

## Assessing impacts to primary productivity at the park edge in Murchison Falls Conservation Area, Uganda

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**Abstract.** Human activities around parks can alter vegetation patterns within them, resulting in edge effects that degrade their ability to sustain ecological processes and support biodiversity. We quantified vegetation patterns and edge effects over a large geographic extent in Murchison Falls Conservation Area, Uganda, using freely available remotely sensed data. Over a 13-yr period, we quantified seasonal patterns in productivity using the Normalized Difference Vegetation Index (NDVI), comparing the park exterior, a boundary zone  $\leq 10$  km from the border inside the park, and the park interior. To identify the extent of edge effects, we further fit mixed models by vegetation type within 1-km bands within the boundary zone. Productivity was higher in the park interior than exterior in both wet and dry seasons, and in the wet season, it was also lower in the boundary zone than the interior. NDVI variability differed between seasons; it declined from exterior to interior in the wet season, but was highest in the boundary zone and similar between interior and exterior during the dry season. Within the boundary zone, edge effects varied by land cover type and extended 4–6 km into MFCA. Abrupt differences in vegetation patterns between the park and adjacent unprotected areas indicated a “hard edge” in this system. While hard edges are readily apparent, the subtle changes in productivity that extend into and degrade park systems are harder to detect. We demonstrated a low-cost and novel approach to detect such effects using readily available satellite imagery, which indicated human influence affecting 29–40% of the park. As human populations grow, parks will become further isolated, and measuring and managing edge effects may be crucial to achieving conservation objectives.

**Key words:** East Africa; edge effect; Normalized Difference Vegetation Index; primary productivity; protected area; remote sensing.

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### INTRODUCTION

The establishment of protected areas (hereafter, parks) with limited human activity is at the forefront of strategies for conserving biodiversity (Chape et al. 2005, UNEP-WCMC 2008, Jenkins and Joppa 2009), with 15.4% of the Earth’s land surface legally protected in 2014 (Juffe-Bignoli

et al. 2014). However, most parks protect only a small portion of their total ecosystems (DeFries et al. 2010). Parks alone may be an inadequate strategy for biodiversity conservation (Margules and Pressey 2000), but nevertheless provide important strongholds for plants and animals (Chape et al. 2005). Minimizing edge effects (i.e., anthropogenic impacts on the environment that

extend into parks), establishing buffer zones around parks, and managing the human-dominated landscape matrix must complement the establishment of parks for effective conservation (UNESCO 1974, Noss 1983, Sánchez-Azofeifa et al. 1999, Alagador et al. 2012, Rudnick et al. 2012, Ryan and Hartter 2012). Without these actions, parks may become increasingly isolated (DeFries et al. 2005, Newmark 2008) and influenced by human settlements and associated disturbances along their borders. Human disturbances may result in edge effects that reduce the effective size of parks and degrade their ability to sustain ecological processes and support biodiversity (Woodroffe and Ginsberg 1998, Parks and Harcourt 2002).

Recent growth in human populations has been disproportionately concentrated in biodiversity hotspots (Cincotta et al. 2000, Balmford et al. 2001, Williams 2013). Notably, Africa's human population is expected to grow from 1.1 billion in 2013 to 2.4 billion in 2050 (Population Reference Bureau 2014), posing significant challenges for conservation on the continent. Whether or not human populations near parks in Africa grow at rates above average rural growth rates due to the availability of resources or jobs (Wittemyer et al. 2008, Joppa et al. 2009, Baird 2014), growing human populations near any given park impact vegetation patterns in the surrounding matrix (Ryan et al. 2015) and can threaten its conservation value.

By definition, edge effects are differences in abiotic conditions, species composition, or species abundance between the interior of a "patch" and areas close to its boundary (Forman and Godron 1986, Collinge 2009). In forest patches, edges are characterized by warmer temperatures, lower humidity, greater light, and higher wind speeds compared to patch interiors (Fetcher et al. 1985, Laurance et al. 1998) and experience higher rates of tree mortality, damage, and turnover (Laurance et al. 1998). Therefore, there can be a gradient of abiotic conditions from edge to interior that drives composition and structure of plant and animal communities (Kristan et al. 2003). Biotic responses to edges may be positive, with "edge-generalist" species benefitting from edge effects, or negative, with "edge-sensitive" species suffering reduced fitness (Knight and Landres 2002). For example, nest predation rates

for edge-sensitive songbirds are higher in small compared to large forest patches due to higher densities of edge-generalist nest predators sustained by the relatively greater amounts of edge per unit area in smaller patches (Wilcove 1985). While most studies of edge effects have focused on forest patches, edge effects also occur in other ecosystems (Kristan et al. 2003). For example, in reserves in the Brazilian cerrado (neotropical savanna), species composition of ant communities was affected by distance to reserve edge (Brandão et al. 2011), and in South Africa, smaller fragments of shrublands contained more alien plant species than larger fragments (Kemper et al. 1999).

Extending the habitat patch analogy to parks, human activities concentrated along boundaries can cause changes in abiotic and biotic conditions some distance into parks that, by extension, affect their ability to sustain ecological communities and services. Edge effects may penetrate into parks as far as 10 km, greatly reducing effective park size (Curran et al. 1999, Laurance 2000). However, they may be difficult to detect in field-based studies, given the large extent of some parks. Quantifying changes in vegetation patterns on a parkwide basis may be greatly aided by satellite sensors that provide the fine spatial resolution, large extent, and seasonal and interannual temporal record required to quantify edge effects on a parkwide basis (Kerr and Ostrovsky 2003, Gibbes et al. 2013). In particular, using Earth Resources Observation and Science Moderate Resolution Imaging Spectroradiometer (eMODIS) and other satellite platforms, the Normalized Difference Vegetation Index (NDVI) can be calculated using measurements of red and near-infrared light (NIR) reflectance. The index ranges from -1 to 1, with negative values indicating water, 0 indicating lack of vegetation, and positive values indicating vegetated areas (McGarigal et al. 2009).

