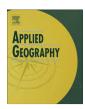
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Population pressure and global markets drive a decade of forest cover change in Africa's Albertine Rift



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ABSTRACT

Africa's Albertine Rift region faces a juxtaposition of rapid human population growth and protected areas, making it one of the world's most vulnerable biodiversity hotspots. Using satellite-derived estimates of forest cover change, we examined national socioeconomic, demographic, agricultural production, and local demographic and geographic variables, to assess multilevel forces driving local forest cover loss and gain outside protected areas during the first decade of this century. Because the processes that drive forest cover loss and gain are expected to be different, and both are of interest, we constructed models of significant change in each direction. Although rates of forest cover change varied by country, national population change was the strongest driver of forest loss for all countries - with a population doubling predicted to cause 2.06% annual cover loss, while doubling tea production predicted to cause 1.90%. The rate of forest cover gain was associated positively with increased production of the local staple crop cassava, but negatively with local population density and meat production, suggesting production drivers at multiple levels affect reforestation. We found a small but significant decrease in loss rate as distance from protected areas increased, supporting studies suggesting higher rates of landscape change near protected areas. While local population density mitigated the rate of forest cover gain, loss was also correlated with lower local population density, an apparent paradox, but consistent with findings that larger scale forces outweigh local drivers of deforestation. This implicates demographic and market forces at national and international scales as critical drivers of change, calling into question the necessary scales of forest protection policy in this biodiversity hotspot. Using a satellite derived estimate of forest cover change for both loss and gain added a dynamic component to more traditionally static and unidirectional studies, significantly improving our understanding of landscape processes and drivers at

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1. Introduction

The Albertine Rift region of Africa, comprising parts of Uganda, Tanzania, Burundi, Rwanda, the Democratic Republic of Congo (DRC), and Zambia, is a biodiversity hotspot (Plumptre et al., 2003,

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2007) (Fig. 1). The juxtaposition of some of the highest human population growth rates and densities in the world, and richest conservation areas, also make it one of the world's most vulnerable conservation-poverty hotspots (Fisher & Christopher, 2007). One of the biggest concerns about the increasingly isolated protected areas in the region is the pressure exerted by deforestation and demand for arable land by a rapidly increasing and dense rural human population outside of protected areas (Hartter & Southworth, 2009; Hartter, Ryan, Southworth, & Chapman, 2011). While rural poverty

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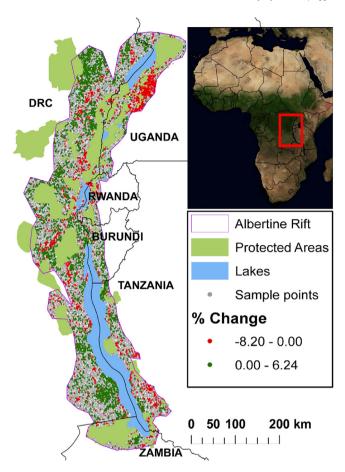


Fig. 1. The Albertine Rift region of Africa. Note lakes and protected areas.

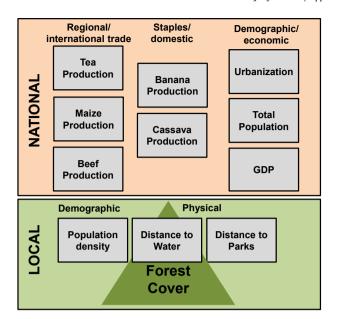
and local population pressure are often cited as reasons for deforestation in developing countries (Sassen, Sheil, Giller, & ter Braak, 2013), reviews suggest that the evidence does not support it (Rudel, 1996), and instead, multiple levels of socioeconomic and political forces at local, national and global levels operate to determine deforestation (Geist & Lambin, 2002; Lambin & Meyfroidt, 2010, 2011; Lambin et al., 2001; Meyfroidt, Rudel, & Lambin, 2010).

The forest transition theory (FT), predicts that as GDP increases, corresponding to development, deforestation due to agricultural conversion accelerates, then plateaus, and finally starts to decrease (Lambin & Meyfroidt, 2010, 2011; Mather, 1992; Meyfroidt et al., 2010; Rudel, Bates, & Machinguiashi, 2002; Walker, 1987). Rather than an increasing poor rural population driving deforestation, large scale human migration patterns associated with urbanization may deplete the rural population, leaving marginal lands to recover, leading to areas of reforestation (Aide & Grau, 2004; Aide et al., 2013; Grau & Aide, 2008). However, an increasingly urban population may also place higher demand on rural fuelwood economies, because cities require charcoal, which is brought in to markets (Mackenzie & Hartter, 2013), creating a counterintuitive signal of population density and deforestation. Importantly, GDP itself does not capture the distribution of wealth, capital, or land tenure in developing countries. An extension of the FT theory is that the rise of urban consumers, driving a demand for more expensive, higher protein diets -the nutrition transition (Popkin, 2001) - and the demand for meat production, also increases pressure on the land. These FT theories and extensions have not been tested in Africa to our knowledge, and instead derive from studies in other tropical forested regions, such as the Amazon, where population density is an order of magnitude lower.

