RESEARCH ARTICLE

Towards systematic and evidence-based conservation planning for western chimpanzees

Stefanie Heinicke[1,2] | Roger Mundry[1] | Christophe Boesch[1,3] | Kimberley J. Hockings[4] | Rebecca Kormos[5] | Papa Ibnou Ndiaye[6] | Clement G. Tweh[7,8] | Elizabeth A. Williamson[9] | Hjalmar S. Kühl[1,2]

[1]Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[3]Wild Chimpanzee Foundation (West Africa Representation), Abidjan, Cote d'Ivoire

[4]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall, United Kingdom

[5]Department of Integrative Biology, University of California, Berkeley, California

[6]Département de Biologie animale, Université Cheikh Anta Diop, Dakar, Senegal

[7]Wild Chimpanzee Foundation, Monrovia, Liberia

[8]School of Biological Sciences, University of Nairobi, Nairobi, Kenya

[9]Faculty of Natural Sciences, University of Stirling, Stirling, Scotland, United Kingdom

Correspondence
Stefanie Heinicke, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
Email: stefanie_heinicke@eva.mpg.de

Abstract

As animal populations continue to decline, frequently driven by large-scale land-use change, there is a critical need for improved environmental planning. While data-driven spatial planning is widely applied in conservation, as of yet it is rarely used for primates. The western chimpanzee (*Pan troglodytes verus*) declined by 80% within 24 years and was uplisted to Critically Endangered by the IUCN Red List of Threatened Species in 2016. To support conservation planning for western chimpanzees, we systematically identified geographic areas important for this taxon. We based our analysis on a previously published data set of modeled density distribution and on several scenarios that accounted for different spatial scales and conservation targets. Across all scenarios, typically less than one-third of areas we identified as important are currently designated as high-level protected areas (i.e., national park or IUCN category I or II). For example, in the scenario for protecting 50% of all chimpanzees remaining in West Africa (i.e., approximately 26,500 chimpanzees), an area of approximately 60,000 km^2 was selected (i.e., approximately 12% of the geographic range), only 24% of which is currently designated as protected areas. The derived maps can be used to inform the geographic prioritization of conservation interventions, including protected area expansion, "no-go-zones" for industry and infrastructure, and conservation sites outside the protected area network. Environmental guidelines by major institutions funding infrastructure and resource extraction projects explicitly require corporations to minimize the negative impact on great apes. Therefore, our results can inform avoidance and mitigation measures during the planning phases of such projects. This study was designed to inform future stakeholder consultation processes that could ultimately integrate the conservation of western chimpanzees with national land-use priorities. Our approach may help in promoting similar work for other primate taxa to inform systematic conservation planning in times of growing threats.

KEYWORDS
Pan troglodytes verus, spatial planning, spatial prioritization, systematic conservation planning, West Africa, western chimpanzee

1 | INTRODUCTION

Land use has changed across the globe, with tropical biomes experiencing large-scale forest loss (Song et al., 2018). Primate range countries are no exception to this trend with a 2 million km² loss in forest cover between 1990 and 2010 (Estrada et al., 2017). Rapid land-use change is typically caused by the expansion of agriculture, logging, mining, hydropower dam construction, and infrastructure development, including roads and power transmission lines (Curtis, Slay, Harris, Tyukavina, & Hansen, 2018; Laurance, Sloan, Weng, & Sayer, 2015). The result has been a decline in species diversity and abundance, which can subsequently lead to deleterious changes in ecosystem function (Dirzo et al., 2014). Responding to these developments not only requires increased investment into conservation actions, but also strategic planning to distribute limited resources effectively while enabling a coexistence of production landscapes and areas under various protection regimes (Margules & Pressey, 2000).

One of the most commonly used frameworks in conservation is spatial planning (Margules & Pressey, 2000; Schwartz et al., 2018). The aim of spatial planning is to optimize where conservation actions are implemented to achieve the long-term protection of targeted species (Schwartz et al., 2018). Spatial planning can take many forms, for example, identifying areas high in biodiversity or other ecosystem services (Law et al., 2015), identifying biodiversity-rich areas under global change scenarios (Ribeiro, Sales, & Loyola, 2018; Struebig et al., 2015), or optimizing the trade-off between costs and benefits for protected area creation (Bicknell et al., 2017; Junker et al., 2015). This approach has also been used to identify hotspots of specific threats (Katsis, Cunneyworth, Turner, & Presotto, 2018) and to spatially prioritize conservation activities (Plumptre et al., 2014).

A recent survey among authors of spatial prioritization studies showed that 74% of the studies that were intended for implementation translated at least to some extent to conservation actions on the ground (Sinclair et al., 2018). While spatial planning is widely used in conservation planning and more than 600 papers have been published on this topic (Sinclair et al., 2018), only a few examples exist for primates. Primate occurrence data have been incorporated into studies that prioritize areas based on the number of species (Lee, 2014; Ribeiro et al., 2018; Struebig et al., 2015), and in studies that identified hotspots of primate species (Castillo Ayala, 2016; Law et al., 2015; Meijaard & Nijman, 2003). In contrast, great ape densities were used by Murai et al. (2013) to identify priority areas across Río Muni in mainland Equatorial Guinea, and by Tédonzong et al. (2018) to identify areas of high conservation value in a logging concession in southeastern Cameroon. Similarly, Junker et al. (2015) used density data to identify priority areas for the protection of western chimpanzees (*Pan troglodytes verus*) and biodiversity across Liberia. At a regional scale, modeled great ape density distribution was used to identify priority landscapes for western lowland gorillas (*Gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) throughout western equatorial Africa (Strindberg et al., 2018).

