


Using abundance and habitat variables to identify high conservation value areas for threatened mammals

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Abstract The present study used abundance and habitat variables to design High Conservation Value Forests for wildlife protection. We considered great apes (*Gorilla gorilla gorilla* and *Pan troglodytes troglodytes*) as model species, and we used nest surveys, dietary analysis and botanical inventories to evaluate whether the traditional methods that use abundance data alone were consistent with the survival of the species. We assumed that setting a local priority area for animal conservation can be made possible if at least one variable (abundance or habitat variables) is spatially clustered and that the final decision for a species may depend on the pattern of spatial association between abundance, nesting habitat and feeding habitat. We used Kernel Density Estimation to evaluate the spatial pattern of each biological variable. The results indicate that all three variables were spatially clustered for both gorillas and chimpanzees. The abundance variables of both animal species were spatially correlated to their preferred nesting habitat variables. But while the chimpanzee feeding habitat variable was spatially correlated to the abundance and nesting habitat variables, the same pattern was not observed for gorillas. We then proposed different methods to be considered to design local priority areas for the conservation of each great ape species. Alone, the abundance variable does not successfully represent the spatial

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distribution of major biological requirements for the survival of wildlife species; we, therefore, recommend the integration of the spatial distribution of their food resources to overcome the mismatch caused by the existence of a biological interaction between congeneric species.

Keywords Priority areas · High conservation value forests · Central chimpanzee · Western lowland gorilla · Kernel density estimation · Spatial conservation planning

Introduction

One of the fundamental issues of wildlife conservation in production landscapes is the gazetting of high conservation value areas for endangered species (Camaclang et al. 2014). This process usually considers only abundance and distribution of the target species, ignoring the contribution of habitat quality (Berger-Tal et al. 2016). Two behavioural factors (animal dispersal and foraging) are closely linked to wildlife population decline due to habitat loss, and must ultimately be considered if conservation measures are to be successful (Berger-Tal et al. 2016). Animal dispersal is mainly controlled by species interactions and habitat quality and configuration (Bowler and Benton 2005), and may consequently influence the abundance and spatial distribution of a species (Gaston et al. 2000). Food is the most obvious resource determinant of habitat quality (Sinclair et al. 2006). It is likely that relying only on abundance distribution to design high conservation value forests for an endangered species is insufficient and biased if the species ranging behaviour is influenced by the food they consume, and if their food does not predict their spatial distribution in their natural environment. In this sense, unoccupied habitat areas should be considered in high conservation value areas if they are to provide significant resources to a population for their long-term persistence and recovery after perturbations (Camaclang et al. 2014; Camphuysen et al. 2012).

As more than three-quarters of the land surface is now dominated by human activities, a great challenge facing conservationists is to conciliate anthropological factors and the ecosystem (Ellis and Ramankutty 2008). In order to mitigate the negative effects of human activities on habitat loss in non-protected areas, sustainable natural resource management via community-based management (Sinclair et al. 2006) features as a strategic goal of the Convention on Biological Diversity (Convention on Biological Diversity 2010). This process is intended to extend the ecosystem integrity of small protected areas, and allow a proper conservation of wide-ranging and migratory species (Sinclair et al. 2006), and also to ensure the long-term persistence of wildlife in forests managed for timber production (Redford et al. 2015). That is the context in which forest certification schemes have grown and emerged as a conservation tool (Auld et al. 2008) and is viewed today as an important guide to foster sustainable forest management (Morgan et al. 2013). The major certification scheme for the management of tropical ecosystems, the Forest Stewardship Council (FSC) (Auld et al. 2008; Rametsteiner and Simula 2003) has outlined principles and criteria to improve the sustainability of forest management (Cauley et al. 2001) that are centred on forest management units (Rametsteiner and Simula 2003). A very important concept in FSC principles and criteria is the concept of High Conservation Value Forests (hereafter referred as HCVF) which is treated in principle 9 (Jennings 2004; Morgan et al. 2013). It takes into account important values about biodiversity, ecosystem services, and society and culture (Morgan et al. 2013). A good consideration of HCVF in forest concessions is a guarantee of the persistence of biodiversity in general, and wildlife in particular (Jennings

2004). The big challenge behind the concept of HCVF is how to identify and maintain high conservation values (Morgan et al. 2013).

The concept of HCVF is synonymous with priority areas for conservation (Pinto et al. 2007) or conservation areas (Denoël and Ficetola 2015), and is widely used in the conservation of endangered species (Ronconi et al. 2012). It is also used to identify small habitat patches pertaining to the survival of threatened species before a perturbation (Jennings 2004; Morgan et al. 2013). Several techniques are often used to identify HCVF. The more commonly used is the abundance-based technique (Berger-Tal et al. 2016), which considers the abundance and distribution of presence signs of a species (Berger-Tal et al. 2016; Vellend and Kharouba 2013). Other methods use ecological niche modelling (Araújo and Williams 2000; Thorn et al. 2009), where occurrence data are used to derive areas environmentally suitable for the persistence of a species (Hirzel et al. 2002), where areas of high abundance of presence signs predict suitable environmental conditions (Hirzel and Arlettaz 2003). High-quality absence data are often challenging to obtain (Hirzel et al. 2002), but it is difficult to evaluate the predictive power of models based only on occurrence data (Hirzel and Arlettaz 2003). In this case, ecological niche modelling (ENM) can be used for species for which distribution data are not easily obtainable (Araújo and Williams 2000), and can also help identify corridors between protected areas (Thorn et al. 2009). The combination of abundance information and habitat variables has rarely been used to design HCVF (Berger-Tal et al. 2016).

Food and habitat are central to niche separation (Schreier et al. 2009), which is the result of biotic interactions that may directly influence the abundance and distribution of two sympatric species on a local basis (Benítez-López et al. 2014). However, food may not be a direct predictor of the abundance and distribution of some animal species (Arnhem et al. 2008; Van Horne 1983), while for others abundance is predicted by food availability (Balcomb et al. 2000; Tweheyo et al. 2004). This biases attempts to identify HCVF based only on the abundance distribution of the species, or using ENM (Vellend and Kharouba 2013), because it is susceptible to missing some specific requirements for the persistence of particular species living in the same site with their direct competitors (Benítez-López et al. 2014). It is thus vital to delineate HCVF that include the distribution of all components necessary for the survival of individual species, rather than focusing only on where the species is present. In this context, considering habitat variables may improve the delineation of HCVF if they are to favour the long-term persistence of species; however, empirical case studies using this approach are lacking.