In a global analysis of drivers of forest loss between 2000 and 2005, DeFries, Rudel, Uriarte, and Hansen (2010), argued that urban population growth and agricultural trade were the biggest drivers of tropical forest loss. However, this was rebutted by Fisher (2010). who provided evidence that, for the 12 African countries in the analysis, deforestation was instead correlated to staple crop production, suggesting a rural domestic crop production link. Our study comprises a more recent set of data (2000-2010), and tests both these sets of drivers (domestic staple and export production). The two previous studies unfortunately only overlap with our countries in one case (DRC), precluding direct comparison, but we can draw parallels in interpretation. In the Albertine Rift, both national and sub-national population trends over the first decade of this century may also have been influenced by armed conflict, rural to urban migrations, climate impacts, and global market forces influencing national commodity and monetary flows (DeFries & Rosenzweig, 2010).

The Albertine Rift has experienced considerable conversion of land to agriculture, from extremely small-scale multi-cropping subsistence agriculture, fragmenting and subdividing rural land-scapes around protected areas, to cooperative farming for tea (Hartter & Southworth, 2009). While tea cooperatives are simply smaller in size, and tend not to require the massive fertilizer inputs and tilling that, for example, U.S. industrial corn production uses, their establishment nonetheless results in substantial and lasting conversion of the landscape (Hartter & Southworth, 2009; Hartter et al., 2011; Ryan & Hartter, 2012; Ryan et al., 2015). Although tropical forest conversion for meat production is well known as an Amazonian frontier problem (Alves et al., 2009), in Africa, an increasingly affluent and urban population, driving higher meat consumption, likely also impacts land cover and land use changes in the Albertine Rift.

We used a spatially random selection of 100,000 points across the Albertine Rift to examine the drivers of forest cover change (percent canopy cover). Our estimate of forest cover change was, derived from moderate resolution satellite imagery (MODIS) from 2000 to 2010 with a spatial resolution of 250 m. The use of this MODIS dataset allows for the development of continuous values of forest cover change to be analyzed, because it is not simply a binary description of forest presence/absence, and allows us to develop models of the rate of both forest cover loss (deforestation) and forest cover gain (reforestation), which is an important contribution to the literature and essential to better understand this differing and often contrasting processes. As different drivers influence deforestation and reforestation processes (Nagendra & Southworth, 2009), assuming that drivers of one are simply the inverse of drivers of the other is a fallacy that arises when modeling the two processes together. Using this MODIS product enables us to separately model these two processes, and assess whether similar or different factors play roles in the separate processes. It is also important to note that we are interested in drivers of the process, a distinction from absolute change that is relevant to management. This is a significant improvement over unidirectional approaches, and allows us to review both deforestation and reforestation drivers and processes across this key landscape. Ten annual estimates of percent canopy cover were used to develop linear regressions for each point. We examined locations with significant rates of forest cover change (loss and gain) over the decade, and analyzed these in a multi-level model to simultaneously assess the impacts of local and national level drivers on local forest change. We examined the relationship between small-scale, local forest cover change and potential demographic, economic, and agricultural production drivers of deforestation at the local and national



Box 1. Hypothesized drivers of significant local forest cover change at multiple level in the Albertine Rift biodiversity hotspot.

level for the six countries that constitute the Albertine Rift (Box 1).

2. Materials and methods

2.1. Data acquisition and processing

We used the MODIS data derived product, VCF (Vegetation Continuous Fields - MOD44B, 250 m resolution) to develop an estimate of forest change across our region of study (DiMiceli et al., 2011). MODIS is a combination of two polar orbiting satellite platforms with sensors that monitor the earth with 36 different spectral bands and generate data products that include the characterization of terrestrial vegetation and atmospheric properties (Braswell, Hagen, Frolking, & Salas, 2003; Giglio et al., 2006). One advantage is that generated products span great spatial and temporal ranges such as our study area. This is specifically helpful in tropical regions that have significant cloud cover, thus causing data acquisition issues for optical satellites (Hill et al., 2017; Morton et al., 2014). The MOD44B is a product that estimates "Percent Tree Cover" in a pixel on an annual basis. Continuous in this instance means a continuous percent value from 0 to 100. This product also provides an error estimate from the models used to generate the estimate. We used both the annual estimate of percent tree cover and the error estimate and did a weighted least square regression. This was done on a per pixel basis across the whole region of study. In this manner, each pixel is a single regression with an estimated rate of change based on slope, with standard error, r-square value, p-value, intercept. Each pixel then can be thought of as a trend of forest loss or forest gain. We used 100,000 spatially random points across the Albertine Rift.

