Informing the transition to evidence-based conservation planning for western chimpanzees

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Dissertation

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Large-scale land-use change across the tropics has led to the decline of animal populations and their habitat. With large investments into mining, hydropower dams and industrial agriculture this trend is likely to continue. Consequently, there is a need for systematic land-use planning to set aside areas for protection and allocate scarce conservation funding effectively. Even though primates are relatively well studied, data-driven systematic planning is still rarely implemented. The overall aim of this dissertation was to investigate population parameters needed for evidence-based conservation planning for the critically endangered western chimpanzee (*Pan troglodytes verus*) in West Africa. To this end, I compiled density datasets covering the entire geographic range of this taxon from the IUCN SSC A.P.E.S. database and modeled chimpanzee densities as a function of 20 social-ecological variables. I found that western chimpanzees seemingly persist within three social-ecological configurations: rainforests with a low degree of anthropogenic threats, steep areas that are less likely to be developed and are harder to access by humans, and areas with a high prevalence of cultural taboos against hunting chimpanzees. The third configuration of reduced hunting pressure is not yet reflected in commonly implemented conservation interventions, suggesting a need for designing new approaches aimed at reducing the threat of hunting. Based on the modeled density distribution, I estimated that 52,811 (95% CI 17,577-96,564) western chimpanzees remain in West Africa, and identified areas of high conservation value to which conservation interventions should be targeted. These results can be used to inform the expansion of the protected area network in West Africa, to quantify the impact of planned industrial projects on western chimpanzees, and to guide the systematic allocation of conservation funding. In addition, this thesis highlights the unique position of taxon-specific databases of providing access to high-resolution data at the scale needed for conservation planning. Data-driven conservation planning has the potential to enable conservationists to respond more proactively to current and emerging threats, and ultimately improve conservation outcomes.

This thesis is based on the following manuscripts:

Characteristics of positive deviants in western chimpanzee populations (2019)

Heinicke, S., Mundry, R., Boesch, C., Amarasekaran, B., Barrie, A., Brncic, T., Brugière, D., Campbell, G., Carvalho, J., Danquah, E., Dowd, D., Eshuis, H., Fleury-Brugière, M.-C., Gamys, J., Ganas, J., Gatti, S., Ginn, L., Goedmakers, A., Granier, N., Herbinger, I., Hillers, A., Jones, S., Junker, J., Kouakou, C. Y., Lapeyre, V., Leinert, V., Marrocoli, S., Molokwu-Odozi, M., N'Goran, P. K., Normand, E., Pacheco, L., Regnaut, S., Sop, T., Ton, E., van Schijndel, J., Vendras, E., Vergnes, V., Welsh, A., Wessling, E. G., & Kühl, H. S.

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Towards systematic and evidence-based conservation planning for western chimpanzees (submitted)

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Introduction

The need for evidence-based conservation planning

In the past decades land use changed strongly across the globe, driven by unsustainable resource exploitation, infrastructure development and expansion of settlements and agriculture (Alamgir et al., 2017; Curtis et al., 2018; Laurance et al., 2014; Song et al., 2018). Large-scale degradation of natural ecosystems has led to the decline of animal populations and their habitats, and in turn also resulted in degraded ecosystem services (Dirzo et al., 2014), a trend likely to continue (Newbold et al., 2015). With increasing pressure on remaining natural habitat, there is a need for informed land-use planning to identify those areas which should be set aside and put under protection (Margules and Pressey, 2000). At the same time, conservation planning can help to distribute scarce funding systematically and will thus make conservation interventions more effective (Mace et al., 2007).

For comprehensive conservation planning, specific data and information are needed. First, population parameters such as abundance, temporal change in abundance, and spatial distribution, describe the conservation status of the targeted taxon (Mair et al., 2018). Second, large-scale planning has been shown to be more efficient in terms of required area than prioritization for each country separately (Moilanen et al., 2013). While density distribution data are still rare for many species, it can inform on the intra-specific variability across a species' geographic range and thus help to identify those areas that are of high conservation value. Third, understanding social-ecological conditions enabling species persistence can be used to design conservation activities that mimick such favorable conditions (Post and Geldmann, 2018).

Systematic conservation planning is particularly warranted in West Africa where 80% of forests were deforested since 1900 and planning of conservation interventions is still often not systematic (Aleman et al., 2018). The region is one of the poorest globally, and with several armed conflicts and the recent Ebola epidemic, large investments into social infrastructure and economic growth are needed (AfDB, 2018; WHO, 2016). West Africa is rich in mineral deposits and remaining forests are of interest to international corporations (Edwards et al., 2014; Malhi et al., 2013). At the same time all West African countries are signatories to the Convention on Biological Diversity and the Aichi Target 11 aiming to protect 17% of terrestrial area, but most have not achieved this goal (UN, 2019).

Conservation planning for western chimpanzees

The geographic range of western chimpanzees (*Pan troglodytes verus*) extends across eight West African countries. Threatened by habitat loss and poaching, the population declined by 80% in 24 years (Kühl et al., 2017). They were uplisted to Critically Endangered by the IUCN Red List of Threatened Species (Humle et al., 2016). One of the main conclusions from the last conservation action plan for western chimpanzees was that large data gaps persist (Kormos and Boesch, 2003). Consequently, the identification of conservation priority areas was based on expert opinion. The evaluation of the action plan revealed that this selection process was contentious and participants emphasized the need for pre-defined selection criteria (Kormos, 2008).

Aims of the research

The overarching aim of my dissertation was to contribute to the scientific basis for the future protection of western chimpanzees regarding spatial planning. Since 2003, more than 50 chimpanzee surveys have been conducted by various NGOs and researchers across West Africa and the data were shared with the IUCN SSC A.P.E.S. database (Kühl et al., 2007). Consequently, with plans to update the conservation action plan for western chimpanzees and the data now available to inform a systematic planning process, the aim of my thesis was threefold. First, to investigate the drivers of chimpanzee densities and examine under which social-ecological conditions some western chimpanzee populations seem to be able to persist, while others have declined strongly. Second, to estimate population parameters needed for evidence-based conservation planning and third, to provide information for the systematic identification of priority areas for western chimpanzee conservation. To this end, I modeled chimpanzee densities as a function of different social-ecological factors to identify drivers of chimpanzee densities, predict the density distribution across their geographic range and determine areas of high conservation value. The three chapters were based on 52 chimpanzee nest count surveys that I compiled via the IUCN SSC A.P.E.S. database with a total sample size of 17,109 transects covering 10,929 km across nine countries. I extracted 20 predictor variables expected to influence chimpanzee densities from the categories habitat, topography, and anthropogenic influences, from publicly available satellite data and aggregated household surveys.

In the **first chapter**, I identified which social-ecological factors influence chimpanzee densities in West Africa. As threats to chimpanzees are already well understood (Campbell et al., 2008;

Kormos et al., 2003; Kühl et al., 2017; Tranquilli et al., 2014), I was interested to understand why chimpanzees are able to persist in some areas (Kühl et al., 2017) and whether specific social-ecological conditions could explain this. I used the 'positive deviance approach', a framework developed in the social sciences and only recently adapted to conservation to study such positive outliers and understand the heterogeneity within species in terms of species persistence (Cinner et al., 2016; Post and Geldmann, 2018). This chapter was the first study applying this approach to terrestrial animals. Specifically, I first identified factors that significantly influence chimpanzee densities based on a Generalized Linear Mixed Model, and then compared configurations of significant social-ecological factors across a total of 66 sites.

For the **second chapter**, I predicted the density distribution of western chimpanzees across their geographic range using spatial modeling techniques to infer total population size and landscape-scale metrics. I also used the predicted density distribution to derive a presence layer and, based on minimum distance between presence pixels, estimated which areas likely have low population connectivity. Lastly, I determined the proportion of western chimpanzees in areas designated as high-level protected areas (i.e., national parks and IUCN category I and II protected areas).

In the **third chapter,** I systematically identified areas of high conservation value to western chimpanzees based on the predicted density distribution. As a diversity of stakeholders is active across the western chimpanzee range, including government agencies, NGOs, researchers, corporations, and community representatives, it is now widely acknowledged that the prioritization of conservation areas is not a purely technical exercise resulting in one 'best' solution but as much a political process in which all stakeholders need to be involved (Grantham et al., 2010; Hadorn et al., 2006; Pressey and Bottrill, 2008). Thus the aim of this chapter was to identify areas of high conservation value to chimpanzees as a first technical step to inform the consultation process among all parties involved in chimpanzee conservation to find a common position. Consequently, I used several scenarios and criteria that accounted for various abundance and area targets and for different spatial scales.

Results

In the first chapter, I found that forest loss had a strong negative impact on chimpanzee densities and for the first time I was able to quantify this effect. No chimpanzee nests were found in areas that were characterized by more than 10% forest loss. The model also revealed that chimpanzees were more abundant in flat terrain. However, in areas characterized by a high intensity of human activity (a compound factor consisting of human density, settlements, nighttime light and armed conflicts), chimpanzee densities were higher in steeper terrain, indicating a refuge effect. Lastly, I found that chimpanzee densities were higher in areas with a high prevalence of hunting taboos and low degree of human activity. Hunting taboos are social customs against killing a specific species based on cultural traditions (Colding and Folke, 2001).

The comparison of the configurations of significant social-ecological factors across all sites revealed that three configurations seem to enable chimpanzee persistence: rainforest areas with low degree of forest loss, steep areas (i.e., areas that are less likely to be developed and are harder to access by humans), and areas with high prevalence of hunting taboos and low degree of human impact. The first two configurations are already reflected in interventions that are commonly implemented in conservation in general and that focus on threat exclusion. These interventions typically restrict access to certain regions by establishing protected areas and through law enforcement. However, conservation interventions aimed at threat reduction, as reflected in the third configuration of reduced hunting pressure, are rare in primate conservation (Junker et al., 2017).

In the second chapter, I first predicted the density distribution of western chimpanzees across their range at 1 km^2 resolution and estimated a total abundance of 52,811 (95% CI 17,577-96,564) individuals. The population analysis revealed that two large populations can be distinguished: one across the Fouta Djallon (a highland region across Guinea and reaching into neighboring countries), characterized by savanna mosaics and a high prevalence of hunting taboos; and a second population across Liberia and neighboring countries mostly characterized by rainforest habitat. I also identified three areas that likely have low population connectivity. Currently, 17% of western chimpanzees occur in high-level protected areas.

In the third chapter, I identified areas of high conservation value to western chimpanzees. Across all scenarios typically less than one third of the areas that I identified as being important are currently designated as high-level protected areas. The comparison to the priority areas from the 2003 action plan showed that although there is a strong overlap, some areas were not previously recognized as important, while chimpanzees are now extirpated from others. This analysis also revealed the importance of maintaining connectivity across the north to south extend of the chimpanzees' geographic range. Based on the range-wide predicted density distribution, I was able to for the first time quantify the relative importance between and within specific areas. This can not only inform the extension of the protected area network but also guide NGOs, donors and governmental agencies in their investment decisions. This type of analysis can be transferred to other primate species, for most of which this type of information is not yet available, but urgently needed (Estrada et al., 2017).

Conclusion

With this dissertation, I for the first time provided population parameters for the entire range of western chimpanzees needed for spatial conservation planning. This information can support conservationists in taking a more proactive approach to planning for the protection of this taxon. For example, environmental guidelines signed by the World Bank and 95 other financial institutions state explicitly that any negative impact on great apes has to be minimized during infrastructure construction and resource extraction (IFC, 2012; The Equator Principles Association, 2019). Results of this dissertation can now be used to estimate how many chimpanzees would be impacted by such industrial projects and thus avoidance and mitigation measures could already be included in the planning phase. The results can also guide donors how to prioritize funding allocation, and can inform negotiations with government agencies and extractive industries on setting aside land for protection. With this dissertation I provided baseline data for western chimpanzees by which the impact of future developments, including infrastructure, resource extraction and conservation projects, could be measured. It can also serve as a starting point for estimating the impact of more complex developments, such as the impact of climate change on western chimpanzees, which has not yet been studied.

I, for the first time, applied the ‘positive deviance approach’ to a terrestrial species and found that this can be a powerful tool to identify conditions or mechanisms that enable species’ persistence. This approach can be applied to any taxon, region and spatial scale, as long as data of sufficient variation across several predictor variables are available. This is especially pertinent as threats to species are rather well-studied, while solutions and suitable conservation interventions are a lot less understood. Thus this work can serve as a template on how this approach can be applied to many more species.

The IUCN SSC A.P.E.S. database (apesportal.eva.mpg.de) provides access to data at a temporal and spatial resolution that is still rare for tropical species, that are generally considered data-deficient (Peterson and Soberón, 2018). However, this level of detail is needed for analyses at the scale relevant for conservation planning. Taxon-specific databases are in a unique position to fill the niche between local data collectors and global databases and can contribute to filling biodiversity data gaps. Such databases already exist for different taxa, but

are largely underfunded. Their value in making data accessible to researchers, planners and decision-makers needs to be recognized, and many more databases could be established. Then a network of taxon-specific databases could be created in which each individual database pools data and expertise of its respective field and users can access data available across the entire network via a central portal. My approach of compiling a suite of datasets from individual research projects to answer broad-scale conservation questions can be applied to many other taxa. A data-driven approach to conservation planning can enable researchers and conservation practitioners to proactively plan in the face of complex future developments in the context of global change.

Zusammenfassung

Einleitung

Notwendigkeit einer evidenzbasierten Naturschutzplanung

Weltweit hat sich die Landnutzung in den letzten Jahrzehnten stark verändert. Verursacht wurde dies durch Ressourcenausbeutung, den Infrastrukturausbau und eine Ausweitung von Siedlungen und landwirtschaftlicher Fläche (Alamgir et al., 2017; Curtis et al., 2018; Laurance et al., 2014; Song et al., 2018). Die großflächige Zerstörung natürlicher Ökosysteme führte zum Rückgang von Tierpopulationen und deren Lebensraum, was wiederum eine Verminderung der Ökosystemleistungen zur Folge hatte (Dirzo et al., 2014), eine Entwicklung, die sich voraussichtlich fortsetzen wird (Newbold et al., 2015). Mit zunehmendem Druck auf den verbleibenden natürlichen Lebensraum, besteht die Notwendigkeit einer fundierten Flächennutzungsplanung, um festzustellen welche Gebiete unter Schutz gestellt werden sollten (Margules und Pressey, 2000). Gleichzeitig kann Naturschutzplanung dazu beitragen, knappe finanzielle Mittel gezielt zu verteilen und damit die Effektivität von Schutzmaßnahmen zu erhöhen (Mace et al., 2007).

Für eine umfassende Naturschutzplanung werden bestimmte Daten und Informationen benötigt. Erstens wird der Erhaltungszustand eines bestimmten Taxons mittels Populationsparametern wie Abundanz, Änderung der Abundanz über die Zeit und räumliche Verteilung beschrieben (Mair et al., 2018). Zweitens wurde gezeigt, dass die Landschaftsnutzungsplanung in Bezug auf den Flächenbedarf für ein großes Gebiet effizienter ist als die Priorisierung für jedes einzelne Land (Moilanen et al., 2013). Obwohl Daten über die Dichteverteilung für viele Arten noch nicht vorhanden sind, können solche Auskunft über die intraspezifische Variabilität im Verbreitungsgebiet einer Art geben und somit helfen, die Gebiete zu identifizieren, die von hohem Erhaltungswert sind. Drittens, wenn die sozial-ökologischen Bedingungen bekannt sind, die zum Fortbestehen der Arten beitragen, können Schutzmaßnahmen konzipiert werden, die die günstigen Bedingungen nachahmen (Post und Geldmann, 2018).

Eine systematische Naturschutzplanung ist insbesondere in Westafrika notwendig, wo 80% der Wälder seit 1900 abgeholzt wurden und die Planung von Schutzmaßnahmen oft noch nicht systematisch erfolgt (Aleman et al., 2018). Die Region ist eine der ärmsten der Welt, und angesichts mehrerer bewaffneter Konflikte und der jüngsten Ebola-Epidemie sind hohe Investitionen in die soziale Infrastruktur und das Wirtschaftswachstum erforderlich (AfDB, 2018; WHO, 2016). Westafrika ist jedoch reich an Bodenschätzen und die verbleibenden

Wälder sind für internationale Holzunternehmen von Interesse (Edwards et al., 2014; Malhi et al., 2013). Gleichzeitig haben alle westafrikanischen Länder das Übereinkommen über die biologische Vielfalt und das Aichi-Ziel 11 zum Schutz von 17% der Landfläche unterzeichnet, jedoch haben die meisten Länder dieses Ziel noch nicht erreicht (UN, 2019).

Naturschutzplanung für den westlichen Schimpansen

Das Verbreitungsgebiet des westlichen Schimpansen (*Pan troglodytes verus*) erstreckt sich über acht westafrikanische Länder. Durch den Verlust von Lebensraum und Wilderei ging die Population innerhalb von 24 Jahren um 80% zurück (Kühl et al., 2017). Der westliche Schimpanse wurde daraufhin auf der Roten Liste der bedrohten Arten der IUCN als vom Aussterben bedrohtes Taxon eingestuft (Humle et al., 2016). Eine der wichtigsten Schlussfolgerungen des letzten Aktionsplanes zur Erhaltung des westlichen Schimpansen war, dass weiterhin große Datenlücken bestehen (Kormos und Boesch, 2003). Die Identifizierung der prioritären Schutzgebiete erfolgte daher auf der Grundlage von Expertenmeinungen. Die Auswertung des Aktionsplans ergab, dass dieser Auswahlprozess umstritten war, und die Teilnehmerinnen betonten die Notwendigkeit, dass Auswahlkriterien bereits im Vorfeld definiert werden müssen (Kormos, 2008).

Forschungsziele

Übergeordnetes Ziel meiner Dissertation war es, zur wissenschaftlichen Grundlage für den Schutz des westlichen Schimpansen im Rahmen der Raumplanung beizutragen. Seit 2003 wurden mehr als 50 Schimpansenzählungen von verschiedenen Nichtregierungsorganisationen und Forschern in Westafrika durchgeführt und die Daten der IUCN SSC A.P.E.S. Datenbank zur Verfügung gestellt (Kühl et al., 2007). Da der Aktionsplan für westliche Schimpansen aktualisiert werden soll und nun umfassende Daten zur Verfügung stehen, die für einen systematischen Planungsprozess notwendig sind, waren die Ziele meiner Dissertation dreifach. Erstens, die Treiber der Schimpansendichte zu bestimmen und zu untersuchen, unter welchen sozial-ökologischen Bedingungen einige westliche Schimpansenpopulationen in der Lage zu sein scheinen, zu bestehen, während andere stark zurückgegangen sind. Zweitens, die für die evidenzbasierte Erhaltungsplanung erforderlichen Populationsparameter zu ermitteln. Und drittens, Informationen für die systematische Festlegung von prioritären Gebieten für den Schutz westlicher Schimpansen zu bestimmen. Zu diesem Zweck habe ich Schimpansendichten als Funktion verschiedener sozial-ökologischer Faktoren modelliert, um Treiber von Schimpansendichten zu bestimmen, die Dichteverteilung im Verbreitungsgebiet zu berechnen und Gebiete mit hohem Erhaltungswert zu bestimmen. Die drei Kapitel dieser Dissertation basierten auf 52 Datensätzen von Schimpansenmonitoring, die ich über die IUCN SSC A.P.E.S. Datenbank zusammengestellt habe, und die insgesamt 17.109 Transsekte über eine Länge von 10.929 km in neun Ländern abdeckten. Ich habe 20 Prädiktorvariablen, die die Schimpansendichte beeinflussen sollen, aus den Kategorien Habitat, Topographie und anthropogene Einflüsse, aus öffentlich zugänglichen Satellitendaten und aggregierten Haushaltserhebungen extrahiert.

Im **ersten Kapitel** habe ich ermittelt, welche sozial-ökologischen Faktoren die Schimpansendichte in Westafrika beeinflussen. Da die Bedrohungen für Schimpansen bereits gut erforscht sind (Campbell et al., 2008; Kormos et al., 2003; Kühl et al., 2017; Tranquilli et al., 2014), wollte ich herausfinden, warum Schimpansen in einigen Gebieten fortbestehen (Kühl et al., 2017) und ob spezifische sozial-ökologische Bedingungen dies erklären könnten. Ich habe dafür den sogenannten „positive deviance approach“ (etwa „positiver Abweichungsansatz“) verwendet, eine in den Sozialwissenschaften entwickelte Methode. Diese wurde erst kürzlich an den Naturschutz angepasst, um positive Ausreißer zu untersuchen und die Heterogenität innerhalb einer Art im Hinblick auf das langfristige Überleben zu verstehen (Cinner et al., 2016; Post and Geldmann, 2018). Dieses Kapitel stellt die erste Studie dar, die diesen Ansatz auf eine terrestrische Art angewendet hat. Basierend auf einem verallgemeinerten linearen gemischten Modell, habe ich zunächst analysiert welche Faktoren die Schimpansendichte signifikant beeinflussen, und anschließend die Konfigurationen von signifikanten sozial-ökologischen Faktoren von insgesamt 66 Standorten verglichen.

Für das **zweite Kapitel** habe ich die Dichteverteilung der westlichen Schimpansen in ihrem Verbreitungsgebiet mit Hilfe von räumlichen Modellierungsmethoden vorhergesagt, um die Gesamtabundanz und Metriken auf Landschaftsebene ableiten zu können. Die Dichteverteilung verwendete ich ebenfalls, um abzuschätzen wo Schimpansen präsent sind und – basierend auf dem Mindestabstand zwischen Pixeln mit Schimpansenpräsenz – geschätzt, in welchen Gebieten es wahrscheinlich ist, dass die Konnektivität von Populationen reduziert ist. Schließlich habe ich bestimmt, welcher Anteil der westlichen Schimpansen in Gebieten vorkommt, die als hochrangige Schutzgebiete ausgewiesen sind (d.h. Nationalparks und Schutzgebiete der IUCN-Kategorien I und II).

Im **dritten Kapitel** bestimmte ich, auf Grundlage der vorhergesagten Dichteverteilung, systematisch Gebiete mit hohem Erhaltungswert für westliche Schimpansen. Da eine Vielzahl von Interessengruppen im gesamten Verbreitungsgebiet des westlichen Schimpansen aktiv sind – darunter Regierungsbehörden, Nichtregierungsorganisationen, Forscher, Unternehmen und Gemeindevertreter – ist es inzwischen allgemein anerkannt, dass die Priorisierung von Schutzgebieten keine rein technische Aufgabe ist, die zu einer "besten" Lösung führt. Dabei handelt es sich ebenso um einen politischen Prozess, an dem alle Interessengruppen beteiligt sein müssen (Grantham et al., 2010; Hadorn et al., 2006; Pressey and Bottrill, 2008). Daher war es das Ziel dieses Kapitels, Gebiete mit hohem Erhaltungswert für Schimpansen als ersten technischen Schritt zu bestimmen, um den Konsultationsprozess zwischen allen am Schimpansenschutz beteiligten Parteien zu unterstützen, um schließlich einen gemeinsamen Standpunkt finden zu können. Folglich habe ich mehrere Szenarien und Kriterien verwendet, die verschiedene Abundanz- und Flächenziele und verschiedene räumliche Dimensionen berücksichtigen.

Ergebnisse

Im ersten Kapitel stellte ich fest, dass Waldverluste einen starken negativen Einfluss auf die Schimpansendichte haben, und zum ersten Mal konnte ich diesen Effekt quantifizieren. In Gebieten, die durch mehr als 10% Waldverlust gekennzeichnet waren, wurden keine Schimpansennester gefunden. Das Modell zeigte auch, dass Schimpansen in flachem Gelände häufiger vorkommen. In Gebieten, die durch eine hohe Intensität menschlicher Aktivität gekennzeichnet sind (ein zusammengesetzter Faktor, der aus Bevölkerungsdichte, Siedlungen, nächtliches Licht und bewaffneten Konflikten besteht), waren die Schimpansendichten in steilerem Gelände jedoch höher, was auf einen Refugiumseffekt hinweist. Schließlich fand ich heraus, dass die Schimpansendichten in Gebieten mit einer hohen Verbreitung von Jagdtabus und einer geringen Intensität an menschlicher Aktivität höher waren. Jagdtabus sind ein gesellschaftlicher Brauch, bestimmte Arten aufgrund kultureller Traditionen nicht zu töten (Colding and Folke, 2001).

Der Vergleich der Konfigurationen signifikanter sozial-ökologischer Faktoren über alle Standorte hinweg ergab, dass drei Konfigurationen das langfristige Überleben von Schimpansen zu ermöglichen scheinen: Regenwaldgebiete mit geringer Entwaldung, steile Gebiete (d.h. Gebiete, die für eine weiterführende Nutzung weniger geeignet sind und für Menschen schwerer zugänglich sind) und Gebiete mit hoher Verbreitung von Jagdtabus und geringer Intensität menschlicher Aktivitäten. Die ersten beiden Konfigurationen spiegeln sich bereits in Interventionen wider, die allgemein im Naturschutz umgesetzt werden und sich auf die Ausgrenzung von Bedrohungen konzentrieren. Diese Maßnahmen beschränken durch die

Einrichtung von Schutzgebieten und die Durchsetzung der Gesetze den Zugang zu bestimmten Regionen. Allerdings werden Naturschutzmaßnahmen, wie sie sich in der dritten Konfiguration des reduzierten Jagddrucks widerspiegeln, im Primatenschutz selten umgesetzt (Junker et al., 2017).

Im zweiten Kapitel habe ich zunächst die Dichteverteilung der westlichen Schimpansen über ihr Verbreitungsgebiet mit einer Auflösung von 1 km^2 vorhergesagt und eine Gesamtabundanz von 52.811 (95% Konfidenzintervall 17.577-96.564) Individuen geschätzt. Die Populationsanalyse ergab, dass zwei große Populationen unterschieden werden können: eine im Fouta Djallon (eine Hochlandregion in Guinea, die bis in die Nachbarländer reicht), die durch Savannen-Wald Mosaike und eine hohe Verbreitung von Jagdtabus charakterisiert ist; und eine zweite Population in Liberia und den Nachbarländern, die hauptsächlich durch Regenwaldhabitat gekennzeichnet ist. Ich habe auch drei Gebiete aufgezeigt, die wahrscheinlich eine geringe Konnektivität von Populationen aufweisen. Derzeit kommen 17% der westlichen Schimpansen in hochrangigen Schutzgebieten vor.

Im dritten Kapitel habe ich ermittelt, welche Gebiete einen hohen Erhaltungswert für westliche Schimpansen haben. Über alle Szenarien hinweg werden typischerweise weniger als ein Drittel der von mir als wichtig identifizierten Gebiete derzeit als hochrangige Schutzgebiete ausgewiesen. Der Vergleich mit den Gebieten, die als besonders schutzwürdig im Aktionsplan von 2003 gekennzeichnet wurden, ergab, dass es starke Überschneidungen gibt. Dennoch konnten einige Bereiche aufgezeigt werden, die bisher noch nicht als wichtig anerkannt wurden oder auch welche in denen Schimpansen bereits ausgestorben sind. Darüber hinaus ergab die Analyse, wie wichtig es ist, die Konnektivität über die Nord-Süd-Ausdehnung des Verbreitungsgebietes des Schimpansen aufrechtzuerhalten. Basierend auf der vorhergesagten Dichteverteilung konnte ich erstmals die relative Bedeutung zwischen und innerhalb bestimmter Gebiete quantifizieren. Diese Ergebnisse können als Informationsgrundlage für den Ausbau des Schutzgebietsnetzes dienen, und Nichtregierungsorganisationen, Geldgebern und Regierungsbehörden bei ihren Investitionsentscheidungen unterstützen. Diese Art der Analyse kann auf andere Primatenarten übertragen werden, für die diese Art von Informationen meist noch nicht verfügbar, aber dringend benötigt ist (Estrada et al., 2017).

Fazit

Mit dieser Dissertation habe ich erstmals Populationsparameter für das gesamte Verbreitungsgebiet des westlichen Schimpansen, die für die Raumplanung benötigt werden, ermittelt. Diese Informationen können Naturschützer dabei unterstützen, einen proaktiveren Ansatz für die Planung zum Schutz dieses Taxons zu verfolgen. So besagen beispielsweise die von der Weltbank und 95 anderen Finanzinstituten unterzeichneten Umweltleitlinien ausdrücklich, dass negative Auswirkungen auf Menschenaffen beim Infrastrukturausbau und bei der Ressourcengewinnung minimiert werden müssen (IFC, 2012; The Equator Principles Association, 2019). Die Ergebnisse dieser Dissertation können nun genutzt werden, um abzuschätzen, wie viele Schimpansen von solchen Industrieprojekten betroffen sein würden, so dass Vermeidungs- und Minderungsmaßnahmen bereits in der Planungsphase berücksichtigt werden könnten. Die Ergebnisse können Geldgebern bei der Priorisierung der Mittelvergabe als Orientierungshilfe dienen. Gleichzeitig können sie bei Verhandlungen mit Regierungsbehörden und der mineralgewinnenden Industrie über die Stilllegung von Land zum Naturschutz unterstützend wirken. Mit dieser Dissertation habe ich Basisdaten für westliche Schimpansen ermittelt, mit denen die Auswirkungen zukünftiger Entwicklungen, einschließlich Infrastruktur-, Ressourcenentnahme- und Naturschutzprojekte, gemessen werden können. Es kann auch als Ausgangspunkt für die Abschätzung der Auswirkungen komplexerer Entwicklungen dienen, die bisher noch nicht untersucht wurden, wie beispielsweise die Folgen des Klimawandels für westliche Schimpansen.

Ich habe zum ersten Mal den "positiven Abweichungsansatz" auf eine terrestrische Art angewandt und festgestellt, dass dies eine effektive Methode sein kann, um Bedingungen oder Mechanismen aufzuzeigen, die das langfristige Überleben einer Art ermöglichen. Sofern Daten mit ausreichender Variation über mehrere Prädiktorvariablen verfügbar sind, kann dieser Ansatz auf jedes Taxon, jede Region und räumliche Dimension angewendet werden. Dies ist besonders relevant, da die Bedrohungen für Arten meist gut untersucht sind, während Lösungen und geeignete Naturschutzmaßnahmen viel weniger erforscht sind. Somit kann diese Arbeit als Vorlage dienen, um diesen Ansatz auf viele weitere Arten anzuwenden.

Die IUCN SSC A.P.E.S. Datenbank (apesportal.eva.mpg.de) bietet Zugang zu Daten mit einer zeitlichen und räumlichen Auflösung, die für tropische Arten noch selten ist und damit eher als datenarm betrachtet werden (Peterson und Soberón, 2018). Dieser Auflösungsgrad ist jedoch notwendig für die Art von Analysen die für die Naturschutzplanung erforderlich sind. Taxonspezifische Datenbanken sind in einer besonderen Position, um die Nische zwischen lokalen Datensammlern und globalen Datenbanken zu besetzen und können dazu beitragen, Lücken in Daten zur biologischen Vielfalt zu schließen. Solche Datenbanken existieren bereits für verschiedene Taxa, sind aber weitgehend unterfinanziert. Ihr Wert bei der Bereitstellung von Daten für Forscher, Planer und Entscheidungsträger muss anerkannt werden, und viele weitere Datenbanken könnten eingerichtet werden. Dann könnte ein Netzwerk von taxonspezifischen Datenbanken geschaffen werden, in dem jede einzelne Datenbank Daten und Fachwissen ihres jeweiligen Bereichs bündelt und Benutzer über ein zentrales Portal auf die im gesamten Netzwerk verfügbaren Daten zugreifen können. Mein Ansatz, aus einzelnen Forschungsprojekten eine Reihe von Datensätzen zusammenzustellen, um breit angelegte Naturschutzfragen zu beantworten, lässt sich auf viele andere Taxa übertragen. Ein datengestützter Ansatz für die Naturschutzplanung kann es Forschern und Naturschutzpraktikern ermöglichen, angesichts komplexer zukünftiger Entwicklungen im Kontext des globalen Wandels, proaktiv zu planen.

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Chapter 1

Characteristics of positive deviants in western chimpanzee populations

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Characteristics of Positive Deviants in Western Chimpanzee Populations

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With continued expansion of anthropogenically modified landscapes, the proximity between humans and wildlife is continuing to increase, frequently resulting in species decline. Occasionally however, species are able to persist and there is an increased interest in understanding such positive outliers and underlying mechanisms. Eventually, such insights can inform the design of effective conservation interventions by mimicking aspects of the social-ecological conditions found in areas of species persistence. Recently, frameworks have been developed to study the heterogeneity of species persistence across populations with a focus on positive outliers. Applications are still rare, and to our knowledge this is one of the first studies using this approach for terrestrial species conservation. We applied the positive deviance concept to the western chimpanzee, which occurs in a variety of social-ecological landscapes. It is now categorized as Critically Endangered due to hunting and habitat loss and resulting excessive decline of most of its populations. Here we are interested in understanding why some of the populations did not decline. We compiled a dataset of 17,109 chimpanzee survey transects (10,929 km) across nine countries and linked them to a range of social and ecological variables. We found that chimpanzees seemed to persist within three social-ecological configurations: first, rainforest habitats with a low degree of human impact, second, steep areas, and third, areas with high prevalence of hunting taboos and low degree of human impact. The largest chimpanzee populations are nowadays found under the third social-ecological configuration, even though most of these areas are not officially protected. Most commonly chimpanzee conservation has been based on exclusion of threats by creation of protected areas and law enforcement. Our findings suggest, however, that this approach should be complemented by an additional focus on threat reduction, i.e., interventions that directly target individual human behavior that is most threatening to chimpanzees, which is hunting. Although changing human behavior is difficult, stakeholder co-designed behavioral change approaches developed in the social sciences have been used successfully to promote pro-environmental behavior. With only a fraction of chimpanzees and primates living inside protected areas, such new approaches might be a way forward to improve primate conservation.

Keywords: behavioral change, conservation planning, hunting, mimicking, positive deviance, West Africa, *Pan troglodytes verus*

INTRODUCTION

With continued human population growth and the associated expansion of human-dominated areas, 75% of land surface areas have been anthropogenically modified (Ellis and Ramankutty, 2008). Human disturbance resulted in an average population decline of 25% for terrestrial vertebrates and of 45% for the majority of invertebrates, with the main drivers being habitat destruction, overexploitation, and invasive species (Dirzo et al., 2014). However, in some instances, species are able to persist and co-exist with humans (Gardner et al., 2009). Threats to species and the resulting species decline are relatively well studied, but considerably less is known about the social-ecological conditions under which some species tend to persist while others disappear.

One approach to understand why species are persisting at certain sites is to understand the heterogeneity across populations with a focus on analyzing positive outliers (Post and Geldmann, 2018). Similarities between areas where species are doing exceptionally well, called exceptional responders (Post and Geldmann, 2018), bright spots (Cinner et al., 2016), or positive deviants (Marsh et al., 2004), could highlight novel solutions to conservation challenges (Cinner et al., 2016; Post and Geldmann, 2018). While this approach has been used widely in medicine and social sciences, applications in ecology and conservation are still rare (Cinner et al., 2016; Frei et al., 2018). Applied to species conservation this approach entails identifying those social-ecological conditions in which a species is likely to persist.

Primates are a taxon that is strongly impacted by anthropogenic factors, and despite their social, cultural, and ecological importance, most populations are severely threatened (Estrada et al., 2017). However, evidence on the effectiveness of conservation interventions for primates remains scarce (Junker et al., 2017). Nonetheless, some primates, and great apes in particular, seem to be able to adapt to and persist in anthropologically impacted landscapes (Hockings et al., 2015; McCarthy et al., 2017; Spehar et al., 2018). The identification of conditions that are enabling species persistence can guide the design of conservation interventions that are mimicking these favorable conditions.

Here we focus on the western chimpanzee (*Pan troglodytes verus*), that occurs in a variety of social-ecological landscapes, meaning that different combinations of biophysical and socio-economic variables characterize their range (Liu et al., 2007). For example, western chimpanzees occur in isolated patches of intact habitat surrounded by human-dominated areas (e.g., Nimba mountains), protected primary rainforest (e.g., Taï National Park), or in agricultural landscapes with forest remnants (e.g., parts of Sierra Leone). A recent evaluation of their status showed a dramatic decline in abundance of 80% and a range reduction of 20% since 1990 (Kühl et al., 2017). This resulted in the up-listing of the species' IUCN status to Critically Endangered (Humle et al., 2016). However, from the 20 sites for which longitudinal data were available, Kühl et al. (2017) found that three sites were exceptions to the general trend of population decline, with two sites in Guinea and one in Côte d'Ivoire seeming to support stable populations. The aim of this study was to apply the positive deviance approach across the entire range of western chimpanzees, to identify social-ecological conditions that might enable chimpanzee persistence. For this we compiled a range-wide dataset of chimpanzee densities, identified drivers of chimpanzee density, and characterized social-ecological conditions across 66 sites.

