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ORIGINAL PAPER

Abundance and spatial distribution of the main food species for mountain gorillas in the Virunga Massif, Rwanda

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Abstract

The conservation of endangered species can benefit from a clear understanding of the quantity and distribution of their main foods. The population of mountain gorillas (*Gorilla beringei beringei*) living in the Virunga Massif of Rwanda, Uganda, and Democratic Republic of Congo has doubled in size since the 1980s, due to success in conservation efforts in and around their habitat. However, this increase in population size along with pressures on gorilla habitat raises concerns about spatial-temporal changes in the gorillas' food plants. This study modelled the abundance and distribution of gorilla food species in the Virunga Massif. A total of 1050 vegetation recordings were collected on five plant species that are known to be frequently consumed by gorillas in one region of the Virungas, the Karisoke area. Two types of datasets collected along vegetation zones were combined: one with plant abundance expressed with Braun-Blanquet scores; and the other with abundance expressed as biomass. Moreover, ecological characteristics of locations where these species occur were extracted from satellite imagery. Analysis of variance and linear regression models were used to examine relationships between food species abundances and predictor variables. Subsequently, maps for the food species were created using boosted regression trees (BRTs). The abundance of species differed across vegetation zones, and the differences were statistically significant among vegetation zones with enough species observations. The accuracy of the BRTs indicated greater than random predictions ($AUC > 0.65$). This study shows the suitable areas for these gorilla food species and relevant ecological variables determining their distribution. The results provide insights into habitat occupancy by mountain gorillas, and help to design a baseline for monitoring changes in the abundance of gorilla food species under changing climate and anthropogenic pressure.

Keywords *Gorilla beringei beringei* · Main food · Species distribution modelling · Virunga Massif

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Introduction

The conservation of flagship species generates particular attention when these species have limited habitat (Williamson and Fawcett 2008). Continuous monitoring of food availability is a key component to understand the spatial and temporal dynamics of food under changing environmental conditions in the species' habitat (McGahey et al. 2013). Mountain gorillas (*Gorilla beringei beringei*) are classified as "Endangered" on the IUCN Red List (previously "Critically Endangered") (Hickey et al. 2018; IUCN 2019); and have a highly restricted geographic distribution, confined to Bwindi Impenetrable National Park, Uganda and the Virunga Massif shared among Rwanda, Uganda and the Democratic Republic of Congo (DRC). In the Virungas, the highest density of gorillas occurs at an elevation range of 2500–3500 m (van Gils and Kayijamahe 2010), which corresponds to vegetation zones that contain high amounts of food for the gorillas (Plumptre 1991; McNeilage 1995). Mountain gorillas in the Virungas are predominantly herbivorous (Watts 1984; Wright et al. 2015) with a diet consisting mainly of leaves and stems of ground plants. Fruits liable to be consumed by gorillas are rare in the Virungas.

In the early 1970s, a census in the Virunga Massif showed a decline in the gorilla population from an estimated 450 down to about 275 individuals. The main cause of the population decline was habitat conversion into agriculture, settlements and cattle grazing that occurred between 1958 and 1973, especially on the Rwandan side (Spinage 1972). Conservation efforts beginning in the 1980s led to an increase of the Virunga mountain gorilla population from 250 in the mid-1980s to a minimum estimate of 480 gorillas in 2010 (Gray et al. 2013). Political unrest and violence characterized the East African region from 1991 to 1998 (Plumptre and Williamson 2001; Kalpers et al. 2003) but research and conservation activities have been re-established and reinvigorated since then and the mountain gorilla population continues to increase (Gray et al. 2013; Robbins et al. 2011). The most recent gorilla census in the Virungas showed an increase from 480 individuals in 2010 to 604 individuals in 2015–2016 (Hickey et al. 2018; Granjon et al. 2019). The increase in the size of the mountain gorilla population has implications for the abundance and availability of the food species consumed by the gorillas (Grueter et al. 2013). Knowing where food species occur throughout the Virunga Massif and how their abundance depends on environmental factors provides relevant information for monitoring the resource base of the gorillas.

In the Karisoke area of the Virunga Massif (Fig. 1), the mountain gorilla diet consists of 54 different plant species, but six species constitute the majority (87%) of their diet (Watts 1984; Table 1). Mountain gorillas at lower elevation in the Virungas (mainly on the DRC side) consume some of the same species but at different frequency as well as other species that do not occur in the Karisoke area (Goodall 1977; McNeilage 2001). Studies have shown that plants favoured by the gorillas are high in protein and relatively low in fibre (Watts 1984; Rothman et al. 2007). Mountain gorillas are more likely to range in areas with higher abundance of preferred food items (Vedder 1984; Seiler et al. 2017; Watts 1998).

Plant consumption exceeding production by the increasing number of gorillas may result in food shortages in the long run. Furthermore, climate change is predicted to affect East African tropical montane rainforests including the habitat of mountain gorillas (Foster 2001). Under global warming conditions, plant species tend to shift to higher latitudes and elevations or migrate within the extent of their current range (Hermes et al. 2018; Chen et al. 2009). Effects of climatic change may include changes in the amount and distribution of available food items for the mountain gorillas (Belfiore et al. 2015). Assuming that

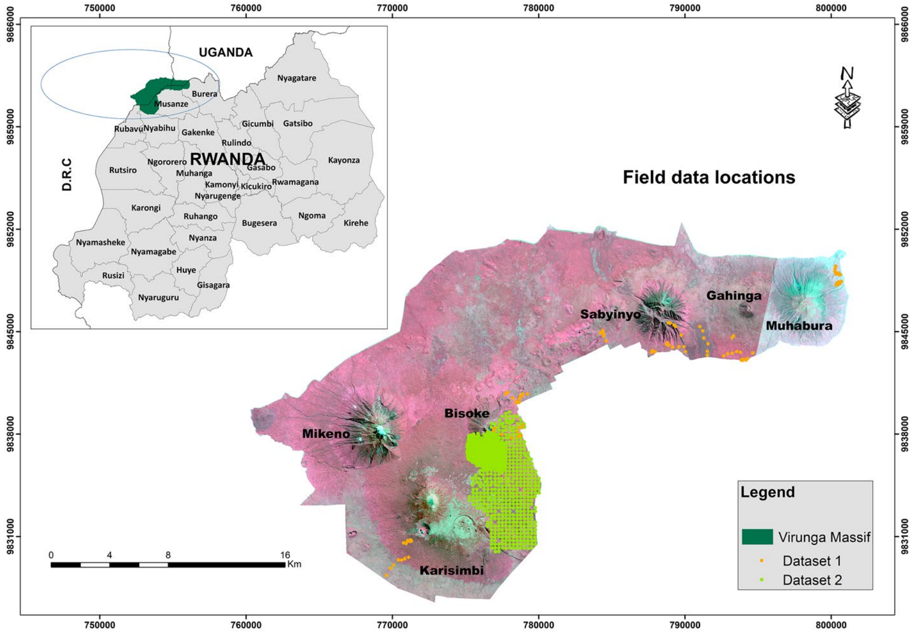

Fig. 1 The extent of Virunga Massif and distribution of field data. Dataset 1 was collected by the first author, while Dataset 2 was existing (Grueter et al. 2013). Dataset 2 covers the area used by gorillas monitored by Karisoke Research Centre. The name for each of the six volcanoes is added in black bold font

the mid-elevation forest has already started shifting uphill because of climate change and agricultural encroachment of gorilla habitat (Plumptre and Williamson 2001; Belfiore et al. 2015), the mountain gorillas may change their dietary and ranging patterns. Assessments of density, abundance, and biomass of gorilla dietary items have been carried out along an altitudinal gradient encompassing several vegetation zones in the Karisoke area (Plumptre 1991; Grueter et al. 2013). Interestingly, Grueter et al. (2013) found a decline in abundance of two among the five most commonly consumed foods in the Karisoke area, and an increase in the other three between 1989 and 2010. However, only limited assessments of gorilla foods abundance have been conducted in other regions of the Virunga Massif (e.g. McNeilage 1995). Additionally, very little is known about the ecological conditions that determine the occurrence of the plant species consumed by the gorillas in the Virunga Massif.

