100 points used to define small datasets (Hernandez et al., 2006).

2.2.2 | Environmental predictor variables

Selecting appropriate and relevant environmental predictors is critical for ensuring accurate and robust models (Elith & Leathwick, 2009). Prior studies of chimpanzees and studies of other non-human primates have found climate, topography, vegetation and other land cover factors influence habitat use/selection (Clee et al., 2015; Fitzgerald et al., 2018; Hickey et al., 2013; Junker et al., 2012; Koops, 2011; Koops et al., 2007; Koops, McGrew, de Vries, et al., 2012; Koops, McGrew, Matsuzawa, et al., 2012; Koops et al., 2013; Mitchell et al., 2015; Serckx et al., 2016; Torres et al., 2010). Using these prior findings and incorporating additional variables generated from new datasets, we identified 47 variables (19 bioclimatic, 12 topographic, 13 vegetation/land cover and three anthropogenic) that might indicate suitable chimpanzee habitat. As multicollinearity between predictor variables can impact the interpretation of the relative contribution of information to the model (Phillips et al., 2006), we removed variables with Pearson’s correlation coefficient $r > \pm 0.7$. We elected a conservative value to have greater confidence in model prediction interpretations, which reduced the set of predictors from 47 to 16 uncorrelated variables (three bioclimatic, four topographic, seven vegetation/land cover and two anthropogenic; Table 1).

**Bioclimatic variables**

Climate defines the bounds of tolerable habitat for all species, including chimpanzees and the species they are dependent on for survival. CHELSA—Climatologies at High Resolution for the Earth’s Land Surface Areas (Karger et al., 2017)—maintains 19 bioclimatic variables derived from monthly temperature and precipitation values. After testing for collinearity, three bioclimatic variables were...
included the following: isothermality, temperature seasonality and precipitation of the wettest month (Table 1).

**Topographic variables**

Topographic variables provide an estimate of the physical complexity of a location and are closely linked to climatic variance. A recent study by Fitzgerald et al. (2018) noted several topographic variables were important predictors of chimpanzee habitat suitability. We derived four variables from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) using the ArcGIS Geomorphometry and Gradient Metrics toolbox (Evans et al., 2014). After collinearity tests, four topographic variables were included elevation, heat load index, hierarchical slope position and roughness (Table 1).

| Predictor variables | Description | Data source | Reference |
|---------------------|-------------|-------------|-----------|
| **Bioclimatic variables** |  |  |  |
| Isothermality | Diurnal range divided by annual temperature range | CHELSA | Karger et al. (2017) |
| Precipitation of wettest month | Precipitation of wettest month | CHELSA | Karger et al. (2017) |
| Precipitation seasonality | Standard deviation of monthly precipitation estimates expressed as percentage of the mean | CHELSA | Karger et al. (2017) |
| **Topographic variables** |  |  |  |
| Elevation (DEM) | Difference between elevation at point and mean elevation | SRTM DEM |  |
| Heat load index | Measurement of heat load considering steepness of slope and aspect | SRTM DEM | McCune and Keon (2002) |
| Hierarchical slope position | Relative topographic exposure | SRTM DEM | Murphy et al. (2010) |
| Roughness | Measure of surface roughness | SRTM DEM | Blaszczynski (1997) and Riley et al. (1999) |
| **Land cover variables** |  |  |  |
| Normalized difference vegetation index (NDVI) | Quantification of biomass | Landsat 8 |  |
| Tasseled cap brightness | Soil brightness | Landsat 8 | Baig et al. (2014) |
| Forest within 1k | Amount of primary forest within a 1,000 m radii of each pixel | Derived from land cover map | N/A |
| Forest within 2k | Amount of primary forest within a 2,000 m radii of each pixel | Derived from land cover map | N/A |
| Forest within 3k | Amount of primary forest within a 3,000 m radii of each pixel | Derived from land cover map | N/A |
| Forest within 5k | Amount of primary forest within a 5,000 radii m of each pixel | Derived from land cover map | N/A |
| Forest within 10k | Amount of primary forest within a 10,000 radii m of each pixel | Derived from land cover map | N/A |
| **Anthropogenic variables** |  |  |  |
| Population | Population density | WorldPop | Linard et al. (2012) |
| Distance to roads | Euclidean distance from each cell to nearest road | Open street map | OSM contributors |

**TABLE 1** Final set of predictor variables used for modelling chimpanzee habitat suitability
Land cover variables

Fifteen land cover variables were categorized into two groups based on their input data: (a) vegetation indices derived from Landsat and (b) land cover fragmentation variables derived from a land cover map developed for Liberia (Sousa et al., 2020).

