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Education and access to fish but not economic development predict chimpanzee and mammal occurrence in West Africa

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ABSTRACT

We are in the midst of an unprecedented environmental crisis. Landscapes have become complex social-ecological systems in which anthropogenic activities and biophysical factors interact across multiple scales. The integration of socio-economic development processes into conservation strategies as a means of sustainable resource management requires a deep understanding of the interactions between human activities and natural processes. Attempts to combine socio-economic and biological datasets for analyses, however, have frequently been hampered by spatial, temporal and methodological incompatibilities. In this study, we investigate the effects of human well-being on their environment in Liberia, West Africa. More specifically, we tested whether regions with improved community and household wealth, better education and access to market towns and fish protein, had higher levels of large mammal species richness and densities of the flagship species of West African forests, the chimpanzee (*Pan troglodytes verus*). Controlling for human pressure, forest cover and cultural diversity, we found that high literacy rates and affordable fish protein correlated with high chimpanzee density. On the other hand, areas with better economic and infrastructure development coincided with reduced large mammal species richness compared to less developed areas. This indicates that wildlife depletion rates can only be understood by including economic and social constraints. These results are important for informing effective future conservation management strategies in Liberia and elsewhere in tropical Africa.

1. Introduction

We are in the middle of a sixth mass extinction characterized by extremely high global rates of biodiversity loss (Barnosky et al., 2011; Dirzo et al., 2014; Pimm et al., 2014). Continued human population growth and increasing resource demands are rapidly changing the environment and few locations remain that have not yet been influenced by man (Sanderson et al., 2002).

Urbanization, agricultural practices, overfishing, biological introductions, and pollution are but a few examples of anthropogenic drivers of biotic homogenization and the subsequent reduction in structural and functional ecosystem complexity (Smart et al., 2006). Such a decrease in system complexity may lead to reduced productivity, resilience, and the system's adaptability to absorb change and persist in the future (Chapin et al., 1998). A decrease in biodiversity, for example, may render systems more vulnerable to human-induced changes (Chapin et al., 2000). Since our persistence depends on the proper functioning of ecosystems that provide natural resources and ecological services, much effort has been made to conserve the remaining pristine wilderness fragments through the establishment of protected areas. The rate at which new protected areas have been established over time has increased substantially over the past 40 years (West et al., 2006). However, protection of the relatively few remaining natural areas often incurs large social costs to local communities (Adams and Hutton, 2007) and their effectiveness varies greatly (Campbell et al., 2008; Craigie et al., 2010; Tranquilli et al., 2011; Coetzee et al., 2014). It is thus unlikely that the global extent of protected areas will substantially increase beyond the 2020 conservation target of 17% (www.cbd.int/sp/sp2010p/).

More recently, there has been a shift away from the "fortress conservation" mentality that typically excluded humans and their needs from conservation planning, towards integrating

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conservation strategies with programs to relief poverty and increase development. However, the effectiveness of integrated strategies remains hotly debated, where evaluation studies of development and conservation projects have yielded mixed results at best (Brooks et al., 2013). For instance, an assessment of ICDPs across Indonesia revealed that very few projects could claim that significant advances had been made towards biodiversity conservation (Wells et al., 1999). An analysis of World Bank projects revealed that only 16% made significant progress on both the conservation and development front (Tallis et al., 2008), and an independent evaluation of the achievements of the World Bank's integrative conservation projects in the forest sector over the past decade found little support for poverty reduction (IEG, 2012).

To know which socio-economic factors influence wildlife depletion and how these can be manipulated to change human behavior and promote conservation requires a profound understanding of the interactions between human and natural processes operating at different spatial and temporal scales (Parrott and Meyer, 2012). This, in turn, requires the amalgamation of spatially compatible socio-economic and biological datasets. Efforts to integrate and analyze ecological and socio-economic patterns across large heterogeneous landscapes however, are frequently hampered by different units of measurement and the fact that the spatial extent of ecological and socio-economic variables frequently does not coincide (Herr, 2007; Norgaard, 2008). Despite these difficulties, several studies have investigated social-ecological drivers of landscape characteristics at global, regional or site-specific scales (e.g., Black et al., 2003; Kronen et al., 2010; Verburg et al., 2011; Campos et al., 2012).

For instance, Black et al. (2003) found that broad-scale social systems including land ownership, economic market structure and cultural values were the key factors explaining forest change in the Interior Columbia River Basin, USA. A global analysis by Verburg et al. (2011) demonstrates that the most intensive modifications of natural land cover, urbanization, land clearing and cultivation are found in areas with the highest market influence. This is supported by a meta-analysis of case studies around the world (Geist and Lambin, 2002) which lists food markets as one of the main determinants of tropical deforestation.

Few studies, however, investigated the effect of socio-economic driving forces on biodiversity loss or wildlife population decline. For example, an analysis of data collected in Pacific Island countries showed that variables characterizing economic household conditions were positively correlated with commercial finfish and overall invertebrate exploitation levels (Kronen et al., 2010). Another recent study on elephants (*Loxodonta africana*) across Africa found that education, measured by literacy rate, was a better predictor of elephant population densities than ecological factors, such as food availability (de Boer et al., 2013). Finally, a number of studies have highlighted the conservation potential of religious and other traditional belief systems and local taboos in the realm of environmental protection (e.g., Brncic et al., 2010, Costa, 2010; Jimoh et al., 2012; Mikusiński et al., 2013).

