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Integrating wildlife conservation with conflicting economic land-use goals in a West African biodiversity hotspot

Jessica Junker[a,*], Christophe Boesch[a,b], Theo Freeman[c], Roger Mundry[a], Colleen Stephens[a], Hjalmar S. Kühl[a,d]

[a] *Max-Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany*
[b] *Wild Chimpanzee Foundation, Deutscher Platz 6, Leipzig, Germany*
[c] *Forestry Development Authority, Wheintown, Mount Barclay, Liberia*
[d] *German Centre for Integrative Biodiversity Research, Deutscher Platz 5e, 04103 Leipzig, Germany*

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Abstract

Half of what remains of the 'Guinean Forests of West Africa hotspot' is located in Liberia. However, only about 2% of the country is officially protected. We systematically identified and evaluated priority areas for the protection of large mammals and biodiversity in Liberia under different conservation scenarios. We also assessed current proposed protected areas (PPAs) in terms of achieving pre-determined conservation targets, and determined potential wildlife and biodiversity loss within logging and mining concessions. We systematically collected nationwide data on chimpanzee (*Pan troglodytes verus*) abundance, large mammal and tree taxonomic diversity, and human threats. We related these to environmental and human impact variables to develop nationwide spatial prediction models that also served as base-layers for spatial prioritization using MARXAN. We improved upon standard software output to evaluate spatial properties of selected sites, determine site-specific target contributions, and estimate potential wildlife and biodiversity loss within logging and mining concessions. The optimal conservation area network contained a candidate list of 92 areas that maximized biodiversity and chimpanzee abundance, minimized threats, and accomplished the preservation of 30% of Liberia's forests. It included more than half of West Africa's second largest chimpanzee population, which spatially coincided with that of some of the most diverse large mammal and tree communities. Logging and mining concessions largely overlapped with existing PPAs and conservation priority areas established in this study, and considerably increased their fragmentation. Existing PPAs, however, only partially covered our areas of prioritization and proved insufficient in meeting conservation targets. We emphasize the need for finding a balance between development and biodiversity conservation, such as through aggregate biodiversity offsets, the use of which is currently being discussed by local government, international investors, and conservation NGOs.

Zusammenfassung

Die Hälfte des 'Guinean Forests of West Africa hotspot' liegt in Liberia, jedoch sind nur ungefähr 2% des Landes offiziell geschützt. Wir haben systematisch Gegenden von hoher Priorität bezüglich des Schutzes großer Säugetiere und Biodiversität unter Verwendung verschiedener Naturschutzszenarien in Liberia identifiziert und evaluiert. Zusätzlich haben wir aktuell vorgeschlagene bzw. zukünftige Naturschutzgebiete (PPAs) dahingehend bewertet, ob vorbestimmte Naturschutzziele erreicht werden können. Außerdem haben wir potentielle Wild- und Biodiversitätsverluste bestimmt, die durch die zukünftige Abholzung und den Abbau von Rohmineralien zu erwarten sind. Hierzu erhoben wir systematisch

*Corresponding author. Tel.: +49 0 341 3550 805; fax: +49 0 341 3550 299.
E-mail address: jessica_junker@eva.mpg.de (J. Junker).

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und landesweit Daten über das Vorkommen von Schimpansen (*Pan troglodytes verus*) und der taxonomischen Diversität großer Säuger und Bäumen sowie der Bedrohung, die von den Menschen ausgeht. Diese Daten setzten wir dann in Relation mit ökologischen und menschlichen Einflüssen, um landesweite räumliche Abundanz- und Verbreitungsmodelle zu entwickeln, welche gleichzeitig als Grundlage für die Priorisierung mit dem Softwareprogramm MARXAN dienten. Die Leistung dieser Software haben wir erheblich verbessert indem wir die Datenausgabe von MARXAN zusätzlich nachbearbeitet haben um so räumliche Eigenschaften von ausgewählten Gegenden besser auszuwerten, ortsspezifische Beiträge zu den vorbestimmten Naturschutzzielen besser bestimmen zu können und die potentiellen Auswirkungen der Konzessionen für Holz- und Rohstoffabbau (Konzessionen) zu bewerten. Die potenziellen Schutzgebiete, welche unter der Prämisse optimaler Landnutzung bestimmt wurden, beinhalteten 92 Gegenden. Diese waren hauptsächlich im stark bewaldeten Nordwesten und dem Südosten lokalisiert unter Berücksichtigung maximaler Biodiversität und Schimpansendichte, bei gleichzeitig minimaler menschlicher Bedrohung und Bezug nehmend auf das Regierungsziel 30% des restlichen Waldes schützen zu wollen. Diese Gebiete beinhalteten mehr als 50% der gesamten liberianischen Schimpansenpopulation. Die Verbreitung dieser Schimpansen korrelierte signifikant mit einigen der artenreichsten Populationen großer Säugetiere und Baumarten. Erteilte Konzessionen erhöhten deutlich die Zersplitterung von Naturschutzgebieten. PPAs überlappten teilweise mit Gebieten hoher Priorität, aber es zeigte sich, dass diese nicht ausreichen um die vorbestimmten Naturschutzziele zu erreichen. Ein Großteil der Konzessionen überlappte mit existierenden PPAs und Gebieten hoher Priorität und zwar so weit, dass momentane Pläne zur Rohstoffentwicklung in Liberia zukünftige Naturschutzbemühungen untergraben und das langfristige Überleben einer der letzten großen Schimpansenpopulationen in Westafrika und der einheimischen Biodiversität gefährden könnte. Wir betonen die Notwendigkeit ein Gleichgewicht zwischen Entwicklung und Naturschutz zu schaffen, wie zum Beispiel durch 'aggregate biodiversity offsets', dessen Nutzung gerade von der Regierung, internationalen Investoren und Nichtregierungsorganisationen, die im Naturschutz tätig sind, diskutiert wird.