Here we focused on western chimpanzees and identified areas of high conservation value to ensure the continued survival of this taxon. The study was designed to inform the revision of a regional conservation action plan for western chimpanzees. Western chimpanzees still occur in eight West African countries (Humle et al., 2016) and the total population is currently estimated at around 52,800 individuals (Heinicke et al., 2019a). In 2016, this taxon was uplisted to Critically Endangered by the IUCN Red List of Threatened Species (Humle et al., 2016) because the population declined by 80% within 24 years (Kühl et al., 2017). The main threats to western chimpanzees are loss and fragmentation of habitat, poaching and disease (Humle et al., 2016). However, chimpanzees are able to persist in areas protected from habitat loss and in which they are not hunted, for example, because of effective law enforcement, the presence of protected area authorities, NGOs or researchers, hunting taboos, or limited access in steep terrain (Boesch, Mundry, Kühl, & Berger, 2017; Campbell, Kuehl, Diarrassouba, N'Goran, & Boesch, 2011; Heinicke et al., 2019b; Tranquilli et al., 2012).

Landscapes across West Africa have changed markedly with total forest cover being reduced by 80% since 1900 (Aleman, Jarzyna, & Staver, 2018). Land-use change is set to continue, considering the large investments that have been made across economic sectors, notably in mining (International Monetary Fund, 2014), agriculture (African Development Bank Group, 2013), and hydroelectric power plants as part of a transition to renewable energies promoted by global initiatives to combat climate change (International Finance Corporation, 2016). These economic developments are likely to incur extensive environmental costs in specific regions (Edwards et al., 2014; Laurance et al., 2015; Norris et al., 2010). Consequently, with the expected increase in land conversion, land-use planning that prioritizes areas for conservation is needed to avoid conservation activities that are implemented in a purely ad-hoc manner or as an afterthought.

It is well-established that conservation planning should not merely be a technical, data-driven exercise with one "optimal" solution, but that involving all relevant stakeholders (e.g., government, local communities, conservation NGOs, researchers) to incorporate their interests in the process of decision-making is critical (Grantham et al., 2010; Pressey & Bottrill, 2008). The socioeconomic context in West Africa requires such an approach for conservation planning for western chimpanzees. West Africa is one of the poorest regions in the world with 43% of the human population living below the poverty line (1.90$; AfDB, 2018), one of the reasons being protracted armed conflicts in the region, including in Côte d'Ivoire (2002–2007, 2010), Guinea-Bissau (1998–1999), Liberia (1989–2003), and Sierra Leone (1991–2002) (Afolabi, 2009). The epidemic of Ebola virus disease from 2014 to 2016 not only caused the death of more than 11,000 people in West Africa (WHO, 2016), but also resulted in decreases in household income, a reduction in crop production of farm households, and a weakening of trust in government institutions (Gatiso et al., 2018). Consequently, as many countries in West Africa are recovering from conflict, and the Ebola epidemic, they require large investments in infrastructure and economic growth to meet their populations' growing needs. At the same time, West Africa is rich in mineral

deposits, and some large forested areas remain, which are of interest to logging companies. In addition, parts of the region have high hydroelectric potential (AECOM, 2018). Thus, global corporations, as well as international financing institutions, have already invested strongly in resource extraction projects and networks of dams and power lines, a trend likely to continue (Edwards et al., 2014). At the same time, and similar to most conservation settings, a diversity of actors is involved in chimpanzee conservation, with long-term chimpanzee research and conservation activities in West Africa dating back to the 1960s (Kormos, Boesch, Bakarr, & Butynski, 2003). The different stakeholders, including government agencies, local communities, conservation NGOs, and researchers, typically have their own mission, obligations to donors and actors are often competing for limited funding. However, identifying priorities can help to unite stakeholders around a common goal and reduce the duplication of effort. This collaboration can strengthen partnerships with government agencies and, to some degree, counterbalance interests of powerful corporations or investors.

The aim of this study was to identify areas important to western chimpanzee conservation as a first technical step to inform the process of finding a common position by all parties involved in chimpanzee conservation. After an agreement has been found on priority areas for western chimpanzees, the essential following step should be a structured decision-making process to include the objectives of all other stakeholders relevant to land-use planning, for example, to integrate other biodiversity targets, concerns of local communities and economic priorities by governments (Pressey, Mills, Weeks, & Day, 2013). While this study focusses on a single species, chimpanzees live in habitats ranging from rainforest to dry savanna areas and co-occur with a number of other species of conservation concern, such as the Temminck's red colobus (*Piliocolobus temminckii*), king colobus (*Colobus polykomos*), pygmy hippopotamus (*Choeropsis liberiensis*), forest elephant (*Loxodonta cyclotis*), African golden cat (*Caracal aurata*), and African wild dog (*Lycaon pictus*) (Bersacola et al., 2018; Brncic, Amarasekaran, McKenna, Mundry, & Kühl, 2015; Brugière & Kormos, 2008; Tweh et al., 2015). Chimpanzees are also considered a charismatic flagship species (Albert, Luque, & Courchamp, 2018). The heightened attention to chimpanzees and other great ape species has led to the International Finance Corporation (IFC), an institution of the World Bank Group focused on financing private-sector projects such as mining or dam construction, explicitly stating in its environmental guidelines that mitigations measures have to be implemented to avoid or minimize the negative impact of a project on great apes (International Finance Corporation, 2019). A total of 96 financial institutions in 37 countries have committed to following these standards established by the IFC (The Equator Principles Association, 2019). Consequently, identifying areas of conservation value to western chimpanzees can inform corporations on whether or not to proceed, and if they do proceed, to what extent negative impacts on chimpanzees need to be mitigated during planning and implementation of projects. Any residual impacts would require an appropriate offset strategy. If implemented appropriately, mitigation could also benefit sympatric species. We chose a design

based on two scenarios, each with different spatial scales and conservation targets, to identify areas that consistently appear as important, identify potential national priorities, and transboundary areas. We then compared selected areas to current protected area coverage and the priority areas identified based on expert opinion and qualitative criteria for a previous regional action plan for western chimpanzees (Kormos & Boesch, 2003).