To better understand the effects of socio-economic drivers on wildlife diversity and abundance in tropical Africa and to go beyond previous efforts to predict population distribution, abundance and proximate threats (e.g., Junker et al., 2012; Tweh et al., 2014), we amalgamated detailed nationwide ecological and socio-economic survey data from Liberia, West Africa in a spatially explicit manner. More particularly, we tested whether human well-being measured by monetary and non-monetary proxies of wealth, rural development, literacy and alternative protein availability, predicted chimpanzee density, large mammal diversity, and hunting pressure.

Rich in biodiversity, Liberia is among the poorest countries on earth (HDI rank: 174/187, UNDP, 2013). At the same time, after almost 15 years of civil unrest, the country is in the process of rapid economic and societal development (LISGIS, 2008; MPEA, 2010; Global Witness/SAMFU/SDI, 2012). These dynamics in ecological and socio-economic conditions result in a complex landscape that makes Liberia an ideal candidate-country for investigating potential social-ecological links.

2. Material and methods

2.1. Data sources

We used four different data sources: (1) chimpanzee density and large mammal species richness data collected on nationwide, systematically-placed line transects; (2) fish prices from interviews conducted near the surveyed line transects; (3) socio-economic information from interviews collected during the Liberia 2008 national population and housing survey (LISGIS, 2008); and (4) information on Landcover (FDA, 2003, modified by MPEA, 2010), human settlements (LISGIS unpublished data, FDA, unpublished data) and market towns (LISGIS, unpublished data, WFP, 2007).

2.2. Data collection

Between August 2010 and May 2012, we conducted a Liberia nationwide chimpanzee and large mammal survey, for which we systematically placed 68 sampling cells, each $9 * 9$ km in size, across Liberia. These were divided into nine, same-sized sampling blocks with one line transect in each center block and one in a second, randomly-chosen block yielding a total of 136 line transects. We followed the IUCN Best Practice Guidelines (Kuehl et al., 2008) to record all chimpanzee nests, presence of mammals on line transects and all human hunting signs, including snares and empty gun shells (cartridges). We restricted our survey to medium and large bodied mammal species (referred to as large mammals hereafter; Appendix A, Section 1, Table A1), because they were relatively easy to observe on line transects. For more details on survey methodology, see Tweh et al. (2014).

Socio-economic national population data were collected by the government of Liberia with the support of the United Nations Population Fund (UNFPA) during the Liberia 2008 national population and housing survey. A total of 1542 interviews with Liberians aged 15 years or older in both urban and rural areas were conducted by trained volunteers across all 136 Liberian districts within a period of seven days in November 2008. For more details on the methods, refer to audiencescapes (http://www.audiencescapes.org).

2.3. Response variables

We ran separate models for five different response variables derived from line transect data: (1) chimpanzee nest density, (2) unweighted and (3) weighted large mammal species richness. While we acknowledge that mammal abundance represents a more sensitive proxy for ecosystem health, particularly hunting pressure, our data did not allow for the estimation of individual species abundance, because several species have become so rare in Liberia that we observed them only on a small number of transects. We therefore included (4) snare and (5) cartridge density as proxies for hunting pressure (e.g. Imong et al., 2013). Although environmental health in the tropics is frequently measured by forest cover (e.g., Bhattarai and Hammig, 2001; Struhsaker et al., 2005), we think that our response variables are more appropriate. Forests still cover about 40% of Liberia's land surface but frequently lack healthy wildlife populations due to extensive poaching (Tweh et al., 2014). For each line transect, we then extracted data on predictor variables that existed either at the district level, the village

Table 1
Description of predictor variables, their hypothesized effects on the response variables, data sources and their spatial resolution.

Measurement	After standardization	Proxy for:	Variable	Anticipated effect[a]	Data source	Spatial resolution
Proportion adults (>15 years of age) who can read and write a simple sentence in any language or dialect	Proportion of literate people	Education	1	Positive	LISGIS[b] (2008)	Per district
Mean fish price (in LD)[c]	Mean fish price (LD)[c]	Availability of fish protein	2	Negative	Liberia nationwide chimpanzee and large mammal survey	Per village interviewed
Weighted (by min. price in USD) average score: proportion of people/district that owned furniture, cell phone, radio, mattress, TV, fridge, motorbike, vehicle	Weighted ownership of amenities	Household wealth	3	Positive	LISGIS[b] (2008)	Per district
Sum of no. people with access to a pump outdoors, pump indoors, public tap, expressed as a proportion of the total no. of people interviewed Inverse of sum of no. people who use wood and palm oil lamps as a lighting source, expressed as a proportion of the total no. of people interviewed Inverse of distance to nearest health facility Parental survival	Summed standardized score	Community well-being	4a	Positive	LISGIS (2008)	Per district
Distance to daily and weekly markets	Distance to markets	Rural development	4b	Positive	LISGIS[b] unpublished data, WFP[d] 2007	Discrete market town locations
Ethnic diversity Proportion Muslims Proportion immigrants	Factor 1 (control)	Cultural diversity (control)	5	Negative	Liberia (2008) national population and housing survey	Per district
Sum of log (human population density in pixel + 1)/distance to that pixel	Human pressure (control)	Human pressure (control)	6	Negative	LISGIS[b] unpublished data, FDA unpublished data[e]	Discrete settlement locations
Forested vs. non-forested habitat types	Proportion forest cover (control)	Proportion forest cover (control)	7	Positive	FDA[e] modified by USAID GEMS[f] unpublished data	$100 * 100$ m pixels