Vegetation indices. To provide an underlying estimate of the health and quality of vegetation, four vegetation indices were computed from Landsat 5 TM data and included the normalized difference vegetation index (NDVI)—found to be an important predictor of chimpanzee occurrence in a prior study (Fitzgerald et al., 2018)—and Tasseled Cap indices (brightness, greenness, wetness). All indices were computed from 8-year image composites covering the data collection event from 2005 to 2013 in Google Earth Engine (Gorelick et al., 2017). This temporal window ensured a value for every pixel as clouds are common. NDVI was computed directly in Google Earth Engine; the Tasseled Cap (TC) indices were computed using ERDAS IMAGINE, both 30 m resolution. After collinearity checks, only NDVI and brightness were included (Table 1).

Land cover fragmentation. To provide an estimate of landscape permeability and human-driven habitat disruption, we included a fragmentation measure derived from the land cover map (Sousa et al., 2020) developed using a random forest classification scheme with Landsat 8 imagery (circa 2015) and ancillary information such as human settlements, existing infrastructure, concessions, administrative borders. The map comprises 10 land cover classes including three separate forest categories: dense/primary, open/secondary and mixed vegetation. As chimpanzees in Liberia are exclusively forest-dwelling (Tweh et al., 2015), we developed five variables representing the proportion of habitat (dense/primary forest) within varying neighbourhoods around each pixel (1,000, 2,000, 3,000, 5,000 and 10,000 radii) using a spatial convolution filter. Distances were selected based on findings that chimpanzee home ranges can be as small as 6 km² (Newton-Fisher, 2003) and as large as 72 km² (Samson & Hunt, 2012). The five radii cover areas of approximately 3, 13, 28, 79 and 314 km², respectively, and span the entire range of observed home range extents. The radii also cover the maximum daily travel distance (9–10 km) for chimps in forest environments (Green et al., 2020; Herbinger et al., 2001). It is anticipated that large proportions of primary forest in the immediate vicinity of a chimpanzee nest will be an important predictor. Fragmentation variables were processed in ArcGIS at a nominal resolution of 30 m.

Anthropogenic indicator variables

To capture anthropogenic effects, we generated three variables related to population and human activities. We obtained population density from the WorldPop database (Linard et al., 2012). We derived “distance to roads” using the humanitarian open street map (HOSM) roads vector data and computing Euclidean distance from every pixel to the closest road. We verified mapped roads against the impervious class in the land cover map (Sousa et al., 2020). We derived a “distance to development” based on the impervious surface class of the land cover map. After testing for collinearity, two variables (population and distance to roads) were included. Examples of several predictor variables are shown in Figure 3.

2.3 Modelling, assessment and prediction

The MaxEnt model was parameterized using a complementary log-log (cloglog) output, which derives from an interpretation of MaxEnt as an inhomogenous Poisson process (IPP; Fithian & Hastie, 2013; Fithian et al., 2015; Phillips, Anderson, et al., 2017; Phillips, Dudík, et al., 2017). Interpreting Maxent as an IPP allows the raw output to be used directly as a model of relative abundance, and the complementary log-log transformation is appropriate for estimating probability of presence based on the relative suitability of one place versus another (Phillips, Anderson, et al., 2017; Phillips, Dudík, et al., 2017). Hereafter, we refer to MaxEnt outputs as habitat suitability, recognizing that others may refer to them differently.