Advancements of statistical techniques together with Geographical Information Systems (GIS) and Remote Sensing tools enable scientists to relate species occurrence data at known locations with ecological characteristics of those locations. Previous studies have demonstrated how these methods can provide “probability of occurrence” maps and identify the best predictors to describe the occurrence of a species (Elith and Leathwick 2009; Duque-Lazo et al. 2016; Guisan and Zimmermann 2000). Modelling the current and future distribution of habitat suitable for mountain gorillas under climate change scenarios has already been carried out (Belfiore et al. 2015; van Gils and Kayijamahe 2010). Both studies combined gorilla presence data with environmental variables using the MaxEnt algorithm (Phillips et al. 2006). These models provide useful predictions for the present and

Table 1 Six plant species frequently consumed by the mountain gorillas in the Karisoke area of the Virungas

Species name	Family	Ecology	Part eaten	Dietary importance (%)
Galium spp.	Rubiaceae	– Vine – Can root under closed canopies, and gets light by climbing up on the stems of trees and shrubs – Altitude: 2800–3600 m	Whole	27.0
Carduus nyassanus (Thistle)	Asteraceae	– Herb – Prefers moist soil conditions – Altitude: 2800–3200 m	Lv, Fl, St, Rt	20.1
Afroligusticum linderi (Wild celery)	Apiaceae	– Herb – Adapted to areas with rich understory (open forest canopies) and moist environments – Altitude: 2800–3200 m	St, Rt	18.7
Yushania alpina (Bamboo)	Poaceae	Shrub	Shoots, Lv	14.8
Rubus spp. (Blackberry)	Rosaceae	– Shrub – Dominate forest gaps and competitively inhibit the recruitment of other species – Can survive in conditions of low soil nutrients – Altitude: 3000–3600 m	Lv, Fr, St	3.6
Laportea alatipes (Nettles)	Urticaceae	– Herb – Grows on nutrient -rich soils – Cannot survive at very low temperatures – Altitude: 2800–3200 m	Lv, St, Rt	2.9

Plants are listed based on a descending order of their dietary importance (Fossey 1974; Watts 1984; Grueter et al. 2013). Bamboo was not targeted with the mapping of food species in this study

Lv Leaves, *St* Stem, *Rt* Roots, *Bk* Bark, *Pi* Pith, *Infl* Inflorescence, *Fl* Flower, *Fr* Fruit future suitable habitat for mountain gorillas. However, relevant input in such models is the distribution of the food species preferred by mountain gorillas and these have not been modelled yet. It would be useful to know to what extent there is overlap between the distribution of food species and the distribution of gorillas. It is also important to find out if the link between food presence and gorilla presence shows spatial differences within the entire Virunga Massif.

The first aim of this paper is to relate gorilla food species abundance and biomass data to ecological and topographic characteristics of the locations where they are found. The second aim is to generate spatial distribution maps with presence/absence data, using a distribution modelling approach and GIS. The five targeted plants constitute the main dietary items for the gorillas ranging in the area monitored by the Karisoke Research Centre. Those species are: *Galium* spp., thistle (*Carduus nyassanus)*, wild celery (accepted name: *Afroligusticum linderi*, synonym: *Peucedanum linderi)*, nettle (*Laportea alatipes)*, and blackberry (*Rubus* spp.). Since these species grow mainly below-canopy and cannot directly be detected by remote sensing, they were mapped indirectly using “Boosted Regression Trees (BRTs)”. The species distribution maps along with variables determining their occurrences are key to understanding the current gorilla habitat occupancy and give room for further modelling of changes in the occurrence of gorilla food species.

Methods

Study area

The Virunga Massif (between 1°20′0″ and 1°40′0″ South and 29°20′0″ and 29°40′0″ East; nearly 454 km^2; Fig. 1) is a montane rainforest experiencing an annual rainfall of approximately 2,000 mm (Plumptre 1991), with a distinct dry season from June to August. The temperature decreases by 5–6 °C every 1000 m of increasing elevation whereas the wind speed increases with altitude (Belfiore et al. 2015; Tuyisingize 2010). The soils in the Virunga Massif are fertile and of volcanic origin, but they vary in composition from one area to another. They are in the category of Andosols and Andic soils with a black colour. In the wetlands, fine alluvial peat formation takes place. Furthermore, soils are generally characterized by high moisture, rich organic matter content, high pH levels and a high permeability (Hitimana et al. 2006).

The Virunga Massif is characterized by nine different vegetation zones (McNeilage 1995); Table 2) four of which have been identified as important for mountain gorillas in the Karisoke area (Weber and Vedder 1983): bamboo, the *Hagenia-Hypericum* zone, the herbaceous zone and the brush-ridge zone. Mountain gorillas consume both bamboo leaves and shoots, but the latter are a favorite and seasonally available in the park during the rainy months of March to May and end-September to mid-December (Vedder 1984; Grueter et al. 2014). Previous studies described *Hagenia-Hypericum* as a vegetation zone that dominates the western part of the Virungas and includes trees with open canopies allowing herbaceous species to proliferate on the forest floor (Weber and Vedder 1983; Fossey 1974). The brush-ridge and herbaceous vegetation zones are dominated by tall herbs and scattered shrubs or trees (Plumptre 1991; Grueter et al. 2013).

Although forests dominated by *Hagenia abyssinica* and *Hypericum revolutum* overlap spatially in the Virunga Massif, in some areas they can be distinguished from each other on the basis of dominance between the two species. The *Hypericum* shrubs dominate the

Table 2 Vegetation zones in the Virunga Massif (Owiunji et al. 2005; Fossey 1974; McNeilage 1995; REMA 2011)

Vegetation zone	Characteristics	Land cover types description	Altitude (in meters a.s.l)
Alpine	Grasses, mosses and lichens, *Dendrosenecio*, giant *Lobelia,* It occupies 6 per cent of the park	Sparse vegetation area including transitional stages from sub-alpine zones to areas where most forms of plant life are extremely limited	Above 3600
Sub-alpine	*Philippia johnstonii*, *Erica arborea*, Giant *Lobelia* Giant *Scenecio*	*Usnea* lichens present, Grasses	3200–3600
Brush ridge	Occurs on volcano slopes, forms the edges of deep ravines	Certain shrubs The main shrub species are *Rubus kirungensis* and *Rubus runssorensis*	3000–3300
Herbaceous	Consists of dense tall herbs with no tree cover	Rich in mountain gorilla foods	2800–3300
Hagenia-Hypericum forest	*Hypericum revolutum*, *Hypericum absi*, *Hagenia abyssinica*	*Hagenia abyssinica* trees (height between 15 and 24 m) and *Hypericum revolutum* (saplings to full-grown tree with a height up to 15 m)	2800–3200
Bamboo	*Yushania alpina*	Closed canopies (when not disturbed), Covers 35% of the park	2500–2800
Mixed forest	Moist semi-deciduous forests with broad leaves	*Dombeya goetzenii* (moist montane forest with *Mimulopsis* shrub), Tall trees (height > 20 m) with broad leaves, Large part cleared for agriculture, Occupies 20% of the park	1600–2500
Grassland	Areas dominated by grass	Meadow and savannah	Occurs at various altitudes
Swamp	Marshy or boggy areas	In the saddles between volcanoes	Occurs at various altitudes

Vegetation belts are categorised starting from the volcanoes' summits moderate to high elevations where dense closed canopies are absent; they support a variety of vines that are eaten by the gorillas. The *Hagenia abyssinica* giant trees with closed canopies are found on the slopes of Karisimbi, Mikeno and the saddle area in between the two volcanoes and Bisoke (Dondeyne et al. 1993).