[a] On chimpanzee density and mammal species richness.
[b] Liberia Institute of Statistics and Geo-Information Services.
[c] Liberian Dollars.
[d] World Food Programme.
[e] Forestry Development Authority.
[f] United States Agency for International Development Governance and Economic Management Support.

level, or as countrywide GIS files (Table 1). For more details, see Appendix A, Section 2.

We weighted large mammal species according to their IUCN category and scored them accordingly (IUCN, 2013; 1 = least concern, 2 = near threatened, 3 = vulnerable, 4 = endangered). Weight increased with IUCN category, meaning that more threatened species contributed more to this score. Note that IUCN category 5 (critically endangered species) was not represented in our dataset, because we never observed any such species on line transects. It has been shown that some large mammal species, such as buffaloes, elephants, chimpanzees and other primates, as well as some ungulate species may survive well in moderately disturbed areas (Meijaard and Sheil, 2008; van Vliet and Nasi, 2008; Brncic et al., 2010; Stokes et al., 2010). We thus used both weighted- and unweighted large mammal species richness because there is a possibility that some moderately disturbed environments (e.g. forest–agriculture mosaics, secondary or degraded forest, rural areas with low to moderate human densities) may not differ substantially from natural environments in terms of mammal species diversity but more in terms of the number of threatened species present and/or the levels of their threat. Fig. A1 illustrates that some areas in central Liberia have relatively high large mammal species richness, despite the forests in these areas being largely degraded.

To control for survey effort in our models, we log-transformed line transect length multiplied by the effective strip width (ESW) and included it as an offset-term (McCullagh and Nelder, 1989) in the chimpanzee density model. We calculated ESW with the software Distance 6.0 Release 2 (Thomas et al., 2009). We included transect length as an offset-term in the other models, because we did not calculate ESW for observations of mammals and hunting signs.

2.4. Predictor variables

To test for a spatial correlation between socio-economic factors and chimpanzee density, large mammal species richness and hunting pressure in Liberia, we included five test predictors into our regression models: (1) proportion of literate people, (2) mean fish price, (3) household wealth, (4) community well-being and (5) distance to market towns. To control for other potential effects that may influence chimpanzee density and large mammal species richness, we also included three control predictors: (1) cultural diversity, (2) proportion of forest cover and (3) human pressure (Table 1, Appendix A, Section 3).

Education has been shown to positively correlate with environmental health (e.g., Heinen, 1993; Fiallo and Jacobson, 1995; Törn et al., 2007; de Boer et al., 2013, but not Struhsaker et al., 2005). We thus expected literacy rate to positively influence chimpanzee density and large mammal species richness (and the opposite effect on snare and cartridge abundance), and used proportion of literate people (adults above 15 years of age who could read and write a simple sentence in any language or dialect) as a proxy for education in our regression models. Including proportion of literate people, rather than proportion of people with secondary education into our models is appropriate, because in Liberia education levels are generally very low (i.e., 40% of the entire population is illiterate (LISGIS, 2008) and secondary level education is rare and varies little across the country). Therefore, even a low level of education is likely to make a difference in terms of employment.

Mean fish price (in LD = Liberian Dollars, LD/USD = 70), was used as an indirect measure for the availability of alternative protein (Brashares et al., 2004). Since fish has been shown to present a dietary substitute for bushmeat (Wilkie et al., 2005) we expected fish price to negatively influence chimpanzee density and large mammal species richness (and the opposite effect on snare and cartridge abundance). To exclude the possibility that fish price was driven by local demand rather than supply, we ran a Spearman correlation between fish price and human pressure (explained below) and found that there was a weak inverse correlation between these two variables ($r_S = -0.178$, $N = 114$, $p = 0.057$; Fig. A2a). Furthermore, we found a significant positive correlation between fish price and forest cover ($r_S = 0.256$, $N = 114$, $p < 0.006$), suggesting that fish price was driven by supply rather than demand (Fig. A2b). We are thus confident that fish prices in Liberia are not driven by demand and that our assumption that people in areas with high fish prices consume more bushmeat is reasonable. Note that fish prices refer to saltwater fish, which make up the bulk of fish on sale in Liberia (Junker personal observation).

We used ranked ownership of amenities (i.e., furniture, radio, mattress, cell phone, motorbike, TV, fridge, vehicle) as a measure of household wealth. We combined indicator variables for infrastructure development (water- and lighting source) and health (walking distance to the nearest health facility, parental survival) into a single measure of community well-being. Data on parent survival were assimilated by reporting whether parents of children/adults not older than 24 years of age were still alive (for details see Appendix A, Section 5). We also included distance to market towns as a test predictor, because this has been suggested a good proxy for rural development (Mwabu and Thorbecke, 2004). Because we were limited in how many predictors we could include, and because community well-being and distance to market towns both represent measures of economic development, we ran two models (one with community well-being and one with distance to markets) for each of the five response variables, referred to as '1' and '2', respectively, throughout the text. In accordance with the development-environment hypothesis, which states that raising local livelihoods may enhance the conservation status of the local environment, we predicted a positive correlation between household wealth, community well-being and rural development with chimpanzee nest density and large mammal species richness (and we predicted the opposite effect on snare and cartridge abundance).