Regressions for each individual pixel were used to derive a rate of annual forest cover change between 2000 and 2010 using ten annual estimates of percent forest cover (Hansen et al., 2005). Because calculation of forest change, on an individual pixel of the MODIS data, provided an estimate of significance, we selectively chose pixels that were experiencing significant change for the development of the models that examined forces acting on loss or gain of forest. Otherwise, we would have been modeling pixels that

showed no change. We only retained significant regressions (at $p \le 0.05$, n = 8175), and removed all points that fell inside protected areas. We divided the remaining points into two datasets: forest cover gain (positive slopes, n = 3835), and forest cover loss (negative slopes n = 2685). We note that using MODIS-derived forest cover change may obscure very small-scale change (less than 250 m) and that VCF often has annual fluctuations and errors. The advantage of this product over more simple binary forest/nonforest cover products (e.g. (Hansen et al., 2013)), is that this MODIS product allows for sub-pixel proportional estimates of tree crown cover and provides an estimate preserving a continuous variable of landscape heterogeneity. It is also important that we model both directions of forest cover change — so we can see direction of change and intensity of change and link these landscape processes to the drivers across multiple spatial scales.

The Albertine Rift contains more than 100 protected areas, and also many important lakes (Fig. 1), which likely influence patterns of human settlement in the region. We controlled for the potential impact of large water bodies on human settlement by including distance to water as a random intercept in the multilevel model. Our 'local' per pixel population density change estimates were derived from the 100 m resolution WorldPop dataset (Linard et al., 2012), aggregated to 250 m resolution for 2010. We chose not to use a change estimate since the data underlying this product for at least one of the countries (Uganda, see Linard et al. (2012), supplementary information) do not permit this. Instead, we preferred to use a single snapshot of estimated local population density. Agricultural and market production measures (tea. maize, meat, bananas, cassava, in tonnes), for countries from 2001 to 2010 were acquired from the Food and Agricultural Organization (FAO) (faostat.org, accessed Sept 10th, 2015), and demographic and economic variables for 2001 and 2010 (population, rural proportion, GDP) were acquired from the World Bank (data.worldbank.org, accessed Sept 10th, 2015). These were included in models as proportional changes.

2.2. Analysis

We used multilevel models in R (version 2.13.2; packages 'lme4', 'arm', 'glmulti') to explore the roles of demographic and environmental change at the local, pixel level, and the additional roles of demographic and market forces at the national level. There are many languages used to describe multilevel, hierarchical, mixed effects, or nested models, which vary between and even within disciplines. For ease of explanation, we refer to this regression as a multilevel model (Gelman & Hill, 2006) and describe the variance components as they appear in our specific case.

We used a basic two-level model to describe the significant slope of forest cover change, y_{ij} , at the pixel level (i), within country (j):

Level 1:
$$y_{ij} = \beta_{0j} + \beta_{1j}(X_{1ij}) + \beta_{2j}(X_{2ij}) + ... + \beta_{nj}(X_{nij}) + e_{ij}$$
 (1)

where $X_{1 \dots n}$ are predictor variables at the pixel level; e_{ij} is the error term subsuming the independent error term for the intercept β_0 and the independent error of the regression coefficients β_1 to β_n , and the predictors X_1 to X_n . β_0 to β_n are the regression coefficients, whose variation depends on explanatory variables at the country level, for example:

Level 2:
$$\beta_{0j} = \gamma_{00} + \gamma_{01}Z_j + \mu_{0j}$$
 (2)

In which γ_{00} is the intercept for the overall model of β_0 , and Z_j is the country-level predictor, with the residual error μ_i at the country

level.

As we had multiple local and country level predictors, this can be summarized with X taking subscript p (1 ... P), and Z taking q (1 ... Q), as:

$$Y_{ij} = \gamma_{00} + \sum_{p} \gamma_{po} X_{pij} + \sum_{q} \gamma_{0q} Z_{qj} + \sum_{p} \sum_{q} \gamma_{pq} X_{pij} Z_{qj} + \sum_{p} \mu_{pj} X_{pij} + \mu_{0j} + e_{ij}$$
(3)

As our hypotheses included predictors that are likely to be correlated, we mean-centered all variables (described below), examined variance inflation factors (VIFs) of the parameters, and kappa statistics for collinearity effects on the overall model, using the package 'mer-utls.R' ('mer-utls.R', https://github.com/aufrank/R-hacks.git, accessed 09 September 2015).

For predictor variables available in 2000 and 2010, we used proportional changes in the indicators, and centered the variable. Centering predictors is useful for interpretation in multi-level models by allowing examination of relative change on the mean (average) property of a level at the higher level. Additionally, it tends to improve model convergence. Distance to parks and distance to water were continuous variables (in meters) that did not change across the decade, and were divided by 10,000 (to create a 100 km variable for model fitting), and centered.