Within the positive data range, NDVI is closely correlated with net primary productivity (Pettorelli et al. 2005, 2011), although the relationship varies across different land cover types. In grassland, the relationships between NDVI and aboveground net primary productivity and biomass are exponential (Paruelo et al. 1997, Frank and Karn 2003), while in dense forests NDVI tends to saturate, making changes in productivity

or canopy structure difficult to detect (Huete et al. 1997). However, recent studies have found NDVI sensitive to drought-induced changes in vegetation, even in dense canopies (Asner and Alencar 2010, Brando et al. 2010, Vicente-Serrano et al. 2013). Despite these differences, in this study, we used NDVI as a useful proxy for primary productivity.

NDVI has been used to monitor vegetation patterns across the globe (Jia et al. 2006, Ma and Veroustraete 2006, Zhao et al. 2012), effectively tracking changes in seasonal, interannual, and spatial vegetation dynamics (Running 1990, Fang et al. 2001, Nemani et al. 2003, Roerink et al. 2003, Pettorelli et al. 2005, Lunetta et al. 2006, Piao et al. 2006, Ryan et al. 2012). Moreover, NDVI has been related to changes in wildlife populations, such as home-range sizes, birth-pulse timing, ranging behavior, and migratory patterns, across a variety of ecosystems (Pettorelli et al. 2005, 2011, Boone et al. 2006, Ryan et al. 2006, 2007, Young et al. 2009). NDVI is particularly useful for differentiating human-disturbed landscapes from natural landscapes. In West Africa, savanna woodlands had higher NDVI values than cropland, while crops and grass savanna had similar values (Achard and Blasco 1990), and in South-East Asia, NDVI was higher in intact tropical forest than in neighboring mosaics of cropland and regenerating forests (Achard and Estreguil 1995). In Nevada, seasonal and interannual NDVI patterns were used to identify areas of invasive cheatgrass (*Bromus tectorum*) (Bradley and Mustard 2006), and in Idaho, NDVI was used to identify vegetation changes caused by livestock grazing (Bradley and O'Sullivan 2011). NDVI has also been used to quantify patterns in spatial heterogeneity of vegetation. In North America, the standard deviation of NDVI was shown to be higher in agricultural landscapes than in natural landscapes (Riera et al. 1998).

Our objective was to quantify the extent of edge effects in Murchison Falls Conservation Area (MFCA), northwest Uganda, by comparing NDVI values among the park interior (>10 km from border), boundary zone ( $\leq 10$  km from border inside the park), and exterior ( $\leq 10$  km from the border outside the park). We calculated overall levels of productivity (mean NDVI) and variation in productivity (NDVI standard deviation), while controlling for the effects of land cover type

and season. We expected primary productivity to be highest, and variation lowest, within the park interior compared to the human-dominated exterior, with intermediate levels of both mean and variation occurring within the boundary zone. Further, within the boundary zone, we expected primary productivity to increase and become less variable along an axis extending from the border to the park interior. Finally, we expected edge effects to be most pronounced in the dry season, when resources for plant growth were most limiting, and that effects would differ in magnitude among major land cover types. We provide not only a comprehensive assessment of edge effects within MFCA, an understudied and rapidly changing park, but also a low-cost and novel approach enabling rapid assessment of edge impacts in parks over large geographic extents.

#### Study area

The Albertine Rift, which extends from northern Uganda to northern Zambia and covers approximately 312,669 km<sup>2</sup>, has been identified as a biodiversity hotspot (Plumptre et al. 2003). Species richness of vertebrates is greater in the Albertine Rift than in any other region in Africa, and the number of endemic species exceeds that of any other region on the mainland (Plumptre et al. 2003). We focused our study on MFCA (2°12' N, 31°49' E), in northwest Uganda (Fig. 1), a flagship park within the Albertine Rift. MFCA is the largest (5595 km<sup>2</sup>) and most visited park in the country, attracting over 70,000 visitors in 2014 (Uganda Bureau of Statistics 2015). The park protects Uganda's only viable populations of crocodile (*Crocodylus niloticus*) and the endangered Rothschild's giraffe (*Giraffa camelopardalis rothschildi*), and the country's largest population of the endangered Lelwel hartebeest (*Alcelaphus buselaphus lelwel*) (Uganda Wildlife Authority 2012).

Murchison Falls Conservation Area is made up of Murchison Falls National Park (3867 km<sup>2</sup>) and three surrounding reserves: Bugungu Wildlife Reserve (336 km<sup>2</sup>), Budongo Forest Reserve (817 km<sup>2</sup>), and Karuma Wildlife Reserve (574 km<sup>2</sup>). Elevation in MFCA ranges from 613 to 1273 m, and temperatures in the region range from a minimum of 22°C to a maximum of 29°C (Prinsloo et al. 2011). Average annual rainfall ranges from approximately 1100 mm in the west

