



Habitat fragmentation, livelihood behaviors, and contact between people and nonhuman primates in Africa

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Abstract

Context Deforestation and landscape fragmentation have been identified as processes enabling direct transmission of zoonotic infections. Certain human behaviors provide opportunities for direct contact between humans and wild nonhuman primates (NHPs), but are often missing from studies linking landscape level factors and observed infectious diseases.

Objectives Our objective is to better understand landscape and livelihood factors influencing human-NHP contact in rural communities whose landscapes undergo deforestation. We investigate core loss and edge density within a buffered area around survey respondent households to identify which landscape changes and behaviors increase the risk of human-NHP contact.

Methods Behavioral survey data were collected from small-scale agriculturists living near forest

fragments around Kibale National Park in western Uganda. We combined spatially explicit behavioral data with high-resolution satellite imagery. Using land cover classification and change detection, we investigated the relationships between forest loss and fragmentation, behavioral data, and human-NHP contact using logistic regression.

Results Between 2011 and 2015, there were differences in the landscape metrics around the households of individuals who had experienced human-NHP contact compared to those who had not had contact. Increased edge density around households, collection of small trees for construction, and foraging and hunting for food in forested habitat significantly increase the likelihood of human-NHP contact.

Conclusion This study provides empirical evidence that forest landscape fragmentation and certain small-holders' behaviors in forest patches jointly increase the likelihood of human-NHP contact events.

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Combining spatially explicit data on land use and human behaviors is crucial for understanding the social and ecological drivers of human-NHP contact.

Keywords Land use and land cover change · Forest fragmentation · Agricultural livelihoods · Human-wildlife contact · Zoonotic risk · Kibale National Park, Uganda

Introduction

People have converted nearly 50% of the world's terrestrial landmass from natural habitats into agricultural land, typically for crops and domestic animal grazing (Assessment 2005). Tropical forests have endured some of the highest rates of agricultural conversion over the last few decades, even those designated as protected areas (Linard et al. 2011; Margono et al. 2012; Hartter et al. 2015). An estimated 75% of recent forest loss in Africa is attributed to agricultural expansion of which more than half is related to subsistence (Hosonuma et al. 2012). Though correlated, habitat loss and habitat fragmentation may influence populations and biodiversity within a landscape in distinct ways (Fahrig 2003; Smith et al. 2009). A characteristic feature of habitat fragmentation, or change in the arrangement and configuration of remaining habitat, is the presence of small patches of forest, or *core*, that are embedded in farmland, pastureland or human settlements known as *matrix* (Skole and Tucker 1993; Forman 1995). Structurally, fragmented landscapes contain a high density of *edges*, defined as the total length of boundary between two habitat types, per unit of core area.

Edge density is a product of core patch shape and composition which influences ecosystem functioning and the movement of humans and other animals (Malcolm 1994; Forman 1995; Ries 2004; Laurance et al. 2009; Ewers et al. 2013). In this conceptualization, the core is the primary habitat for large-bodied wild mammals such as nonhuman primates (NHPs) (Fagan et al. 1999) and the matrix is the primary habitat for humans engaged in agricultural livelihoods (Skole and Tucker 1993; Forman 1995). In African landscapes with diverse wildlife populations, edges are the interfaces between NHPs and humans, with

which physical encounters increase the risk of harm, infection transmission, and local biodiversity loss.

Core loss and habitat fragmentation are dynamic processes that affect species' population sizes, densities, and the probability of interspecies contacts in various ways at different points during a landscape transition (Skole and Tucker 1993; Forman 1995; Faust et al. 2017). Figure 1 conceptually illustrates three potential stages of core loss that increase landscape fragmentation. Initially, when core area is lost, the edge density increases and the number of core patches increases. As core fragmentation progresses, the area of core patches decreases, the isolation of core patches increases, and eventually edge density declines (Bascompte and Solé 1996; Hargis et al. 1998; Fahrig 2003; Faust et al. 2018). Core area interacts with edge density to determine animal carrying capacity, survival, and movement across landscape types (Pfeifer et al. 2017).

The processes by which core is converted to matrix determines the fragmentation pattern trajectory and the chronology of interactions between wild animals and people sharing these spaces (Zipperer 1993; Hargis et al. 1998; Pellissier et al. 2017). Some species of NHPs persist temporarily or permanently in core patches depending on their home ranges, their population sizes, the availability of resources, their resilience to degraded habitat, and their social structure (Chapman and Lambert 2000; Nunn and Altizer 2006; Bonnell et al. 2016). In small-holder agricultural landscapes, changes to matrix extent and quality also influence the size and density of human populations. The movement of NHP species into matrix and the movement of humans into core for livelihood and foraging behaviors are mediated by the boundaries between these two habitat types, as described by the edge density (Naughton-Treves 1997, 1998; Hill 2004).

Previous research suggests that fragmentation occurs more rapidly in a concentrated area around a household where livelihood activities are shaped by economic and social factors as well as resident perceptions of wildlife (Ryan et al. 2015). Intensified levels of core loss and increased human encroachment on wild animal habitats lead to periods of time during which edge creation and edge density are maximized (Ostfeld et al. 2005; Faust et al. 2018). Increased core fragmentation can restrict wild animal movement, leading to concentrated wild animal habitat use in