We conducted predictor selection in a multi-model comparison using Akaike's Information Criterion (AIC) to select the best candidate set of variables (Burnham & Anderson, 2002), using the R package 'glmulti' (Calcagno & de Mazancourt, 2010). The base (or intercept only) model $y_{ij} = \beta_{0j} + e_{ij}$, was used to establish the structure in the data at the country level, to compare the impact on model fit of adding predictors at the two levels (pixel (i) and country (j)). We created baseline models for negative and positive slopes (cover loss and gain, respectively), and derived AIC values. We then stepped through two stages of predictor and factor addition: adding a random component to the model, country, then the distance to water, and then using model selection for the fixed component on the remaining predictors constraining the number of variables to 4 to avoid overfitting, at the country and pixel level.

We included national production estimates of meat, maize, banana, cassava, and tea. We also included GDP, national total population, the proportion of rural population derived from FAO and World Bank data, local population density, and the distance to nearest water body and protected area as independent variables. In each stage, model improvement over the previous was assessed, with the criteria of 'improvement' at Δ AIC \geq 2 (Anderson, Link, Johnson, & Burnham, 2001; Burnham & Anderson, 2002).

For the best model fits, we report the significance of parameters using t-tests, understanding that our large sample size and relatively few estimated parameters obscured the uncertainty about estimating degrees of freedom (DF), which would exceed 500, often the point of reported convergence of the critical value at 1.96 for $\alpha=0.05$.

3. Results

The MODIS data regressions quantifying the rate of annual change in the Albertine Rift reveals a dynamic landscape of gain and loss of forest cover (Fig. 2). We see that the rate of deforestation ranges much greater (-23%) than reforestation (8.66%), but both processes are widespread. Fig. 2 also reveals spatial patterns in rates of loss and gain, with respect to the lakes, suggesting strong physical geographic influences on the drivers of change.

There was considerable variation across the Albertine Rift countries in the rate of significant local forest cover change in our

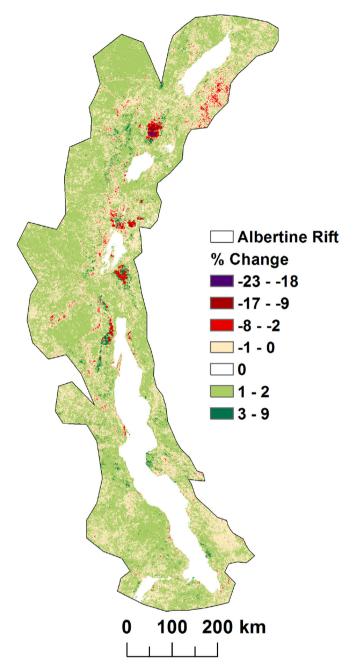


Fig. 2. Annual forest cover change rate 2001–2010 (% annual change) from MODIS44B VCF (vegetation continuous fields) data highlighting spatial differences in reforestation (positive values, greens) versus deforestation rates (negative values, reds) and patterns across the study region.

random sample from 2000 to 2010 [ANOVA: cover loss: F = 108.48, df = 5, p < 0.0001; cover gain: F = 11.44, df = 5, p < 0.0001]. The mean and range of rates of gain and loss were 1.28% [0.13–6.97] and -1.98% [-0.19 to -7.20] respectively, suggesting higher rates of loss than gain from 2000 to 2010 (Fig. 3). Within our random sample, there were more pixels with significant forest cover gain (positive slopes, n = 3835), than forest cover loss (n = 2685), indicating that both processes occurred during the decade, and that while the rate of significant loss was greater than the rate of gain, more pixels were significantly gaining cover.

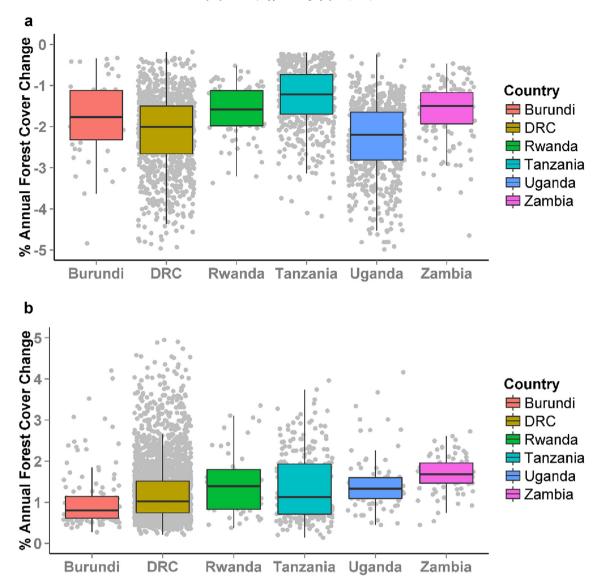


Fig. 3. Significant rates of annual forest cover change 2001–2010 (%/yr of (a) loss and (b) gain), in six countries, outside protected areas and water bodies in the Albertine Rift, from a geographically random sample of 100,000 points. Boxes encompass 25–75% quartiles of the mean.