The rationale for including ethnic diversity, proportion immigrants and proportion Muslims as control predictors was as follows: We predicted that: (1) more ethnically diverse communities have traditions that are more diluted and thus less socially enforced, potentially leading to a weakening of taboos on killing and eating chimpanzees and/or other mammal species (Colding and Folke, 2001; Jones et al., 2008; Jimoh et al., 2012) and a corresponding decrease in wildlife abundance; (2) in areas with a large immigrant population, traditions and local taboos are also weakened, because laws/rules of the migrants' homeland might no longer apply to the area that they migrated to, possibly resulting in higher hunting pressure (Bowen-Jones and Pendry, 1999); (3) proportion Muslims positively affects chimpanzee densities and/or mammal species diversity as Muslims frequently follow a taboo against killing and/or consuming chimpanzees (e.g., East et al., 2005; Costa, 2010) and possibly other mammals. We expected a correlation between proportion immigrants, proportion Muslims and ethnic diversity, because presence of immigrants from different cultural backgrounds would lead to increased ethnic and religious diversity. We thus ran a principal components analysis, which revealed one principal component with an Eigenvalue >1. We then conducted a factor analysis to extract one factor including the variables ethnic diversity, proportion immigrants, and proportion Muslims, which we from now on refer to as cultural diversity (Appendix A, Section 4, Table A2).

We included human pressure, a measure combining distance to human settlements and their respective population size, and proportion of forest cover as control predictors. Both are well known to influence chimpanzees (e.g., Junker et al., 2012) and other mammals, as well as hunting pressure (e.g., Muchaal and Ngandjui, 1999). We further included an autocorrelation term to account for potential spatial non-independence in the residuals (derived as described in Fürtbauer et al., 2011). For more details see Appendix A, Section 5.

2.5. Models

We excluded all interaction terms, because including them would have made the model too complex for the given sample size (Field, 2005). We analyzed the data using Generalized Linear Models (GLMs, McCullagh and Nelder, 1989) with a negative binomial (in case of overdispersed residuals) or Poisson error structure and log link function, respectively. To establish the significance of the full models (Forstmeier and Schielzeth, 2011) we used likelihood ratio tests (Dobson, 2002), comparing their deviance with that of the respective null models. Null models comprised only the intercept, the offset-term, the control predictors (i.e., cultural diversity, proportion forest and human population density), and the autocorrelation term when it had a significant and positive effect in the full model.

Due to some collinearity among certain predictors, we used multi-model-inference (Burnham and Anderson, 2002) to ensure that our models did not suffer from it and our conclusions are sound. For each response (i.e., chimpanzee density, weighted and unweighted large mammal species richness, and snare and cartridge density), we ran all $_{\text{possible}}$ combinations of test and control predictors ($N = 128$). For each predictor we then determined its Akaike weight as the summed Akaike weights of the models comprising it. We also calculated weighted averages of model coefficients for each predictor, where weights were the models' Akaike weights. For details on model terms, full-and null model comparisons, model stability, model implementation, data compatibility, and model robustness see Appendix A, Sections 6–11.

3. Results

3.1. Data collection

We surveyed 116 line transects (total survey effort: 326 km) to gather data on encounter rates of chimpanzee nests, number of large mammal species, as well as snares and cartridges. At the same time we also interviewed 276 people from 70 locations (mean number of respondents/location: 3.9, range: 1–6) across the entire country to document fish prices (Fig. 1). We recorded a total of 113 chimpanzee nests on 28 transects and 26 large mammal species on 92 transects. Chimpanzees and other large mammals ranged widely and occurred predominantly within the two large continuous forest blocks in the south-east and north-west of the country (Figs. A1a–c). Snares were predominantly found in agricultural areas in central Liberia, whereas cartridges were most frequently encountered in forested areas in the north-west, north-east and east of the country (Figs. A1d–e). For more details on survey results see Tweh et al. (2014).

3.2. Models

For simplicity, we only show the results of one of the chimpanzee density, weighted large mammal species richness, and snare