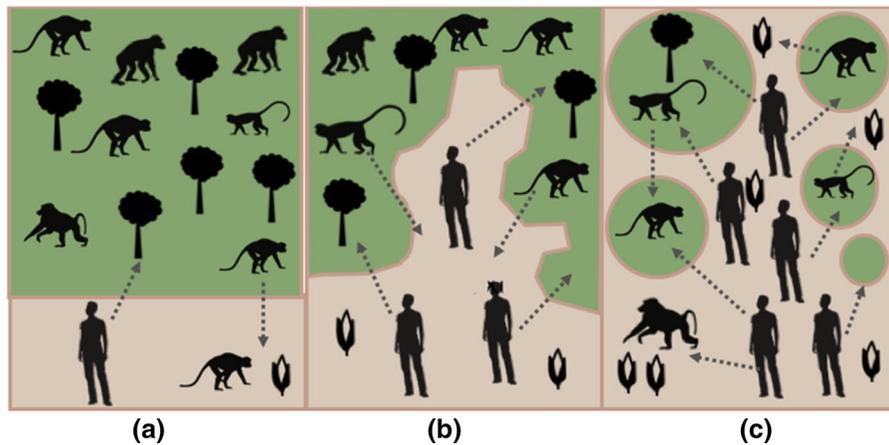


Fig. 1 Conceptual illustration of core fragmentation progression: **a** The first panel illustrates a mostly intact core that has a minimum edge density, a high NHP population, and minimal movement of both humans and NHPs across the edge. **b** The second panel illustrates a fragmented core that has decreased core, increased edge density, decreased NHP population,

increased human population, and increased movement across the edge. **c** The third panel illustrates the creation of core patches embedded in matrix that has decreased core, increased edge density, decreased NHP population, but increased NHP density, increased human population, increased matrix quality, and increased movement across edges

particular areas of the landscape (Bonnell et al. 2013, 2018). Edge length and human use of wild animal habitat has been positively correlated with interspecies contact rates and increased pathogen sharing (Chapman et al. 2005; Nunn et al. 2008; Li et al. 2012; Lane-deGraaf et al. 2013; Paige et al. 2014; Wilkinson et al. 2018).

Recent core loss and fragmentation have been identified as landscape processes that are mediated by human behaviors, and which enable directly transmitted zoonotic infections (Bausch and Schwarz 2014; Olivero et al. 2017). In particular, the transmission of infected bodily fluids from NHPs through direct contact has led to the emergence of new infections in human populations, most notably the origin of HIV almost a century ago (Gonzalez et al. 2005; Wolfe et al. 2005; Goldberg et al. 2008; Pepin 2011; Frieden et al. 2014; Genton et al. 2015). Pathogens from humans also have negative consequences for wild NHP populations (Ferber 2000; Woodford et al. 2002). For this study, we define a contact event as a direct physical interaction (i.e. touching, biting, scratching or slaughtering) between a human and a living or deceased NHP.

To date, models of emerging infections rarely incorporate landscape level analyses. Furthermore, very few empirical studies have analyzed the relationship between landscape patterns, human behaviors, and interspecies contact events (Faust et al. 2018;

Wilkinson et al. 2018). The objective of this study is to better understand which landscape and livelihood factors influence the likelihood of human-NHP contact events in communities near Kibale National Park in western Uganda. Our hypothesis is that recent loss of core and increased edge density influence the likelihood of direct contact events between humans and NHPs. The underlying assumptions are that: (1) core loss indicates increased human encroachment on core areas that are primarily NHP habitat and (2) increased levels of edge density create more entry points for humans and NHPs into their non-dominant habitats (i.e. core for people and matrix for NHPs).

This study relies on self-reported cross-sectional survey data and landscape analyses. We investigate core loss and edge density within a buffered area around household locations of survey respondents reflecting the average distance people who utilize core resources live from a core patch (Hartter 2010). The buffered area defines the space in which human and NHP movements are most likely to overlap. By placing human livelihood activities in a geographically explicit area, we link spatial and behavioral variables that influence human-NHP contact. In the next sections, we introduce the study site, data collection, spatial analysis and statistical methods, and results, before discussing our findings. Our results highlight the value of investigating spatial and behavioral data to better understand the potential

association of landscape variables and human livelihood activities to human-NHP contact events.

Background

Study site

In 1993, Kibale Forest Reserve and the Kibale Corridor Game Reserve were combined into one continuous protected area forming Kibale National Park (0° 13'– 0° 41' N, 30° 19'– 30° 32' E), located in western Uganda spanning the Kaberole, Kamwenge, Kasese, Kyenjojo counties (Statute 1996). Covering approximately 766 km², Kibale National Park is one of six forested national parks in Uganda and contains a high level of ecological diversity including a high abundance of NHPs (Struhsaker and Leland 1979; Chapman and Chapman 1999; Wanyama et al. 2010). Beginning in the early twentieth century, the British colonial government prohibited local people near the land that has become Kibale National Park from hunting wild animals in core habitat (Hartter et al. 2015). Since its Park designation, the Uganda Wildlife Authority has monitored and restricted access to the Kibale National Park boundary by fining trespassers and poachers. The punishment for illegal entry into protected land can also include arrest, physical assault or even death (Naughton-Treves 1997; Mackenzie and Hartter 2013).

Human population density around Kibale National Park is exceptionally high, estimated to exceed twice the national average of 120 people per km² (Of Statistics 2006; Mackenzie and Hartter 2013; Hartter et al. 2015). Such density contributes to a mosaic of intensive small-holder agriculture and large tea estates that are interspersed with patches of core and wetlands that restrict further development (Hartter and Southworth 2009). Migration to the area around Kibale National Park is the result of decades of land scarcity and a high population density in southwestern Uganda, which was once sparsely populated (Hartter et al. 2015). Small-scale farming (plots of less than 5 hectares) composes greater than 80% of the matrix area and the vast majority of households are considered subsistence farmers (Of Statistics 2009; Hartter and Southworth 2009; Hartter et al. 2015).