Data collection

Data were collected on gorilla food species abundance and biomass as well as the ecological characteristics of the locations where these species occur were recorded. Five gorilla food species were targeted in this study: *Galium* spp., *Carduus nyassanus*, *Afroligusticum linderi* (accepted name for wild celery), *Rubus* spp., and *Laportea alatipes*. There are in total five species of *Rubus* in the Virunga Massif (Owiunji et al. 2005): *Rubus runssorensis*, *Rubus kirungensis*, *Rubus apelatus*, *Rubus steudneri* and *Rubus pinnatus*, all combined into *Rubus* spp. in this study. Owiunji et al. (2005) also listed four species of *Galium* in the Virungas: *Galium chloroionanthum*, *Galium simense*, *Galium aparinoides* and *Galium thunbergianum,* all combined into *Galium* spp. in this paper. They were combined because they are difficult to tell apart and there is evidence that the gorillas feed on all of them.

Two different and complementary datasets on vegetation were used in this study. The first dataset was collected during September–October 2015 in Rwanda (Dataset 1), consisting of 94 sample plots that are spread across the Rwandan part of the Virunga Massif. The second dataset (Dataset 2; from Grueter et al. 2013) comprises 956 sample plots in a very dense sampling grid, however, across a smaller portion of the park (Fig. 1). Dataset 1 was collected as part of an MSc research over a rather short time period and therefore is relatively small, and without using grid sampling as in Dataset 2. Therefore Dataset 1 on its own did not allow running more robust and complete analysis of gorilla food species abundances and distribution. It contains data on abundance of gorilla food species according to the Braun-Blanquet scale (Wikum and Shanholtzer 1978). Dataset 2 contains abundance of gorilla food species expressed as biomass (Grueter et al. 2013). Sampling for Dataset 2 was done in circular plots of different sizes; 1 m^2 plots for herbs and vines, and 5 m^2 plots for shrubs.

For Dataset 1, circular plots with a radius of 12.6 m were used, resulting in an overall plot size of 500 m^2. This plot size is less vulnerable to errors and characterizes the vegetation in a dense forest (Bergseng et al. 2015). Due to the topography, dense vegetation in the area, and limited time for fieldwork, purely random or systematic sampling strategies were difficult to apply and a more practical approach was used. At each 300 m trail distance and 100 m buffer (distance perpendicular to the trail), a sample plot was taken alternatively at the left and right side of the trail (see Online Resource 1). The buffer was used to avoid effects of proximity to the trail such as human disturbances. Nevertheless, the sampled vegetation plots in Dataset 1 are not necessarily representative of the forest type at each elevation class, mainly because over decades, humans have modified areas close to the trail by collecting resources from the forest. A slope correction was applied where necessary. Within these plots, smaller subplots were created to collect different variables:

- 500 m^2: diameter at the breast height (DBH), tree height, dominant species, stem density of trees taller than 5 m and canopy cover (as percentage),
- 5 m^2: dominant species of shrubs (height between 50 cm and 5 m),
- 1 m^2: for herbs; species abundance was recorded using the Braun-Blanquet approach which estimates plant cover from the vertical plant shoot-area projection as a percent-

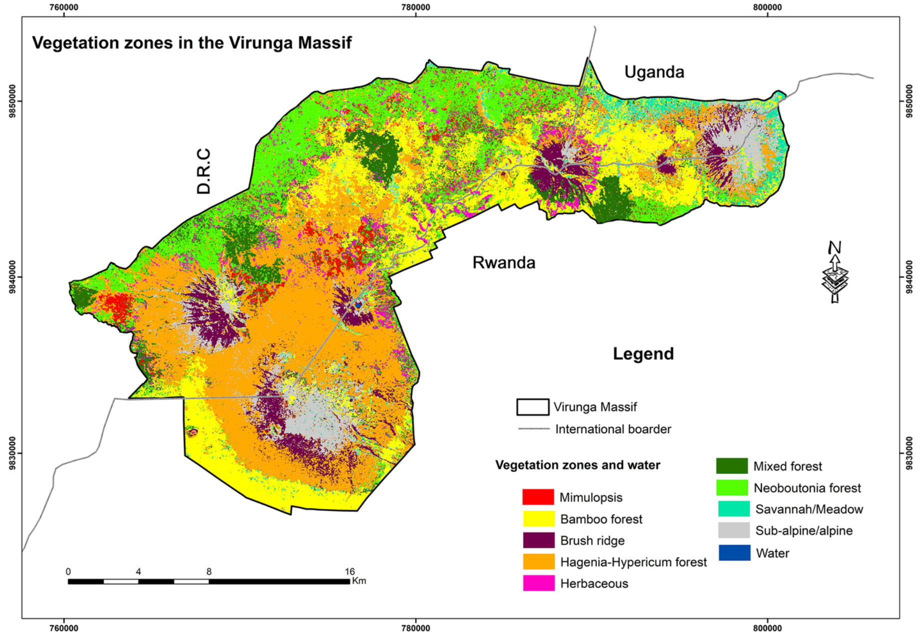

Fig. 2 Vegetation zones of the Virunga Massif. The map is based on the classified ASTER imageries for the years 2005 and 2006. Each of these imageries covers a section of the Virunga, and was classified separately

age of quadrat area (Wikum and Shanholtzer 1978). Scores representing gorilla food species abundance were then assigned. In each 1 m^2 subplot, one gorilla food species or in some cases a maximum of three species could be found in the same subplot. The assigned scores are: 0.5 (cover < 1%), 1 (cover 1–5%), 2 (cover 6–25%), 3 (cover 26–50%), 4 (cover 51–75%), 5 (cover 76–100%) (Ellenberg and Mueller-Dombois 1974).

Remote sensing variables

Bands from two ASTER scenes (see Online Resource 2), were all resampled to 15 m resolution and classified using the maximum likelihood algorithm into nine vegetation zones (Fig. 2). For this supervised classification, 732 observations (70% of the total observations) were used and an accuracy assessment was performed based on the remaining 318 observations (30% of the total observations). The overall accuracy was 80% with a kappa (κ) of 0.688 and 0.685 for the 2006 and 2005 imagery respectively. It was difficult to distinguish between the reflectance of the sub-alpine and the alpine vegetation zones and this affected the overall image classification accuracy. Therefore, the sub-alpine and alpine zones were combined into one class. The two ASTER scenes were classified separately and then mosaicked to produce a vegetation map of the Virunga Massif (Fig. 2).