3.1. Model fits

The simple model of forest cover change by country was our base model (Gain: AIC = 8745; Loss: AIC = 7, 147). Adding the distance-to-water component to the random effect improved model fit considerably (Gain: AIC = 8,433, Δ AIC = 309; Loss: AIC = 7, 065, Δ AIC = 81).

We then performed model selection on our fixed component, constraining the number of variables to 4 to avoid overfitting, and arriving at the top models, with Gain: AIC = 8418 (Δ AIC = 15); and Loss: AIC = 7044 (Δ AIC = 21), demonstrating considerable improvement in support. The best-fit model for forest cover loss included national tea production, national population change, local population density, and distance to protected areas, as drivers of forest cover loss (Table 1). The best-fit model for forest cover gain included national banana and cassava production, meat production, and local population density (Table 1). We show the trajectories of these drivers across prediction space in Fig. 4.

Table 1Parameter estimates and significance (*p*-value) for the best-fit model of significant deforestation across the Albertine Rift, Africa.

Model	Variable	Estimate ^a	p-value
Cover loss	Total Population	-2.06	<0.0001
	Tea	-1.90	< 0.0001
	Park Distance (100 km)	0.394	< 0.0001
	Population Density	0.026	< 0.0001
Cover gain	Banana	-0.049	<0.001
	Cassava	0.25	< 0.0001
	Meat	-0.707	< 0.0001
	Population Density	-0.009	< 0.05

^a % annual rate of forest cover change.

3.2. Model stability

When we examined the final models for collinearity, using the Kappa statistic ('mer-utls.R', https://github.com/aufrank/R-hacks. git), we obtained values of $\kappa=1.72$ for the loss model, and 1.88

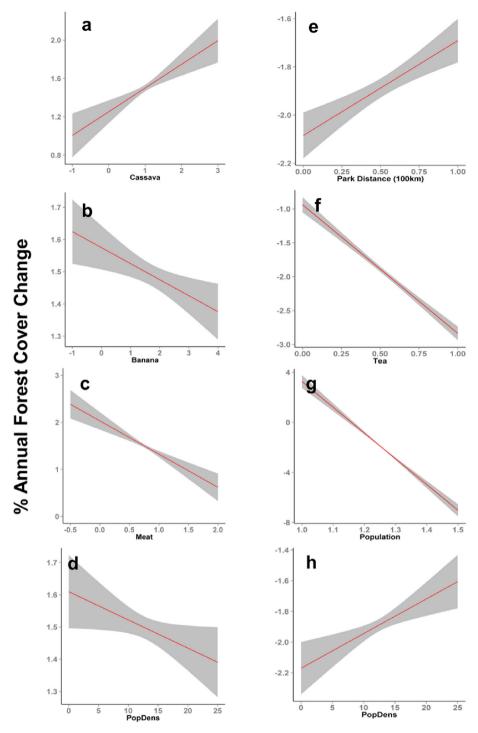


Fig. 4. The individual partial effects of the predictors in the top models (with 95% confidence interval bands in grey), for forest cover gain (a–d) and loss (e–h), as a function of a. cassava production change; b. banana production change; c. meat production change; d. local population density; e. distance from nearest park (in 100 km units); f. tea production change; g. national population change; and h. local population density.

for the gain model, suggesting low collinearity and high stability. We calculated variance inflation factors (VIFs) to assess all predictors, and found that our predictors all fell below 1.5, indicating little inflation and thus we could be confident in our estimates of model fit (Gelman & Hill, 2006).

4. Discussion

An analysis of significant forest cover change outside of

protected areas in the first decade of the 21st century across the Albertine Rift suggests that a dynamic process of forest cover gain and forest cover loss is occurring on the landscape, with different drivers emerging at local and national scales, and signals of higher rates of forest cover loss, but greater areas of forest cover gain (Fig. 2). This again serves to highlight the advantages of using both the continuous MODIS derived forest cover product and modeling both cover loss and forest cover gain, to more fully understand our landscape and its patterns and drivers of change.

National level population change was the biggest driver of forest loss rate; a doubling in population is predicted to cause 2.06% forest loss per year at the local level. In Uganda, which has a population growth rate of 3.24% (Central Intelligence Agency, 2015), population doubling would occur in just over 20 years. The increase in population across the Rift will put ever more pressure on remaining forests for fuelwood, timber for housing, and other resources, in addition to continued land clearing for agriculture.

