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Development and biodiversity conservation in Sub-Saharan Africa: A spatial analysis

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Abstract

The current study seeks to provide a sound analysis of the relationship between economic development and species loss in Sub-Saharan African countries. The motivation is that a better understanding of the impact of economic development on species loss is of great relevance, given the current rapid extinction of species along with challenges born from the context of economic development in poor countries. The analysis draws on the most up-to-date data on threatened species from 48 sub-Saharan African countries. Assuming that spatial autocorrelation is a typical problem for biodiversity data, we use Maximum-likelihood estimators to account for spatial-autoregressiveness in the dependent variable, as well as in the explanatory variables of the models. We find evidence that supports a decrease of biodiversity loss, measured as the percent of threatened bird species, with increasing income per capita. The results also reveal some species-level differences in the biodiversity-development relationship, since we find no significant impact of economic development measured as per capita income on threatened mammal species. This analysis contributes to the literature by partially challenging the paradigm of a strictly positive relationship between biodiversity loss and economic growth in a developing countries context.

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Abstract

The current study seeks to provide a sound analysis of the relationship between economic development and biodiversity loss in Sub-Saharan African countries. The motivation is that a better understanding of the impact of economic development on biodiversity loss is of great relevance, given the current rapid extinction of species along with challenges born from the context of economic development in poor countries. The analysis draws on the most up-to-date data on threatened species from 48 sub-Saharan African countries. Assuming that spatial autocorrelation is a typical problem for biodiversity data, we use Maximum-likelihood estimators to account for spatial-autoregressiveness in the dependent variable, as well as in the explanatory variables of the models. We find evidence that supports a decrease of biodiversity loss, measured as the percent of threatened bird species, with increasing income per capita. The results also reveal some species-level differences in the biodiversity-development relationship, since we find no significant impact of economic development measured as per capita income on threatened mammal species. This analysis contributes to the literature by partially challenging the paradigm of a strictly positive relationship between biodiversity loss and economic growth in a developing countries context.

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Introduction

The depletion of biodiversity is now one of the most important environmental threats that humanity faces (Chapin et al. 2000; Tilman et al. 1997; MEA 2005). Regarding the consequences of biodiversity loss, not all people are impacted equally. Changes in ecosystems disproportionately harm many of the world's poorest people, who are less able to adjust to these changes and for whom poverty means they have limited access to substitutes or alternatives (MEA 2005). The less developed regions in the world, where the poorest people who are most vulnerable to biodiversity loss live, are also regions where threats to biodiversity are the highest (Turner et al. 2012; Roe 2010; Billé et al. 2012). The Sub-Saharan Africa (SSA) region is a good illustration of such a developing region that is at the forefront of priorities in terms of conservation as well as development needs (Fisher and Christopher 2007). Indeed, the needs for reducing poverty and vulnerability are the greatest in SSA according to World Bank reports (Monchuk 2014). The SSA region is also home to almost one-quarter of the "biodiversity hotspots," i.e. areas around the world where exceptional concentrations of endemic species are undergoing exceptional loss of habitat (Myers et al. 2000).

The CBD (Convention on Biological Diversity) decisions (UNEP 2012) and Aichi targets (UNEP 2010) recommend moving forward with integrated strategies that tackle conservation and development issues together. Despite some progress being made towards achievement of these goals through the implementation of incentives like REDD+ (Reducing Emissions from Deforestation and forest Degradation) and PES (Payments for Ecosystem Services), it would be a fairly safe assumption that the current impacts of these pro-conservation tools are not very perceptible in the on-going development strategies in developing areas. It is therefore important to further discuss whether continued efforts to meet development and poverty reduction targets will not lastingly compromise biodiversity. In others words, since we need to deal with development and poverty challenges for regions which are also "biodiversity hotspots," shall we be optimistic or pessimistic about biodiversity and the maintenance of related environmental services?