The aim of this study was to evaluate whether using abundance variables alone to define priority areas is consistent with the long-term survival of sympatric species. Because niche partitioning may affect the distribution of sympatric animal species (Benítez-López et al. 2014), we evaluated whether including habitat variables in the identification of priority areas for two sympatric species leads to different approaches for each species. To this end, we studied populations of sympatric great apes, western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) in the northern periphery of the Dja Biosphere Reserve, as model species. Western lowland gorillas and central chimpanzees are highly frugivorous; fruit species represent 50–98% of their diet (Cipolletta 2004; Doran-Sheehy et al. 2009; Tutin and Fernandez 1993; Tweheyo et al. 2004), and more than 87% of those fruit species are trees and lianas (Tutin and Fernandez 1993). Fruit consumption by great apes is generally significantly correlated with availability (Buij et al. 2002; Doran-Sheehy et al. 2009). Those fluctuations in fruit availability have important consequences on great ape ranging behaviour (Doran-Sheehy et al. 2004; Doran and Greer 2002; Wartmann et al. 2010). When fruits are abundant, great apes increase the

quantity and diversity in their diet, and gorillas increase their daily path lengths (Cipolletta 2004; Doran-Sheehy et al. 2004, 2009; Doran and Greer 2002). Woody plant species are important to great apes as they provide fruit (Balcomb et al. 2000) and nesting material (Stanford and O'Malley 2008), but are more likely to be affected during logging operations, thus making it essential to establish sound approaches for identifying HCVF where conservation efforts will be more focused toward woody plant species. Great apes exhibit some preferences for nesting habitats (Morgan et al. 2006; Willie et al. 2013): gorillas prefer nesting in open canopy secondary forests and swamps (Morgan et al. 2006; Willie et al. 2013), while chimpanzees prefer nesting in closed canopy old secondary forests (Morgan et al. 2006). It is evident that chimpanzees and gorillas may have become specialised in resource use due to their sympatry (Head et al. 2011, 2012), and the distribution of resources (nesting habitats and food) is likely to have affected their patterns of spatial distribution. Since all great ape species are threatened with extinction, and more than 50% of their populations lie in logging concessions and other human-dominated land-use types (Morgan and Sanz 2007), they are among the mammals most threatened due to habitat degradation (Schipper et al. 2008). There is an urgent need to develop approaches to design HCVF for their preservation in managed forests (Morgan et al. 2013), that consider both the spatial distribution of habitat variables and presence signs.

Methods

Study site

The study area lies in the tropical rainforest of south-east Cameroon, between 13°2' and 13°11'E, and 3°20'–3°27'N (Fig. 1). It covers an area of about 200 km² and is located in the Forest Management Unit 10–047a, that is planned to be exploited for timber production in the near future. The topography is relatively without relief, with a mean elevation of 680.58 m, SD = 17.53 m (range: 633–751 m) (Fig. 1). The area is traversed by several tributaries of the Dja river, many of which are seasonal, and among which the most important are Moun, Djo'o, Nkoun, and Mpou'o. The climate is characterized by two dry seasons and two rainy seasons (Willie et al. 2014). The long dry season lasts from November to February and the short dry season lasts from July to August. The long rainy season lasts from February to July while the short rainy season lasts from August to November. Mean annual rainfall is about 1637.9 (SD = 105.1), and the average daily temperatures are 19.5° (SD = 1.3°) for the minimum daily temperature and 26.3° (SD = 2.4°) for the maximum daily temperature (Willie et al. 2014). There are seven habitat types found in the study area [Near Primary Forests (NPF), Old Secondary Forests (OSF), Young Secondary Forests (YSF), Light Gaps (LG), Swamps, Riparian Forests (RF) and Fallows]. We present a description of the different habitat types in [Appendix](#).

Data collection

Transect surveys

We set a sample grid with 1000 × 1000 m cell size. In each cell, we established a 1200 m transect at 45° bearing, extending diagonally 600 m both ways from the centre of the cell

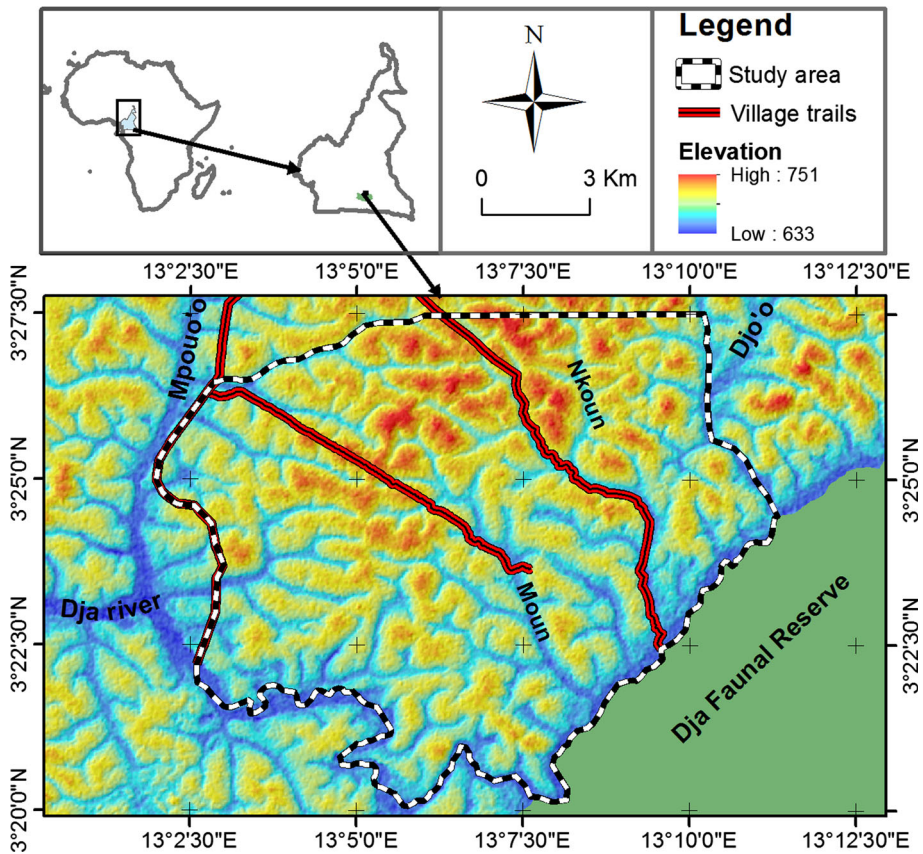


Fig. 1 Study area drawn on the hill shade of the digital elevation model obtained from the Shuttle Radar Topography Mission (SRTM) one arc-second global (<https://earthexplorer.usgs.gov/>)

(Online Resource 1). A total of 133 cells was used, giving a total distance of 159.6 km of transect walked.

On each transect, we noted the habitat type as well as the geographical coordinate at each 50-m interval, with one point at the start and end of the transect, resulting in 25 habitat points per transect. For each habitat type, availability was calculated as the number of points recorded for the selected habitat over the total number of points recorded for all habitats. We also recorded the geographical location of all great ape nests of all ages and noted the habitat type. A random sample of grid cells was selected for survey each month for 11 months, from October 2015 to August 2016. Each cell was surveyed once. Fresh nests had characteristics that facilitated their attribution to either gorillas or chimpanzees; those are the presence of signs such as urine, hairs, faeces, and prints (Morgan et al. 2006). We considered a nest site as a cluster of nests of the same age category within 50 m of each other (Morgan et al. 2006). For nests that could not be assigned to either gorillas or chimpanzees, because of the lack of site-specific parameters (Sanz et al. 2007), we considered a nest site as being made by chimpanzees when at least one nest of the same site was made in a tree at more than 2 m high; and we assigned a nesting site to gorillas if all nests of the same site were present on the ground or in trees at less than 2 m high.

Great ape tracking and faecal analysis

Faecal analysis was employed to identify fruit remains consumed by great apes (Head et al. 2011). Faecal samples were collected by two teams of local trackers from November 2013 to September 2016 (for chimpanzees) and January 2014 to September 2016 (for gorillas). Chimpanzee faeces were not found in March 2014, March–April 2015, January–February 2016 and June 2016; while gorilla faeces were not found in March 2014. Faecal samples were collected when the presence of signs such as the shape, size, associated odours, hairs or nests helped distinguish the primate species (Head et al. 2011).