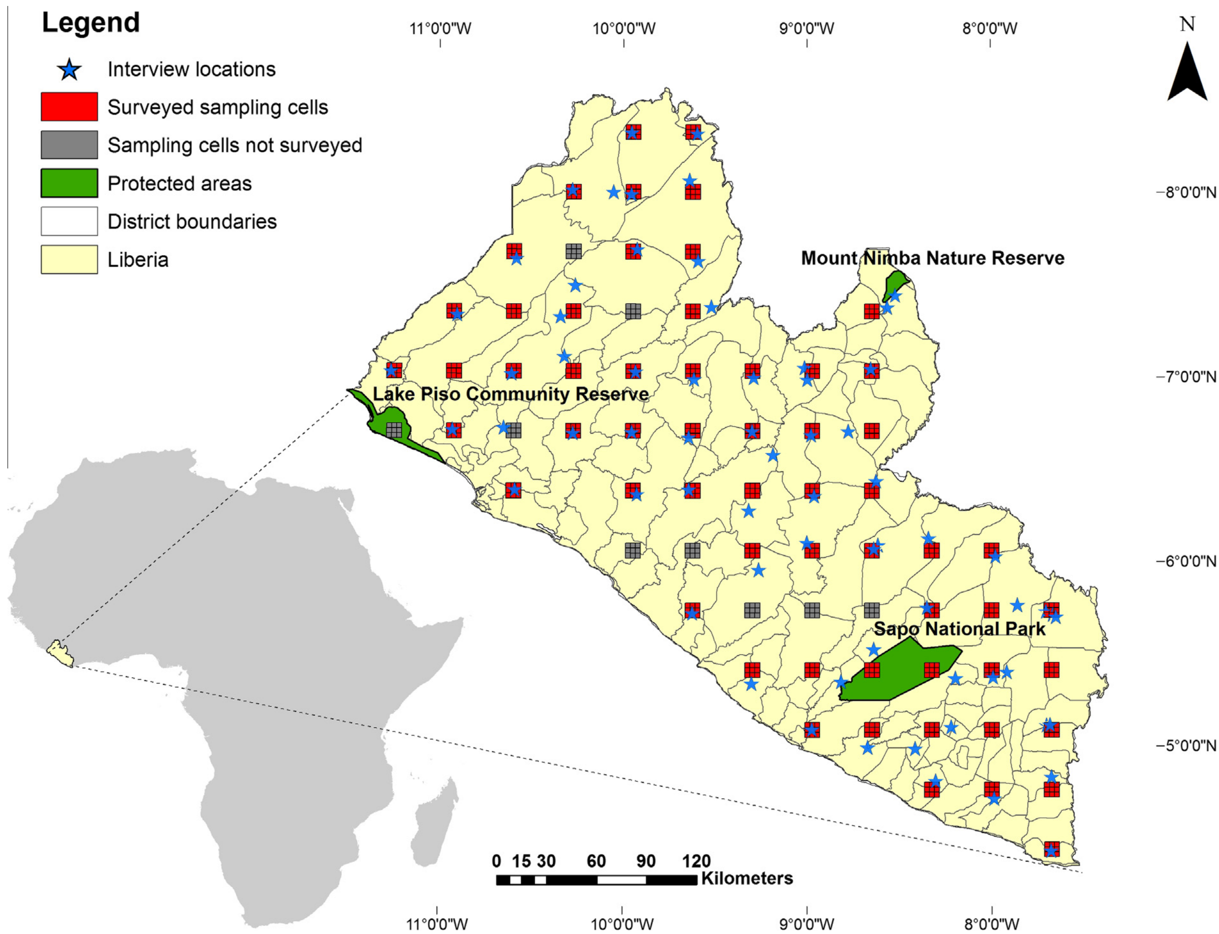

Fig. 1. Map of Africa showing Liberia, the sampling locations and surveyed line transects of the Liberia nationwide chimpanzee and large mammal survey, interview locations, fully protected areas and district boundaries in which socio-economic data were collected during the Liberia 2008 national population and housing survey. Please note that nine sampling cells were inaccessible due to physical barriers and local political conflict.

density models in the main text. For raw data outputs of the other models, please refer to Appendix A. We could retrieve information on socio-economic variables for all but one district in Liberia, which we assigned to a total of 114 line transects. Therefore, our models were run on a dataset including 114 transects for which we extracted information on all predictor variables.

Both full models that included chimpanzee density as a response and the models that included unweighted and weighted large mammal species richness as a response and distance to markets as one of their predictors, fitted the data significantly better than their respective null-models (chimpanzee density 1: $\chi^2 = 10.777$, $df = 4$, $p = 0.029$; chimpanzee density 2: $\chi^2 = 9.949$, $df = 4$, $p = 0.041$; unweighted large mammal species richness 2: $\chi^2 = 9.624$, $df = 4$, $p = 0.047$; weighted large mammal species richness 2: $\chi^2 = 9.629$, $df = 4$, $p = 0.047$). The models that included weighted and unweighted large mammal species richness as a response and community well-being as one of their predictors, and the models predicting snare and cartridge density did not differ significantly from their respective null-models (for details, see Appendix A7).

Variable contributions differed between models with different response variables (Tables 2, A3). With the exception of distance to market towns and household wealth, observed effects of predictor variables that contributed significantly to a model supported our hypotheses about their correlation with chimpanzee density, large mammal species richness, and snare and cartridge density. Contrary to what we had anticipated, economic development, measured by household wealth, community well-being, and distance to markets had no significant effect on chimpanzee density. Additionally, areas closer to market towns coincided with low levels of both unweighted (Table A3) and weighted (Table 2, Fig. 2a) large mammal species richness.