The matter of whether economic development worsens or strengthens biodiversity conservation has been widely analyzed in the literature. A number of researchers share a pessimistic view and forecast a conflict between economic growth and biodiversity conservation (Chambers et al. 2000; Czech 2003; Trauger 2003). Some works have found that increased growth of the economy implies higher threats to biodiversity (Asafu-Adjaye 2003; Freytag et al. 2009). Other scholars reject the monotonic relationship assumption and argue that the relationship between economic growth and biodiversity conservation varies along the development path. They predict a "virtuous circle" after a threshold of development is reached (Naidoo and Adamowicz 2001; McPherson and Nieswiadomy 2005; Pandit and Laband 2007a; Mills and Waite 2009) and advocate for a biodiversity Kuznets curve (BKC). The logic is that when enough financial wealth accumulates, especially in per capita terms, society refocuses on solving environmental problems (Czech 2008). As we can see, empirical findings have not yet provided a clear-cut answer to the question of the impact of economic development on biodiversity. In this paper, we propose further investigation on the issue and provide the first sound analysis for the SSA region with a focus on spatial interactions in our modeling techniques.

Including spatial interactions in the development-biodiversity relationship is important for several reasons. First, the distribution of species is determined by geophysical, atmospheric, and ecological factors that cut across political jurisdictions (Kerr and Burkey 2002; Pandit and Laband 2007a). Factors that threaten biodiversity may extend or operate beyond arbitrary political boundaries and risks to biodiversity in one country may similarly impact biodiversity in neighboring countries through spillover effects (see (McPherson and Nieswiadomy 2005;

Pandit and Laband 2007a; Mills and Waite 2009)). Second, national policies for conservation may be influenced by policies in neighboring countries or by regional policies, resulting in a pattern of political spatial dependence (Sauquet et al. 2012). Third, unobserved variables may be related by a spatial process; in the case of biodiversity, these may be climatic variables. As a matter of fact, regarding biodiversity, there may be several sources of spatial dependence between countries.

McPherson and Nieswiadomy (2005) were the first to consider the problems surrounding spatial autocorrelation, investigating biodiversity-development relationship. They find evidence for both endogenous interaction effects (spatial autoregressive model-SAR) and interaction effects among the error terms (spatial error model-SEM). In others words, they find that the percentage of threatened species in one country is jointly determined with that of neighboring countries and that unobserved shocks follow a spatial pattern. Evidence of significant spatial autocorrelation with respect to biodiversity indicators through SAR model have been found in different works (Pandit and Laband 2007a; Pandit and Laband 2007b; Pandit and Laband 2009; Tevie et al. 2011). Only one study establishes that SEM models result in greater explanatory power than SAR models for threatened mammals, birds, amphibians, and vascular plants (Pandit and Laband 2007b). Development of spatial econometrics advocates for models that include both endogenous and exogenous interaction effects (LeSage and Pace 2009; Elhorst 2010; Corrado and Fingleton 2011), in a model labelled spatial Durbin model (SDM). This model admits that the dependent variable of a particular unit depends on independent explanatory variables of others units (Elhorst 2014). Face to the plethora of alternative model specifications, LeSage (2014) indicates that there are only two model specifications worth considering for applied work, SDM (spatial Durbin model) and SDEM (spatial Durbin error model) that subsume other specifications. Given the fact that there is more evidence in previous findings for a spatial pattern related to endogenous interaction in literature as described earlier, we then run a spatial Durbin model. This is in line with the hypothesis previously presented. In this way, our paper is the first to consider a spatial Durbin model, investigating the impact of economic development on biodiversity loss at regional scale.

The argument proceeds in five parts. First, we present previous findings in analyzing the link biodiversity-development by focusing on methodological issues. Second, we describe our methodology. Third, we present the data. Fourth, we present our results. Then we discuss the results, while a final section concludes and shows how our findings can inform policymakers.

Methodology

Firstly, in order to choose the functional form between biodiversity and economic development (lin-lin, log-log, lin-log, or log-lin form relationship), we shall test a Box-Cox transformation, as described below:

$$Y_i^{(\theta)} = \alpha_0 + \sum_{k=1}^{K_1} \alpha_k . x_{1ik}^{(\lambda)} + \sum_{k=K_1}^{K_2} \alpha_k . x_{2ik} + u_i \ , \qquad (1)$$

where $i = 1, \dots, 48$ countries; Y_i: the biodiversity threat measure in country i; x_{1k}: the K$_1$ transformed quantitative variables; and x_{2k}: the other K$_2$ quantitative variables. And where $Y_i^{(\theta)}$and $x_{1ik}^{(\lambda)}$ are respectively, the Box-Cox transformations of the biodiversity threat measure and countries' characteristics.