Keywords: Biodiversity offsets; Chimpanzees; Economic development; Guinean Forests of West Africa; IUCN SSC A.P.E.S. database; Liberia; MARXAN; Systematic conservation planning (SCP)

Introduction

The 'Guinean Forests of West Africa hotspot' (Mittermeier, Meyers, & Thomsen 1998) is one of the most critically fragmented regions on the planet (Mittermeier et al. 2004). It is estimated that almost 60% of all endemic plants and vertebrates in this eco-region are either threatened with extinction or have gone extinct already (Brooks et al. 2002). Despite its conservation importance and urgency, to date less than 10% of this eco-region is within protected areas (Jenkins & Joppa 2009; Schmitt et al. 2009), many of which have failed to safeguard the biodiversity within their boundaries from encroaching human threats (e.g., Campbell, Kuehl, N'Goran, & Boesch 2008). The systematic identification of conservation gaps and the effective management of protected areas can contribute to the long-term persistence of one of the world's richest land areas for threatened amphibians, birds, and mammals.

Systematic conservation planning (SCP; Margules & Pressey 2000) is widely considered the most effective approach to conservation prioritization (Pressey, Cabeza, Watts, Cowling, & Wilson 2007) and various software tools have been developed to identify conservation area networks. MARXAN, the most widely used software tool, identifies networks of cohesive sites that meet pre-defined conservation targets while simultaneously minimizing costs (Ball, Possingham, & Watts 2009). Its output however, would be even more valuable if it allowed for the evaluation of spatial attributes of selected sites, such as mean patch size and connectivity, as well as proportional and relative target contributions of individual reserves for which external statistics packages are currently still needed (Ardron, Possingham, & Klein 2010). This information is crucial, because resources for conservation are limited and entire reserve networks will almost never be implemented at once (except Fernandez et al. 2005). Similarly, activities that are destructive to nature are expanding and initial plans may become partly unachievable, because of the loss or degradation of some selected areas. Therefore, success of eventual reserve networks in representing biodiversity and promoting long-term species persistence will not only depend on how carefully individual reserves have been located and how spatially coherent they are (Williams, ReVellea, & Levin 2005), but also on whether information on their relative conservation importance can easily be accessed by conservation managers, environmental consultants, international investors, and policy-makers.

About half of the remaining Guinean Forests of West Africa are located within Liberia (Mittermeier et al. 2004). Liberia's two largely continuous forest blocks in the north-west and south-east display high levels of biodiversity and endemism (CEPF 2003), are a likely source of as-yet-unknown species (Jenkins, Pimm, & Joppa 2013), and are home to one of the last viable chimpanzee (*Pan troglodytes verus*) populations in West Africa (Tweh et al. 2014). In spite of this, Liberia currently only holds three officially protected areas (PAs) that include about 2% of its total land area, which is relatively low as compared to other countries in the region (e.g., Côte d'Ivoire = 23%, Ghana = 15%, Nigeria = 13%; http://www.unep-wcmc.org).

In 2003, the Liberian Forestry Development Authority (FDA) signed an agreement to establish "a biologically representative network of protected areas covering at least 30% of the existing forest area" (MFA 2003). Nebel and colleagues (2006) defined a reserve network of 12 proposed protected areas (PPAs) that covers almost 14% of Liberia's forests (FDA 2007; Appendix B: Fig. 1). However, this network was neither evaluated in terms of its biological representativeness, cost-efficiency or spatial coherence, nor were the identified sites ever gazetted as officially protected areas, which was due mainly to a lack of data, expertise and financial resources. Furthermore, because of a substantial increase over the past ten years in the demand for land by the private sector in Liberia, many of the PPAs now overlap completely or at least partially with mining and forestry concessions (Global Witness 2012; Blair 2013; Global Witness 2013). Fortunately though, in September 2014, the Government of Norway entered into a US$ 150 million partnership with the Government of Liberia "to halt the destruction of Liberia's rainforest"(http://www.oecd.org/tax/exchange-of-tax-information/46386375.pdf). Central to this agreement are Liberia's commitment to conserving 30% or more of its forests as protected areas, as well as reviewing all proposed concession licenses as to their legality.

In light of these developments, it will be key to assess the efficiency and biological value of the current PPA network, propose spatial adjustments if necessary, identify additional conservation areas to meet Liberia's 30% conservation target, and assess the extend of land-use conflict between the private- and the conservation sector. In this study, we therefore (1) systematically identified priority areas for the protection of large mammals and biodiversity in Liberia, (2) mapped conservation priority areas under different conservation scenarios, and (3) assessed both, conservation priority areas and the current PPA network in terms of target contributions. We also post-processed MARXAN's analytical output to (4) assess spatial attributes of selected sites and rank them according to their relative conservation importance and (5) determine potential wildlife and biodiversity loss in logging and mining concessions.

Materials and methods

Our methods included four major steps: (1) collection of distribution and abundance data on large mammals, human threats, and trees across Liberia during a nationwide chimpanzee and large mammal survey (Tweh et al. 2014). (2) Relating these data to environmental and human impact variables to develop spatial prediction models for chimpanzee abundance and large mammal and tree diversity, which, among others, served as base layers for the (3) spatial prioritization with MARXAN. (4) Post-processing of MARXAN output maps to assess spatial properties of selected sites and determine site-specific contributions to achieving pre-determined conservation targets (Appendix B: Fig. 2). Because we partly used published data on nationwide distribution and abundance of large mammals and human threats (Tweh et al. 2014) as a baseline for our spatial prioritization, we focus on steps 3 and 4 in Materials and methods and Results sections and refer readers to Appendix B for details on field methods (step 1) not presented by Tweh et al. (2014) and a more in-depth description of step 2. Please also note that our analyses focus on one mammal species in particular, namely the West African chimpanzee. They are a flagship species for West African forests and the target of the spatial prioritization due to the relative importance of Liberia for the conservation of this species (Tweh et al. 2014). We therefore refer to them separately from other large mammal species throughout the text.

