

RESEARCH ARTICLE

Distribution and Numbers of Pygmies in Central African Forests

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Abstract

Pygmy populations occupy a vast territory extending west-to-east along the central African belt from the Congo Basin to Lake Victoria. However, their numbers and actual distribution is not known precisely. Here, we undertake this task by using locational data and population sizes for an unprecedented number of known Pygmy camps and settlements ($n = 654$) in five of the nine countries where currently distributed. With these data we develop spatial distribution models based on the favourability function, which distinguish areas with favourable environmental conditions from those less suitable for Pygmy presence. Highly favourable areas were significantly explained by presence of tropical forests, and by lower human pressure variables. For documented Pygmy settlements, we use the relationship between observed population sizes and predicted favourability values to estimate the total Pygmy population throughout Central Africa. We estimate that around 920,000 Pygmies (over 60% in DRC) is possible within favourable forest areas in Central Africa. We argue that fragmentation of the existing Pygmy populations, alongside pressure from extractive industries and

dictate or influence the results or discussions in this paper.

sometimes conflict with conservation areas, endanger their future. There is an urgent need to inform policies that can mitigate against future external threats to these indigenous peoples' culture and lifestyles.

Introduction

Locational information and population estimates are crucial for developing appropriate human rights and land security safeguards for indigenous peoples [1]. However, there are considerable challenges to evaluating numbers or their actual geographic ranges. In the case of the Pygmies (see [S1 File](#)), there is uncertainty on current numbers living in Central Africa. For example, there may be between 100,000 and 250,000 Pygmies in DRC as a whole, though some estimates mention up to 660,000 [2]. The main difficulty in estimating Pygmy population numbers in DRC is the lack of proper census data, but some approximations are available from censuses for CAR and Gabon, though only households in villages but not forest camps. In the CAR, only 0.3% of the population are likely to be Pygmies, in Gabon the percentage is also well below 1% [2]. Pygmies are thus a small minority in the countries in which they live, politically insignificant, but a central component of national culture and history. Despite small numbers by modern standards, they are the largest group of hunter-gatherers in Africa, and possibly the world.

The geographic distribution of Pygmies in Central Africa has been represented in a number of published maps [3–6]. Although there are some coincidences between these maps, they are imprecise because they have relied on unverified range approximations from verbal or informal reports of field workers. Published distribution ranges of the various Pygmy groups are therefore difficult to compare. Generally, three main groups of Pygmy populations are recognised [3], each containing different ethnic groups: 1) a Western group composed of the Gyeli, Bongo, Kola, and Zimba, inhabiting the western Atlantic forest; 2) the BaYaka (Aka, Luma, Mikaya, Mbendjele, Ngombe and Baka) who inhabit forest west of the Congo River towards the Atlantic coast and speak Bantu and Ubangian languages; 3) Twa (Tua, Toa, Cwa, Boone, Langi, Chua, and many others) living east from the Congo River to Burundi and Rwanda and speak a wide diversity of languages, and 4) an Eastern group, the Mbuti (Efe, Asua, Sua and Kango), living in the Northeasternmost part of the Central African belt in the region of the Ituri rainforest and Lake Victoria, who speak Bantu and Central Sudanic languages.

Although accumulated knowledge on culture and lifestyles of Pygmies has increased in recent years [7], no one has attempted to predict the occurrence or areas of ecological importance for the largest groups of remaining active hunter-gatherers in the world. Here, we employ a species distribution modelling (SDM) technique [8] based on the favourability function [9, 10], to forecast the distribution of Pygmies in the Congo Basin. Favourability is a measure of the degree to which local conditions lead to a local probability higher or lower than that expected at random, being this random probability defined by the overall prevalence of an organism [9]. SDM techniques have been utilised to predict contemporary [1, 11] and Palaeolithic [12] human populations.