2 | METHODS

2.1 | Study area

The study area extended across the geographic range of western chimpanzees, comprising eight countries in West Africa, and covering 524,100 km^2 (Kühl et al., 2017). Chimpanzee abundance is highest in Guinea, followed by Liberia and Sierra Leone (Table 1). Western chimpanzees occur in a variety of habitats, including dry and moist tropical lowland forests, savanna mosaic habitat with gallery forests, and agricultural landscapes dominated by human activities but with forest remnants (Hockings et al., 2015; Humle et al., 2016; Ndiaye et al., 2018).

2.2 | Data

The area selection was based on estimated chimpanzee density distribution that was recently modeled across its entire range using 20 social and ecological factors, including habitat, climate, threats to chimpanzees such as forest loss and human activities, and factors having a positive effect on chimpanzee densities such as protected areas, prevalence of hunting taboos, and steepness of terrain (Heinicke et al., 2019b). This data layer has a spatial resolution of half a minute (of a longitude/latitude degree, approximately 0.9 × 0.9 km) and is available via the IUCN SSC A.P.E.S. database (http://apes.eva.mpg.de). We further used spatial polygons of high-level protected areas from the World Database of Protected Areas, meaning protected areas designated as "national park" or IUCN category I or II (UNEP-WCMC & IUCN, 2019; listed in Table S1). The spatial polygon for the national parks Boé and Dulombi in Guinea-Bissau were not up-to-date, so we used park outlines according to the Instituto da Biodiversidade e das Áreas Protegidas. We focused on high-level protected areas as conservation activities are mostly taking place in these areas, while data on whether conservation activities are implemented in other types of managed areas were not available across the entire geographic range of western chimpanzees. The size of the total land area for western chimpanzee range countries was taken from the World Database of Protected Areas (UNEP-WCMC & IUCN, 2019).

2.3 | Scenarios for area selection

The objective of the analysis was to optimize area selection along three dimensions: maximizing chimpanzee abundance, minimizing the size of the required area, and minimizing area fragmentation. The

TABLE 1 Protected area coverage and estimated chimpanzee abundance in western chimpanzee range countries

Country	Total land area (km^2)	Land area designated as high-level protected area (km^2)[a]	Percentage of high-level protected areas relative to total area[a]	Estimated chimpanzee abundance (95% confidence interval)
Côte d'Ivoire	324,108	20,408	6.3	1,093 (329 – 3,299; Heinicke et al., 2019a)
Ghana	240,330	11,513	4.8	24 (1 – 212; Heinicke et al., 2019a); 264 (18–843; Danquah, Oppong, Akom, & Sam, 2012)
Guinea	246,427	8,136	3.3	33,139 (8,796 – 68,203; Heinicke et al., 2019a)
Guinea-Bissau	34,016	5,326	15.7	1,908 (923 – 6,121; Heinicke et al., 2019a)
Liberia	96,634	3,880	4.0	6,050 (2,902 – 13,690; Heinicke et al., 2019a), 7,008 (4,260–11,590; Tweh et al., 2015)
Mali	1,256,684	1,930	0.2	2,029 (322 – 9,228; Heinicke et al., 2019a)
Senegal	197,924	9,960	5.0	2,642 (1,077 – 13,293; Heinicke et al., 2019a)
Sierra Leone	72,709	2,472	3.4	5,580 (3,052–10,446; Brncic, Amarasekaran, & McKenna, 2010), 5,925 (1,951 – 12,668; Heinicke et al., 2019a)

[a]A high-level protected area was defined as an area designated as national park or IUCN category I or II according to the World Database of Protected Areas (UNEP-WCMC & IUCN, 2019).

latter criterion was chosen because the protection of larger coherent areas is less expensive, and they are considered ecologically more viable (Balmford, Gaston, Blyth, James, & Kapos, 2003; Hodgson, Thomas, Wintle, & Moilanen, 2009). We analyzed two different scenarios: (a) by chimpanzee abundance and (b) by area size. Specifically, this approach implies that for the first scenario, the chimpanzee abundance was preset at a specific target, and the algorithm aimed to find an optimal balance between minimizing the size of required area while also minimizing the area fragmentation. For the second scenario, the area was preset, whereas the algorithm aimed to find an optimal balance between maximizing chimpanzee abundance and minimizing area fragmentation.

For the first scenario (i.e., by chimpanzee abundance), we further differentiated three spatial scales: chimpanzee abundance across the geographic range of western chimpanzees (sub-scenario 1a), in each range country (sub-scenario 1b), and separately for each of the three largest populations (sub-scenario 1c). These sub-scenarios were implemented for targets ranging from protecting 10–90% of chimpanzee abundance, in 10% increments. The aim of sub-scenario 1a was to identify areas that are of conservation value for this taxon in general and to determine important transboundary areas. Sub-scenario 1b identified areas at the national level, where conservation actions are typically planned and implemented. We compared sub-scenarios 1a (abundance across geographic range) with 1b (abundance per country) because chimpanzee densities and population sizes differ strongly across the range, and national prioritizations can be less effective in terms of reaching conservation targets and financial costs than large-scale prioritizations (Kark, Levin, Grantham, & Possingham, 2009; Moilanen, Anderson, Arponen, Pouzols, & Thomas, 2013). The sub-scenario 1c (abundance per population) was motivated by two considerations. First, protecting a species in several locations across its range can reduce extinction risk because an event, for example, a disease outbreak, a fire, or a sudden increase in anthropogenic

pressure at one site is less likely to affect the entire population (van Teeffelen, Vos, & Opdam, 2012). Second, chimpanzees differ strongly across sites regarding socially learned behaviors (e.g., Kühl et al., 2019, 2016; Whiten et al., 1999) and might also differ genetically. Consequently, sub-scenario 1c ensures that areas from each population are selected, as delineated in Heinicke et al. (2019a).