Spatial prediction models

To identify conservation priority areas, we first made countrywide interpolations based on transect data for the entire country. First, we predicted nationwide abundance of chimpanzees using Generalized Linear Models (GLMs; McCullagh & Nelder 2008). We also used tree and large mammal taxonomic diversity (from here on we refer to taxonomic diversity as 'td') as indicators of terrestrial biodiversity (Lawler, White, Sifneos, & Master 2003). We predicted countrywide IUCN-weighted large mammal td (i.e., number of species per unit area) and tree td. We weighted large mammal species according to their IUCN category (IUCN 2014; category 1 = least concern, 2 = near threatened, category 3 = vulnerable, category 4 = endangered) to prioritize conservation of rare and threatened species over more abundant, less-threatened species. We could not model individual species distributions, because wildlife densities for many species were low and resulted in insufficient transect observations. Additionally, we modeled nationwide empty gun shell and snare density. We could not develop spatial models for other human threats observed on line transects, because of too few observations. We used eight environmental predictor variables representing various ecological and human impact conditions. Ecological variables included soil organic carbon content, Compound Topographic Index (CTI), annual mean rainfall, rainfall seasonality, and forest cover. Variables relating to human impact included distance to markets, distance to roads, and human population pressure (Table 1). A detailed description of the different models can be found in Appendix B.

Study area

Our study area included the entire country of Liberia. Although the government committed to protecting 30% of Liberia's forests, we decided to include not only forested areas into our study area, but the entire country. We did this

Table 1. List of response and predictor variables included in the GLMs, details on how they were measured and their data source.

Variable name	Measurement	Type of variable	Year	Source
IUCN-weighted mammal taxonomic diversity	Sum of the iucn-weight of the unique large mammal species recorded on each line transect	Response	2011–2012	Tweh et al. (2014)
Tree taxonomic diversity	Number of tree species (dbh> 10 cm) recorded on each strip transect	Response	2011–2012	Nationwide chimpanzee and large mammal survey, unpublished data
Chimpanzee abundance	Number of chimpanzee nests recorded on each line transect	Response	2011–2012	Tweh et al. (2014)
Empty gun shell abundance	Number of empty gun shells recorded on each line transect	Response	2011–2012	Tweh et al. (2014)
Snare abundance	Number of snares recorded on each line transect	Response	2011–2012	Tweh et al. 2014
Soil organic carbon content	Mean organic carbon content (g/kg) of the top soil layer (0-5 cm)	Predictor	1950–2005	ISRI-World Soil Information 2013
Compound Topographic Index (CTI)	Measure of soil wetness	Predictor	1996	(HYDRO1k) USGS[a]
Annual mean rainfall	Annual mean rainfall (mm)	Predictor	1980–1997	Bioclim/WorldClim-Global Climate Data (Hijmans, Cameron, Parra, Jones, & Jarvis 2005)
Rainfall seasonality	Coefficient of variation of annual mean rainfall	Predictor	1980–1997	Bioclim/WorldClim-Global Climate Data (Hijmans et al. 2005)
Forest cover	Forest/non-forest/intermediate forest	Predictor	2003	FDA[b] modified by USAID GEMS[c] unpublished data
Distance to markets	Distance to daily and weekly markets	Predictor	2007	LISGIS[d]/WFP[e] 2007 unpublished data
Distance to roads	Distance to primary and secondary roads, paved and unpaved	Predictor	2007	MLME[f] unpublished data
Human population pressure	For each pixel: sum of log (inhabitants in settlements +1)/distance of settlements to that pixel	Predictor	2007	LISGIS[d] unpublished data; FDA[b] unpublished data

[a] U.S. Geological Survey.
[b] Liberia Forestry Development Authority.
[c] United States Agency for International Development Governance and Economic Management Support.
[d] Liberia Institute of Statistics and Geo-Information Services.
[e] World Food Programme.
[f] Liberia Ministry of Lands, Mines and Energy.

because areas that are not within forest may still have conservation value for some species, be important in the context of adjacent reserve patches, and even be reforested if necessary. We thus divided our study area into a grid of 29,976 ‘planning units’ (i.e., grid cells), each $1810.077 \times 1810.077\, m^2$ in size. A habitat patch (hereafter ‘patch’) included two or more planning units that shared common borders. We used ArcMap (v. 9.2, ESRI 2011) to convert raster layers into shapefiles.

Spatial prioritization – Conservation features

We used the software MARXAN v. 1.8.10 to identify systems of cohesive sites (hereafter patches) that met our

Table 2. Conservation features included in the MARXAN analysis and described in the table below were measured either quantitatively or qualitatively, stemmed from various sources and were each assigned conservation targets.

Conservation feature	Type of measure	Description	Source	Conservation target (%)
Chimpanzee abundance	Quantitative	Number of chimpanzee nests per unit area	Tweh et al. (2014)	25
Large mammal taxonomic diversity	Quantitative	Number of IUCN-weighted large mammal species per unit area	Tweh et al. (2014)	25
Large tree taxonomic diversity	Quantitative	Number of large tree (> 10 dbh) species per unit area	Nationwide chimpanzee and large mammal survey	25
Elephant presence-absence	Binary	Elephant(s) present/absent (1/0); buffer = elephant home range size	WCF 2009, unpublished results; WCF 2012, unpublished results; AML/WCF/CI 2010–2011, unpublished results; RSPB 2010–2012, unpublished results; MPIEVA 2013, unpublished results	25
Forest cover	Binary	Forest present/absent (1/0)	FDA, modified by USAID GEMS, unpublished results	30
Threatened large mammal presence-absence	Binary	Threatened large mammal species present/absent (1/0); buffer = species-specific home range size	WCF 2009, unpublished results; WCF 2012, unpublished results; AML/WCF/CI 2010–2011; RSPB 2010-2012, unpublished results; MPIEVA 2013, unpublished results	25
Future threat	Binary	High/low altitude (1/0); low altitude (<300 m), high altitude (> 300 m)	Jarvis, Reuter, Nelson, and Guevara (2008)	30

conservation targets while minimizing management costs. In the text that follows, we use standard MARXAN terminology (Ball et al. 2009).