Following federal protection, the mean core patch size around Kibale National Park increased and the number of core patches decreased within the Park border indicating reforestation and cessation of fragmentation inside the border. In contrast, deforestation and fragmentation have increased in the area surrounding Kibale National Park (Hartter and Southworth 2009). Between 1984 and 2003, 25% of core patches supporting NHPs were lost, the number of core patches increased, their sizes decreased, and the core patches became more isolated within the matrix similar to the progression illustrated by Fig. 1 (Southworth et al. 2010). Degradation of remaining core patches also declined (as measured by a vegetation index established by remote sensing, NDVI), indicating potential ecological consequences from continued fragmentation (Hartter and Southworth 2009). Core patches outside of the Kibale National Park provide unrestricted access to livelihood materials such as water, firewood, poles (defined as small trees for house and fence construction), handicraft materials, food and medicinal herbs, land for grazing domestic animals, and areas to hunt wild animals (Naughton-Treves 1997, 1998; Naughton-Treves et al. 2005; Mackenzie et al. 2012; Ryan et al. 2015). Generally, local people avoid hunting and eating NHPs due to cultural preferences and a commonly held local perception that these animals carry harmful infections (Paige et al. 2014; Hill 2015).

Since each species of NHP has different home ranges, group sizes, and foraging behaviors that determine whether isolated core patches can support them, there is no generalized model to estimate NHP presence and population sizes in patches (Clutton-Brock 1975; Rudran 1978; Struhsaker and Leland 1979; Butynski 1990; Chapman et al. 2000; Onderdonk and Chapman 2000). The consensus from field observations is that most species of NHPs prefer living in intact core, however, NHPs may adapt to changing landscape features (Naughton-Treves 1998; Onderdonk and Chapman 2000; Wallace and Hill 2012; Hill 2015). Additionally, evidence suggests that smaller NHP species may prefer living in smaller core patches that pose less risk of predation from chimpanzee groups that require larger core areas (Onderdonk and Chapman 2000; Wallace and Hill 2012).

Crop-raiding events by wild animals, particularly elephants and NHPs, are increasingly common and lead to substantial household crop losses for

individuals living close to the border of Kibale National Park (Mackenzie and Ahabyona 2012). Households located near core patches have reported average annual losses of 4–7% of total agricultural land from wild animal crop-raiding (Naughton-Treves 1997), with higher average losses of maize crops (10%) (Hill 2004) and with individual farmers losing up to 60% of an annual harvest (Hill 2004; Paige et al. 2014). NHPs living in core patches embedded in matrix respond to a changing environment. During periods of low forest fruit availability, NHPs may take advantage of increased access to cropland that provide predictable sources of nutrition (Strum 2010). Increasing NHP habituation may also lead to more frequent raids of cropland that range further from intact core into matrix (Hill et al. 2017). Crop-raiding events are less likely on plots of tea than plots of maize, indicating that variations in core resources increase pressure on desirable crops or that desirable crops are a potent attractant to wild animals (Naughton-Treves 1998; Hill 2004; Tweheyo et al. 2005). Observational studies reveal that collectively NHPs travel an average of 15 m from the edge of core to crop-raid whereas chimpanzees and baboons will travel up to 50 m to do so (Wallace and Hill 2012).

Proximity to protected forests and associated crop losses influence local land-use decisions and pose social, economic, and behavioral consequences. Although previous studies reported that farmers who have experienced damaging crop-raiding events are more likely to hunt for bushmeat and forage for food in the core as a way to cope with food insecurity, a recent study around Kibale National Park could not confirm this relationship (Hill 2004; Webber 2006; Hill and Wallace 2012; MacKenzie 2018). A history of NHP crop-raiding has led people to position maize further from the edge of Kibale National Park and modify behaviors that lead to NHP exposure. Crop-raiding has also led to decreased primary school attendance for male children who remain at home to guard crops (Mackenzie et al. 2015). Households may invest in physical deterrents, such as fencing, which are both costly and often ineffective (Hill and Wallace 2012).

In addition to economic concerns associated with crop-raiding, individuals living near Kibale National Park report fear of wild animal infections, particularly those from NHPs (Paige et al. 2014; Hill 2015). Crop-raiding from NHPs may result in aggressive physical contact and injuries causing people concern for

potential exposure to infectious agents (ITFC and WCS 2003; Paterson and Wallis 2005; Woodroffe et al. 2005). NHPs in and near the Park carry a diversity of viral infections, some of which have been detected in humans (Goldberg et al. 2009). These complex relationships make the rural communities situated near core patches at the boundary of Kibale National Park an ideal setting to investigate the link between landscape level processes, livelihood behaviors, and human-NHP contact.

Methods

Survey data

Study communities were selected based on previous work with collaborators from the Kibale EcoHealth Project which had identified communities where households were located within 500 m of a core patch containing wild NHPs. Previous studies have referred to these communities as *fragment* communities due to the influence of local residents on the land cover. We selected sites around the northern aspect of Kibale National Park which was historically Kibale Forest Reserve. A pilot survey was field tested with enumerators in January 2014 and feedback was incorporated in the final survey and data collection methods. We administered standardized behavioral surveys between July 2014 and January 2015 to participants living in households selected from a previous census-based survey. Enumerators visually confirmed that the core areas around survey households were known habitat for NHPs.

Ugandan research assistants collected data on human-NHP contact and livelihood behaviors in the local languages, Rutooro and Rakiga, using verbal informed consent. Consent was received by adult guardians for minors. We did not exclude anyone from the study who was able to consent, though multiple individuals in the same household were excluded from the analysis. One half kilogram of sugar, the equivalent of 3000 Ugandan shillings (< 1 USD), was provided as compensation following survey completion. Participation was confidential and survey information was de-identified prior to analysis (Fig. 2).

Self-reported survey data included the frequency and extent of core use, the activities participants conducted in both core and matrix, whether NHPs

were observed during these activities and the estimated distance of NHPs during these activities, known contact with NHP excrement, and detailed information on physical contact events with both living and deceased NHPs. Study participants indicated up to four behaviors in the core and up to five behaviors in matrix. Answers were coded based on focus group answers to typical categories of behaviors described during the pilot phase of the study. For consistency with the dates of the satellite data, only households in which a resident had a NHP contact event between January 2011 and December 2014 were included as a contact in our analysis. Participants with a history of NHP contact were asked to indicate the type and severity of contact, the land cover type where the contact event occurred, and the livelihood activity associated with the NHP contact event.