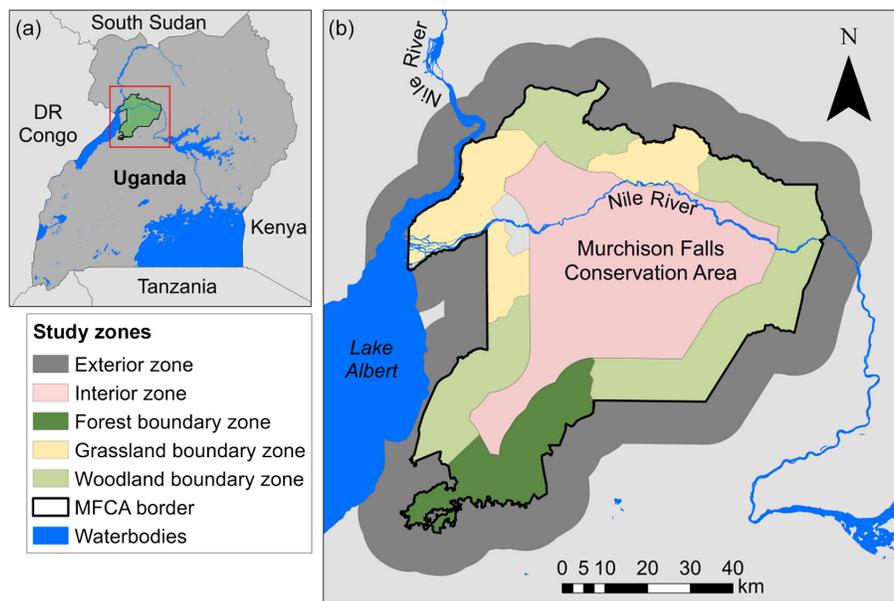


Fig. 1. (a) Location of Murchison Falls Conservation Area (MFCFA) in northwest Uganda. (b) Study zones for Normalized Difference Vegetation Index (NDVI) analysis: park interior (>10 km from MFCFA border), boundary zone divided by dominant land cover type ( $\leq 10$  km from MFCFA border), and exterior study zone ( $\leq 10$  km from MFCFA border).

to 1500 mm in the east and far south and occurs in a bimodal seasonal pattern (Laws et al. 1975, Prinsloo et al. 2011). The region has experienced a drying trend over the last 20 yr, with a 20% decrease in rainfall during the growing seasons (Diem et al. 2014). MFCFA is the only example of the Sudanian vegetation form in East Africa (Prinsloo et al. 2011), and major vegetation types in the national park and the two wildlife reserves include grassland and woodland, while Budongo Forest Reserve is made up of semideciduous forest (Nampindo et al. 2005, Ayebare 2011). The region surrounding MFCFA is dominated by agriculture and human settlements (Mwavu and Witkowski 2008).

Uganda has one of the highest natural rates of population increase (3.4%) in the world (Population Reference Bureau 2014), and increasing human population densities around MFCFA are also driven by several factors drawing immigration into the region. Following the departure of the Lord's Resistance Army in 2006, local residents returned from internally displaced persons camps to villages near the northern border of MFCFA (Uganda Wildlife Authority 2012). On the east side of MFCFA, the government

has relocated refugees from landslides around Mt. Elgon (Jeanne and Asiimwe 2012). In the southwest, recent immigration (1998–2008) was motivated by perceived land availability, family connections, and lack of war in the region (Zommers and MacDonald 2012). Additional immigration to the area is drawn by anticipated employment opportunities in the expanding oil, hydropower, sugarcane, and tourism industries (Mwavu and Witkowski 2008, Kityo 2011, Total E&P Uganda 2013, Uganda Human Rights Commission 2013). As population growth continues in the region and available land becomes scarcer, illegal activities already underway within MFCFA are likely to intensify, such as cattle grazing, timber harvesting, charcoal burning, collection of grass and firewood, encroachment of settlements and farms within the park, and wildlife poaching (Uganda Wildlife Authority 2012).

## METHODS

We acquired one eMODIS NDVI East Africa image (Jenkinson et al. 2010) in each of two seasons for each year from 2001 to 2013. Wet season

Table 1. Model selection criteria for linear mixed models of mean Normalized Difference Vegetation Index (NDVI) inside and outside Murchison Falls Conservation Area (MFCA), Uganda, in the wet and dry seasons, 2001–2013.

Rank	Model components	K	LL	$\Delta$ AIC	$w_i$
1	S, Z, L, BD, BD <sup>2</sup> , S × Z, S × L, S × BD, S × B, L × BD, L × BD <sup>2</sup>	24	1758.9	0.0	0.82
2	Less S × BD <sup>2</sup>	21	1754.4	3.0	0.18
3	Less BD <sup>2</sup> , S × BD <sup>2</sup> , L × BD <sup>2</sup>	18	1731.2	43.5	0.00
4	Less L × BD <sup>2</sup>	20	1732.9	44.1	0.00
5	Less S × BD <sup>2</sup> , L × BD <sup>2</sup>	19	1731.7	44.5	0.00
6	Less BD <sup>2</sup> , S × BD, S × BD <sup>2</sup> , L × BD <sup>2</sup>	15	1715.5	68.9	0.00
7	Less BD <sup>2</sup> , S × BD <sup>2</sup> , L × BD <sup>2</sup> , L × BD	14	1712.3	73.3	0.00
8	Less BD <sup>2</sup> , S × BD, S × BD <sup>2</sup> , L × BD <sup>2</sup> , L × BD	13	1707.4	81.2	0.00
9	S, Z, L, S × Z, S × L	12	1703.7	86.5	0.00
10	S, Z, L, S × Z	10	1385.1	719.7	0.00
11	S, Z	6	761.4	1959.1	0.00
12	S, Z, S × Z	8	762.0	1961.9	0.00
13	S	4	754.8	1968.3	0.00
14	Z	5	599.7	2280.4	0.00
15	Random intercept	3	595.3	2285.3	0.00

Notes: Year was included in all models as a random intercept. Models are listed with number of parameters estimated (K), model log-likelihood (LL), change in Akaike’s information criterion ( $\Delta$ AIC; AIC of top model = -3469.9), and Akaike weights ( $w_i$ ). Interaction terms are indicated by “×.” S = Season (dry vs. wet); Z = Zone (interior, boundary, or exterior); L = Land cover type (forest, grassland, or woodland), nested variable within boundary zone; BD = Buffer distance to MFCA boundary (1 indicates buffer from 0 to 1 km), nested variable within boundary zone; BD<sup>2</sup> = Buffer distance-squared.

images ( $n = 13$ ) were obtained from the end of September, while dry season images ( $n = 13$ ) were obtained mid-January. These images consisted of 250-m-resolution, temporally smoothed, 10-d composites. The smoothing procedure followed Swets et al. (1999), using weighted least-squares regression to reduce noise caused by clouds or other atmospheric contamination.