For the second scenario (i.e., by area size), optimization was done separately for each range country and we analyzed two sub-scenarios: area with highest chimpanzee densities (sub-scenario 2a), and area with highest chimpanzee densities added to areas already designated as high-level protected areas (i.e., the algorithm first selected all protected areas and then added cells with highest chimpanzee densities to reach the area target, sub-scenario 2b). We chose an area target of 17% following the Aichi target 11 of the Convention on Biological Diversity which specifies that at least 17% of the terrestrial area of each country should be protected and which all countries within the western chimpanzee range have signed (UN, 2019). This scenario does not imply that protecting western chimpanzees alone would meet the biodiversity goals set out by this Aichi target. Instead, we chose this target because it is the most widely recognized target in terms of how much area should be protected. With calls for higher area protection targets (Noss et al., 2012) and as biodiversity targets are in the process of being updated, we ran additional analyses for area targets of 20–50% of the area (Table 2, Figure S1).

2.4 | Implementation of area selection

We first reduced the resolution of the chimpanzee density layer to 5x5 km^2 to consist of 25,430 cells, because computation time scales quadratically with the number of cells for optimization algorithms. We implemented the optimization in R (R Core Team, 2018) instead of specialized planning software. Specialized programs were developed to optimize multi-dimensional prioritization problems typically

TABLE 2 Results for each scenario identifying areas of high conservation value for western chimpanzees

Scenario	Sub-scenario	Target	Estimated chimpanzee abundance	Area (km^2)	Percentage of chimpanzees occurring in a high-level protected area [a]	Overlap with priority areas identified by Kormos and Boesch (2003) (%)
1) by chimpanzee abundance	1a) across range	10%	5,323	4,708	57.3	91.5
		20%	10,644	13,243	44.5	70.4
		30%	15,956	24,845	34.7	67.6
		40%	21,275	40,509	27.8	62.7
		50%	26,586	59,805	24.4	59.6
		60%	31,889	85,487	21.7	55.8
		70%	37,149	118,567	20.0	51.8
		80%	42,403	166,324	18.7	47.1
		90%	47,640	244,478	17.4	42.2
	1b) by country	10%	5,336	6,570	53.0	77.5
		20%	10,628	17,460	44.2	70.4
		30%	15,929	32,131	35.9	68.0
		40%	21,236	51,466	29.8	69.2
		50%	26,542	75,076	26.3	64.3
		60%	31,817	105,828	23.7	61.1
		70%	37,094	146,376	21.7	57.5
		80%	42,355	199,846	19.9	52.0
		90%	47,616	286,009	18.2	45.2
	1c) by population	10%	5,223	5,508	48.6	79.3
		20%	10,393	15,067	41.5	68.0
		30%	15,525	27,149	34.8	62.9
		40%	20,634	43,011	30.2	62.8
		50%	25,679	62,434	25.8	60.5
		60%	30,557	85,676	22.9	56.8
		70%	35,305	114,585	20.6	52.9
		80%	39,844	150,075	19.0	48.8
		90%	44,078	195,341	18.1	45.4
2) by area size	2a) by country	17%	34,643	193,640	24.1	56.5
		20%	36,943	216,849	23.0	55.1
		30%	42,671	267,036	20.4	51.9
		40%	46,385	312,021	18.9	48.1
		50%	48,785	354,586	18.0	44.6
	2b) by country added to current protected areas	17%	33,418	177,598	26.3	59.6
		20%	35,946	198,244	24.5	56.9
		30%	41,968	259,784	21.0	52.5
		40%	45,831	302,383	19.2	48.6
		50%	48,385	344,998	18.2	45.2

[a]A high-level protected area was defined as an area designated as a national park or IUCN category I or II according to the World Database of Protected Areas (UNEP-WCMC & IUCN, 2019).

aimed at maximizing a number of species protected as well as minimizing costs of conservation. However, in multi-dimensional prioritization problems, there is the danger of selecting "residual areas," meaning areas that are easier to protect but not necessarily most important for the targeted species (Pressey, Weeks, & Gurney, 2017). As the aim of this analysis was to inform the process by first identifying priority areas for western chimpanzees, we instead opted for a scenario-based analysis using the modeled chimpanzee density distribution which already encompasses how suitable areas are for this taxon (i.e., the model was based on ecological and socioeconomic predictor variables). While conservation planning software programs are very powerful, they can be perceived as a "black box" by stakeholders, which can lead to a distrust of the results (Ball, Possingham, & Watts, 2009; Brooks, 2010). An algorithm implemented in R has the advantage that this computational environment is widely used in ecology and that the code is explicit and transparent.

Specifically, the algorithm starts by ranking all cells according to chimpanzee density and selects all cells with highest chimpanzee densities that together reach the specified abundance (i.e., 10–90% of chimpanzee abundance) or area target (i.e., 17–50% of the area). Then the algorithm iteratively looks for cells that could replace those from the current selection that, while keeping the abundance/area target constant, reduce the edge-to-area ratio, meaning replacing the original selection with cells that reduce the fragmentation of each patch so that it becomes more coherent. Specifically, this approach implies that for the first three sub-scenarios a higher density cell is replaced by two lower density cells that together comprise an equal or larger abundance than the current cell. Thus, this approach implies that for the first scenario a larger area is selected than the minimum required one. Table S2 shows this trade-off for each sub-scenario and target: from a total of 108 runs (because analyses were done separately by country and population for some of the sub-scenarios), 78 runs required an additional area of less than 10%, 25 runs of more than 10%, 4 runs of more than 20%, and only one run of more than 30%. The detailed "pseudo code" and the R-code can be found in the Supporting Information.

Finally, we determined for each scenario the proportion of chimpanzees in areas currently designated as high-level protected areas and the spatial overlap with priority areas identified in the last western chimpanzee action plan (Kormos & Boesch, 2003). All analyses were implemented in R (vers. 3.4.x; R Core Team, 2018).