At the local level, higher population density was associated with lower rates of cover loss, but was also associated with higher gain in our forest cover gain model. While this seems contradictory, it supports recent work suggesting that local population pressure is not a main driver of deforestation (DeFries et al., 2010), yet reversion to forest is likely slowed by the need for arable land. In sub-Saharan Africa, rural livelihoods depend on land and natural resources (Abulu & Hassan, 1998); increasing population growth and a trend towards middle-income economies is placing everincreasing pressures on land use and natural resources (Hartter & Ryan, 2010).

The increase in production of both tea and meat at the national level were found to be drivers of cover change, tea was responsible for 1.90% annual forest loss, while meat corresponded to -0.71%annual forest gain, with a doubling in production. These two markets may operate in different ways to exert this change. Tea is largely produced for global export markets (Chapagain & Hoekstra, 2007), exported to, and departing from Kenya (FAOSTAT.org, accessed Sept 10th, 2015), while meat produced in the countries of the Rift is largely traded within sub-Saharan Africa (FAOSTAT.org. accessed Sept 10th, 2015). While tea production was initially a holdover from colonial land ownership and markets oriented toward supporting Great Britain, it clearly continues to be a major market force in the region. Tea transforms the landscape by introducing a perennial crop, rather than seasonal subsistence level crops. Tea requires larger land parcels, added transportation infrastructure, and fuelwood for drying. It also transforms the scale of economy, as tea businesses may induce cooperatives, requiring a steady labor force. Potentially of significance for biodiversity maintenance, in a region where almost no chemical fertilizers are used, tea is heavily fertilized (Freeman & Omiti, 2003), adding potential ecotoxicological impacts on landscape health. Meat production, on the other hand, appears to be a largely regionally traded commodity, and is a signal of the rising demand for meat in affluent, more urbanized systems.

In contrast to these trade commodities, we found that forest cover gain was influenced by staple crop production. Following Fisher (2010), in ascertaining the role of domestic agriculture in the form of staple crop production, we found there was a small but positive association between forest cover gain and cassava production, suggesting that perhaps this staple is not a primary driver displacing forest cover in the region, despite its increasing production levels throughout the decade in all countries considered. In contrast, we found that banana production was negatively correlated with forest cover gain, indicating that perhaps rural lands used to produce bananas slow the process of reforestation. Unfortunately, we did not have the resolution of data to ascertain what type of banana was involved in this production measure – banana is a term used for both starchy cooking staple types of banana, and the sweet banana, which may be part of a regional or even international production market.

We found a small (0.4% per 100 km per year), but significant, trend of decrease in forest cover loss rate as the distance from protected areas increased, across six countries. This finding aligns with previous work suggesting that human density is higher near protected areas (Wittemyer et al., 2008), but may be more indicative not of settlement patterns, rather highly dynamic land-use in

the wake of park border establishment (Ryan & Hartter, 2012; Ryan et al., 2015). The process of increasing isolation of remnant forest cover continues to challenge protected area management, indicating a need to understand and manage drivers of deforestation.

As protected area management and human livelihoods continue to exert impacts on the landscape of the Albertine Rift, it is important to identify the driving forces behind forest cover gain and loss, as this information is needed to guide conservation strategies. We saw that different drivers of cover change are acting on forest cover. We found that national production markets for both meat and tea are significant drivers of both direct loss, and a reduction in cover gain, respectively, but serve different scales of consumers. Tea is meeting a global demand, whereas meat production is meeting regional dietary shifts towards higher meat consumption in more affluent urban areas. We saw that staples, cassava and banana, which were the proxy for domestic production and consumption – rural small scale agriculture – yielded a mixed signal, but were important to the processes driving cover gain over the decade. Population growth and local population density were also very important drivers, and are more complicated to address as conservation policy than production markets. Targeting policy at the appropriate scale to protect forest cover, and identifying the scope of population pressure on remaining fuelwood supplies is fundamental to protecting this biodiversity hotspot.

This study indicates that the coupled forest transition and development spectrum are not restricted to Latin America and the Caribbean, and point to the need to understand how development, land tenure legislation, and population growth will proceed in conjunction with forest and timber trade policies at multinational scales. While African deforestation rates have been found to be slower than other tropical forested areas (DeFries et al., 2010; Fisher, 2010), and most countries in this analysis are far lower on development trajectories than those of primary focus for FT theory (e.g. Brazil), our findings indicate emergence of similar market and consumption drivers, at multiple scales. Most importantly, our methods of using multi-level modeling in association with a continuous measure of forest cover change, allowing us to understand both forest cover loss and forest cover gain, as well as intensity versus area of these changes, is a significant step forward in understanding the drivers of change across such important, biodiversity hotspots.