METHODS

General Workflow

We compiled a western chimpanzee density dataset covering the entire range of this taxon and extracted publicly available social-ecological data for all surveyed sites. We first determined which of the factors influenced chimpanzee densities significantly by fitting a Generalized Linear Mixed Model (McCullagh and Nelder, 1989; Baayen, 2008). After the model established which factors influenced chimpanzee densities significantly, we compared the configuration of significant social-ecological factors across a total of 66 sites.

Statistical Modeling

Model Response and Offset Term

Great ape density estimates are usually based on the counting of nests they built as resting places, instead of counting individuals themselves. Nests are more visible, more numerous, and do not move, meaning that there is no correlation between detectability of nests and intensity of threats (Kühl et al., 2008). Following a procedure that is commonly used for modeling ape densities, we used number of nests per transect as the model response and constructed an offset term to let the model output directly express chimpanzee densities (Murai et al., 2013; Wich et al., 2016; Voigt et al., 2018).

The number of nests was derived from chimpanzee nest surveys. In total we compiled 52 chimpanzee nest surveys across nine countries (**Figure 1**, **Supplementary Table 1**) via the IUCN SSC A.P.E.S. database (Kühl et al., 2007). These included line transect and reconnaissance surveys (Kühl et al., 2008) conducted between 2001 and 2015. We only included reconnaissance surveys for which the survey effort was known, based on GPS tracklog data. The entire dataset consisted of 17,109 transect or reconnaissance segments (hereafter referred to as "transect") with a total survey effort of 10,929 km (mean transect length: 0.64 km, range: 0.02–14.00 km).

The offset term (McCullagh and Nelder, 1989) was calculated as $D = N/(2^{*}L^{*}ESW^{*}p^{*}r^{*}t)$ where D is chimpanzee density, N number of nests, L transect length, ESW effective strip width, p proportion of nest builders, r nest production rate, and t nest decay time (Kühl et al., 2008). Hence, the offset term in the model was the log of the denominator of the above equation [i.e., $log(2^{*}L^{*}ESW^{*}p^{*}r^{*}t)$].

To determine the ESW we only used nests for which the perpendicular distance from the transect line was recorded ($n = 12{,}728$ nests), meaning that we did not use nest observations from reconnaissance surveys for this specific analysis. We determined the ESW separately for different habitat types to account for varying nest detectability due to habitat type. For nest observations the habitat type was typically recorded during the survey. To standardize habitat types across datasets we assigned them to the land cover categories defined by the Global land cover dataset (Friedl et al., 2010), namely "evergreen broadleaf forest," "mixed forest," "permanent wetlands," "woody savanna," "savanna," "croplands," "cropland natural vegetation mosaic." For <10% of nest observations the habitat was not recorded during the survey, and we extracted habitat type from satellite data (Global land cover dataset, Friedl et al., 2010). To get approximately balanced sample sizes for each habitat type we pooled habitat type to three categories: forest ("evergreen broadleaf forest," "mixed forest," "permanent wetlands"), savanna ("savannah," "woody savannah," "closed shrubland"), and cropland ("cropland," "cropland/natural vegetation mosaic"). We determined the ESW using DISTANCE (6.2 Release 1, Thomas et al., 2010, further details in Supplementary Material, **Supplementary Tables 2**, **3**, **Supplementary Figure 1**). We then extracted the habitat type for an area of 0.5 km around each transect from the Global land cover dataset (Friedl et al., 2010), and used the same assignment to the three habitat categories as above. Lastly, we assigned the habitat-specific ESW to each transect. ESW assignment for transects that traversed more than one habitat type was based on a majority vote.

Nest decay times vary between sites and seasons and are influenced by rainfall (Walsh and White, 2005; Kühl et al., 2008; Kouakou et al., 2009). Hence, we first fitted models to determine the mean nest decay time separately for each of the eight nest decay datasets and then fitted a separate model to estimate decay time as a function of rainfall. We then assigned a nest decay time to each transect based on that model and the mean rainfall at the respective transect. The model revealed a minimum fitted decay time of 85.45 days and a maximum fitted decay time of 229.03 days. Model uncertainty was assessed by deriving 10,000 bootstraps (additional details on nest decay methods and results in **Supplementary Tables 4, 5**, **Supplementary Figures 2**, **3**). We used a proportion of nest builders of 0.83 (Plumptre and Cox, 2006) and a nest production rate of 1.143 (Kouakou et al., 2009).

Model Predictors

We modeled chimpanzee density as a function of different social-ecological factors relevant for chimpanzee abundance, such as habitat, climate, topography, and socio-economic context. For this we used 19 predictor datasets that were available for the entire study area (predictor descriptions, temporal and spatial resolution of datasets detailed in **Table 1**). For quantitative predictors we calculated the mean of values within a fixed extraction radius around each transect, and for categorical predictors we determined the proportion of each category within the extraction radius. We transformed predictors when necessary to derive approximately symmetric distributions (details on predictor data extraction, transformation, and post-processing in **Supplementary Table 6**).

Spearman correlations among predictors indicated that some predictors were highly interrelated (**Supplementary Table 7**); hence, we used factor analyses to reduce redundancy among them, which resulted in three factors. On the factor that we termed "environment" *tree cover* and *vegetation height* loaded negatively, while *savanna*, *temperature,* and *rainfall seasonality* loaded positively (**Supplementary Table 8**). On the factor termed "socio-economic status" *education* and *corruption control* loaded positively, while *poverty* and *malnourishment* loaded negatively. On the factor termed "human activity" *settlements*, *human density*, *nighttime light,* and *conflicts* loaded positively (details on factor analyses in **Supplementary Table 9**). We did not include the variables *cropland*, *forest loss*, *hunting taboo*, *slope*, *river,* and *road* in the factor analyses either because they did not load strongly on any factor with Eigenvalue ≥1, or because it was the only predictor that loaded strongly on a factor. We therefore included them as separate predictors in the model.

We differentiated between test and control predictors (Mundry, 2014), and included 13 model terms as test predictors into the model (details on anticipated effects, also for interactions and squared terms, in **Table 2**). Distance to the closest river and

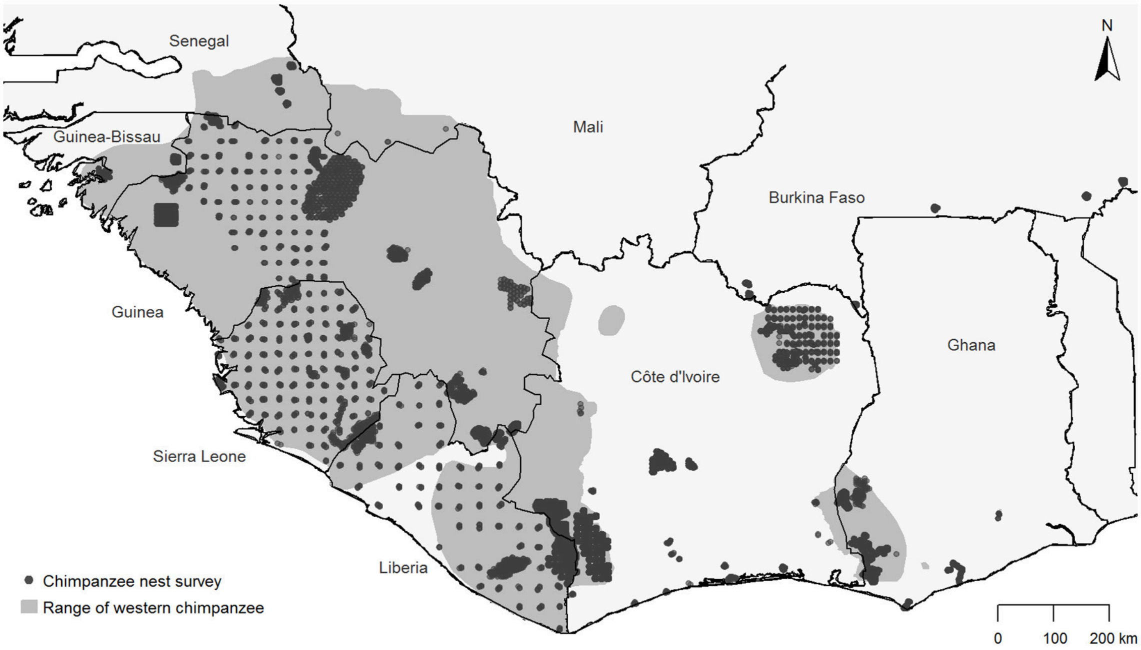

FIGURE 1 | Location of the 52 chimpanzee nest surveys compiled for this study and the geographic range of western chimpanzees (Humle et al., 2016).

road were included as control predictors, because they are known to influence animal densities (Boesch et al., 2017). All predictors were standardized to a mean of zero and a standard deviation of one to facilitate comparability of model parameters and ease interpretation of interactions (Schielzeth, 2010).

Model Implementation

We fitted a Generalized Linear Mixed Model (McCullagh and Nelder, 1989; Baayen, 2008) with a negative binomial error distribution and log link function, because the response was highly skewed with no nest observations on most transects (90.24%) and a large number of nests on some transects (range number of nests per transect: 0–430). The latter speaks against a Poisson distribution. With ape surveys being very cost and time intensive, they are usually targeted toward areas with possible chimpanzee presence, and hence we decided against a zero-inflated error distribution.

We included an autocorrelation term into the model to account for spatial autocorrelation, i.e., nest counts from transects that were closer to one another were more similar, even after accounting for the predictors in the model, and therefore the model residuals were not independent (details on implementation in **Supplementary Material**). The full model was:

number of nests per transect ∼ cropland + date + environment + forest loss + human activity + hunting taboo + slope + socio-economic status + socio-economic status ^{2} + human activity:hunting taboo + human activity:slope + human activity:socio-economic status + human activity:socio-economic status ^{2} + hunting taboo:slope + hunting taboo:socio-economic status + hunting taboo:socio-economic status ^{2} + river + road + spatial autocorrelation + offset term.

Chimpanzee densities are likely to differ among countries. This can be due to past events, for example chimpanzee densities are likely to be lower in Sierra Leone due to excessive chimpanzee captures in the 70's and 80's (Hanson-Alp et al., 2003). To account for these between-country differences and to control for the non-independence of data points from the same country, i.e., pseudoreplication, we included country as a random effect.

Additionally, the strength of effects can differ among countries, i.e., the slopes of the response against the predictor. For example, in a country with high poaching intensity, forests have lower than expected mammal densities, so that the positive effect of forests on mammal density will be smaller than in a country with less intense poaching. Such country-specific differences in poaching intensity can have many reasons among which could be differences in law enforcement capacity, or access to alternative protein sources or livelihoods. Consequently, we included the random slopes of all predictors within country (Schielzeth and Forstmeier, 2009; Barr et al., 2013).

The check of model assumptions revealed overdispersion (dispersion parameter = 1.71), causing standard errors to be underestimated. We corrected for this by adjusting the estimated standard errors and then re-determining *z*- and *p*-values (Gelman and Hill, 2007). We also tested for multicollinearity and found that it was not an issue (details on implementation in **Supplementary Material**, **Supplementary Table 10**, **Supplementary Figure 4**).

To test the significance of fixed effects as a whole, we compared the fit of the full model with that of a null model lacking all test predictors, but comprising the same control predictors

TABLE 1 | Dataset sources for predictors in the statistical model.

Predictor	Dataset	Variable used	References	Temporal resolution*	Spatial resolution
Conflicts	Armed Conflict Location and Event Data project (ACLED)	Location of violent conflicts	Raleigh et al., 2010	1997–2015 (continuous)	Point locations
Corruption control	Worldwide governance indicators	Control of corruption (measures perception of extent of corruption, ranges from −2.5 to 2.5)	World Bank, 2015	2000–2014 (annually, not 2001)	Country
Cropland	Global land cover MCD12Q1	Land cover classified as "cropland" and "cropland/natural vegetation mosaic"	Friedl et al., 2010	2001–2012 (annually)	0.5 km
Education	Sub-national African education and infrastructure access data	Net secondary attendance rate (proportion of children attending secondary school)	CCAPS, 2013	year of DHS/MICS survey (2005-2011)	Subnational region
Forest loss	Global forest change—forest loss year	Year of forest cover loss	Hansen et al., 2013	2000-2014 (annually)	0.03 km
Human density	AfriPop	Estimated number of people	Linard et al., 2012	2010	0.0083° (ca. 0.10 km)
Hunting taboo	World religion database based on USAID demographic and health survey (DHS)	Proportion of Muslims	Johnson and Grim, 2008	most recent DHS survey available in database (2003–2008)	Subnational region
Malnourishment	World Health Organization Global Database on Child Growth and Malnutrition	Prevalence of stunting among 0–5 year-old children (stunting is the result of suboptimal health and/or nutritional conditions)	de Onis and Blössner, 2003	1992–2013 (1–6 datasets per region)	Subnational region
Nighttime light	Nighttime lights composite	Stable lights (presence of lighting, is associated with intensity of economic activity, integer scale from 0 to 63)	NOAA, 2013	2000–2013 (annually)	30 arc s (ca. 1.00 km)
Poverty	Multidimensional poverty index 2015 [based on most recent USAID demographic and health survey (DHS) and UNICEF multiple indicator cluster survey (MICS)]	Poverty index (ranges from 0 to 1)	Alkire and Robles, 2015	most recent DHS or MICS survey (2006–2014)	Subnational region
Rainfall	Tropical rainfall measuring mission (TRMM) 3B43	Rainfall	TRMM and GES DISC, 2011	Jan 2000–Oct 2015 (monthly)	0.25°
River	River-surface water body network (RWDB2)	Location of rivers	FAO, 2007	2006	Vector map
Road	Roads of the world (Vmap0)	Location of roads	FAO, 2005	1997	Vector map
Savanna	Global land cover MCD12Q1	Land cover classified as "savannah," "woody savannah," "open shrubland," or "closed shrubland"	Friedl et al., 2010	2001–2012 (annually)	0.50 km
Settlements	Global urban footprint	Land cover classified as built-up area	Esch et al., 2012	2011/2012	0.084 km
Slope	Global multi-resolution terrain elevation data (GMTED2010)	Slope (derived as maximum elevation change between a cell and its eight neighbors)	Danielson and Gesch, 2011	2010	7.5 arc s (ca. 0.25 km)
Temperature	Land surface temperature and emissivity MOD11B3	Day time land surface temperature	Wan and Hulley, 2015	Feb 2000–Dec 2011 (monthly)	6.00 km
Tree cover	Vegetation continuous fields MOD44B	% tree cover	DiMiceli et al., 2011	2000-2010 (annually)	0.25 km
Vegetation height	Vegetation height estimate	Average vegetation height	Woods Hole Research Center, 2007	2007	0.03 km

"most recent" refers to the latest data point prior to when the area was surveyed.

TABLE 2 | Anticipated effects of model terms included as test predictors into the model.

Model term*	Anticipated effect	Explanation/hypothesis
Cropland	negative	Land-use conversion to cropland results in habitat loss and fragmentation. It also increases contact between humans and chimpanzees, e.g., when chimpanzees feed on crops, increasing the likelihood of conflict or disease transmission.
Date	negative	Chimpanzee populations have continuously declined over the last decades Kühl et al., 2017.
Environment	negative	*Tree cover* and *vegetation height* loaded negatively on this factor, and *savanna*, *temperature* and *rainfall seasonality loaded* positively, i.e., low values of this factor indicate rainforest conditions and high values indicate savanna conditions. It can be expected that chimpanzee densities are lower in savanna than in forest habitat due to differences in resource availability.
Forest loss	negative	Forest loss leads to habitat loss and fragmentation. It entails secondary threats such as increased bush meat hunting around settlements in resource concessions.
Human activity	negative	*Conflicts, human density, nighttime light,* and *settlements* loaded positively on this factor. Increased intensity of human activity leads to increased resource use which negatively influences chimpanzees.
Hunting taboo	positive	Due to cultural traditions Muslims are less likely to kill great apes for food than non-Muslims Davis et al., 2013. In areas with a higher proportion of Muslims there is a higher prevalence of cultural taboos against eating chimpanzee meat Ham and Carter, 1998.
Slope	positive	Steep terrain is characterized by less anthropogenic disturbances and could serve as a refuge area for chimpanzees.
Socio-economic status^2	positive quadratic	*Education* and *corruption control* loaded positively on this factor, and *poverty* and *malnourishment* loaded negatively. Improvement of the socio-economic status, e.g., economic development, is often accompanied by an increase in resource use resulting in environmental degradation. Based on the concept of the environmental Kuznets curve Mills and Waite, 2009, further economic growth might allow a community or country to invest into environmental protection.
Human activity : Hunting taboo	positive	The effect of hunting taboos increases when the intensity of human activity increases, because in areas with a very low intensity of human activity the pressure on chimpanzees might be too low to reveal the positive effect of hunting taboos.
Human activity : Slope	positive	The effect of steep terrain as a refuge area increases with increasing intensity of human activity in surrounding areas.
Human activity : Socio-economic status^2	positive quadratic	The effect of socio-economic status increases with increasing intensity of human activity, because in areas with a low intensity of human activity the pressure on chimpanzees might be too low to reveal an effect of socio-economic status.
Hunting taboo : Slope	positive	The effect of steep terrain as a refuge area increases with decreasing hunting pressure, because the positive effect of steep terrain might not be observable in areas with very strong hunting pressure.
Hunting taboo : Socio-economic status^2	positive quadratic	In areas with a high prevalence of hunting taboos changes in socio-economic conditions might impact chimpanzee densities, while there could be no such effect in areas without hunting taboos.

**Model term followed by superscripted 2 refers to a squared term.*

and random effects structure as the full model (Forstmeier and Schielzeth, 2011) using a likelihood ratio test (Dobson and Barnett, 2008). All models were fitted with the R function "glmer.nb" of the R package "lme4" (version 1.1–11, Bates et al., 2015). Model stability was assessed by comparing model estimates based on all data, with model estimates based on data excluding countries one at a time. The model was stable regarding the effects of all significant predictors (minimum and maximum estimates in **Table 3**). To derive confidence limits, we fitted parametric bootstraps. For this, we randomly selected one nest decay bootstrap, determined the fitted nest decay rate, and derived an adjusted offset term. We then fitted the full model with the new offset term and derived one bootstrap with the R function "bootMer" (package "lme4"). This was repeated 1,000 times. Unless specified otherwise, all analyses were implemented in R (version 3.2.3, R Core Team, 2015).

Characterization of Positive Deviant Sites

We assigned the transects to 19 of the 20 sites delineated in the previous study on western chimpanzee population trends (Kühl et al., 2017). We did not have data for Mount Péko in Côte d'Ivoire, but it is thought that chimpanzees are now extirpated there (Kühl et al., 2017). The remaining transects covered 47 additional sites, usually according to protected area delineation. For each of the total 66 sites and each factor that was significant in the statistical model we calculated the median, lower and upper quartile of the predictor variable. We then compared characteristics for the three sites that were previously identified as having stable populations, namely Fouta Djallon and Sangaredi in Guinea and Cavally in Côte d'Ivoire (Kühl et al., 2017). We also analyzed sites with transects that deviated by more than two standard deviations from the mean chimpanzee density of transects with chimpanzee presence, as suggested by Post and Geldmann (2018). Due to lower densities of feeding trees, chimpanzee densities are naturally lower in savanna-mosaics than in rainforest habitat (Pruetz and Bertolani, 2009). As chimpanzees have adapted to these challenging conditions (Wessling et al., 2018a,b), low chimpanzee densities in these habitats do not imply population decline. We therefore, focus interpretation of results on populations which have been shown

TABLE 3 | Results of the full model to identify drivers of chimpanzee densities (Generalized Linear Mixed Model, $n = 17{,}109$).

Predictor[a]	Estimate	SE	z	p	$\mathrm{SE}_{\mathrm{cor}}$[b]	z_{cor}[b]	p_{cor}[b]	min[c]	max[c]	$\mathrm{CL}_{\mathrm{lower}}$[d]	$\mathrm{CL}_{\mathrm{upper}}$[d]
Intercept	−3.176	0.761	[e]	[e]	0.995	[e]	[e]	−3.783	−2.765	−4.359	−2.101
Cropland	−0.160	0.231	−0.695	0.487	0.301	−0.532	0.595	−0.507	0.009	−0.689	0.302
Date	−0.390	0.291	−1.338	0.181	0.381	−1.023	0.306	−0.586	−0.255	−1.075	0.246
Environment	−1.037	0.414	−2.501	0.012	0.542	−1.913	0.056	−1.649	−0.789	−2.312	−0.302
Forest loss	−0.571	0.085	−6.736	< 0.001	0.111	−5.152	< 0.001	−0.681	−0.496	−0.743	−0.399
Human activity	−0.009	0.136	[e]	[e]	0.178	[e]	[e]	−0.462	0.256	−0.216	0.349
Hunting taboo	0.385	0.424	[e]	[e]	0.554	[e]	[e]	−0.058	1.201	−0.250	1.645
Slope	0.490	0.200	[e]	[e]	0.261	[e]	[e]	0.225	0.594	0.072	0.869
Socio-economic status	0.469	0.239	[e]	[e]	0.313	[e]	[e]	−0.578	0.463	−1.510	1.081
Socio-economic status^2	−0.259	0.232	[e]	[e]	0.304	[e]	[e]	−0.632	0.050	−0.963	0.399
Human activity : hunting taboo	−0.302	0.099	−3.053	0.002	0.130	−2.335	0.020	−0.430	−0.052	−0.531	−0.078
Human activity : slope	0.175	0.050	3.476	0.001	0.066	2.658	0.008	−0.050	0.259	0.042	0.283
Human activity : socio-economic status	−0.047	0.126	−0.370	0.711	0.165	−0.283	[e]	−0.096	0.333	−0.301	0.321
Human activity : socio-economic status ^{2}	0.004	0.098	0.040	0.968	0.128	0.031	0.976	−0.166	0.310	−0.289	0.189
Hunting taboo : slope	0.217	0.102	2.118	0.034	0.134	1.620	0.105	0.162	0.291	−0.064	0.472
Hunting taboo : socio-economic status	0.122	0.313	0.389	0.697	0.409	0.298	[e]	−0.298	0.548	−0.632	0.953
Hunting taboo : socio-economic status^2	0.504	0.207	2.437	0.015	0.271	1.864	0.062	0.054	0.692	−0.084	0.939
River [f]	−0.419	0.130	−3.228	0.001	0.170	−2.469	0.014	−0.533	−0.328	−0.683	−0.124
Road [f]	0.013	0.140	0.095	0.924	0.184	0.073	0.942	−0.039	0.124	−0.284	0.329
Spatial autocorrelation [f]	0.704	0.074	9.502	< 0.001	0.097	7.267	< 0.001	0.660	0.756	0.532	0.852

[a] *All predictors were z-transformed to a mean of zero and a standard deviation of one (mean and sd of predictors before being z-transformed in* ***Supplementary Table 13****).*

[b] *Corrected for overdispersion.*

[c] *Minimum and maximum value of model stability.*

[d] *95% confidence limits.*

[e] *P- and z-values not shown for intercept and model terms that are conditional on other model terms because of very limited interpretation.*

[f] *Control predictor.*

to have remained stable (Kühl et al., 2017) and also ordered sites in **Figure 3** according to environmental conditions.

RESULTS

In total, 13,464 nests were recorded. Estimated chimpanzee density ranged between 0.00 and 46.33 individuals/km^2, with average densities of 0.14 ± 0.93 individuals/km^2 (mean ± SD) across all transects and average densities of 1.42 ± 2.67 individuals/km^2 on transects with chimpanzee presence.

Statistical Model

The full model explained chimpanzee density significantly better than the null model (likelihood ratio test comparing full model and null model without test predictors: $\chi^2 = 40.28$, df $=$ 16, $p < 0.001$, model results in **Table 3**, random effects and random slopes in **Supplementary Tables 11**, **12**). The factor "environment" had a marginally significant negative effect, with lower chimpanzee densities in dry and sparsely forested areas, and higher chimpanzee densities in rainforest habitat (**Table 3**). "Forest loss" had a significant negative effect on chimpanzee density. Except for two transects in Marahoué National Park, Côte d'Ivoire, chimpanzee nests were only found on transects with <10% forest loss (**Figure 2A**). We also found a positive synergistic effect of human activity and slope. Chimpanzee densities were higher in areas with low intensities of human activity. However, in areas characterized by relatively high intensities of human activity, chimpanzee densities were higher in steeper terrain (**Figure 2B**). There was also a positive synergistic effect of human activity and hunting taboo, with the highest chimpanzee densities in areas with a high prevalence of hunting taboos and low degree of human activity. Socio-economic status had no significant effect (**Table 3**), i.e., chimpanzee density was not significantly influenced by education, poverty or malnourishment levels. Cropland did not have a significant effect on chimpanzee densities, but highest densities were recorded on transects with <25% cropland. Overall, absolute model estimates showed that the factor "environment" had the strongest influence on chimpanzee densities, followed by "forest loss" and "slope".

Characteristics of Positive Deviant Sites

In addition to the three sites identified as exceptional based on stable populations in a previous study (Kühl et al., 2017), we identified five sites with transects with very high estimated chimpanzee densities (>6.76 individuals/km^2 corresponding to the mean+2SD), namely Tai (Côte d'Ivoire), Grebo (Liberia), Nimba (Côte d'Ivoire and Guinea part), and Boé (Guinea-Bissau, **Figure 3**, **Supplementary Figure 5**). Characterization of those sites could be grouped into three social-ecological configurations. The first group was characterized by rainforest habitats with low degree of forest loss and low intensity of human activity,

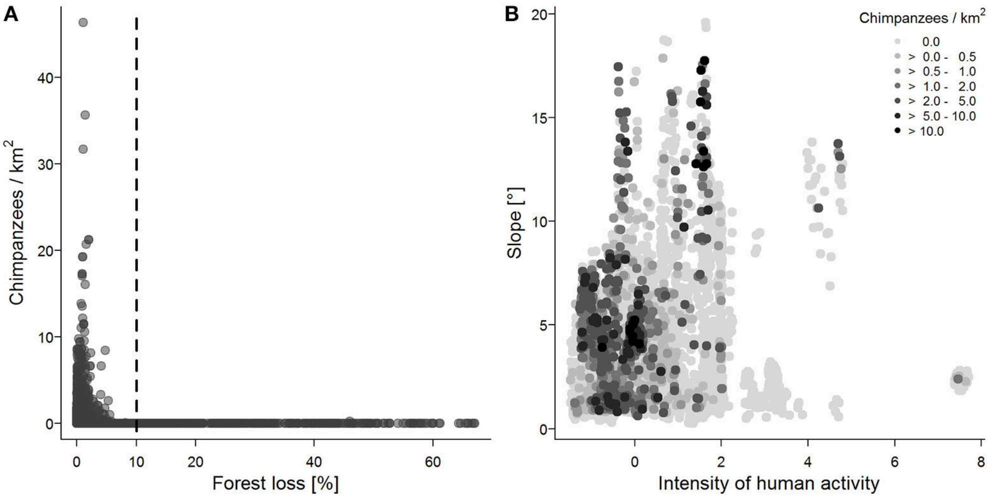

FIGURE 2 | Chimpanzee density as a function of **(A)** forest loss (data points drawn in transparent colors to visualize overlapping points), and **(B)** slope and human activity. Chimpanzee nests were found on transects with <10% forest loss (dashed vertical line). Chimpanzees mainly occurred on transects with low intensity of human activity, but in areas with higher human activity higher chimpanzee densities were found in steeper areas, i.e., a refuge effect.

e.g., Cavally (Côte d'Ivoire), Grebo (Liberia), and Tai (Côte d'Ivoire). The second group was characterized by steep terrain, e.g., Nimba mountains in Guinea and Côte d'Ivoire. The third was characterized by a high prevalence of hunting taboos and low intensity of human activity, e.g., Boé in Guinea-Bissau, and Fouta Djallon and Sangaredi in Guinea (**Figure 3**). Nimba (Liberian part), Gola (Sierra Leone), and Goin-Débé (Côte d'Ivoire) also each had one transect with exceptionally high chimpanzee densities, but as this was only one transect each, we did not base any conclusions on these three sites.

DISCUSSION

In our study we found that three configurations of social-ecological factors enabled chimpanzee persistence: rainforest habitat with low degree of human impact, steep areas, and areas with a high prevalence of hunting taboos and low degree of human impact. While the conditions of the first and second configuration are mirrored in conservation interventions aiming at threat exclusion, such as the expansion of protected areas and law enforcement, conservation interventions focusing on threat reduction, as reflected in the third configuration, are still very rare in primate conservation.

Social-Ecological Conditions Enabling Chimpanzee Persistence

The results underlined the importance of intact habitat for chimpanzee persistence, as chimpanzees seemed to only be able to tolerate a surprisingly low threshold of a maximum of 10% forest loss (**Figure 2A**). Habitat loss not only implies a loss of feeding and nesting trees, but often also an increase in other disturbances, such as hunting or human-wildlife conflicts (Estrada et al., 2017). This is in line with previous findings that chimpanzees are sensitive to habitat disturbance (Junker et al., 2015; Morgan et al., 2018). At those sites in our dataset for which we found high forest loss levels, such as Monogaga (median forest loss: 40.88%), Duékoué (14.19%) and Marahoué (15.20%) in Côte d'Ivoire, chimpanzees are now thought to be extirpated (Campbell et al., 2008; Kühl et al., 2017). In contrast, median forest loss ranged between 0.09 and 1.51% at sites with exceptional chimpanzee densities. Consequently, very low levels of forest loss seem to be a prerequisite for chimpanzee persistence.

Regarding the three social-ecological configurations enabling chimpanzee persistence, we first found exceptionally high chimpanzee densities at rainforest sites with low human activity. The low level of human activity in some of these areas is due to conservation interventions, such as law enforcement, presence of researchers and NGOs, which have a scientifically proven positive effect on great ape persistence (Campbell et al., 2011; Tranquilli et al., 2012; Tagg et al., 2015). For other sites in this category, the relative remoteness and the large distances to the next city (Weiss et al., 2018) might have enabled chimpanzee persistence, as it has been shown that increased market integration has a negative influence on chimpanzee densities (Boesch et al., 2017).

Second, exceptionally high chimpanzee densities were found in steep terrain, especially when surrounding areas were strongly impacted by humans (**Figure 2B**). The steep terrain likely reduced access for humans, as has been found elsewhere (Adanu et al., 2011; Sesink Clee et al., 2015), and such areas are less favorable for conversion to other land-uses (Kinnaird et al., 2003; Silva et al., 2007), so that they seem to function as refuge areas for chimpanzees. In savanna environments, steep terrain also seem to be favored sleeping sites due to the higher tree cover and access to water sources (Pintea and Plumptre, 2006). Consequently, individual transects with very high densities may indicate favored sleeping sites, while surrounding areas are likely characterized by less favorable conditions. For those sites in

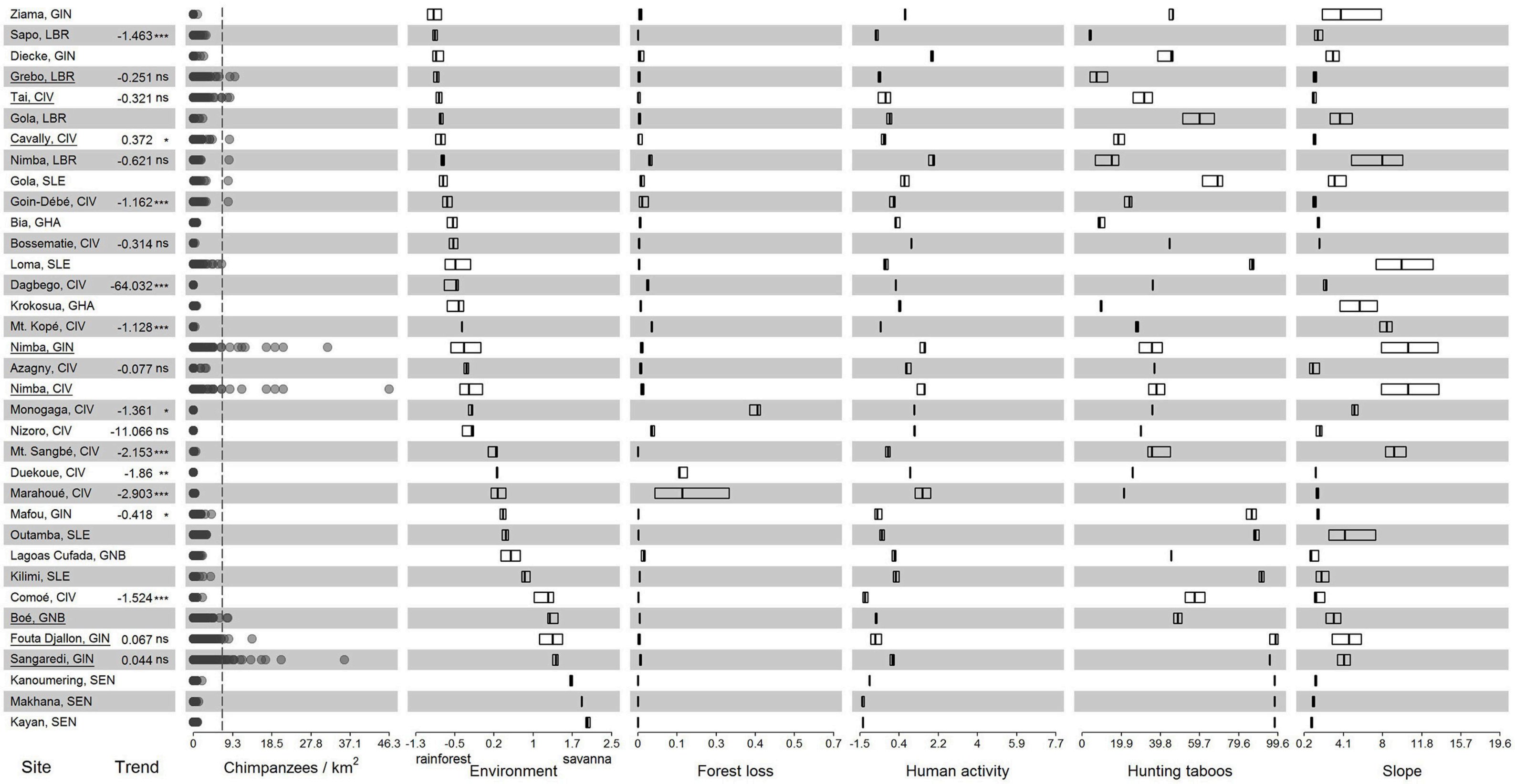

FIGURE 3 | Chimpanzee densities and significant factors from statistical model plotted for all sites analyzed in Kühl et al. (2017) and additional sites included in our dataset (additional sites **Supplementary Figure 5**) all sorted according to environment from rainforest habitat (top) to savanna habitat (bottom). Positive deviant sites are underlined. Population trend estimates are based on Kühl et al. (2017) and were only available for certain sites. In the chimpanzee density panel data points are drawn in transparent gray, so that overlapping data points appear in a darker shade, meaning sites with low chimpanzee density do not necessarily have less data points. The vertical dashed line in the chimpanzee density panel marks the threshold for exceptional density [6.76 individuals/km^2 corresponding to the mean + 2SD as suggested by Post and Geldmann (2018)]. Due to the data being based on nest count surveys individual transects with very high chimpanzee densities likely indicate favored sleeping sites, while surrounding areas are likely characterized by less favorable conditions. Horizontal axes depict the range of values in the dataset. Bars represent the lower and upper quartiles and thick vertical lines the median. Country names are abbreviated as CIV, Côte d'Ivoire; GHA, Ghana; GIN, Guinea; GNB, Guinea-Bissau; LBR, Liberia; SEN, Senegal and SLE, Sierra Leone.

our dataset with steep terrain and high chimpanzee densities, including the Nimba mountains in Guinea and Côte d'Ivoire, and to a lesser extent Loma mountains in Sierra Leone, the population trend is not known. Chimpanzees might be restricted to small refuge areas, and their long-term survival at those refuges could be constrained due to reduced dispersal possibilities and increased vulnerability, for example to diseases. This is illustrated by examples from Côte d'Ivoire such as Mount Kopé and Mount Sangbé for which strong population declines have been shown (Kühl et al., 2017). While these mountains are isolated areas of steep terrain, there are regions where extensive areas are characterized by relatively steep slopes, for example the Fouta Djallon (**Figure 3**, **Supplementary Figure 6**). Here, loss in dispersal ability is less likely to be of concern for chimpanzee survival. In addition, mineral exploitation poses a threat as mountains often contain mineral deposits, and several mining sites operate in the Nimba mountains, entailing further threats to wildlife such as infrastructure expansion (Edwards et al., 2014).