3 | RESULTS

For scenario 1 (10–90% abundance at three spatial scales), cells that were most frequently selected were in the Fouta Djallon Highlands, which extends from Guinea-Bissau and Senegal across Guinea into Sierra Leone, as well as in the border area between Liberia and Sierra Leone (Figure 1, Figure 2, outline c in Figure 2b). Specifically, cells of high conservation value to chimpanzees were in Moyen Bafing (outline 16 in Figure 2a) in Guinea, Outamba (outline 22 in Figure 2a) and Loma (outline 14 in Figure 2a) in Sierra Leone, and Gola in Sierra

Leone and Liberia. Transboundary areas that were frequently selected include the Guinea-Senegalese, Guinea-Malian, Guinea-Sierra Leonean and Côte d'Ivoire-Liberian border (Figure 1a). In the countrywide sub-scenario 1b, cells in protected areas were frequently selected, especially in Côte d'Ivoire and Ghana (Figure 1b). Overall, the range-wide sub-scenario 1a required the smallest area compared to the two other sub-scenarios (Table 2). Required area differed because chimpanzee densities vary strongly among countries but also among the three populations. Consequently, for the countrywide scenario, more cells in countries with low chimpanzee densities were selected. The comparison between the range-wide and the countrywide selections showed that for the range-wide criterion selection was higher for Guinea and Sierra Leone, and at the border areas of Guinea, Guinea-Bissau, Senegal, and Mali (Figure 1d). In the population-wide scenario (sub-scenario 1c), more cells from the population marked as "blue" and "red" in Figure 1c were selected which have lower densities than the "green" one and therefore this sub-scenario selected a larger area than the range-wide scenario (each population was assigned a color so that it can be differentiated in Figure 1c, but colors have no further meaning).

Of the areas selected in the second scenario (17–50% of area per country), 24.1% (sub-scenario 2a for area target 17%) are currently designated as high-level protected areas, or are in the final stages of designation. Considering only these high-level protected areas, no range country has met the 17% terrestrial area protection target countries committed to when signing the Convention on Biological Diversity (Table 1). The selection scenario based on reaching 17% area protection (sub-scenario 2b) identified cells in Guinea in the Fouta Djallon (outline c in Figure 2b), in northern Sierra Leone, and in northern and southern Liberia (Figure 3b).

Selected areas overlapped strongly with the priority areas identified by Kormos and Boesch (2003), with 40% of the selected cells across all scenarios falling within one of the priority areas (Table 2, Figure 2b). Notable exceptions were the priority areas "Haute Sassandra & Mt. Péko" and "Marahoué" (outline f and k in Figure 2b) from which chimpanzees are thought to now be extirpated (Kühl et al., 2017). Areas that were frequently selected, but are not within the priority areas identified by previous studies, were the Kourandou and Simandou mountain ranges in eastern Guinea, Mt. Sangbé in Côte d'Ivoire (outline 17 in Figure 2a), and the cross-border area at Oure Kaba in Guinea and Outamba in Sierra Leone (outline 22 in Figure 2a, but see below for discussion of limitations and uncertainties of this analysis). Spatial overlap was also large with prioritization areas identified in a study focused on Liberia (Junker et al., 2015, results in Table S3; Figure S2). All results are made available via the IUCN SSC A.P.E.S. database.

4 | DISCUSSION

Our study provides the first attempt to use quantitative analyses to identify areas that are important for western chimpanzee conservation across their entire range. Instead of providing a single "optimal"
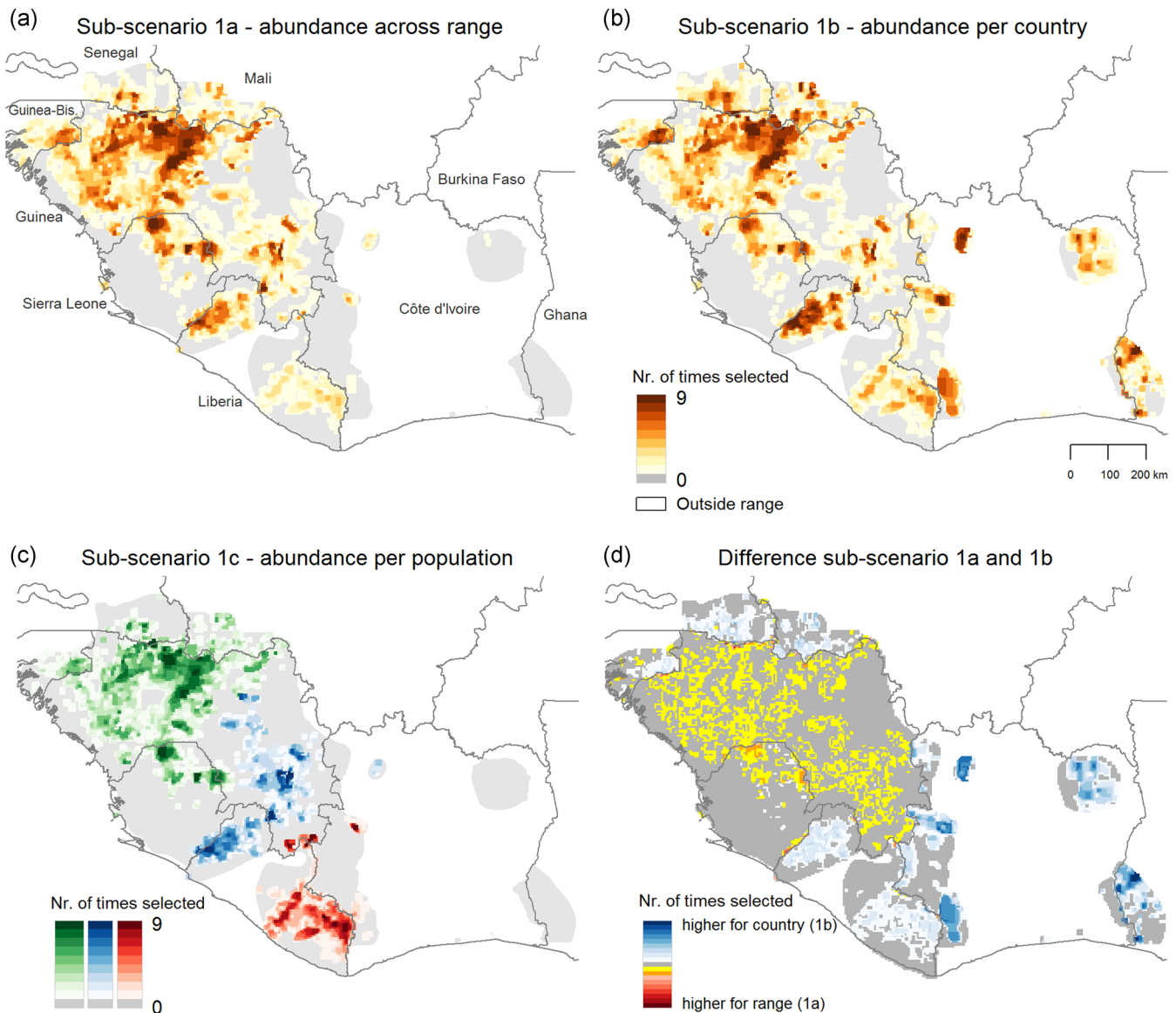
FIGURE 1 Mapped areas of high conservation value for western chimpanzees for the first scenario based on chimpanzee abundance with three sub-scenarios for different spatial scales: (1a) across the geographic range of western chimpanzees, (1b) in each range country, and (1c) separately for each of the three largest populations. Colors correspond to the number of times a cell was selected and can range from 0 to 9, as each sub-scenario was implemented for nine targets ranging from 10% to 90% of chimpanzee abundance in 10% increments. Panel (d) illustrates the difference between sub-scenario (1a) and (1b)