$Y_i^{(\theta)} = (Y_i^{(\theta)} - 1)/\theta$ if $\theta \neq 0$, $Y_i^{(\theta)} = \ln(Y_i)$ otherwise.
$x_{1ik}^{(\lambda)} = (x_{1ik}^{(\lambda)} - 1)/\lambda$ if $\lambda \neq 0$, $x_{1ik}^{(\lambda)} = \ln(x_{1ik})$ otherwise.

We shall then estimate the model on a set of different values of θ and λ and find out the best functional form.

Secondly, to capture spatial dependence among countries, we shall use spatial econometric techniques. To take into account spatial dependence and its magnitude among countries belonging to our sample, we look for evidence that the values for the percentage of threatened species of a taxon in SSA countries are more spatially clustered than they would be under random assignment. Spatial autocorrelation measures the intensity of the relationship between observations and their degree of resemblance. Each observation is described by one attribute (the dependent variable) and by proximity relations (weight matrices). If the presence of the attribute in one country makes its presence in a nearby country more or less likely, then there is spatial autocorrelation. There is no spatial autocorrelation if there is no relationship between the proximity of countries and their degree of resemblance. Whatever the source of spatial dependence, standard econometric techniques are no longer appropriate, especially the method of ordinary least squares. Instead, other estimators are proposed in the literature (see Anselin 1988, LeSage and Pace, 2009).

We define two weight matrices: (i) Matrix W^{c}_{ij} is based on 1st order contiguity, i.e. two countries are neighbors if they share a common border and (ii) Matrix W^{B}_{ij} contains the length of common borders between two countries. Both are row-standardized.

Following recent developments in spatial econometrics (Elhorst 2010; Corrado and Fingleton 2011; LeSage 2014), and, given the arguments discussed earlier, we estimate a spatial Durbin model, such that

$$\begin{gathered} Y = \lambda WY + \beta X + \theta WX + \varepsilon \\ \varepsilon \sim N(0, \sigma^2 I) \end{gathered} \tag{2}$$

Y is the $N \times 1$ vector of values of the dependent variable. W is an $N \times N$ spatial weight matrix. X is an $N \times K$ matrix of K explanatory variables. β is a $K \times 1$ vector of parameters. ε is an $N \times 1$ vector of errors terms. WX is an $N \times k$ matrix of spatially lagged explanatory variables. λ and θ are scalar spatial parameters. λ reflects the magnitude of spatial dependence between observations. This spatial parameter measures the intensity of spatial interactions through the lagged dependent variable, i.e. the dependence of a country on nearby countries. θ is a measure of exogenous interactions effects. This spatial parameter measures the intensity of spatial interactions through independent explanatory variables of others units.

Data

The definition, interpretation, and sources of data are given in Appendix A. The Percentages of Threatened Species (PTS) for birds and mammals at the country level for SSA countries measure the pressure on biodiversity. Birds and mammals species are the only taxonomic groups for which all species have been reviewed by the International Union for Conservation of Nature (IUCN) (Hilton-Taylor and Mittermeier 2000). Hence we will estimate the model for two dependent variables, $\mathrm{PTS}_{\mathrm{BIRD}}$ and $\mathrm{PTS}_{\mathrm{MAM}}$. We calculate the latter for each taxon as the percentage of threatened species to known species in 2011 for mammals and in 2012 for birds. Gross domestic product per capita (PCGDP) in constant 2005 US$, normalized for purchasing power, is used as an indicator of economic development.

Socio-economic and ecological characteristics of countries are introduced as control variables. For socio-economic data, we use population density (per km^2) at the country level (DENS), as Dietz and Adger (2003), Asafu-Adjaye (2003), and Pandit and Laband (2007). Following Kerr and Currie (1995), and Asafu-Adjaye (2003), we also employ the percentage of agricultural land area (AGRI). We use as ecological variable, the percentage of endemism in birds (PES_{BIRD}) and in mammals (PES_{MAM}) in each country, as Naidoo and Adamowicz (2001), McPherson and Nieswiadomy (2005), Pandit and Laband (2007), and Pandit and Laband (2009). We consider national conservation policies as Naidoo and Adamowicz (2001), Freytag et al. (2009). To do so, we use the duration of existence of the first protected area in the country (DURPA). For the specific context of SSA, we control for experience of political instability and violence (PV) and for high rates of poverty (POV).