The five fragmentation variables are highly correlated ($r > .9$), but since determining the importance of this variable is a specific objective, we adopted two modelling approaches. We first included all five variables in a “full” model that also included the other two land cover, three bioclimatic, four topographic and two anthropogenic variables (i.e., all variables in Table 1). As MaxEnt uses a machine-learning approach where the algorithm decides which variables are important, past work has suggested forgoing an input variable downselect altogether (Merow et al., 2013). However, multicollinearity can cloud the interpretation of relative contribution information (Phillips et al., 2006). Therefore, we also developed separate models that included each of the five forest variables along with the 11 other variables. Running six sets of models (one for all variables, five additional with each individual forest variable plus the remaining variables) allows us to interpret the per cent contributions of the fragmentation variables while also understanding their relative importance to each other. The final models included 12 or 16 variables, depending on the run.

Models were run with 10 bootstrap replicates at each of the six resolutions using a random seed, a maximum of 500 iterations with a convergence threshold of 0.00001, and a maximum 10,000 background points. Data were randomly partitioned into 80% training and 20% testing for each replicate. Model performance was assessed using a combination of measures including area under the receiver operating characteristic curve (AUC), overall accuracy and the true skill statistic (TSS; Alouche et al., 2006). While AUC is generally accepted as the best for evaluating model performance (Elith et al., 2006) and is preferred over other measures because it does not require arbitrary threshold selections (Peterson et al., 2008; Phillips et al., 2006), it does not distinguish between useful and non-useful predictions (Peterson et al., 2007). Therefore, TSS was also computed following Jiménez-Valverde (2014). We also assessed response plots as a plausibility check (Zurell et al., 2020).
Maintaining connectivity between suitable areas of chimpanzee habitat in Liberia is critical for ensuring reproduction, sharing of beneficial genetic variance and maintaining sufficient ecological functioning. Circuitscape, based on circuit theory (McRae & Beier, 2007; McRae et al., 2008), has been used to model connectivity of chimpanzee habitat in other regions (Bonnin et al., 2020). Unlike other methods for assessing landscape connectivity such as landscape pattern indices (McGarigal et al., 2012), graph-based metrics (Minor & Urban, 2008; Saura & Torne, 2009) or least-cost path models (Adriaensen et al., 2003), the circuit-based approach has a theoretical basis in random walk theory and allows for the evaluation of contributions from multiple dispersal pathways (McRae et al., 2008). In this case, the suitability map from the MaxEnt model was used as the input conductance surface (i.e., ease of movement between points), where highly suitable habitat values are assigned high conductance values for movement. The same set of chimpanzee occurrence points were used to analyse pairwise connections between occurrences using an 8-neighbour (queen) connectivity parameterization. As the north and south populations are largely isolated from each other (Figure 1), we also modelled their “within group” connectivity separately. Modelling was performed using Circuitscape v4. Connectivity results were overlain with extraction concessions (i.e., timber, mining, palm oil) and existing and proposed protected areas to inform natural capital accounting and the current wave of conservation projects and efforts taking place in Liberia.
RESULTS

Habitat suitability modelling results show two main areas of highly suitable chimpanzee habitat in the north and south, with a swath of low suitability through the central portion of the country (Figure 4). There is also a small area of suitable habitat in the peninsula of land bordering Guinea and Cote D’Ivoire. These findings corroborate those of Junker et al. (2012). The map depicts results from the full model at the 120 m scale. A comparison of all models and scales is provided below.

3.1 | Habitat suitability model comparisons and variable importance

All models performed generally well, and AUC values (Table 2) were consistently high across all resolutions with small standard deviations (Table 2). An AUC value of 0.9 is considered the threshold for very good model fit (Pearce & Ferrier, 2000) as it indicates a high sensitivity rate relative to the false-positive rate (Swets, 1988). All six modelling scales were above 0.9, although values were lower for the 960 model. AUC values tend to be higher for species with narrow ranges relative to the study area described by the environmental data. In this case, the very high AUC values may be indicative of a narrow range within Liberia. Overall accuracies and TSS were similarly high across all modelling resolutions, with accuracy declines at the 960 model.