Based on the ASTER Digital Elevation Model (DEM) with 15 m resolution (after resampling), five topographic variables (Table 3) were derived and values for each field observation site were extracted. The slope aspect is a circular variable which was transformed into eastness and northness using respectively the sine and cosine functions to obtain linear

Table 3 Predictor variables and their connection with gorilla food abundance (only herbaceous plant species) in the Virunga Massif

Variable name	Proxy for food abundance	Expected effect on food abundance	Units (range)	Processing steps	Type
Elevation	Vegetation zone, amount of temperature and rainfall	Low abundance in high and low elevation (i.e. >3600 m and <2400 m)	Meters	From the ASTER imagery package	Continuous
Slope steepness	Soil nutrient, plant growth	High abundance in either gentle or steep slopes	Degrees (0° to 90°)	From the DEM	Continuous
Solar radiation	Amount of light	High abundance of vines when the incoming insolation is also high	Watts-h/m^2	From the DEM	Continuous
Eastness	Soil moisture content, amount of heat (sunshine)	High abundance of some species on the west-facing slopes	West or east (-1 or $+1$)	Map algebra: Sine of the aspect (in absolute radians)	Continuous
Northness	Soil moisture content, amount of heat	Slight preference of species to either the north or south-facing slopes; mainly because the Virungas is close to the equator	South or North (-1 or $+1$)	Map algebra: Cosine of the aspect (in absolute radians)	Continuous
Stem density	Amount of light reaching the ground	Low abundance when there are many trees. Can be favourable for the growth of vines	Number of trees per plot	Counted in the field	Continuous
Canopy cover	Amount of light reaching the ground, abundance of understory plant species	Low food species abundance in very dense forest with closed canopies	Percentage (%)	Measured in the field using a densiometer	Continuous
DBH	Forest age, soil nutrient	Low abundance in dense forest with big trees. Tree falls allow the growth of some herbaceous plants and vines	Meters (m)	Measured in the field using a diameter tape	Continuous
Tree height	Space for vines to climb	Low abundance when trees are tall and in a dense forest	Meters (m)	Measured in the field using a laser distance meter	
Vegetation zone	Canopy cover, amount of light reaching the ground, competition for nutrient	High abundance in vegetation zones with open canopies	–	Based on literature, altitude and dominant species	Categorical

Only five variables were extracted from the ASTER's DEM: elevation, slope steepness, eastness, northness, solar radiation

DEM Digital elevation model, *DBH* Diameter at the breast height, *ASTER* Advanced spaceborn thermal emissions and reflection radiometer gradients that indicate how much a slope is facing east and north (Piedallu and Gégout 2008).

Multiple linear regression was carried out between estimates of the canopy cover measured in the field and the calculated ASTER band reflectance values. With this model, a continuous canopy cover map of the Virunga Massif was created (see Online Resource 3). The data on canopy cover was part of Dataset 1 and only measured on the Rwandan side, but the analysis was extrapolated to the whole Virungas.

Statistical analysis

Differences in species abundance between vegetation zones

To check whether the samples come from a normally distributed and homogenous population, the Shapiro-Wilk and Levene's tests were applied, respectively. One-way Analysis of Variance (ANOVA) was used to determine if there is a significant difference in the abundance of gorilla food species among the different vegetation zones. The ANOVA test appears to be robust to minor violations of normality assumption (Blanca et al. 2017; Quinn and Keough 2002). Because population variances were not equivalent, a Games-Howell post hoc test was used for pairwise comparison when a significant difference was detected (Quinn and Keough 2002). Analyses were run separately for the different datasets because Dataset 1 included abundance and Dataset 2 was comprised of biomass values. Additionally, two vegetation zones (*Neoboutonia* and *Mimulopsis*) were not sampled in Dataset 2. This analysis was not performed for *Laportea alatipes* for Dataset 1 because of too few observations in some vegetation zones.

Site characteristics relevant for food species

Explanatory variables included field measured and remote sensing based variables that potentially contribute to explaining variations in the abundances and distribution of gorilla food species (Table 3). These variables were first tested for multicollinearity before including them in a multiple linear regression model. Variables included in the regression model were selected based on Variance Inflation Factors (VIF) < 10 and insignificant predictors were removed from the model in a stepwise fashion (Field 2009; Quinn and Keough 2002). The response variable was abundance (Dataset 1) or biomass (Dataset 2) of gorilla food species. Both abundance and biomass were continuous variables.

Species distribution modelling

Boosted Regression Trees (BRTs) were used to model the gorilla food species distribution. Studies have demonstrated that BRTs generally perform better than traditional modelling techniques such as Generalized Linear Model (GLM) and Generalized Additive Model (GAM) (Albeare 2009; Leathwick et al. 2006). The BRT model was selected because it is advantageous in handling different types of predictor variables, relevant for fitting complex non-linear relationships, and settles effects of missing data and collinearity between predictors (Elith et al. 2008).

BRT is a machine learning algorithm that improves the accuracy of a single regression tree model through fitting several models and combining them for prediction. The BRT model consists of two components: regression trees and boosting (De'ath and Fabricius 2013). Model fitting, training, validation and plotting maps was done in R 3.1.2 software using the gbm package (R Development Core Team 2014); ArcGIS version 10.3 was used to create the maps.

The gorilla food species abundance and biomass data were converted into absence/presence data for every species recorded. With the species distribution modelling, abundance could not be used as a response variable because not all points had matching abundances for the combined datasets (which is required for transforming biomass into abundance). All 1036 observations (80 for Dataset 1 and 956 for Dataset 2) were used for each gorilla food species to fit the BRT model. The eastern part of the Virungas (around Muhabura volcano) was not considered, given that the most recent image (ASTER 2006), used for extracting remote sensing variables, did not cover that region. For each food species, the dataset was split randomly into 70% for training and 30% for validation (Liu et al. 2011). The BRT model was parameterized with a learning rate of 0.001, a tree complexity of 5 and a bag fraction of 0.5 (Elith and Leathwick 2009).

Three complementary measures of model accuracy were used: the Area Under the Curve (AUC), the True Skill Statistic (TSS), and the percentage explained deviance (D^2). The AUC measures the ability of a model to discriminate between sites where a species is present, versus sites where a species is absent (Hanley and McNeil 1982). The AUC values range from 0.5 to 1, where a score of 1 indicates a perfect model discrimination capacity; a score of 0.5 implies predictive discrimination that is no better than a random guess. The TSS ranges from -1 to $+1$; where $+1$ indicates a perfect agreement, and a value of -1 shows a perfect inverse prediction i.e. predicted presences are absences and vice versa (Elith and Leathwick 2009). The percentage deviance explained by the model acts as a pseudo R-square (De'ath 2007). The threshold at which Kappa would be maximum was selected (Liu et al. 2013) before plotting species distribution maps in R software. The BRT's resulted in maps that indicate ([0–1]) the probability of finding a species in a certain area. Since the species observations were collected on the Rwandan side only, predicting species occurrences on the DRC and Uganda sides of the Virunga Massif should be regarded as extrapolations.

Results

Food species abundance among vegetation zones

For Dataset 1, none of the gorilla food species showed a statistically significant difference in abundance between vegetation zones (Fig. 3), which is very likely caused by the relative small sample size and rather few species observations in each of the vegetation zones. Nevertheless, both *Galium* spp. and *Rubus* spp. seem to occur in relative high abundances in the brush ridge vegetation zone.

For Dataset 2, significant differences in abundance (expressed as biomass) between vegetation zones were found. For instance, significant differences in biomass for *Galium* spp. were found between brush ridge and meadow, between meadow and herbaceous, between *Hagenia*-*Hypericum* and herbaceous and between brush ridge and *Hagenia*-*Hypericum* (Fig. 4).