result, we used different scenarios and spatial scales to take into account that stakeholders use different metrics for their decision-making, depending on the scale at which they work and their objectives. Areas that were consistently identified as important for chimpanzees can guide where governments, NGOs and funding organizations target conservation activities. In addition, our results can be used to estimate how many chimpanzees would likely be affected by infrastructure and resource extraction projects. This information can help to identify areas that should be avoided and to quantify the required mitigation measures for areas that are being developed.

Overall there was strong agreement among different scenarios concerning which areas were identified (Figures 1–3). However,

scenarios differed regarding the amount of area required to reach the respective targets. Specifically, the range-wide sub-scenario (1a) needed the smallest area for protecting the same number of chimpanzees (Table 2). This result is in line with previous findings that large-scale prioritizations are more efficient than national prioritizations (Moilanen et al., 2013). Even though country- and population-wide scenarios required larger areas, because they selected more cells with low chimpanzee densities, they had the advantage of selecting cells from more dispersed areas. Protecting a species across several locations can reduce the risk that a negative event at a single location will affect the entire population (van Teeffelen et al., 2012). As it has been proposed that behavioral diversity needs to be considered in conservation planning for
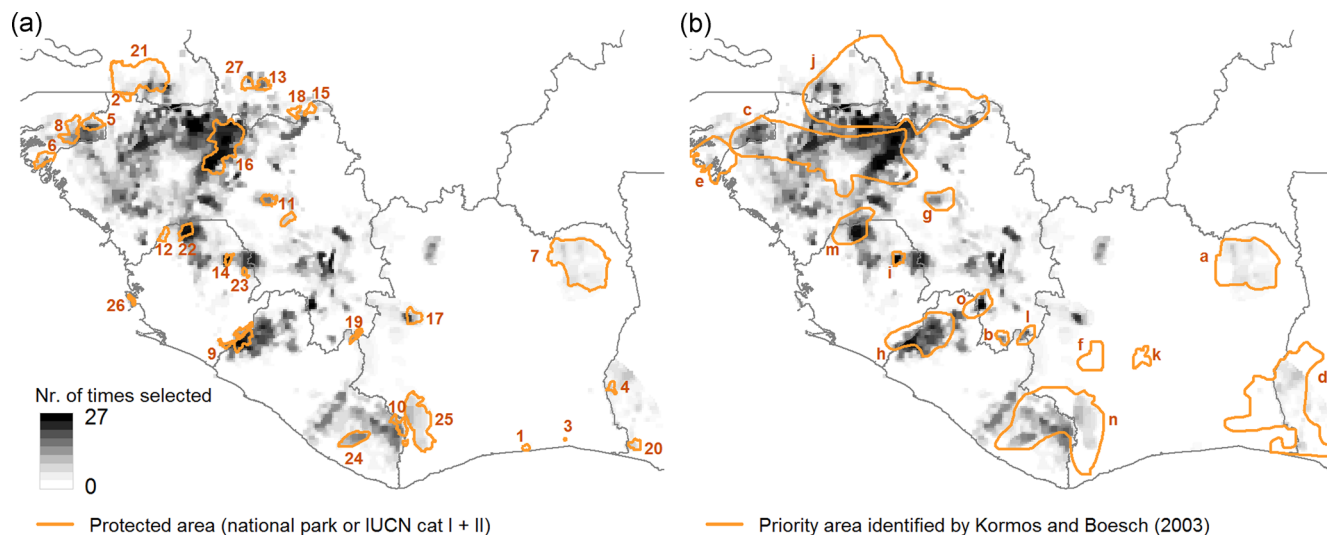
FIGURE 2 Mapped areas of high conservation value for western chimpanzees summed up for all three sub-scenarios based on chimpanzee abundance (i.e., the number of times a cell was selected was summed up across scenarios 1a-c). Shown is the overlap with (a) high-level protected areas (i.e., national park or IUCN category I or II) and (b) priority areas identified by Kormos and Boesch (2003). Protected areas: 1 Azagny, 2 Badiar, 3 Banco, 4 Bia, 5 Boé, 6 Cantanhez, 7 Comoé, 8 Dulombi, 9 Gola, 10 Grebo-Krahn, 11 Haut Niger, 12 Kilimi, 13 Kouroufing, 14 Loma, 15 Mandé Wula, 16 Moyen Bafing, 17 Mt. Sangbé, 18 Néma Wula, 19 Nimba, 20 Nini-Suhien, 21 Niokolo Koba, 22 Outamba, 23 Sankan Biriwa, 24 Sapo, 25 Taï, 26 Western Area, 27 Wongo. Priority areas: a Comoé, b Diéke, c Fouta Djallon, d Ghana-Côte d'Ivoire border, e Guinea-Guinea-Bissau coastal, f Haute Sassandra & Mt Péko, g Haut Niger, h Lofa-Mano-Gola forests, i Loma mountains, j Manding plateau, k Marahoué, l Nimba mountains, m Outamba-Kilimi & Guinea border, n Taï-Grebo-Sapo-Cestos, o Ziama & Wonegizi