Explanatory variables are averaged over the 1992-2011 period (except for PES_{BIRDS} and PES_{MAM}) in line with McPherson and Nieswiadomy (2005). The intuition behind this procedure is to account for the fact that an indefinite span of time exists between anthropogenic factors and changes in biodiversity. This procedure also makes our study immune to short-term effects. Our sample consists of 48 observations which gather all SSA countries (cf. Appendix B for the list of countries). Table 1 presents descriptive statistics for all variables.

Table 1. Descriptive statistics

Variables	Unit	N	Mean	S.D.	Min	Max	Year
PTS_{BIRDS}	%	48	3.64	3.41	0.66	15.29	2012
PTS_{MAM}	%	48	9.44	5.81	3.22	31.58	2011
PCGDP	constant 2005 US$	48	2747.83	4079.16	311.89	18245.49	
POV	%	48	51.12	15.35	9.53	81.2	
DENS	hab./km^2	48	76.62	106.68	2.32	587.74	
AGRI	%	48	47.94	21.25	8.24	86.54	
PV	score	48	-0.41	0.95	-2.69	1.36	
DURPA	number of years	48	63.81	25.82	6	117	
PES_{BIRDS}	%	48	2.86	8.02	0	43.98	2012
PES_{MAM}	%	48	4.17	11.93	0	80.09	2011

Unless otherwise stated all variables are averaged over the 1992-2011 period

Results

The estimation procedure[1] of the linear Box-Cox functional form (equation 1) indicates that the value of θ and λ are, respectively, 0.61 and 1.24 for mammals and 0.46 and -0.44 for birds. We perform a comparison test model which calculates the value of the following test: -2($LM_{constraint}$ - $LM_{non\ contsraint}$) where the term $LM_{constraint}$ (resp. $LM_{non\ constraint}$) corresponds to the value of the logarithm of the maximum likelihood of the constrained model (respectively of the non-constrained model). This formula can be adjusted by iterations to obtain the best possible transformation, according to maximum likelihood criterion. It allows estimating the model parameters with or without restrictions. This test follows, asymptotically, a χ^2 with two degrees of freedom. In the case of birds, the hypothesis θ=0 is accepted at the 1% threshold (the transformation of λ is rejected). The log-linear form is retained for the subsequent estimation for birds models. For mammals, the linear form is retained.

In our model, there is no issue of multicollinearity. We use Variance Inflation Factors (VIFs) to detect it. VIF values for variables other than PCGDP and $PCGDP^2$ do not exceed 2.02[2], which is in line with the most conservative rule of thumb.

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[1] The econometric analysis is performed using STATA software.

[2] Mean VIFs range from 1.33 and 1.47 and reach 5.54 when both PCGDP and $PCGDP^2$ are included.

Following the spatial tests in Appendix C, we can reject the hypothesis that the models allow for both sources of spatial dependence, i.e. spatial lag on the dependent variable and spatially autocorrelated residuals. Furthermore, the robust LM tests validate a spatial lag term instead of spatially correlated error structure. Testing the SDM, which adds spatially lagged independent variables to the model, the Likelihood Ratio test (WX's=0) does not reject the hypothesis that the set of spatially lagged independent variables are significant in all specifications and with the two matrices for birds and mammals models (see Table 2 and Table 3). We retain, therefore, the SDM specification for birds and mammals models.

Spatial models fit better than models that omit spatial dependence, with respect to some model selection diagnostic criteria (adjusted R^2, log-likelihood and Akaike information criterion (Table 2 and Table 3). The spatial analysis reveals also some species-level differences. We find that the percentage of threatened mammal species in one country depends mainly on the level of threatened mammal species in neighboring countries (the spatial lag of the dependent variable is significant). The source of spatial dependence for threatened bird species is, however, mainly due to the intensity of some characteristics of neighboring countries (the spatial lag and spatially autocorrelated residuals are not significant). These results corroborate that spatial analysis needs to be done in order to explain the pattern of threatened species.

As robustness check for the specification, we compare SDM model to SDEM (model with spatially auto-correlated residuals) and to SLX (model with no spatial dependent variable) and we find SDM model more appropriate in all cases using the Akaike information criteria (Cf. Appendix D).