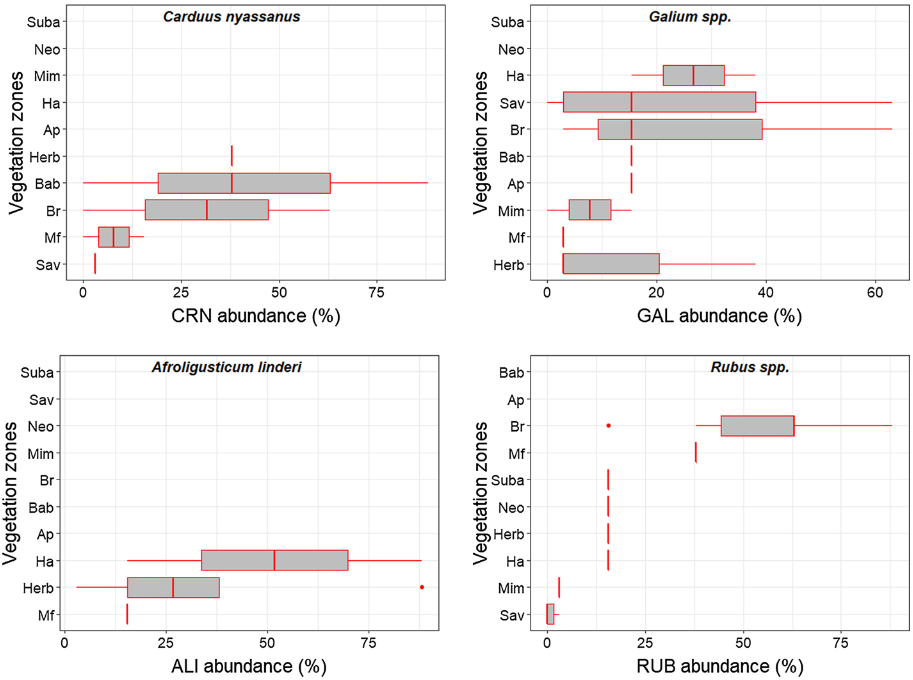

Fig. 3 The abundance (in %) of mountain gorilla food species in different vegetation zones (Dataset 1). The boxplots are arranged by increasing order of the means. There was no statistically significant difference between pairs of vegetation zones (significance treshold at $p < 0.05$). *Ap* Alpine, *Bab* Bamboo, *Br* Brush ridge, *Ha Hagenia-Hypericum*, *Herb* Herbaceous, *Mf* mixed forest, *Mim Mimulopsis*, *Neo Neoboutonia*, *Sav* Savannah/meadow, *Suba* Sub-alpine vegetation zones. *CRN Carduus nyassanus*, *GAL Galium* spp., *LAP Laportea alatipes*, *ALI Afroligusticum linderi*, *RUB Rubus* spp.

Relatively high amounts of biomass for *Galium* spp. were observed in the herbaceous, *Hagenia-Hypericum*, brush ridge, alpine and sub-alpine vegetation zones. In contrast, low values of *Galium* spp. biomass were found in the bamboo and meadow vegetation zones. *Carduus nyassanus* was observed in only five vegetation zones, with relatively high biomass in the brush ridge, the *Hagenia-Hypericum* and the herbaceous zone.

Rubus spp. was found in all vegetation zones, although there were significant differences in biomass (Fig. 4). High biomass values of *Rubus* spp. were found in the brush ridge, sub-alpine and alpine vegetation zones. *Afroligusticum linderi* was found in only three vegetation zones, without significant differences in biomass between these vegetation zones. *Laportea alatipes* biomass was observed in five different vegetation zones, but also no significant differences in its biomass were found between vegetation zones (Fig. 4).

Site characteristics relevant for food species

The abundance or biomass of *Galium* spp. and *Rubus* spp. increased with elevation in analysis of both datasets. For Dataset 1, only *Galium* spp. and *Rubus* spp. had significant regression equations (*Galium* spp.: $F_{2,75} = 9.18$; $R^2 = 0.19$; *Rubus* spp.: $F_{4,73} = 8.059$; $R^2 = 0.30$). In contrast, for Dataset 2 all regression models were significant ($p < 0.05$).

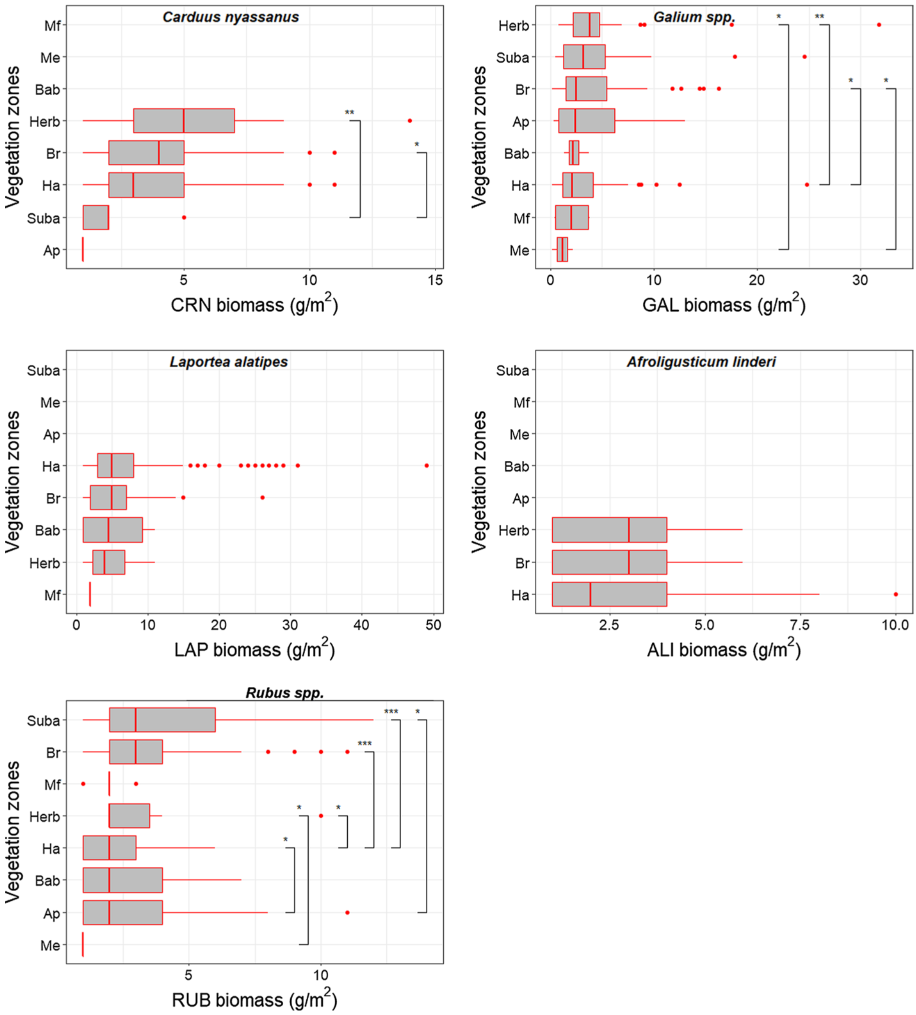

Fig. 4 Mountain gorilla food species biomass (in g/m^2) in different vegetation zones (Dataset 2). The boxplots are arranged by increasing order of the means. Pairwise differences are indicated by asterisks. Significance codes: "*"0.05; "**"0.01; "***"0.001. *Ap* Alpine, *Bab* Bamboo, *Br* Brush ridge, *Ha Hagenia-Hypericum*, *Herb* Herbaceous, *Me* Meadow, *Mf* Mixed forest, *Suba* Sub-alpine vegetation zones. *CRN Carduus nyassanus*, *GAL Galium* spp., *LAP Laportea alatipes*, *ALI Afroligusticum linderi*, *RUB Rubus* spp.

However, a low variance ($R^2 < 0.15$) was explained by the models (Table 4). For Dataset 2, *Afroligusticum linderi* and *Laportea alatipes* biomass decrease with increased elevations.