We included the following conservation features: chimpanzee abundance, IUCN-ranked large mammal td, and tree td. In addition, we used four binary measures: forest cover, altitude, elephant occurrence, and threatened large mammal occurrence (Table 2, Appendix B: Fig. 3). We included occurrences of threatened mammal species only, because previous studies showed that this provides adequate protection to those species not yet considered endangered, while at the same time delivering cost-efficient outcomes (e.g., Drummond et al. 2009). We treated elephants and other threatened large mammal species as separate features to ensure appropriate representation of the latter in the prioritization model (Pimm et al. 2014). We buffered occurrence records of elephants and other threatened large mammals. Buffer size corresponded to the approximate home range of the species (for details see Appendix B: "MARXAN spatial prioritization–details on conservation features"). We included threatened large mammal occurrence locations in addition to our modelled prediction layers for large mammal td to ensure that we did not miss areas where specific species were known to occur.

We included forest as a conservation feature, because Tweh et al. (2014) demonstrated that the majority of chimpanzees and threatened large mammal species in Liberia live in forested habitats. Parren and de Graff (1995) estimated that 90% of the exploitable forests are situated in the relatively flat south-eastern parts of the country, whereas those in the north of Liberia are partly located in rough terrain (Shearman 2009) characterized by higher altitudes, making them less economically accessible (Verschuren 1983). We categorized altitude into (1) high and (2) low altitude, at > and <300 m ASL, respectively. We used this relatively low altitude cut-off, because more than 95% of the country's surface area is below 500 m. At our cut-off, 28% of the country's total area is included in the high altitude category. The reason for converting altitude into a categorical variable is that it facilitated setting proportional targets in MARXAN (T. Wiens personal communication). We included altitude as a proxy for potential future resource exploitation (e.g., logging) and thus named this feature ‘future threat’.

Spatial prioritization – Costs

We combined modeled empty gun shell and snare density into one conservation cost layer by simply summing the values of each. This is legitimate as the units of both measurements (i.e., number of signs per unit area) were the same (T. Wiens personal communication). We observed relatively few signs of artisanal mining and logging on line transects and thus did not consider either of these as cost layers for the model. We also did not include slash-and-burn agriculture in the model, as we did not consider agricultural areas priorities for biodiversity conservation.

Spatial prioritization – Conservation targets

We set the conservation target for chimpanzee abundance, large mammal td, tree td, elephant and other threatened large mammal occurrence at 25%. By default, MARXAN tries to achieve conservation targets while, at the same time minimizing area (Ball et al. 2009). Thus, we can assume that the algorithm favours planning units with high values for conservation features over those with low values to achieve targets within a smaller area. In other words, the planning units selected to achieve our conservation target represent the 25% highest chimpanzee abundance areas, the 25% most diverse large mammal and tree communities (T. Wiens personal communication), and at least 25% of all buffered elephant and threatened large mammal occurrences recorded in Liberia. We previously also mapped reserve networks to achieve 50% and 75% conservation targets. However, after inspecting the results, we decided to remove these again as we considered them unrealistic. We also set 30% proportional targets for forest and future threat (i.e., 30% high altitude areas), where the former is in accordance with FDA’s commitment of protecting 30% of Liberia’s remaining forest cover.

Spatial prioritization – Conservation scenarios

We defined four conservation scenarios (hereafter scenarios 1–4) and included them one at a time in MARXAN (Table 3, Appendix B: Fig. 4). These represent different land-use management scenarios and were defined by whether land currently set aside for logging and mining activities was excluded from selection and whether or not PPAs were included in the selection (Ardron et al. 2010). PAs were always included in the reserve system. PPAs were included in the reserve system only in scenario 4. Concessions were excluded from the area available for selection in scenario 2 and illegally issued, so-called ‘Private-Use-Permits’ (PUPs; Global Witness 2012; Blair 2013) were excluded from selection in scenario 3. For scenario 4, selection was restricted to PAs and PPAs only.

Table 3. Description of land-use conditions for each conservation scenario.

Scenario	Description
1	PAs included in the selection; all other planning units available for conservation
2	PAs included in the selection; logging & mining excluded from selection
3	PAs included in the selection; logging & mining excluded from selection; PUPs excluded from selection
4	PAs & PPAs included in the selection; all other planning units excluded from selection

Post-processing of MARXAN outputs

MARXAN does not evaluate spatial attributes of individual patches, although these may considerably influence wildlife persistence (Diamond 1975) and management costs (Bruner et al. 2004). In addition, MARXAN does not assess target contributions of individual patches (Ardron et al. 2010), which is important for estimating their efficiency. We therefore post-processed MARXAN output maps to determine for each of the four conservation scenarios total patch network area (km^2), individual patch size (km^2), total patch edge length (km), and a patch proximity index, which, for each patch, was the sum of the area of all other patches divided by their respective minimum edge-to-edge distance (squared) to the focal patch (modified from McGarigal 2014).

Because MARXAN only allows for setting a minimum, but not a maximum conservation target, we selected from each MARXAN output the ‘best’ 30% of patches (defined by the number of chimpanzees that they included) in order to not exceed FDA’s area limit. We based our selection of the ‘best’ 30% of patches on chimpanzees only, which we justified by testing for a correlation between chimpanzee abundance and large mammal and tree td (see following section). To determine for each patch (for all scenarios) how many chimpanzees it included, we estimated chimpanzee abundance per patch from the GLM results.

We also estimated each patch’s contribution to achieving the 25% conservation target for each scenario, and its rank in terms of conservation importance, which we defined as the number of chimpanzees, other large mammal species, and tree genera present within each patch. To determine the minimum number of patches that maximizes the cumulative number of unique large mammal species/tree genera over the number of selected patches, we iteratively selected patches, at each step adding the patch that maximized the total number of large mammal species/tree genera in these. To determine which large mammal species and tree genera were included in patches, we first assigned each planning unit in each patch the large mammal species and tree genera found on the transect closest to it, to then determine the mammal species and tree genera found per patch. Removing duplicate species/genera we could then estimate which large mammal species/tree genera were likely to occur in each selected patch. To determine the minimum number of patches that maximizes the cumulative number of unique large mammal species/tree genera over the number of selected patches, we iteratively selected patches, at each step adding the patch that maximized the total number of large mammal species/tree genera in these.