Activities in core included: any use of core habitat, collecting firewood, collecting poles, collecting water, core agriculture, touring and collecting handicraft materials, and foraging and hunting for food. In Ugandan forestry, poles are defined as trees naturally

growing in the core with a diameter between 5 and 14 cm measured at 1.4 m above the ground; those grown on plantations have a diameter between 5 and 24 cm measured at 1.4 m above the ground (Kakudidi 2007). Activities in the matrix included digging land, collecting firewood, collecting water, domestic activities (i.e., sweeping, washing dishes, washing clothes, preparing food), preparing gardens, and grazing domestic animals.

Spatial analysis

To create information concerning land cover, we performed supervised classification in ENVI on RapidEye (L3A product, spatial resolution: 6.5 m) satellite images of the study area from January 2011 and January 2015 with cloud coverage below 5% (Planet Application Program Interface: In Space for Life on Earth 2017). The images were classified into six classes via supervised classification: water, core, cropland, grassland, roads/impermeable urban surfaces, and bare ground. Core region of interest (ROI)

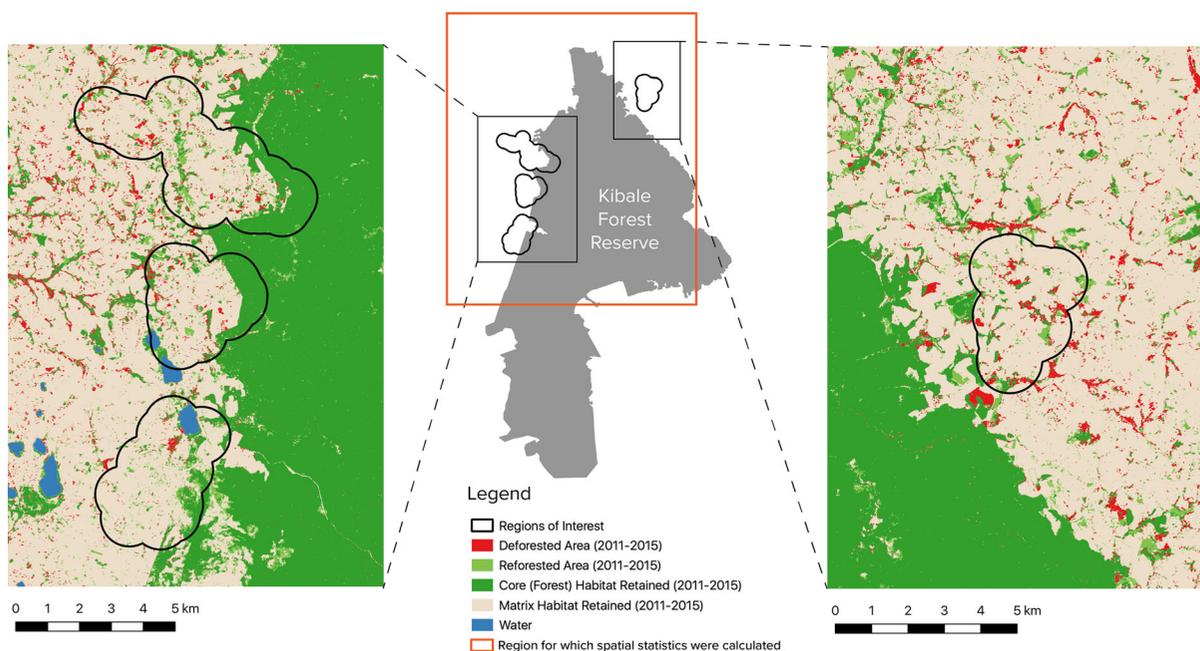


Fig. 2 Classification map of study area: The gray area represents the border of Kibale Forest Reserve, Uganda which is protected as the northern part of Kibale National Park. The orange box outlines the extent of satellite imagery available for January 2011 and January 2015 for which spatial statistics were calculated. The black rectangles outline the areas represented by

the change detection maps on the left and right of the figure. The black rounded areas within the change detection maps represent the community regions of interest, areas in which study households were located. These community regions of interest were created by overlapping 900 m radius buffered areas around each household

selection in spatially complex areas was informed by forest delineation shapefiles acquired from researchers in the region, as well as by visual change detection to identify stable core patches and minimize the possible selection of woodlots as ROI samples. Following classification, all classes except for water and core were merged into a single class describing human-modified land: matrix. A majority filter was then applied to both images and change detection from 2011 to 2015 was performed. Results were exported to shapefiles in ArcGIS to create layers of: (1) core that remained throughout 2011–2015, (2) core loss between 2011 and 2015, (3) core reforested during 2011–2015, then (4) matrix areas throughout 2011–2015.

Core patches within 50 m of one another were aggregated into multi-part features and analytically treated as a single core patch in order to assess potential NHP distribution (Onderdonk and Chapman 2000). The 50 m distance corresponds to the furthest NHP movement across matrix observed near Kibale National Park and is equivalent to half of the furthest distance from an adjacent patch (100 m) in which a NHP has been observed (Onderdonk and Chapman 2000; Wallace and Hill 2012). Aggregated core patches smaller than 0.8 hectares were removed based on observational data indicating that NHPs in this setting do not live in core patches of this size or smaller (Onderdonk and Chapman 2000). We then calculated the distance from surveyed participant households to Kibale National Park, to the closest core patch, to the closest core habitat of any type (to either Kibale National Park or to a core patch), and to the closest main road. If participants recalled the exact location of a NHP contact event, they were asked to lead enumerators to the location where it occurred and the coordinates were recorded.