Mapping the distribution of food species

Boosted Regression Tree (BRT) models for four species showed predictions with an AUC > 0.65, while one species (*Galium* spp.) had lower accuracies (AUC = 0.65; Table 5). The highest discrimination ability was observed for *Laportea alatipes*, and the lowest for *Galium* spp.

Table 4 Relationship between gorilla food species abundance/biomass (response variable) and forest structure characteristics together with topography variables (explanatory variables)

Gorilla food species	Dataset 1			Dataset 2		
	Coefficients	Estimate	F and R^2	Coefficients	Estimate	F and R^2
GAL	Intercept	**−20.98***	$F_{2,75}=9.18$	Intercept	−2.47	$F_{4,951}=3.99$
	Elevation	**0.008****	$R^2=0.190$	Elevation	**0.001***	$R^2=0.016$
	Eastness	**−3.09***		HAG	**−0.31***	
				Slope	0.013	
CRN	Intercept	**5.49****	$F_{2,75}=2.23$	Intercept	**0.687*****	$F_{3,952}=4.952$
	Eastness	−3.32	$R^2=0.056$	Eastness	**−0.27****	$R^2=0.0145$
	HT	−0.31		Slope	**0.013***	
				HAG	−0.17	
ALI	Intercept	**8.392****	$F_{1,76}=3.88$	Intercept	**1.757****	$F_{3,952}=4.007$
	CC	−0.11	$R^2=0.048$	Elevation	**−0.0004****	$R^2=0.0124$
				Northness	−0.083	
RUB	Intercept	**−59.00*****	$F_{4,73}=8.059$	Intercept	**−8.891*****	$F_{5,950}=21.58$
	Elevation	**0.021*****	$R^2=0.306$	Elevation	**0.003*****	$R^2=0.102$
	HT	0.315		HYR	**0.117****	
	Eastness	−3.68		Eastness	0.164	
LAP	Intercept	**0.497***	$F_{2,75}=2.173$	Intercept	**19.276*****	$F_{3,952}=22.36$
	Northness	0.554	$R_2=0.054$	Elevation	**−0.005*****	$R^2=0.065$
	Eastness	−0.43		Eastness	**−0.317****	
				HYR	**−0.317****	

For both datasets, only coefficients retained after a stepwise regression are presented. The significant values are in bold. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05. CC: canopy cover; HT: tree height; HAG/HYR: *Hagenia/Hypericum* tree densities (number of stems/m2). GAL, CRN, ALI, RUB, LAP stand for *Galium* spp., *Carduus nyassanus*, *Afroligusticum linderi*, *Rubus* spp. and *Laportea alatipes* biomass or abundance

Table 5 BRT model performance for each of the five mountain gorilla food species

Gorilla food species	Nt	MaxKappa	Sens.	Sens. sd.	Spec.	Spec. sd.	TSS	AUC	AUC sd.	D^2
RUB	3250	0.37	0.61	0.047	0.84	0.024	0.45	0.78	0.028	0.31
GAL	2150	0.34	0.45	0.051	0.79	0.026	0.24	0.65	0.034	0.17
CRN	2050	0.30	0.53	0.056	0.83	0.023	0.36	0.77	0.028	0.21
ALI	1300	0.13	0.53	0.090	0.81	0.023	0.34	0.72	0.051	0.18
LAP	2700	0.41	0.71	0.043	0.76	0.030	0.47	0.80	0.025	0.32

The model accuracy was measured based on the TSS, AUC and D^2

Nt number of trees from the boosted regression tree model (BRT), *sd* standard deviation, D^2 percentage explained deviance (pseudo-R-square), *AUC* (validation) area under the ROC curve, *Sens* sensitivity, *Spec* specificity, *TSS* true skill statistic, *RUB Rubus* spp., *GAL Galium* spp., *CRN Carduus nyassanus*, *ALI Afroligusticum linderi*, *LAP Laportea alatipes*

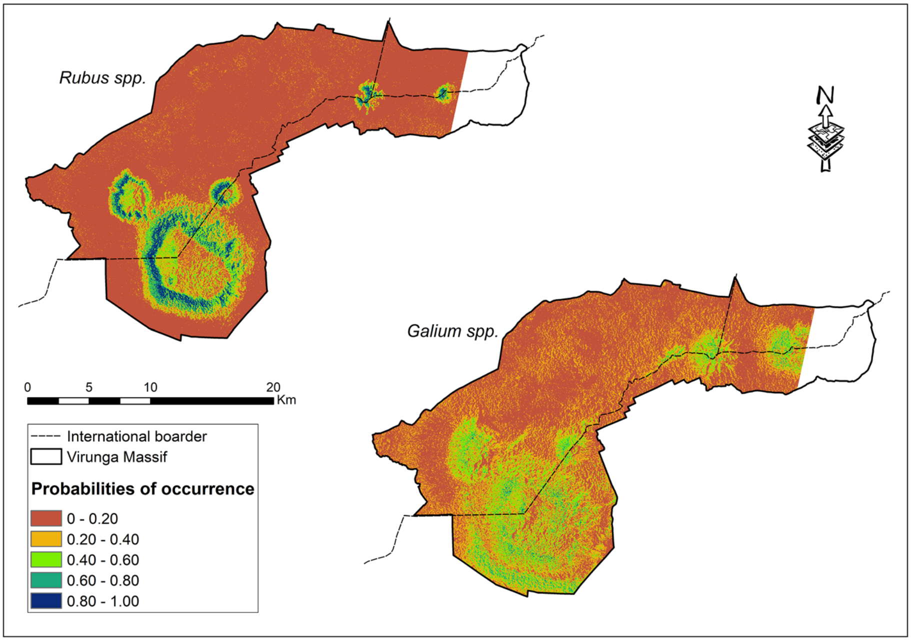

Fig. 5 Spatial distribution of *Rubus* spp. and *Galium* spp. in the Virunga Massif. Georeferenced maps are available online as electronic supplementary material (Online Resource 6)

Topographic variables were important predictors for the distribution of the gorilla food species. Elevation and eastness were among the three most important predictors for the occurrence of each of the five gorilla food species. Three of the modelled species did not show a remarkable preference of the east or west-facing slopes. *Galium* spp. and *Afroligusticum linderi* showed a more pronounced preference of west-facing slopes and hence eastness was the most important predictor for the occurrence of these two species (see Online Resource 5). All the five species showed different preferences towards elevation ranges. *Laportea alatipes, Afroligusticum linderi* and *Carduus nyassanus* have very low probabilities of occurrence in higher elevations (Fig. 6) especially on volcano summits (3600–4500 m). The opposite occurred for *Galium* spp. and *Rubu*s spp. (Figure 5). The optimal suitable elevation range for *Rubus* spp. was between 3200 and 3500 m with probabilities of occurrence in elevations < 3000 m very close to zero (see Online Resource 4). Both *Rubus* spp. and *Galium* spp. seem to occur primarily around the Karisimbi volcano, in the Karisoke area (Fig. 5).

Carduus nyassanus was found in the middle elevation of the Virungas. Its probability of occurrence increases from an altitude of 2800 m upwards and reaches a maximum at 3200 m (see Online Resource 4). Compared to the other species, *Afroligusticum linderi* showed a higher probability of occurrence in the lower elevations, below 2800 m (see Online Resource 5). These elevation zones of the park are mainly found in the territory of the Park National des Virunga in the Democratic Republic of Congo (DRC).