Materials and Methods

Study Area

Pygmy groups are found in forests within the limits of the Rainforest Biotic Zone (RBZ) of central Africa. The RBZ, as defined by Happold & Lock [13] encompasses six main countries

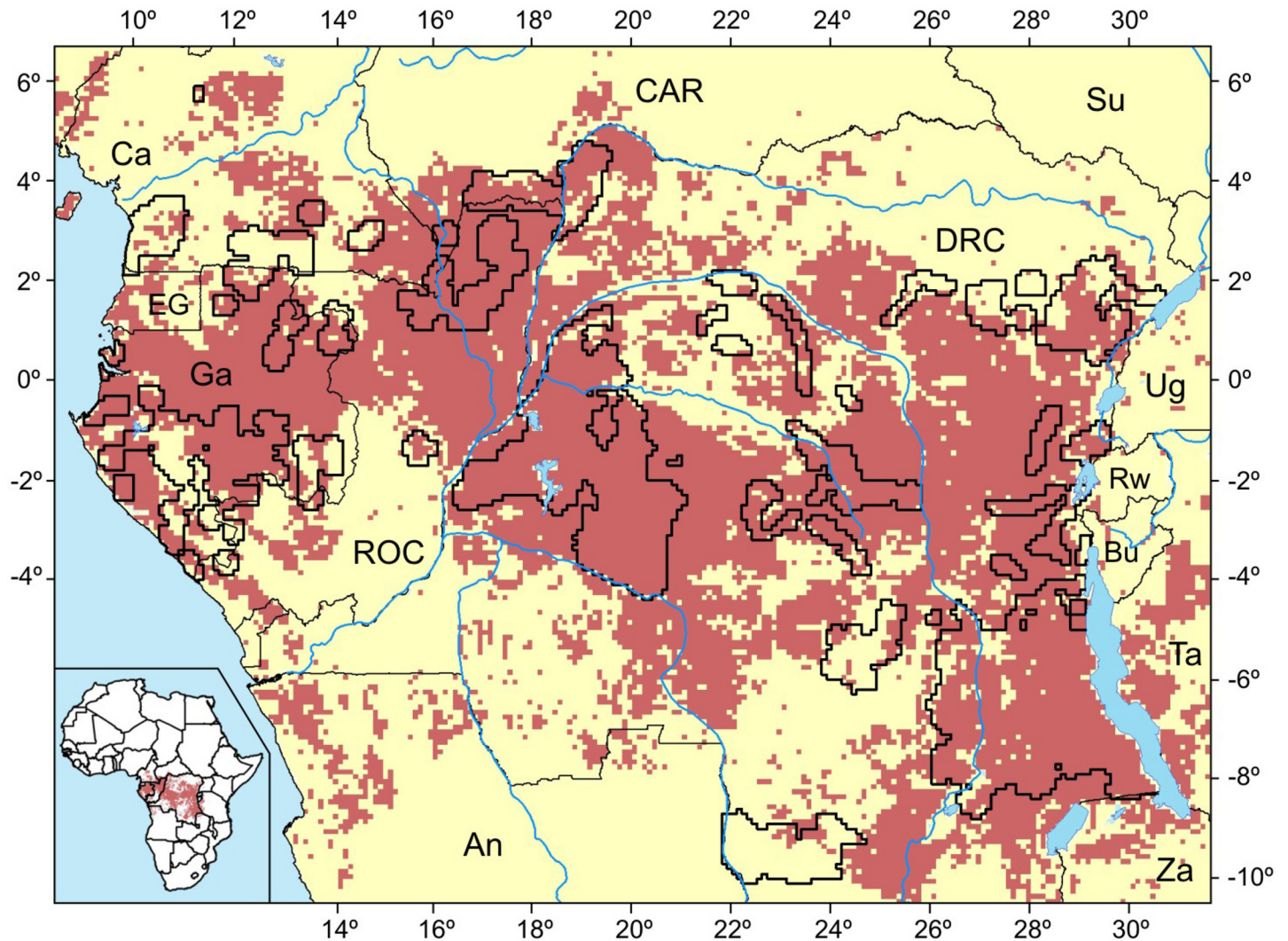


Fig 1. Environmental favourability (F) model for Pygmies. Red: $F > 0.5$; yellow: $F < 0.5$. Presence areas are delimited with a thick black line. (Ca: Cameroon; CAR: Central African Republic; Su: Sudan; EG: Equatorial Guinea; Ga: Gambia; RoC: Republic of Congo; DRC: Democratic Republic of the Congo; Ug: Uganda; Rw: Rwanda; Bu: Burundi; Ta: Tanzania; An: Angola; Za: Zambia).

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(DRC, ROC, CAR, Cameroon, Gabon and Equatorial Guinea), as well as parts of another three (Angola, Burundi and Rwanda) (Fig 1). The main vegetation type in the region is Guineo-Congolian lowland rainforest, concentrated in the Congo basin, corresponding to the second largest (close to 2 million km²) and the least degraded area of contiguous tropical rainforest in the world. These forests constitute almost 91% of Africa’s rainforests—they are the continent’s main forest resource and home to an extraordinary biological and cultural diversity.