The third social-ecological configuration was characterized by relatively low levels of human activity in combination with a high prevalence of hunting taboos at sites characterized by higher proportions of savanna habitat. It was surprising to find that this group of sites not only has seemingly stable populations (Kühl et al., 2017), but also exceptionally high chimpanzee densities, despite the fact that our analysis showed that overall chimpanzee densities are lower in savanna areas compared to rainforest areas (**Table 3**). It appears that the adherence to hunting taboos by humans reduced hunting pressure on chimpanzees, and thereby the key threat to chimpanzees was removed. This is in accordance with a site-based sociological study from Côte d'Ivoire that showed that people adhering to hunting taboos generally do not eat primate meat (Bachmann et al. submitted). These important chimpanzee areas are now partly protected by the recently established Boé National Park (Guinea-Bissau) and the Moyen Bafing National Park (Guinea) that is currently being created. However, large-scale open pit mining is underway at Sangaredi (Guinea), and the current status of the chimpanzee communities there is unclear.

However, there are exceptions to these patterns, i.e., there are sites which are characterized by one of the above-mentioned combination of factors but still have low chimpanzee densities or decreasing populations. This shows that additional factors for which data were not available across the entire study area and could therefore not be included in our analysis might influence chimpanzee persistence, for example absence of diseases (Ryan and Walsh, 2011). Also, historic events, such as intensive hunting in the past at specific sites (Hanson-Alp et al., 2003), might influence current chimpanzee densities. Due to their slow life history apes are especially susceptible to such threats and communities can take decades to recover from single mortality events (Ryan and Walsh, 2011). In addition, due their behavioral flexibility, chimpanzees might be able to adapt to savanna and anthropogenic habitat mosaics and persist there long-term, though likely at lower densities (Hockings et al., 2015). For example, it has been shown that although chimpanzees at Fongoli, Senegal, a site with strong seasonality in temperature and rainfall, experience heat and dehydration stress, chimpanzees likely developed mechanisms for avoiding costs of energetic constraint (Wessling et al., 2018b). However, these types of landscapes are still less surveyed, and longitudinal data from more sites are needed to determine the population trend, especially from Guinea-Bissau, Mali, Senegal, and Sierra Leone for which such data are lacking. Consequently, this study can only be regarded as a first step and follow-up studies are needed to substantiate our findings.

Threat Reduction Through Behavioral Change

Our study revealed three factors having a positive effect on chimpanzee densities; habitat protection, reduced accessibility, and hunting taboos. The first two factors are already reflected in commonly implemented conservation interventions, such as protected areas, law enforcement, and the presence of researchers, NGOs and tourism activities, which have also been shown to have a positive effect on ape persistence (Campbell et al., 2011; Tranquilli et al., 2012; Strindberg et al., 2018). The mechanism underlying those activities is threat exclusion, meaning threats are excluded from delineated areas. In contrast, the positive effect of hunting taboos is based on a different mechanism, namely the reduction of a threat, in this case due to a particular human behavior. While threat exclusion addresses the symptoms of conservation challenges, threat reduction aims to focus on the root causes. Previous studies argued that for conservation to be successful, threats need to be actively reduced (Allison et al., 1998; Clout, 2001; Challender and MacMillan, 2014; Crees et al., 2016). Considering that only a small proportion of chimpanzees are living in protected areas (Kühl et al., 2017), conservation interventions reducing threats outside of protected areas are needed, that thereby also reduce the pressure on protected areas. However, in a recent compilation of available evidence for the effectiveness of conservation interventions for primates, the majority of interventions was aimed at threat exclusion, for example through protected areas, law enforcement, and species management (Junker et al., 2017). There is considerably less evidence for interventions targeting threat reduction (Junker et al., 2017).

While the positive effect of hunting taboos we found for chimpanzees cannot be directly transferred to other areas, conservation interventions mimicking these conditions could complement current conservation efforts. The positive effect of hunting taboos is a challenge for conservationists, because they generally have a religious or a supernatural basis, both in their origin and in their maintenance (Colding and Folke, 2001). While taboos can be strengthened or reinforced where they already exist (Junker et al., 2017), they cannot simply be introduced to other areas, where they never existed or disappeared. An additional concern is the loss of power of traditional taboos through modernization and migration, with people from different cultural or religious background being less likely to accept local taboos (Golden and Comaroff, 2015).

Mimicking hunting taboos would mean to reduce the demand for chimpanzees by consumers and discourage the supply by hunters and traders. From a consumer perspective, chimpanzees are not a notable protein source, and the provision of alternative protein sources is a common intervention aimed at reducing the economic incentive to consume bushmeat, including chimpanzee. Junker et al. (2015) have, for example, shown that affordable fish protein correlated positively with chimpanzee densities. Another important conservation intervention includes awareness raising activities, especially because in certain areas medicinal or magical properties are assigned to chimpanzee parts and chimpanzee bone powder (Hanson-Alp et al., 2003). There are studies that have shown a positive effect of such interventions on bushmeat consumption, for example in the context of repeated multimedia campaigns (Kouassi et al., 2017) and Ebola information campaigns (Ordaz-Németh et al., 2017). However, hunting chimpanzees is also strongly driven by a demand for chimpanzee parts and live animals from urban areas and even international markets (Kuehl et al., 2009; Greengrass, 2016; Strindberg et al., 2018). Awareness raising activities at national or even regional scale specifically targeting urban consumers is absent from West Africa, but could be an important tool to reduce the acceptability of chimpanzee consumption. Evidence from China suggests that an ambitious nation-wide awareness raising campaign championed by the most popular Chinese athlete, Yao Ming, resulted in a change in government policy and a strong decrease in shark fin demand across China (Whitcraft et al., 2014). In general, research on behavioral change in conservation highlights the need to go beyond awareness raising because often a change in awareness alone is not enough to lead to pro-environmental behavior (Schultz, 2011; Amel et al., 2017). Stakeholder co-designed behavioral change tools therefore try to identify barriers to behavioral change as well as providing benefits (Schultz, 2014). Successful examples of behavioral change interventions aimed at reducing bushmeat consumption include the so-called community-based social marketing tool, that has been implemented to reduce consumer demand for wild meat in a Brazilian town, and that explicitly identified and then reduced barriers to the consumption of domesticated meat (Chaves et al., 2018).

From a supplier perspective, chimpanzees are mostly killed or captured opportunistically, but because of their large size, hunters make high profits from a single catch, and young chimpanzees can be sold for the pet trade (Hanson-Alp et al., 2003). Even such single catches can have detrimental effects on chimpanzee populations due to their long time to maturation and long inter-birth intervals. As discussed above, law enforcement aiming to exclude hunters from certain areas often seems not to be sufficient, mainly due to the virtual impossibility of stopping every single hunter. Conservation interventions aiming at reducing chimpanzee supply are scarce, and here again stakeholder co-designed behavioral change tools might be a way forward to first understand what is driving certain behaviors and how hunters could be motivated to not kill or capture chimpanzees despite their high monetary value. While there is evidence that monetary and non-monetary benefits can have a positive effect on primate populations, there are also studies showing no effect (Junker et al., 2017). In addition, studies looking at the entire supply chain from individual hunters via traders to sellers have identified multiple entry points for conservation interventions (Bachmann et al., submitted).

Application of the Positive Deviance Approach to Other Study Systems and Challenges

The positive deviance approach can be a useful tool for conservation science because it focuses on identifying conditions or mechanisms that have already proven to work. While understanding threats to species is a prerequisite for conservation planning, solutions are often a lot less understood. The positive deviance approach allows directing research toward possible answers to conservation challenges. In general, this approach can be applied to any taxon, region and at different spatial scales, if matched with data of corresponding resolution and quality. Importantly, the spatial scale needs to be chosen so that there is sufficient variation along multiple predictor variables.

Similarly to Frei et al. (2018) who applied this approach to agricultural landscapes, we found that applying it to a specific species comes with several challenges. First, it is difficult to differentiate between the influence of historic and current conditions, i.e., past events such as disease outbreaks might have long-lasting effects on a population independent of current conditions. This is of particular concern for species with slow life histories. Second, the data, especially when it pertains to human behavior or socio-economic context, might not be available at a small resolution for a large area, which makes large-scale analyses difficult. Here, multi-scale studies might give additional insights. In general, many more studies using the positive deviance approach would be needed to determine whether this is truly a useful approach that can provide novel insights for species conservation.

CONCLUSIONS

Conservation interventions, especially for the conservation of primates, still largely focus on habitat protection and reducing accessibility for humans through protected areas and law enforcement. However, with about 80% of western chimpanzees living outside of high-level protected areas, i.e., national parks and strict nature reserves, the focus on excluding threats from delineated areas might not be sufficient to ensure the long-term survival of western chimpanzees. By using the positive deviance approach, we found high chimpanzee densities and seemingly stable population trends for sites with a high prevalence of hunting taboos, even though those areas were not set aside under any high-level protective status. This suggests that these enabling conditions can be mimicked by using stakeholder co-designed behavioral change approaches (Schultz, 2011, 2014; Chaves et al., 2018) to reduce hunting pressure and thereby complement current conservation interventions. While new behavioral change tools have been applied to different environmental problems, they remain largely absent from primate conservation (Junker et al., 2017). With a lot of organizations already working for the protection of chimpanzees across West Africa and the relatively strong support that chimpanzee protection garners within and outside its range, this might be an opportunity to pioneer and test new conservation approaches, which, if successful, could inform protection of other primates. Applications of the positive deviance approach to species conservation are still rare, and many more studies and methodological advancements would be needed to establish this method as a useful conservation science tool.

DATA AVAILABILITY

The raw data will be made available via the IUCN SSC A.P.E.S. database (http://apesportal.eva.mpg.de).

AUTHOR CONTRIBUTIONS

HK, SH, RM, and CB conceived and designed the study; SH and TS curated the data; SH and RM analyzed the data; SH and HK wrote the initial draft; all remaining authors contributed data, and provided comments on model formulation. All authors contributed to the reviewing and editing of the manuscript, and approved its submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00016/full#supplementary-material

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The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor declared a collaboration with two of the authors, JJ and HK.

Supplementary Material

Characteristics of positive deviants in western chimpanzee populations

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1 Data extraction and processing

1.1 Chimpanzee data

Transects longer than 1 km were split into sections of approximately 1 km to reduce predictor variation along a single transect. This could only be done for transects for which the spatial data for transect start and end were available. In total 1,838 transects were split.
For two recce datasets the tracklog data did not include timestamps. We connected consecutive GPS points and noticed that they were in a wrong order which resulted in an overestimation of survey effort (Supplementary Figure 7). Due to missing timestamps the original order of GPS points could not be restored. Hence, we chose an approach for all recce datasets, for which we first imposed a 0.5x0.5km grid on all connected tracklog data points and then determined which grid cells were surveyed. Grid cells with less than 0.1km walked therein were omitted because we assumed that these were an artefact of the above described wrong order of GPS points. For the remaining grid cells we assumed an effort of 0.5km. Supplementary Table 14 compares the survey effort reported in the study with the survey effort we estimated. For data extraction we used the spatial coordinates of the midpoint of each cell.

1.2 Nighttime light

The nighttime light dataset was collected using three different satellites (F15, F16, F18) for which the values are known to not be fully comparable (Doll 2008). We eliminated the effect of satellite by fitting a set of models with the aim to standardize the data to a given satellite (F18).
To derive models representative for the entire region, we derived a grid with a resolution of half a minute (ca. 0.9km) across the range of western chimpanzees covering a total area of ca. 1.58 mio km^2. We identified the coordinates of each cell center. For each cell (n=1,854,765) and transect (n=17,109) we extracted the mean nighttime light within 50 km of the midpoint

for the years 2000-2007 (F15), 2004-2009 (F16) and 2010-2013 (F18). We consequently had 18 values for each cell and transect (more details on data extraction Supplementary Table 6).
First we split the dataset for cells and transects into those where extracted values were zero in all 18 combinations of year and satellite, i.e., there was never any nighttime light ('never' data), those where extracted value were always larger than zero ('always' data), and the remainder ('sometimes' data). Year was z-transformed to a mean of zero and a standard deviation of one.
For the 'never' data there was no need to correct for not fully comparable values, and we simply set standardized nighttime light to zero. To determine the effect of satellite on the value of recorded light, we selected all combinations of cell/transect, year and satellite where extracted values were larger than zero from the 'always' and 'sometimes' data. We fitted a linear mixed model (LMM, Baayen 2008) with nighttime light (log-transformed) as the response; year, satellite and their interaction as fixed effects; year (as a factor) and cell/transect ID as random intercepts and year within cell/transect as random slope. We fitted the model using a Gaussian error structure and identity link.
To determine the effect of satellite on whether light was recorded or not, we fitted a Generalized linear mixed model (GLMM, Baayen 2008) to the ‘sometimes’ data with nighttime light as a binary response (yes/no). This model was identical to the above mentioned LMM, but we did not include the interaction between year and satellite because the model did not converge otherwise. This model was fitted using a logistic error structure and logit link function (McCullagh & Nelder 1989). From both models we extracted predicted values for satellite F18, whereby predicted values were extracted in probability space for the GLMM.
We finally derived the fitted nighttime light (assuming satellite F18) as follows: for the 'never' dataset we simply set it to zero; for the 'always' dataset we set it to the exponential of the predicted values from the LMM; and for the 'sometimes' data we set it to the product of the predicted values from the LMM exponentiated and the GLMM. Models were fitted using the functions lmer (LMM) and glmer (GLMM), respectively, of the R package lme4 (version 1.1-12, Bates et al. 2015).

1.3 Malnourishment data

The temporal resolution differed strongly between countries. We extracted one value for each year for which there were data in any of the datasets, i.e., 1992, 1993, 1994, 1995, 1998, 1999, 2000, 2001, 2003, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013. For each subnational region and year we extracted the value from the closest year that was available. For example, for Côte d’Ivoire we had data for the years 1994, 2006, 2011. So for the years 1992 to 2000 we extracted the values from the 1994 survey, for the years 2001 to 2008 from the 2006 survey and for 2009 to 2013 from the 2011 survey.

2 Factor analyses of predictor data

Spearman correlations among predictors indicated that some predictors were highly interrelated (Supplementary Table 7); hence, we used Factor Analyses (FA) to reduce redundancy among them. To retain explanatory value, we grouped thematically related predictor variables and ran two separate FAs using the R function ‘factanal’ with varimax rotation. We conducted one FA with habitat and climate predictors, i.e., tree cover, vegetation height, savanna, temperature and rainfall. The FA was justified as shown by the Kaiser-Meyer-Olkin measure of sampling adequacy (0.84) and Bartlett’s test of sphericity (χ^2=106,778, df=10, P<0.001, McGregor 1992). An initial Principal Component Analysis (PCA) revealed

that only one principal component had an Eigenvalue >1 and the following FA showed that all five predictors loaded strongly on one factor with an Eigenvalue of 4.06 (Supplementary Table 8). The variance explained by this factor was 81.27% and we termed this factor “environment”.
Into the second FA we included eight of the socio-economic predictors (Supplementary Table 9; Kaiser-Meyer-Olkin measure of sampling adequacy: 0.76, Bartlett’s test of sphericity: χ^2=100,299, df=28, P<0.001). The initial PCA revealed two principal components with an Eigenvalue >1 and the FA resulted in two factors with Eigenvalues of 3.03 and 2.31, respectively. Together the two factors explained 66.80% of the total variance. On the first factor education and corruption control loaded positively, while poverty and malnourishment loaded negatively. We termed this factor “socio-economic status”. On the second factor settlements, human density, nighttime light and conflicts loaded positively. We termed this factor “human activity”. For subsequent analyses the second factor was transformed as sqrt(x-min(x)) to derive an approximately symmetric distribution.
We did not include the variables cropland, forest loss, hunting taboo, slope, rivers, and roads in the FA because either they did not load strongly on any factor with Eigenvalue ≥ 1, or because it was the only predictor that loaded strongly on a factor. We therefore included them as separate predictors in the model.

3 Spatial autocorrelation

We included an autocorrelation term into the model to account for spatial autocorrelation, i.e., that nest counts from transects that were closer to one another were more similar, even after accounting for the predictors in the model, and therefore the model residuals were not independent. To obtain the autocorrelation term, we first extracted residuals for each data point from the full model. We then, separately for each data point, averaged the residuals of all other data points, each weighted by the spatial distance to the focal data point. The weight was normally distributed with a mean of zero and we derived the optimal standard deviation by maximizing the log-likelihood of the full model with the derived autocorrelation term included as an additional predictor.

4 Nest decay time

To convert chimpanzee nest density to chimpanzee density, nest decay times are needed. Nest decay times vary strongly between sites and seasons (Walsh & White 2005; Kühl et al. 2008), but because data collection is very laborious, only few studies exist. Instead researchers often rely on already published decay times and use one from a site similar in habitat or climatic characteristics, or the one that is spatially the closest. To assign decay times to transects across our entire study area using this approach would lead to arbitrary cut-off points, but decay times vary gradually across the region.
It has been shown that nest decay times are strongly influenced by rainfall (Walsh & White 2005; Kouakou et al. 2009). Hence, we first fitted models to determine the mean nest decay time separately for each of the eight nest decay datasets and then fitted a separate model to estimate decay time as a function of rainfall. We then assigned a nest decay time to each transect based on that model and the mean rainfall at the respective transect.
In a first step, to calculate mean nest decay times we fitted three models that estimate the probability of nest decay as a function of time, separately for each of the eight sites for which nest decay data were available: a logistic model with left-truncation (Laing et al. 2003), a logistic model with reciprocal transformation of time (Laing et al. 2003), and a Markov model

(Spehar et al. 2010). For each nest decay dataset we fitted the three models and weighted the resulting estimated decay times by the corresponding models' AIC weight (Burnham & Anderson 2002) to derive a mean estimated decay time. These varied between 85 days in Djouroutou, Côte d'Ivoire, and 243 days in Dindefelo, Senegal (Supplementary Table 4).
In a second step, we modelled decay time as a function of rainfall. To this end, we extracted mean rainfall across the study period and study site for each decay dataset from the Tropical Rainfall Measuring Mission dataset (TRMM & GES DISC 2011). We fitted a sigmoidal non-linear least squares model (Pinheiro & Bates 2000) using the R function 'nls' to estimate four parameters describing the influence of rainfall on decay time as:

$$\text{nest decay time} \sim c_1 + c_2 * (1/(1 + \exp(-(c_3 - c_4 * \text{rainfall}))))$$

where c_x are the estimated model parameters. The model revealed a minimum fitted decay time of 85.45 days and a maximum fitted decay time of 229.03 days (Supplementary Figure 2). To assess model uncertainty we derived 10,000 non-parametric bootstraps based on a resampling with replacement of the eight decay rates (Supplementary Figure 3). As only 795 unique bootstrap datasets converged, variance might be underestimated. We used this model, which estimates decay time as a function of rainfall, to calculate nest decay times for each transect, based on the rainfall at each transect. We assumed that decay times were influenced by rainfall up to eight months prior to when the transect was surveyed, as this was the maximum decay time calculated for the above decay datasets. As the range of rainfall covered by the study sites was limited, we used the model only for interpolation. Transects with lower rainfall were assigned the minimum fitted decay time and transects with higher rainfall the maximum fitted decay time (Supplementary Figure 2).

5 Effective strip width

We determined the effective strip width (ESW) using DISTANCE 6.2 Release 1 (Thomas et al. 2010). We used a truncation distance of 50m with which 12,025 observations remained. We grouped the data according to three habitat types (cropland, forest and savanna) and calculated the ESW separately for each habitat type, using different key functions and adjustment terms (Supplementary Table 2). We selected the best fitting model based on lowest AIC and χ^2-tests.

6 Multicollinearity

To rule out multicollinearity, we determined Variance Inflation Factors (VIF, Field 2009) using the function 'vif' of the R package 'car' (version 2.1.1, Fox & Weisberg 2011) applied to a standard linear model excluding all random effects and interactions. The predictors 'environment' and 'hunting taboo' had the largest VIFs with 3.16 and 3.57, respectively. An inspection of the two predictors plotted against each other revealed good variation of each of the two predictors across the entire range of the respective other, which indicated no collinearity problem (Supplementary Figure 4). But to ensure that possible collinearity did not bias model results, we fitted two additional models excluding each of the factors. This did not reveal a significant change in model estimates and standard errors (Supplementary Table 10).

7 Supplementary Tables

Supplementary Table 1: Chimpanzee nest surveys used in the study.

Country	Study site(s)	Survey year(s)	Reference	Survey type
Burkina Faso	several sites	2012	Ginn et al. 2013	recce
Côte d'Ivoire	Azagny NP	2007	WCF 2007a	transect
Côte d'Ivoire	Banco NP	2007-2008	WCF 2008	transect
Côte d'Ivoire	Banco NP	2008	WCF 2008	transect
Côte d'Ivoire	Cavally	2008-2009	WCF 2010a	transect
Côte d'Ivoire	Cavally	2010	WCF 2010a	transect
Côte d'Ivoire	Comoé	2009	WCF 2009a	transect
Côte d'Ivoire	Comoé	2012	WCF 2012a	transect
Côte d'Ivoire	Goin-Débé	2006-2007	WCF 2010a	transect
Côte d'Ivoire	Goin-Débé	2009-2010	WCF 2010a	transect
Côte d'Ivoire	Marahoué	2006	WCF 2006	transect
Côte d'Ivoire	Marahoué	2007	WCF 2007b	transect
Côte d'Ivoire	Mt Sangbé	2001	WCF 2001	transect
Côte d'Ivoire	Nationwide	2007	Campbell et al. 2008	transect, recce
Côte d'Ivoire	Nimba	2008-2009	WCF 2009b	transect
Côte d'Ivoire	Tai NP	2013	WCF 2013a	transect
Côte d'Ivoire	Tai NP	2013-2014	WCF 2014a	transect
Côte d'Ivoire	Tai NP	2014-2015	WCF 2015	transect
Ghana	Atewa Range FR	2006	Granier & Awotwe-Pratt 2007	transect
Ghana	Bia Goaso	2009-2010	Danquah et al. 2012	transect
Ghana	several sites	2006-2009	Gatti 2009	recce
Ghana	several sites	2015	PanAf	recce
Guinea	Bafing River	2013-2014	WCF 2014b	transect
Guinea	Foutah Djallon	2011-2012	WCF 2012b	transect
Guinea	Haut Niger NP	2001	Fleury-Brugiere & Brugiere 2010	transect
Guinea	Haut Niger NP	2002	Fleury-Brugiere & Brugiere 2010	transect
Guinea	Pic de Fon	2002	WCF 2002	transect
Guinea	several sites	2008-2011	WCF 2012b	transect
Guinea-Bissau	Boé	2013	Chimbo Foundation 2016 & PANAF	recce
Guinea-Bissau	Lagoas Cufada NP	2010	Carvalho et al. 2013	transect
Guinea-Bissau	Lagoas Cufada NP	2011	Carvalho et al. 2013	transect
Liberia	Gola NF	2011-2012	Hillers 2012	transect
Liberia	Grebo NF	2005-2006	Gamys 2006	transect
Liberia	Grebo NF	2012	WCF 2012c	transect
Liberia	Grebo NF	2013	PanAf	transect
Liberia	Nationwide	2010-2012	Tweh et al. 2015	transect
Liberia	Nimba Arcelor Mittal	2010	WCF 2011a	transect

Liberia	Nimba Arcelor Mittal	2011	WCF 2011a	transect
Liberia	Nimba East	2013-2014	PanAf	transect
Liberia	Proposed Grebo NP	2013	WCF 2013b	transect
Liberia	Proposed Grebo NP	2014	WCF 2014c	transect
Liberia	Sapo NP	2009	WCF 2010b	transect
Liberia	Sapo NP	2012	PanAf & WCF	transect
Liberia	Sapo NP	2014	FFI 2014	transect
Mali / Guinea	APT Bafing-Falémé	2003-2004	Granier & Martinez 2004	transect
Senegal	Heremakhono	2013-2014	Wessling unpublished data	transect
Senegal	Kanoumering	2013-2014	Wessling unpublished data	transect
Senegal	Kayan	2012	PanAf	transect, recce
Senegal	Makhana	2013-2014	Wessling unpublished data	transect
Sierra Leone	Bumbuna	2013	Barrie 2016	transect
Sierra Leone	Gola RNP	2009	Ganas 2009	transect
Sierra Leone	Nationwide	2009-2010	Brncic et al. 2015	transect

Supplementary Table 2: Effective strip width estimated for three habitat types and function used for the analysis.

Habitat type	No. observations	ESW (m)	Key function	Adjustment term
Cropland	1029	20.25	half-normal	simple polynomial
Forest	5649	18.58	uniform	cosine
Savanna	5347	24.56	uniform	cosine

Supplementary Table 3: Detection model selected for each habitat type for the estimation of the effective strip width (ESW) and results of the χ^2-goodness of fit test for each detection model. Results include point estimate, standard error (SE), coefficient of variation (CV), and 95% Confidence limits (Cl) for the parameters (A) in the probability density function, the probability density function evaluated at distance zero (f(0)), the detection probability (p), and ESW.

Habitat type	Selected detection model	Model parameters						χ^2-goodness of fit test on detection model		
		Parameter	Point estimate	SE	CV (%)	95 % Cl		total χ^2-value	degrees of freedom	Probability of a greater χ2 value
Cropland	Half-normal key, $k(y) = Exp(-y^2/(2*A(1)^2))$	A(1)	15.58	0.878				4.27	3	0.23
	Simple polynomial adjustments of orders: 4, 6	A(2)	-4.21	1.832						
		A(3)	13.20	4.828						
		f(0)	0.05	0.002	3.20	0.046	0.053			
		p	0.41	0.013	3.20	0.380	0.431			
		ESW	20.25	0.649	3.20	19.020	21.569			
Forest	Uniform key, k(y) = 1/W	A(1)	1.13	0.014				2.12	2	0.35
	Cosine adjustments of orders: 1, 2, 3, 4	A(2)	0.37	0.018						
		A(3)	0.14	0.019						
		A(4)	0.06	0.015						
		f(0)	0.05	0.001	1.78	0.052	0.056			
		p	0.37	0.007	1.78	0.359	0.385			
		ESW	18.58	0.332	1.78	17.943	19.244			
Savanna	Uniform key, k(y) = 1/W	A(1)	0.86	0.016				3.41	4	0.49
	Cosine adjustments of orders: 1, 2	A(2)	0.18	0.017						
		f(0)	0.04	0.001	1.38	0.040	0.042			
		p	0.49	0.007	1.38	0.478	0.505			
		ESW	24.56	0.340	1.38	23.901	25.233			

Supplementary Table 4: Nest decay time estimates based on eight nest decay datasets.

Study site	Reference	No. nests	Study period	Rainfall*	Model	AIC	AIC weight	Decay time (days)	Lower CI	Upper CI
Liberia Sapo NP (forest)	PanAf	142	2010-2012	0.22	left truncated	140.93	0.97	153.97	135.38	178.15
					reciprocal	148.22	0.03	154.13	131.85	177.21
					markov	164.30	0.00	187.93	153.83	233.90
					mean			**153.97**	**135.29**	**178.13**
Liberia Sapo NP (marshes)	PanAf	62	2010-2012	0.21	left truncated	54.20	0.78	145.94	101.32	182.08
					reciprocal	56.74	0.22	145.67	104.43	181.82
					markov	66.01	0.00	186.81	141.08	261.01
					mean			**145.97**	**102.09**	**182.19**
Guinea Foutah Djalon	WCF 2012b	226	2011-2012	0.10	left truncated	119.16	0.30	220.44	216.60	229.82
					reciprocal	117.42	0.70	216.36	210.19	224.43
					markov	404.00	0.00	394.81	347.04	462.38
					mean			**217.57**	**212.08**	**226.02**
Guinea Haut Niger	Fleury-Brugiere & Brugiere 2010	151	2002-2003	0.21	left truncated	924.83	0.00	212.25	172.44	259.90
					reciprocal	889.67	1.00	229.21	157.63	291.33
					markov	921.51	0.00	209.56	172.84	259.45
					mean			**229.21**	**157.63**	**291.33**
Senegal Dindefelo	IJGE Senegal	419	2013-2016	0.14	left truncated	2462.57	0.20	241.42	217.97	270.01
					reciprocal	2474.24	0.00	233.37	174.26	258.31
					markov	2459.75	0.80	243.67	217.32	272.09
					mean			**243.22**	**217.42**	**271.68**
Côte d'Ivoire TaÏ NP	Kouakou et al. 2009	141	2005-2006	0.24	left truncated	728.44	0.25	94.36	72.73	114.14
					reciprocal	730.65	0.08	94.18	78.81	113.09
					markov	726.42	0.67	94.59	79.31	112.65
					mean			**94.50**	**77.66**	**113.05**
Côte d'Ivoire Djouroutou	WCF 2011b	139	2010-2011	0.23	left truncated	125.17	0.22	87.05	70.84	109.87
					reciprocal	125.70	0.17	72.10	54.52	117.48
					markov	123.16	0.61	87.50	67.57	109.41
					mean			**84.77**	**66.07**	**110.89**
Côte d'Ivoire TaÏ NP	WCF 2011b	176	2010-2011	0.20	left truncated	217.90	0.22	163.48	135.05	192.14
					reciprocal	218.45	0.17	146.78	118.98	275.66

markov	215.89	0.61	164.57	135.51	199.03
mean			**161.31**	**132.61**	**210.46**

*mean rainfall across study area and study period extracted from the Tropical Rainfall Measuring Mission product 3B43 in mm/hr per 0.25°x0.25° pixel

Supplementary Table 5: Parameters of the nest decay time model to estimate the influence of rainfall on decay time.

Model parameter	**Estimate**
c_1	-82.44
c_2	311.75
c_3	12.31
c_4	50.91

Supplementary Table 6: Predictor data extraction and post-processing

Covariate	Extraction radius	Data extraction per transect	Post-processing of extracted data per transect	Transformation for model/ factor analysis
Conflicts	15km	number of conflicts within a circle around the transect midpoint weighted by inverse time lag in years between conflict and transect survey	none	none
Corruption control	20km	mean of values within the extraction radius (ER) around the transect, weighted according to the proportion with which the resulting area overlapped with different countries	we used the mean across all years	none
Cropland	5km	proportion of pixels within the ER around transect classified as cropland and cropland/natural vegetation mosaic	we used the mean across all years	square root (x)
Education	20km	mean of values within the ER around transect, weighted according to the proportion with which the resulting area overlapped with different subnational regions	none	none
Forest loss	5km	frequency of pixels with forest loss per year within the ER around transect	we used the proportion of pixels with forest loss for the years before the survey was conducted (excluding year of survey)	square root (x)
Human density	15km	mean of values within the ER around transect	none	log(x)
Hunting taboo	20km	mean of values within the ER around transect, weighted according to proportion with which the resulting area overlapped with different subnational regions	none	none
Malnourishment	20km	mean of values within the ER around transect, weighted according to the proportion with which the resulting area overlapped with different subnational regions (additional information below in ‘Text 2: Malnourishment data extraction’)	we used the mean across all years	none
Nighttime light	50km	mean of values within the ER around transect	for details on how we derived the predicted value for each year refer below to ‘Text 3: Nighttime light data processing’; each transect was assigned the predicted value for the year the survey was conducted, all surveys conducted after 2013 were assigned the value for 2013	square root (x)

Poverty	20km	mean of values within the ER around transect, weighted according to the proportion with which the resulting area overlapped with different subnational regions	none	none
Rainfall		mean of values of all pixels transversed by transect, weighted by transect length per pixel; for transects with NA for a certain month we used the mean of values of neighbouring pixels	to determine the seasonality in rainfall, we calculated the effect size (partial R^2) of season for each transect by comparing a model with date (in days) and season (sine and cosine of Julian date converted to radians) as predictor, and a model with only date as predictor (model based on regression with R function 'lm', model comparison with ‘anova’)	none
River		distance between transect midpoint and closest river in km	none	square root (x)
Road		distance between transect midpoint and closest road in km	none	square root (x)
Savanna	5km	proportion of pixels within the ER around transect classified as savanna, woody savanna, open shrubland, or closed shrubland	we used the mean across all years	none
Settlements	50km	mean of values within the ER around transect (original values were binary with 0 for ‘no settlement’ and 1 for ‘settlement’)	none	square root (x)
Slope	2km	mean of values within the ER around transect	none	log(x)
Temperature		mean of values of all pixels transversed by transect, weighted by transect length per pixel; for transects with NA for a certain month we used the mean of values of neighbouring pixels	we used the mean across all months	none
Tree cover	5km	mean of values within the ER around transect	variation among years within transects was very large; for each transect we fitted a regression (R function ’lm’) with extracted values as response and date (in days) as a predictor, we then estimated tree cover for each year (R function ‘predict.lm’), each transect was assigned the predicted value for the year the survey was conducted, all surveys done after 2010 were assigned the value for 2010	none
Vegetation height	5km	mean of values within the ER around transect	none	none

Supplementary Table 7: Spearman correlations between predictors.

	Tree cover	Vegetation height	Savanna	Cropland	Temperature	Precipitation	Slope	Human density	Settlements	Forest loss	Night-time light	Conflicts	Hunt. taboo	Malnourishment	Poverty	Education	Corruption	Road
Tree cover																		
Vegetation height	0.89																	
Savanna	-0.84	-0.83																
Cropland	-0.40	-0.51	0.31															
Temperature	-0.86	-0.83	0.74	0.31														
Precipitation	-0.62	-0.62	0.78	0.09	0.55													
Slope	-0.25	-0.22	0.32	0.26	0.17	0.36												
Human density	-0.17	-0.26	0.13	0.69	0.07	0.11	0.41											
Settlements	0.16	0.04	-0.16	0.50	-0.22	-0.22	0.22	0.77										
Forest loss	-0.11	-0.14	0.07	0.57	0.02	-0.05	0.19	0.57	0.53									
Night-time light	-0.01	-0.13	-0.11	0.49	0.02	-0.28	0.06	0.55	0.77	0.38								
Conflicts	0.02	0.05	0.05	0.05	-0.08	0.10	0.12	0.21	0.15	0.18	-0.14							
Hunting taboo	-0.50	-0.52	0.68	-0.05	0.55	0.73	0.24	-0.12	-0.28	-0.22	-0.23	0.08						
Malnourishment	0.23	0.29	-0.07	-0.43	-0.31	0.15	-0.19	-0.46	-0.46	-0.22	-0.70	0.23	0.00					
Poverty	-0.31	-0.24	0.50	-0.25	0.33	0.61	0.20	-0.29	-0.46	-0.29	-0.59	0.25	0.73	0.46				
Education	-0.01	-0.10	-0.13	0.35	0.04	-0.45	-0.15	0.3	0.51	0.22	0.65	-0.12	-0.22	-0.66	-0.59			
Corruption	0.25	0.30	-0.46	0.06	-0.30	-0.57	-0.21	0.17	0.25	0.14	0.21	0.07	-0.74	-0.12	-0.54	0.41		
Road	0.43	0.38	-0.43	-0.20	-0.40	-0.53	-0.34	-0.27	0.11	-0.17	0.21	-0.31	-0.35	-0.12	-0.44	0.40	0.24	
River	-0.16	-0.18	0.18	0.04	0.27	0.10	0.08	-0.05	-0.01	-0.09	0.16	-0.09	0.33	-0.27	0.21	0.05	-0.30	-0.03

Supplementary Table 8: Loadings of habitat and climate predictors on the factor “environment” as derived from the first Factor Analysis.

	Environment
Temperature	0.97
Savanna	0.91
Tree cover	-0.91
Vegetation height	-0.91
Rainfall seasonality	0.80

Supplementary Table 9: Loadings of socio-economic predictors on the two factors “Socio-economic status” and “Human activity” as derived from the second Factor Analysis.

	Socio-economic status	Human activity
Education	0.88 *	0.21
Poverty	-0.83 *	-0.23
Corruption control	0.76 *	0.05
Malnourishment	-0.71 *	-0.22
Settlements	0.36	0.91 *
Human density	0.26	0.77 *
Nighttime light	0.52	0.69 *
Conflicts	-0.05	0.53 *

* largest absolute loading for each predictor

Supplementary Table 10: Results for models each fitted without one of the two factors that showed increased Variance Inflation Factors and might therefore be influenced by possible multicollinearity. For the model ‘Environment excluded’ we removed the predictor ‘Environment’ from the full model, and for the model ‘Hunting taboo excluded’ we removed all model terms that contained the predictor ‘Hunting taboo’. For both models the model estimates and standard errors (SE) did not change significantly compared to the full model.