Faecal samples were washed through a 1-mm sieve, in order to identify the fruit species consumed by the great ape species via their seeds (Doran et al. 2002), using a seed bank previously collected for our site. Many species were only identified to the genus level (e.g. *Uapaca* spp., *Landolphia* spp., *Nauclea* spp.) (Head et al. 2011), genera for which seeds are similar.

Botanical inventories

To carry out botanical inventories, we overlaid a second grid of 500×500 m cell size, in such a way that each of the original 1000×1000 m cells (big grid cell) comprised four 500×500 m cells (small grid cell). We set a 25×25 m plot at the centre of each small grid cell (Online Resource 1). In each plot, we measured all trees with a DBH ≥ 10 cm, and all lianas with a DHB ≥ 5 cm. Plant specimens for species for which identification was not possible on site were collected for later identification at the National Herbarium of Cameroon. At least two botanical plots were set in each big grid cell to calculate the mean abundance of plant species in those cells.

Data analysis

Nesting habitat selection

We evaluated habitat selection for nesting by gorillas and chimpanzees using the Cheason index of selection, followed by a goodness of fit test (Manly et al. 2002). The Cheason index allowed us to evaluate if a habitat was preferred, avoided or randomly used by great apes as sleeping sites; and the goodness of fit test determined whether or not the avoidance or preference of a habitat was significant (Manly et al. 2002). We calculated the Cheason index using the Eq. 1:

$$\alpha_i = \frac{\frac{r_i}{p_i}}{\sum_{i=1}^m \frac{r_i}{p_i}} \quad (1)$$

$$\alpha_i' = m\alpha_i \quad (2)$$

where r_i is the proportion of nests in habitat i over all nests; p_i is the availability of habitat i , and m is the total number of habitat types. The values of α vary between 0 (complete avoidance) and 1 (complete preference). We calculated a second value α' using Eq. 2. For $\alpha_i' > 1$, the habitat is considered preferred by the animal in function of its availability; for $\alpha_i' < 1$, the habitat is avoided in function of its availability; and for $\alpha_i' = 1$, the habitat is used randomly in function of its availability. All habitats preferred or avoided through the

Cheason index, but not significant through the exact goodness of fit test, were considered randomly used for nesting.

We considered a habitat as a chimpanzee or gorilla nesting habitat if significantly preferred by the respective species. Additionally, we also considered habitats randomly used, but accounting for more than 20% of the observed proportion of use by a great ape species (Gregory and Baillie 1998). This is consistent with the assumption that a habitat may not be preferred by a species but, may nevertheless support a higher number of individuals of the population (Gregory and Baillie 1998).

Important fruit species to great apes

We used the method described by Doran et al. (2002) to determine important fruit species consumed by gorillas and chimpanzees. Doran et al. (2002) defined four ‘importance types’, three of which we used: Importance type 1: present in more than 50% of faecal samples in at least 1 month and consumed for more than 50% of months; importance type 2: present in faecal samples for more than 50% of months; importance type 3: present in more than 50% of faecal samples in at least 1 month (Doran et al. 2002). The fourth importance type deals with direct observations, so we did not consider it as we conducted indirect observations through faecal sample analysis. Before defining important plant species, we excluded from the plant list those for which remains were found in less than 1% of faecal samples (Doran et al. 2002).

Spatial analyses

We used three methods of spatial analyses: The Global Moran’s I, the Kernel Density Estimation (KDE) and the spatial correlation. The Global Moran’s I spatial autocorrelation statistic was used to measure the degree to which features were spatially associated (Scott and Janikas 2010). A significant clustered pattern in each variable is evidence of the existence of HCVF (Lin et al. 2017). We used KDE to describe the distribution of great ape nesting sites as well as that of important fruit trees and suitable habitats.

The KDE is a non parametric method that is generally used to estimate home range of individual animals (Worton 1989), but can also be used at population level to study their range, or applied to data other than animal locations that are vital to a population, such as habitat availability (Seaman and Powell 1996). KDE uses location points recorded with GPS to derive a probability distribution that illustrates the likelihood that the study target is going to be present at any particular point (Kie et al. 2010). The term utilization distribution is often used in home range studies to denote that probabilistic distribution, but in this work, we will use the terms ‘abundance distribution’ and ‘availability distribution’ for abundance and habitat variables, respectively. An important aspect of KDE is that its output results vary according to several parameters such as the method used (fixed or adaptive), the grid cell size, and the bandwidth (Powell 2000; Worton 1989). All our variables presented a clumped distribution (Table 2); consequently, we used the fixed kernel method in KDE for this study (Lawson and Rodgers 1997). Furthermore, the method may produce less variable home range sizes at different sampling sizes (Wartmann et al. 2010). The spatial resolution was 106×106 m. The value of the bandwidth (also called the smoothing parameter), is evidently the most influential parameter in the KDE implementation (Hemson et al. 2005). Several methods were developed to determine the bandwidth value for implementing KDE (Signer and Balkenhol 2015). The best method for bandwidth selection is ideally the one that minimizes the mean integrated square error

(Seaman and Powell 1996; Worton 1989). In that sense, the least square cross validation (LSCV) was recommended for bandwidth selection in KDE (Seaman and Powell 1996), and it has been widely used in home range studies (Laver and Kelly 2008). The KDE used together with LSCV, though producing accurate results (Seaman and Powell 1996), has been criticized because it yields smaller bandwidths and then produces utilization distributions (home ranges) that are more fragmented (Powell 2000). A recent study has shown that the LSCV produces home ranges with a negative bias for smaller samples and a positive bias for larger samples (Kie 2013). Using KDE with LSCV may result in missing potential corridor areas between important feeding sites and nesting sites (Kie et al. 2010). An alternative to the LSCV is the reference bandwidth (Worton 1989). This method yields large bandwidths that lead to over-smoothing of the sampling points, particularly when data points are clumped (Kie et al. 2010). An ad-hoc approach is proposed to overcome the problem of under-smoothing by the LSCV method and over-smoothing by the reference method; an approach which consists of reducing the value of the reference bandwidth until the extent of the home range starts to divide into two parts (Kie 2013). This ad-hoc method was used to determine the smoothing parameter of all variables. We used 50 and 95% isopleths to represent the abundance and availability distribution from KDE (Hemson et al. 2005). Following Laver and Kelly (2008), we also performed a distribution core analysis using an objective method based on the abundance and availability distribution of our data. It allows us to draw a third contour level of the abundance and availability distributions, which was further used to define HCVFs. The method produces different percentages at different probabilities of abundance and availability (Powell 2000).