Pygmy occurrence data

We gathered georeferenced location data (S1 Table) for a total of 654 documented Pygmy camps (S1 Fig) in five Central African countries (Cameroon: 240, CAR: 76, Gabon: 82, ROC: 39, DRC: 217) available for our study. All camps considered in this study were of Pygmy groups only, since Pygmies are intermixed with Bantu families in some villages. These data, derived from field observations of Pygmies in forest during 1985–2014 (though >75% were

post-2008), were treated as definite presence of Pygmies at the time of each field study. Registered localities were a mixture of ancestral areas, as well as sites used by Pygmies after displacements by other ethnic groups [14] and forced relocation and sedentarisation [15,16].

We supplemented the more precise Pygmy camp information with published extent-of-occurrence maps of Pygmy distributions for Gabon [17] and DRC [18]. These maps contained distribution polygons within which Pygmy occurrence had been established through national consultations with Pygmy support organizations, representatives of the government and donors.

Although the interplay of social structure, environmental conditions, and cultural factors affect hunter-gatherer population size and demography, there is evidence that similar factors to other mammals, condition how human societies interact with their resource base. Generally speaking, area used and population size of human settlements is positively correlated [19]. In the case of Pygmies, according to data for measured subsistence areas ($n = 29$ camps, S2 Table), published in Hoare [20], average camp size was 248.03 ± 43.95 people (mean \pm SE, range 12–842) and mean subsistence area was $1,079.38 \pm 98.0$ km² (range 214–5,964 km²). Population sizes and subsistence areas were significantly positively correlated ($R^2 = 0.14$, $P < 0.05$).

Although there is still a scarcity of data on Pygmy movement ecology and space use, territory sizes are unlikely to be circular, because Pygmies, like most human resource users, are central place foragers [21]. Therefore, movements for hunting and foraging away from settlements are likely to be linear, consisting of an outward journey, a period of resource extraction and a return journey [34]. Recorded maximum travel distance is almost 76 km [22] although the average from 36 studies is 21.0 ± 3.65 km [20,22–25], varying by group and possibly habitat. Among Aka Pygmies, movements between 0–20km and 60–80km have been recorded [24].

For the purpose of this study, we generated a theoretical unit area of land around each known Pygmy camp liable to be exploited for natural resources. To determine this area, we first determined the mean radius (18.5 ± 1.0 km) encircling a settlement, by using average subsistence area. From this, we created a buffer zone of 20-km, on the basis of the mean radius calculated and on the average travel distance of 21 km (see above). We then applied this buffer to all camps in our database to plot onto a $0.1^\circ \times 0.1^\circ$ map of the study area (6.7°N , 10.5°S , 31.6°E , 8.4°E). This resulted in 5,926 grid cells of Pygmy presence, out of the total of 35,340 cells that covered the entire study area (Fig 1). With this grid approach, which is equivalent to a systematic sampling that covered the whole extent of the study area, we aimed at minimizing bias outcomes resulting from spatial dependence among observations (i.e. autocorrelation [26]). We then considered absences to be those grid cells not included in the presence-grid-cells subset, and used the Pygmy presences/absences for modelling environmental favourability.

Distribution modelling of environmental favourability

To model the potential distribution of Pygmies throughout Central Africa, we used the Favourability Function [9]. The Favourability Function is based on logistic regression, but cancels out uneven proportions of presences and absences in the modelled data. Favourability thus assesses the extent to which the environmental conditions change the probability of occurrence of an organism with respect to its overall prevalence in the study area. Here, we take this approach to model the relationships between human societies and environmental variables.

We first built an environmental favourability model for Central Africa, by considering 34 predictor variables (S3 Table). Ecological factors that could condition environmental favourability for hunting and gathering were based on habitat descriptors such as climate, topo-hydrography and ecosystem type. Alongside these, we included descriptors of human land use and human activity to represent anthropogenic impacts.