Given that edge effects may extend 10 km into parks (Curran et al. 1999, Laurance 2000), we created 1-km-wide concentric buffers from the border to 10 km inside MFCA and considered this area to be the “boundary” zone. Buffers within the boundary zone were further divided into regions based on dominant land cover type (Wildlife Conservation Society 2010), which included forest, grassland, and woodland. NDVI composite images from each year were clipped to each buffer and cover type in the boundary zone, as well as to the MFCA “interior” zone (core area >10 km from the boundary) and the “exterior” zone (areas extending 0–10 km outside of the park boundary; Fig. 1). We removed waterbodies from the analysis by masking pixels below a threshold NDVI of 0.1 (Riera et al. 1998).

For each zone, year, and season, we quantified overall primary productivity using mean

NDVI values, and variation in primary productivity as the standard deviation (SD) in NDVI. We assessed differences in overall productivity and its variation among the zones in each season using each year as a replicate and one-way ANOVA and conducted post hoc pairwise comparisons using Tukey’s honest significant difference (HSD) test (experiment-wise  $\alpha = 0.05$ ). We fit linear mixed-effects models using maximum-likelihood estimation to estimate the effects of season and zone on mean primary productivity, and generalized linear mixed-effects models using Laplace approximation (Bolker et al. 2009) to estimate the effects on variation in primary productivity, with year as a random intercept (Tables 1 and 2). Within the boundary zone only, we also included fixed effects for dominant land cover type and distance from boundary, including quadratic distance terms to capture potential nonlinear changes or thresholds. Candidate models included interaction terms between each variable and season, and between land cover and distance terms within the boundary zone. For models predicting variation in primary productivity, we included a log link to ensure that predicted values of the response variable were greater than zero. We compared full and reduced

Table 2. Model selection criteria for generalized linear mixed models (log link) of Normalized Difference Vegetation Index (NDVI) standard deviation inside and outside Murchison Falls Conservation Area (MFCA), Uganda, in the wet and dry seasons, 2001–2013.

Rank	Model variables	K	LL	ΔAIC	$w_i$
1	S, Z, L, BD, BD <sup>2</sup> , S × Z, S × L, S × BD, S × B, L × BD, L × BD <sup>2</sup>	24	2268.0	0.0	1.00
2	Less S × BD <sup>2</sup>	21	2258.5	12.9	0.00
3	Less L × BD <sup>2</sup>	20	2232.6	62.7	0.00
4	Less S × BD <sup>2</sup> , L × BD <sup>2</sup>	19	2230.8	64.4	0.00
5	Less BD <sup>2</sup> , S × BD <sup>2</sup> , L × BD <sup>2</sup>	18	2225.5	73.1	0.00
6	Less BD <sup>2</sup> , S × BD, S × BD <sup>2</sup> , L × BD <sup>2</sup>	15	2216.2	85.5	0.00
7	Less BD <sup>2</sup> , S × BD, S × BD <sup>2</sup> , L × BD <sup>2</sup> , L × BD	13	2186.3	141.4	0.00
8	Less BD <sup>2</sup> , S × BD <sup>2</sup> , L × BD <sup>2</sup> , L × BD	14	2186.3	143.3	0.00
9	S, Z, L, S × Z, S × L	12	2151.8	208.4	0.00
10	S, Z, L, S × Z	10	2132.2	243.5	0.00
11	S, Z, S × Z	8	1937.5	629.1	0.00
12	S, Z	6	1929.8	640.4	0.00
13	S	4	1912.6	670.9	0.00
14	Z	5	1887.6	722.8	0.00
15	Random intercept	3	1869.0	755.9	0.00

Notes: Year was included in all models as a random intercept. Models are listed with number of parameters estimated (K), model log-likelihood (LL), change in Akaike’s information criterion (ΔAIC; AIC of top model = -4488.0), and Akaike weights ( $w_i$ ). Interaction terms are indicated by “×”. S = Season (dry vs. wet); Z = Zone (interior, boundary, or exterior); L = Land cover type (forest, grassland, or woodland), nested variable within boundary zone; BD = Buffer distance to MFCA boundary (1 indicates buffer from 0 to 1 km), nested variable within boundary zone; BD<sup>2</sup> = Buffer distance-squared.

candidate models using Akaike’s information criterion (AIC) and model weights ( $w_i$ ) (Burnham and Anderson 2002).

RESULTS

Mean primary productivity was lower during the dry season than during the wet season (Fig. 2), and within season, primary productivity differed among zones (ANOVA; dry season:  $F_{(2, 36)} = 3.63, P = 0.04$ ; wet season:  $F_{(2, 36)} = 210.69, P < 0.01$ ). In the dry season, productivity in the interior zone was 9.7% higher than in the exterior zone ( $P = 0.05$ ), whereas the boundary zone did not differ from either the interior or exterior ( $P \geq 0.10$ ; Fig. 2a). In the wet season, primary productivity differed among all three zones, being 4.4% higher in the interior than the boundary zone and 14.5% and 9.7% higher in the interior and boundary zones, respectively, compared to the exterior zone (all  $P < 0.01$ ; Fig. 2b).