Results for the full model indicate that variable importance rankings shifted considerably across resolutions (Figure 5), supporting the decision to investigate multiple scales. Within the full model, the amount of forest within 1 km (Forest 1k) was the top-ranked variable and also the only variable that maintained a consistent rank across all six models. Forest 1k was also the most important variable for all six resolutions based on percent contribution. The results for the individual model including Forest 1k (without the other Forest variables) were similar, with Forest 1k ranking first in importance and maintaining that rank across all resolutions (Appendix: Table S1.1). When the forest variable was replaced with the other distances (i.e., 2k, 3k, etc.), the results remained the same for Forest 2k and Forest 3k, with those variables taking and holding the top rank across all resolutions. For the Forest 5k model, the forest variable dropped to the second rank (replaced by Roughness), and for the Forest 10k model, the forest variable dropped to fourth rank for all but the 240 m resolution (Appendix: Tables S1.2–S1.5).

There is consistency across the full (Figure 5, Table 3) and individual forest models (Tables S1.1–S1.5) in terms of the top-ranking variables. In the individual models, the top six variables were always: the forest variable, roughness, elevation, distance to roads, isothermality and precipitation in the wettest month. For the Forest 1k, 2k and 3k models, the forest variable was the most important according to all measures at all scales. Along with the forest variable, roughness, elevation and distance to roads consistently filled the top four ranks. In the full model, the same six variables were most important, although Forest 3k was ranked ahead of distance to roads (Table 3). However, this rank should be interpreted with caution because it is correlated with forest 1k. Although elevation was not the most important variable in any of the models, it often contributed the highest gains to the model.

3.2 | Optimal scale selection

The multiscale findings provide evidence of a scale domain for the top-ranking variables between 30 and 120 m. The full model is used here as the example (Figure 5), but similar patterns were found for the individual models (Tables S1.1–S1.5). The top five variables—forest 1k, elevation, distance to roads, wetness, isothermality—remained consistent in terms of their ranks between 30 and 120 m, indicating the species–habitat relationships do not change between these scales. There is also support for a positive relationship between rank and rank stability for the most important variables in all models. This relationship is particularly evident in the full model results (Figure 5), where an increase in rank was accompanied by an increase in the length of the scale.
The stability in rank of the top five predictors along with the decline in rank consistency of all variables at resolutions coarser than 120 m suggests that finer resolutions (30–120 m) are more appropriate for modelling chimpanzee occurrence. Accuracy metrics (Table 2) confirm that any of these resolutions is suitable for modelling. As the 120 m resolution better captures the scale of the general landscape patterns and heterogeneity (Figure 2) and is computationally more efficient than the finer resolutions, the 120 m result was used as the Circuitscape input. It should be noted that the climate variables (1 km nominal resolution) were downsampled, not statistically downscaled. Therefore, interpretation of rank shifts should be interpreted in context with their relative importance to the other variables.

### 3.3 | Connectivity results

Circuitscape results across Liberia show current densities at each cell resulting from a pairwise analysis that analysed movement corridors between each focal node (chimpanzee occurrence location) to every other focal node (Figure 6a). Higher values (darker colours) indicate greater current densities that must flow through that path and thus more important corridors. Several choke points are clear from the results. There is a narrow corridor of high-density flow linking the southern and northern areas. Additionally, there is an area of high-density flow running from the southern area up through the eastern peninsula. As this area is bounded by Guinea and Côte D’Ivoire, it is possible suitable habitat exists beyond the boundaries of Liberia that provide connectivity.

As the northern and southern chimpanzee groups are largely isolated from each other due to anthropogenic disturbances in the central region including major transportation arteries as well as considerable agriculture, it is unlikely that these subpopulations are connecting via the main path flowing through the centre of the country (Figure 6a). Results for “within group” connectivity (Figure 6b) show critical connectivity paths in the north-central portion of the southern group and hotspots around several clusters of occurrences in the northern group. These more local connectivity analyses provide a means to focus conservation efforts and are discussed in the context of existing efforts in the following section.