Discussion

The model for bird species shows evidence of a statistically significant relationship between income per capita and the percentage of threatened bird species in linear and hyperbolic specification with all weight matrices. The model for mammal species shows, on the contrary, that the percentage of threatened mammals in a SSA country is not related to income per capita. Income per capita is not significant in all mammals models, except the variable GDP_LAG, whose marginal effect (cf. Appendix E) is however null. Previous works (McPherson and Nieswiadomy 2005; Pandit and Laband 2007c) have found a significant relationship between threatened mammals and GDP but for a group of developed and developing countries. This result advocates for studies on homogenous group of countries and geographical areas.

The results reveal also some species-level differences in the biodiversity-development relationship, in line with previous findings (Kerr and Currie 1995; Naidoo and Adamowicz 2001; Pandit and Laband 2007a). The results confirm then that the development-biodiversity relationship is complex and non-homogeneous across taxa groups. They also confirm the fact that the use of synthetic indicators in the biodiversity-development relationship is problematic.

The results advocate for a hyperbolic, non-linear relationship between threatened birds and income per capita, rather than an inverted-U relationship. This is in line with Dietz and Adger (2003). The data also support a negative linear relationship between threatened birds and income per capita. The magnitude of the effect of income per capita in the linear model is however negligible (cf. Appendix E).

Table 2. Non-spatial and DURBIN models log threatened birds (1992–2011 averages of independent variables)

	Non-spatial models			DURBIN models with W^{C}_{ij}			DURBIN models with W^{B}_{ij}		
	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic
PCGDP	-0.000027*	-0.000060		-0.000035***	0.000001		-0.000049***	-0.000020	
	0.000015	0.000053		0.000011	0.000035		0.000018	0.000042	
PCGDP2		2.14E-09			3.24E-09			-1.83E-09	
		-2.32E-09			2.17E-09			2.38E-09	
PCGDP^{-1}			211.484216**			122.962215**			112.001415*
			89.083841			59.497480			58.097306
POV	-0.012726***	-0.013644***	-0.016128***	-0.007756***	-0.005948*	-0.010009***	-0.009460***	-0.008488***	-0.010949***
	0.004070	0.004328	0.004507	0.002671	0.003278	0.003603	0.002748	0.003211	0.003263
DENS	0.001121*	0.001058*	0.000758	0.000178	0.000045	0.000376	-0.000073	-0.000211	0.000337
	0.000562	0.000574	0.000563	0.000425	0.000443	0.000446	0.000515	0.000544	0.000477
AGRI	0.003733	0.004440	0.006451**	0.002500	0.002260	0.004374**	0.003503*	0.003337*	0.004690**
	0.002788	0.003005	0.002732	0.001762	0.001798	0.001994	0.001868	0.001895	0.002033
PV	-0.108687*	-0.103986*	-0.076012	-0.096081***	-0.093240**	-0.080268**	-0.101736***	-0.102601***	-0.084195**
	0.057563	0.058407	0.057009	0.033902	0.037360	0.035791	0.032740	0.033837	0.033735
DURPA	-0.005094**	-0.005169**	-0.005063**	-0.001810	-0.001724	-0.001991	-0.002346*	-0.002356*	-0.002766*
	0.002227	0.002245	0.002143	0.001281	0.001309	0.001432	0.001285	0.001288	0.001369
PES$_{BIRDS}$	0.056446***	0.055998***	0.056767***	0.040058***	0.041893***	0.057247***	0.038572***	0.038551**	0.062243***
	0.006703	0.006785	0.006520	0.008158	0.010303	0.006083	0.014217	0.015066	0.007144
PCGDP_LAG				0.000065***	0.000085		0.000057	0.000037	
				0.000025	0.000108		0.000037	0.000098	
PCGDP2_LAG					-2.06E-09			1.27E-09	
					8.03E-09			7.34E-09	
PCGDP^{-1}_LAG						-149.866437			91.019929
						135.745637			129.161276