Model	Predictor	Estimate	SE
‘Environment’ excluded	Intercept	-3.263	0.755
	Cropland	-0.184	0.226
	Date	-0.429	0.317
	Forest loss	-0.564	0.085
	Human activity	0.020	0.130
	Hunting taboo	0.252	0.430
	Slope	0.496	0.196
	Socio-economic status	0.465	0.239
	Socio-economic status ^{2}	-0.263	0.233
	Human activity : Hunting taboo	-0.306	0.097
	Human activity : Slope	0.172	0.050
	Human activity : Socio-economic status	-0.054	0.125
	Human activity : Socio-economic status ^{2}	-0.007	0.096
	Hunting taboo : Slope	0.229	0.102
	Hunting taboo : Socio-economic status	0.038	0.314
	Hunting taboo : Socio-economic status ^{2}	0.490	0.208
	River	-0.425	0.133
	Road	0.022	0.142
	Spatial autocorrelation	0.702	0.073
‘Hunting taboo’ excluded	Intercept	-3.189	0.855
	Cropland	-0.237	0.228
	Date	-0.392	0.282
	Environment	-0.913	0.350
	Forest loss	-0.573	0.086
	Human activity	-0.259	0.193
	Slope	0.542	0.227
	Socio-economic status	0.248	0.237
	Socio-economic status ^{2}	-0.440	0.229
	Human activity : Slope	0.124	0.060
	Human activity : Socio-economic status	-0.018	0.139
	Human activity : Socio-economic status ^{2}	0.187	0.111
	River	-0.425	0.126
	Road	0.042	0.141
	Spatial autocorrelation	0.701	0.074

Supplementary Table 11: Estimated random effects for the full model indicate the overall among country variation for the effect of each model term on the response.

Predictor	SD
Intercept	1.845
Cropland	0.487
Date	0.699
Environment	0.911
Forest loss	0.000
Human activity	0.175
Hunting taboo	0.699
Slope	0.475
Socio-economic status	0.000
Socio-economic status ^{2}	0.000
Human activity : Hunting taboo	0.000
Human activity : Slope	0.000
Human activity : Socio-economic status	0.000
Human activity : Socio-economic status ^{2}	0.000
Hunting taboo : Slope	0.000
Hunting taboo : Socio-economic status	0.000
Hunting taboo : Socio-economic status ^{2}	0.000
River	0.274
Road	0.290
Spatial autocorrelation	0.162

Supplementary Table 12: Estimated random intercepts and slopes for the full model indicate the between country variation for the effect of each model term on the response, relative to the model estimates.

Predictor	Burkina Faso	Côte d'Ivoire	Ghana	Guinea	Guinea-Bissau	Liberia	Mali	Senegal	Sierra Leone
Intercept	-1.765	-0.667	-1.532	-0.128	3.750	-0.177	0.040	0.187	0.792
Cropland	0.068	-0.529	0.792	-0.328	-0.107	0.253	-0.013	-0.126	0.023
Date	-0.156	0.194	1.357	0.017	-0.738	-0.252	-0.019	-0.463	0.105
Environment	-0.800	-0.545	0.216	1.170	0.398	-0.954	0.023	-0.017	0.757
Forest loss	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Human activity	0.021	0.221	-0.071	-0.164	-0.034	-0.034	-0.002	-0.007	0.076
Hunting taboo	-0.150	0.990	0.029	-0.097	0.074	-0.849	0.005	0.046	-0.072
Slope	0.144	0.019	-0.304	0.605	0.607	-0.362	-0.007	-0.237	-0.509
Socio-economic status	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Socio-economic status ^{2}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Human activity : Hunting taboo	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Human activity : Slope	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Human activity : Socio-economic status	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Human activity : Socio-economic status ^{2}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Hunting taboo : Slope	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Hunting taboo : Socio-economic status	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Hunting taboo : Socio-economic status ^{2}	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
River	0.053	-0.119	-0.081	-0.001	0.074	0.458	-0.002	-0.069	-0.297
Road	0.026	-0.526	0.112	0.092	-0.074	0.172	0.000	0.007	0.161
Spatial autocorrelation	-0.010	0.135	-0.058	0.041	0.030	-0.185	0.000	0.200	-0.160

Supplementary Table 13: Mean and standard deviation of predictors before being z-transformed to a mean of zero and a standard deviation of one.

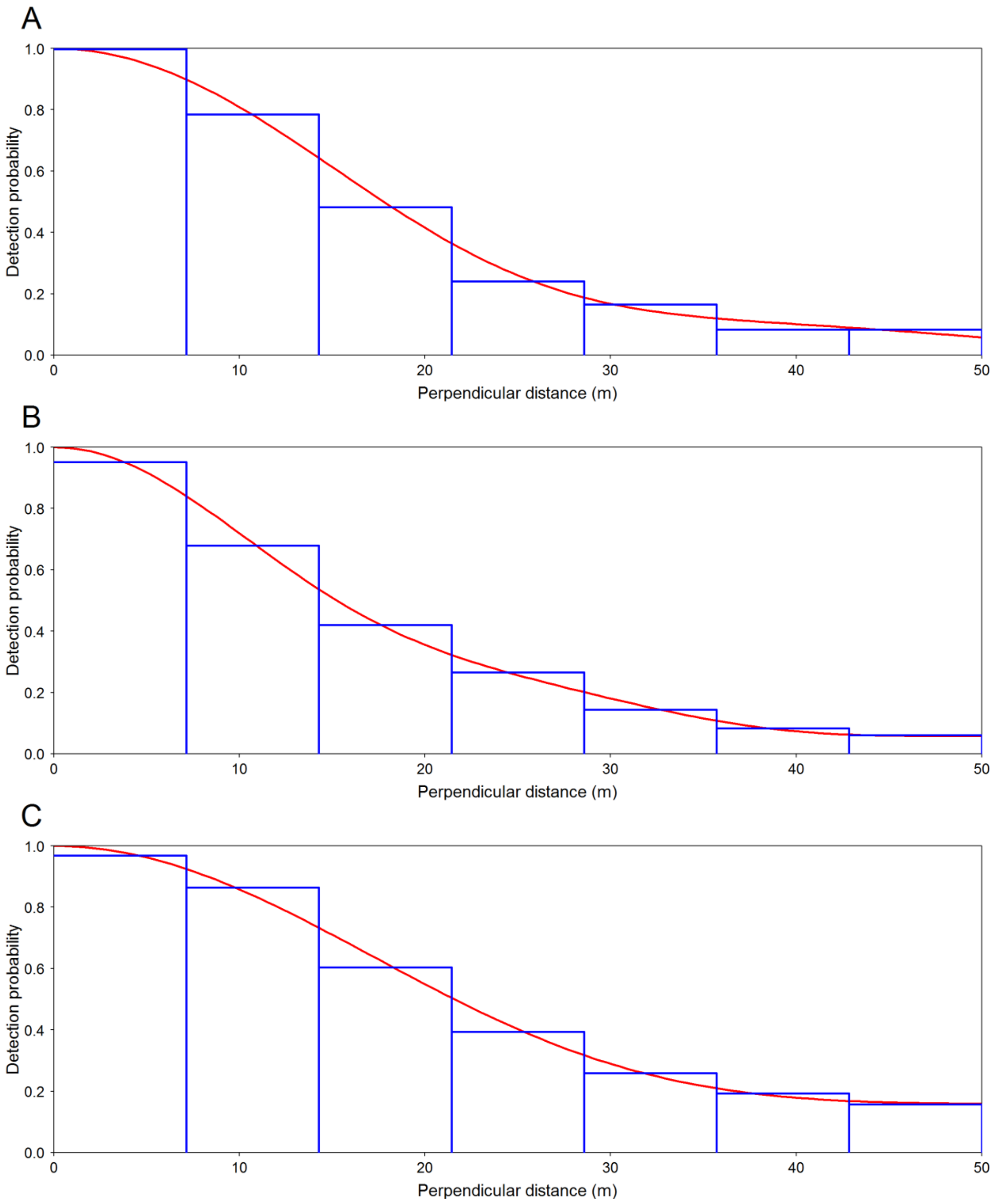
Predictor	mean	SD
Cropland	0.246	0.244
Date*	14980.107	882.374
Environment	0.000	0.984
Forest loss	0.104	0.094
Human activity	1.420	0.292
Hunting taboo	40.330	33.240
Slope	0.667	0.673
Socio-economic status	0.000	0.945
River	3.675	1.670
Road	3.047	1.376
Spatial autocorrelation	-0.292	0.300

* Julian date

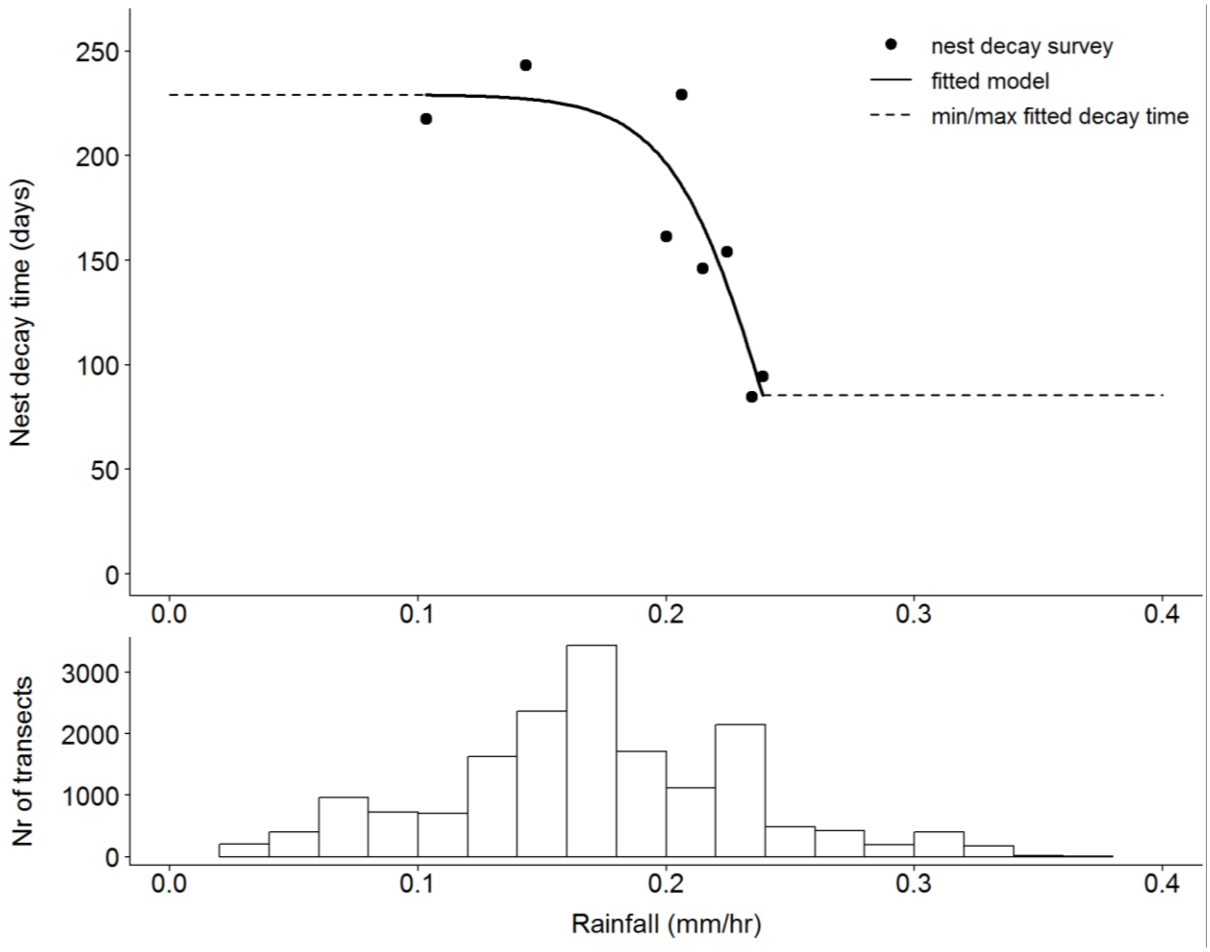
Supplementary Table 14: Comparison of survey effort reported and survey effort estimated for recconnaisance datasets.

Dataset	**Survey effort reported [km]**	**Survey effort derived for this study [km]**	**Comment**
Burkina Faso – several sites 2012	250.00	207.50	No chimpanzee signs were found on any of the recces, so that chimpanzee density was 0. Our underestimate of survey effort therefore did not bias estimated chimpanzee density.
Ghana – several sites 2006-2009	not reported	1138.50	
Ghana – several sites 2015	not reported	258.00	
Guinea-Bissau – Boé 2013	181.39	181.50	
Senegal – Kayan 2012	69.25	69.50	

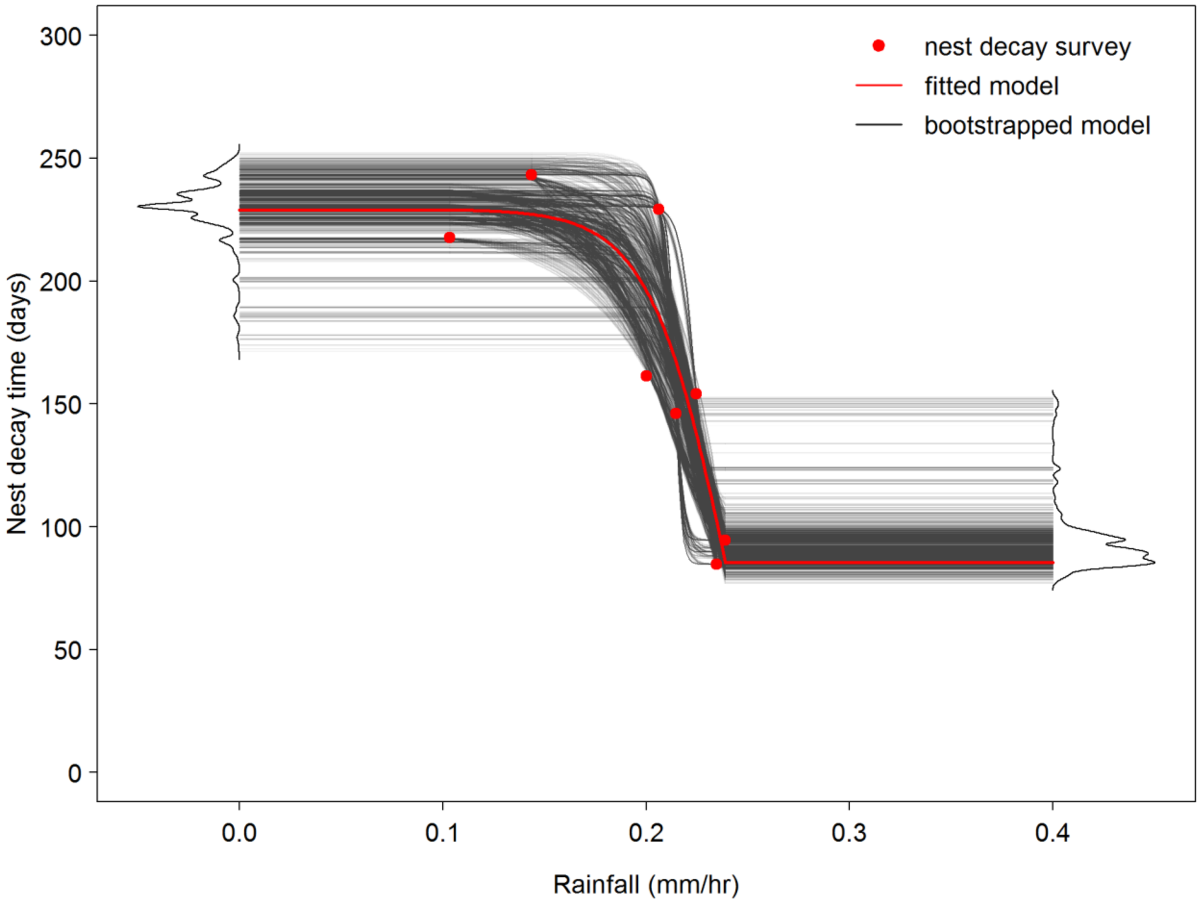
8 Supplementary Figures



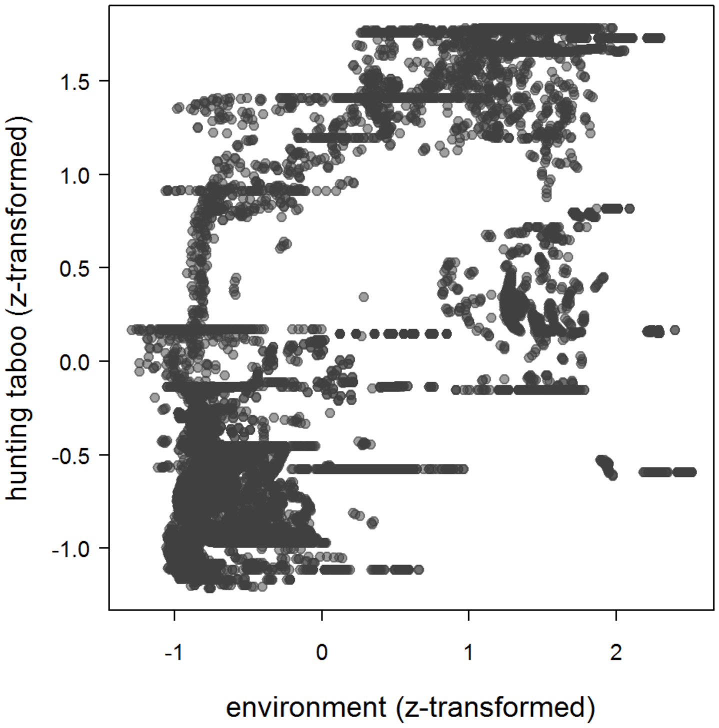
Supplementary Figure 1: Detection probability (red lines) along perpendicular distance and the proportion of observations (blue bars) in distance intervals for the estimation of effective strip width for each of the three habitat types: cropland (A), forest (B) and savanna (C).



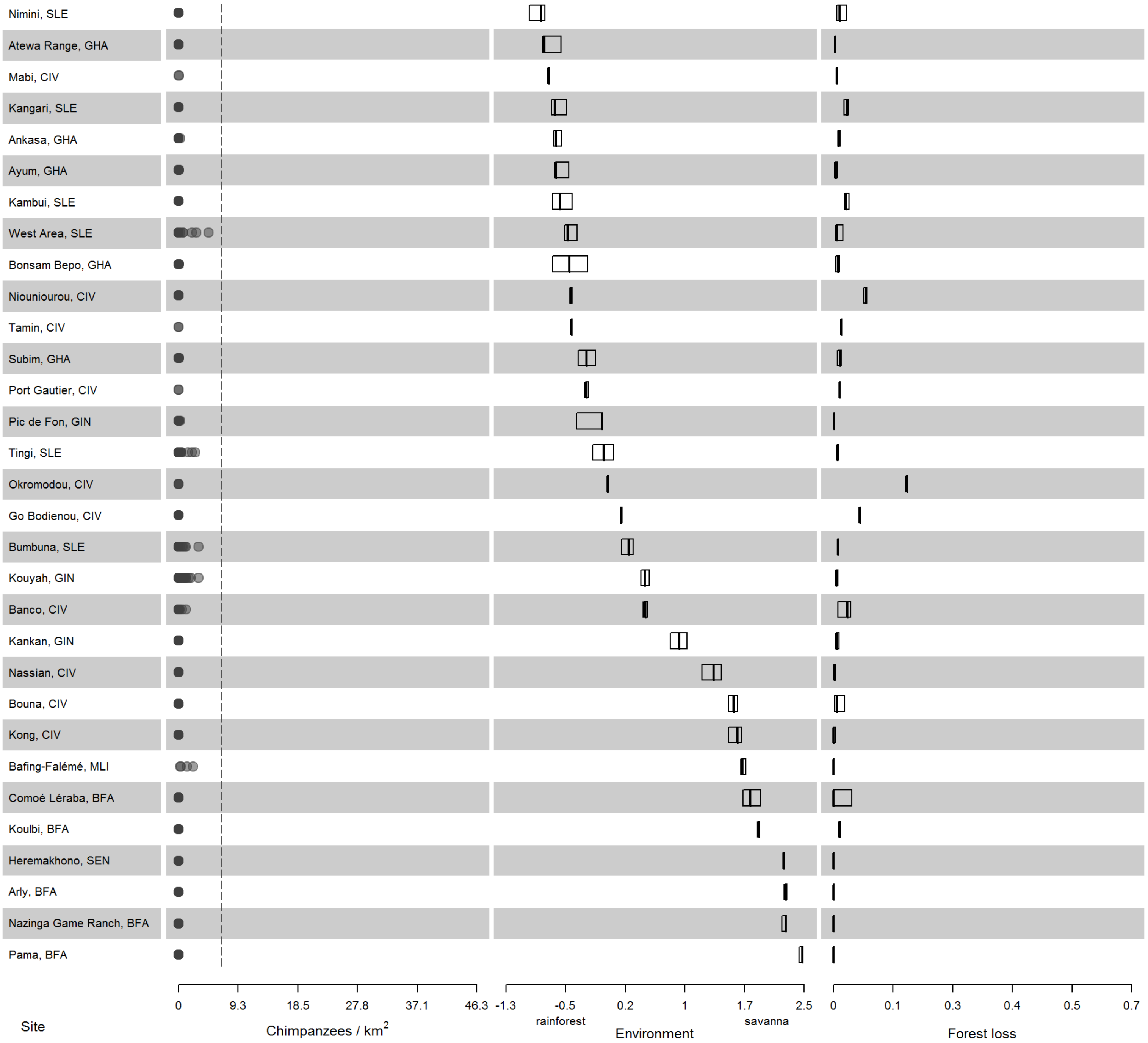
Supplementary Figure 2: Top: Nest decay time as a function of rainfall (solid line). Transects with lower rainfall were assigned the maximum fitted decay time (dashed line) and transects with higher rainfall the minimum fitted decay time (dashed line). Bottom: The majority of transects had an intermediate rainfall and was assigned a nest decay time from the fitted model.

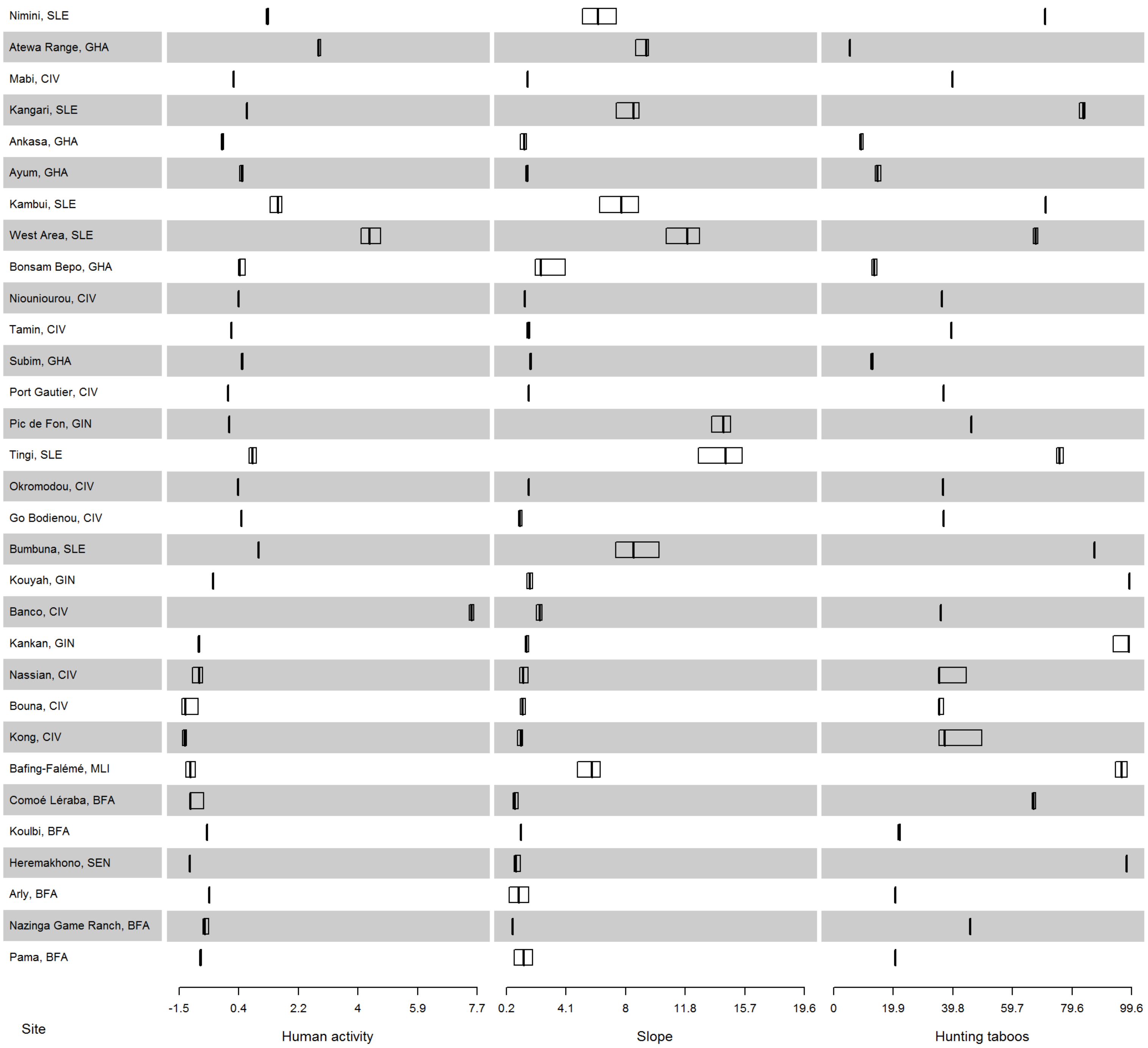


Supplementary Figure 3: Bootstraps for the model of nest decay time as a function of rainfall (grey lines, n=10,000). The two black vertical graphs show the density distribution of the bootstrapped minimum/maximum nest decay time.



Supplementary Figure 4: The two predictors ‘environment’ and ‘hunting taboo’ had the largest Variance Inflation Factors among the model predictors. Here we plotted the two variables against each other to check for collinearity. This plot showed good variation of each of the two predictors across the entire range of the respective other.


Nimini, SLE
Atewa Range, GHA
Mabi, CIV
Kangari, SLE
Ankasa, GHA
Ayum, GHA
Kambui, SLE
West Area, SLE
Bonsam Bepo, GHA
Niouniourou, CIV
Tamin, CIV
Subim, GHA
Port Gautier, CIV
Pic de Fon, GIN
Tingi, SLE
Okromodou, CIV
Go Bodienou, CIV
Bumbuna, SLE
Kouyah, GIN
Banco, CIV
Kankan, GIN
Nassian, CIV
Bouna, CIV
Kong, CIV
Bafing-Falémé, MLI
Comoé Léraba, BFA
Koulbi, BFA
Heremakhono, SEN
Arly, BFA
Nazinga Game Ranch, BFA
Pama, BFA
0
9.3
18.5
27.8
37.1
46.3
-1.3
-0.5
0.2
1
1.7
2.5
0
0.1
0.3
0.4
0.5
0.7
Site
Chimpanzees / km^2
rainforest
savanna
Environment
Forest loss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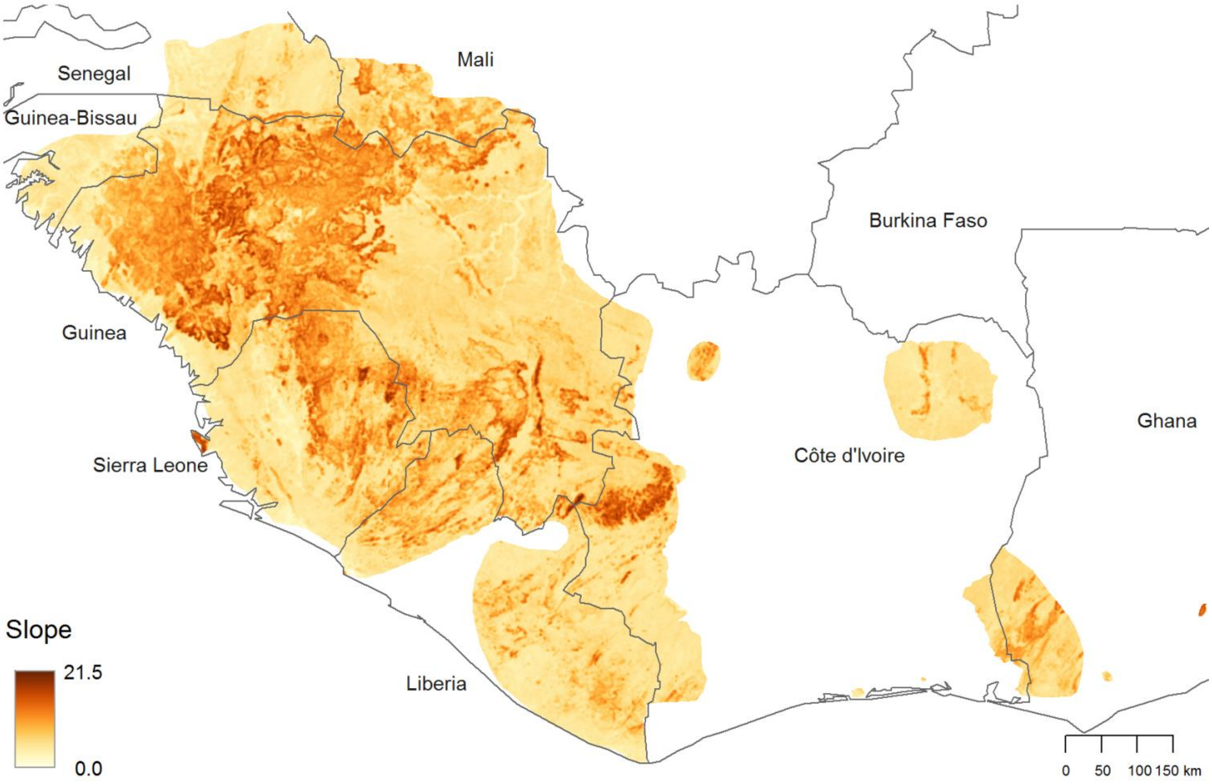
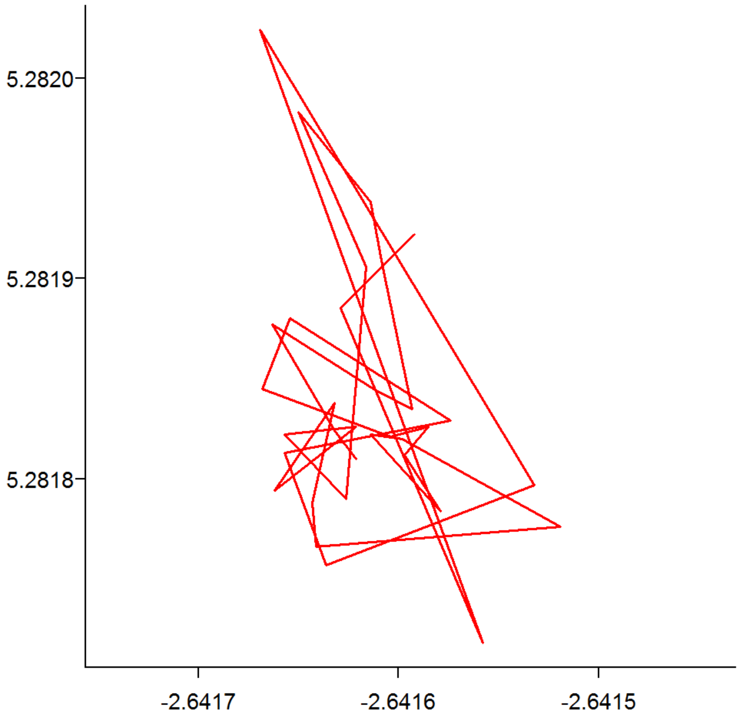
Mabi, CIV
Kangari, SLE
Ankasa, GHA
Ayum, GHA
Kambui, SLE
West Area, SLE
Bonsam Bepo, GHA
Niouniourou, CIV
Tamin, CIV
Subim, GHA
Port Gautier, CIV
Pic de Fon, GIN
Tingi, SLE
Okromodou, CIV
Go Bodienou, CIV
Bumbuna, SLE
Kouyah, GIN
Banco, CIV
Kankan, GIN
Nassian, CIV
Bouna, CIV
Kong, CIV
Bafing-Falémé, MLI
Comoé Léraba, BFA
Koulbi, BFA
Heremakhono, SEN
Arly, BFA
Nazinga Game Ranch, BFA
Pama, BFA
-1.5
0.4
2.2
4
5.9
7.7
0.2
4.1
8
11.8
15.7
19.6
0
19.9
39.8
59.7
79.6
99.6
Site
Human activity
Slope
Hunting taboos

Supplementary Figure 5. Chimpanzee densities and significant factors from statistical model plotted for additional sites not included in the main body. Sites are sorted according to environment from rainforest habitat (top) to savanna habitat (bottom). Trend estimates were not available. In the chimpanzee density panel data points are drawn in transparent grey, so that overlapping data points appear in a darker shade, meaning sites with low chimpanzee density do not necessarily have less data points. The vertical dashed line in the chimpanzee density panel marks the threshold for exceptional density (6.76 individuals/km^2 corresponding to the mean+2SD as suggested by Post & Geldmann (2018)). Horizontal axes depict the range of values in the dataset. Bars represent the lower and upper quartiles and thick vertical lines the median.



Supplementary Figure 6. Distribution of steep terrain across the range of western chimpanzees based on data extracted from the Global multi-resolution terrain elevation data (GMTED2010, Danielson and Gesch, 2011).



Supplementary Figure 7. Example of connected consecutive tracklog data points without timestamps for a specific recce.

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Chapter 2

Advancing conservation planning for western chimpanzees using IUCN SSC A.P.E.S. – the case of a taxon-specific database

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LETTER

Advancing conservation planning for western chimpanzees using IUCN SSC A.P.E.S.—the case of a taxon-specific database

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Abstract

Even though information on global biodiversity trends becomes increasingly available, large taxonomic and spatial data gaps persist at the scale relevant to planning conservation interventions. This is because data collectors are hesitant to share data with global repositories due to workload, lack of incentives, and perceived risk of losing intellectual property rights. In contrast, due to greater conceptual and methodological proximity, taxon-specific database initiatives can provide more direct benefits to data collectors through research collaborations and shared authorship. The IUCN SSC Ape Populations, Environments and Surveys (A.P.E.S.) database was created in 2005 as a repository for data on great apes and other primate taxa. It aims to acquire field survey data and make different types of data accessible, and provide up-to-date species status information. To support the current update of the conservation action plan for western chimpanzees (*Pan troglodytes verus*) we compiled field surveys for this taxon from IUCN SSC A.P.E.S., 75% of which were unpublished. We used spatial modeling to infer total population size, range-wide density distribution, population connectivity and landscape-scale metrics. We estimated a total abundance of 52 800 (95% CI 17 577–96 564) western chimpanzees, of which only 17% occurred in national parks. We also found that 10% of chimpanzees live within 25 km of four multi-national 'development corridors' currently planned for West Africa. These large infrastructure projects aim to promote economic integration and agriculture expansion, but are likely to cause further habitat loss and reduce population connectivity. We close by demonstrating the wealth of conservation-relevant information derivable from a taxon-specific database like IUCN SSC A.P.E.S. and propose that a network of many more such databases could be created to provide the essential information to conservation that can neither be supplied by one-off projects nor by global repositories, and thus are highly complementary to existing initiatives.

1. Introduction

In conservation planning there is an increasing need for detailed information on the density distribution of species, population trends, and habitat suitability to support evidence-based decision-making (Schwartz *et al* 2018). To derive these parameters different types of data are needed across large areas, an extent that usually exceeds the scope of individual research projects. Consequently, the curation of existing data has been the focus of various databases, many of them compiling data at a global scale, such as the Global Biodiversity Information Facility (GBIF 2018), Map of Life (Jetz *et al* 2012), and Living Planet Index (Collen *et al* 2009). However, large data gaps remain regarding spatial and taxonomic coverage and type of data, especially for Africa and the Middle East, and occurrence data are more readily available than abundance or trend data (Boakes *et al* 2010, Kindsvater *et al* 2018, Peterson and Soberón 2018).

For many taxa the challenge is not necessarily that data are not available. In contrast, researchers and conservation organizations go to great lengths to collect species survey data, which requires extensive human and financial resources. However, only a fraction of these data are shared, despite their value for broad-scale and comparative analyses (Costello *et al* 2013). Impediments to data sharing include first and foremost a lack of perceived benefit, workload, and concern of losing intellectual property (Thessen and Patterson 2011). In addition, the amount of survey data published in the gray literature greatly exceeds that published in peer-reviewed journals (Corlett 2011). To inform conservation planning, these data need to be centralized, standardized, and quality checked, whilst assuring data collectors of their intellectual property rights (Reichman *et al* 2011, Thessen and Patterson 2011, Costello *et al* 2013).

Apes are particularly well studied (Wich and Marshall 2016), and western chimpanzees (*Pan troglodytes verus*) are no exception, as illustrated by the IUCN Status Survey and Conservation Action Plan (Kormos *et al* 2003). However, the action plan stated that information available at the time was insufficient because data were only available for specific sites, and large data gaps remained. Consequently, the identification of priority areas for conservation activities was based on expert opinion (Kormos and Boesch 2003). Besides the call for filling data gaps (Kormos and Boesch 2003), conservationists and researchers saw the need of compiling available ape survey datasets and make them accessible through a platform to better inform conservation planning.