We employed a combination of five climate variables (*maximum annual temperature, minimum annual temperature, maximum annual temperature range, annual precipitation, and intra-annual pluviometric irregularity*), four topo-hydrographic indicators (*elevation, slope, distance to water masses, and distance to minor rivers*) as well as 8 ecosystem type descriptors based on vegetation structure (*broadleaf evergreen/semideciduous rainforests, swamp forests, deciduous forests, woody savannas, shrublands, grasslands, deserts, intact forest*). Additionally, we considered 17 indicators of anthropogenic activity in terms of human concentration (*rural population density and distance to populated places*), infrastructures (*distance to roads and distance to railroads*), agriculture (*intensive croplands, non-intensive croplands, cropland [$>50\%$]/vegetation mosaics, vegetation [$>50\%$]/cropland mosaics, global constraints for cropping activities, and percentage of area equipped for irrigation*), livestock (*pasture and browse, density of poultry farms, density of pigs, density of cattle, and density of small ruminants*), nature conservation policies (*distance from protected areas*), and exploitation of fauna (*bushmeat extraction*). All variables defining types of land-cover/use were computed as cover percentages in every grid cell, and the rest of variables were estimated by averaged grid-values. All spatial operations, including the calculation of distances to water flows, infrastructures and populated places, were performed using ArcGIS 10.0.

We excluded nonlinear and interaction effects from the model, in order to keep its mathematical formulation as simple as possible for explanatory purposes. To account for Type-I errors caused by the large number of variables considered in our analyses, we controlled the False Discovery Rate (FDR) [27]. Thus, using the presence/absence of Pygmy settlements as the dependent variable, we ran a logistic regression on each of the 34 predictor variables, and only significant ($P < 0.05$) variables under an FDR of $q < 0.05$ were accepted as part of a multivariate environmental model. Only then did we perform a multiple logistic regression employing forward stepwise variable selection (using IBM SPSS statistics 22), and finally transformed probability outputs into favourability values [9, 10].

The model was finally assessed for calibration using the Hosmer-Lemeshow [28] index and the Rooted Mean Square Error (RMSE) [29]; for discrimination capacity using the Area Under the receiver-operating-characteristic Curve (AUC) [30]; and for classification capacity using sensitivity, specificity, Cohen's Kappa [31], and under- and overprediction rates [32]. For calibration purposes, we used 10 probability bins based on equal distribution of presences; classification measures were based on the 0.5 favourability threshold, because probability is equal to the overall prevalence at this level [10]. Classification and discrimination capacities were expected to be moderate, given the scattered and incomplete knowledge of Pygmy distribution, and the differing underlying causes affecting site selection by Pygmies. Despite this, we still expected to find a favourability model significantly explained by predictor variables, well calibrated, and discriminative.

Explanatory analysis of variables in the model

We employed a variation partitioning procedure to measure the relative participation of three factors [macroecological indicators (i.e. climate), habitat descriptors (i.e. topo-hydrography and ecosystem types) and anthropogenic influences] on the model explanation of favourability for Pygmy occurrence [26,33]. In this way, we specified how much of the variation in favourability was accounted for by the pure effect of each factor (i.e., variation that is not affected by covariation with other factor), and what proportion was clearly attributable to more than one factor (i.e. shared effect).

The significance of the influence of all variables in the model was assessed using the univariate Wald test statistic [28]. Stepwise methods tend to select variables acting on a larger scale in

the first steps and add at subsequent steps only variables significantly related to the residuals not accounted for by previously incorporated variables [34]. The regional relevance of every variable was, thus, analysed using two approaches. Firstly, we measured the correlation (Spearman R) of each variable with the favourability output, and compared the sign of R (which indicates global relationship within the study area) with the sign of the variable coefficient in the model equation (which indicates the sign of the variable contribution to explaining favourability). Secondly, we visualized the regional contribution of each variable to the model by mapping the difference between favourability values obtained in successive steps, along the stepwise variable selection.

Estimating Pygmy population densities

VanDerWal *et al.* [35] have suggested a positive association between environmental favourability values and population size. Empirical evidence for a large number of vertebrate species shows that local population density is positively related to environmental suitability [36]. This relationship is expected to be triangular, since many factors may reduce the theoretical maximum density that a species can reach at a certain location. Favourability, in particular, has been shown to reflect maximum density better than probability when prevalence is uneven, as is the case in this study [37].