	Non-spatial models			DURBIN models with W^{C}_{ij}			DURBIN models with W^{B}_{ij}		
	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic
POV_LAG				0.009150	0.009965	0.006474	0.003533	0.004215	-0.002640
				0.007371	0.009199	0.009583	0.007465	0.007763	0.007401
DENS_LAG				-0.000763	-0.000399	-0.001859*	-0.001131	-0.001033	-0.003140***
				0.001019	0.001059	0.000995	0.001517	0.001537	0.001065
AGRI_LAG				0.008022**	0.008046**	0.007488*	0.004666	0.004871	0.008123**
				0.003743	0.003724	0.004112	0.003681	0.003815	0.003790
PV_LAG				0.020605	0.015574	-0.083412	0.024711	0.023533	-0.008348
				0.080658	0.085974	0.075830	0.067908	0.067565	0.067824
DURPA_LAG				-0.005037	-0.004595	-0.005558	-0.004550	-0.003952	-0.002970
				0.003284	0.003331	0.003581	0.003173	0.003251	0.003221
PES_{BIRDS}_LAG				0.023551**	0.029235**	0.011661	0.031221**	0.033690**	0.009202
				0.010757	0.011762	0.011197	0.014067	0.014359	0.010474
_cons	1.624110***	1.690984***	1.426297***	0.815406	0.653679	1.167588*	1.381285**	1.264737**	1.358000***
	0.310246	0.328429	0.250876	0.605645	0.767659	0.660897	0.578971	0.617318	0.515970
λ				-0.074602	-0.159354	-0.116715	-0.071663	-0.096252	-0.110810
				0.147508	0.169865	0.152893	0.143594	0.161671	0.145804
N	48	48	48	48	48	48	48	48	48
r2_a	0.70	0.70	0.72	0.69	0.67	0.69	0.70	0.68	0.72
Log-likelihood	-12.581834	-12.314517	-11.280631	15.767048	16.60192	12.970548	13.450666	13.753208	12.125306
AICc	45.9005	48.5750	43.2981	17.7116	23.7633	17.7101	17.7065	23.7615	17.6961
LR test (wX's =0)									
P-Value > Chi2				0.0002	0.0002	0.0120	0.0019	0.0036	0.0225

*p<0.1; **p<0.05; ***p<0.01. Parameters estimation of the SDM is performed by Maximum Likelihood Estimation (MLE). For each variable we present the coefficient and the standard errors.

According to these results the pressure on biodiversity in the SSA context, measured as a percentage of threatened birds, could slow down as income per capita rises. Based on these findings, we can temper the pessimistic view concerning the development-biodiversity relationship in a developing country context with data from SSA countries. We can argue that economic development is not totally incompatible with species conservation even in developing areas like SSA countries. In fact, our analysis provides evidence that a lessened threat on bird species is associated with higher income per capita in SSA.

Previous works have demonstrated that in wealthy countries birds receive greater conservation attention than other taxonomic groups, regardless of relative degrees of threat (Simon et al. 1995). Based on our findings, we can also suppose that the protection of bird species is more stringent in wealthier countries in SSA. It seems more likely that certain institutions may make conservation of birds less difficult than that of other taxonomic groups (Naidoo and Adamowicz 2001). Conservation efforts for mammal species could be more challenging, as many mammal species are relatively large and require much larger tracts of undisturbed habitat than birds to maintain viable populations (Noss et al. 1996). In addition, mammals, particularly large mammals, have also been vulnerable to the expansion of subsistence-oriented human economies for several reasons, including competition for resources, danger as predators, and value as food and clothing (Burghardt and Herzog 1980; Kellert 1985).

The results enable additional conclusions to be drawn explaining some sources of pressure on bird and mammal species in SSA. It seems that in the SSA context, the poorest countries where more people are below the poverty line exert less pressure on species. This could reflect the lack of *means* of these countries to implement intensive economic activities that would threaten biodiversity. This finding justifies the issue that is addressed in this study, as development and thus intensive economic activities, can lead to greater threats to biodiversity. The effect of poverty on threatened species is significant in all models for birds as well as for mammal species.

Threatened mammal species increase with increasing human population density. This indicates that the threat on mammal species increases in more densely populated countries. This result is in line with an anthropogenic theory of biodiversity loss, according to which population pressure leads to habitat destruction and reduction of resources for animal species. A number of papers have found evidence for this theory and show that high population density increases the percentage of threatened species (Asafu-Adjaye 2003; McPherson and Nieswiadomy 2005; Pandit and Laband 2007c; Freytag et al. 2009). The effect of human density on threatened birds is less clear. The significant effect of human density on bird species' imperilment disappears with spatial dependence. It seems that the influence of some adjacent countries' characteristics trumps the effect of human density on the imperilment of birds in a given country.