Levels of variation in primary productivity were similar in magnitude between the wet and dry seasons (Fig. 3), but within each season, there were significant differences among zones (dry season:  $F_{(2, 36)} = 61.12, P < 0.01$ ; wet season:  $F_{(2, 36)} = 141.26, P < 0.01$ ). In the dry season,

variation in productivity did not differ between interior and exterior zones ( $P = 0.33$ ), but variation in the boundary zone was 41.5% and 51.9% higher compared to the exterior and interior zones, respectively (all  $P < 0.01$ ; Fig. 3a). In the wet

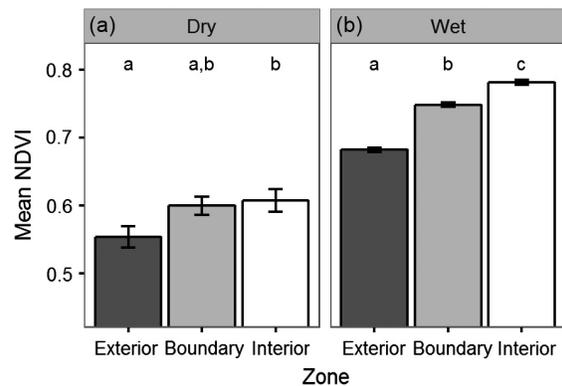


Fig. 2. Mean Normalized Difference Vegetation Index (± standard error) from 2001 to 2013 in the (a) dry and (b) wet seasons in the three study zones in Uganda: Murchison Falls Conservation Area (MFCA) interior (>10 km from border), MFCA boundary zone (≤10 km from border), and MFCA exterior (≤10 km from border). Letters indicate Tukey HSD groups, with zones sharing letters not differing significantly.

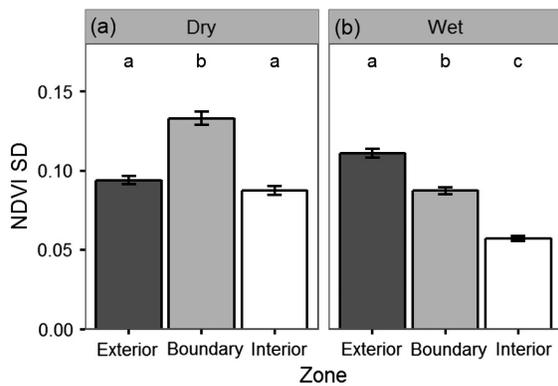


Fig. 3. Normalized Difference Vegetation Index (NDVI) standard deviation ( $\pm$  standard error) from 2001 to 2013 in the (a) dry and (b) wet seasons in the three study zones in Uganda: Murchison Falls Conservation Area (MFCA) interior (>10 km from border), MFCA boundary zone ( $\leq 10$  km from border), and MFCA exterior ( $\leq 10$  km from border). Letters indicate Tukey HSD groups, with zones sharing letters not differing significantly.

season, variation in productivity varied among all three zones, declining 26.9% from the exterior to the boundary zone, and 52.4% and 93.4% from the boundary and exterior zones, respectively, to the interior of the park (all  $P < 0.01$ ; Fig. 3b).

*Productivity patterns within the boundary zone*

For boundary zone models, we found considerably more support for the full model, including a full suite of interaction terms and nonlinear effects, over any reduced model for both mean primary productivity ( $w_i = 0.82$ ,  $\Delta AIC$  of reduced models  $\geq 3.0$ ; Table 1) and variation in productivity ( $w_i = 1.00$ ,  $\Delta AIC$  of reduced models  $\geq 12.9$ ; Table 2). Based on the importance of interactions, mean productivity was similar between seasons for the forest cover type, but was considerably lower during the dry season for both the grassland and woodland types (Table 3, Fig. 4). Furthermore, variation in productivity was greater in the dry season than in the wet season, and greater in woodland and grassland than the

Table 3. Coefficient estimates with standard error and confidence intervals (CI) for highest-ranked linear mixed model predicting mean Normalized Difference Vegetation Index (NDVI) inside and outside Murchison Falls Conservation Area (MFCA), Uganda, in the wet and dry seasons from 2001 to 2013.

Model variables	$\beta$	SE	Lower CI	Upper CI
Intercept†	0.6076	0.0102	0.5876	0.6275
Wet	0.1735	0.0111	0.1516	0.1953
Edge	0.1111	0.0121	0.0873	0.1349
Exterior	-0.0536	0.0111	-0.0754	-0.0318
Wet $\times$ Edge	-0.0997	0.0172	-0.1334	-0.0661
Wet $\times$ Exterior	-0.0454	0.0157	-0.0763	-0.0146
Edge:Grassland	-0.1754	0.0131	-0.2011	-0.1498
Edge:Woodland	-0.1386	0.0131	-0.1642	-0.1129
Edge:Buffer distance	0.0261	0.0039	0.0186	0.0337
Edge:Buffer distance <sup>2</sup>	-0.0021	0.0003	-0.0028	-0.0014
Wet $\times$ Edge:Woodland	0.0932	0.0185	0.0570	0.1295
Wet $\times$ Edge:Grassland	0.0701	0.0185	0.0338	0.1064
Edge:Grassland $\times$ Buffer distance	-0.0419	0.0055	-0.0526	-0.0312
Edge:Woodland $\times$ Buffer distance	-0.0248	0.0055	-0.0355	-0.0141
Wet $\times$ Edge:Buffer distance	-0.0170	0.0055	-0.0278	-0.0063
Edge:Grassland $\times$ Buffer distance <sup>2</sup>	0.0031	0.0005	0.0022	0.0041
Edge:Woodland $\times$ Buffer distance <sup>2</sup>	0.0021	0.0005	0.0011	0.0030
Wet $\times$ Edge:Buffer distance <sup>2</sup>	0.0015	0.0005	0.0005	0.0024
Wet $\times$ Edge:Grassland $\times$ Buffer distance	0.0251	0.0077	0.0100	0.0403
Wet $\times$ Edge:Woodland $\times$ Buffer distance	0.0181	0.0077	0.0030	0.0333
Wet $\times$ Edge:Grassland $\times$ Buffer distance <sup>2</sup>	-0.0016	0.0007	-0.0029	-0.0002
Wet $\times$ Edge:Woodland $\times$ Buffer distance <sup>2</sup>	-0.0014	0.0007	-0.0028	-0.0001