The ad-hoc bandwidth performed well by producing joint polygons for all variables at 95% contour. However, the areas produced for habitat variables were highly fragmented (Online Resource 1). Consequently, we chose the smallest bandwidth obtained from abundance variables to produce a continuous shape of distribution cores. Certainly, our sampling intervals resulted in spatially irregular data points (Katajisto and Moilanen 2006). This is due to the fact that data were collected on predefined transects that were established at a certain distance from each other, leading to missed observations and spatial aggregation of data points (Katajisto and Moilanen 2006). To solve this problem, we weighted each variable by grid cell and rounded all decimal values to one (Katajisto and Moilanen 2006). We then generated random points in each grid cell corresponding to its weight for each variable. The weight of abundance variables was the number of nesting sites recorded in each grid cell. For suitable habitat, the weight was the total number of points of all suitable habitats in the grid cell. We calculated the weights (W_k) for important plant species as in Eq. 3:

$$W_k = \sum_{i=1}^X \sum_{j=1}^Y \frac{B_{ij}}{N} \quad (3)$$

where X is the number of important fruit species in the cell k ; Y is the number of individuals of species i in the cell k ; N is the number of plots counted in the cell, and B_{ij} is the basal area of the plant j .

The spatial correlation was conducted to evaluate the local relationship between two abundance or availability distributions. We applied two techniques to delineate HCVF if the two species show different patterns of habitat use: (1) if a larger part of the nesting site distribution correlated to both the distribution of nesting habitats and important fruit species, the HCVF comprised a single area composed of the zone of overlap between high abundance of nesting sites, high densities of important fruit species and preponderance of

preferred nesting habitats; (2) if the distribution of nesting sites was not simultaneously correlated to nesting habitats and important fruit species, the HCVF was composed of two areas, one where nesting sites are more abundant in an area of high nesting habitat availability and one zone of overlap of high densities of important fruits and high densities of nesting sites.

The R software version 3.3.1 (R Core Team 2016) was used to conduct exact goodness of fit test, KDE and core analysis distribution [package *rhr* version 1.2.909 Signer and Balkenhol 2015)], and spatial correlation (package *spatialEco* version 0.1-7). We used ArcGIS 10.3.1 to conduct the Moran's I index of spatial autocorrelation and draw maps. HCVF were defined using the ArcGIS tool *raster calculator*.

Results

Great ape habitat use

From the 133 1000 × 1000 m cells, we recorded 272 chimpanzee nests and 89 gorilla nests. Great ape nests were absent from 59 cells. Chimpanzee nests were found in 55 cells, while gorilla nests were found in 33 cells. Both chimpanzee and gorilla nests were found only in 14 grid cells. Mean nest encounter rate per kilometer was 4.97 (SD = 4.5) for chimpanzees and 3.48 (SD = 4.7) for gorillas. The mean number of nests per site was 1.91 (SD = 1.36) for chimpanzees and 3.18 (SD = 3.97) for gorillas. A total of 4375 habitat points was recorded and assigned to either Fallow (26), Old secondary forest (2069), Near primary forest (57), Young secondary forest (1396), Swamp (575), Riparian (191) and Light gap (61). The Cheason indexes indicate that chimpanzees and gorillas exhibit habitat preferences for nesting, as confirmed by the exact goodness of fit test (df = 6; p = 0.000). Chimpanzees significantly preferred nesting in old secondary forests ($\alpha_i = 2.772$), while

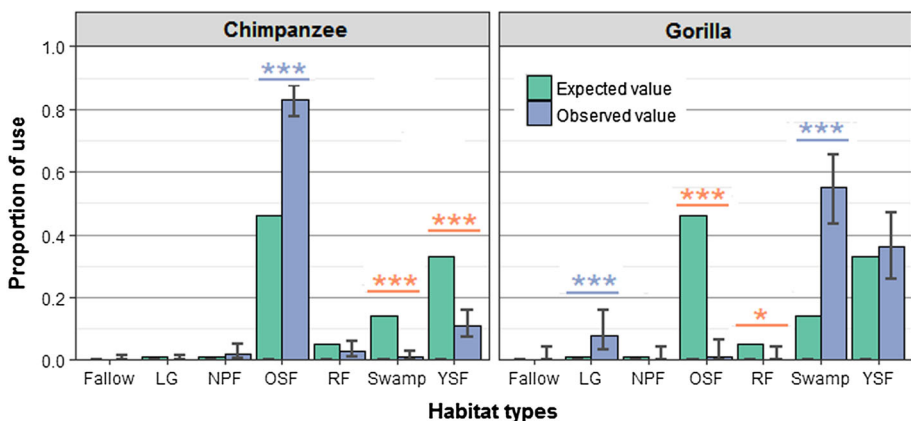


Fig. 2 Gorilla and chimpanzee habitat use. Expected values are presented with confidence intervals as error bars. The observed values are significantly higher or lower than the predicted values if that value \pm the confidence value is always greater or lower than the expected value, otherwise, they are non-significant at a probability of 0.05. Significant values are marked with asterisks (*p < 0.05; ***p < 0.001). Blue asterisks indicate habitats significantly preferred, and red asterisks indicate habitats significantly avoided. LG light gap, NPF near primary forest, OSF old secondary forest, RF riparian forest YSF young secondary forest. (Color figure online)

gorillas preferred nesting in swamps ($\alpha_i = 2.389$) and light gaps ($\alpha_i = 3.914$) (Fig. 2). It is noteworthy that gorillas avoided all habitats that chimpanzees preferred and vice versa. Both animal species randomly used riparian forests and young secondary forests, though this pattern was insignificant and varied: riparian forests constituted only 2.98% of use by chimpanzees, while young secondary forests constituted 36.05% of use by gorillas. We found no nest in fallows for neither chimpanzees nor gorillas.

Important fruit species

We classified 15 and 14 fruit species as important for chimpanzees and gorillas, respectively, based on the analysis of faecal samples (Table 1). Three species were classified as type 1, 11 as type 2 and one as type 3 for chimpanzees; while four species were classified as type 1 and 10 as type 2 for gorillas. No species was classified as type 3 for gorillas. *Duboscia macrocarpa* classified as type 3 for chimpanzees appeared as type 1 for gorillas.

Spatial distribution of great ape nests, suitable habitats, and important fruit species

Features of all variables (nest abundance distribution, suitable nesting habitats, and important fruit species) were spatially clumped for both chimpanzees and gorillas (Table 2). This means that the distribution of great ape nesting sites, suitable nesting habitats, and important fruit species exhibit high values in some areas, that can be set as HCVF. Aggregation areas differ from one variable to another (Fig. 3). Chimpanzee nesting sites are more abundant in the southern and south-western areas, with some small patches in the north-eastern area; while gorilla nesting sites are more abundant in the eastern, north-eastern and central areas (Fig. 3a). Chimpanzee suitable nesting habitats are more abundant in the southern and north-western areas; while gorilla suitable nesting habitats occur more in the eastern areas (Fig. 3b). The distributions of important fruit species for both chimpanzees and gorillas are all concentrated in the south and south-east of the site (Fig. 3c).

The correlation maps indicate that the spatial correlation between nesting site abundance, nesting habitat and important fruit distribution do not show a clear pattern for both animal species (Fig. 4). However, chimpanzees appear to show more affinity for the distribution of their nesting habitat and important fruits than do gorillas. Gorilla nesting site distribution is locally correlated with nesting habitats (east) and important fruit species distribution (centre and south) (Fig. 4b1.b2, b1.b3). The correlation between chimpanzee nesting habitats and their important fruit distribution is high (Fig. 4a2.a3), but relatively low for gorillas (Fig. 4b2.b3). In addition, the correlation between chimpanzee and gorilla nesting habitat is very low (Fig. 4a2.b2), while it is very high between chimpanzee and gorilla important fruit species distribution (Fig. 4a3.b3). This implies that chimpanzee and gorilla habitats are available at different spatial locations, while gorilla important fruit species are more abundant in areas of high chimpanzee habitat availability.