### 4 | DISCUSSION

We modelled habitat suitability of western chimpanzee habitat in Liberia, focusing specifically on determining the relevance of novel
variables not previously included in modelling efforts (i.e., forest fragmentation) and determining the most appropriate scale for modelling species–habitat relationships. Using the habitat suitability information as an input representing ease of movement, we assessed where important corridors of chimpanzee connectivity are located throughout the country. Below we discuss the importance of these findings and implications for ongoing land management and conservation efforts in Liberia.

4.1 | Variable importance in the context of modelling scale

Primary forest cover (specifically the amount of primary forest within 1–3 km of an occurrence) was the most important predictor of chimpanzee habitat suitability at all spatial scales. We were able to identify this relationship based on the recent land cover mapping effort by Sousa et al. (2020), from which we derived these novel habitat fragmentation proxies. This finding is key because it illustrates the need to conserve primary forest to preserve biological diversity in the tropics. It can be difficult to develop and implement conservation plans based on vegetation proxies, such as NDVI, that fluctuate seasonally and are difficult to measure on the ground. The spatial convolutional filtering approach employed in this study also overcame the limitation of including categorical data in SDMs. While we only measured forest proportion, more complex spatial pattern metrics can be computed (e.g., landscape metrics; Frazier & Kedron, 2017) to better inform conservation planning.

The population (density) variable did not rank highly in any model, but distance to roads was consistently in the top set, suggesting that infrastructure and development (e.g., roads) may be more important for predicting chimpanzee habitat than sustained human presence or density. However, these findings should be interpreted in context as there may be a more nuanced relationship between chimpanzee occurrence and settlements. Junker, Boesch, Mundry, et al. (2015) found that certain social drivers including literacy may be related to large mammal occurrences in the country. We were unable to include these surveyed social variables directly in this study due to their spatial discontinuity.

4.2 | Scale dependency of species–environment relationships

The scale dependency of the species–environment relationships was evident through the multiscale analysis. The explanatory power of the environmental predictor variables shifted considerably among the six modelling scales, and variation was particularly broad for variables with less explanatory power. Our findings support the need to include at least two, but preferably more, spatial resolutions when examining landscape variables. The scale of landscape impact is variable and dependent on the species–environment relationship being examined. It is therefore impossible to know the correct scale to examine a priori; thus, multiple scales of analysis are required to determine an appropriate modelling scale with the data at hand. We suggest contextualizing the relative explanatory power of each variable with a visualization of its geographic variance (see Figure 2) and

![Figure 6](image-url)
relative explanatory power across spatial resolutions to determine the optimal scale of analysis. The finding here that finer resolutions (30–120 m) are most appropriate for modelling chimpanzee occurrence is logically consistent with chimpanzee ranging behaviours and distances for foraging trips (Jang et al., 2019).

4.3 | Connectivity and conservation priorities in Liberia

Landscape connectivity is critically important for maintaining chimpanzee population, particularly in human-disturbed landscapes (Bonnin et al., 2020). The connectivity analysis indicates areas with high flow in both the northern and southern groups but also areas where connectivity is fragmented by the lack of suitable habitat. Moving forward, it is important to incorporate these findings in the many conservation planning activities currently underway in Liberia. Notably, Liberia’s Pro-poor Agenda for Prosperity and Development (PAPD), supported by the 2020–2024 Country Programme Document, aims to achieve a more sustainable pathway to renewed progress and prosperity in Liberia (MFDP, 2018; Republic of Liberia, 2018). One of the PAPD pillars focuses on infrastructural development such as road construction, electricity and agriculture: sectors that could significantly transform Liberia’s landscape including the areas identified by this study as important connectivity corridors for chimpanzee populations. Liberia plans to expand their road network, specifically along development corridors that will further isolate the northern and southern groups and also potentially bisect highly important conductance paths in the northeast “peninsula” adjacent to Guinea and Côte D’Ivoire.