We ranked individual patches for each scenario as follows: we determined averages of large mammal td and tree td across all planning units within patches. We also estimated weighted large mammal td by species-specific IUCN categories. Additionally, we determined chimpanzee abundance for all planning units within individual patches. We ranked patches for each one of these four variables and then averaged the ranks whereby we gave large mammal td and IUCN-weighted large mammal td half the weight of the other two, to give large mammal diversity the same weight as the other two. We reversed the revealed score so that the best patch had the lowest rank (starting at 1). Similarly, we ranked mining and logging concessions to assess their potential impact on chimpanzees and large mammal and tree diversity. We refer to the highest-ranked patches as those patches that have the most chimpanzees, and highest average values for (weighted) large mammal and tree td. These are also the patches that are most vulnerable to potential impact.

Chimpanzees as surrogates for biodiversity

We used a Spearman correlation test to investigate whether chimpanzee abundance correlated with large mammal td and tree td within patches selected by MARXAN. To calculate chimpanzee abundance, we summed the number of chimpanzees predicted per planning unit. We did the same for each patch for large mammal td and tree td: we assigned those large mammal species and tree genera to a patch that were observed on the line or strip transect located closest to it. After removing duplicate species and genera, we could estimate the total number of large mammal species and tree genera present in (or nearest to) each patch.

Results

Spatial prediction models

Overall, IUCN-weighted large mammal td, tree td, and chimpanzee abundance were clearly influenced by environmental variables and to a lesser extent by human impact variables. The only human impact variable that showed a trend was distance to markets in the chimpanzee abundance model (Appendix B: Table 5). Based on our spatial prediction model for chimpanzees, we estimated the country's total population at 6514 chimpanzees (as compared to 7008 chimpanzees estimated by Tweh et al. 2014). Modelled empty gun shell abundance was affected by the interaction between forest cover and human population pressure and that between forest cover and distance to markets (Appendix B: Table 6, Fig. 7). More gun shells occurred in forested areas when these were far away from human populations. Additionally, more gun shells were found in forested areas when they were near markets. The interaction between distance to roads and human population pressure also had a significant influence on empty gun shell abundance, suggesting that when human population pressure was low, distance to roads had a negative effect on empty gun shell abundance. Snares appeared significantly more abundant in non-forested areas.

Spatial prioritization

Depending on the scenario, MARXAN selected between 30 and 35% (between 5321 and 6140 planning units of a total of 17,737 forested planning units in Liberia) of the country's forest cover to achieve the conservation target for chimpanzees, large mammal diversity, tree diversity, and threatened species, respectively (Appendix B: Table 8). Scenario 4, which was restricted to PAs and PPAs, included 15% of the country's forests and 21% (1373 individuals) of Liberia's chimpanzees. Scenario 4 did not meet conservation targets for four out of the seven conservation features (Appendix B: Table 8). The optimal conservation scenario 1 contained >50% of Liberia's chimpanzees, >50% and >25% of the country's most diverse large mammal and tree communities, respectively, as well as >50% and >60% of the reported range of elephants and other threatened large mammals, respectively. As the proportion of land available for conservation decreased from scenario 1 to scenario 3, fragmentation of patches increased considerably (Fig. 1).

Post-processing of MARXAN outputs

The total patch area that was needed to achieve all conservation targets simultaneously, lay slightly above the 30% forest cover conservation target for scenarios 1–3 (Fig. 2A). As patch fragmentation increased, patch size decreased from scenario 1 to scenario 3 (Fig. 2B). Total edge length increased considerably (Fig. 2C), and proximity between neighboring patches decreased from scenario 1 to scenario 3 (Fig. 2D). Scenario 4 did not fit any of the above described patterns, because area selection was constrained to PAs and PPAs.

Scenario 1 also performed best in terms of patch contribution to achieving the conservation target for chimpanzees. Relatively few patches (ca. 30 patches) contributed to protecting >50% of Liberia's chimpanzees, whereas in scenario 2 about 60 patches were needed to protect <40% of the population (Appendix B: Fig. 8A). Scenario 3 performed worst, because more than 100 patches were necessary to protect<30% of the chimpanzee population. Scenarios