Author contributions

SJR conceived the framework, conducted statistical analysis; MP processed data and contributed to analysis; SJR, MP, JED, CAC, JH and JS wrote and edited the manuscript.

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References

Abulu, G., & Hassan, R. (1998). Agricultural activity and natural resource use in South Africa. *Food Policy*, 23, 477–490.

Aide, T. M., Clark, M. L., Grau, H. R., López-Carr, D., Levy, M. A., Redo, D., et al. (2013). Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica*, 45, 262–271. http://dx.doi.org/10.1111/j.1744-7429.2012.00908.x.

Aide, T. M., & Grau, H. R. (2004). Globalization, migration, and Latin American ecosystems. *Science*, *305*, 1915–1916. http://dx.doi.org/10.1126/science.1103179. Alves, D. S., Morton, D. C., Batistella, M., Roberts, D. A., & Souza, C. (2009). The changing rates and patterns of deforestation and land use in Brazilian Amazonia. In *Amazonia and global change* (pp. 11–23).

- Anderson, D. R., Link, W. A., Johnson, D. H., & Burnham, K. P. (2001). Suggestions for presenting the results of data analysis. *Journal of Wildlife Management*, 65, 373–378.
- Braswell, B. H., Hagen, S. C., Frolking, S. E., & Salas, W. A. (2003). A multivariable approach for mapping sub-pixel land cover distributions using MISR and MODIS: Application in the Brazilian Amazon region. *Remote Sensing of Environment*, 87, 243–256. http://dx.doi.org/10.1016/j.rse.2003.06.002.
- Burnham, K. D., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach (Second). New York: Springer-Verlag New York. Inc.
- Calcagno, V., & de Mazancourt, C. (2010). Glmulti: An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, 24.1—20
- Central Intelligence Agency. (2015). Uganda. In The World Factbook. Retrieved from https://www.cia.gov/library/publications/the-world-factbook/geos/ug.html.
- Chapagain, A. K., & Hoekstra, A. Y. (2007). The water footprint of coffee and tea consumption in The Netherlands. *Ecological Economics*, 64, 109–118.
- DeFries, R., & Rosenzweig, C. (2010). Toward a whole-landscape approach for sustainable land use in the tropics. Proceedings of the National Academy of Sciences, 107, 19627–19632. http://dx.doi.org/10.1073/pnas.1011163107.
- DeFries, R. S., Rudel, T., Uriarte, M., & Hansen, M. (2010). Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nature Geoscience*, *3*, 178–181.
- DiMiceli, C., Carroll, M., Sohlberg, R., Huang, C., Hansen, M., & Townshend, J. (2011). Annual global automated MODIS vegetation continuous fields (MOD44B) at 250 m spatial resolution for data years beginning day 65, 2000–2010. collection 5 percent tree cover.
- Fisher, B. (2010). African exception to drivers of deforestation. *Nature Geoscience*, 3, 375–376. http://dx.doi.org/10.1038/ngeo873.
- Fisher, B., & Christopher, T. (2007). Poverty and biodiversity: Measuring the overlap of human poverty and the biodiversity hotspots. *Ecological Economics*, 62, 93–101. http://dx.doi.org/10.1016/j.ecolecon.2006.05.020.
- Freeman, H. A., & Omiti, J. M. (2003). Fertilizer use in semi-arid areas of Kenya: Analysis of smallholder farmers' adoption behavior under liberalized markets. Nutrient Cycling in Agroecosystems, 66, 23–31.
- Geist, H. J., & Lambin, E. F. (2002). Proximate causes and underlying driving forces of tropical deforestation. *Bioscience*, 52, 143–150.
- Gelman, A., & Hill, J. (2006). Data analysis using regression and multilevel/hierarchical models. Cambridge: Cambridge University Press.
- Giglio, L., Van der Werf, G., Randerson, J., Collatz, G., & Kasibhatla, P. (2006). Global estimation of burned area using MODIS active fire observations. *Atmospheric Chemistry and Physics*, 6, 957–974.
- Grau, H. R., & Aide, T. M. (2008). Globalization and land-use transitions in Latin America. *Ecology and Society*, *13*, 16.
- Hansen, M. C., Townshend, J. R., DeFries, R. S., & Carroll, M. (2005). Estimation of tree cover using MODIS data at global, continental and regional/local scales. *International Journal of Remote Sensing.*, 26(19), 4359–4380.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., et al. (2013). High-resolution global maps of 21st-Century forest cover change. *Science*, 342, 850–853.
- Hartter, J., & Ryan, S. J. (2010). Top-down or bottom-up?: Decentralization, natural resource management, and usufruct rights in the forests and wetlands of western Uganda. *Land Use Policy*, 27, 815–826.
- Hartter, J., Ryan, S. J., Southworth, J., & Chapman, C. A. (2011). Landscapes as continuous entities: Forest disturbance and recovery in the Albertine Rift landscape. *Landscape Ecology*, 26, 877–890. http://dx.doi.org/10.1007/s10980-011-9616-0.
- Hartter, J., & Southworth, J. (2009). Dwindling resources and fragmentation of landscapes around parks: Wetlands and forest patches around Kibale National