The connectivity maps can also guide production area planning (e.g., oil palm and rubber), to ensure that intervention designs contribute towards prosperity of both humans and chimpanzees, particularly as they concern existing and future mining and logging concessions (Figure 7). Concessions confer rights to private companies to manage and extract resources. Existing timber concessions currently overlap considerably with important connectivity corridors in both the southern and northern areas (Figure 7a). Oil palm concessions interfere to a lesser degree but are present along the southern coast (Figure 7b). Mining concessions (Figure 7c), which have resulted in widespread tropical deforestation in Liberia in the past (Wilson et al., 2017), largely avoid the areas of high connectivity.

**FIGURE 7** Chimpanzee connectivity layer overlain with concessions and protected areas in Liberia (administrative boundaries included in basemap). Darker paths are more important for connectivity. In (e), protected areas partially or fully obscured by connectivity surface have outline also layered on top of the surface to facilitate visualization.
importance in the northern and southern networks, but they may interfere with connectivity in the northeast peninsula (Figure 6a). Recall that this area was not included in a separate subregion connectivity analysis due to its proximity to international boundaries.

Addressing the threat of timber, oil palm and mining concessions to chimpanzee conservation represents a critical step for conservation planning. Liberia’s Forestry Reform Law of 2006 mandates the establishment of “a Protected Forest Areas Network, together with Conservation Corridors, and incorporating existing National Forests, to cover at least 30% of the existing forested area of Liberia, representing about 1.5 million hectares.” Liberia currently maintains several official protected areas (Figure 7e, dark green) that account for only about 5% of its total land area (FAO, 2015; World Bank, 2018). The gazetting process for another national park (Krahn-Bassa; Figure 7e) was recently initiated, but the protected areas in total only minimally overlap the northern and southern networks, leaving large areas important for chimpanzee habitat and connectivity unprotected (Figure 7e). In 2018, Conservation International and the Government of Liberia launched The Liberia Conservation Fund to provide sustainable, long-term financing for protecting areas (Conservation International, 2018). As a result of this and other initiatives related to the National Forestry Reform Law of 2006, planning activities are being expedited and have resulted in the delineation of several proposed protected areas (Figure 7e, light green areas) some of which partially overlap the connectivity networks. As an example, the Liberian government has been working to formally demarcate the boundaries of Sapo National Park, after a contentious expansion in 2003, to prevent illicit hunting and illegal activities (Mukpo, 2020). For key connectivity areas that fall beyond protected areas, other conservation approaches should be prioritized such as allowing local stewardship and sustainable harvesting of natural resources in community forests.

The information generated by this work will also be valuable for the current wave of conservation efforts taking place in Liberia. One of the flagship projects being undertaken by the Government of Liberia in partnership with Global Environmental Facility (GEF) is the Good Growth Partnership (GGP). The GGP, which is implemented by the United Nations Development Programme and involved Conservation International, aims to support the sustainable production of palm oil while conserving biodiversity and safeguarding the rights of forest-dependent communities. The GGP landscape (Figure 7f) is located in the north-western part of Liberia and covers more than one million hectares. The area is rich in biodiversity and plays an important role in maintaining the well-being of its 320,000 inhabitants but is also an area of timber and palm oil concessions (Figure 7a,b). The habitat suitability and connectivity maps produced by this research along with other relevant information can be utilized to design an optimal configuration of the landscape with areas designated for oil palm production, food production and conservation or restoration of natural habitat and/or wildlife corridors. Other conservation efforts that are likely to benefit from this work include several emerging projects related to natural capital accounting that Liberia is committed to implement under the Gaborone Declaration for Sustainability in Africa (GDSA, 2012).