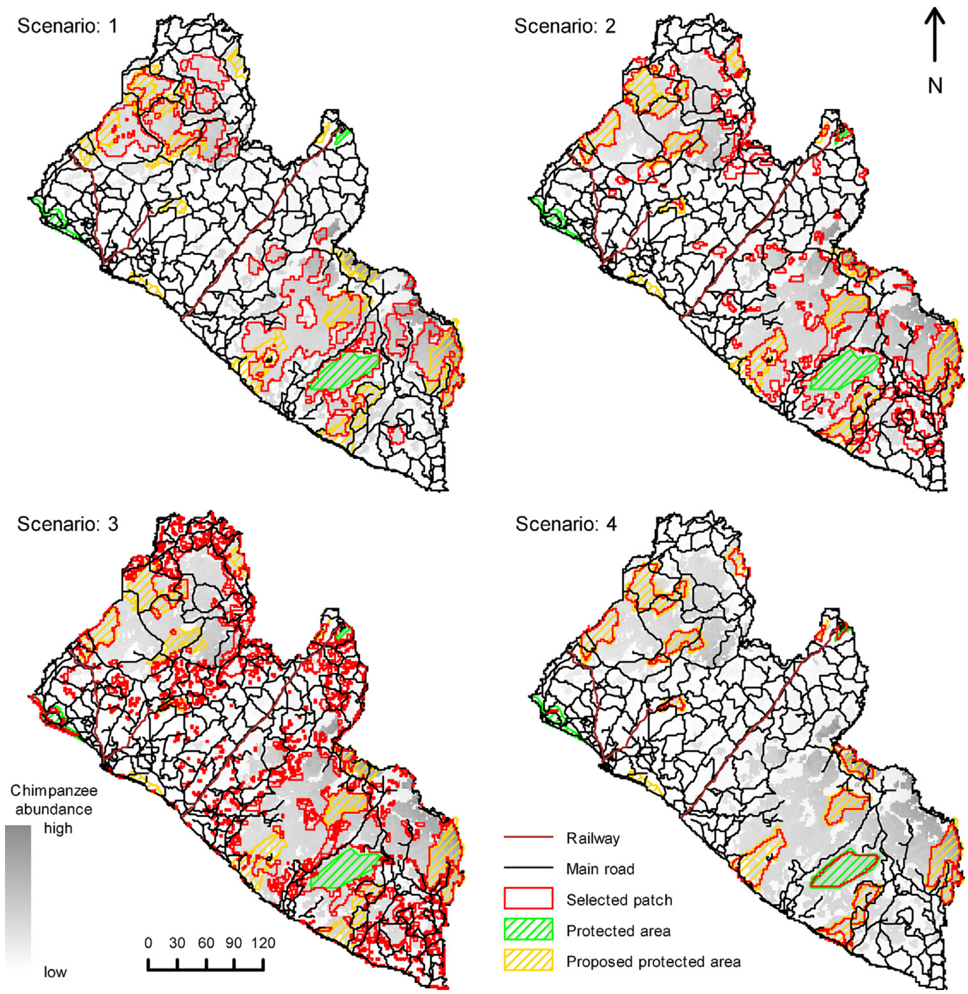

Fig. 1. Maps showing 30% best patches in terms of chimpanzee abundance for each of four conservation scenarios. Maps relate locations of selected patches to Liberia's current rail and road system and the protected and proposed protected areas.

performed similarly well when we evaluated patch contribution to large mammal and tree diversity (Appendix B: Fig. 8B and C). Relatively few patches were needed (<8 patches for large mammals, <25 patches for trees) to protect the majority of large mammal species and tree genera found during our survey in Liberia. However, scenario 4 performed considerably worse than scenarios 1–3 in terms of protecting tree diversity, as it included only about 65% of all the tree genera recorded across Liberia.

The majority of patches identified for scenario 1 that were within the 30% area limit, overlapped with proposed or ratified logging and mining concessions (Fig. 3A). Several patches also overlapped with Important Bird Areas (IBAs, Robertson 2001; Fig. 3B). Together, the six best patches covered approximately 14,500 km^2 and included 2360 chimpanzees, or 36% of Liberia's chimpanzee population (Fig. 3B, raw data for upload into a GIS is available in Appendix C). The eight worst concession areas were ratified or proposed forestry concessions, the latter of which also overlapped greatly with PUPs (Appendix B: Fig. 9). Together, the ten worst concessions included roughly 20,000 km^2 and 2820 chimpanzees (43% of the total population; detailed raw data on individual patches and concessions are available in Appendices D and E, respectively).

Chimpanzees as surrogates for biodiversity

The correlations between patch-specific chimpanzee abundance and large mammal- and tree td for the four scenarios were all significant (indicated are ranges of *rho*-values for scenarios 1–4: $rho_{\text{large mammal td}} = 0.35$- 0.75, $rho_{\text{tree td}} = 0.22–0.85$; all $p < 0.001$). Furthermore, for both large mammal td and tree td, correlations were highest for scenario 1, followed by scenarios 2 and 3, respectively. Correlations were highest for scenario 4, which was the scenario in which conservation priorities were spatially constrained to PAs and PPAs (Appendix B: Fig. 6).

Discussion

While the results of this study are specific to Liberia, we believe that the methodological approach presented here

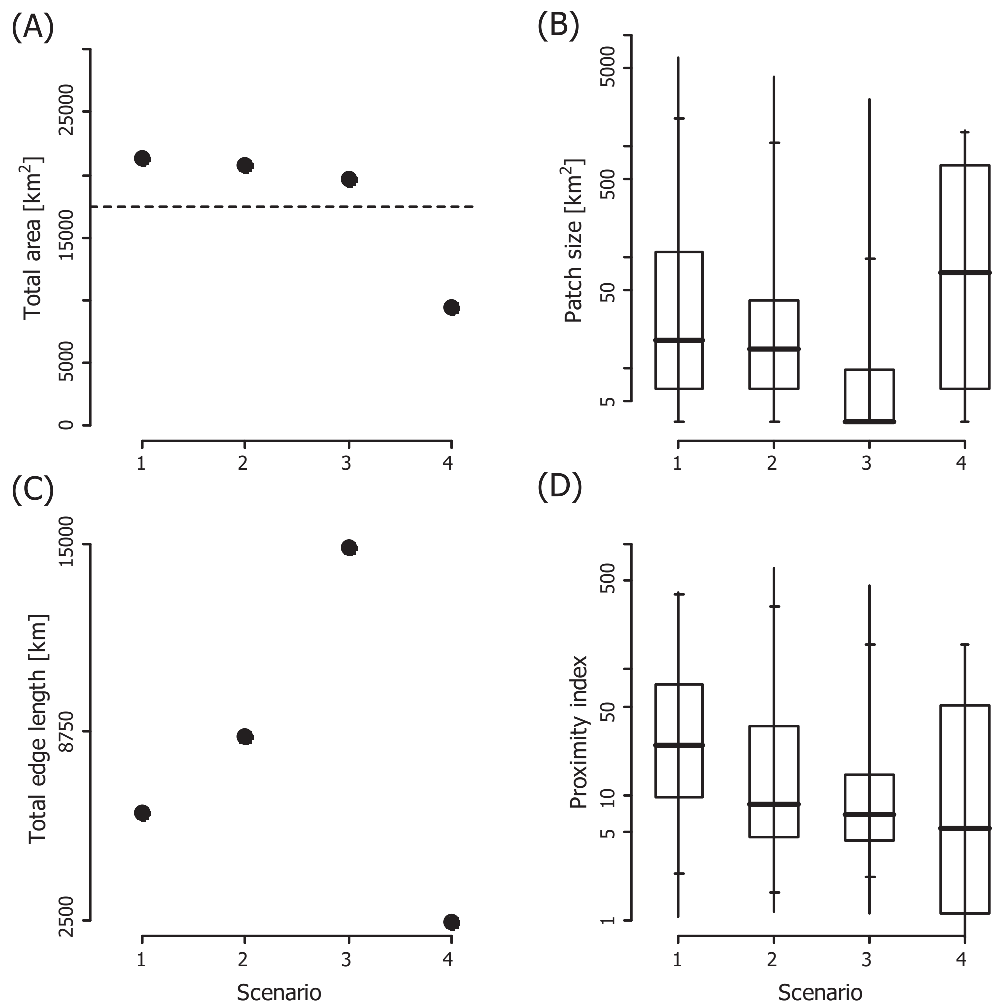

Fig. 2. (A) Total patch area, (B) average individual patch size (median, quartiles, percentiles, range), (C) total patch edge length and (D) average patch proximity (median, quartiles, percentiles, range) estimated for conservation scenarios 1–4 for the 25% conservation target. The stippled line represents the 30% area goal for protected areas set by the government. Note that patch size and proximity index are shown on a log-scale.