As expected, areas with a high proportion of literate people co-occurred with high chimpanzee densities (Table 2, Fig. 2b; Table A3). Furthermore, areas where fish prices were high, had low chimpanzee densities (Table 2, Fig. 2c, Table A3). However, neither of these variables obviously influenced large mammal species richness. Except for cartridge density, forest cover showed a significant effect in all models. This effect was positive, except in the case of snares, which we observed more frequently outside forests. Apart from forest cover, snare density also appeared to be weakly influenced by household wealth: we found more snares in areas where people were wealthier. Human pressure did not significantly influence any of our response variables. Predictors that showed a significant effect on the response in our original models also had the highest summed Akaike weights, confirming our results (Tables 2, A3).

4. Discussion

Our study highlights two key issues. First, it shows the need to use integrative approaches to improve our understanding of the dynamic relations between socio-economic conditions and current resource (e.g. bushmeat) exploitation levels in complex social-ecological systems to successfully prevent over-exploitation and ensure the livelihoods of rural communities. We found that in Liberia, chimpanzee density was spatially linked to livelihood

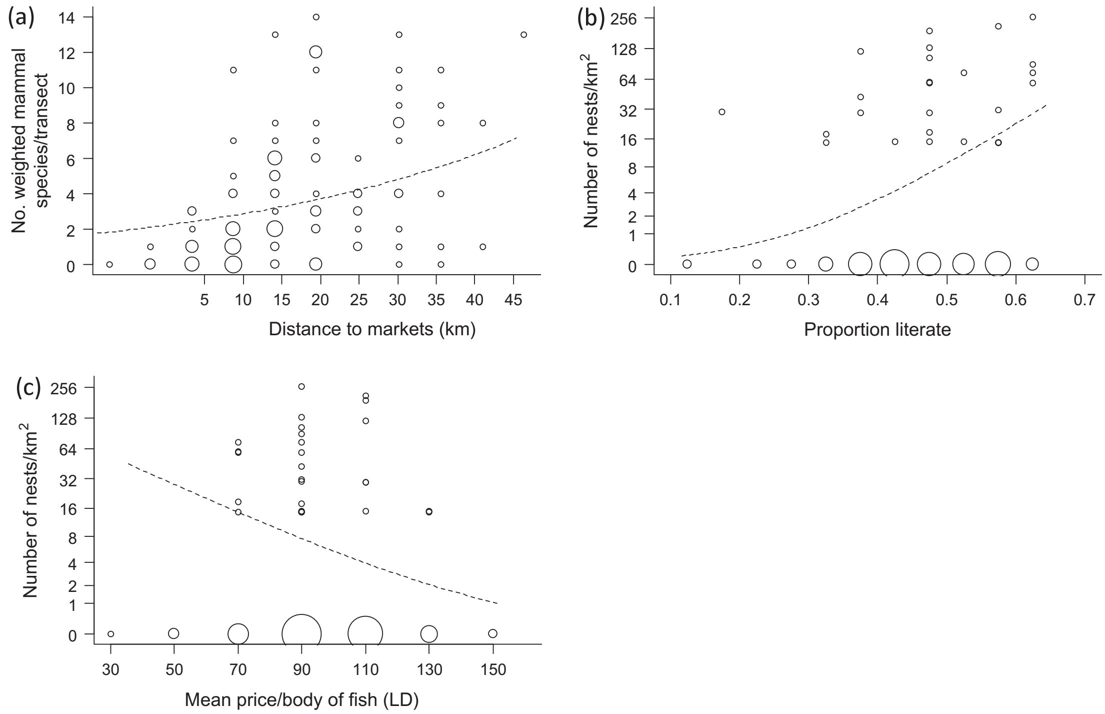

Fig. 2. Weighted large mammal species richness as a function of distance to markets (a), and chimpanzee density as a function of proportion of literate people (b) and fish price (c). The size of each circle corresponds to the number of transects for a given combination of values of the respective predictor and response variable (both binned), and the dashed lines indicate the fitted model.

Table 2
AIC values, estimated model coefficients, weighted average of coefficients, standard errors, *z*-values, *p*-values, and summed AIC weights for three full models, including chimpanzee density, weighted large mammal species richness, and snare density as a response. Significant effects and trends are indicated in bold.

Model/response	Predictor	Estimate (full model)	Weighted average of coefficients	SE	*z*	*p* (Full model)	Summed AIC weights
Chimpanzee density 2	Intercept	1.828	1.933	0.269	[a]	[a]	1
	Proportion of literate people	0.654	0.597	0.317	2.061	**0.039**	0.896
	Cultural diversity (control)	0.275	0.183	0.256	1.074	0.283	0.331
	Human pressure (control)	−0.109	−0.110	0.354	−0.309	0.758	0.285
	Mean fish price	−0.612	−0.544	0.252	−2.427	**0.015**	0.582
	Forest cover (control)	1.107	1.151	0.333	3.320	**0.001**	0.998
	Household wealth	−0.215	−0.158	0.265	−0.811	0.417	0.302
	Distance to markets	0.150	0.125	0.302	0.496	0.620	0.295
Weighted large mammal species richness 2	Intercept	1.235	1.243	0.082	[a]	[a]	1
	Proportion of literate people	0.101	0.097	0.097	1.043	0.297	0.399
	Cultural diversity (control)	−0.152	−0.176	0.088	−1.723	**0.085**	0.749
	Human pressure (control)	−0.027	−0.059	0.112	−0.245	0.806	0.308
	Mean fish price	−0.044	−0.036	0.085	−0.510	0.610	0.290
	Forest cover (control)	0.382	0.396	0.108	3.536	**<0.001**	0.997
	Household wealth	−0.093	−0.074	0.090	−1.043	0.297	0.345
	Distance to markets	0.274	0.286	0.102	2.686	**0.007**	0.940
Snare density 2	Intercept	0.538	0.579	0.182	[a]	[a]	1
	Proportion of literate people	−0.328	−0.222	0.205	−1.599	0.110	0.365
	Cultural diversity (control)	0.101	0.086	0.192	0.527	0.598	0.293
	Human pressure (control)	−0.221	−0.136	0.225	−0.983	0.325	0.307
	Mean fish price	−0.019	0.007	0.190	−0.100	0.920	0.270
	Forest cover (control)	−0.979	−0.978	0.258	−3.788	**<0.001**	0.999
	Household wealth	0.337	0.247	0.199	1.687	**0.092**	0.428
	Distance to markets	−0.045	−0.025	0.237	−0.189	0.850	0.274
	Ac-term	0.578	NA	0.166	3.478	**0.001**	NA