An important consideration for future studies using SDMs in tropical and developing areas is estimating shifting agriculture. Liberia experiences frequent and dynamic changes in land cover patterns from clearing vegetation from plots, cultivating them for a period, then abandoning them until soil fertility has been restored. Recent evidence from Planet imagery shows dynamic land cover changes on monthly time-scales (Figure 8). Shifting agriculture is nearly impossible to detect through the multiyear satellite imagery composites used to create land cover maps (e.g., Homer et al., 2015). However, as more than 60% of the Liberian population relies on agriculture as a primary livelihood (Liberia-Agricultural Sectors report from export.gov), these dynamic land cover shifts are likely to persist in the future. While most of the current area for shifting agriculture is located in the central part of the country where habitat suitability was found to be low (Figure 5), analysis of time series images suggests these activities are pushing north closer to the GGP boundary. It is not clear how proposed development activities in these areas will affect these land cover changes, but developing methods to capture these dynamic changes for distribution modelling and spatial analysis will be critical. Very high spatial and temporal resolution remote sensing datasets are underexploited but have a strong potential to contribute to conservation.

### 4.4 Summary and conclusions

This study modelled habitat suitability and connectivity for the western chimpanzee (P. troglodytes verus) in Liberia with a specific focus on the inclusion of appropriate and relevant environmental predictors and an analysis of optimal modelling scale. Several key findings emerged. First, the most important variable for predicting chimpanzee occurrence was the proportion of dense/primary forest within 1–3 km. This variable, which was novel to this study, remained the most important across all six scales tested despite...
rank shifting from the other variables. Given the importance of the amount of primary forest at 1–3 km radii, additional habitat fragmentation variables may be useful to include in future modelling efforts. For example, landscape metrics such as the number of land cover patches or statistics on the shape and area of these patches may prove useful. Second, we found modelling resolution impacted the importance of the predictor variables. When they exist, scale domains can provide an indication of where results remain stable when the choice of optimal scale is not clear. Contextualizing importance rankings alongside a visualization of the typical scales at which land cover changes are taking place in the landscape can also aid in determining optimal modelling scales. Third, by overlaying key connectivity corridors with concessions and planned protected areas, it was clear that logging concessions threaten chimpanzee habitat connectivity and conservation. Lastly, it should be noted that as almost 10 years have passed since the chimpanzee survey was completed, it is possible that areas where chimpanzees were sighted in the past may have undergone land cover changes that are not reflected in the results.

ACKNOWLEDGEMENTS

We would like to acknowledge the contributions of George Ilebo and Solomon Carlon from Conservation International—Liberia, who commented on an earlier version of the manuscript. This work was initiated through a partnership between Arizona State University and Conservation International, and we thank both institutions for their support of this work. The work was partially funded by US NSF Grant #1934759.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/dli.13270.

DATA AVAILABILITY STATEMENT

The data used to derive the environmental covariates that support the findings of this study are openly available from public domain resources including Google Earth Engine and Chelsa (https://chelsa-climate.org/bioclim/). Core files for the land cover map are available from the https://github.com/celioholder/Liberia-Classification repository, and raster files are available from https://figshare.com/s/49937c4eadd7b12b2dbb. The chimpanzee occurrence data are provided as Supporting Information and Appendix S2.

ORCID

Amy E. Frazier https://orcid.org/0000-0003-4552-4935
Miroslav Hanzak https://orcid.org/0000-0001-6563-3130
Celio de Sousa https://orcid.org/0000-0002-2136-284X
Sylvain Nyandwi https://orcid.org/0000-0002-3482-4839
Andrew B. Trgovac https://orcid.org/0000-0002-1390-9868

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**BIOSKETCH**

The research team is part of the Arizona State University-Conservation International partnership, which was launched in 2018 to actively engage ASU faculty and conservation practitioners to drive collaborative research and education on global conservation and ensure valuable research informs and impacts real-world efforts.

Author contributions: A.E.F., M.H., C.H., R.P., A.T. and K.G. conceived the ideas; A.E.F., J.J., C.S., T.L., C.H., R.P., and A.T. collected and/or generated the data; A.E.F., J.J., C.S., T.L., C.H., R.P., and A.T. completed the analysis; all authors contributed to reviewing and revising the manuscript.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Frazier AE, Honzák M, Hudson C, et al. Connectivity and conservation of Western Chimpanzee (*Pan troglodytes verus*) habitat in Liberia. *Divers Distrib*. 2021;27:1235–1250. https://doi.org/10.1111/ddi.13270