The relationship between Pygmy population density and environmental favourability was examined in 90 grid cells ($n = 188$ localities) for which camp-size data were available (S1 Table, S1 Fig). We calculated Pygmy population densities from the sum of all Pygmy population figures reported for the same $0.1^\circ \times 0.1^\circ$ grid cell (123 km^2 at the Equator). Coverage of existing camps for the study areas included here is likely to be fairly complete (given the manageable size of the grid cell used). However, two caveats exist: first, camps varied in their dependence on forest resources, i.e. all hunted and gathered, but some relied upon farming more than others; and second, not all reported population sizes were taken during the same time period. We examined the shape of the population—favourability values point cloud, after population-size outliers were eliminated following Tukey [38] [i.e., if population size $> Q3 + 1.5 \times (Q3 - Q1)$, where $Q1$ and $Q3$ are the first and the third quartiles, respectively] and found a typical wedge-shaped relationship. We were then able to use ordinary linear regression to test the significance of a positive relation, and a quantile regression [39] to extrapolate the upper limit of population size to the whole study area, as a function of favourability.

Estimating Pygmy populations

We calculated the Pygmy metapopulation in Central Africa. We use the term metapopulation here to encompass all spatially separated populations of Pygmy groups, which may interact at some level. First, we divided the range of environmental favourability into three distinct categories, unfavourable: <0.2 , medium: $0.2-0.5$, favourable: >0.5 . We then calculated the average Pygmy population size empirically observed in all 123-km^2 grid cells with favourability values belonging to the three categories; these averages were built upon the 90 grid cells for which data on settlement size were available (excluding outliers). Using these figures, we then calculated the potential population size (PPS) for every grid cell in the study area, according to their favourability values. Finally, we summed all PPS values for the entire study area, but applied the following correction to take territoriality into account:

$$\text{Metapopulation} = GPPS \times GCS / ASA \quad (1)$$

where the metapopulation is the net potential population size; $GPPS$ is the gross potential population size resulting from the sum of the PPS values; GCS is the size of a grid cell (i.e.

123 km²); and ASA is the average subsistence area estimated for Pygmies (i.e. 1,079 km², see [Pygmy Occurrence Data](#) above). The resulting metapopulation number was estimated for the entire Central African study area, and then individually computed for each of the eight countries in which Pygmies occur.

Relationship between Pygmy camps and roads

From colonial to recent times, a large number of Pygmies have been subject to relocations, voluntary and forced, along roads [15]. We analysed the link between environmental favourability and proximity to roads as a means of testing whether Pygmy camps are disadvantaged close to roads. We used box plots to examine the relationship between favourability and distance to roads for those localities where Pygmy presence has been recorded (see above). Favourability was divided into the three distinct categories for estimating metapopulation size (i.e. unfavourable: <0.2, medium: 0.2–0.5, favourable: >0.5). We used an analysis of variance (ANOVA) to determine whether differences between the three classes are significant, for the log-transformed distance values [40]. Tukey's honestly significant difference (HSD) post hoc tests were applied when significant differences ($p < 0.05$) were found between the favourability classes.

Results

We obtained a significant environmental favourability model for Pygmy distribution in Central Africa ([Fig 1](#) and [S1 Fig](#)). The model was significantly well calibrated (Hosmer-Lemeshow index = 14.18; $P_{10} > 0.05$), with a low deviation between observed and predicted presences (RMSE = 49.9; for a total of 5926 presences). The model had an acceptable discrimination capacity (AUC = 0.770), and a fair classification capacity (Cohen's Kappa = 0.246). The proportion of correctly classified presences was higher than that of absences (sensitivity = 0.733; specificity = 0.659), meaning that favourable areas covered recorded presences but were not restricted to them. Although under-prediction was low (0.073), meaning that Pygmies were observed to occur in a low proportion (7%) of unfavourable areas, the model had a high over-prediction rate (0.704), thus indicating that Pygmy presence was not reported in 70% of favourable areas.

Our favourability model combined 26 of the 34 proposed variables to explain significantly the presence of Pygmies in 5,926 of the 35,340 cells ([Table 1](#)). Habitat descriptors and anthropogenic influences explained a similar proportion of the spatial variation in favourability: 54.5% and 62.6% respectively ([S2 Fig](#)). However, climate only explained 23.4%. Shared effects between different factors (meaning either cross or indistinguishable explanatory power) were found; habitat and anthropogenic factors shared 26.2% of their influence, whilst climate shared 14% with the other two factors. As a result, the pure effect of habitat and anthropogenic influences respectively only explained around 30% of favourability each. The pure effect of climate explained less than 10%.