[a] Not shown because of not having a meaningful interpretation.

constraints, more specifically, lack of education and limited fish protein supply. Second, areas with better economic and infrastructure development coincided with reduced large mammal species richness compared to less developed areas. This demonstrates that different measures of socio-economic conditions can have opposing effects on wildlife populations, which is important in the context of future conservation management.

To better understand these results, it is important to reflect on the mechanisms underlying economic well-being and education that bring about the observed differences in chimpanzee density and mammal species richness. Our results showing that literacy was the most important predictor for chimpanzee density after controlling for forest cover are in line with the few previous studies that empirically tested for a relationship between education and environmental health (e.g., Heinen, 1993; Fiallo and Jacobson, 1995; Törn et al., 2007; de Boer et al., 2013, but not Struhsaker et al., 2005). We speculate that one of the following mechanisms may be responsible for the observed effect: (1) educated people may more likely be involved in cash income activities and thus depend less on local wildlife resources for food. This is supported by results of a Spearman's Rank Order post hoc correlation test showing a positive link between education and household wealth ($r_S = 0.604$, $N = 114$, $p < 0.001$), and community well-being ($r_S = 0.614$, $N = 114$, $p < 0.001$); (2) educated people may be more aware of potential negative environmental consequences of their actions, or possible health hazards related to preparing and eating bushmeat and thus employ more sustainable or alternative ways to satisfy their needs. This hypothesis however, does not likely explain the observed spatial patterns, as people's attitudes alone generally do not seem to predict behavior well (Holmes, 2003; Heberlein, 2012); (3) a more likely reason for the observed effect is that the majority of present-day hunters fall into an age group that had very limited access to education during times of civil war in Liberia (1989–1997 and 2003–2004).

We also showed that chimpanzee densities in forests close to relatively developed communities were comparable to those in more remote and underdeveloped areas. This suggests that chimpanzees can, to some extent, survive in areas that are relatively close to moderately impacted areas, which may be facilitated by the fact that hunters in many areas in Liberia do not specifically target chimpanzees but rather kill them opportunistically or not at all (Liberia: Junker personal observation; Sierra Leone: Brncic et al., 2010; Guinea: Regnaut personal communication). For example, in some forests in Liberia, signs of chimpanzees were the only large mammal signs we frequently observed. This is in contrast to the notion that chimpanzees are environmental indicator species (Wrangham et al., 2008) and can serve to monitor the health of an ecosystem.

Perhaps one reason for chimpanzees to survive in forests close to relatively developed communities may be that people in these areas have better access to affordable non-bushmeat protein, such as fish, a hypothesis that was supported by the results of our analysis correlating fish price with human pressure and forest cover. Lower fish prices in these more densely populated areas may be the result of better road infrastructure and lower transport costs of fish from coastal towns to these areas. In contrast, people in remote forest areas probably rely more on bushmeat (for personal consumption and/or commercial trade) and consequently also hunt more chimpanzees. They may occasionally supplement their diet with freshwater fish caught from nearby rivers since market prices for salt water fish in these remote inland areas may not be affordable on a daily basis for the majority of people who live in these communities. Our results on the spatial link between fish prices and chimpanzee density are in line with previous studies that demonstrated a direct link between fish supply and price and bushmeat demand (Apaza et al., 2002; Brashares et al., 2004), suggesting that fish represents an important dietary substitute for bushmeat in many parts of west and central Africa (Wilkie et al., 2005).

The reason why neither proportion of literate people, nor fish prices showed an effect on large mammal species richness may be that the latter is not a sufficiently sensitive proxy for hunting pressure or habitat disturbance. It is expected that species detection on transects is not 100%. While some species may disappear over time, the overall number of species observed will likely remain similar, as generalist species can survive and even increase in abundance in moderately-impacted environments and thus be regularly detected on transects (e.g., Meijaard and Sheil, 2008). We hypothesized that hunting pressure may be more sensitive towards the effect of these predictors, which is why we ran additional models including snare and cartridge density as responses. None of these models however, revealed any correlations between either measure of hunting pressure and literacy levels or fish prices. We ascribe this to the fact that the disappearance of cartridges and the actual disappearance of animals act on different time scales. Snares on the other hand were more common in non-forested, agricultural areas and used by people mainly to deter crop-raiding animals from private farms (Junker personal observation), rather than specifically hunt animals for their meat. This may also explain the lack of significant effects of literacy or fish prices on snare abundance. Instead, snare density weakly correlated with household wealth. In rural Liberia, wealthier people own larger farms, which may have resulted in the higher snare densities observed in these areas.