- Park, Uganda. *Landscape Ecology*, 24, 643–656. http://dx.doi.org/10.1007/s10980-009-9339-7
- Hill, M. J., Zhou, Q., Sun, Q., Schaaf, C. B., & Palace, M. (2017). Relationships between vegetation indices, fractional cover retrievals and the structure and composition of Brazilian Cerrado natural vegetation. *International Journal of Remote Sensing*, 38, 874–905. http://dx.doi.org/10.1080/01431161.2016.1271959.
- Lambin, E. F., & Meyfroidt, P. (2010). Land use transitions: Socio-ecological feedback versus socio-economic change. Land Use Policy, 27, 108–118. http://dx.doi.org/ 10.1016/i.landusepol.2009.09.003.
- Lambin, E. F., & Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. Proceedings of the National Academy of Sciences, 108, 3465–3472. http://dx.doi.org/10.1073/pnas.1100480108.
- Lambin, E. F., Turner, B. L., Geist, H. J., Agbola, S. B., Angelsen, A., Bruce, J. W., et al. (2001). The causes of land-use and land-cover change: Moving beyond the myths. Global Environmental Change, 11, 261–269.
- Linard, C., Gilbert, M., Snow, R. W., Noor, A. M., & Tatem, A. J. (2012). Population distribution, settlement patterns and accessibility across Africa in 2010. PloS One, 7, e31743.
- Mackenzie, C. A., & Hartter, J. (2013). Demand and proximity: Drivers of illegal forest resource extraction. *Oryx*, 47, 288–297.
- Mather, A. S. (1992). The forest transition. Area, 367–379.
- Meyfroidt, P., Rudel, T. K., & Lambin, E. F. (2010). Forest transitions, trade, and the global displacement of land use. Proceedings of the National Academy of Sciences of the United States of America, 107, 20917–20922.
- Morton, D. C., Nagol, J., Carabajal, C. C., Rosette, J., Palace, M., & Cook, B. D. (2014). Amazon forests maintain consistent canopy structure and greenness during the dry season. *Nature*, 506, 221–224.
- Nagendra, H., & Southworth, J. (2009). *Reforesting landscapes: Linking pattern and process*. Springer Science & Business Media.
- Plumptre, A. J., Behangana, M., Davenport, T. R. B., Kahindo, C., Kityo, R., Ndomba, E., et al. (2003). The biodiversity of the Albertine Rift. Kampala, Uganda: Wildlife Conservation Society.
- Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., et al. (2007). The biodiversity of the Albertine Rift. *Biological Conservation*, 134, 194.
- Popkin, B. M. (2001). The nutrition transition and obesity in the developing world. *The Journal of Nutrition*, 131, 8715–873S.
- Rudel, T. (1996). Regional patterns and historical trends in tropical deforestation, 1976-1990: A qualitative comparative analysis. *Ambio*, 25, 160.
- Rudel, T. K., Bates, D., & Machinguiashi, R. (2002). A tropical forest Transition? Agricultural change, out-migration, and secondary forests in the Ecuadorian Amazon. Annals of the Association of American Geographers, 92, 87–102. http:// dx.doi.org/10.1111/1467-8306.00281.
- Ryan, S. J., & Hartter, J. (2012). Beyond ecological success of corridors: Integrating land use history and demographic change to provide a whole landscape perspective. *Ecological Restoration*, 30, 320–328. http://dx.doi.org/10.3368/ er.30.4.320.
- Ryan, Sadie J., Southworth, J., Hartter, J., Dowhaniuk, N., Fuda, R. K., & Diem, J. E. (2015). Household level influences on fragmentation in an African park land-scape. *Applied Geography*, *58*, 18–31.
- Sassen, M., Sheil, D., Giller, K. E., & ter Braak, C. J. F. (2013). Complex contexts and dynamic drivers: Understanding four decades of forest loss and recovery in an East African protected area. *Biological Conservation*, 159, 257–268. http:// dx.doi.org/10.1016/j.biocon.2012.12.003.
- Walker, R. T. (1987). Land use transition and deforestation in developing countries. *Geographical Analysis*, 19, 18–30. http://dx.doi.org/10.1111/j.1538-4632.1987.tb00111.x.
- Wittemyer, G., Elsen, P., Bean, W. T., Burton, A. C. O., & Brashares, J. S. (2008). Accelerated human population growth at protected area edges. *Science*, 321, 123–126. http://dx.doi.org/10.1126/science.1158900.