High conservation value areas for great ape protection

The assessment of the spatial relationship between abundance and habitat variables led to the designation of one area HCVF for chimpanzees and two separate areas as HCVF for gorillas (Fig. 5). The chimpanzee HCVF covers the south and western part of the study

Table 1 Important fruit species for great apes

Scientific name	Family	Lifeform	Importance type
<i>Pan troglodytes troglodytes</i>			
<i>Chrysophyllum lacortianum</i>	Sapotaceae	Tree	1
<i>Landolphia</i> spp. ^a	Apocynaceae	Liana	1
<i>Uapaca</i> spp. ^b	Euphorbiaceae	Tree	1
<i>Celtis tessmannii</i>	Ulmaceae	Tree	2
<i>Cissus dinklagei</i>	Vitaceae	Liana	2
<i>Dialium pachyphyllum</i>	Cesalpiniaceae	Tree	2
<i>Enantia chlorantha</i>	Annonaceae	Tree	2
<i>Ficus</i> spp. ^c	Moraceae	Tree and stranglers	2
<i>Heisteria parvifolia</i>	Olacaceae	Tree	2
<i>Milicia excelsa</i>	Moraceae	Tree	2
<i>Nauclea</i> spp. ^d	Rubiaceae	Tree	2
<i>Polyalthia suaveolens</i>	Annonaceae	Tree	2
<i>Santiria trimera</i>	Burseraceae	Tree	2
<i>Strephonema pseudocola</i>	Combretaceae	Tree	2
<i>Duboscia macrocarpa</i>	Tiliaceae	Tree	3
<i>Gorilla gorilla gorilla</i>			
<i>Chrysophyllum lacortianum</i>	Sapotaceae	Tree	1
<i>Duboscia macrocarpa</i>	Tiliaceae	Tree	1
<i>Landolphia</i> spp. ^a	Apocynaceae	Liana	1
<i>Uapaca</i> spp. ^b	Euphorbiaceae	Tree	1
<i>Antrocaryon klaneanum</i>	Anacardiaceae	Tree	2
<i>Celtis tessmannii</i>	Ulmaceae	Tree	2
<i>Cissus dinklagei</i>	Vitaceae	Liana	2
<i>Dialium pachyphyllum</i>	Cesalpiniaceae	Tree	2
<i>Ficus</i> spp. ^c	Moraceae	Tree and stranglers	2
<i>Heisteria parvifolia</i>	Olacaceae	Tree	2
<i>Klainedoxa gabonensis</i>	Irvingiaceae	Tree	2
<i>Santiria trimera</i>	Burseraceae	Tree	2
<i>Sorindeia grandifolia</i>	Anacardiaceae	Tree	2
<i>Tetrapleura tetraptera</i>	Mimosaceae	Tree	2

Importance type 1: present in more than 50% of faecal samples in at least 1 month and consumed for more than 50% of months; importance type 2: present in faecal samples for more than 50% of months; importance type 3: present in more than 50% of faecal samples in at least 1 month

^aIncludes *L. glabra*, *L. jumellei*, *L. landolphioides*, *L. mannii*, *L. maxima*, *L. owariensis*, *L. violacea*, *L. jumellei* and two unidentified species

^bIncludes *U. acuminata*, *U. guineensis*, *U. paludosa*, *U. vanhoutei*

^cIncludes *Ficus mucoso*, and some stranglers

^dIncludes *N. diderrichii*, *N. pobeguinii*

Table 2 Results of the Moran's index I test for spatial autocorrelation

Autocorrelation analysis	Moran's index (I)	Z-score	P value
<i>Gorilla gorilla gorilla</i>			
Nesting site distribution	0.836	5.764	0.000
Nesting habitat distribution	0.967	118.771	0.000
Important fruit distribution	0.974	33.955	0.000
<i>Pan troglodytes troglodytes</i>			
Nesting site distribution	0.836	5.764	0.000
Nesting habitat distribution	0.857	67.925	0.000
Important fruit distribution	0.955	48.908	0.000

A positive Moran's index (I) indicates that features are concentrated, while a negative value indicates dispersion. The z-score is a summary value indicating the degree to which features of the measured variable are clustered or dispersed. z-scores greater than 2.58 indicate that data points are clustered at more than 99% confidence level

area (Fig. 5b). The two gorilla HCVF (Fig. 5b, c) occur in the centre area where gorilla nesting sites and their important fruits intersect, and in the north-eastern part of the study area where gorilla nesting habitats are more available. Between the two areas is a transitional zone composed of gorilla high-quality nesting habitats (Fig. 5c), and should be considered as a corridor.

Discussion

In contrast to techniques based solely on species abundance distribution, incorporating habitat variables, such as nesting habitat and fruit tree distribution, allowed us to objectively define HCVF that do not only designate areas of high densities of great apes, but that also consider factors that are indispensable to their long-term survival. Gorillas and chimpanzees significantly preferred different sets of habitat types, but a similar set of fruit species was important for their survival. In addition, those habitat variables and nesting site locations presented a clumped distribution. Spatial correlations between variables show different patterns for the two great ape species. Chimpanzee nesting sites exhibited a high degree of aggregation in areas of high fruit and high nesting habitat availability; while gorilla nesting sites occurred in two important clumps: one in an area of highly preferred nesting habitat availability and the other in an area of important fruit availability. Areas of high nesting habitat availability for gorillas and chimpanzees did not overlap, while areas of highly important fruit availability greatly overlapped between the two species. The results show that apes may move seasonally according to the distribution of their resources. However, our data do not allow us to confirm the effect of seasons on the spatial distribution of nesting sites. Using such a method that integrates habitat variables with abundance distribution, results in HCVF that are consistent with ecological requirements of the animal species. Additionally, we showed that considering the distribution of fruit species would result in different approaches for defining HCVF when dealing with two competing species that coexist in the same environment. This method provides more valuable supplement to other techniques based only on the animal abundance distribution, especially