chimpanzees (e.g., Kühl et al., 2019), protecting a diversity of areas can be one way of accounting for intraspecific behavioral variation by covering different habitat types and degrees of anthropogenic influence. However, more specific analyses would be needed once detailed information on the genetic and behavioral composition of individual chimpanzee communities can be determined and approaches for how to account for these in conservation planning have been designed.

4.1 | Comparison to previously identified priority areas

Areas of high conservation value overlapped to a large degree with the areas identified by Kormos and Boesch (2003); (Table 2, Figure 2 b). The main differences were that for the priority areas "Haute Sassandra & Mount Péko" and "Marahoué" (outline f and k in Figure 2b) chimpanzees are thought to now be extirpated (Kühl et al., 2017), likely because of hunting and large-scale deforestation (Campbell,
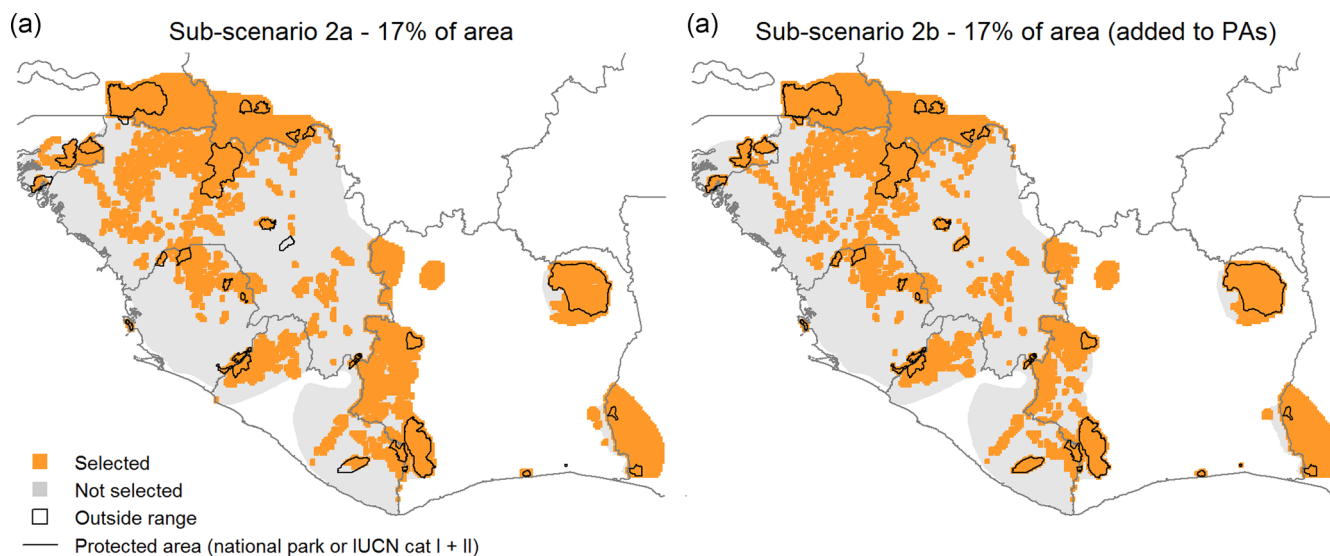

FIGURE 3 Mapped areas of high conservation value for western chimpanzees for the second scenario based on area size for 17% of the terrestrial area for each country with (a) highest chimpanzee density and (b) highest chimpanzee density in addition to high-level protected areas (i.e., national park or IUCN category I or II)

Kuehl, N'Goran Kouamé, & Boesch, 2008; Herbinger, Boesch, & Tondossama, 2003). Similarly, the extent of the chimpanzees' geographic range in the "Ghana-Côte d'Ivoire border area" (outlined in Figure 2b) has contracted since 2003, driven by the expansion of industrial agriculture and resulting deforestation as well as hunting (Kühl et al., 2017). Furthermore, our study provides a detailed picture at a high resolution in terms of relative importance between and within selected areas. Our results also show that areas between the "Mandag Plateau," "Fouta Djallon," and "Outamba-Kilimi & Guinea border area" (outline j, c, and m in Figure 2b) are of high conservation value. While Kormos and Boesch (2003) emphasized the east-west extension of those areas, it seems that north-south connectivity between all three areas is also important for ensuring population connectivity (Figure 2b).

4.2 | Limitations

The aim of this analysis was to provide a large-scale overview of areas important for western chimpanzee conservation. The main limitation lies in the accuracy of the modeled chimpanzee density distribution which was the basis for this analysis. Chimpanzee densities might be over- or underestimated for specific areas and could thus distort the derived area selection. For several countries model estimates were in line with previous design-based estimates, namely, for Côte d'Ivoire, Guinea, Liberia and Sierra Leone (Table 1). However, as limited data were available for Guinea-Bissau, Mali, and Senegal, this analysis has to be considered as preliminary for those three countries until further surveys are undertaken. Chimpanzee densities may have been underestimated for coastal areas in Guinea-Bissau for which higher chimpanzee densities have previously been estimated in four forest patches (Sousa, Barata, Sousa, Casanova, & Vicente, 2011). In contrast, densities may have been overestimated for the Simandou and Kourandou ranges in eastern Guinea which are characterized by very dry conditions. Field surveys for data-scarce areas are needed to ground-truth the input chimpanzee density distribution and this analysis (details, including a map of survey gaps, in Heinicke et al., 2019a). A further limitation is that we were able to consider only chimpanzee densities, which are naturally lower in savanna habitat (Pruetz & Bertolani, 2009). The sub-scenarios by country and population were implemented to counterbalance this constraint. In contrast, habitat destruction can lead to high chimpanzee densities in small refuge areas and the importance of areas, such as the Nimba Mountains (outline 19 in Figure 2a), might have been overestimated.