The IUCN SSC Ape Populations, Environments and Surveys database (A.P.E.S.; Kühl *et al* 2007) was initiated in 2005, and its creation was facilitated by a collaboration between the section on Great Apes of the IUCN Primate Specialist Group, ape range country authorities, academic institutions, and conservation organizations. IUCN SSC A.P.E.S. contains geo-referenced survey data of all 14 taxa of extant great apes covering 21 of the 23 ape range countries (data not available for South Sudan, and Cabinda Province in Angola, figure 1). The database holds almost 500 standardized and quality-checked datasets consisting of more than three million records, including information on abundance, density, population trends, presence-absence, and spatial distribution (as of November 2018).

For western chimpanzees, data deposited in IUCN SSC A.P.E.S. have been used to predict the distribution of habitat suitability and its trends (Junker *et al* 2012, Jantz *et al* 2016), and to determine their population trend as well as geographic range (Kühl *et al* 2017). These assessments estimated a population decline of 80% and a range reduction of 20% within 24 years (Kühl *et al* 2017). As a result, western chimpanzees were uplisted to Critically Endangered by the IUCN Red List of Threatened Species (Humle *et al* 2016). Currently, the conservation action plan for this taxon is being updated. As various researchers and conservation organizations conducted surveys on this ape in the past 15 years and shared their data with IUCN SSC A.P.E.S., we were now able to use a dataset representative of the entire range of western chimpanzees, 75% of which had not been published. For the first time, we could thus model the range-wide density distribution

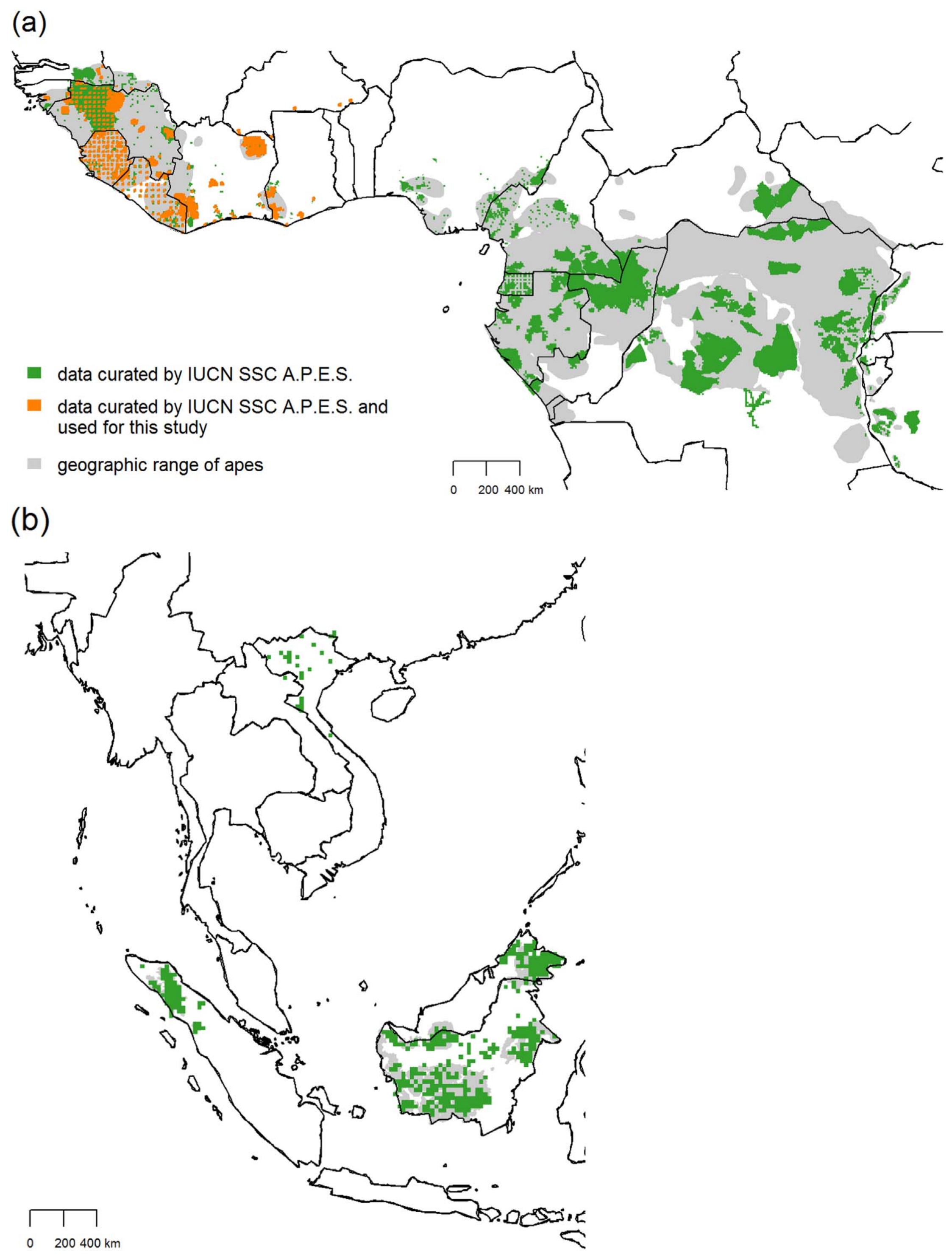

Figure 1. Data contained in IUCN SSC Ape Populations, Environments and Surveys (A.P.E.S.) database with spatial distribution of datasets for (a) African apes, and (b) Asian apes.

for this ape. We then derived information on western chimpanzees important for the update of the conservation action plan, including areas with high chimpanzee densities, or those where population connectivity has been reduced, estimated total abundance, and proportion of chimpanzees occurring in proximity to settlements and infrastructure.

2. Methods

2.1. IUCN SSC A.P.E.S. database

The IUCN SSC A.P.E.S. database currently holds 498 survey datasets contributed by more than 200 conservation scientists, wildlife authorities, and non-governmental organizations. A dataset is defined as a set of data that was collected for a specific area and time period. Datasets had been collected as part of single or repeated surveys, and range from small scale (20 km^2) to large areas, or even entire countries. The database stores different types of data that are standardized and quality-checked, including point and reconnaissance survey data that can be used to determine presence and absence, line transect data which are the basis for density estimates, and camera trap data. IUCN SSC A.P.E.S. also holds 280 abundance polygons, meaning abundance estimates for various resource management areas such as protected areas or resource concessions. The available data also include 24 spatial layers, for example, species density distribution and range layers, abundance layers, and suitable ecological conditions layers. Additionally, IUCN SSC A.P.E.S. contains nest decay datasets, which are needed to convert counts from ape nest surveys into individual ape density and abundance estimates. Most datasets not only include sightings of the ape taxa targeted in the survey, but also include phenology of ape food plants, records of other taxa, human signs, and records of covariates such as vegetation type and slope. Furthermore, the database stores 950 publications and reports, of which 280 are unpublished field survey reports. For this study we used 58 chimpanzee nest count surveys and nest decay datasets, only 13 of which had been published to date (figure 1, table S1 is available online at stacks.iop.org/ERL/0/000000/mmedia).

2.2. Modeling chimpanzee density distribution

We followed a commonly used procedure to predict ape density distributions (Murai *et al* 2013, Wich *et al* 2016, Strindberg *et al* 2018, Voigt *et al* 2018). Specifically, we first fitted a full model to establish the relationship between chimpanzee densities and several social-ecological predictor variables, and then predicted chimpanzee density distribution based on multi-model inference (Burnham and Anderson 2002).

The response variable in the full model was the number of nests per transect with a sample size of 17 109 transects and a total survey effort of 10 929 km, covering all western chimpanzee range states (figure 1(a)). For the model output to directly express number of individuals per km^2 and to account for varying transect lengths, we included an offset term comprising transect length, effective strip width, proportion of nest builders, nest production rate, and nest decay time (details supplementary material). We then extracted 20 predictor variables for each transect using publicly available satellite and aggregated household-survey data which approximate known drivers of chimpanzee density including both environmental variables and anthropogenic pressure (details in table S2 and table S3). We originally started with a model comprising the same predictors used in an earlier study to identify drivers of chimpanzee densities (Heinicke *et al* 2019), but the initial evaluation of the derived density distribution revealed an underestimation of chimpanzee densities for protected areas. We therefore added 'protected area' as a binary predictor, meaning whether the midpoint of a transect was within the boundaries of a protected area designated as 'national park' or IUCN category I or II based on data from the World Database of Protected Areas (UNEP-WCMC and IUCN 2017). For the full model (table S4), we fitted a Generalized Linear Mixed Model (Baayen 2008) with a negative binomial error distribution (Hilbe 2011). Details on model implementation, namely spatial autocorrelation, random effects, check for multicollinearity and overdispersion can be found in the supplementary material.

We then extracted all predictors across the entire range of western chimpanzees by deriving a grid with a resolution of half a minute (ca. 0.9 km) and identifying the coordinates of each cell center. The total area was approximately 523 000 km^2. For each cell we extracted, processed and transformed the predictors using the same procedure and parameters as for the transect data (table S3).

To avoid nuisance parameters, namely parameters with an overestimated contribution, and model selection uncertainty, we based the range-wide density prediction on qAICc-weighted multi-model inference (Burnham and Anderson 2002). Specifically, we first derived all possible models on the basis of the test predictors (5824 models). Six of those models did not converge, and we used the remaining 5818 models to derive a density prediction for each grid cell ($n = 620\,043$ cells) for the year 2015. These predictions were made in link space and weighted by the corresponding models' qAICc, summed for each cell, and were finally exponentiated to produce chimpanzee densities (Cade 2015). We calculated 95% confidence intervals based on non-parametric bootstrapping ($n = 1\,000$) with the sampling units being the datasets (Manly 1997).

2.3. Identifying populations and low-connectivity areas

To estimate where connectivity between chimpanzee populations might be reduced, we first identified grid cells with a high likelihood of chimpanzee presence based on modeled chimpanzee density and expert opinion (details in supplementary material). We then determined patches of connected presence cells. Cells were iteratively assigned to the same patch when they were within a threshold distance or connected via cells separated by no more than the threshold distance. There is little information for dispersal distances between chimpanzee communities, for example when females transfer from their natal group. Published maximum daily travel distances range from 9 km in rainforest habitat (Herbinger *et al* 2001) to 16 km in drier habitat (Humle *et al* 2011), and may be larger in very dry areas where chimpanzees have larger home ranges (Pruetz 2018). However, this is likely only the case within suitable habitat and in the absence of barriers such as areas densely populated by humans. As this is a broad-scale analysis, we did not account for conditions between presence cells. Therefore, we present three scenarios for possible dispersal distances, namely 5, 15, and 25 km, to identify areas where connectivity might be low or be reduced in the near future in case of land-use change or increase of other threats.

2.4. Spatial distribution of chimpanzees in relation to infrastructure

Large-scale land-use change across West Africa is mainly driven by the expansion of agricultural areas, resource extraction, and development of associated infrastructure (Norris *et al* 2010, Edwards *et al* 2014, Laurance *et al* 2015). While most of the land surface has essentially been divided into mining and timber concessions, as well as areas for renewable energy production, such as hydropower plants, spatial data are not available for the entirety of the western chimpanzee range. We therefore focused on only one of these planned development projects, namely proposed 'development corridors' (Laurance *et al* 2015), to illustrate how such developments could affect western chimpanzees if they were implemented. Development corridors center on the expansion of roads, railroads, pipelines, and ports, to improve the movement of people and goods between remote areas and urban centers. The aim is to enable rural communities' access to markets and social services, and ultimately improve agricultural productivity, market integration, and regional trade (Mulenga 2013, Weng *et al* 2013, Laurance *et al* 2015). However, these infrastructure projects could lead to environmental damage by opening up formerly inaccessible areas and intersecting protected areas (Laurance *et al* 2015, Sloan *et al* 2017). Four corridors have been proposed for West Africa: Conakry-Buchanan (Guinea, Liberia, Sierra Leone), Dakar-Port Harcourt (Mali, Senegal), Gulf of Guinea (Côte d'Ivoire, Ghana, Liberia), and Sekondi/Ouagadougou (Burkina Faso, Ghana) (Laurance *et al* 2015). The recent $22.7 Mio agreement between the Economic Community of West African States and the African Development Bank to upgrade roads on the 'Gulf of Guinea' corridor (African Development Bank 2019) and feasibility studies for the upgrade of the Dakar-Bamako railroad on the 'Dakar-Port Harcourt' corridor (PIDA 2018) suggest that these developments might threaten apes and their habitat (Laurance 2018). To estimate how many chimpanzees occur in proximity to these corridors, we overlaid the 50-km wide corridor bands from Laurance *et al* (2015) and Sloan *et al* (2017) with the modeled chimpanzee density distribution.

To provide further contextual information for conservation planning we determined the proportion of chimpanzees in three habitat types based on the Global land cover dataset (Friedl *et al* 2010): forest ('broadleaf forest', 'mixed forest'), savanna-mosaic ('savanna', 'woody savanna', 'open shrubland', 'closed shrubland'), and cropland ('cropland', 'cropland/natural vegetation mosaic'). We also determined the distance of each grid cell to the closest road (FAO 2005) and settlement (Esch *et al* 2012) to estimate how many chimpanzees live within 5 km and 10 km of roads and settlements. All analyses were implemented in R (vers. 3.4x, R Core Team 2018).

Table 1. Estimated western chimpanzee abundance by country (within geographic range delineated by IUCN SSC A.P.E.S. database).

Country	Estimated chimpanzee abundance (95% CI)	% chimpanzees living in national parks and IUCN category I or II protected areas
Guinea	331 39 (8796–68 203)	12.21
Liberia	6050 (2902–13 690)	14.22
Sierra Leone	5925 (1951–12 668)	31.20
Senegal	2642 (1077–13 293)	31.55
Guinea-Bissau	1908 (923–6121)	34.45[a]
Mali	2029 (322–9228)	10.00
Côte d'Ivoire	1093 (329–3299)	46.92[b]
Ghana	24 (1–212)	14.40
Total	52 811 (17 577–96 564)	16.98

[a] As the spatial outline of Boé and Dulombi National Parks provided by the World Database of Protected Areas is not up to date (A Goedmakers pers. obs.), we used the outline provided by the 'Instituto da Biodiversidade e das Áreas Protegidas' (Agency of Guinea-Bissau government responsible for national parks) for this calculation.

[b] It is noteworthy that while this number seems high, chimpanzees have declined by more than 90% across Côte d'Ivoire including regional extinctions resulting in a strong contraction of their range (Campbell *et al* 2008, Kühl *et al* 2017).

3. Results

3.1. Modeled chimpanzee density distribution

We estimated a total western chimpanzee abundance of 52 811 (95% confidence interval: 17 577–96 564), with the highest numbers in Guinea, Liberia and Sierra Leone (table 1). Densities ranged between <0.01 and 6.3 individuals km^{-2}. The highest densities were predicted for the Fouta Djallon highland region (figure 2). We estimated that 7.66% of western chimpanzees range in high-level protected areas (i.e. national parks and IUCN Cat I + II) as of 2015. Since then several new national parks have specifically been created for the protection of western chimpanzees, e.g. Boé and Dulombi (Guinea-Bissau), and Gola and Grebo-Krahn (Liberia), while Moyen Bafing (Guinea) is currently being created. Consequently, 8.56% of the current range is now a high-level protected area which

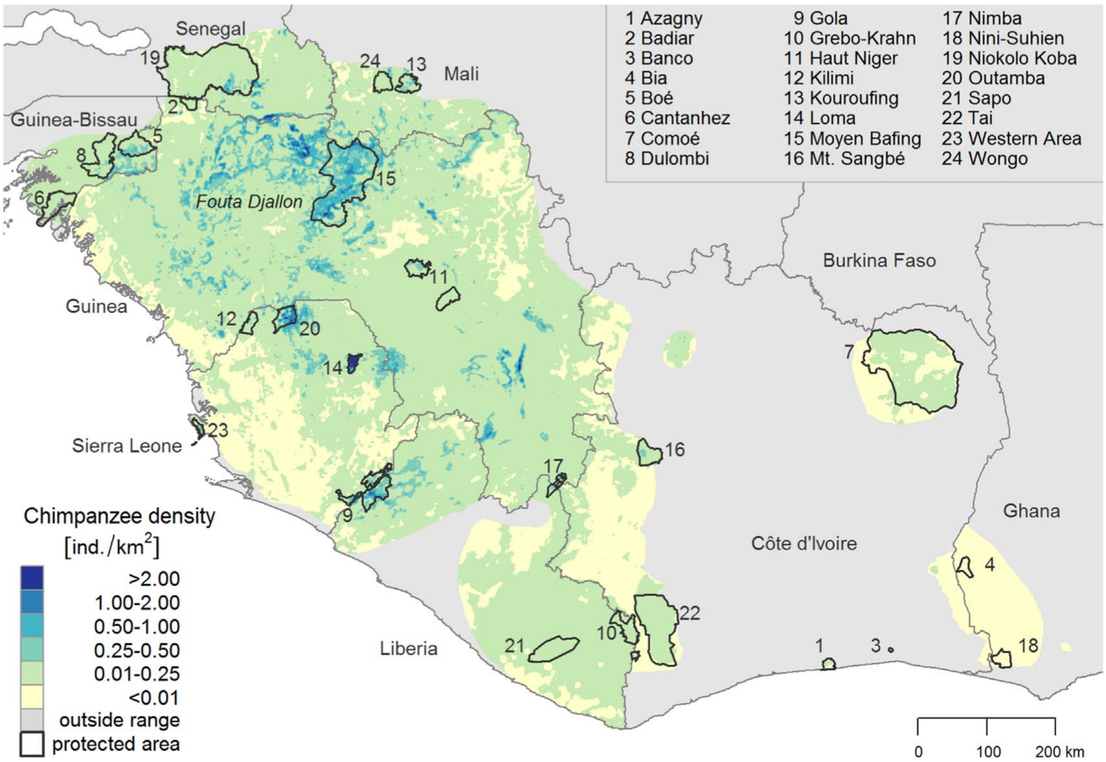

Figure 2. Modeled western chimpanzee density distribution (within geographic range delineated by IUCN SSC A.P.E.S. database, protected area outline from UNEP-WCMC and IUCN 2017, Boé and Dulombi National Parks outline from Instituto da Biodiversidade e das Áreas Protegidas in Guinea-Bissau). For plotting purposes we truncated densities at two because <0.04% of cells had estimated values larger than two, and otherwise low density cells would not be discernible. Maps of lower and upper confidence limit are in the supplementary material (figure S1).

corresponds to 16.98% of the estimated western chimpanzee population.

3.2. Population connectivity analysis

We estimated that there is one large chimpanzee population across the Fouta Djallon highland region and adjacent areas, extending from Senegal and Guinea-Bissau, across Guinea and Mali and into Sierra Leone (figure 3). This population comprises at least half of the remaining chimpanzees in West Africa (>33 000 individuals, details table S5). The southern population that extends from eastern Guinea across Liberia to Taï National Park in western Côte d'Ivoire comprises the remaining half of western chimpanzees (table S5). Our analysis revealed that connectivity between these two populations might be low in certain areas, specifically across the Upper Niger Basin in Guinea, and where the three countries Guinea, Liberia and Sierra Leone meet (green and blue patch in figure 3(a)), and in the Zone Forestière in southern Guinea (green and red patch in figure 3(b), population estimates for all scenarios in table S5 and results for additional minimum density thresholds in figure S2).

3.3. Spatial distribution of chimpanzees in relation to infrastructure

We estimated that 10.44% of chimpanzees lived within 25 km of the four aforementioned development corridors. The planned Dakar-Port Harcourt corridor in Senegal and Mali would intersect the northernmost distribution of western chimpanzees, while the Conakry-Buchanan corridor would intersect Outamba-Kilimi National Park and the above identified low-connectivity area at the tri-national border of Guinea, Liberia, and Sierra Leone (figure 4). Azagny and Banco National Park in Côte d'Ivoire, which still hold small chimpanzee populations, are entirely within 25 km of the proposed Gulf of Guinea corridor.

For further contextual information relevant for conservation planning, we estimated that 77.93% of western chimpanzees live in savanna-mosaic habitat, 16.38% in forest habitat, and 5.32% in cropland habitat. We also estimated that 38.59% of chimpanzees live within 5 km and 67.43% within 10 km of settlements, while 59.25% live within 5 km and 88.11% within 10 km of roads (figure 5).

4. Discussion

4.1. Implications for western chimpanzee conservation

As IUCN SSC A.P.E.S. provides access to a large number of ape survey datasets, many of which have not been published in peer-reviewed journals, we were able to compile a dataset representative of the entire range of western chimpanzees. For the first time, we

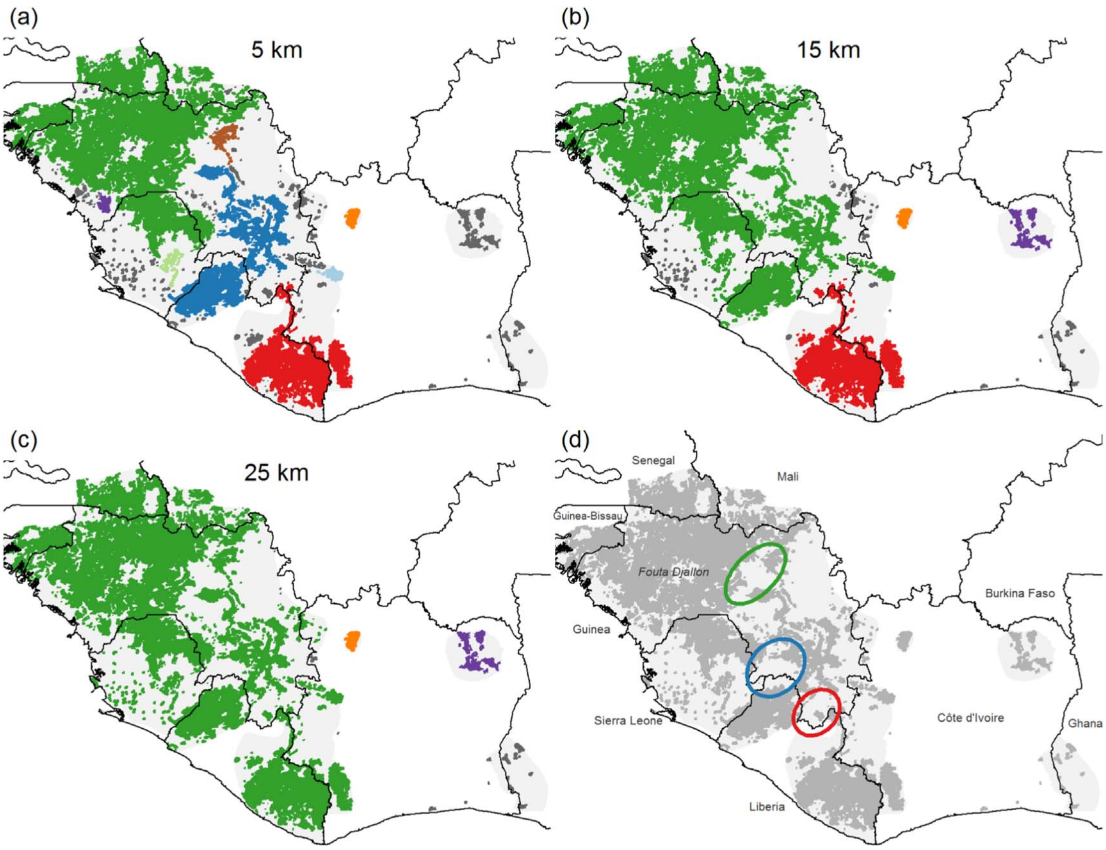

Figure 3. Scenarios for sub-populations based on three minimum distance thresholds (a) 5 km, (b) 15 km and (c) 25 km (i.e. for a larger threshold more presence cells are clustered to the same patch). Large patches are shown in color, smaller ones (typically less than 100 chimpanzees) in gray. (d) Areas with low population connectivity across all three scenarios marked (green: upper Niger Basin in Guinea, blue: tri-national border of Guinea, Liberia, and Sierra Leone, red: zone Forestière in southern Guinea).

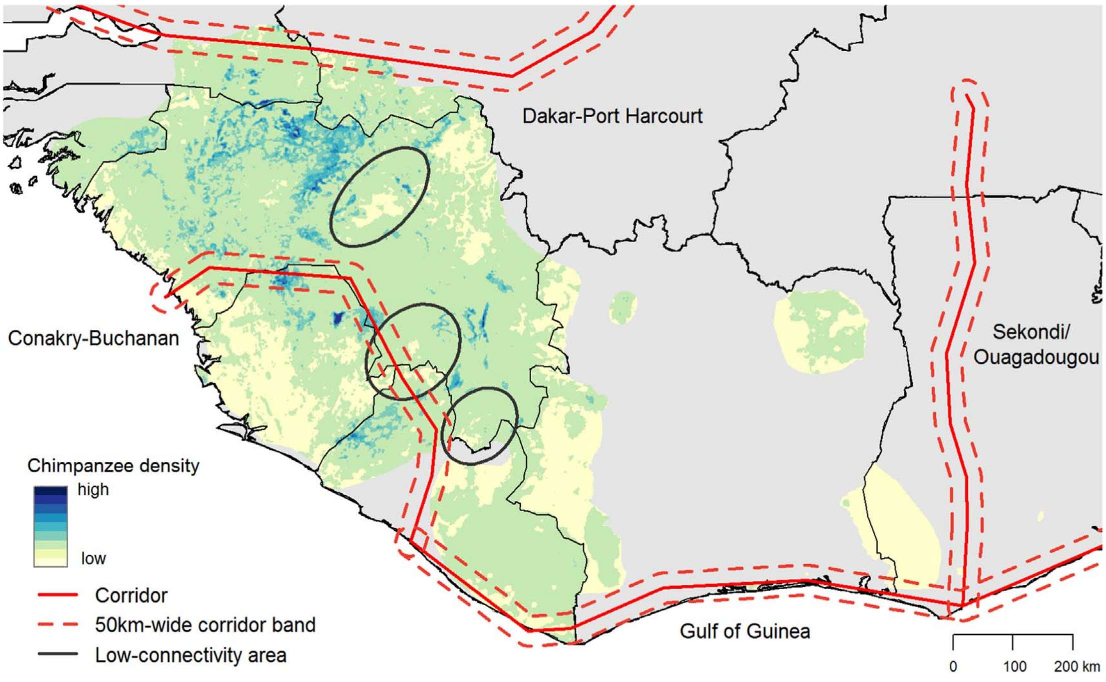

Figure 4. Spatial overlap between the four 'development corridors' planned for West Africa (Laurance *et al* 2015, Sloan *et al* 2017) and modeled western chimpanzee density distribution with estimated low population connectivity areas marked.

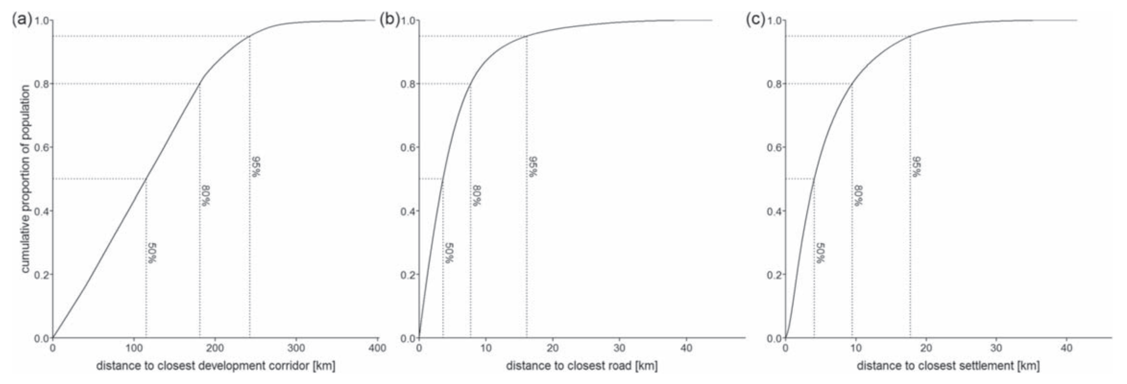

Figure 5. Cumulative proportion of western chimpanzees living within increasing distance to (a) 'development corridors', (b) roads, and (c) settlements. Plot (b) shows, for example, that 80% of western chimpanzees live less than 10 km from the nearest road.

could thus model range-wide density distribution of this taxon and derive information on chimpanzee status important for conservation planning.

The analysis showed that two main populations can be distinguished (figure 3). Chimpanzees in the Fouta Djallon and adjacent areas appear to be a large population characterized by savanna-mosaic habitat. Despite challenging ecological conditions (Wessling *et al* 2018), chimpanzees persist here at high densities due to relatively low levels of anthropogenic threats and a high prevalence of hunting taboos (Boesch *et al* 2017, Heinicke *et al* 2019). Chimpanzees in the second largest population live in a habitat mostly characterized by rainforest. Our analysis indicated that these two populations might have low connectivity at present (figure 3). The other chimpanzee populations remaining in Côte d'Ivoire and Ghana are already completely isolated (Kühl *et al* 2017), and due to their small size these populations are particularly vulnerable to stochastic events, such as disease outbreaks, that can cause local extinctions (Knight *et al* 2016).

If implemented as planned, the multi-national infrastructure projects, including development corridors, hydropower plants and powerlines, could pose multiple threats to chimpanzees (Laurance 2018). First, infrastructure development is likely to incur direct loss of chimpanzee communities, because chimpanzees cannot shift their home range to move away from disturbances as they are highly territorial (Morgan *et al* 2018). Large-scale habitat loss can especially ensue from infrastructure developments that entail expansion of settlements and agriculture, one of the explicit objectives of development corridors (Laurance *et al* 2015). For example, large-scale deforestation and wide-spread hunting as a result of industrial agriculture led to strong declines of chimpanzee populations in Côte d'Ivoire and Ghana (Kormos *et al* 2003, Campbell *et al* 2008). Beyond the direct reduction in chimpanzee abundance this may also lead to loss in behavioral diversity, as even neighboring communities can differ in their behavioral repertoire (Luncz *et al* 2012). Q1 Second, infrastructure expansions often carry secondary threats, especially an increase in hunting due to the arrival of more people, who potentially also do not adhere to established hunting taboos (Golden and Comaroff 2015). For example, in northern Congo the development of a logging concession with road construction and influx of workers led to a 64% increase in bushmeat supply (Poulsen *et al* 2009). However, a recent study of apes in Western Equatorial Africa underlined that this is context dependent, as central chimpanzee densities were significantly lower close to roads, but this effect disappeared with the presence of law enforcement (Strindberg *et al* 2018). Third, infrastructure projects lead to habitat fragmentation and act as dispersal barriers for a wide range of species (Laurance *et al* 2009). Although, chimpanzees have been observed to cross unpaved roads (Hockings *et al* 2015), genetic studies demonstrate that habitat fragmentation reduced chimpanzee population connectivity (Knight *et al* 2016, da Silva Borges 2017). A notable example is the case of Bossou, Guinea, where habitat fragmentation led to the isolation of a chimpanzee group, and there has been no female immigration from neighboring groups for the last 30 years (Matsuzawa *et al* 2011). What the impact on western chimpanzees will be remains to be seen and will strongly depend on the context. However, the list of potential negative impacts emphasizes the necessity to apply the mitigation hierarchy during the planning and construction of infrastructure (i.e. avoid, minimize, restore, and offset; BBOP 2013).

4.2. Comparison to previous estimates and data gaps

Overall, our abundance estimates are in line with previous studies that estimated around 7000 chimpanzees in Liberia (Tweh *et al* 2015), 5600 in Sierra Leone (Brncic *et al* 2015), and 17 700 in the Guinean part of the Fouta Djallon (WCF 2012). Kühl *et al* (2017) compiled abundance data for 35 sites across West Africa, covering 40% of the western chimpanzee range, and estimated a minimum of 35 000 chimpanzees. Our predicted abundance for Senegal is notably higher than previous estimates of 200–400 which were

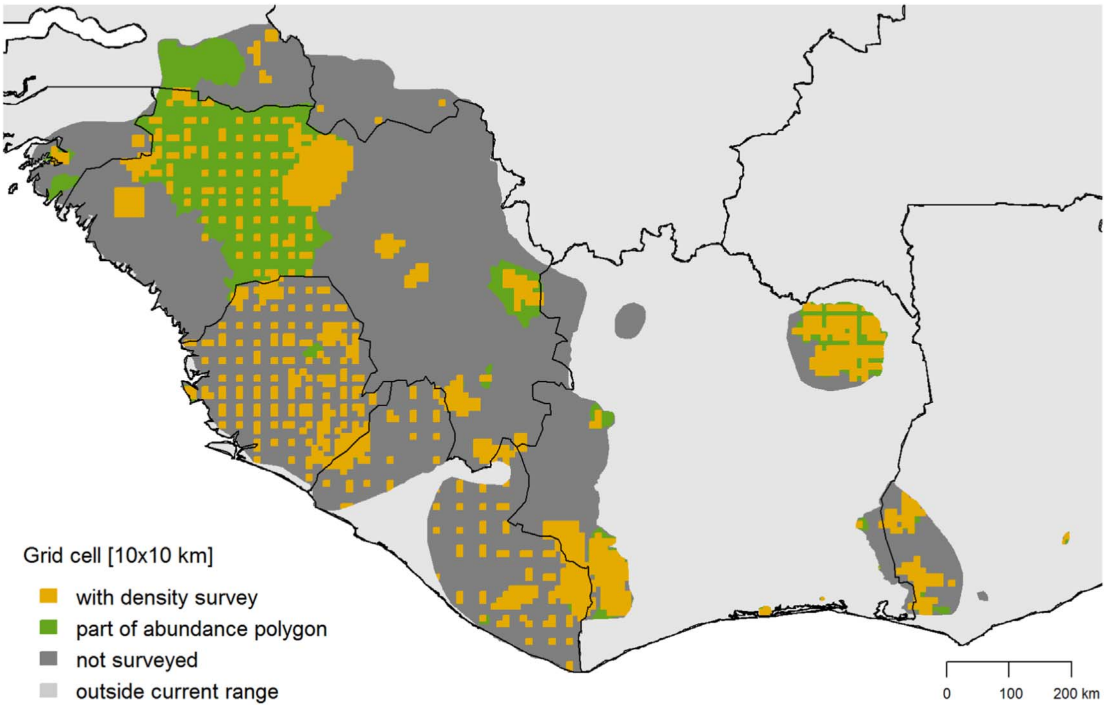

Figure 6. Surveyed areas and survey gaps for western chimpanzees. For each grid cell of 10 × 10 km we determined whether a survey was conducted in that cell. Abundance polygon is the spatial outline of an area for which an abundance estimate was available from the IUCN SSC Ape Populations, Environments and Surveys (A.P.E.S.) database.

extrapolated from small-scale surveys (Kormos *et al* 2003). Similarly, our estimate is higher than the 600–1000 estimated for Guinea-Bissau, but that estimate was not based on quantitative data (Kormos *et al* 2003).

Modeled estimates are associated with uncertainties (figure S1) due to the possibility of missing predictors, and differences in spatial scale of different predictor datasets (table S2). Uncertainties are more pronounced for areas with fewer data and those that differ strongly from surveyed areas regarding predictor space coverage. While substantial data are already available for large parts of the western chimpanzee's range, notable data gaps exist (figure 6). Identifying such gaps can inform where further surveys are needed, and shows where results are uncertain and need to be interpreted with care (see also figure S1). In particular, further field surveys are needed for Mali, for which only few data points are available. However, this is difficult due to the on-going political instability there. Considering that our estimates are significantly higher than previous estimates for Senegal and Guinea-Bissau and have large confidence intervals, more intensive and representative future surveys in these countries would be instrumental in verifying our estimates. Similarly, high densities were predicted for the Kourandou and Simandou mountain ranges in eastern Guinea, but considering that this region is very dry, densities might have been overestimated and further surveys would be needed to validate these predictions. The aim of the model was thus to predict general patterns in chimpanzee density distribution across its range. However, its usefulness is limited at the local scale, for which site-based surveys are clearly superior.

4.3. Contribution of a taxon-specific database

Our study exemplifies the multi-facetted advantages of the IUCN SSC A.P.E.S. database. First, it can design data sharing policies reflecting the data sharing culture of its research field (Thessen and Patterson 2011), and by building trust and collaborations with a variety of data collectors, it can compile data in greater depth and provide access to unpublished datasets for a wider community. It also provides contextual information on the data, such as ecological and anthropogenic variables. Second, IUCN SSC A.P.E.S. not only ensures data attribution to data collectors so that their efforts are credited (Thessen and Patterson 2011), but it can also provide direct benefits to data collectors, for example, by collaborating on research projects and sharing authorship. In addition, database staff can support data collectors during study design and data analysis. Third, IUCN SSC A.P.E.S. hosts different types of data which can be used to derive different population parameters, including species abundance, density distribution, population trend, population connectivity, and habitat suitability (table 2). Fourth, databases can pool expertise and technical skills to process data to be directly fed into conservation decision-making. For example, data contained in IUCN SSC A.P.E.S. had been used for a range of applications, including assessments for the IUCN Red

Table 2. Information on western chimpanzees that has been or could be derived from datasets archived in IUCN SSC A.P.E.S.