should be applied to many other regions in Africa, where conservation increasingly has to compete with land used for settlement, production systems and infrastructure. Despite the region's underrepresentation in terms of protected area coverage (Brooks et al. 2004), its critical importance for biodiversity conservation, growing importance for logging (e.g. Laporte, Stabach, Grosch, Lin, & Goetz 2007), mining (Edwards et al. 2014) and industrial agriculture (Wich et al. 2014) and its rapidly increasing human populations (Cincotta, Wisnewski, & Engelman 2000), very few reserve selection case studies have been published from sub-Saharan Africa to date (but see Rondinini, Chiozza, & Boitani 2006; Smith et al. 2008; Nackoney & Williams 2013). The success of future conservation planning studies in this policy-relevant region will directly depend on how well these address thematic, disciplinary and implementation gaps (Habel et al. 2013). More specifically, focus should be placed on solution-oriented research that is of direct interest to conservation practitioners, on cross-disciplinary approaches, and on facilitating knowledge transfer from scientists to conservation managers and policy-makers on the ground.

In an attempt to bridge these gaps, we proposed optimal protected area networks under different conservation scenarios, which aimed at maximizing biodiversity and wildlife abundance, while, at the same time, accomplishing Liberia's promise to protect 30% of its remaining forest cover. The conservation network under optimal land-use conditions (i.e., scenario (1) included more than half of the country's chimpanzee population, a landscape species (Coppolillo, Gomez, Maisels, & Wallace, 2004) that acts as an umbrella for some of the most species-diverse large mammal and tree communities in Liberia. Our network also minimized management costs likely associated with anti-poaching activities, and accounted for negative impacts imposed by roads and railways (e.g., Laurance et al. 2006), and high human population densities near settlements, market centers, and large towns (e.g., Kuehl et al. 2009; Murai et al. 2013).

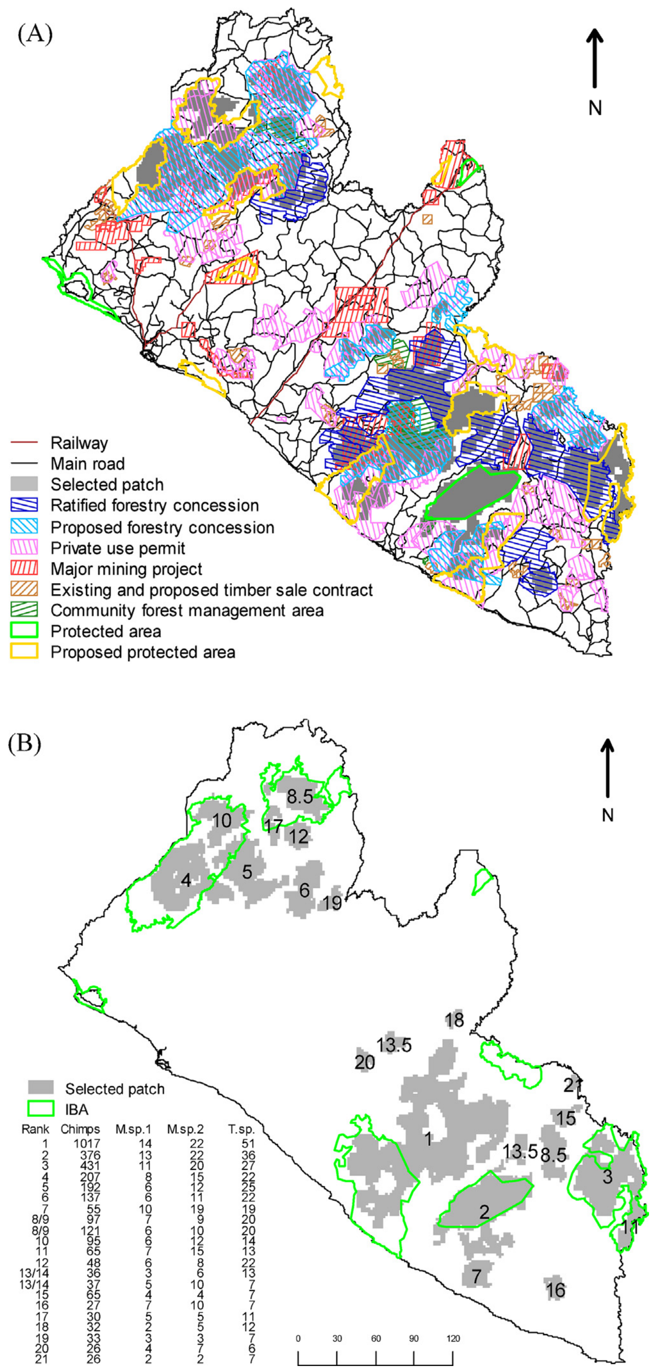

Fig. 3. (A) 30% best patches selected by MARXAN for scenario 1 for the 25% conservation scenario in relation to the location of railways and roads, protected and proposed protected areas and the different types of logging and mining concessions. (B) The same patches ranked (Rank) from best (=1) to worst (=21) in terms of chimpanzee abundance ("Chimps"), number of unique large mammal species ("M.sp.1"), sum of the IUCN-weight of the unique large mammal species ("M.sp.2") and number of unique tree genera ("T.sp."), in relation to the location of Important Bird Areas (Robertson 2001).