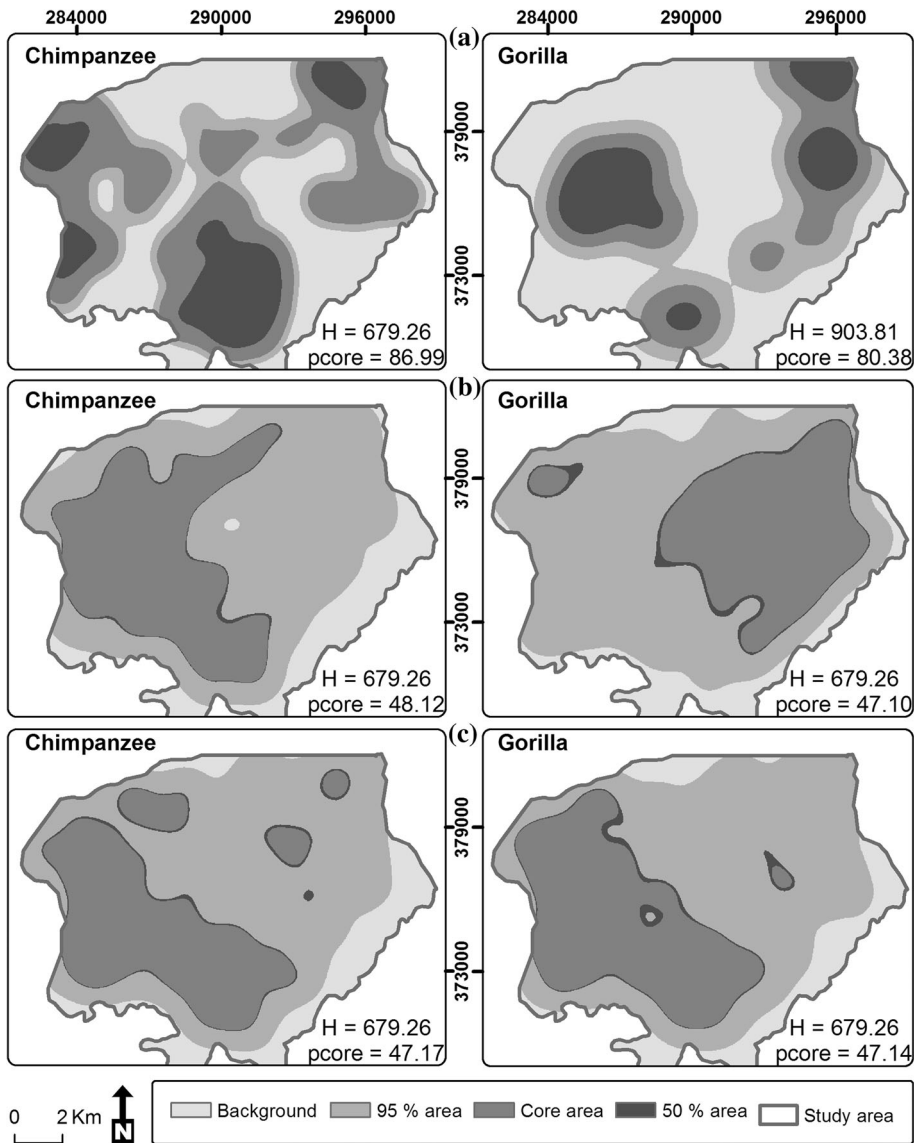


Fig. 3 Spatial distribution of great ape nests and resources: **a** great ape nesting sites, **b** great ape suitable habitat, **c** great ape important fruits; maps on left represent chimpanzee and maps on right represent gorilla. The abundance is classified into three categories using 95 and 50% contours and the core area. *H* bandwidth, *pcore* percentage of the core area

when character displacement may have been at the centre of sympatry between the species and its competitor (Hickman Jr. et al. 2008).

The patterns observed in this study (Fig. 4) are due to the evidence of niche partitioning between gorillas and chimpanzees (Oelze et al. 2014). Seasonal variation of fruit availability in great ape habitat results in a shift in fruit consumption by gorillas in terms of diversity, quantity and quality, in comparison to chimpanzees (Oelze et al. 2014). Recent

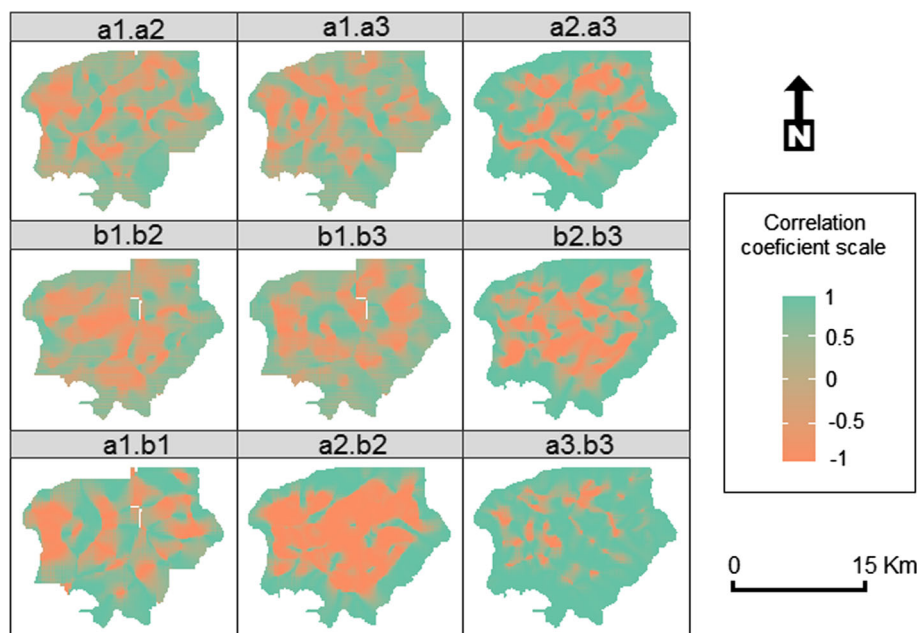


Fig. 4 Spatial correlation between the different variables for each species: **a** Chimpanzee, **b** Gorilla, **1** nesting site distribution, **2** nesting habitat distribution, **3** important fruit species distribution

works have underlined the importance of adding habitat features to design HCVF, as a mean to enhance the protection of important ecological processes that govern the maintenance of ecosystem integrity (Berger-Tal et al. 2016; Camphuysen et al. 2012). Camphuysen et al. (2012) found that birds are generally in transit to or from food sources. This implies that relying solely on inventory data without considering behaviour may lead to set priority areas that cannot protect key food resources necessary for the survival of the target populations. Using camera traps, Matsuda et al. (2015) demonstrated that orang-utans and other mammals require natural salt licks for mineral access, and subsequently proposed the inclusion of natural licks in HCVF. Buij et al. (2002) found that due to seasonal variation in fruit availability at different altitudes, orang-utans seasonally show high densities in habitats where fruit availability was the highest. They then concluded that HCVF should include a range of different altitudes to allow the survival of orang-utans in the forest. Using ecological niche modelling, Brambilla and Saporetto (2014) found that habitat suitability with nesting habitats and feeding habitats resulted in different spatial distributions. Consequently, nesting habitats and feeding habitats were functionally different and should be considered separately when designing priority areas for conservation (Brambilla and Saporetto 2014). This is congruent with the case of gorillas in our study where their nesting and feeding habitats were not spatially correlated and have resulted in different functional responses (Fig. 4).