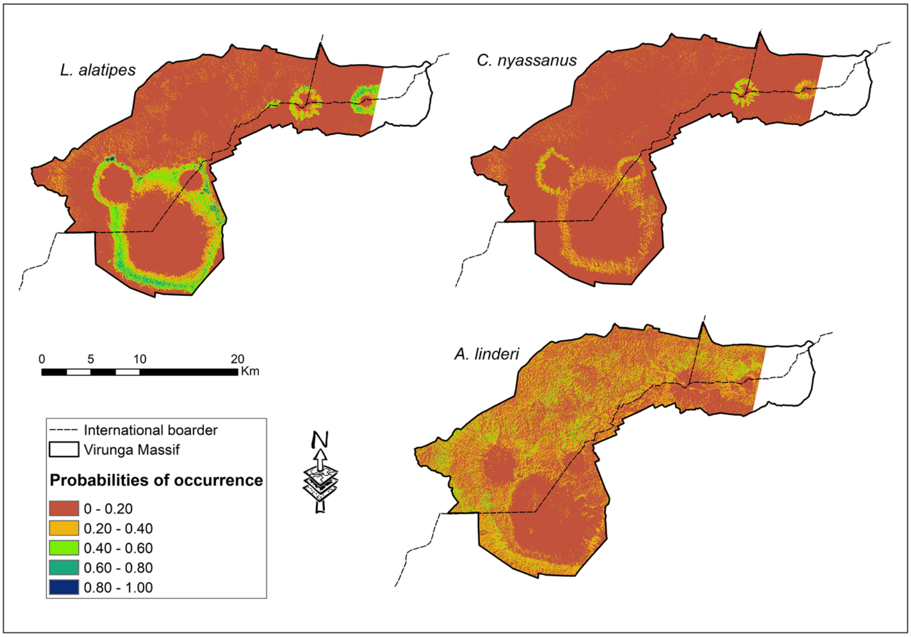

Fig. 6 Spatial distribution of *Laportea alatipes*, *Carduus nyassanus* and *Afroligusticum linderi* (accepted name for *Peucedanum linderi*) in the Virunga Massif. Georeferenced maps are available online as electronic supplementary material (Online Resource 6)

Discussion

Various studies have showed that mountain gorilla food species are abundant and perennially available across their habitat (e.g. Watts 1998; Plumptre 1991). Continuous monitoring of the abundances and distribution of gorilla food resources will help assess the ecology and quality of the mountain gorilla habitat under changing conditions. This research determined the abundances and mapped five plant species that are frequently consumed by mountain gorillas in the Karisoke area of the Virunga Massif, Rwanda. Gorillas in other areas of the park may consume other species, but studies need to be conducted to better understand variability in the gorillas' diet in relation to food species availability. This discussion reflects on the choice of predictor variables, model accuracies and gorilla food species occurrences throughout the entire Virungas.

Biophysical variables selection

The set of topographic and vegetation variables selected to model the abundance and distribution of gorilla food species appeared suitable for modelling. Significant relationships between individual food species and various environmental variables provide improved insight into ecological characteristics of gorilla's foraging areas. The fact that elevation was an important variable was expected but it was interesting to see that also solar radiation and eastness are relevant variables for the gorilla food occurrences in the Virunga Massif. This study showed that it is possible to predict plant species abundances based on topographic variables (Table 3) calculated from remote sensing data (ASTER).

Topographic variables such as elevation indirectly correlate with plant growth and abundance (Kübler et al. 2015). In the Virungas, a strong correlation between altitudinal gradients and climate (temperature and rainfall) is observed (Kayijamahe 2008). Climate parameters were not available for this study, but keeping elevation as a predictor variable gives indication on the temperature and rainfall amounts. More direct predictors that may play a role in the abundance and distribution of gorilla food species include the amount of light in the forest understory and the soil moisture content. The unavailability of a detailed soil map of the area or resources to execute detailed soil sampling and analysis prevents including soil variables in the modelling approach. Measuring the light intensity in the field under the tree canopy requires daily measurements (Joshi et al. 2006) and does not allow for easy extrapolation. However, by using remote sensing based techniques, suitable proxies could be modelled.

Model accuracies and study limitations

The accuracies were judged to be reasonable for the Boosted Regression Trees, but low accuracies were observed for the regression models. For instance, for Dataset 1 (the smaller dataset), no significant differences in food species abundance between vegetation zones were found and the regression models were not all significant. For the larger dataset (Dataset 2), they were significant but the variance explained by the regression models (R^2) was low. Improvements can potentially be made by expanding the sampling area and use the grid method as in the previous studies by Plumptre (1991) and Grueter et al. (2013). Also including additional environmental variables, such as soil moisture content, soil pH, and light intensity, in the prediction models may improve the models.

In the Virungas, vegetation characteristics vary with the history of each park (Owiunji et al. 2005) and encroachment on some volcanoes led to the disappearance of the lower montane forest. But there are similarities in vegetation zones at some altitudinal ranges on both sides of the volcanoes (Owiunji et al. 2005). Also, it was possible to extract environmental variables across the park in a consistent way from 15 m by 15 m resolution satellite imagery. Hence, although the field observations were from the Rwandan side of the park, the analysis could be extrapolated to the entire Virunga Massif. Estimations on the probability of occurrence of gorilla food species outside the Rwandan part of the park might be less accurate, but should be indicative in a relative way. There was also a time lag between the time of the image acquisition (the year is 2006; see Online Resource 2) and the time the field data was collected (2009–2010 and 2015). But vegetation dynamics are not expected to change at such a rate that this should be a major cause for low R^2 values. However, it could be worthwhile to estimate food species distributions based on higher resolution images (e.g. 1 m by 1 m) that match the field sampling period and conducting vegetation sampling at the DRC and Uganda portions of the Virunga Massif. More importantly, using the grid sampling as it was done in Dataset 2, and going further from the forest edge to avoid effects of human disturbance on the vegetation sampling would be additional measures to find stronger associations.

The predictions with boosted regression trees (BRTs) for four of the species were reasonable, but hardly better than random for *Galium* spp. The area under the curve (AUC) and the true skill statistic (TSS), have been selected as better indicators of accuracy than

Kappa, given that Kappa is criticised to be too dependent on prevalence (the proportion of presence sample points in the whole sample; Allouche et al. 2006). Less discriminating predictions for *Galium* spp. can be related to the fact that it is widely distributed and seems to have very few environmental conditions that really determine its distribution (Duque-Lazo et al. 2016). However, BRTs could also have been impacted by spatial autocorrelation and extrapolation of data collected on the Rwandan side to the entire Virunga Massif. Further follow up on this study's findings would be to carry out fieldwork validation to check whether the predicted distributions of the various food plants on the non-Rwandan side are correct.

Effect of soil, soil moisture and elevation

The five gorilla food species respond differently towards environmental conditions. Each of the seven variables considered is part of the three most important predictors for at least one of the species (see Online Resource 4 and 5). The abundance (Dataset 1) and biomass (Dataset 2) are both termed as "abundances" in the following descriptions.

Higher probabilities of occurrence of both *Rubus* spp. and *Galium* spp. are predicted in the elevation range of 3200–3500 of the Virunga Massif. Grueter et al. (2013) also highlight that thickets of *Rubus* spp. are associated with the giant lobelia belt in the sub-alpine zone, which corresponds to high elevation range (3300–3600 m). This elevation range is characterised by high annual rainfall amounts and low temperature values (Plumptre 1991). Moreover, the high altitudinal gradients of mountainous landscapes are characterized by decreased soil fertility (Tanner et al. 1998). These observations suggest that *Rubus* spp. and *Galium* spp. do not require high soil nutrient levels and prefer open canopy areas for their optimum growth. In contrast, the results of this study show that the occurrence of *Laportea alatipes*, *Afroligusticum linderi* and *Carduus nyassanus* decrease with increased elevation. These three species are therefore likely to grow under nutrient-rich soil, which is scarce in the higher elevations of the Virungas (Dondeyne et al. 1993). The high elevation range > 3200 m was also reported as a harsh environment for most plants, because of extremely low temperatures and the presence of frost during some seasons (Smith 1977).