Based on published data describing the average distance that individuals travel from their household to a core patch for ecosystem goods or services, we created a circular buffer with a radius of 300 m (Area = $3 \times 10^5 \text{ m}^2$) around each respondent household to describe the local landscape in which an individual lives and engages in livelihood activities (Hartter 2010). For known contact locations, we calculated the distance metrics described above in addition to the distance of the known contact location to the participant's household. Within each buffered area, we used the program Fragstats to calculate distance to the

closest core habitat, total core area, core area loss during 2011–2015, and edge density, if present. These metrics were chosen based on prior research attributing these landscape features to human-NHP contact and informed the independent variables included in our logistic regression models.

Edge density is the ratio between the length of edge and core area. The equation for edge density is McGarigal and Marks (1995):

$$\text{Edge Density} = \frac{\text{Edge (m)}}{\text{Area (m}^2\text{)}} (10,000) \quad (1)$$

We used edge density as a landscape permeability index to indicate the amount of edge across which an individual could move from primary to non-primary habitat (i.e., a NHP moving from core into matrix or a human from matrix into core). Figure 3 illustrates examples of low, medium, and high levels of edge density within the household buffered area.

We conducted spatial analyses for each participant, with individuals being assigned the outcome of contact (1) or no contact (0) based on self-reported survey data responses. Due to spatial clustering of households and spatial overlap between their buffered areas, we employed a stepwise technique to correct for the non-independence of data and reduce spatial autocorrelation as measured by Moran's I. For each buffered area around households, we calculated the area of overlap shared with every other household buffered area, weighted overlapping areas by the total shared area, ordered participants by amount of overlap, and iteratively removed participants whose buffered areas had the greatest spatial overlap with those of other participants until Moran's I reflected that autocorrelation and the potential for overrepresentation in the sample had been reduced. This process reduced the total number of households in the sample used for analysis from 268 to 220 (82% of the original sample) and the total number of participants from 364 to 220 (60% of the original sample).

Logistic regression models

We described the relationship between independent variables and the binary outcome of human-NHP contact (0, 1) from 2011 to 2015 using a logistic regression model. Prior to determining our logistic models, we investigated the significance of many

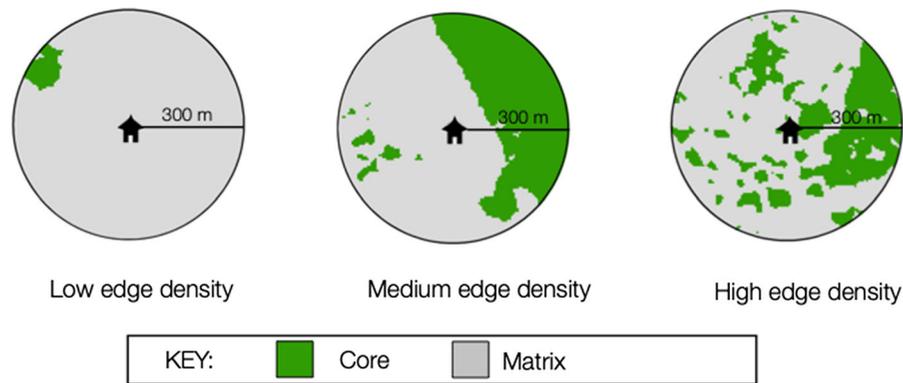


Fig. 3 Edge density: Examples of edge density within the household buffered area (Radius = 300 m and Area = 3×10^5 m²)

variables from landscape analysis and survey data. The landscape metrics within the household buffered area which we tested prior to determining our final model were: distance to Kibale National Park, distance to nearest core, number of core patches, change in number of core patches, core area in 2011, core area in 2015, core loss between 2011 and 2015, edge density in 2011, edge density in 2015, and edge density change between 2011 and 2015. The landscape metrics within the buffered area around contact locations that we tested were: distance to Kibale National Park, distance of contact location to nearest core habitat in 2011, distance of contact location to nearest core in 2015, distance from contact location to household of participant, core area in 2011, core area in 2015, core loss from 2011 to 2015, edge density in 2011, edge density in 2015, and edge density change between 2011 and 2015.

We investigated the significance of core activities: daily core use, weekly core use, collecting firewood, collecting poles, collecting water, agricultural activities in the core, touring the core, collecting handicraft materials, and foraging and hunting for food in the core. We also tested the significance of matrix activities: digging in domestic gardens, collecting firewood, collecting water, engaging in domestic activities (i.e., sweeping, washing dishes, washing clothes, preparing food), preparing gardens for planting, and grazing domestic animals.

We removed variables that had high correlation coefficients with other explanatory variables and those that had minimal explanatory power. We developed three models to test the relative explanatory power of landscape metrics around participant households and

participant behaviors on the occurrence of NHP contact. In the first model, we tested the association between local spatial metrics previously linked to interspecies contact with the likelihood of a human-NHP contact event. These variables were core loss, edge density (Faust et al. 2018), and distance to core patches (Genton et al. 2015). The independent variable core area was not incorporated based on its covariance with edge density. In the second model, we tested whether participant behaviors were associated with an increased likelihood of a participant reporting a NHP contact event. In the third model, we tested the combined association of landscape metrics and specific participant behaviors on the risk for a reported NHP contact event.

Results

Descriptive statistics

Land cover change

Land cover change analysis was performed for the entire area for which satellite data was available for 2011 and 2015 (bounded by the orange box depicted in Fig. 2). In January 2015, nearly 50% (461.5 km²) of the land cover was composed of core, nearly 50% (457.8 km²) of land cover was composed of matrix, and less than 1% was composed of water. In 2015, 97% (448.7 km²) of core area was determined to be suitable NHP habitat after the removal of core patches that did not meet the aforementioned specifications for hosting a NHP. Between 2011 and 2015, there was a

7% (31.9 km²) gross loss of core. Most detected core loss was from the core patches and not from within the boundary of Kibale National Park where there was a net increase in core area of 1.6 km².