Our study accepts a number of limitations. We collected data over 11 months, but our analysis did not focus on seasonal spatial variations in the different variables. Also, we did not consider the nest decay rate in our analyses. Evaluating patterns of habitat use by great apes often requires the use of signs other than nests (footprints, feeding remains, etc.) (Morgan et al. 2006). Those additional signs are generally difficult to observe after several

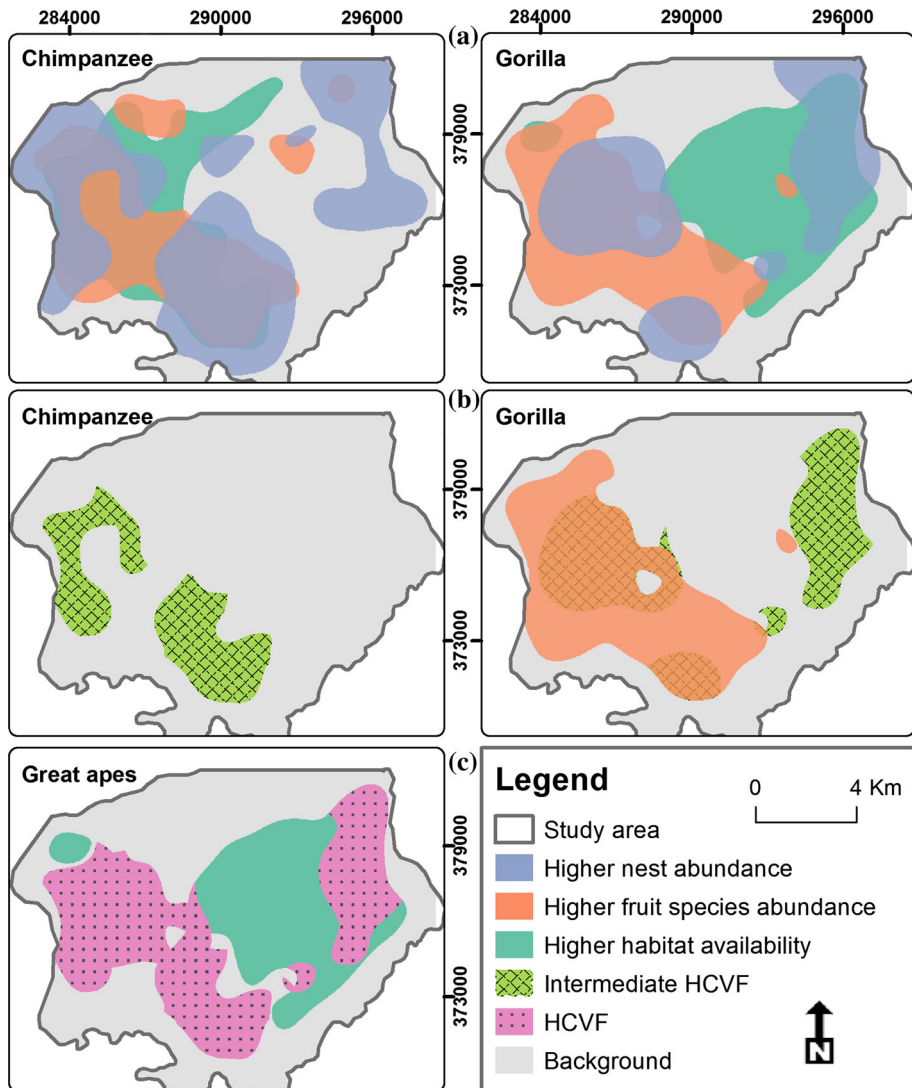


Fig. 5 Delimitations of high conservation value areas for great ape conservation: **a** an overlay of high nesting site abundance distribution, high nesting habitat availability and high fruit plant density; **b** the intersection of all spatially correlated variables; **c** the final HCVF for both gorillas and chimpanzees with a corridor for gorilla ranging between the two HCVF

days or even when fresh in the dry season in *terra firma* habitats (Sanz et al. 2007). As such, we used nest data as the only available ecologically-sound and unbiased information on abundance distribution. Nest decay rate was shown to vary between gorilla and chimpanzee, and is also influenced by habitat types, nesting material and seasons (Morgan et al. 2016). It is evident that such variable nest decay rate may have influenced our observed nesting site distribution. Great apes are social primates, and many nests of the same site may have disappeared at the time the nesting site is discovered. Then, by using nesting sites instead of individual nests (Funwi-Gabga and Mateu 2012), we reduced not

only the effect of variability in the number of nests per site, but also minimized the influence of nest decay rate. The distribution of different variables obtained from KDE is not a unique output, because it depends on several variable parameters. It is likely that a change of a parameter like the bandwidth may result in a different distribution. The different parameters and the model are chosen based on some properties and constraints defined in the literature. Now, no single method is consistent with all studies (Laver and Kelly 2008), and the intended use of KDE outputs remain the important factor governing the choice of a parameter for KDE (Worton 1989).

As a home range estimation technique, using KDE allowed us to derive spatial distribution of density probabilities of our survey data. This particularity of KDE makes it more suitable than other methods, such as Minimum Convex Polygons (Laver and Kelly 2008), to design HCVF. The improvement of KDE implementation (Kie 2013) and their integration in open source R software (Signer and Balkenhol 2015), along with their possible application on habitat variables (Seaman and Powell 1996), make it a useful tool for defining ecologically meaningful conservation areas that are more consistent with the long-term persistence of wildlife species. The resultant HCVF do not consider factors that can affect the distribution of animals, such as roads and human settlements (Clark et al. 2009). This is an important issue that needs to be considered, because some areas may be set as HCVF that are not accessible or suitable for the animal. Our results revealed that unoccupied areas should be included in HCVF to allow long-term survival of wildlife (Camaclang et al. 2014). In this case, ecological niche modelling appears to be a good complement to KDE to design HCVF (Denoël and Ficetola 2015), as it will help to focus conservation efforts only on areas that may support population persistence.

Habitat requirements and HCVF

Using a combination of abundance and habitat variables, it was possible to set HCVF that differ from those set from abundance data alone. Our results are consistent with those of Balcomb et al. (2000) when considering chimpanzees alone. They found that the abundance of chimpanzees can be predicted by the distribution of large fruiting trees and high fruit species density may be a proxy of habitat chimpanzee quality. However, great apes are generally sympatric range wide, and sound conservation measures are those that consider the evolutionary factors that condition the coexistence of these two sympatric species. Our study demonstrates that the prediction of the abundance of an animal species by habitat quality holds true under the assumption that it is a dominant species, but it is not necessarily the case when dealing with its direct competitor. With this in mind, considering the distribution of nesting habitats and fruit species made it possible to set less subjective HCVF that are more compatible with the persistence of the target animals. HCVF are at the centre of biodiversity mainstreaming (Morgan et al. 2013; Redford et al. 2015), and considering both abundance distribution and habitat variables to delineate them provides a tool that should be incorporated into conservation decisions. A similar approach was used by Martins et al. (2013), considering animal abundance distribution and the intensity of anthropogenic activities. Also, abundance alone was considered by Murai et al. (2013) to address hunting pressures in large mammals. It is then evident that the approach used to design HCVF may differ depending on the conservation objectives, but sound conservation measures that intend to favour the long-term survival of animals are those that put forward the distribution of suitable habitat components such as food sources (see Balcomb et al. 2000).

The importance of our study lies in the combination of the distribution of important components of their ecology in defining HCVF. The study considers the distribution of plant species providing fruit to great apes. However, not all trees considered will bear fruits at the same time; therefore, this parameter will not necessarily reflect the actual distribution of fruit available to great apes. As the phenology of fruit species can vary annually within the same species (Chapman et al. 2005; Tweheyo and Lye 2003; Yamagiwa et al. 2008), it is possible that the distribution of fruits available to great apes will vary from year to year. One solution to this issue is to consider the distribution of foraging sites rather than that of fruit species consumed (Brambilla and Saporetti 2014; Camphuysen et al. 2012; Soanes et al. 2016). Recording foraging site distribution is difficult for unhabituated great ape populations, because dietary analysis based on trails is insufficient to describe great ape diet without being in complement with faecal analysis, and is more commonly used for the identification of herbaceous plant species that are not identifiable in faecal samples (Doran et al. 2002). Relying on feeding sites to derive feeding habitat suitability (Brambilla and Saporetti 2014) may lack the spatial pattern of the consumption of fruit species, the important resources for great ape survival. Our study is among the few that consider feeding habitat suitability by incorporating the spatial distribution of potential sources of important feeding resources (see Brambilla and Saporetti 2014; Buij et al. 2002; Matsuda et al. 2015). A similar approach was used by Martins et al. (2013) to consider important breeding areas in the setting of priority area.