Notes: Terms nested within the boundary zone only are indicated by “:” and interaction terms are indicated by “ $\times$ .”  
 † Reference levels for factor variables were as follows: Season: Dry; Zone: Interior; Land cover (within boundary zone only): Forest. Therefore, the intercept represents the mean NDVI in the interior of MFCA during the dry season.

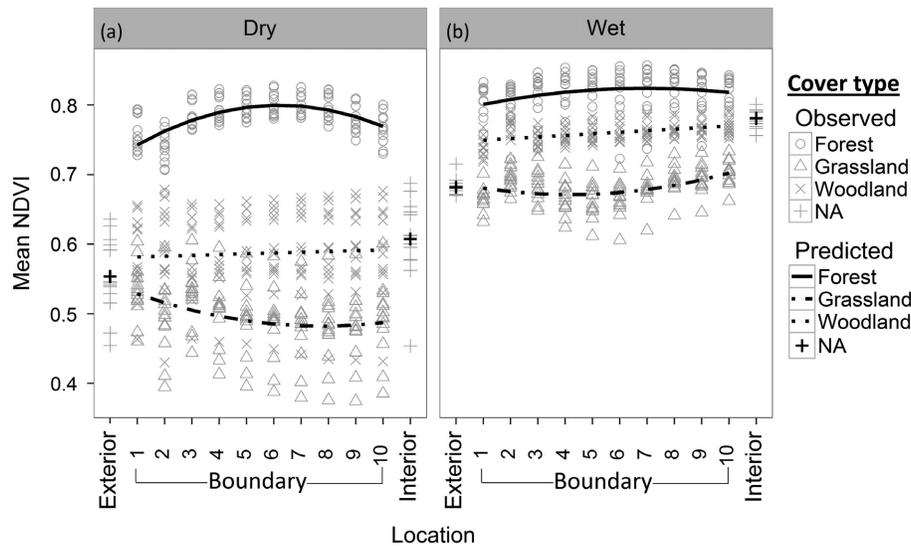


Fig. 4. Observed and predicted mean Normalized Difference Vegetation Index (NDVI) values from 2001 to 2013 in the three study zones of Murchison Falls Conservation Area (MFCA), Uganda, in the (a) dry and (b) wet seasons. The exterior zone extended  $\leq 10$  km from MFCA border, and the interior zone extended  $>10$  km from MFCA border. The numbers 1–10 indicate buffers within the boundary zone, with “1” indicating the area from 0 to 1 km inside the MFCA border. The boundary zone was further divided based on three dominant land cover classes: forest, grassland, and woodland. Exterior and interior zones were not divided by buffer or land cover (NA).

forest cover type (Table 4, Fig. 5). Mean productivity was similar between grassland in the boundary region and the exterior zone, which was dominated by agriculture and pasture. However, there was a stark difference in mean NDVI between the park exterior and the first km of the boundary zone for the forest and woodland cover types in the wet season (Fig. 4). Additionally, in the wet season, variability was considerably lower across all land cover types in the first km of the boundary zone compared to the exterior zone. Nonlinear changes in productivity within the boundary zone implied that edge effects extended 4–6 km into the park (Figs. 4 and 5). As expected, thresholds in edge effects were most pronounced, for both mean productivity and variability, during the dry season.

## DISCUSSION

We found strong evidence for edge effects in MFCA. Our observations support Laurance’s (2000) claim that edge effects can occur over large spatial scales, and we demonstrate that such

effects were detectable in MFCA using readily available remotely sensed data. We observed the greatest overall differences in productivity, and largest threshold distances in edge effects, during the dry season, yet the wet season provided the clearest evidence for the expected trend of high productivity in the core of the park, intermediate levels in the boundary region, and low levels exterior to the park. The magnitude and direction of change in primary productivity from the park border to its interior differed considerably among land cover types, indicating that ignoring differences among land cover types may confound the detection of edge effects. Nonlinear changes in productivity within forest and grassland indicated that edge effects extended up to 4–6 km into the park. Edge effects extending considerable distances, such as we observed, may have important implications, especially for smaller parks in which very little protected land may exist outside of the influence of edge effects (Joppa et al. 2008). In MFCA, edge effects covered roughly 29–40% of the park. While a few studies have documented edge effects occurring

Table 4. Coefficient estimates with standard error and confidence intervals (CI) for highest-ranked generalized linear mixed model (log link) predicting Normalized Difference Vegetation Index (NDVI) standard deviation inside and outside Murchison Falls Conservation Area (MFCA), Uganda, in the wet and dry seasons from 2001 to 2013.