In 2015, within the community regions of interest (bounded by the black rounded buffered areas around survey households in Fig. 2), 26% (14.1 km²) of land cover was composed of core and 74% (40.2 km²) was composed of matrix. Between 2011 and 2015, there was a 16% (2.7 km²) gross loss of core in community regions of interest. On average, households were located 48 m from the nearest core (range 0, 174 m). In the buffered areas around participant households 3×10 m², there was an average 3 m² of core area (range 0, 22 m²), an average loss of 1 m² of core area (range 0, 7 m²), and an average edge density of 84 m⁻¹ (range 0, 256 m⁻¹).

We compared landscape metrics for the buffered areas around contact and noncontact households. In Fig. 4, average core loss between 2011 and 2015 and average edge density in 2015 are both higher in the buffered areas around the households of participants who experienced NHP contact compared to the buffered areas around households of participants who did not experience contact. In contrast, the average distance to core in 2015 for participants who experienced NHP contact was less than the distance to core for those who did not experience contact. Though the mean values for the selected landscape metrics are not substantially different between contact and non-contact groups, the shape of the distributions are distinct.

Location of contact events

Of the 90 participants with at least one NHP contact event between 2011 and 2015, 57 self-reported a specific GPS location for the contact event that was accessible during data collection. These contact locations were located an average 858 m (range 0, 2723 m) from the Kibale National Park border, 32 m (range 0, 117 m) from the nearest core patch, and 84 m (range 0, 1339 m) from the participant's household. In the buffered areas around contact locations (3×10^5 m²), there was an average 5 m² (range 1, 22 m²) of core area, an average 2 m² (range 0, 8 m²) of core loss, and an average edge density of 152 m⁻¹ (range 47, 262 m⁻¹). Compared to buffered areas around the

households of participants who experienced NHP contact, buffered areas around NHP contact locations were closer to core area, had higher core area, higher average core loss, and higher edge density.

Survey data

In the original study population, 364 individuals from 268 households were represented with an average 1.4 participants per household. In the original participant population, 70% (255/364) were adults (15 years and older) and the average age of participants was 27 years. 51% (186/364) were Mutooro and 38% were Mukiga (138/364), the two dominant ethnic groups in the region. 73% (266/364) of people used core for livelihood activities with an average of 2.7 core visits per week. 12% (44/364) of participants used the core daily.

Concerning livelihood activities in the core, 67% (244/364) of participants collect firewood, 17% collect poles (62/364), 13% collect water (47/364), 11% engage in core agriculture (40/364), 3% tour and collect handicraft materials (10/364), and 16% forage and hunt in the core (58/364). Concerning livelihood activities in the matrix, 56% of people dig land for crops (204/364), 5% collect firewood (18/364), 6% collect water (22/364), 23% sweep and wash around the house (84/364), 27% prepare gardens (98/364), and 20% graze domestic animals (73/364).

32% (115/364) of participants in the sample experienced at least one NHP contact event between 2011 and 2015 and provided complete information about 160 NHP contact events. There was an average 1.4 (range 1, 5) contact events per participant who experienced NHP contact between 2011 and 2015. There were 249 participants included in the full sample who did not experience any NHP contact between 2011 and 2015.

After the reduction in auto-correlation during spatial analysis, there were 220 households in the final sample. 90 household points represented a participant who had experienced at least one physical contact event with a NHP between 2011 and 2015. Of these 90 participants, 57 (63%) specified a location for the contact event and a willingness to take an enumerator to that specific geographic location. In Fig. 5, we represent the livelihood activities in core and matrix of participants included in the spatial analysis (N = 220). A greater percentage of

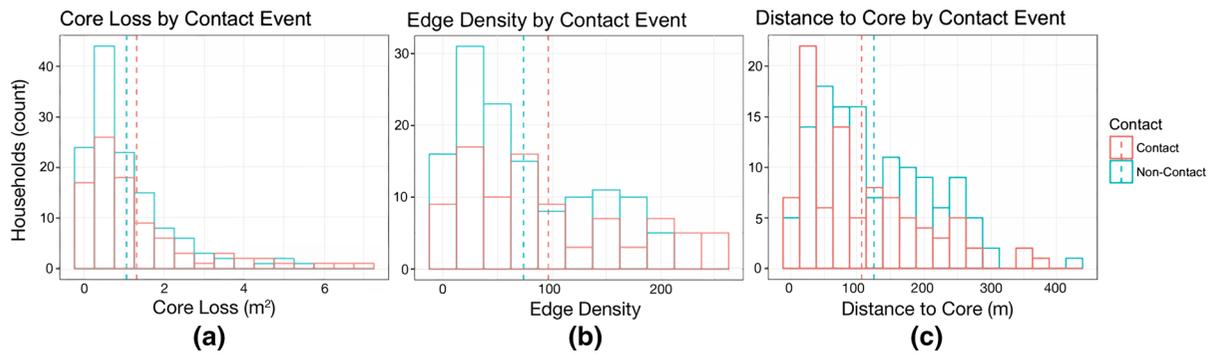


Fig. 4 Distribution of Household Landscape Metrics by NHP Contact Status between 2011 and 2015: Red bars represent households of participants who experienced NHP contact. Blue bars represent households of participants who did not experience NHP contact. Dashed lines represent mean values of the

distributions for contact and noncontact households. **a** Core Loss within 3×10^5 m² buffered area, **b** Edge Density within 3×10^5 m² buffered area, **c** Distance to Core (Kibale National Park or core patch) from households

participants who experienced NHP contact participated in the core activities of collecting poles and foraging and hunting compared to the percentage of participants who did not experience contact.