Land in Liberia is rapidly being sold to resource developers (MPEA 2010), which caused the almost complete overlap of concessions with conservation priority areas identified in this study. The latter are at risk of becoming degraded unless concessions are managed sustainably and their environmental impact is mitigated. Our analysis showed that, given current wildlife densities, protecting 30% of Liberia's current forest cover will not be sufficient to achieve the 25% conservation targets for chimpanzees, large mammal diversity, tree diversity, and threatened species, simultaneously. Moreover, assuming that all concession areas will become unsuitable for future conservation (scenario 3), this could lead to considerable fragmentation of selected patches, thereby decreasing patch size, increasing total patch edge, and decreasing connectivity among neighboring patches. It also substantially decreased the efficiency of the conservation area network (measured as target contributions of individual patches) to the extent that it became biologically and financially unfeasible to implement. Based on our results, anti-poaching patrols would have to travel about 15,000 km to once walk along the highly fragmented conservation network's boundary proposed in scenario 3 (Fig. 1). This is two-and-a-half times the boundary length of the reserve network identified without any spatial restrictions (scenario 1). Similarly, effectively managing 795 reserves with an average size of 25 km^2 as proposed by scenario 3 (as compared to 92 reserves averaging 230 km^2 proposed by scenario 1) will likely be impossible with the limited financial and human resources currently available. We showed that a minimum of 100 patches would have to be preserved to include about 30% of the country's chimpanzee population (which amounts to less than 2000 individuals) in scenario 3, whereas only about 30 patches would be necessary to conserve more than 50% of chimpanzees in scenario 1.

Furthermore, we could show that the optimal conservation scenario proposed in this study (scenario 1) not only maximized chimpanzee abundance, but it also ensured the protection of the country's most diverse mammal and tree communities. This spatial overlap between chimpanzee abundance and biodiversity, which decreased with increasing patch fragmentation, was greatest for scenario 4. However, this does not mean that scenario 4 performed best in terms of maximizing conservation targets for chimpanzees, and large mammal and tree diversity (see below). Rather, we ascribe this to the fact that scenario 4 neither optimized costs (i.e. areas of low hunting pressure) nor minimized human threats (i.e. human population pressure, proximity to roads, railways, and markets, which is a proxy for human threat) because area selection was constrained to the existing PA and PPA network in Liberia.

Although some PPAs overlapped with conservation priority areas, PAs and PPAs were not sufficient in meeting even the minimum conservation targets for chimpanzees, and large mammal and tree diversity. Liberia's PPA network covers 15% of the country's forests, but includes only 20% of the country's chimpanzee population (about 1300 individuals) and even less of its most species-diverse large mammal

(18%) and tree (11%) communities. Thus, even if the Liberian government implemented full protection status of all PPAs, more than 5000 chimpanzees along with many other threatened and endemic species and their natural habitats would remain unprotected and thus vulnerable to increasing human impact. These projections are not encouraging, especially when considering the very slow progress in the establishment of protected areas in the country, with only two proclaimed protected areas since the establishment of Sapo National Park in 1983 (EPA 2012).

However, we hope that through our continuous collaboration with the Liberian government and with the financial support from Norway, we will be able to bridge an important implementation gap and contribute to the decision-making processes that address Liberia's conservation challenges, before commercial operators, such as mining (Edwards et al. 2014), forestry or oil palm investors (Wich et al. 2014) purchase more licenses in not yet legally protected areas of high conservation priority.

Biodiversity offsets

One possibility to partially finance the identified conservation network in Liberia could be through a large-scale aggregate biodiversity offset system, the use of which is currently being investigated by the World Bank (WBG 2013). In biodiversity offsetting, different types of biodiversity measures are being traded off across space and time (Kiesecker et al. 2009). To date, offsetting has generally not achieved its anticipated conservation goals (Walker, Brower, Stephens, & Lee 2009). This may partially be ascribed to the lack of a robust and transparent methodology for quantifying and translating impact into offsets to achieve 'no net loss' or net environmental benefits (Overton, Stephens, & Ferrier 2013) and the lack of accurate and up-to-date datasets and expertise to systematically identify offsets within a landscape context (McKenney & Kiesecker 2010). Our systematic approach to identifying conservation priorities and assessing potential negative impact of proposed and ratified logging and mining concessions in Liberia, however, provides a scientific platform for accurately estimating impact-offset transactions, and will allow multiple stakeholders to co-invest into an effective nationwide aggregate biodiversity offset system. More specifically, our study estimated values for chimpanzee abundance, species diversity, and the number and type of threatened species present in each concession in Liberia. Based on these, we could rank each concession in terms of its 'biological importance', a metric that could be used (among others) during the impact evaluation process. For any residual impact (after applying the mitigation hierarchy; IFC 2012) developers could offset areas within the conservation priority network defined by this study to achieve 'no net loss' or 'net positive impact' of their activities within the concession. Contrary to project specific biodiversity offsets, an aggregate offset scheme would therefore provide an opportunity for the private sector to offset their residual environmental impact in a nationally-coherent manner and at the same time support governments in establishing a biologically representative and efficient protected area network (Johnson 2014).

Conclusions

The effective protection of only the best six of the 92 conservation areas outlined by our study under optimal land-use conditions would ensure the long-term survival of a chimpanzee population of approximately 2500 individuals and some of the most diverse forest communities in Liberia. Conservation actions will have to be implemented rapidly (see Appendix B: "Recommendations") as plans for economic development are competing heavily with wildlife preservation. This study provides the scientific basis for government, conservation authorities, international donors and environmental consultants to decide where limited funds are best invested to maximize conservation outputs and protect viable populations of chimpanzees and other wildlife species. Resource development and conservation management plans need to be integrated, where future strategies may range from area reservation to restoration depending on the biology, threats, and sociopolitical conditions of the area. We emphasize the possibility of a Liberia nationwide aggregate biodiversity offset scheme managed and financed by multiple stakeholders and with the potential to make Liberia a global model for conservation success.

Data accessibility

All data collected during the nationwide chimpanzee and large mammal survey in Liberia are available from the IUCN SSC A.P.E.S. database: http://apesportal.eva.mpg.de.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.07.002.

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