Variables with the highest explanatory power within the model (Wald statistic > 250) were primarily habitat type descriptors ([Table 1](#)). In fact, the correlation (Spearman R) between favourability and forest surface area (i.e. the sum of *broadleaf evergreen/semideciduous forests*, *swamp forests* and *deciduous forests*) is highly significant: $R = 0.667$, $P_{35, 341} < 0.001$ ([S3 Fig](#)). Broadly speaking, habitat variables, and descriptors of the intersection between farming and forest areas, were positively related to high environmental favourability areas for Pygmies. In contrast, most anthropogenic variables limited the environmental favourability for Pygmies in the model (*livestock*, *indicators of intensive agriculture*, and *communication infrastructure*). Some variables, such as *broadleaf evergreen/semideciduous rainforests*, *swamp forests*, *short distance to water masses*, and *long distance to roads and railroads*, had a positive influence on the

Table 1. Descriptor variables of the environmentally favourable areas for Pygmies according to the favourability model. Step: Order or entrance in the model; W: Univariate Wald test statistic quantifying variable significance in the model (all the variables shown were significant with $P < 0.05$); CfS: Sign of the variable coefficient in the model; CrS: Sign of the correlation (Spearman) between the variable and favourability values; AGI: Area of geographic influence of the variable in the model within the Central African study area (N = North, S = South, E = East, SE = South-East, W = West).

Variable	Step	W	CfS	CrS	AGI
Variables describing favourable areas for Pygmies globally					
Rainforest	3	499.3	+	+	
Distance to water masses	2	420.3	-	-	
Flooded forest	5	269.8	+	+	
Distance to railway	12	232.7	+	+	
Distance to roads	1	193.4	+	+	
Min. temperature	22	29.7	+	+	
Bushmeat extraction	17	25.1	-	-	
Intact forest	19	19.7	+	+	
Constraints for agriculture	20	12.6	-	-	
Variables describing favourable areas for Pygmies regionally					
Deciduous forest	4	482.5	+	-	E, SE
Cropland	9	372	+	-	N, E, SE
Woody savanna	6	288.1	+	-	N, E, SE
Rainfall seasonality	13	137.2	+	-	E, SE, W
Veg./crop mosaic	14	128.4	+	-	E, SE
Herbaceous vegetation	15	50.7	+	-	W
Altitude	21	43.2	+	-	E, SE
Sheep/goat prod.	24	12	+	-	N, E, SE
Variables apparently outlining unfavourable areas for Pygmies					
Beef production	8	211.4	-	-	
Distance to populated places	7	144.4	-	+	
Temperature range	11	141.6	-	-	
Precipitation	10	80.8	-	+	
Poultry production	16	63.1	-	-	
Rural population density	18	23	-	-	
Irrigation equipment	23	14.3	-	-	
Pork production	26	11.1	-	-	
Agricultural land	25	4.7	-	-	

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presence of Pygmies, i.e. they showed identical signs within the model equation and in the variable correlations with the model, and their entry into the model produced a generalized increase of favourability (Table 1, S4 Fig). Other variables [*deciduous forests* and *vegetation/cropland mosaics* (East/South-East), *woody savannas* and *non-intensive croplands* (also in the North), *annual pluviometric irregularity* and the *distance to populated places* (also in the West)] also had positive influences, though they were limited to a regional context, mostly to the east and the south-east (i.e. the sign within the model equation was positive, whereas that of the correlation with the model was negative; and their entry into the model produced a regional increase of favourability). Finally, a set of variables, most of them indicators of farming practices (livestock and intensive agriculture), represented environmental constraints to Pygmy occurrence, especially in the peripheral areas (i.e. both signs within the model equation and of variable correlations with the model were negative; and their entry into the model produced a regional decrease of favourability).