We find significant evidence that the level of imperiled species among birds depends on increasing agricultural land in a given country, as well as in its neighboring countries. This finding is consistent with previous ones that evidence the negative influence of agriculture on threatened species (Asafu-Adjaye 2003; Kerr and Currie 1995) and goes further by demonstrating the influence of a spillover effect through agriculture.

The percentage of threatened species in SSA is influenced by conservation policies. We find that the longer the conservation experience in a given country, the less species are threatened. That can support the establishment of protected areas as an instrument for species conservation.

Table 3. Non-spatial and DURBIN models percent threatened mammals (1992–2011 averages of independent variables)

	Non -spatial models			DURBIN models with W^{C}_{ij}			DURBIN models with W^{B}_{ij}		
	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic
PCGDP	0.000108	-0.000455		-0.000154	0.000318		-0.000138	0.000431	
	0.000121	0.000425		0.000111	0.000327		0.000112	0.000348	
PCGDP2		3.59E-08			-2.89E-08			-2.90E-08	
		2.60E-08			2.07E-08			2.04E-08	
$PCGDP^{-1}$			-193.464235			558.954728			419.550252
			755.114432			613.849717			544.443887
POV	-0.061598*	-0.076948**	-0.067915*	-0.033149	-0.064118**	-0.065649*	-0.042443*	-0.051062*	-0.056581*
	0.033618	0.035048	0.038514	0.028895	0.029050	0.036968	0.025802	0.027463	0.031119
DENS	0.028951***	0.027753***	0.029467***	0.016315***	0.011875**	0.018405***	0.013401**	0.012273**	0.017500***
	0.004484	0.004518	0.004638	0.004818	0.004633	0.004600	0.005077	0.004955	0.004411
AGRI	-0.044237*	-0.032220	-0.050289**	-0.016361	-0.023437	-0.016980	-0.017841	-0.020570	-0.019004
	0.022934	0.024287	0.023232	0.018597	0.017175	0.020575	0.016528	0.015618	0.017922
PV	-0.325011	-0.252375	-0.371468	-0.389101	-0.824367**	-0.364655	-0.330986	-0.504235*	-0.268147
	0.468508	0.466240	0.482428	0.362194	0.343970	0.370236	0.313539	0.297027	0.323140
DURPA	-0.047798**	-0.048745**	-0.050830***	-0.024122	-0.029609**	-0.036639**	-0.029546**	-0.034177***	-0.033840**
	0.018254	0.018063	0.018194	0.014756	0.013322	0.015088	0.012441	0.011695	0.013286
PES_{MAM}	0.312331***	0.308823***	0.314585***	0.194388***	0.115499**	0.249545***	0.146249**	0.161045***	0.207586***
	0.035233	0.034931	0.035506	0.054145	0.053688	0.041146	0.058495	0.055427	0.043364
PCGDP_LAG				0.000317	-0.002949***		0.000366	-0.002079**	
				0.000233	0.000934		0.000251	0.000887	
PCGDP2_LAG					2.28E-07***			1.67E-07**	
					6.33E-08			5.79E-08	
$PCGDP^{-1}$_LAG						1026.251698			-99.454843
						1267.506154			1147.229130