4.3 | Applications

In this study, we identified areas of high conservation value for western chimpanzees and the resulting maps can be used to decide to which areas conservation activities should be targeted to maximize conservation impact. The type of activity to be implemented depends on the specific social-ecological context at each site and can include the designation of new protected areas, conservation activities for chimpanzee strongholds outside of protected areas and in transboundary areas, or the designation of "no-go zones" for industry.

First, legally protecting chimpanzee habitat is a common conservation action that can have a positive effect on chimpanzee densities (Stokes et al., 2010; Strindberg et al., 2018), when these areas are actively managed and conservation actions are implemented (e.g., law enforcement, research or NGO presence, Campbell et al., 2011; Tranquilli et al., 2012). While protected area coverage across western chimpanzee range countries is low (Kühl et al., 2017), several national parks have been created recently, including Boé and Dulombi in Guinea-Bissau, and Gola and Grebo-Krahn in Liberia (outline 5, 8, 9, and 10 in Figure 2a). Moyen Bafing in Guinea is in the final stages of official designation. Still, only 17% of chimpanzees occur in high-level protected areas (including Moyen Bafing, Heinicke et al., 2019a). While Figure 3b is of limited use for countries which harbor only a small part of the western chimpanzees' range (i.e., Ghana, Mali, Senegal), this analysis can inform the designation of protected areas in countries with the largest western chimpanzee populations (Figure 3b). Protected area extension would likely not only benefit chimpanzees, but also sympatric species, as western chimpanzees have been shown to coincide with other threatened mammal species (Bersacola et al., 2018; Brncic et al., 2015; Brugière & Kormos, 2008; Junker et al., 2015; Tweh et al., 2015). However, there is an on-going debate on the socioeconomic effects of protected areas on communities living inside and immediately adjacent to protected areas (West, Igoe, & Brockington, 2006). With research showing both positive (Naidoo et al., 2019) and negative effects (Poudyal et al., 2018), it is now well-established that social concerns need to be considered in protected area planning and governance (e.g., loss of livelihoods or increase in human–wildlife conflicts; Woodhouse, Bedelian, Dawson, & Barnes, 2018).

Second, with more than 80% of western chimpanzees living outside protected areas, conservation activities targeting chimpanzees in these areas are also needed to ensure the long-term survival of the sub-species. Chimpanzees live in a diversity of habitat types including mosaics of forests and agricultural areas (Hockings et al., 2015). They are able to persist in areas where hunting pressure is low, usually because local residents have long-held traditions of not hunting chimpanzees (Boesch et al., 2017; Heinicke et al., 2019b; Kormos et al., 2003). Although the effectiveness of conservation activities outside protected areas is under-studied (Junker et al., 2017), it is recognized that measures such as reducing hunting pressure are essential (Kühl et al., 2017).

Third, our analysis underlined the importance of transboundary conservation efforts, as areas of high conservation value were identified at most border areas across the geographic range of western chimpanzees (Figures 1–3). Even though collaboration across international borders is challenging, for example, because of differences in legal and institutional structures, it can improve ecological connectivity (Vasilijevic et al., 2015). With increasing

habitat fragmentation across West Africa, habitat connectivity might become an important point to address in conservation planning.

Fourth, environmental guidelines by many international institutions that finance development projects state that the negative impact on great apes during the planning and construction of infrastructure or during resource extraction needs to be limited (IFC, 2019; Kormos et al., 2014; Laurance, 2018). Therefore, the results of this study can be used to inform mitigation measures and the identification of areas that should be avoided by such projects (e.g., "no-go zones"). Furthermore, similar to the suggestion that rare and important habitat types merit higher compensation ratios when they are impacted by dam construction (Rainer, 2018), areas that are particularly important to western chimpanzees could require a higher compensation ratio, meaning that activities leading to the destruction or disturbance of areas particularly important to chimpanzees would require more compensatory measures. In this context, our study can also guide the identification of areas that qualify as potential offset sites (Kormos et al., 2014). Chimpanzees are a charismatic flagship species and attract a lot of international attention, which can put pressure on corporations to follow best-practice guidelines and, if implemented appropriately, can also benefit sympatric species that typically get less attention.

This analysis is intended to maximize the number of chimpanzees that come under the protection and can serve as a basis for protected area authorities, NGOs and researchers working for the preservation of western chimpanzees to identify priority conservation areas. The incorporation of expert opinion for under-surveyed areas, for example, following the approach by Pérez-García, DeVault, Botella, and Sánchez-Zapata (2017), might be required at this stage. Then a consultation process with the government, local communities, and representatives from industry should follow, ultimately to incorporate chimpanzee conservation priorities within national biodiversity and development targets (Kormos et al., 2014; Laurance, 2018). The approach we used here could be applied to any primate taxon for which density distribution data are available. With so many primate taxa listed as Endangered (Estrada et al., 2017), systematic conservation planning has the potential to inform the effective allocation of scarce conservation funding, respond to emerging threats more strategically, and improve the long-term survival prospects of these threatened species.

The research adhered to German law and the ASP Principles for the Ethical Treatment of Non-Human Primates.

ORCID

Stefanie Heinicke http://orcid.org/0000-0003-0222-5281
Elizabeth A. Williamson http://orcid.org/0000-0001-6848-9154
Hjalmar S. Kühl http://orcid.org/0000-0002-4440-9161

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SUPPORTING INFORMATION

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

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