Management of HCVFs

Delineating HCVF should involve all stakeholders (Lascelles et al. 2012) who have an influence on the region (Hanski 2011). Thus, our HCVF (Fig. 5c) is proposed as an area suitable for the target species based on the considered criteria (Ronconi et al. 2012), to be put forward and discussed with other stakeholders with a view to the on-the-ground application. It is not yet clear, however, how to objectively delineate HCVF. Some authors propose to delineate an area comprising about 10% of the forest area (Hanski 2011). The final area allocated as HCVF may reflect a solution to the trade-off between conservation, economic development and other stakeholders (Lascelles et al. 2012). It is not necessarily feasible to assign all areas where a species is present to its protection (Denoël and Ficetola 2015); instead, HCVF is a valuable tool to contribute to the preservation of threatened species in managed forests. Considering habitat variables (preferred nesting habitats and important foods) certainly improves the conservation objective of HCVF. However, the habitats designated for HCVF must be sufficient to allow the persistence of wildlife populations (Fahrig 1999).

Our design can be applied to many ecosystems where HCVF are useful for the protection of wildlife species. We focused on two model species in our study, both of which are classified as endangered or critically endangered, which is an important criterion for setting conservation areas (Galetti et al. 2009). Additionally, our final HCVF encompasses many habitat types as it covers both chimpanzee and gorilla preferred nesting habitats (Fig. 5c), and is consequently suitable for the preservation of many other wildlife species for which survival depends on these habitats. Also, as our design considers areas of high fruit species densities, the HCVF could also benefit many primate species other than great apes, as well as birds and many other frugivorous mammal species (Fleming and Kress 2011). Therefore, the choice of great apes as focal species to identify HCVF can result in the preservation of many species in the faunal community, thus reducing the effort, expertise, finance and time needed to identify HCVF for multiple threatened species. This

method can be likened to the ‘umbrella species’ approach proposed by Rainho and Palmeirim (2013) and applied by Martins et al. (2013) to drive conservation decisions for a coral reef ecosystem.

Importance of habitat-based HCVF for great apes

The frugivorous character of great apes necessitates conservation practices that consider fruit species protection. In the context of human disturbance, this implicates the management of logging practices. Although selective logging may not affect plant species richness, diversity and evenness (Testolin et al. 2016), it can significantly reduce species abundances (Meijaard and Sheil 2008) and affect plant community and structure (Potts 2011; Testolin et al. 2016), resulting in a significant dissimilarity in plant species composition between logged and unlogged forests (Testolin et al. 2016). These affected plant species may include those preferred by great apes: for example, in Kanyawara, logging led to a change in the basal area of 18 fruit species consumed by chimpanzees, and many additional species of the chimpanzee diet were directly extracted for commercial purposes (Potts 2011). However, the seven most consumed fruit species were not extracted (Potts 2011), therefore suggesting that logging may not detrimentally affect chimpanzee food supply in this area (McLennan 2013). Furthermore, selective logging may not negatively affect great ape abundance: gorillas appear temporally resilient to logging activities (Haurez et al. 2016) and exist at higher abundances in logged forests (Clark et al. 2009), and chimpanzees exhibit no spatial changes in range use during logging activities (Arnhem et al. 2008). Velázquez-Vázquez et al. (2015) found similar results in a study on the distribution of spider monkeys in logged and unlogged forests. Great apes exhibit a significantly positive response to the gradient of the distance from logged forest (Clark et al. 2009); however, the spatial or temporal patterns of great ape abundance may be due to a spatial relocation of great ape populations in relation to logging activities, but not a loss of individuals (Morgan et al. 2015). Although great apes are highly frugivorous, they exhibit some flexibility in their diet (Meijaard and Sheil 2008), and increase their consumption of non-fruit food when fruit is scarce (Head et al. 2011; Yamagiwa and Basabose 2009), thus enabling a degree of resilience to disturbance (Milton et al. 2005). However, fruits continue to play a crucial role in great ape socio-ecology (Doran et al. 2002). Consequently, it is important to differentiate between short-term fluctuations in fruit availability to which great apes exhibit resilience (Milton et al. 2005), and long-term loss of fruit resources in the forest habitat as a result of habitat degradation, an alteration that could ultimately lead to great ape extirpation (Behie and Pavelka 2015; McLennan 2013; Rosa et al. 2016).

Conclusion

HCVF is an important management tool that proposes sustainable natural resource management outside of protected areas. The major challenge of HCVF is to define areas that comprise important resources necessary for populations to survive (Morgan et al. 2013). We have demonstrated that setting priority areas for species conservation by considering abundance alone is inappropriate for species survival, and instead recommend considering both species abundance and resource distribution when formulating conservation decisions. HCVF constitute areas consisting a high availability of the target species’ preferred habitat conditions, and the highest abundance of presence signs. Therefore, extractive activities

should be managed in areas allocated to resource production, to avoid habitat fragmentation or degradation that may lead to the isolation of the priority area (Fahrig 1999). Subsequently, restoration activities will be required following resource extraction (Shi et al. 2005). The designation of priority areas for conservation implies setting aside an area for conservation while assigning surrounding areas to extractive activities. It is worth noting, however, that areas set aside as HCVF are not necessarily the only areas where animal presence indices are observed, and landscape-wide conservation should be considered. For example, in this study, the proposed HCVF is composed of two zones exemplifying the relationship between gorillas and their habitat requirements. Meanwhile, the distribution of gorilla suitable nesting habitats offers the possibility to consider in the final HCVF map (Fig. 5c), a corridor that will allow the apes to move between areas of key resources when necessary. An important contribution for the improvement of the conservation of threatened mammals may be research into the evaluation of factors affecting their spatial distribution.

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Appendix: Description of the different habitat types present in the study site

The different habitat types considered in our study were adapted from Willie et al. (2013, 2014). We distinguished seven habitat types in our study site: Near primary forests (NPF) comprise large and tall tree species (Diameter at Breast Height (DBH) > 60 cm and height > 30 m) with an almost open canopy (examples of common species include *Piptadeniastrum africanum* and *Distemonanthus benthamianus* of families Mimosaceae and Ceasalpiniaceae, respectively); Old secondary forests (OSF) are characterized by the presence of large trees (DBH > 60 cm) relatively less tall than those of NPF (height 25–30 m); Young secondary forests (YSF) are characterized by the presence of pioneer tree species with relatively small diameters (DBH < 25 cm and height < 25 m), and dense understory (e.g. *Tabernaemontana crassa*, Apocynaceae); Light gaps (LG) are the result of an original vegetation where some trees were felled by elephant activity, branch fall or natural death, leading to an open canopy; Swamps are vegetation types growing in hydromorphic soils characterized by the presence of *Raphia spp.* as dominant species. Riparian forests (RF) develop on soils temporally inundated; consequently, they share many plant species with many other habitat types (*terra firma* and swamps); Fallows are forests with signs of the existence of old farms (e.g. cocoa, palm trees, etc.).

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