Logistic regression results

Our logistic regression results indicate a significant positive association between edge density and the occurrence of a NHP contact event. Our regression results also indicate a significant association between collecting poles and foraging and hunting for food in the core and a NHP contact event. We used an odds ratio (OR) to measure the association between edge density, collecting poles, foraging and hunting, and the outcome of NHP contact. For each additional unit of edge density within the buffered area around a household, an individual was 1.01 times more likely to have experienced a NHP contact between 2011 and 2015 (Table 1). Participants who collected poles or participated in foraging and hunting within the core were more than twice as likely to have experienced a NHP contact event between 2011 and 2015 (Table 2). A model including edge density, pole collection, and foraging and hunting in core showed that all were significant explanatory variables for NHP contact (Table 3).

Discussion

Our results show that at the landscape level, there was nearly equivalent core gain (7% conversion of matrix to core) through reforestation within Kibale National Park as there has been gross deforestation (7% loss of core area) outside of the protected area between 2011 and 2015. Unprotected core patches proportionally experienced the most concentrated loss of core. Therefore, core area loss per patch may have relatively more impact on the ecology of the local NHP populations that reside in core patches compared to those living in the main Park. The increase in edge density of core patches may also make these areas more accessible to people, increasing the potential for physical overlap of humans and NHPs. The core area loss in core patches and increased edge density outside of the boundary of Kibale National Park are the result of increasing pressure from local communities whereas reforestation within the Park border is the result of both enforcement and a carbon sequestration reforestation program managed jointly by the Uganda Wildlife Authority and the organization Face the Future that has planted over 1.5 million trees.

The most significant result from our analysis is that local edge density is an explanatory variable for human-NHP contact ($p < 0.01$ in Model 1 and $p < 0.001$ in Model 3). The confidence interval does not cross 1, however, it is narrowly above 1 indicating that while significant, edge density for participants experiencing NHP contact and those not experiencing contact are similar at the population level. Edges are

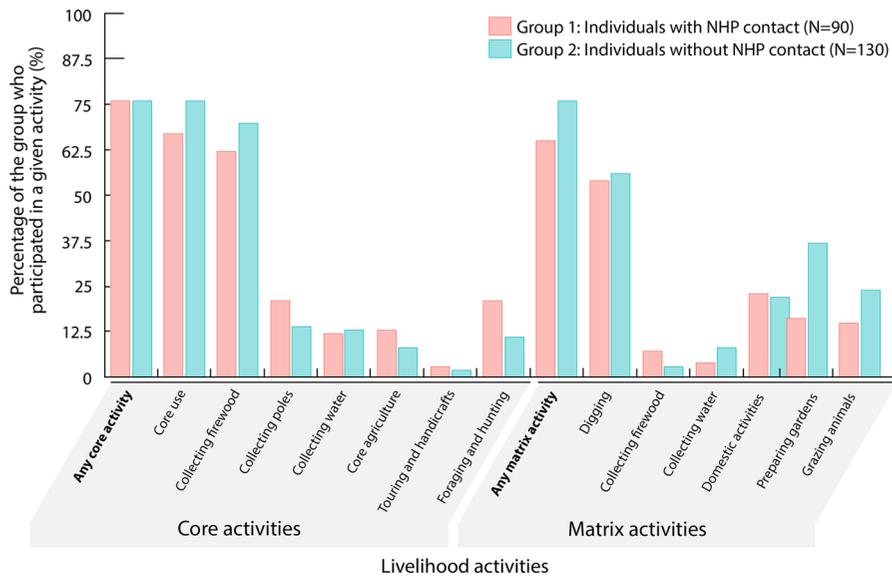


Fig. 5 Core and matrix activities: Survey data on livelihood behaviors of participants who experienced NHP contact compared to participants who did not experience NHP contact between 2011 and 2015 (N = 220)

Table 1 Model 1: Edge density and NHP contact (N = 220)

Independent variable	OR	Std. err.	P > z	95% CI
Edge density	1.01	0.00	0.01**	(1.00, 1.01)

**Significant at the 0.01 level

Table 2 Model 2: Selected core activities and NHP contact (N = 220)

Independent variable	OR	Std. err.	P > z	95% CI
Collecting poles	2.2	0.81	0.03*	(1.07, 4.53)
Foraging and hunting	2.3	0.87	0.03*	(1.07, 4.81)

*Significant at the 0.05 level

the conduit of interactions between species that live in core and species that live in matrix (Pellissier et al. 2017). If increased edge density explains increased likelihood of NHP contact, then continued loss of core may pose future risks of NHP exposure and higher potential for the spillover of infections from NHP to humans. This effect is likely to occur until the area of core patches decreases below the size that supports NHP populations and these animals no longer survive in this landscape.

Globally, approximately half of remaining core area is within 500 m of an edge shared with matrix, indicating that people may physically access most core

areas on this planet through an edge (Pfeifer et al. 2017). This empirical relationship from our study supports conceptual models of landscape change and interspecies contact events (Faust et al. 2018). The high edge density in the landscape around Kibale National Park indicates that much of the remaining core habitat is under the influence of matrix processes and that the abundance of many core species may continue to decrease through human-induced changes to the landscape. NHP species in this area of Uganda are already considered threatened. As core to matrix conversion continues, it is likely that core patches will disappear along with the NHP that currently live or forage in them, thus reducing their habitat to the boundaries of Kibale National Park and reducing buffered areas around the park itself.

Our data revealed a significant relationship between the livelihood activities of pole collection, foraging and hunting, and the likelihood of at least one contact event with at least one NHP. The confidence intervals for these explanatory variables for this regression model do not cross 1 and indicate that these activities increase the odds of NHP contact. According to local participants and literature on Ugandan forest resources, poles are created from larger diameter trees than firewood collection which is often from smaller timber debris. Since many species of NHPs in Kibale National Park spend time in larger trees, we

Table 3 Model 3: Edge density, selected core activities, and NHP contact (N = 220)

Independent variable	OR	Std. err.	P > z	95% CI
Intercept	0.21	0.08	0.00***	(0.10, 0.43)
Edge density	1.01	0.00	0.00***	(1.00, 1.01)
Collecting poles	2.17	0.82	0.04*	(1.04, 4.54)
Foraging and hunting	2.57	1.01	0.02*	(1.18, 5.57)

*Significant at the 0.05 level

***Significant at the 0.001 level

hypothesize that pole collection may correspond to participants entering areas of the core where NHPs spend time. Similarly, foraging for wild foods and hunting wild animals in the core are activities that take place in dense brush where participants have reported finding carcasses of deceased NHP. In the model combining landscape metrics and human behaviors (Model 3), edge density, pole collection, and foraging and hunting for food in the core remained significant independent variables. This result supports the explanatory power of both spatial and behavioral data in describing the likelihood of human contact with NHPs.