In contrast to household wealth, improved rural development is likely to affect the environment differently. Distance to market towns relates primarily to infrastructure development and trade. This may affect the environment in three ways: (1) through modification and removal of vegetation cover (Theobald et al., 1997), (2) increased accessibility (Blake et al., 2008; Stokes et al., 2010) and human immigration (Laporte et al., 2007), possibly leading to increased human disturbance and hunting pressure in these regions and (3) an increase in commercial hunting fueled by the bushmeat trade. It is possible that the combination of physical damage to the environment and commercial hunting is the reason why distance to market towns, but not increased household wealth or community well-being, co-varied with mammal species richness. However, these are speculations and more detailed data on different aspects and scales of economic development are needed to further investigate these hypotheses.

We were not able to demonstrate a causal link between specific development project's activities and local wildlife populations, because information on the location, type, activities, duration, and spatial extend of such projects was not available on a nationwide scale. Liberia is no exception and there appears to be a general lack of quantitative evidence on the effectiveness of integrated conservation and development projects and an urgent need to make socio-ecological data sets more widely available for detailed and large-scale evaluation studies (e.g., for data on great apes, see IUCN SSC A.P.E.S. database: http://apesportal.eva.mpg.de).

Nevertheless, our study is one of the few to provide quantitative data to suggest that projects that provide bushmeat protein alternatives and promote education may complement existing strategies to conserve chimpanzees in Liberia and possibly other countries in tropical Africa. Liberia's 2008 population census showed that 40% of Liberians were illiterate (LISGIS, 2008). Additionally, results from our 2010–2012 interview survey on meat protein availability indicate the lack of domestic livestock in many rural Liberian communities (unpublished results). There thus seems to be much opportunity and a great need for implementing education projects and programs to promote domestic meat stocks and fisheries into future conservation and development action plans. Such programs should be initiated around protected areas to raise conservation awareness, provide livelihood-alternatives through better education (e.g., Borchers et al., 2014) and relieve resource pressure inside these areas. Our results may also become important for managing aggregate biodiversity offset areas, the use of which is currently being investigated by the World Bank (World Bank Group, 2013).

In addition, because the majority of development strategies go hand in hand with infrastructure growth, it will be key to install appropriate control measures along with development projects to minimize negative effects of infrastructure growth on wildlife populations in the future. For example, strategically located road blocks, frequent ranger patrols (Tranquilli et al., 2011; N'Goran et al., 2012), long-term research or conservation presence (Campbell et al., 2011), and eco-tourism (N'Goran et al., 2012) may help to reduce poaching pressure in these areas. While all of these measures have been implemented at various locations in Liberia at some or other point in time, high corruption levels, a lack of capacity and equipment, insufficient distribution of funds, political instability, and disease outbreaks, such as the recent Ebola crisis, continue to hamper efficient conservation efforts.

5. Conclusions

This study provides a national perspective on the spatial links between human well-being and biodiversity protection which may aid in informing future sustainable resource management in Liberia. Understanding the social-ecological processes acting at the landscape level may also increase our ability to predict future patterns of resource use to effectively promote the maintenance of current biodiversity levels and ensure the long-term survival of rare and threatened species, such as the West African chimpanzee. This is particularly relevant in tropical developing countries, where the scale and magnitude of current anthropogenic landscape transformation represents a serious threat to global biodiversity (Campos et al., 2012).

We argue that multipurpose regional surveys such as ours can yield valuable datasets to address these conservation challenges, enhance collaboration and build capacity in the future. As many countries conduct regular human population surveys, we contend that biological data should more frequently be integrated with existing socio-economic datasets to conduct similar analyses.

While Liberia currently still holds the largest continuous forest blocks in West Africa (Christie et al., 2007), several commercial logging and mining industries have already purchased large tracts of pristine land with the intend to commence extraction activities in the forthcoming years (MPEA, 2010; Global Witness/SAMFU/SDI, 2012). Thus, Liberia's landscape will progressively transform into a mosaic of different land-use patterns, where few areas will remain devoid of human impact. In the light of these developments, there is a need for researchers, conservationists and environmental managers to monitor the complex social-ecological processes that will continue to shape Liberia's natural ecosystems and incorporate this knowledge into current and future conservation plans. These should incorporate food-security and education projects, appropriate anti-poaching measures and strict environmental policies to guide sustainable development and resource extraction activities.

There is no panacea to be applied to all environmental problems, and trade-offs between economic development and conservation will continue to exist. However, with sufficient scientific knowledge and a good understanding of the complex mechanisms driving ecological systems in a human-dominated world, we may be able to provide human populations with the resources and ecological services they need without jeopardizing the long-term survival of our rich natural heritage.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.11.034. These data include Google maps of the most important areas described in this article.

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