Both *Afroligusticum linderi* and *Galium* spp. showed an increase in probability of occurrence with negative values of eastness (i.e. high occurrences on the west-facing slopes; see also Online Resource 5) and the eastness was their most important predictor variable. The three other food species do not show such a pronounced preference of the west-facing slopes, but the eastness is among the three most important predictor variables (see Online Resource 4). The east-facing slopes receive direct sunshine in the morning when they are still damp from the night while the west-facing slopes get heated in the afternoons, when they are already drier, and hence can heat up more. This suggests that *Afroligusticum linderi* and *Gallium spp.* prefer warmer and drier conditions, but how this differs between the studied species requires further study. Additionally, the prevailing winds can contribute in modifying the soil moisture of either the east or the west-facing slopes (Bader and Ruijten 2008), although it is not known whether there is a noticeable orographic effect in the Virungas. While the east and west facing slopes can be distinguished in this study (see Online Resource 7), further research is important to understand which slopes are drier or wetter. This would enable us to determine if the gorilla food plants prefer the dry or wet conditions at either each of the slope aspects. It is worthwhile to note that both east and west facing slopes were included in the sampling (see Fig. 1), but that north facing slopes were underrepresented. This could be a partial explanation why we do not observe a distinction between north and south facing slopes as predictor variables, although at the given position of the park relative to the equator, we do not expect this orientation of slopes to be of major importance.

Effect of radiation, undergrowth and canopy closure

Galium spp. occurrences showed a positive relationship with solar radiation. The four other species also showed a slight incline towards high values of incoming solar radiation. Therefore the closed bamboo canopies (non-disturbed bamboo), obstructing the sunlight and hence supporting very little undergrowth (Vedder 1984; Owiunji et al. 2005), may explain relatively low abundances of the gorilla food species in the bamboo zone. The open canopies correspond to a high amount of sunlight reaching the forest floor, and supporting the growth of understory plant species (Lowman 1986). However, *Galium* species that survive in the bamboo zone, are more likely to do so because they can root easily under the poor undergrowth and can escape the light limitation by climbing up with their vines. The plant species growing in the bamboo zone also take advantage of the disturbed bamboo zones, where there are old bamboo plants that fall over and give space to herbaceous plants.

Role of food species for gorilla's habitat

Knowing the suitable foraging areas for the mountain gorillas in a transboundary habitat is key to reinforcing existing and future conservation efforts of the Virunga Massif. Because the gorillas prefer areas with high food abundance (Vedder 1984), it is crucial to clearly describe areas with high density of foods but that are not frequently used by gorillas. However, there could be additional reasons why gorillas are absent there. More importantly, an understanding of the suitable conditions for the plant species mostly consumed by gorillas would help if forest restoration and expanding the gorilla habitat were to occur in the areas adjacent to the protected areas in the Virunga Massif (Belfiore et al. 2015).

This study predicted high probabilities of occurrence of five gorilla food species in the Karisoke area (Figs. 5 and 6); especially in the medium to high elevation ranges (2800–3500 m). This central Virunga zone around Bisoke, Karisimbi, Mikeno, and the saddles between Bisoke and Sabyinyo volcanoes, corresponds to the location of the majority of gorilla groups (Gray et al. 2010; Granjon et al. 2019). Also, most of the high abundances of gorilla food species were found in the *Hagenia-Hypericum* vegetation zone, which was reported by previous studies to be frequented by mountain gorillas (van Gils and Kayijamahe 2010).

Relative lower probabilities of occurrence of the five gorilla food species were observed in the lower altitudinal ranges of the Democratic Republic of Congo (DRC) and Uganda portions of the Virungas. This result supports the observation that the mountain gorillas on the DRC and Uganda areas eat other plants (Goodall 1977), particularly because these five mostly consumed plants (in the Rwandan portion of the park) do not occur on the DRC and Ugandan sides in high abundance. However, because the species distribution model used extrapolation on the entire Virunga area, additional research in the DRC and Uganda are needed to confirm the occurrences and species mostly consumed by gorillas in these areas.

Conclusion

This study determined the suitable conditions for the abundance and occurrence of five frequently consumed gorilla food species: *Galium* spp., *Carduus nyassanus*, *Afroligusticum linderi*, *Rubus* spp., and *Laportea alatipes*. Seven predictors, with five that are based on topography (slope steepness, eastness, northness, elevation and solar radiation) were used in this study. For each of the 1050 total plots, the main vegetation zone was recorded, while the canopy cover was measured in only 80 plots. All samples covered only the Rwandan portion of the Virunga Massif, but the mapping was extrapolated over the entire area including the parts in the Democratic Republic of Congo (DRC) and Uganda. This resulted in continuous maps for the five food species for the entire habitat of this mountain gorilla population. Researchers have shown differences in plant food choice among mountain gorillas in Bwindi Impenetrable National Park and the Virunga Massif (Ganas et al. 2004; Wright et al. 2015). The diet of mountain gorillas in the Virungas has also been studied but focusing on gorilla groups in the Karisoke area in Rwanda (Watts 1984). However, there is need to increase knowledge of the diet of mountain gorillas on the DRC side of the Virungas and explore areas that are predicted as highly suitable for the five gorilla food species mapped in this study. It would also be useful to do repeated vegetation sampling over time to assess the vegetation cover changes and impacts on the gorilla feeding habits.

Given the observed importance of some topographical variables (elevation, eastness, solar radiation), it would be interesting to focus future research on including measurements or estimates of light and soil moisture for the entire Virunga Massif and link these with the gorilla food abundances and distribution. This would give more direct indications of the importance of these variables for the gorilla food species, and deduce the wetter or warmer sides of the volcanoes and how they favour plant species occurrences. With continuous advances made in remote sensing techniques (e.g. LiDAR and Radar), other forest characteristics such as tree height, canopy cover or forest biomass might be estimated over the entire park area, which could prove to be useful for creating species distribution maps.

The results of the current study show high probabilities of occurrence of *Rubus* spp. and *Galium* spp. at the elevation ranges > 3200 m. This probably explains to some extent why the gorillas prefer to spend some time at the higher elevations including the volcano peaks (only for Bisoke volcano). However, it may not just be the top five food species in the gorilla diet that dictate their habitat use. Other nutrient factors can also play role, especially less frequently eaten resources that contain high levels of micronutrients. For instance, Grueter et al. (2018) found that some of the *Senecios* and *Lobelias* in the sub-alpine zone are very rich in sodium, which could attract the gorillas to these high altitude areas. Previous research has addressed the question of why gorillas are confined to some areas of their habitat, including medium to higher slopes (Vedder 1984; Watts 1998). Severe human disturbances in the past including poaching, political unrest and encroachment probably contributed to restricted use of the lower elevation slopes of the Virungas by the gorillas (Gray et al. 2010; Kalpers et al. 2003; van Gils and Kayijamahe 2010).

Our models also make it feasible to make predictions of the potential future distribution of food species for mountain gorillas in light of climate change. A better understanding of the relative importance of food species occurrence compared to other factors (e.g. intergroup encounters among gorilla groups, anthropogenic pressure) in shaping habitat use by the gorillas will be useful to further prioritize conservation efforts. Nevertheless, food availability will always be relevant for mountain gorillas, and hence the distribution maps created in this study will help in determining critical areas for the gorillas (maps shared as raster data in the Online Resource 6).

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Data availability The georeferenced distribution maps for each of the targeted food species are submitted as electronic supplementary material and will be made available online as raster data (Online Resource 6).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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