Model variables	$\beta$	SE	Lower CI	Upper CI
Intercept†	-2.4412	0.0518	-2.5427	-2.3397
Wet	-0.4262	0.0921	-0.6067	-0.2458
Edge	0.1175	0.0875	-0.0540	0.2889
Exterior	0.0642	0.0690	-0.0710	0.1995
Wet × Edge	-0.0998	0.1570	-0.4075	0.2080
Wet × Exterior	0.5917	0.1109	0.3742	0.8091
Edge:Grassland	0.2635	0.0893	0.0886	0.4385
Edge:Woodland	-0.1178	0.0894	-0.2931	0.0574
Edge:Buffer distance	-0.2293	0.0330	-0.2940	-0.1647
Edge:Buffer distance <sup>2</sup>	0.0201	0.0030	0.0143	0.0259
Wet × Edge:Woodland	0.3794	0.1539	0.0777	0.6810
Wet × Edge:Grassland	0.2381	0.1520	-0.0598	0.5360
Edge:Grassland × Buffer distance	0.0812	0.0420	-0.0012	0.1636
Edge:Woodland × Buffer distance	0.3067	0.0396	0.2290	0.3844
Wet × Edge:Buffer distance	0.1195	0.0573	0.0072	0.2319
Edge:Grassland × Buffer distance <sup>2</sup>	-0.0129	0.0039	-0.0204	-0.0053
Edge:Woodland × Buffer distance <sup>2</sup>	-0.0274	0.0035	-0.0344	-0.0205
Wet × Edge:Buffer distance <sup>2</sup>	-0.0118	0.0052	-0.0219	-0.0017
Wet × Edge:Grassland × Buffer distance	-0.0691	0.0693	-0.2050	0.0668
Wet × Edge:Woodland × Buffer distance	-0.1755	0.0679	-0.3086	-0.0424
Wet × Edge:Grassland × Buffer distance <sup>2</sup>	0.0103	0.0063	-0.0021	0.0228
Wet × Edge:Woodland × Buffer distance <sup>2</sup>	0.0156	0.0061	0.0037	0.0276

Note: Terms nested within the boundary zone only are indicated by “.” and interaction terms are indicated by “×.”

† Reference levels for factor variables were as follows: Season: Dry; Zone: Interior; Land cover (within boundary zone only): Forest. Therefore, the intercept represents the mean NDVI in the interior of MFCA during the dry season.

over large spatial scales (>1 km from edge; Woodroffe and Ginsberg 1998, Curran et al. 1999, Peters 2001, Cochrane and Laurance 2002), our study is unique in that it assesses impacts to primary productivity, which can have implications for species richness, distribution, and abundance, on a parkwide basis.

Immediately at the park boundary, within the first km of the edge, we observed a sharp difference in productivity at the transition from agricultural matrix to woodland and forest. That hard edge, however, was not apparent for the grassland cover type. This difference is unsurprising as productivity of agricultural fields is generally more similar to that of grasslands than forest or woodland (Wang et al. 2003). The differences we observed in vegetation productivity and variability indicate that the matrix surrounding MFCA may be limited in its ability to act as a buffer zone for the park, especially for forest-dependent species. Despite widespread recognition that managing buffer zones and matrices

between parks is necessary to ensure the conservation value of parks (Margules and Pressey 2000), hard edges, like those we observed here, have been documented in many park systems (Dobson et al. 1999). For example, Joppa et al. (2008) found that percent cover by natural vegetation immediately outside park borders in West Africa and the South American Atlantic coast was dramatically lower than immediately inside park borders. Abrupt transitions between parks and human-dominated landscapes are common in the Albertine Rift, where local residents are often excluded from parks but cultivate land immediately outside their boundaries (Mackenzie and Hartter 2013, Hartter et al. 2016). In MFCA, the hard edge we observed could present challenges to the successful preservation and establishment of proposed wildlife corridors in the greater landscape extending south to Semuliki National Park (Wildlife Conservation Society 2010).

We chose NDVI as a proxy for measuring productivity and variability because NDVI has

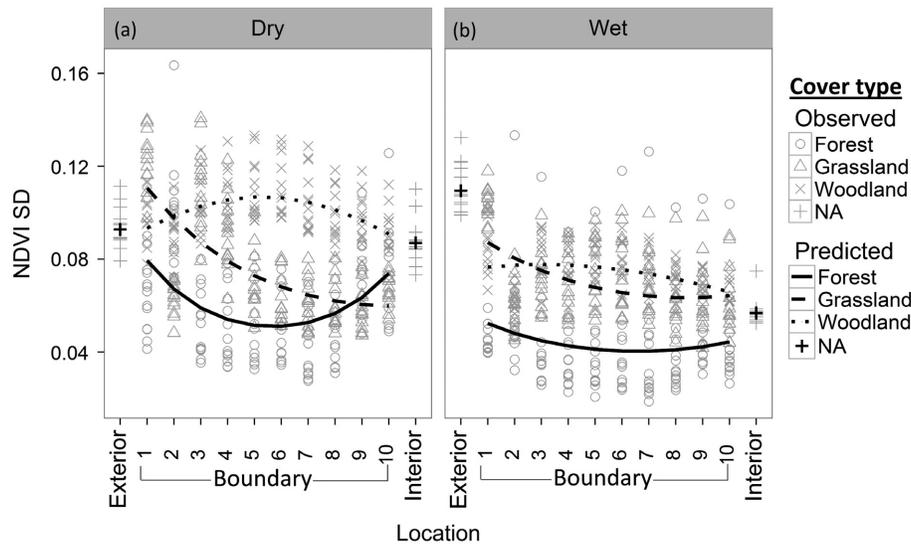


Fig. 5. Observed and predicted Normalized Difference Vegetation Index (NDVI) standard deviation (SD) values from 2001 to 2013 in the three study zones of Murchison Falls Conservation Area, Uganda, in the (a) dry and (b) wet seasons. The exterior zone extended  $\leq 10$  km from MFCA border, and the interior zone extended  $>10$  km from MFCA border. The numbers 1–10 indicate buffers within the boundary zone, with “1” indicating the area from 0 to 1 km inside the MFCA border. The boundary zone was further divided based on three dominant land cover classes: forest, grassland, and woodland. Exterior and interior zones were not divided by buffer or land cover (NA).