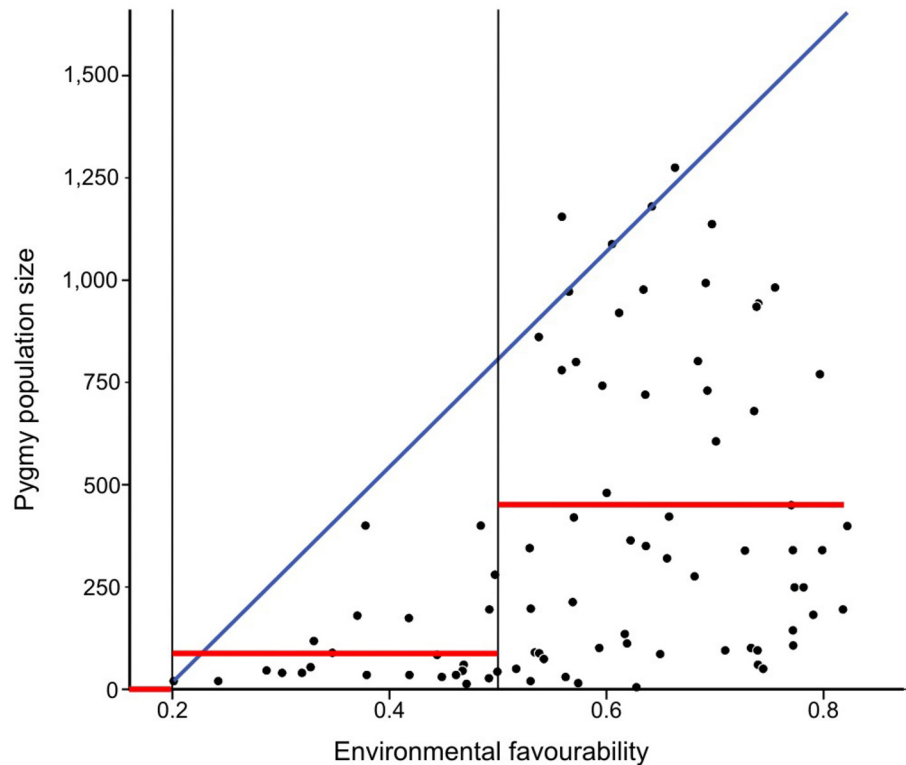


Fig 2. Space defined by predicted environmental favourability (x-axis) and population size (y-axis). The scatter plot shows a polygonal wedge-shaped spread of points with the upper limit increasing at higher favourability values. The blue line fits the quantile regression with the 95th percentile, representing the upper limit of potential population size. Red lines indicate average population size considered, in every favourability category (<math><0.2</math>, $0.2-0.5$, >0.5), for estimating net potential population size in the Central African studied area.

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Predicted environmental favourability (x-axis) and population size (y-axis) exhibited a polygonal wedge-shaped spread of points with the upper limit increasing at higher favourability values (Fig 2); five outliers (population size > 1,563 inhabitants / km²) were eliminated from the dataset. Population size and environmental favourability were positively correlated ($F_{1,82} = 13.3, P < 0.001$). The quantile regression with the 95th percentile outlined very narrowly the upper limit of population size as a function of favourability: Upper limit of population size = $-509.767 + 2,633.026 \times \text{Environmental Favourability}$ (see Fig 2 and S1 Fig).

We calculated a Pygmy potential metapopulation size for Central Africa of $919,500 \pm 226,500$. By country, the largest potential population of Pygmies was estimated for the DRC, followed by Gabon, ROC, Cameroon and CAR; the smallest populations were for Rwanda, Burundi and Uganda (Fig 3).

Distance to the road network was significantly related to environmental favourability (ANOVA: $F_{2, 5923} = 262.5, P < 0.001$; Fig 4). This distance was significantly higher in the most favourable areas (favourability value > 0.5) compared to unfavourable (< 0.2; HSD = 21,833.3; $p < 0.001$) and intermediate-favourability areas (0.2–0.5; HSD = 23,309.4; $P < 0.001$).

Discussion

This paper is the first to have compiled such a large collection of known location and population data of Pygmy camps in Central Africa. These records (75% gathered after 2008, and 81% post-2000) allow for a valid comparison given that Pygmy dispersal is strongly localized.