Type of analysis	Results for western chimpanzees	Example studies
Abundance	52 811 (17 577–96 564) individuals	This study
Climate change	To be investigated	
Density distribution	Figure 2 this study	This study
Ecosystem service provision through habitat protection (e.g. carbon storage, watershed protection, human cultural traditions associated with the habitat)	To be investigated	
Geographic range	524 100 km^2	Kühl *et al* 2017
IUCN Red List assessment	Critically Endangered	Humle *et al* 2016
Landscape-scale metrics	Figure 5 this study	This study
Land-use across species range	77.93% in savanna-mosaic, 16.38% in forest habitat, 5.32% in croplands	This study
Population trend	Annual decline of 5.96%, decline of 80.2% between 1990–2014	Kühl *et al* 2017
Population connectivity	Figure 3 this study	This study
Presence estimation for individual grid cells	Figure 3 this study	This study
Protected area coverage	16.98% of chimpanzees occur in high-level protected areas	This study
Species co-occurrence	To be investigated	
Suitable environmental conditions	Decline of area with suitable environmental conditions from 1990 to 2000	Junker *et al* 2012, Jantz *et al* 2016
Survey gaps	Figure 6 this study	This study

List (e.g. Fruth *et al* 2016, Humle *et al* 2016, Maisels *et al* 2018), conservation action plans (e.g. IUCN and ICCN 2012, IUCN 2014), CITES, UNEP, and funding organizations (e.g. GRASP and IUCN 2018). Fifth, due to their knowledge of the field, database staff can also convey contacts to relevant experts and thereby improve information flow between different stakeholders, for example for the verification of study results. Thereby, research efforts can be streamlined and duplication avoided. Lastly, funders and journals increasingly require that research results are made publicly available. Accordingly, study results based on IUCN SSC A.P.E.S. data are also stored in the database (table 2). IUCN SSC A.P.E.S. thus enables a two-way information and knowledge exchange and functions as an intermediary to bridge the gap between stakeholders collecting data and those basing their research or decision-making on that data.

Taxon-specific databases already exist for different taxonomic groups and regions, for example the North American Breeding Bird Survey (Sauer *et al* 2013), African Elephant Database (Thouless *et al* 2016), Biological Records Centre in the UK (Pocock *et al* 2015), or Entomofauna Germanica (Bleich *et al* 2019). Despite their fundamental role in curating data relevant for conservation planners and policy makers, databases face severe funding shortages. We suggest that their contribution to filling data gaps for under-represented taxa and regions needs to be recognized, and that many more databases could be established. Similar to initiatives in the biomedical sciences that set up database networks, such as bioDBnet (Mudunuri *et al* 2009) and BioMart Central Portal (Guberman *et al* 2011), a network of taxon-specific databases could be grown incrementally to complement global data repositories. Within such a network each database would pool data and expertise of the respective research field, while data users can retrieve data available across the entire network, for example, for a specific country or region. Taxon-specific databases can thus fill the niche between local data collectors and global data repositories.

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Supplementary Material

Advancing conservation planning for western chimpanzees using IUCN SSC A.P.E.S. – the case of a taxon-specific database

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1. Modeling chimpanzee density distribution

We fitted a Generalized Linear Mixed Model (Baayen 2008) with a negative binomial error distribution (Hilbe 2011). As commonly done for modeling ape densities (Murai *et al* 2013, Wich *et al* 2016, Strindberg *et al* 2018, Voigt *et al* 2018), we used an offset term consisting of effective strip width, proportion of nest builders, nest production rate, nest decay time, and transect length so that the model output directly expresses the number of individuals per km^2 and accounts for varying transect lengths (Heinicke *et al* 2019). This offset term was calculated as $D = N/(2 * L * \mathrm{ESW} * p * r * t)$ (D chimpanzee density, N number of nests, L transect length, ESW effective strip width, p proportion of nest builders, r nest production rate, t nest decay time; Kühl et al., 2008). The ESW was calculated based on the transect data using DISTANCE 6.2 Release 1 (Thomas *et al* 2010). Nest decay time was based on a nest decay time model from an earlier study (Heinicke *et al* 2019) for which we had fitted nest decay time as a function of rainfall. Further details on ESW and nest decay can be found in Heinicke et al. (2019).

To control for spatial autocorrelation of the residuals of the response, we derived a spatial autocorrelation term for the full model. For this we first extracted residuals for each data point from the full model. Separately for each data point we averaged the residuals of all other data points, and weighted each by the spatial distance to the focal data point. To derive the optimal standard deviation, we included the derived autocorrelation term as an additional predictor and maximized the log-likelihood of the full model.

All predictors were z-transformed to a mean of zero and standard deviation of one to facilitate model convergence. Distance to the closest river and distance to the closest road, as well as the spatial autocorrelation term, were included as control predictors (Mundry 2014). We fitted the following full model (details on each model term in Table S4):

number of nests per transect ~ cropland + date + environment + forest loss + human activity + hunting taboo + protected area + slope + socio-economic status + socio-economic status ^{2} + human activity:hunting taboo + human activity:slope + human activity:socio-economic status + human activity:socio-economic status ^{2} + hunting taboo:slope + hunting taboo:socio-economic status + hunting taboo:socio-economic status ^{2} + river + road + spatial autocorrelation + offset term.

To account for general differences between countries we included country as a random effect (Baayen 2008). As we only had one dataset each for Burkina Faso and Mali, the variation within a predictor covered by the transect data did not adequately reflect the variation encountered across the entire country. Consequently, the random slopes components could not be fitted reliably predictions and we, therefore, did not include random slopes for individual predictors within country, but only a random intercept for country. All models were fitted with the R function *glmer.nb* of the R package *lme4* (Bates *et al* 2015). We tested for multicollinearity using the R function *vif* of the package *car* (Fox and Weisberg 2011), applied to a standard linear model lacking the random effect, but this was not an issue (largest Variance Inflation factor = 3.54). As the check of model assumptions revealed a dispersion parameter of 1.96, we used the qAICc, the AIC corrected for overdispersion, in subsequent analyses (Burnham and Anderson 2002).

2. Identifying populations and low-connectivity areas

To estimate where connectivity between chimpanzee populations might be reduced, we first identified grid cells with a high likelihood of chimpanzee presence based on predicted chimpanzee density and expert opinion. As modeled density estimates never reach zero, a minimum density threshold had to be specified, below which chimpanzees are considered absent. Due to differences in group size and home- range size, these minimum thresholds are likely to differ depending on habitat and threat context, and there is no generally established minimum threshold for chimpanzee densities. Consequently, we used the judgment of chimpanzee experts with on-the-ground experience in the respective countries to determine minimum density thresholds by visually examining maps with thresholds that ranged from 0.001 to 0.1 individuals/km^2. The final minimum thresholds used were: Côte d'Ivoire: >0.02 in individuals/km^2, Ghana: >0.004, Guinea: >0.08, Guinea-Bissau: >0.08, Liberia: >0.03, Mali: >0.08, Senegal: >0.04, Sierra Leone: >0.05. Figure S1 shows additional results for analyses with the entire range of thresholds. We then added all presence points from the nest count surveys used above, with a buffer of 5 km, which is the approximate radius of the largest reported home-range size for western chimpanzees (90 km^2, Pruetz 2018). Lastly, we added polygons for areas for which surveys confirmed chimpanzee presence. This presence map was validated by chimpanzee experts who attended chimpanzee conservation action planning workshops in Guinea and Liberia in 2017 and suggested changes were incorporated accordingly.

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Table S1: Chimpanzee nest count datasets used in the study (reproduced from Heinicke *et al* 2019, CC BY 4.0).

Country	**Study site(s)**	**Survey year(s)**	**Reference**	**Survey type**
Burkina Faso	several sites	2012	Ginn *et al* 2013	recce
Côte d'Ivoire	Azagny NP	2007	WCF 2007a	transect
Côte d'Ivoire	Banco NP	2007-2008	WCF 2008	transect
Côte d'Ivoire	Banco NP	2008	WCF 2008	transect
Côte d'Ivoire	Cavally	2008-2009	WCF 2010a	transect
Côte d'Ivoire	Cavally	2010	WCF 2010a	transect
Côte d'Ivoire	Comoé	2009	WCF 2009b	transect
Côte d'Ivoire	Comoé	2012	WCF 2012c	transect
Côte d'Ivoire	Goin-Débé	2006-2007	WCF 2010a	transect
Côte d'Ivoire	Goin-Débé	2009-2010	WCF 2010a	transect
Côte d'Ivoire	Marahoué	2006	WCF 2006	transect
Côte d'Ivoire	Marahoué	2007	WCF 2007b	transect
Côte d'Ivoire	Mt Sangbé	2001	WCF 2001	transect
Côte d'Ivoire	Nationwide	2007	Campbell *et al* 2008	transect, recce
Côte d'Ivoire	Nimba	2008-2009	WCF 2009a	transect
Côte d'Ivoire	Tai NP	2013	WCF 2013a	transect
Côte d'Ivoire	Tai NP	2013-2014	WCF 2014a	transect
Côte d'Ivoire	Tai NP	2014-2015	WCF 2015	transect
Ghana	Atewa Range FR	2006	Granier and Awotwe-Pratt 2007	transect
Ghana	Bia Goaso	2009-2010	Danquah *et al* 2012	transect
Ghana	several sites	2006-2009	Gatti 2009	recce
Ghana	several sites	2015	PanAf	recce
Guinea	Bafing River	2013-2014	WCF 2014c	transect
Guinea	Foutah Djallon	2011-2012	WCF 2012a	transect
Guinea	Haut Niger NP	2001	Fleury-Brugière and Brugière 2010	transect
Guinea	Haut Niger NP	2002	Fleury-Brugière and Brugière 2010	transect
Guinea	Pic de Fon	2002	WCF 2002	transect
Guinea	several sites	2008-2011	WCF 2012a	transect
Guinea-Bissau	Boé	2013	Chimbo Foundation 2016 & PanAf	recce
Guinea-Bissau	Lagoas Cufada NP	2010	Carvalho *et al* 2013	transect
Guinea-Bissau	Lagoas Cufada NP	2011	Carvalho *et al* 2013	transect
Liberia	Gola NF	2011-2012	Hillers 2012	transect
Liberia	Grebo NF	2005-2006	Gamys 2006	transect

Liberia	Grebo NF	2012	WCF 2012b	transect
Liberia	Grebo NF	2013	PanAf	transect
Liberia	Nationwide	2010-2012	Tweh *et al* 2015	transect
Liberia	Nimba Arcelor Mittal	2010	WCF 2011	transect
Liberia	Nimba Arcelor Mittal	2011	WCF 2011	transect
Liberia	Nimba East	2013-2014	PanAf	transect
Liberia	Proposed Grebo NP	2013	WCF 2013b	transect
Liberia	Proposed Grebo NP	2014	WCF 2014b	transect
Liberia	Sapo NP	2009	WCF 2010b	transect
Liberia	Sapo NP	2012	PanAf & WCF	transect
Liberia	Sapo NP	2014	FFI 2014	transect
Mali / Guinea	APT Bafing-Falémé	2003-2004	Granier and Martinez 2004	transect
Senegal	Heremakhono	2013-2014	Wessling unpublished data	transect
Senegal	Kanoumering	2013-2014	Wessling unpublished data	transect
Senegal	Kayan	2012	PanAf	transect, recce
Senegal	Makhana	2013-2014	Wessling unpublished data	transect
Sierra Leone	Bumbuna	2013	Barrie 2016	transect
Sierra Leone	Gola RNP	2009	Ganas 2009	transect
Sierra Leone	Nationwide	2009-2010	Brncic *et al* 2015	transect

Table S2: Sources of the 20 predictor variables used (reproduced and modified from Heinicke *et al* 2019, CC BY 4.0).

Predictor	**Dataset**	**Variable used**	**Reference**	**Temporal resolution***	**Spatial resolution**
Conflicts	Armed conflict location and event data project (ACLED)	location of violent conflicts	Raleigh et al., 2010	1997-2015 (continuous)	point locations
Corruption control	Worldwide governance indicators	control of corruption (measures perception of extent of corruption, ranges from -2.5 to 2.5)	World Bank, 2015	2000-2014 (annually, not 2001)	country
Cropland	Global land cover MCD12Q1	land cover classified as 'cropland' and 'cropland/natural vegetation mosaic'	Friedl et al., 2010	2001-2012 (annually)	0.5 km
Education	Sub-national African education and infrastructure access data	net secondary attendance rate (proportion of children attending secondary school)	CCAPS, 2013	year of DHS/MICS survey (2005-2011)	subnational region
Forest loss	Global forest change – forest loss year	year of forest cover loss	Hansen et al., 2013	2000-2014 (annually)	0.03 km
Human density	AfriPop	estimated number of people	Linard et al., 2012	2010	0.0083° (ca. 0.10 km)
Hunting taboo	World religion database based on USAID demographic and health survey (DHS)	proportion of Muslims	Johnson and Grim, 2008	most recent DHS survey available in database (2003-2008)	subnational region
Malnourishment	World Health Organization global database on child growth and malnutrition	prevalence of stunting among 0-5 year-old children (stunting is the result of suboptimal health and/or nutritional conditions)	Onis and Blössner, 2003	1992-2013 (1-6 datasets per region)	subnational region
Nighttime light	Nighttime lights composite	stable lights (presence of lighting, is associated with intensity of economic activity, integer scale from 0 to 63)	NOAA, 2013	2000-2013 (annually)	30 arc sec (ca. 1.00 km)

Poverty	Multidimensional poverty index 2015 (based on most recent USAID demographic and health survey (DHS) and UNICEF multiple indicator cluster survey (MICS))	poverty index (ranges from 0 to 1)	Alkire and Robles, 2015	most recent DHS or MICS survey (2006-2014)	subnational region
Protected area	World Database of Protected Areas	National Parks and IUCN category I or II protected areas	UNEP-WCMC and IUCN 2017	2015	spatial outline of protected area
Rainfall	Tropical rainfall measuring mission (TRMM) 3B43	rainfall	TRMM and GES DISC, 2011	Jan 2000 – Oct 2015 (monthly)	0.25°
River	River-surface water body network (RWDB2)	location of rivers	FAO, 2007	2006	vector map
Road	Roads of the world (Vmap0)	location of roads	FAO, 2005	1997	vector map
Savanna	Global land cover MCD12Q1	land cover classified as ‘savanna’, ‘woody savanna’, ‘open shrubland’, or ‘closed shrubland’	Friedl et al., 2010	2001-2012 (annually)	0.50 km
Settlements	Global urban footprint	land cover classified as built-up area	Esch et al., 2012	2011/2012	0.084 km
Slope	Global multi-resolution terrain elevation data (GMTED2010)	slope (derived as maximum elevation change between a cell and its eight neighbours)	Danielson and Gesch, 2011	2010	7.5 arc sec (ca. 0.25 km)
Temperature	Land surface temperature and emissivity MOD11B3	day time land surface temperature	Wan and Hulley, 2015	Feb 2000 - Dec 2011 (monthly)	6.00 km
Tree cover	Vegetation continuous fields MOD44B	% tree cover	DiMiceli et al., 2011	2000-2010 (annually)	0.25 km
Vegetation height	Vegetation height estimate	average vegetation height	Woods Hole Research Center, 2007	2007	0.03 km

* ‘most recent’ refers to the latest data point prior to when the area was surveyed

Table S3: Details on data extraction and post-processing for each predictor variable (reproduced and modified from Heinicke *et al* 2019, CC BY 4.0).

Covariate	**Extraction radius**	**Data extraction per transect**	**Post-processing of extracted data per transect**	**Transformation for model/ factor analysis**
Conflicts	15km	number of conflicts within a circle around the transect midpoint weighted by inverse time lag in years between conflict and transect survey	none	none
Corruption control	20km	mean of values within the extraction radius (ER) around the transect, weighted according to the proportion with which the resulting area overlapped with different countries	we used the mean across all years	none
Cropland	5km	proportion of pixels within the ER around transect classified as cropland and cropland/natural vegetation mosaic	we used the mean across all years	square root (x)
Education	20km	mean of values within the ER around transect, weighted according to the proportion with which the resulting area overlapped with different subnational regions	none	none
Forest loss	5km	frequency of pixels with forest loss per year within the ER around transect	we used the proportion of pixels with forest loss for the years before the survey was conducted (excluding year of survey)	square root (x)
Human density	15km	mean of values within the ER around transect	none	log(x)
Hunting taboo	20km	mean of values within the ER around transect, weighted according to proportion with which the resulting area overlapped with different subnational regions	none	none
Malnourish-ment	20km	mean of values within the ER around transect, weighted according to the proportion with which the resulting area overlapped with different subnational regions (additional	we used the mean across all years	none

		information below in ‘Text 2: Malnourishment data extraction’)		
Nighttime light	50km	mean of values within the ER around transect	for details on how we derived the predicted value for each year refer below to ‘Text 3: Nighttime light data processing’; each transect was assigned the predicted value for the year the survey was conducted, all surveys conducted after 2013 were assigned the value for 2013	square root (x)
Poverty	20km	mean of values within the ER around transect, weighted according to the proportion with which the resulting area overlapped with different subnational regions	none	none
Protected area		whether the midpoint of a transect was within the boundaries of a protected area	none	none
Rainfall		mean of values of all pixels traversed by transect, weighted by transect length per pixel; for transects with NA for a certain month we used the mean of values of neighbouring pixels	to determine the seasonality in rainfall, we calculated the effect size (partial R^2) of season for each transect by comparing a model with date (in days) and season (sine and cosine of Julian date converted to radians) as predictor, and a model with only date as predictor (model based on regression with R function 'lm', model comparison with ‘anova’)	none
River		distance between transect midpoint and closest river in km	none	square root (x)
Road		distance between transect midpoint and closest road in km	none	square root (x)
Savanna	5km	proportion of pixels within the ER around transect classified as savanna, woody savanna, open shrubland, or closed shrubland	we used the mean across all years	none
Settlements	50km	mean of values within the ER around transect (original values were binary with 0 for ‘no settlement’ and 1 for ‘settlement)	none	square root (x)
Slope	2km	mean of values within the ER around transect	none	log(x)

Temperature		mean of values of all pixels traversed by transect, weighted by transect length per pixel; for transects with NA for a certain month we used the mean of values of neighbouring pixels	we used the mean across all months	none
Tree cover	5km	mean of values within the ER around transect	variation among years within transects was very large; for each transect we fitted a regression (R function ’lm’) with extracted values as response and date (in days) as a predictor, we then estimated tree cover for each year (R function ‘predict.lm’), each transect was assigned the predicted value for the year the survey was conducted, all surveys done after 2010 were assigned the value for 2010	none
Vegetation height	5km	mean of values within the ER around transect	none	none

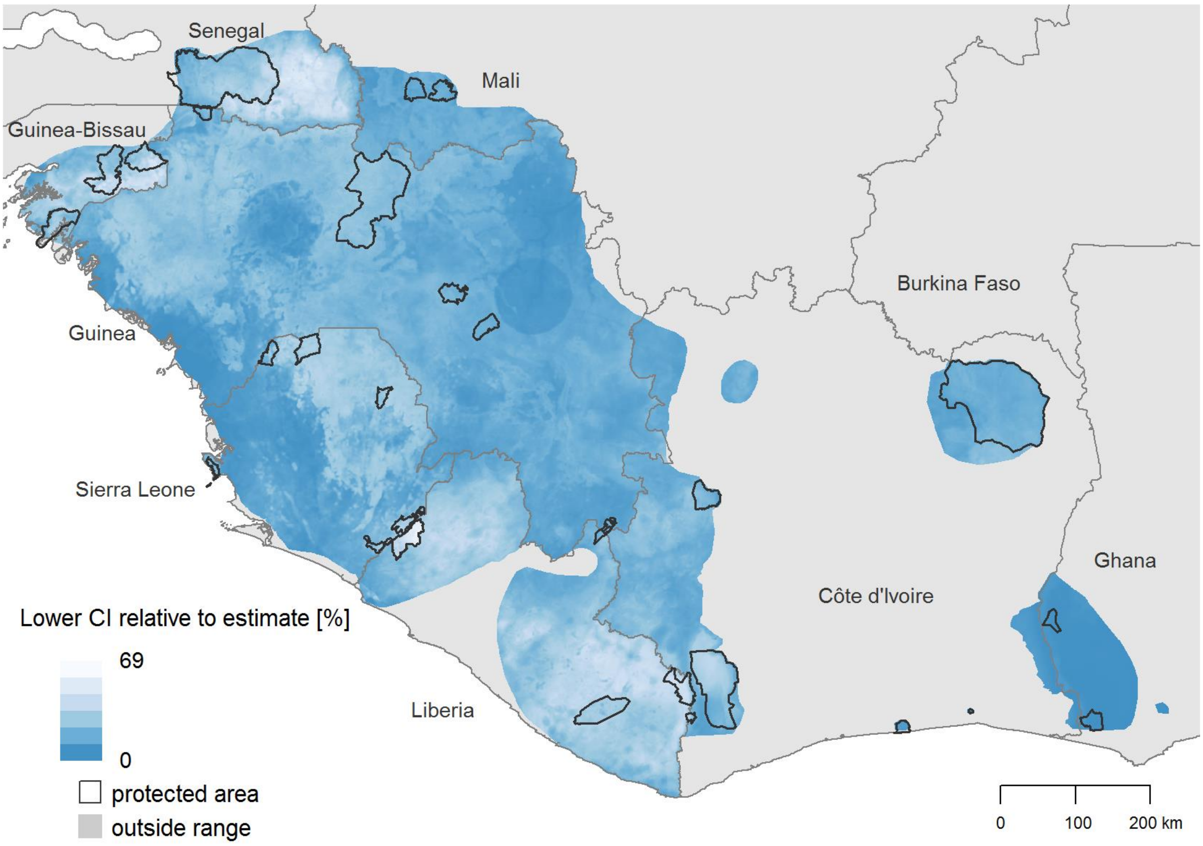
Table S4: Details on each model term in the full model.

type of model term	model term	additional explanation
response	number of nests per transect	
test predictor	cropland	
	date	date when transect was surveyed
	environment	derived from a factor analysis with temperature, proportion savanna and seasonality in rainfall loading positively, and percent tree cover and vegetation height loading negatively
	forest loss	
	human activity	derived from a factor analysis with settlements, human density, nighttime light and conflicts loading positively
	hunting taboo	measured as proportion of Muslims; due to cultural traditions Muslims are less likely to kill great apes for food than non-Muslims (Davis *et al* 2013); in areas with a higher proportion of Muslims there is a higher prevalence of cultural taboos against eating chimpanzee meat (Ham and Carter 1998).
	protected area	
	slope	
	socio-economic status ^{2}	derived from a factor analysis with education and corruption control loading positively and poverty and malnourishment loading negatively; we added a quadratic term based on the concept of the environmental Kuznets curve (Mills and Waite 2009), which postulates that improvement of the socio-economic status is accompanied by an increase in resource use resulting in environmental degradation, but that further economic growth allows a community or country to invest into environmental protection
	human activity * hunting taboo	The effect of hunting taboos increases when the intensity of human activity increases, because in areas with a very low intensity of human activity the pressure on chimpanzees might be too low to reveal the positive effect of hunting taboos.
	human activity * slope	The effect of steep terrain as a refuge area increases with increasing intensity of human activity in surrounding areas.
	human activity * socio-economic status ^{2}	The effect of socio-economic status increases with increasing intensity of human activity, because in areas with a low intensity of human activity the pressure on chimpanzees might be too low to reveal an effect of socio-economic status.
	hunting taboo * slope	The effect of steep terrain as a refuge area increases with decreasing hunting pressure, because the positive effect of steep terrain might not be observable in areas with very strong hunting pressure.
	hunting taboo * socio-economic status ^{2}	In areas with a high prevalence of hunting taboos changes in socio-economic conditions might impact chimpanzee densities, while there could be no such effect in areas without hunting taboos.

control predictors	distance to river	
	distance to road	
	spatial autocorrelation	to account for non-independence of the residuals of the response, details above (Supplementary Material 1.2)
offset term	offset term	calculated from number of nests, transect length, effective strip width, proportion of nest builders, nest production rate, nest decay time

Table S5: Number of chimpanzees and patch size for all large sub-populations plotted in color in figure 3 based on three minimum distance thresholds (3A) 5 km, (3B) 15 km and (3C) 25 km.

Figure	Patch ID	nr. of chimpanzees	patch size (in nr. of pixels)	patch colour (in Fig. 3)
3A	1	33,015	138,912	green
	2	7,095	38,105	blue
	3	2,698	39,298	red
	4	521	2,522	brown
	5	249	1,092	purple
	6	138	1,715	light green
	7	133	1,507	orange
	8	127	1,404	light blue
3B	1	41,518	187,905	green
	2	2,799	40,781	red
	3	133	1,507	orange
	4	125	3,695	purple
3C	1	44,498	232,515	green
	2	133	1,507	orange
	3	125	3,695	purple


Senegal
Mali
Guinea-Bissau
Burkina Faso
Guinea
Sierra Leone
Ghana
Côte d'Ivoire
Liberia
Lower CI relative to estimate [%]
69
0
☐ protected area
▨ outside range
0
100
200 km

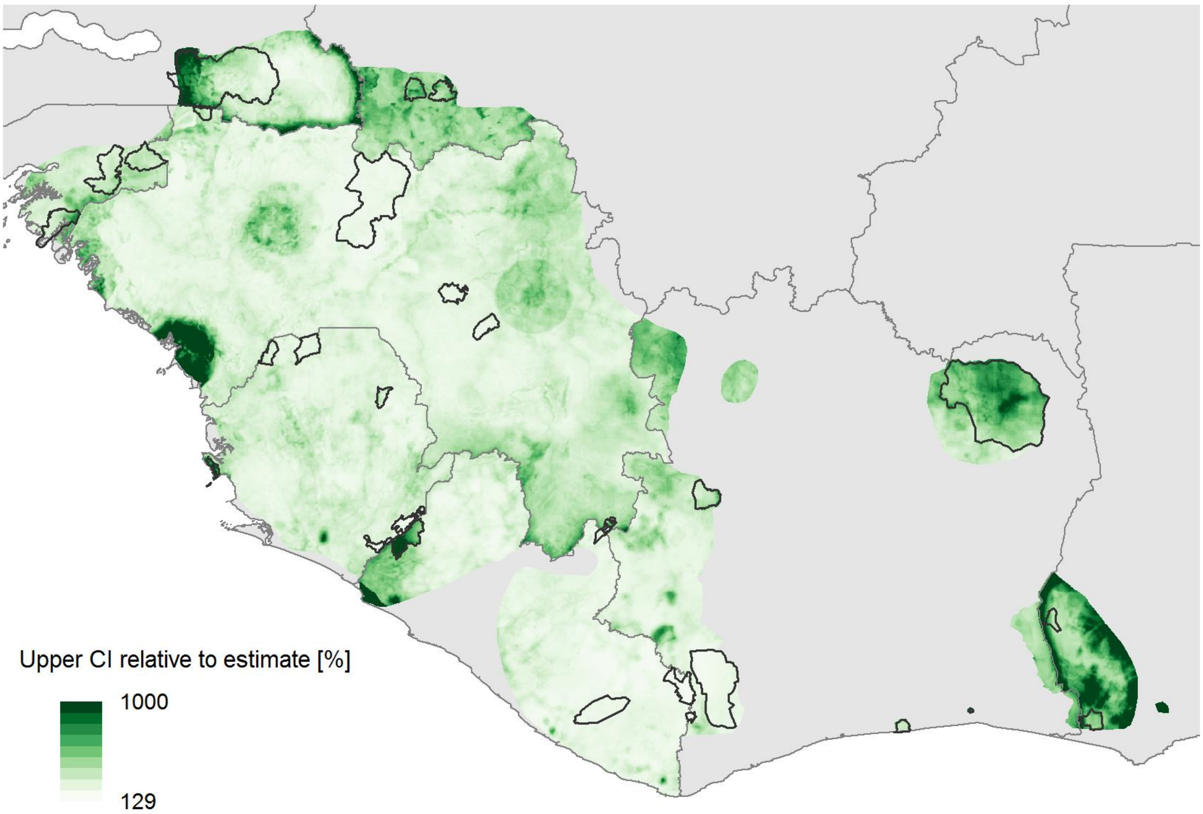
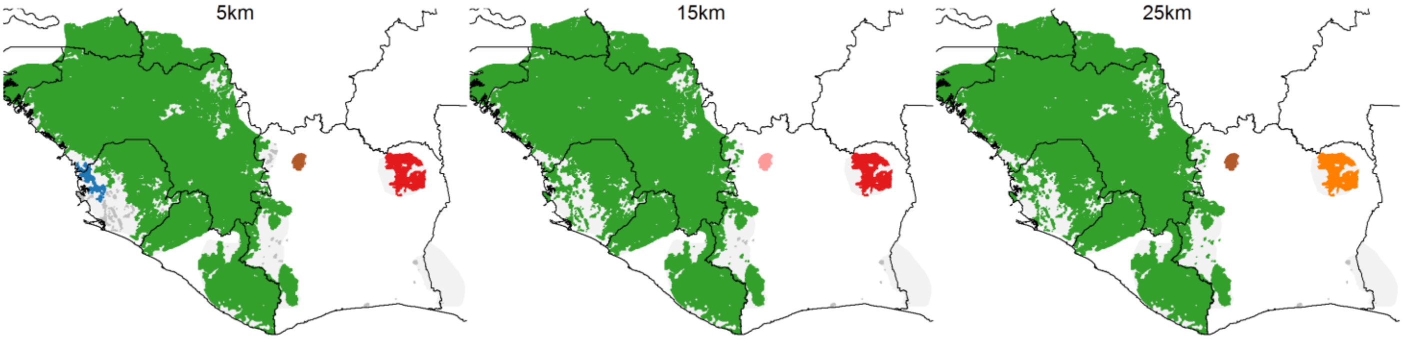
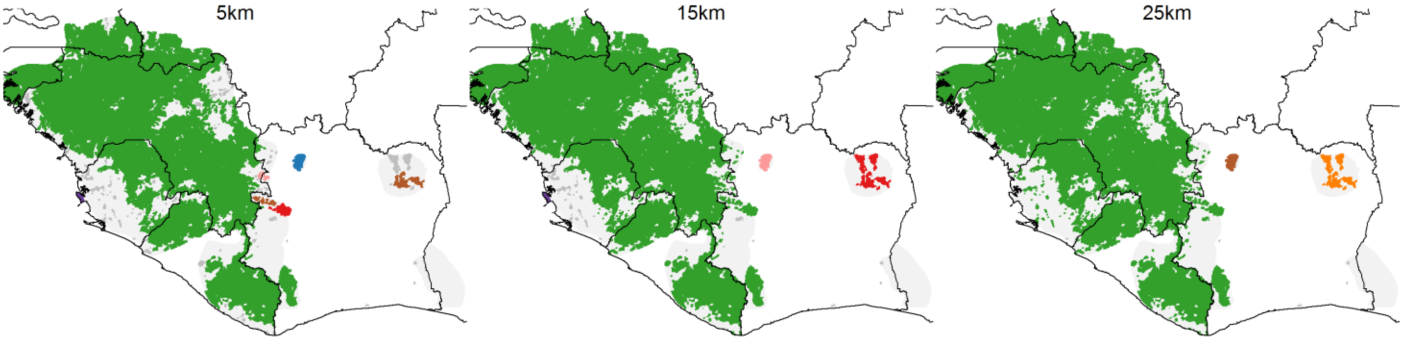

Upper CI relative to estimate [%]
1000
129

Figure S1: Lower and upper 95% confidence limits plotted for each cell of modeled chimpanzee density distribution. Values were calculated as percentage relative to estimated chimpanzee density from Figure 2, meaning that darker cells are associated with more uncertainty than lighter cells. Uncertainties are particularly high for cells for which fewer chimpanzee data were available and for which predictions were low. For the predictors 'settlement' and 'nighttime light' values were extracted for a radius of 50 km and averaged. The circles that can be seen in Guinea pertain to the increased uncertainty for areas around large towns or cities. Note that low chimpanzee densities were estimated for those areas (Figure 2).