been successfully used in numerous wildlife studies to predict species richness, distribution, abundance, and migration patterns (Pettoirelli et al. 2005, 2011). Vegetation productivity and spatial heterogeneity have important implications for ecosystem functioning. Species diversity has been shown to increase with primary productivity (Brown 1981, Currie and Paquin 1987, Currie 1991, Bailey et al. 2004) or to peak at intermediate levels (Abramsky and Rosenzweig 1984, Leibold 1999, Dodson et al. 2000, Virtanen et al. 2013), and to vary as a function of the spatial variability of vegetation cover (Riera et al. 1998, Kerr et al. 2001, Bailey et al. 2004, Lunetta et al. 2006, Costanza et al. 2011). These relationships depend on numerous factors such as scale (Chase and Leibold 2002, Pärtel et al. 2010) and the taxa of interest (Mittelbach et al. 2001). Young et al. (2009) documented that in southern Africa during the wet season, home-range size for elephants was negatively correlated with mean NDVI. Therefore, a reduction in mean NDVI in the MFCA edge effect area could drive elephants in this region to need larger average home-range sizes than in the park interior.

A potential driver of the edge effects we observed is changes to the fire regime related to human activities, a concern that has been voiced by park management (Uganda Wildlife Authority 2012). Outside MFCA, fires are set to hunt Gambian pouched rats (*Cricetomys gambianus*) and cane rats (*Thryonomys* spp.), and these fires often spread into the park. Poachers also purportedly set fires inside the park to attract game to resulting new vegetation growth. Various fire regimes at the park edges could contribute to patterns of vegetation productivity and variability in the edge effect area of MFCA. In savanna ecosystems with  $>700$  mm annual rainfall, fire is the primary factor driving tree cover, with higher fire frequencies limiting tree density (Bond 2008, Sankaran et al. 2008, Mayer and Khalyani 2011), and thus correlating with lower NDVI values (Campo-Bescós et al. 2013a, b). Cochrane and Laurance (2002) found increased fire frequencies within 2.4 km of forest edges in Amazonia and speculated that this edge effect had the potential to degrade even very large parks in Amazonia, especially in areas with distinct dry seasons.

Another driver of vegetation patterns, especially in African systems, is herbivory. Elephants

tend to reduce tree cover through browsing and trampling and exacerbate the effects of fire on trees by debarking them (Sankaran et al. 2008). Changes in elephant populations have previously driven large-scale shifts in land cover in MFCA, with a rapid increase in the elephant population following park establishment in 1952 resulting in the conversion of large areas of woodland and forest to grassland (Buechner and Dawkins 1961, Buechner et al. 1963, Laws et al. 1975). Following intense poaching of elephants and other herbivores in the 1970s and 1980s, much of this grassland reverted to woodland south of the Nile (Mann 1995). Other browsers and mixed feeders also suppress woody biomass, while grazers may suppress woody plant growth at low and moderate densities, but promote it at high densities (Sankaran et al. 2008). Differences in fire frequencies and herbivore distribution between seasons, among land cover types, and with relative proximity to the park border may contribute to the patterns observed in our study.

Our study was limited by a lack of available land cover data for MFCA, and our land cover zones were approximate delineations based on dominant cover type. Variations in land cover within these zones with distance from the park edge could potentially have contributed to observed patterns of NDVI. Other contributing factors could include abiotic factors such as topography (Teillet and Staenz 1992, Burgess et al. 1995) and soil type (Huete 1988, Farrar et al. 1994, Nicholson and Farrar 1994). A post hoc examination of soil types (FAO-UNESCO 2012) revealed that MFCA is dominated by sandy clay loams, with some clay soils in the region of Budongo Forest Reserve. While a larger proportion of clay soils occurred within the buffer zone compared to the park interior, there was little variation within the buffer zone and so it is unlikely that these differences would explain NDVI patterns observed within the buffer zone. Furthermore, most of the clay soils overlapped with our forest land cover zone, and so any effects of soil on NDVI patterns would likely be masked by the differences between land cover zones. Total elevation change in MFCA is a moderate 660 m; therefore, topography may explain some variation in NDVI measurements. However, elevation increases relatively gradually in the park primarily from west to east, rather than with

distance from the edge, and the terrain is not mountainous. Therefore, it is unlikely that elevation would explain the observed patterns in NDVI. Matsushita et al. (2007) found that topography had less of an effect on NDVI than on other vegetation indexes and can usually be ignored.

## CONCLUSION

We observed an abrupt change in vegetation productivity and variation in productivity along the border of MFCA in Uganda, with edge effects covering as much as 40% of the park. Satellite imagery provided a rapid and cost-efficient means of quantifying edge effects on vegetation in this region. Quantifying the extent of edge effects in parks is an important step toward mitigating the drivers of change and preserving integrity, especially as human populations continue to expand and parks become increasingly isolated. Our approach yielded a novel, low-cost means of measuring edge effects on the landscape, which may prove particularly useful as climate change progresses and human populations continue to grow. The population in Africa will double over the next few decades, and Uganda's population is projected to nearly triple by 2050 (World Population Review 2014). Higher-than-average population growth rates in global biodiversity hotspots raise concerns about the long-term sustainability of parks in these areas (Cincotta et al. 2000, Hartter et al. 2016). Increasing populations and lack of available land elsewhere may further exacerbate edge effects by driving people to move closer to parks like MFCA (Hartter et al. 2014). Furthermore, expanding crop production driven by both population growth and lower agricultural yields caused by land degradation and shortened rainy seasons will put further pressure on parks in the region (Diem et al. 2014, 2016). Replication of our approach in other park systems will facilitate exploration of how impacts to primary productivity at park edges may vary in different land cover types and with varying levels of human disturbance.

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