Previous studies have shown that individuals further from Kibale National Park place more pressure on core patches (Hartter 2010). This study did not reveal significant relationships between the spatial distribution of households and frequency of visits to core patches. Individuals living further than 290 m from the nearest core did not use of core for resources or services in the year preceding the survey, suggesting a possible maximum distance of travel for core resource collection. However, there is also no clear effect of distance from core on the probability of NHP contact below this threshold distance. We did not collect geographic information on where individuals were performing core activities beyond land classification in either core or matrix. Logistic regression models indicate that edge density, pole collection, and foraging and hunting are better explanatory variables for the likelihood of human-NHP contact compared to household distance from core or loss of core area between 2011 and 2015.

Limitations

Spatial analysis results presented here are valid under the assumption that NHP habitat was accurately

selected during classification, change detection, and the removal of core patches. For consistency, land cover change analysis was performed using satellite imagery from January of both 2011 and 2015. However, change detection across years may have been influenced by year-to-year variation in rainfall, climate, and corresponding vegetation attributes. During data collection, participants confirmed that NHPs lived in core areas near their households, but participants did not verify that all core patches included in our spatial analyses had NHPs. One of the most likely sources of error in NHP habitat selection is the presence of woodlots larger than 0.8 hectares planted near Kibale National Park, which would have been identified as core due to the difficulty of distinguishing woodlots from core. Our classification method omitted core if it did not meet the published size criteria for NHP residence or match spectral characteristics of intact core or confirmed core habitat, which may not be accurate for all NHP species. We did not explicitly measure core quality or the presence of particular fruiting trees that attract NHP groups, which may be good indicators of where NHPs are distributed across the landscape.

Contact locations that are self-reported and geolocated by participants are likely biased toward contact events that occurred at or near households because contact locations further from households were more difficult to visit and many participants were unwilling to take enumerators to these locations. While the core inside the park was expected to remain intact, agricultural lands outside of the park were modified by local residents during the study period. Nevertheless, this study included all core patches that met the specified criteria. There are a few reasons why some spatial factors that were anticipated to increase the likelihood of contact may not have been significantly explanatory of NHP contact. First, we used the

January 2015 image for spatial associations that does not correspond to the exact timing of all contact events. We attempted to control for land changes over time by restricting the analysis to the four year period bounded by our January 2011 and January 2015 images.

Another limitation of this study is that data on contact events between people and NHPs were collected by self-reporting, not observation. There are two primary issues with self-reporting, social undesirability bias and recall bias. Foraging and hunting are legal activities in the core fragments, however, they are illegal activities to conduct in Kibale National Park. Due to social undesirability bias, households close to Kibale National Park may be more likely to respond that they do not conduct activities in the Park compared to those further from the Park. This limitation to the study may be more severe for core activities such as hunting than activities like firewood collection due to the potentially severe repercussions of poaching in Kibale National Park.

Asking individuals to recall past events also poses opportunities for recall bias, particularly in the accuracy of a specific time frame. Studies have supported that individuals under-report past events particularly those outside of a recent past, often beyond a few weeks. However, the acuity of an event may modify this recommended recall window. Additionally, narrowing the window of recall may lead to a large loss of information, particularly with infrequent events (Clarke et al. 2008). A physical encounter with a NHP likely holds greater salience than other daily life events in an individual's memory. Studies have shown that while people under-recall the frequency of ordinary life events, people are more accurate in recalling potentially traumatic events (Lalande and Bonanno 2011). A future prospective study would provide an alternative study design that could remove this recall bias. However, the infrequency of contact events over an individual's lifetime in this geographic context makes this design less feasible for the temporal constraints of this study.

Participants provided information on livelihood activities and behaviors based on self-perception of frequency and time spent completing activities in the core and the matrix. Although an activity log of the previous week was collected to confirm the occurrence of activities recalled by each participant, these

activities were not observed or prospectively accounted. Each individual was represented once in the sample and therefore repetition or risk of multiple NHP contacts were not included in our models. Reduction of sample size to reduce spatial autocorrelation may have removed observations that would modify the currently observed relationships. However, selection of the subset was not biased and we expect that the sub-sample is representative of the entire study population.

Conclusion

Physical contact between humans and nonhuman primates can result in physical harm, transmission of infectious diseases, and may increase tension between populations of humans and nonhuman primates in rural populations living near protected forests in Africa. This study points to the importance of particular local landscape metrics and livelihood activities in core that significantly increase the likelihood of human contact with a nonhuman primate. This study provides empirical evidence that links increased edge density, pole collection, and hunting and foraging for food in core to an individual's increased likelihood of experiencing a human-nonhuman primate contact event. Collecting spatially explicit data on land use and human behaviors is crucial for understanding the proximate ecological and social drivers of contact between humans and nonhuman primates. Improved prediction of the likelihood of physical interactions between humans and nonhuman primates is key to assessing the risk of zoonotic emergence in rapidly changing landscapes across the globe.

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Data availability The data generated and analyzed during the current study are not publicly available due to the sensitive nature of geographically explicit data on individual behaviors and personal health information of the survey respondents. Sharing of composite data or future collaborative projects may be possible from the corresponding author upon reasonable request.

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