	Non -spatial models			DURBIN models with W^{C}_{ij}			DURBIN models with W^{B}_{ij}		
	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic	Linear	Quadratic	Hyperbolic
POV_LAG				0.037454	-0.144310*	-0.072379	0.035126	-0.026937	-0.040341
				0.074200	0.083594	0.088774	0.072474	0.073564	0.065227
DENS_LAG				-0.005933	-0.007395	-0.016765	0.009104	-0.005956	-0.003285
				0.011784	0.010888	0.010912	0.014036	0.014529	0.012353
AGRI_LAG				-0.019300	0.042633	-0.028624	-0.038586	0.013578	-0.039332
				0.033217	0.034165	0.034574	0.026577	0.031118	0.028715
PV_LAG				1.567454**	0.387841	1.057711	1.774661***	1.227032**	1.370603**
				0.792075	0.785348	0.733728	0.565932	0.587370	0.568363
DURPA_LAG				-0.002276	-0.034723	-0.012938	0.011149	0.029920	0.004286
				0.036115	0.034057	0.037548	0.028303	0.027744	0.030626
PES$_{MAM}$_LAG				-0.016321	0.043178	-0.020567	-0.011410	-0.029318	-0.028375
				0.056449	0.057277	0.055383	0.050502	0.049049	0.050145
_cons	13.811493***	14.907195***	15.035367***	5.738416	19.786818***	14.147784**	6.140375	9.184159	12.114996***
	2.564259	2.656649	2.141980	6.563942	7.318008	6.355431	5.963428	6.153718	4.426447
λ				0.602803***	0.552139***	0.553047***	0.648907***	0.618085***	0.601919***
				0.144265	0.147094	0.147543	0.131305	0.132110	0.135087
N	48	48	48	48	48	48	48	48	48
r2_a	0.70	0.70	0.72	0.69	0.67	0.69	0.70	0.68	0.72
Log-likelihood	-12.581834	-12.314517	-11.280631	15.767048	16.60192	12.970548	13.450666	13.753208	12.125306
AICc	45.9005	48.5750	43.2981	17.7116	23.7633	17.7101	17.7065	23.7615	17.6961
LR test (wX's =0)									
P-Value > Chi2				0.0002	0.0002	0.0120	0.0019	0.0036	0.0225

*p<0.1; **p<0.05; ***p<0.01Parameters estimation of the SDM is performed by Maximum Likelihood Estimation (MLE). For each variable we present the coefficient and the standard errors.

Moreover political instability and violence have an influence on threatened species. Low instability is associated with less threat on species. The effect, however, is more significant on bird species than mammal species. The level of threatened mammal species depends also on the risk of instability in neighboring countries.

Finally, the results suggest that the percentage of threatened birds and mammals in SSA is positively and strongly correlated with the percentage of endemic species. This result is constant across all taxa groups. So countries in SSA that have a great number of species that are located exclusively within their borders are subject to higher imperilment. For bird species specifically, a greater number of endemic species in neighboring countries may also increase the threat to bird species in a given country.

As birds' species are very mobile, some are migratory species, it is likely the case that more species in neighboring countries (endemic or not) contribute to an increase in the total number of species that could be threatened in a given country at a given period. This must draw policymakers and donors attention to focus on endemic areas for species conservation.

Conclusion

Our paper seeks to answer the question of whether and how economic development influences biodiversity in SSA. Our main contribution is to take spatial interdependencies into account. To this extent, we estimated a series of linear and non-linear spatial models, using percent of threatened bird and mammal species and per capita PPP income levels for 48 countries in SSA. The following are the main findings of the study.

Our result indicates that a biodiversity-income relationship may exist for birds but not for mammals in SSA. There is thus no significant empirical link between economic development as measured by per capita GDP and threatened mammal species in SSA, while a robust and significant link exist for bird species in SSA. As regards how economic development influences biodiversity, we find evidence for a linear negative relationship between GDP and percent of threatened bird species and a hyperbolic nonlinear relationship. That means, empirically, that -ceteris paribus- the wealthier a country is in SSA the less threatened bird species there are. Moreover, our results do not support a quadratic biodiversity Kuznets curve that claims for a replenishment of species in almost the same magnitude of species loss once a certain economic level is attained in SSA. The results support a hyperbolic biodiversity Kuznets curve, thus a slowing of biodiversity loss with economic development in SSA. These results attenuate the pessimistic view of the link between development and biodiversity in developing area contexts. They do not however advocate promoting development while disregarding conservation needs, since the difficulties of considering irreversibility and uncertainty in the models leads us to interpret the findings with caution.

Our findings also evidence that spatial econometric techniques provide a much clearer picture of the evolution of biodiversity. Indeed, we find that the imperilment of mammal species in one country is affected by pressure on mammal species in adjacent countries. These interactions are however conditional on ecological and socio-economic characteristics in neighboring countries. Our results also suggest that omitting spatial dependence alters statistical inference.

From a policy perspective, these findings suggest that development and conservation are not strictly separate policy realms, even in the context of underdevelopment, as found in SSA. Furthermore, the presence of spatial interactions supports the promotion of regional strategies for maintaining biodiversity and related environmental services in SSA.

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