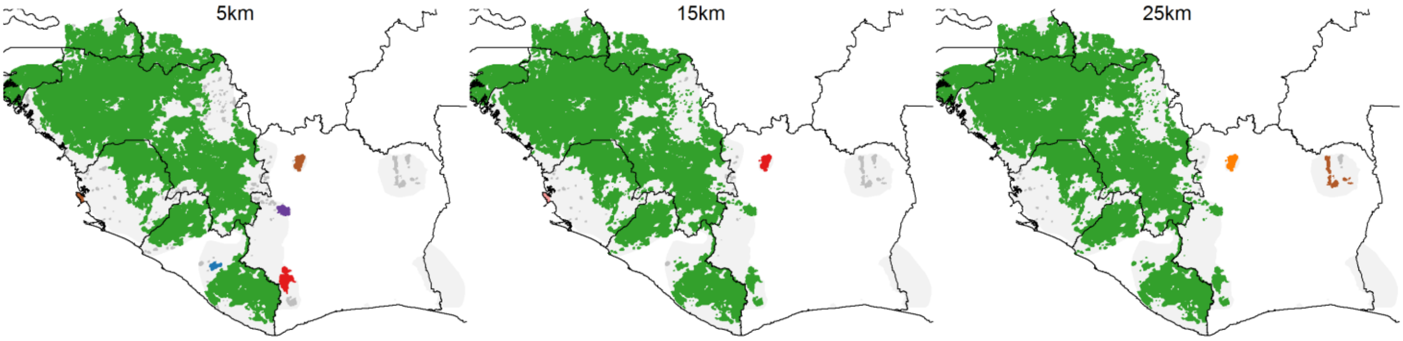
Pixels for density > 0.01 chimpanzees/km2

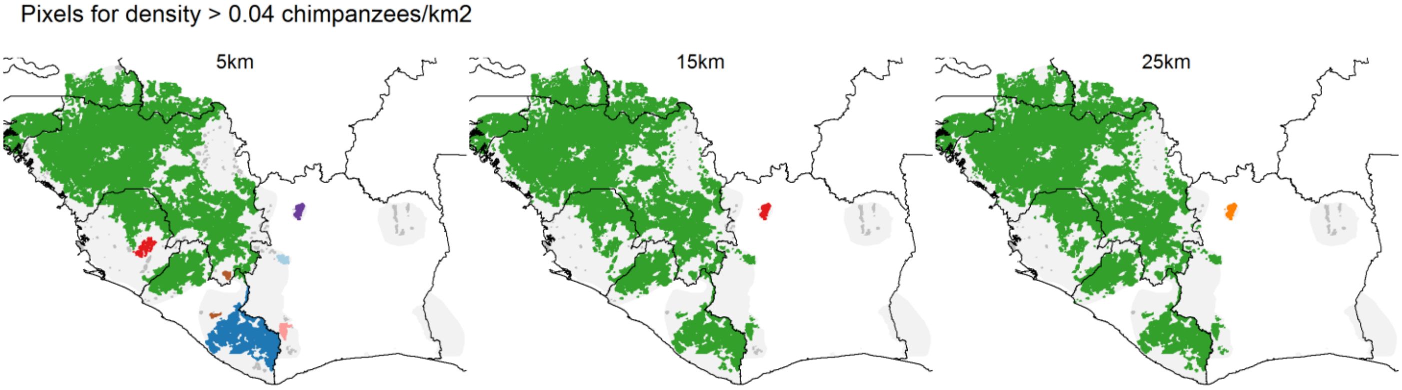


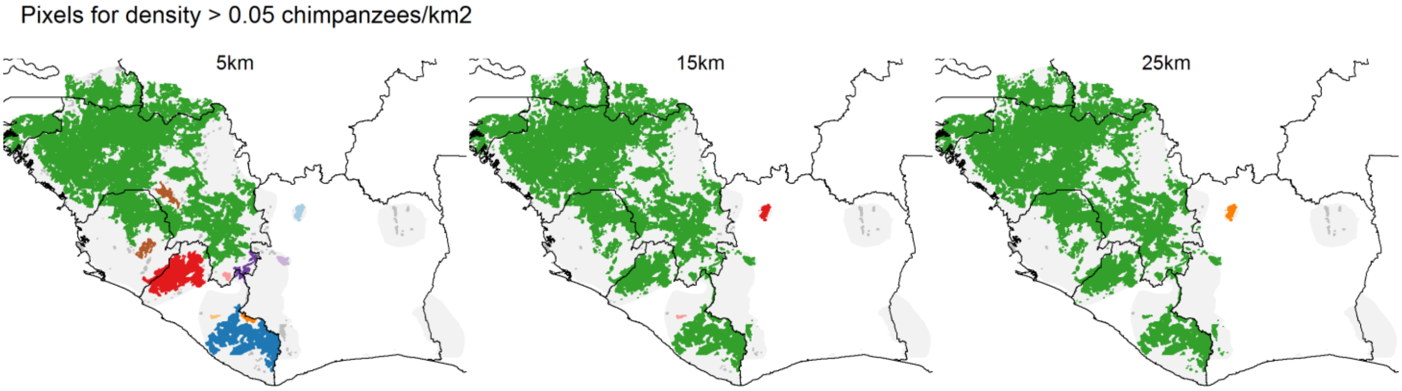
Pixels for density > 0.02 chimpanzees/km2

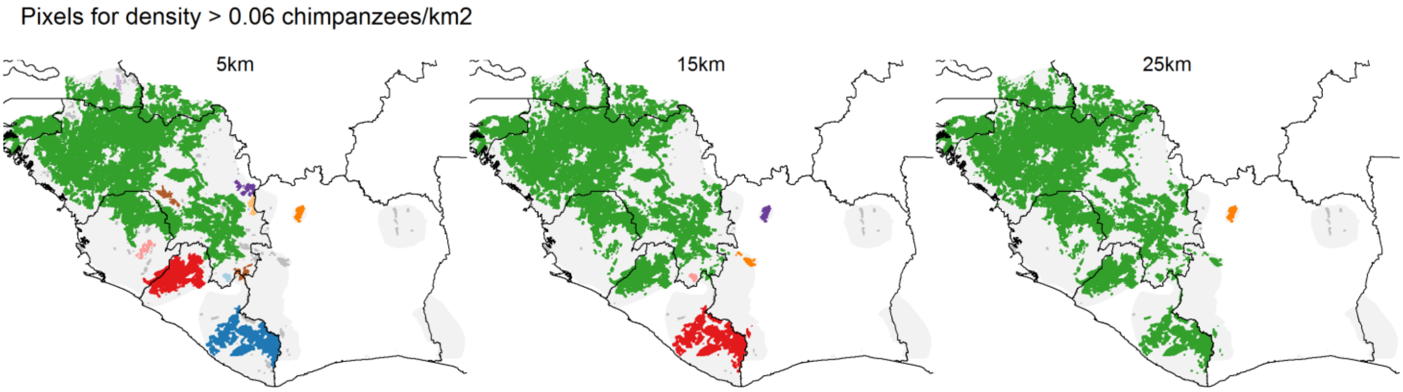


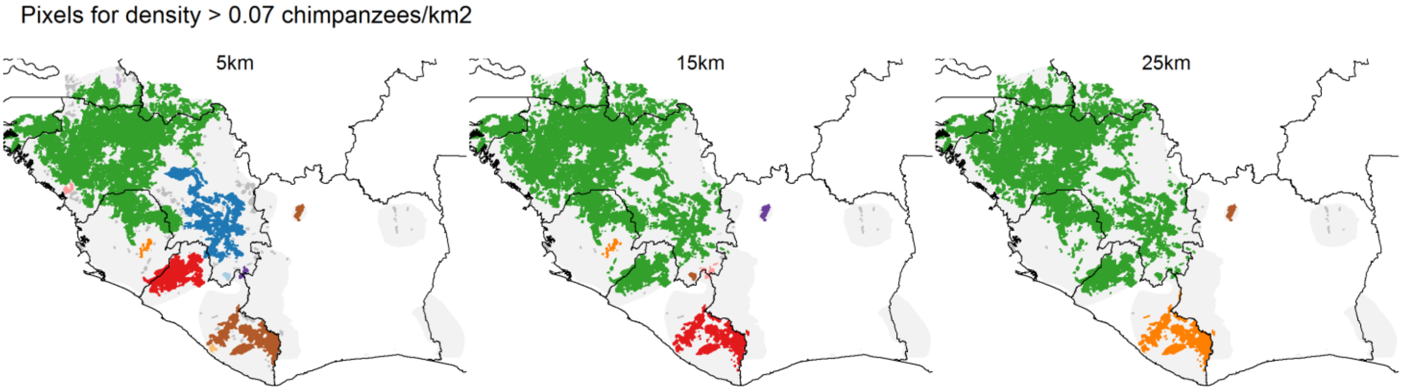
Pixels for density > 0.03 chimpanzees/km2




Pixels for density > 0.04 chimpanzees/km2
5km
15km
25km


Pixels for density > 0.05 chimpanzees/km2
5km
15km
25km


Pixels for density > 0.06 chimpanzees/km2
5km
15km
25km


Pixels for density > 0.07 chimpanzees/km2
5km
15km
25km

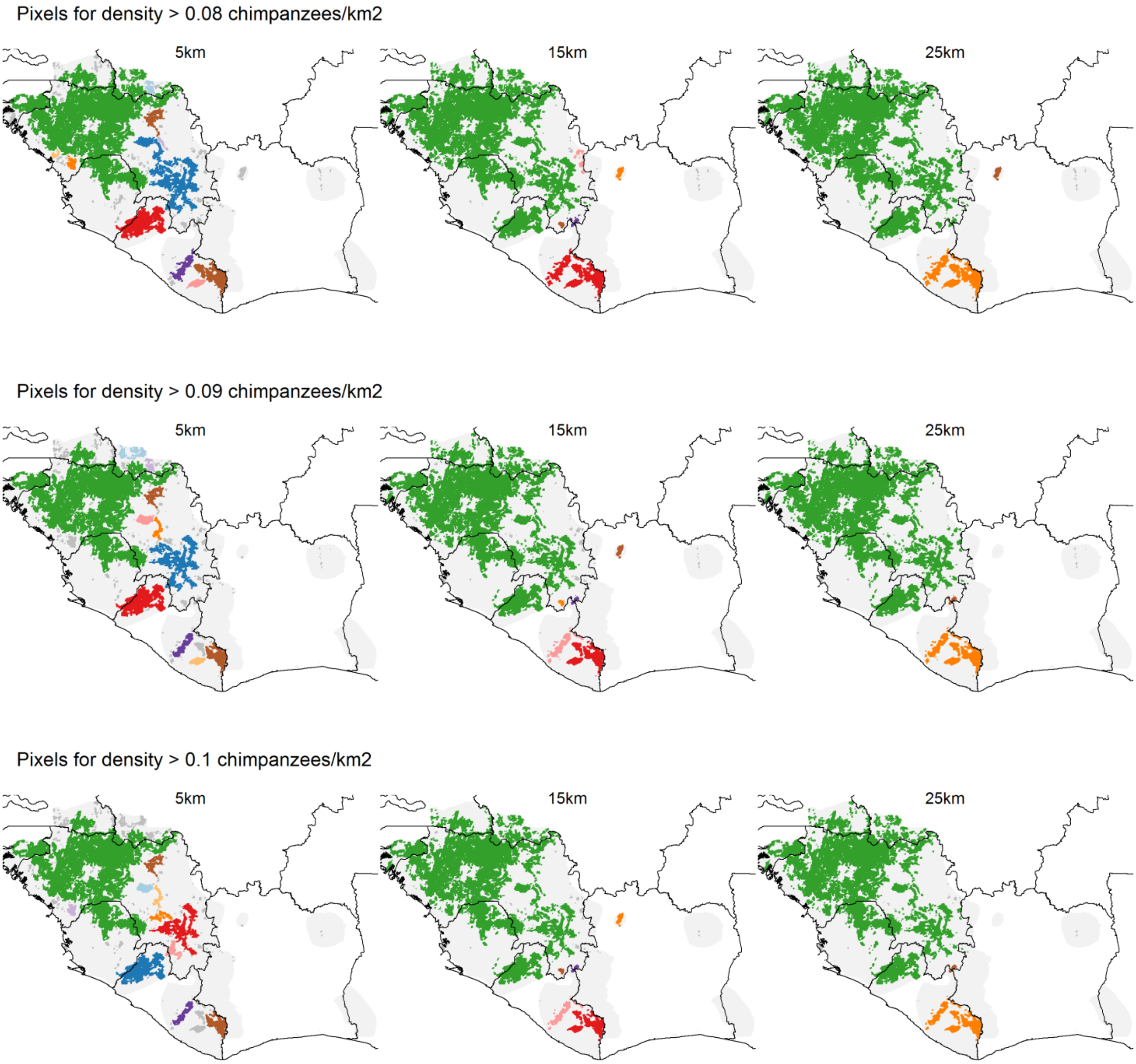


Figure S2: Results for population analyses using different chimpanzee density thresholds for assigning a cell as inhabited by chimpanzees for each minimum distance threshold, i.e., 5 km, 10 km, and 15 km.

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Chapter 3

Towards systematic and evidence-based conservation planning for western chimpanzees

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Towards systematic and evidence-based conservation planning for western chimpanzees

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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 dataset 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 27% 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 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 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 being characterized by large-scale forest loss (Song et al., 2018). Primate range countries are no exception to this with a 2 million km^2 loss in forest cover between 1990 and 2010 (Estrada et al., 2017). Rapid land-use change is typically caused by expansion of agriculture, logging, mining, hydropower dam construction, and infrastructure development, including roads and power transmission lines (Alamgir et al., 2017; 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; Johnson et al., 2017). Responding to these developments not only requires increased investment into conservation actions, but also strategic planning to distribute limited resources effectively while enabling a co-existence of production landscapes and areas under various protection regimes (Margules & Pressey, 2000).

One of the most commonly used frameworks in conservation is spatial planning (Kukkala & Moilanen, 2013; 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 (Groves & Game, 2016; Schwartz et al., 2018). This can take many forms, for example, identifying areas high in biodiversity or other ecosystem services (Asaad, Lundquist, Erdmann, & Costello, 2018; 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 (Schwartz et al., 2018), only few examples exist for primates. Primate occurrence data have been incorporated into studies that prioritize areas based on 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 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) due to a population decline of 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, due to 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 (AfDB, 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 that conservation activities 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; Hadorn, Bradley, Pohl, Rist, & Wiesmann, 2006; Pressey & Bottrill, 2008). The socio-economic 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 Ebola virus disease epidemic 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, 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 into 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 efforts.

This can strengthen partnerships with government agencies and, to some degree, counter balance interests of powerful corporations or investors.

The aim of this study was therefore 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 badius temminckii*), king colobus (*Colobus polykomos*), Pygmy hippopotamus (*Choeropsis liberiensis*), forest elephant (*Loxodonta africana*), African golden cat (*Profelis aurata*), and African wild dog (*Lycaon pictus*) (Bersacola et al., 2018; T. 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 fact that 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 states in its environmental guidelines that mitigations measures have to be implemented to avoid or minimize negative impact of a project on great apes (IFC, 2012). 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. 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; Heinicke et al. 2019a). 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 (details in Heinicke et al. 2019b). This data layer has a spatial resolution of half a minute (of a longitude / latitude degree, approximately 0.9 x 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, and 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 required area, and minimizing area fragmentation. The 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: (1) by chimpanzee abundance and (2) by area size. Specifically this means 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, while 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 (1a) across the geographic range of western chimpanzees, (1b) in each range country, and (1c) separately for each of the three largest populations. These were implemented for targets ranging from protecting 10 to 90% of chimpanzee abundance, in 10% steps. 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, because this is 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 it has been shown that 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 (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007; van Teeffelen, Vos, & Opdam, 2012). Second, chimpanzees differ strongly across sites regarding their behavioral repertoire (e.g., Kühl et al., 2019, 2016; Whiten et al., 1999). 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: (2a) area with highest chimpanzee densities, and (2b) 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). We chose an area target of 17% following the Aichi target 11 of the Convention on Biological Diversity which states to protect at least 17% of the terrestrial area of each country and which all countries within the western chimpanzee range have signed (UN, 2019). This 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 to 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 aimed at maximizing 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 socio-economic predictor variables). While conservation planning software programs are very powerful, they can be perceived as a ‘black box’ by stakeholders and this 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 to 90% of chimpanzee abundance) or area target (i.e., 17 to 50% of 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 implies that for the first three 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 scenario and target: from a total of 108 runs (because analyses were done separately by country and population for some of the 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 region, 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). Specifically, cells of high conservation value to chimpanzees were in Moyen Bafing in Guinea, Outamba and Loma 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). This was 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 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 (1c) selected a larger area than the range-wide scenario.

Of the areas selected in the second scenario (2a, 17-50% of area per country), 24.33% 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 (2b) identified cells in Guinea in the Fouta Djallon, 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' 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 Guinea, Mt. Sangbé in Côte d'Ivoire, and the cross-border area at Oure Kaba in Guinea and Outamba in Sierra Leone (but see below for discussion of limitations and uncertainties of this analysis). 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' 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 they work at 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 to 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 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 (Pressey et al., 2007; van Teeffelen et al., 2012). As it has been proposed that behavioral diversity needs to be considered in conservation planning for chimpanzees (e.g., Kühl et al., 2019) protecting a diversity of areas can be one way of accounting for intra-specific behavioral variation by covering different habitat types and degrees of anthropogenic influence. However, more specific analyses would be needed once detailed information on genetic and behavioral composition of individual chimpanzee communities can be determined and approaches for how to account for this in conservation planning have been designed.

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 2b). Main differences were that for the priority areas ‘Haute Sassandra & Mount Péko’ and ‘Marahoué’ chimpanzees are thought to now be extirpated (Kühl et al., 2017), likely due to hunting and large-scale deforestation (Geneviève Campbell, 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’ has contracted since 2003, driven by 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’ (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). 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).

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. Of particular note are Guinea-Bissau, Mali and Senegal for which limited data were available, and thus 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 and overestimated for the Simandou and Karandou ranges in eastern Guinea. Field surveys for data-scarce areas are needed to ground-truth the input chimpanzee density distribution and this analysis (details, including map of survey gaps, in Heinicke at al. 2019a).

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. 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. Moyen Bafing in Guinea is in the final stages of official designation. Still, only 17% of chimpanzees occur in high-level protected areas (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 socio-economic effects of protected areas on communities living inside and immediately adjacent to protected areas (West, Igoe, & Brockington, 2006). With research showing both, positive (Braber, Evans, & Oldekop, 2018; Naidoo et al., 2019) and negative effects (Poudyal et al., 2018), it is now well-established that social and ecological concerns need to be considered in protected area planning and governance (Pagdee, Kim, & Daugherty, 2006; 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 to 3). Even though collaboration across international borders is challenging, for example, due to 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, 2012; Kormos et al., 2014; Laurance, 2018). Therefore, the results of this study can be used to inform mitigation measures by, for example, identification of areas that should be avoided by such projects (e.g., 'no-go zones'). Furthermore, areas that are particularly important to western chimpanzees could require a higher mitigation 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 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 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. This might require incorporating expert opinion for under-surveyed areas, for example, following the approach by Pérez-García et al. (2017). This should be followed by a consultation process with government, local communities, and representatives from industry, to ultimately incorporate chimpanzee conservation priorities with national biodiversity and development targets. 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.

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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] §**	**Proportion of high-level protected areas relative to total area [%] §**	**Estimated chimpanzee abundance (95% confidence interval)**
Côte d'Ivoire	324 108	20 407.86	6.30	1,093 (329 – 3,299 ; Heinicke et al. 2019a)
Ghana	240 330	11 512.50	4.79	24 (1 – 212; Heinicke et al. 2019a); 264 (18–843; Danquah, Oppong, Akom, & Sam, 2012)
Guinea	246 427	8 136.00	3.30	33,139 (8,796 – 68,203; Heinicke et al. 2019a)
Guinea-Bissau	34 016	5 326.10	15.66	1,908 (923 – 6,121; Heinicke et al. 2019a)
Liberia	96 634	3 879.88	4.02	6,050 (2,902 – 13,690; Heinicke et al. 2019a), 7,008 (4,260–11,590; Tweh et al. 2015)
Mali	1 256 684	1 930.49	0.15	2,029 (322 – 9,228; Heinicke et al. 2019a)
Senegal	197 924	9 959.79	5.03	2,642 (1,077 – 13,293; Heinicke et al. 2019a)
Sierra Leone	72 709	2 471.58	3.40	5,580 (3,052–10,446; Brncic, Amarasekaran, & McKenna, 2010), 5,925 (1,951 – 12,668; Heinicke et al. 2019a)

§ 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).

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]	Proportion of chimpanzees occurring in high-level protected area § [%]	Overlap with priority areas identified by Kormos and Boesch (2003) [%]
1) by chimpanzee abundance	1a) across range	10%	5 323	4 708	57.28	91.53
		20%	10 644	13 243	44.50	70.45
		30%	15 956	24 845	34.68	67.55
		40%	21 275	40 509	27.83	62.72
		50%	26 586	59 805	24.37	59.64
		60%	31 889	85 487	21.68	55.84
		70%	37 149	118 567	20.03	51.75
		80%	42 403	166 324	18.67	47.14
		90%	47 640	244 478	17.42	42.20
	1b) by country	10%	5 336	6 570	53.01	77.54
		20%	10 628	17 460	44.21	70.39
		30%	15 929	32 131	35.93	68.03
		40%	21 236	51 466	29.80	69.18
		50%	26 542	75 076	26.33	64.28
		60%	31 817	105 828	23.70	61.10
		70%	37 094	146 376	21.73	57.45
		80%	42 355	199 846	19.87	51.97
		90%	47 616	286 009	18.23	45.20
	1c) by population	10%	5 223	5 508	48.56	79.30
		20%	10 393	15 067	41.51	68.01
		30%	15 525	27 149	34.76	62.88
		40%	20 634	43 011	30.22	62.84
		50%	25 679	62 434	25.75	60.47
		60%	30 557	85 676	22.89	56.76
		70%	35 305	114 585	20.58	52.85
		80%	39 844	150 075	19.02	48.84
		90%	44 078	195 341	18.11	45.39
2) by area size	2a) by country	17%	34 643	193 640	24.12	56.49
		20%	36 943	216 849	23.02	55.07
		30%	42 671	267 036	20.35	51.90
		40%	46 385	312 021	18.89	48.05
		50%	48 785	354 586	18.01	44.58
	2b) by country added to current protected areas	17%	33 418	177 598	26.34	59.61
		20%	35 946	198 244	24.48	56.88
		30%	41 968	259 784	20.97	52.51
		40%	45 831	302 383	19.20	48.61
		50%	48 385	344 998	18.19	45.18

§ 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).

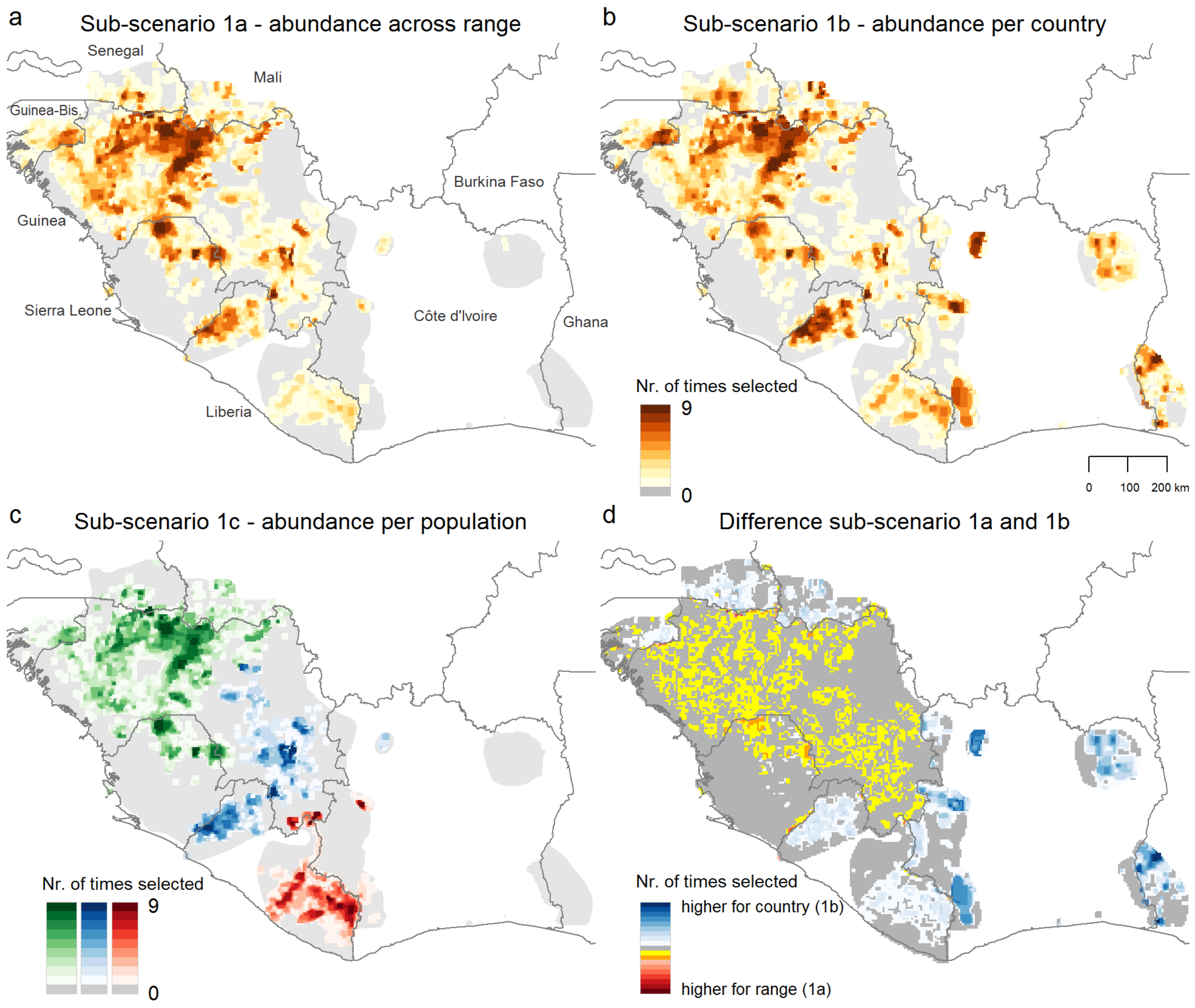
a
Sub-scenario 1a - abundance across range
Senegal
Mali
Guinea-Bis.
Guinea
Burkina Faso
Sierra Leone
Côte d'Ivoire
Ghana
Liberia
b
Sub-scenario 1b - abundance per country
Nr. of times selected
9
0
0
100
200 km
c
Sub-scenario 1c - abundance per population
Nr. of times selected
9
0
d
Difference sub-scenario 1a and 1b
Nr. of times selected
higher for country (1b)
higher for range (1a)

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 10-90% of chimpanzee abundance in 10% steps. Panel (d) illustrates the difference between sub-scenario (1a) and (1b).

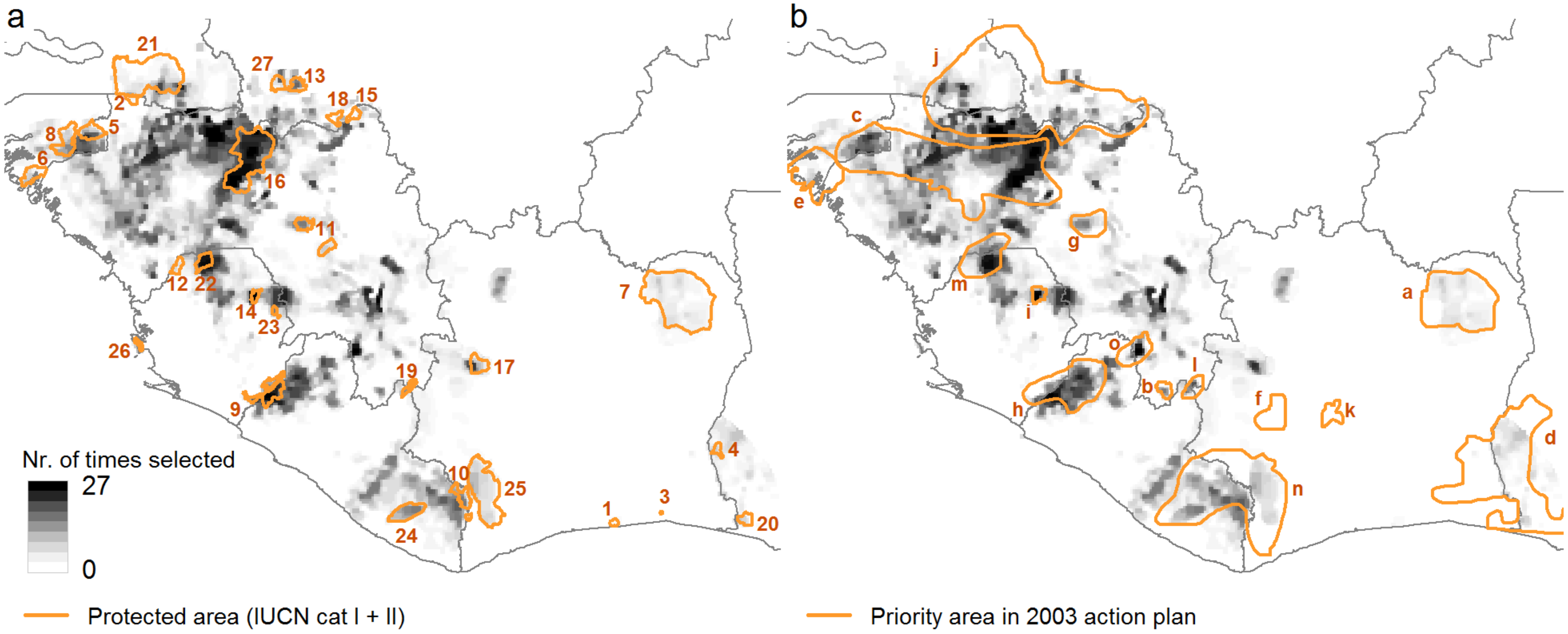

Figure 2. Mapped areas of high conservation value for western chimpanzees summed up for all three sub-scenarios based on chimpanzee abundance (i.e., the number of times a cell was selected was summed up across scenarios 1a-c). Shown is the overlap with (a) high-level protected areas (i.e., national park 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 Tai, 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.

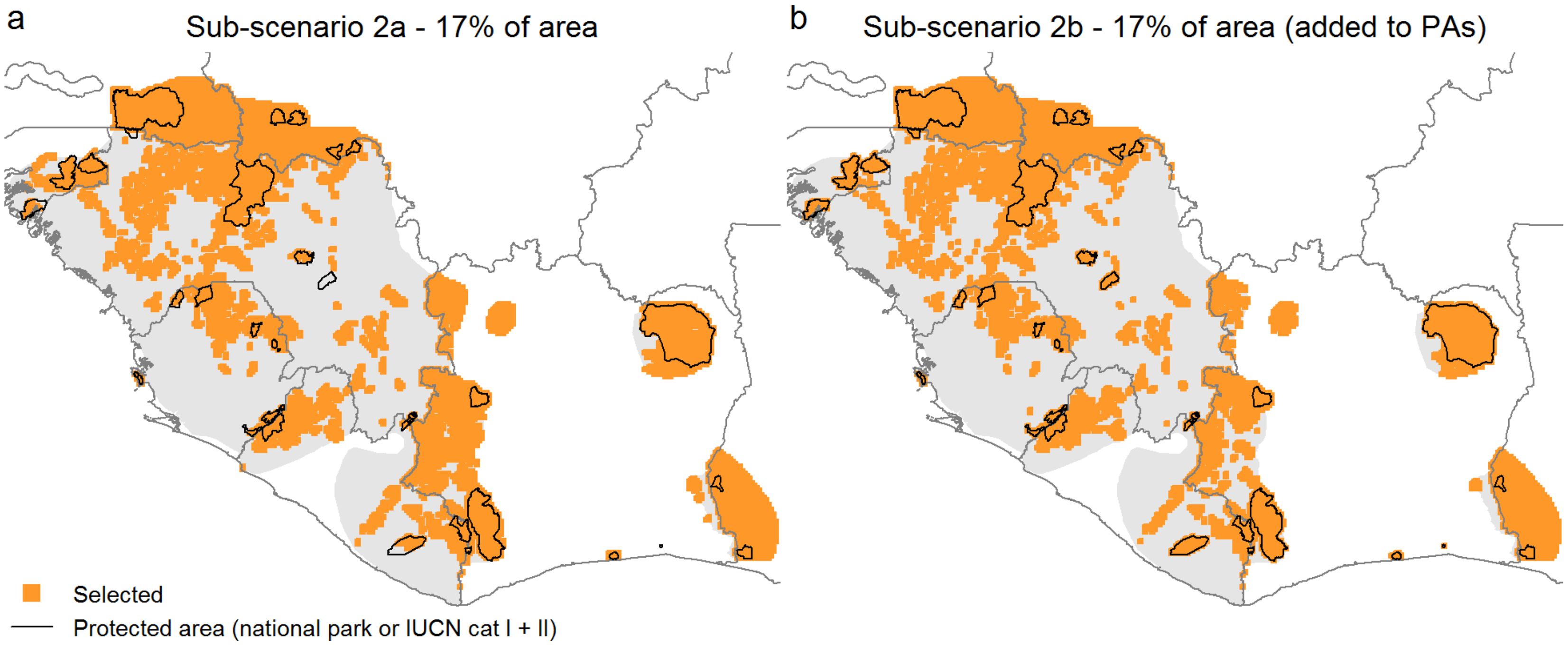

Figure 3. Mapped areas of high conservation value for western chimpanzees for the second scenario based on area size for 17% of the terrestrial area in each country with (a) highest chimpanzee density alone and (b) highest chimpanzee density in addition to high-level protected areas (i.e., national park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

Supporting Information

Towards systematic and evidence-based conservation planning for western chimpanzees

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Supporting methods

Pseudo code for optimization algorithm

```
1. Sort cells by decreasing chimpanzee abundance
2. Select initial set of cells. For this include cells beginning with the cell with largest chimpanzee abundance until the cumulative abundance reaches the proportion of the total abundance to be protected (e.g., for a scenario with a target of 10% of chimpanzee population, all cells with the highest chimpanzee abundance that together make up 10% of the chimpanzee abundance are selected).
3. For this initial set of cells determine the following parameters:
    total area
    total edge length (i.e., not considering edges between neighboring cells)
    ruggedness (i.e., total edge length / total area)
    radius of a circle of the size of the total area (i.e., the radius a perfectly round selected area would have)
    ideal ruggedness (i.e., the edge length to area ratio the above circle has, namely 2/radius)
4. Iteratively change the set of cells selected: at each iteration first one or several cells are removed from those currently selected and subsequently one or several cells that were not included prior to the removal were included
    4.1. removal
    -is done iteratively (i.e., cell by cell) as long as the proportion of chimpanzee abundance of the currently selected cells is larger than the targeted proportion of chimpanzee abundance
    -criteria for exclusion: cell which leads to the greatest decrease in the overall ruggedness of the set of selected cells (when several cells revealed the same change in the overall ruggedness the one with the smallest abundance was excluded)
    4.2. inclusion
    -is done iteratively (i.e., cell by cell) as long as the proportion of chimpanzee abundance of the currently selected cells is smaller than the targeted proportion of chimpanzee abundance
```

-criteria for inclusion: cell which leads to the smallest increase in the overall ruggedness of the selected area (when several cells revealed the same change in the overall ruggedness, the one with the largest abundance was included)

→ Over the course of the iterations, the total area of the selected cells increases and the total ruggedness of the selected area decreases. As a consequence, the ratio of ideal area to current area decreases and the ratio of ideal ruggedness to current ruggedness increases.

5. The algorithm stops when the current configuration of selected cells reveals a value for (ideal area / current area)*(ideal ruggedness / current ruggedness) that is smaller than or equal to that of the previous configuration.

R code for function used for the first scenario based on abundance targets

```
# exemplary for 20% of abundance to be protected
# argument map expects a matrix with abundance values for each cell and rows and columns for latitude and
# longitude bands

find.prop.ab<-function(map, prop.to.protect=0.2){

  ## 1. Sort cell values by decreasing chimpanzee abundance
  xx=rev(sort(unlist(map)))

  ## 2. Select initial set of cells
  #determine abundance threshold to be selected
  thresh=xx[min(which(cumsum(xx)/sum(xx)>=prop.to.protect))]
  #determine initial set of cells proposed to be selected
  in.pa=map>=thresh
  colnames(in.pa)=colnames(map)
  rownames(in.pa)=rownames(map)

  ## 3. For this initial set of cells determine the following parameters:
  ideal.area=sum(in.pa, na.rm=T)           #total area
  long.map=which(in.pa, arr.ind=T          #create object to be used later; comprises only the currently #selected
                                           cells
  tot.circ=sum(4-n.neighb(xmap=long.map))  #total edge length (uses a function n.neighb which determines per #cell in
                                           long.map the number of immediately adjacent cells that #are also in
                                           long.map)
  current.ruggedness=tot.circ/sum(in.pa, na.rm=T)      #ruggedness
  rad=sqrt(sum(in.pa, na.rm=T)/pi)                     #radius of a circle with the area that was selected
  ideal.ruggedness=2/rad                               #ideal ruggedness
  xcount=0

  # save all parameters in data.frame (i.e., corresponds to process output from Table S2)
  all.res=data.frame(
       iteration=xcount, current.ab=sum(map[in.pa], na.rm=T), current.rug=current.ruggedness,
       current.prop.inside=sum(map[in.pa], na.rm=T)/sum(map, na.rm=T),
       area.score=1, rug.score=(ideal.ruggedness/current.ruggedness),
       comb.score=(1)*(ideal.ruggedness/current.ruggedness), #times (1) because ideal.area/current.area is 1 #during
                                                             the initial setup
```

```r
    n.sel.cells=sum(in.pa, na.rm=T))
    old.comb.score=(1)*(ideal.ruggedness/current.ruggedness)

## 4. Iteratively change the set of cells selected
continue=T
while(continue){
  # 4.1. removal
  #remove 1 cell; criterion: ruggedness (if tied observation: criterion abundance)
   if(sum(map[in.pa], na.rm=T)/sum(map, na.rm=T)>prop.to.protect){ #if proportion selected is larger than #the
                                                                   proportion aimed at
   print(c(xcount, -1))                 #print process progress on monitor
   long.map=which(in.pa, arr.ind=T)     #create object for later processing
   n.inside=nrow(long.map)-1            #-1 because one is to be removed
   #determine total circumference for each cell in area being removed:
   e1 <- new.env(parent = baseenv())
   assign(x="long.map", value=long.map, envir=e1)
   assign(x="n.neighb", value=n.neighb, envir=e1)
   clusterExport(cl=cl, varlist=c("long.map", "n.neighb"), envir=e1)  # for parallelization
   tot.circ=unlist(parLapply(cl=cl, X=1:nrow(long.map), fun=function(x){
     sum(4-n.neighb(xmap=long.map[-x, , drop=F]))
   }))
   current.ruggedness=tot.circ/n.inside#edge to area ratio of the current PA configuration
   #determine ruggedness for all possible configurations derived when excluding currently selected cells #one at a
   time:
   to.sel=which(current.ruggedness==min(current.ruggedness))   #indices of candidate cells to be #removed (those
                                                               that minimize ruggedness)
   ab.of.cand=map[as.matrix(long.map[to.sel, , drop=F])]  #determine abundance of candidate cells loss in #new
                                                          selection
   to.sel=to.sel[ab.of.cand==min(ab.of.cand)]       #keep indices of candidate cells with min. abundance
   to.sel=resample(to.sel, 1)                       #in case there are >1 left: randomly select one cell
   xx=in.pa[as.matrix(long.map[to.sel, , drop=F])]
   in.pa[as.matrix(long.map[to.sel, , drop=F])]=F #exclude the finally chosen cell from the selected #ones
  }

  # 4.2. inclusion
  #add 1 cell; criterion: ruggedness (if tied obs: criterion abundance)
  while(sum(map[in.pa], na.rm=T)/sum(map, na.rm=T)<prop.to.protect){ #while proportion selected cells is #smaller
                                                                     than aimed at
   print(c(xcount, 1))                          #print process progress on monitor
```

```
  long.map=which(in.pa, arr.ind=T)
  n.inside=nrow(long.map)+1                  # +1 because one is to be added
  out.rows=long.map                          # begin with the cells currently selected
  out.rows=rbind(                            # determine their immediately adjacent neighbors
    cbind(out.rows[, 1], out.rows[, 2]-1),
    cbind(out.rows[, 1], out.rows[, 2]+1),
    cbind(out.rows[, 1]-1, out.rows[, 2]),
    cbind(out.rows[, 1]+1, out.rows[, 2])
  )
  #some formatting:
  out.rows=out.rows[!duplicated(out.rows), ] #remove duplicate cells
  out.rows=as.data.frame(out.rows)
  names(out.rows)=colnames(long.map)
  out.rows=subset(out.rows, row>0 & row<=nrow(in.pa) & col>0 & col<=ncol(in.pa)) #remove cells outside #the
                                                                           borders of the input map
  xx=in.pa[as.matrix(out.rows)]  #remove cells from out.rows that already are selected
  out.rows=subset(out.rows, !is.na(xx)) #remove cells not having an abundance value (e.g., because they #are
                                       outside of the country considered or subspecies' range)
  xx=in.pa[as.matrix(out.rows)]
  out.rows=subset(out.rows, !xx)      #remove cells that are already selected
  #determine circumference for each scenario (i.e., cell to be added)
  e1 <- new.env(parent = baseenv())
  assign(x="long.map", value=long.map, envir=e1)
  assign(x="n.neighb", value=n.neighb, envir=e1)
  assign(x="out.rows", value=out.rows, envir=e1)
  clusterExport(cl=cl, varlist=c("long.map", "n.neighb", "out.rows"), envir=e1)
  tot.circ=unlist(parLapply(cl=cl, X=1:nrow(out.rows), fun=function(o){
    long.map2=rbind(long.map, out.rows[o, , drop=F])
    return(sum(4-n.neighb(xmap=long.map2)))
  }))
  current.ruggedness=tot.circ/n.inside #edge to area ratio of the current PA configuration one per #possible
                                      scenario
  to.sel=which(current.ruggedness==min(current.ruggedness))  #indices of candidate cells to be included #(those
                                                            that minimize ruggedness)
  ab.of.cand=map[as.matrix(out.rows[to.sel, , drop=F])]  #abundance of candidate cells to be removed
  to.sel=to.sel[ab.of.cand==max(ab.of.cand)]       #keep indices of candidate cells with max. abundance
  to.sel=resample(to.sel, 1)                       #in case there are >1 left: randomly sample 1 cell
  in.pa[as.matrix(out.rows[to.sel, , drop=F])]=T   # mark chosen cell as selected
}
```

```
    long.map=which(in.pa, arr.ind=T)
    #determine new parameters for current iteration:
    tot.circ=sum(4-n.neighb(xmap=long.map))
    current.ruggedness=tot.circ/sum(in.pa, na.rm=T)
    rad=sqrt(sum(in.pa, na.rm=T)/pi)
    ideal.ruggedness=2/rad#circumference to area ratio of an ideal circle with the given area
    current.area=sum(in.pa, na.rm=T)
    current.comb.score=(ideal.area/current.area)*(ideal.ruggedness/current.ruggedness)
    xcount=xcount+1
    #... and store them in object comprising process details
    all.res=rbind(all.res, data.frame(
      iteration=xcount, current.ab=sum(map[in.pa], na.rm=T), current.rug=current.ruggedness,
      current.prop.inside=sum(map[in.pa], na.rm=T)/sum(map, na.rm=T),
      area.score=ideal.area/current.area, rug.score=(ideal.ruggedness/current.ruggedness),
      comb.score=current.comb.score,
      n.sel.cells=current.area))
    image(in.pa, main=xcount)

## 5. algorithm stops when the current configuration of selected cells reveals a value for (ideal area / current
area)*(ideal ruggedness / current ruggedness) that is smaller than or equal to that of the previous configuration:
   if(current.comb.score<=old.comb.score){
     continue=F
   }else{
     old.comb.score=current.comb.score
   }
  }
  return(list(process=all.res, in.pa=in.pa))
}

# Function used above to determine for each cell in a map the number of neighbors
n.neighb<-function(xmap){
  xres=unlist(lapply(1:nrow(xmap), function(xrow){
    return(
      sum((abs(xmap[xrow, 2]-xmap[-xrow, 2])==1) & (abs(xmap[xrow, 1]-xmap[-xrow, 1])==0))+
      sum((abs(xmap[xrow, 2]-xmap[-xrow, 2])==0) & (abs(xmap[xrow, 1]-xmap[-xrow, 1])==1)))
  }))
  return(xres)}
```

Supporting Results

Table S1. List of high-level protected areas (i.e., national park or IUCN category I and II) used to calculate protected area coverage for each western chimpanzee range country as listed in Table 1 of the manuscript.

Country	Name	Designation	IUCN Category	Area in km2
Côte d’Ivoire	Azagny	National Park	II	194.00
	Banco	National Park	II	30.00
	Comoe	National Park	II	11491.50
	Haut Bandama	Fauna and Flora Reserve	Ia	1230.00
	Iles Ehotile	National Park	II	5.50
	Lamto	National/Scientific Reserve	Ia	25.00
	Marahoue	National Park	II	1010.00
	Mont Peko	National Park	II	340.00
	Mont Sangbe	National Park	II	950.00
	Mount Nimba	(Integral) National Reserve	Ia	50.00
	Tai	National Park	II	5081.86 [1]
Ghana	Bia	National Park	II	77.70
	Bui	National Park	II	1820.60
	Digya	National Park	II	3478.30
	Kakum	National Park	II	207.00
	Kogyae	Strict Nature Reserve	Ia	385.70
	Kyabobo	National Park	not reported	359.80
	Mole	National Park	II	4840.40
	Nini-Suhien	National Park	II	343.00
Guinea	Badiar	National Park	II	382.00
	Haut Niger (Gban/Kouya and Mafou)	National Park	not reported	1198.00
	Mount Nimba	Strict Nature Reserve	Ia	130.00
	Moyen Bafing	National Park	not reported	6426.00 [2]
Guinea-Bissau	Boé	National Park	not reported	1081.90 [3]
	Cantanhez Forest	National Park	not reported	1057.67
	Dulombi	National Park	not reported	1604.18 [3]
	Orango	National Park	II	1582.35
Liberia	East Nimba	Nature Reserve	not reported	135.00
	Gola Forest	National Park	not reported	979.75
	Grebo-Krahn	National Park	not reported	961.50 [4]
	Sapo	National Park	not reported	1803.63
Mali	Kouroufing	National Park	II	557.70
	Mandé Wula	Total Wildlife Reserve	II	390.50
	Néma Wula	Total Wildlife Reserve	II	447.30
	Wongo	National Park	II	534.99
Senegal	Basse-Casamance	National Park	II	50.00
	Delta du Saloum	National Park	II	599.34
	Langue de Barbarie	National Park	II	20.00

	Magdalen Islands	National Park	II	0.45
	Niokolo Koba	National Park	II	9130.00
	Oiseaux de Djoudj	National Park	II	160.00
Sierra Leone	Gola Rainforest	National Park	II	710.70
	Kilimi	National Park	not reported	388.50
	Loma Mountains	National Park	II	332.01
	Outamba	National Park	II	738.15
	Sankan Biriwa (Tingi Hills)	Non-hunting forest reserve	II	118.85
	Western Area Peninsula Forest	National Park	II	183.37

[1] According to the Office Ivorien des Parcs et Réserves the national park was enlarged in 2018 and the new area size was taken from OIPR website http://www.oipr.ci/index.php/parcs-reserves/parcs-nationaux/parc-national-de-tai.

[2] Area size taken from press release of the Wild Chimpanzee Foundation from October 2017 via www.wildchimps.org.

[3] Spatial outline of Boé and Dulombi National Parks provided by the World Database of Protected Areas were not up to date, so we used the outline provided by the “Instituto da Biodiversidade e das Áreas Protegidas” to calculate area sizes.

[4] Area size taken from the Wild Chimpanzee Foundation annual report 2017 via www.wildchimps.org.

Table S2. Details on the optimization process for each scenario with starting configuration (iteration 0) and final configuration of selected cells. For scenario 1 the chimpanzee abundance was preset at a specific target, and the algorithm optimized for a balance between size of required area and minimizing area fragmentation (i.e., the area score decreases). For scenario 2 the area was preset, and the algorithm optimized for a balance between maximizing chimpanzee abundance and minimizing area fragmentation (i.e., the proportion of chimpanzee abundance decreases slightly). Country codes are CIV Côte d'Ivoire, GHA Ghana, GIN Guinea, GNB Guinea-Bissau, LBR Liberia, MLI Mali, SEN Senegal, SLE Sierra Leone. Population codes correspond to the following colors in Figure 1c: Pop 1 (green), Pop 2 (blue), Pop 3 (red).

Scenario	Sub-scenario	Target	Country/ population (if appl.)	Iteration	Ruggedness	Proportion of chimpanzee abundance	Area score (ideal area divided by current area)	Number of cells selected
1) by chimpanzee abundance	across range	10%		0	2.15	0.100092	1.00	193
				60	0.90	0.100096	0.86	224
		20%		0	1.79	0.200126	1.00	555
				138	0.74	0.200141	0.88	630
		30%		0	1.68	0.300088	1.00	1072
				234	0.73	0.300013	0.91	1182
		40%		0	1.46	0.400017	1.00	1758
				301	0.66	0.400036	0.91	1926
		50%		0	1.27	0.500094	1.00	2654
				357	0.60	0.500037	0.93	2843
		60%		0	1.06	0.600032	1.00	3820
				391	0.49	0.600025	0.94	4063
		70%		0	0.86	0.700006	1.00	5391
				418	0.44	0.700029	0.96	5632
		80%		0	0.69	0.800028	1.00	7648
				414	0.38	0.800003	0.97	7897
		90%		0	0.50	0.900008	1.00	11380
				404	0.28	0.900006	0.98	11603
	by country	10%	CIV	0	1.74	0.101582	1.00	23
				5	1.15	0.100758	0.88	26
			GHA	0	2.33	0.101527	1.00	18
				4	1.60	0.101821	0.90	20
			GIN	0	2.35	0.100043	1.00	136
				45	0.94	0.100102	0.87	156

	GNB	0	2.75	0.102259	1.00	16
		7	1.47	0.102316	0.84	19
	LBR	0	2.31	0.101323	1.00	45
		12	1.14	0.100558	0.88	51
	MLI	0	3.20	0.102929	1.00	20
		6	2.17	0.102256	0.87	23
	SEN	0	3.00	0.102924	1.00	8
		4	1.56	0.102470	0.89	9
	SLE	0	2.00	0.100022	1.00	7
		2	1.50	0.103128	0.88	8
20%	CIV	0	1.75	0.200059	1.00	71
		17	0.79	0.200337	0.85	84
	GHA	0	1.95	0.202036	1.00	40
		7	1.29	0.202314	0.89	45
	GIN	0	1.88	0.200229	1.00	351
		99	0.70	0.200023	0.86	408
	GNB	0	2.16	0.203622	1.00	38
		12	1.05	0.200768	0.90	42
	LBR	0	1.82	0.200137	1.00	122
		21	0.95	0.200516	0.92	133
	MLI	0	2.81	0.201561	1.00	47
		14	1.25	0.200718	0.77	61
	SEN	0	2.48	0.200264	1.00	21
		4	1.29	0.204235	0.75	28
	SLE	0	1.46	0.203167	1.00	26
		4	1.14	0.201206	0.93	28
30%	CIV	0	1.65	0.300609	1.00	154
		37	0.65	0.301401	0.77	200
	GHA	0	1.74	0.303081	1.00	68
		11	1.36	0.300340	0.94	72
	GIN	0	1.74	0.300286	1.00	644
		146	0.75	0.300078	0.90	718
	GNB	0	1.78	0.301761	1.00	65
		17	0.54	0.300493	0.88	74
	LBR	0	1.27	0.300054	1.00	225
		29	0.62	0.300032	0.92	244
	MLI	0	2.37	0.300349	1.00	81

		22	1.02	0.300418	0.84	96
	SEN	0	2.28	0.301245	1.00	43
		11	1.03	0.302692	0.74	58
	SLE	0	1.48	0.301259	1.00	61
		9	0.83	0.300195	0.97	63
40%	CIV	0	1.40	0.400378	1.00	272
		54	0.68	0.400021	0.85	320
	GHA	0	1.55	0.401057	1.00	106
		13	1.11	0.400322	0.96	110
	GIN	0	1.53	0.400201	1.00	1023
		195	0.64	0.400028	0.90	1135
	GNB	0	1.27	0.402066	1.00	99
		14	0.58	0.400436	0.93	106
	LBR	0	1.08	0.400018	1.00	361
		43	0.53	0.400384	0.94	384
	MLI	0	1.94	0.401335	1.00	124
		24	0.99	0.400660	0.87	143
	SEN	0	1.90	0.400237	1.00	77
		20	0.63	0.401404	0.66	117
	SLE	0	1.57	0.400535	1.00	115
		24	0.77	0.400297	0.91	127
50%	CIV	0	1.23	0.500453	1.00	432
		56	0.66	0.500291	0.91	477
	GHA	0	1.42	0.500626	1.00	158
		23	0.89	0.500361	0.95	167
	GIN	0	1.38	0.500069	1.00	1508
		223	0.63	0.500086	0.92	1644
	GNB	0	1.21	0.500484	1.00	141
		17	0.64	0.501358	0.97	146
	LBR	0	0.99	0.500466	1.00	535
		55	0.57	0.500320	0.96	559
	MLI	0	1.87	0.501764	1.00	175
		34	0.86	0.500795	0.87	202
	SEN	0	1.57	0.500275	1.00	130
		22	0.73	0.500620	0.82	159
	SLE	0	1.39	0.500082	1.00	190
		31	0.71	0.500516	0.92	207

60%	CIV	0	1.15	0.600262	1.00	643
		77	0.63	0.600088	0.92	698
	GHA	0	1.31	0.601185	1.00	223
		25	0.93	0.600697	0.97	229
	GIN	0	1.21	0.600000	1.00	2128
		259	0.56	0.600036	0.93	2290
	GNB	0	1.16	0.600919	1.00	195
		27	0.60	0.600220	0.96	203
	LBR	0	0.80	0.600126	1.00	747
		41	0.58	0.600155	0.98	764
	MLI	0	1.51	0.601030	1.00	237
		33	0.79	0.600498	0.88	268
	SEN	0	1.42	0.600194	1.00	211
		33	0.63	0.600216	0.85	247
	SLE	0	1.16	0.600720	1.00	292
		48	0.51	0.600282	0.91	320
70%	CIV	0	1.01	0.700256	1.00	924
		99	0.53	0.700008	0.93	998
	GHA	0	1.18	0.700865	1.00	301
		28	0.81	0.700378	0.97	309
	GIN	0	0.97	0.700050	1.00	2937
		248	0.46	0.700091	0.95	3106
	GNB	0	1.02	0.700164	1.00	260
		25	0.62	0.701164	0.97	269
	LBR	0	0.70	0.700020	1.00	1022
		56	0.45	0.700140	0.97	1051
	MLI	0	1.39	0.700491	1.00	318
		42	0.73	0.700969	0.90	355
	SEN	0	1.32	0.700474	1.00	326
		48	0.53	0.700212	0.86	379
	SLE	0	0.99	0.700488	1.00	432
		54	0.49	0.700380	0.91	474
80%	CIV	0	0.77	0.800218	1.00	1292
		68	0.51	0.800150	0.95	1354
	GHA	0	0.95	0.800417	1.00	396
		24	0.69	0.800632	0.98	403
	GIN	0	0.75	0.800014	1.00	4060

			258	0.37	0.800008	0.96	4248
		GNB	0	0.84	0.800799	1.00	345
			31	0.50	0.801133	0.96	358
		LBR	0	0.59	0.800011	1.00	1397
			59	0.40	0.800033	0.98	1428
		MLI	0	1.21	0.800793	1.00	426
			34	0.69	0.800536	0.91	470
		SEN	0	1.00	0.800247	1.00	486
			46	0.46	0.800475	0.89	547
		SLE	0	0.78	0.800027	1.00	647
			39	0.49	0.800101	0.97	667
	90%	CIV	0	0.60	0.900053	1.00	1825
			76	0.39	0.900049	0.94	1949
		GHA	0	0.64	0.900089	1.00	523
			14	0.54	0.900276	0.99	529
		GIN	0	0.54	0.900035	1.00	5880
			242	0.28	0.900036	0.97	6056
		GNB	0	0.62	0.900196	1.00	465
			24	0.41	0.900139	0.96	483
		LBR	0	0.47	0.900041	1.00	1975
			63	0.30	0.900017	0.98	2015
		MLI	0	0.94	0.900113	1.00	581
			33	0.46	0.900181	0.90	643
		SEN	0	0.72	0.900289	1.00	720
			46	0.37	0.900229	0.90	797
		SLE	0	0.60	0.900046	1.00	1066
			31	0.41	0.900058	0.98	1084
by population	10%	Pop 1	0	2.08	0.100202	1.00	129
			35	1.01	0.100229	0.90	144
		Pop 2	0	2.27	0.100010	1.00	45
			14	1.19	0.100473	0.83	54
		Pop 3	0	1.90	0.101019	1.00	61
			12	1.37	0.100121	0.97	63
	20%	Pop 1	0	1.76	0.200085	1.00	371
			94	0.75	0.200095	0.89	417
		Pop 2	0	2.08	0.200026	1.00	127

		32	1.13	0.200027	0.89	143
	Pop 3	0	1.59	0.200288	1.00	150
		22	1.14	0.200581	0.97	154
30%	Pop 1	0	1.69	0.300074	1.00	707
		143	0.80	0.300164	0.92	766
	Pop 2	0	1.85	0.300285	1.00	244
		47	1.02	0.300116	0.93	263
	Pop 3	0	1.24	0.300539	1.00	256
		26	0.89	0.300672	0.98	260
40%	Pop 1	0	1.54	0.400108	1.00	1140
		219	0.67	0.400098	0.92	1236
	Pop 2	0	1.54	0.400390	1.00	393
		63	0.80	0.400096	0.93	422
	Pop 3	0	0.97	0.400057	1.00	379
		26	0.76	0.400145	0.99	383
50%	Pop 1	0	1.33	0.500120	1.00	1688
		241	0.62	0.500120	0.93	1809
	Pop 2	0	1.29	0.500052	1.00	580
		80	0.67	0.500127	0.94	618
	Pop 3	0	0.95	0.500612	1.00	529
		37	0.68	0.500489	0.99	535
60%	Pop 1	0	1.17	0.600106	1.00	2373
		280	0.58	0.600109	0.95	2494
	Pop 2	0	1.14	0.600110	1.00	816
		88	0.65	0.600222	0.96	851
	Pop 3	0	0.84	0.600427	1.00	709
		42	0.60	0.600429	0.99	719
70%	Pop 1	0	0.98	0.700086	1.00	3225
		292	0.47	0.700081	0.96	3355
	Pop 2	0	1.04	0.700061	1.00	1111
		95	0.65	0.700077	0.98	1137
	Pop 3	0	0.74	0.700399	1.00	929
		56	0.49	0.700100	0.99	943
80%	Pop 1	0	0.75	0.800041	1.00	4305
		277	0.38	0.800068	0.98	4404
	Pop 2	0	0.92	0.800228	1.00	1472
		93	0.63	0.800151	0.99	1489

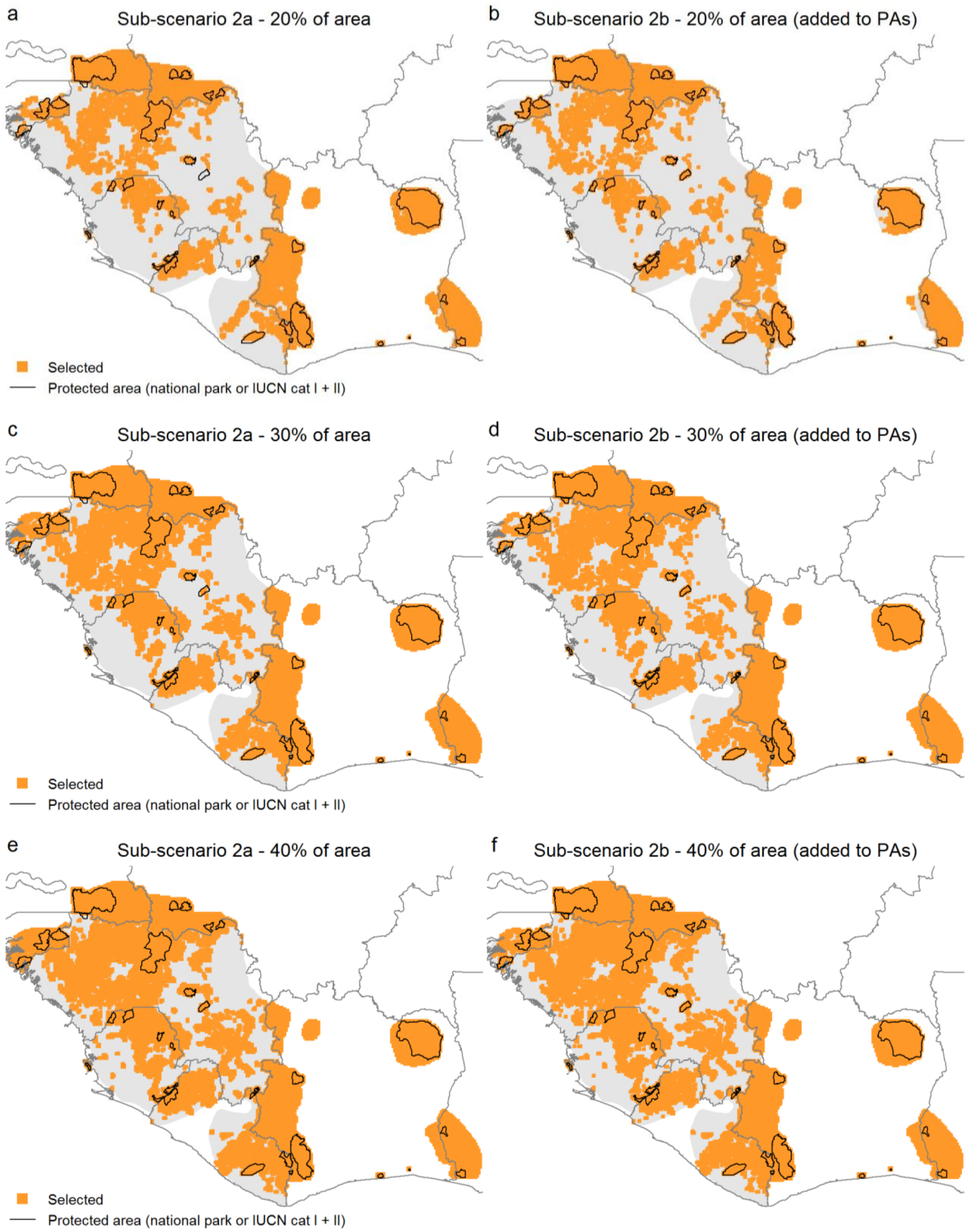
			Pop 3	0	0.64	0.800281	1.00	1204
				62	0.40	0.800033	0.98	1226
				0	0.56	0.900046	1.00	5710
		90%	Pop 1	226	0.36	0.900007	0.99	5768
				0	0.77	0.900194	1.00	1894
			Pop 2	95	0.58	0.900076	0.99	1915
				0	0.49	0.900202	1.00	1566
			Pop 3	38	0.38	0.900036	0.99	1584
by area size	by country	17%	CIV	0	0.41	0.976924	1.00	2597
				8	0.40	0.975728	1.00	2597
			GIN	0	1.24	0.579639	1.00	1989
				55	1.13	0.577988	1.00	1989
			GNB	0	0.95	0.721496	1.00	276
				4	0.92	0.720853	1.00	276
			LBR	0	0.79	0.610454	1.00	772
				7	0.77	0.610107	1.00	772
			SLE	0	0.82	0.775634	1.00	584
				10	0.78	0.774996	1.00	584
		20%	CIV	0	0.31	0.996203	1.00	3056
				8	0.30	0.994702	1.00	3056
			GIN	0	1.14	0.629142	1.00	2340
				55	1.06	0.627536	1.00	2340
			GNB	0	0.85	0.778623	1.00	324
				7	0.78	0.777774	1.00	324
			LBR	0	0.74	0.662052	1.00	908
				10	0.71	0.661664	1.00	908
			SLE	0	0.78	0.813533	1.00	687
				10	0.74	0.813071	1.00	687
		30%	GIN	0	0.84	0.755973	1.00	3511
				45	0.79	0.754954	1.00	3511
			GNB	0	0.62	0.914270	1.00	487
				4	0.60	0.914077	1.00	487
			LBR	0	0.61	0.792145	1.00	1363
				9	0.58	0.790604	1.00	1363
			SLE	0	0.63	0.894221	1.00	1030
				13	0.59	0.893779	1.00	1030

	40%	GIN	0	0.67	0.840944	1.00	4681
			44	0.64	0.840068	1.00	4681
		GNB	0	0.39	0.989083	1.00	649
			4	0.38	0.988870	1.00	649
		LBR	0	0.49	0.878201	1.00	1817
			7	0.48	0.878081	1.00	1817
		SLE	0	0.52	0.935663	1.00	1374
			14	0.48	0.935369	1.00	1374
	50%	GIN	0	0.54	0.898847	1.00	5851
			50	0.51	0.898255	1.00	5851
		LBR	0	0.39	0.932386	1.00	2271
			18	0.36	0.932203	1.00	2271
		SLE	0	0.54	0.958382	1.00	1717
			19	0.50	0.958068	1.00	1717
by country additive to current protected areas	17%	CIV	0	0.53	0.929134	1.00	2068
			10	0.52	0.927911	1.00	2068
		GIN	0	1.23	0.564633	1.00	1932
			7	1.22	0.564372	1.00	1932
		GNB	0	0.89	0.443332	1.00	190
			4	0.86	0.441324	1.00	190
		LBR	0	0.85	0.586856	1.00	732
			2	0.84	0.585696	1.00	732
		SEN	0	0.25	0.997456	1.00	1151
			2	0.25	0.996927	1.00	1151
		SLE	0	0.85	0.767656	1.00	571
			2	0.85	0.767127	1.00	571
	20%	CIV	0	0.44	0.963035	1.00	2407
			4	0.44	0.962906	1.00	2407
		GIN	0	1.15	0.615126	1.00	2271
			35	1.09	0.614311	1.00	2271
		GNB	0	0.91	0.574844	1.00	227
			5	0.84	0.573444	1.00	227
		LBR	0	0.75	0.641722	1.00	862
			3	0.74	0.641536	1.00	862
		SLE	0	0.77	0.806963	1.00	670
			6	0.75	0.806687	1.00	670

30%	GIN	0	0.86	0.744288	1.00	3402
		16	0.85	0.744012	1.00	3402
	GNB	0	0.78	0.791510	1.00	348
		1	0.78	0.791477	1.00	348
	LBR	0	0.65	0.775366	1.00	1296
		4	0.64	0.775321	1.00	1296
	SLE	0	0.65	0.889191	1.00	1001
		2	0.65	0.888416	1.00	1001
40%	GIN	0	0.69	0.831354	1.00	4533
		16	0.68	0.830986	1.00	4533
	GNB	0	0.59	0.901313	1.00	470
		2	0.59	0.901032	1.00	470
	LBR	0	0.52	0.864267	1.00	1729
		2	0.52	0.864179	1.00	1729
	SLE	0	0.53	0.931947	1.00	1332
		3	0.53	0.931700	1.00	1332
50%	GIN	0	0.56	0.890685	1.00	5664
		23	0.55	0.890436	1.00	5664
	GNB	0	0.50	0.967719	1.00	592
		2	0.50	0.965966	1.00	592
	LBR	0	0.40	0.921526	1.00	2162
		1	0.40	0.921432	1.00	2162
	SLE	0	0.55	0.955465	1.00	1663
		4	0.55	0.954665	1.00	1663

Table S3. Results for each scenario identifying areas of high conservation value to western chimpanzees in Liberia only.

Scenario	Sub-scenario	Target	Estimated chimpanzee abundance	Area [km^2]	Overlap with priority areas identified by Junker et al. (2015) [%]
1) by chimpanzee abundance	1a) across range	10%	109	85	0.00
		20%	319	382	33.33
		30%	620	1,083	60.78
		40%	1,318	3,163	65.10
		50%	1,879	5,349	64.67
		60%	2,326	7,495	64.87
		70%	3,367	14,050	67.33
		80%	4,250	22,327	60.30
		90%	5,138	35,695	52.16
	1b) by country	10%	608	1,083	64.70
		20%	1,212	2,823	68.42
		30%	1,814	5,179	65.97
		40%	2,421	8,154	64.58
		50%	3,025	11,879	66.38
		60%	3,627	16,242	65.98
		70%	4,231	22,349	60.05
		80%	4,828	30,375	56.87
		90%	5,423	42,869	46.36
	1c) by population	10%	427	1,043	71.46
		20%	1,042	3,512	70.93
		30%	1,854	6,937	73.02
		40%	2,756	11,488	71.49
		50%	3,471	16,381	66.11
		60%	3,999	21,170	62.51
		70%	4,527	27,129	60.71
		80%	4,856	32,580	55.32
		90%	5,235	39,923	48.45
2) by area size	2a) by country	17%	3,685	16,412	65.42
		20%	3,997	19,306	63.89
		30%	4,769	28,992	57.60
		40%	5,289	38,654	49.93
		50%	5,610	48,316	42.50
	2b) by country added to current protected areas	17%	3,541	15,563	68.32
		20%	3,876	18,329	66.37
		30%	4,678	27,565	57.88
		40%	5,205	36,781	51.54
		50%	5,547	45,997	44.18


a
Sub-scenario 2a - 20% of area
b
Sub-scenario 2b - 20% of area (added to PAs)
Selected
Protected area (national park or IUCN cat I + II)
c
Sub-scenario 2a - 30% of area
d
Sub-scenario 2b - 30% of area (added to PAs)
Selected
Protected area (national park or IUCN cat I + II)
e
Sub-scenario 2a - 40% of area
f
Sub-scenario 2b - 40% of area (added to PAs)
Selected
Protected area (national park or IUCN cat I + II)

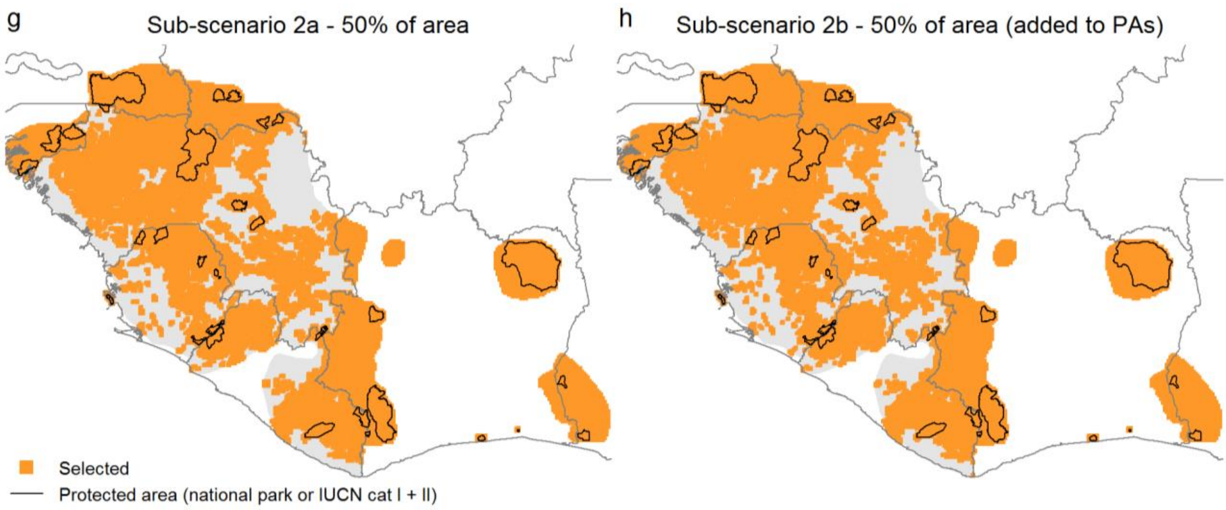


Figure S1. Mapped areas of high conservation value for western chimpanzees for the second scenario based on area size (a, c, e, g,) highest chimpanzee density alone and (b, d, f, h) highest chimpanzee density in addition to high-level protected areas (i.e., national park or IUCN category I and II) for area targets in each country of 20% (a, b), 30% (c, d), 40% (e, f) and 50% (g, h).

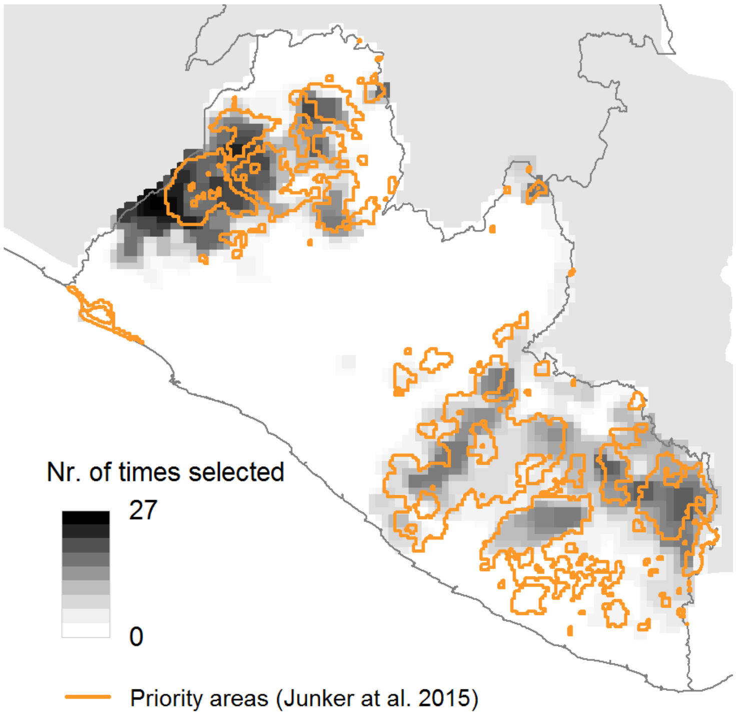


Figure S2. Mapped areas of high conservation value for western chimpanzees summed up for all three sub-scenarios based on chimpanzee abundance (i.e., number of times a cell was selected was summed up across scenarios 1a-c). Shown is the overlap with priority areas in Liberia identified by Junker at al. (2015).

References

Junker, J., Boesch, C., Freeman, T., Mundry, R., Stephens, C., & Kühl, H. S. (2015). Integrating wildlife conservation with conflicting economic land-use goals in a West African biodiversity hotspot. *Basic and Applied Ecology*, *16*(8), 690–702. https://doi.org/10.1016/j.baae.2015.07.002

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Journal: Environmental Research Letters

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Journal: American Journal of Primatology

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LIST OF PUBLICATIONS

Heinicke, S., Mundry, R., Boesch, C., Hockings, K. J., Kormos, R., Ndiaye, P. I., Tweh C.G., Williamson E. A. & Kühl, H. S. (submitted) Towards systematic and evidence-based conservation planning for western chimpanzees. *American Journal of Primatology*

Heinicke, S., Mundry, R., Boesch, C., Amarasekaran, B., Barrie, A., Brncic, T., Brugière, D., Campbell, G., Carvalho, J., Danquah, E., Dowd, D., Eshuis, H., Fleury-Brugière, M.-C., Gamys, J., Ganas, J., Gatti, S., Ginn, L., Goedmakers, A., Granier, N., Herbinger, I., Hillers, A., Jones, S., Junker, J., Kouakou, C. Y., Lapeyre, V., Leinert, V., Maisels, F., Marrocoli, S., Molokwu-Odozi, M., N'Goran, P. K., Pacheco, L., Regnaut, S., Sop, T., Ton, E., van Schijndel, J., Vergnes, V., Voigt, M., Welsh, A., Wessling, E. G., Williamson, E. A., & Kühl, H. S. (accepted) Advancing conservation planning for western chimpanzees using IUCN SSC A.P.E.S. – the case of a taxon-specific database. *Environmental Research Letters*, DOI: 10.1088/1748-9326/ab1379

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Voigt, M., Wich, S. A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G., Campbell-Smith, G., d'Arcy, L. J., Delgado, R. A., Erman, A., Gaveau, D., Goossens, B., **Heinicke, S.**, Houghton, M., Husson, S. J., Leiman, A., Sanchez, K. L., Makinuddin, N., Marshall, A. J., Meididit, A., Miettinen, J., Mundry, R., Musnanda, Nardiyono, Nurcahyo, A., Odom, K., Panda, A., Prasetyo, D., Priadjati, A., Purnomo, Rafiastanto, A., Russon, A. E., Santika, T., Sihite, J., Spehar, S., Struebig, M., Sulbaran-Romero, E., Tjiu, A., Wells, J., Wilson, K. A., & Kühl, H. S. (2018). Global demand for natural resources eliminated more than 100,000 Bornean orangutans. *Current Biology*, 28(5): e5, pp. 761-769

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Kalan, A. K., Mundry, R., Wagner, O. J. J., **Heinicke, S.**, Boesch, C., & Kühl, H. S. (2015). Towards the automated detection and occupancy estimation of primates using passive acoustic monitoring. *Ecological Indicators*, 54, 217-226.

SELBSTÄNDIGKEITSERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Arbeit mit dem Titel „Informing the transition to evidence-based conservation planning for western chimpanzees“ selbstständig und nur unter Verwendung der angegebenen Hilfsmittel angefertigt habe.

Leipzig, den 21.05.2019

S. Heinicke

Stefanie Heinicke