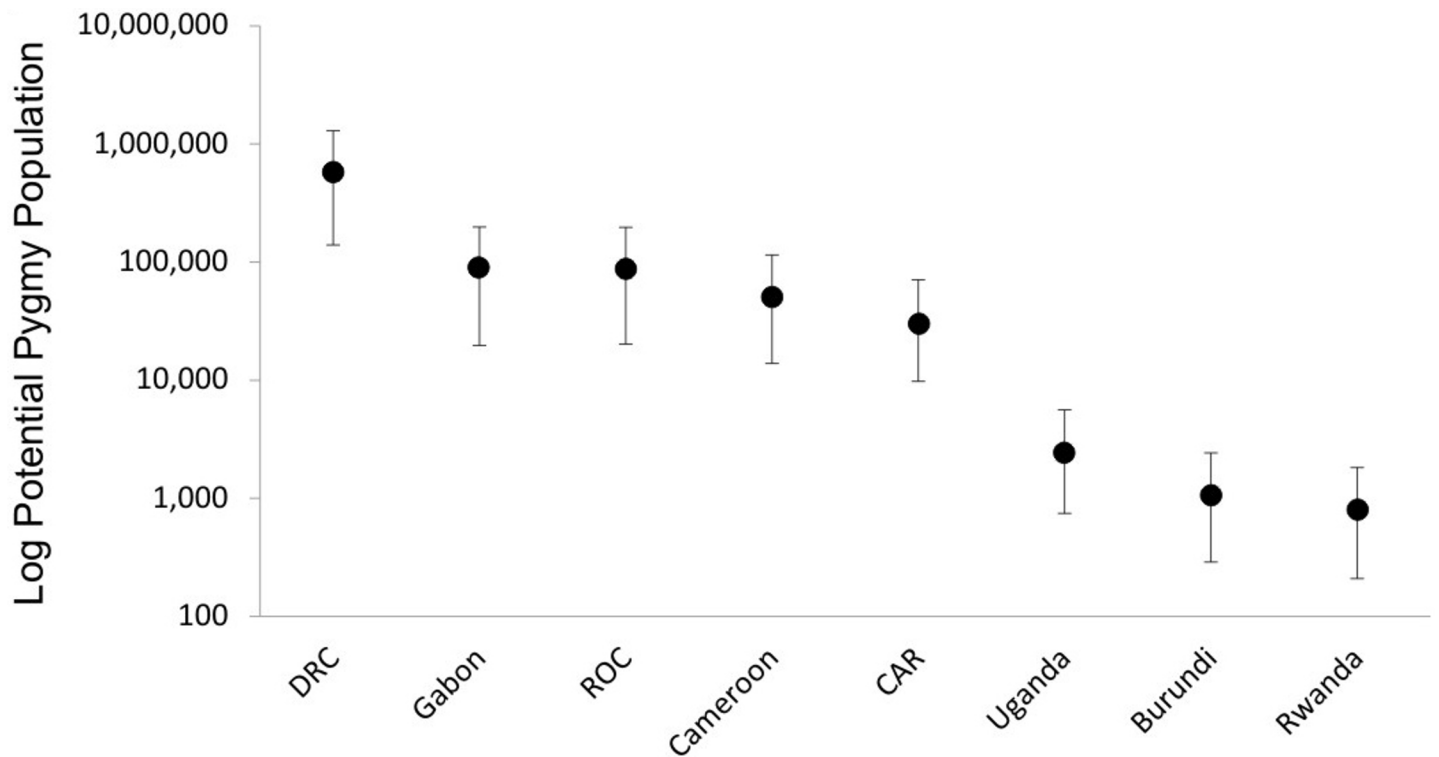


Fig 3. Estimates of potential Pygmy population size by countries in Central Africa.

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Genetic studies of Western Central African Pygmies indicate a strong differentiation, suggesting that in the Baka, dispersal over wide geographical areas rarely occur [41], though population concentration (further travel at lower densities) and culture can alter this (B. Hewlett, pers. comm.). Thus, All things being equal, camp movements, if they did occur between our first (1985) and last studies (2014), were unlikely to have significantly changed the location of the sites to have affected our modelling outputs.

Our model classified potentially suitable areas for Pygmy settlements in a fairly robust manner, despite the relatively sparse data available on Pygmy presence. Although we were able to cover only 17% of the total surface of the study area, we did not find any evidence that our model was biased by overfitting [42]. The most favourable areas for Pygmies according to our model are those areas contained within Guineo-Congolian forests of Central Africa (technically the Congo–Ogooué Basin and contiguous forests, hereafter termed the Congo Basin for brevity), which accounts for 89% of African rainforests. In our model, three forest variables (*broadleaf evergreen/semideciduous rainforest*, *deciduous forests* and *swamp forests*), included among the first five variables entered in the stepwise variable selection procedure, were the most important descriptors of Pygmy presence. In fact, the correlation between the complete favourability model and the 5th step-model (from the first five variables) was 0.783, thus confirming that all variables other than the five main ones were of lower significance. Hence, rainforest variables had a wide-scale positive influence on Pygmy presence. This relationship is strong, not just in those countries where we were able to obtain direct camp data, but also in those others (Rwanda, Burundi, Uganda) where Pygmies also occur [7] but for which no location data were available.

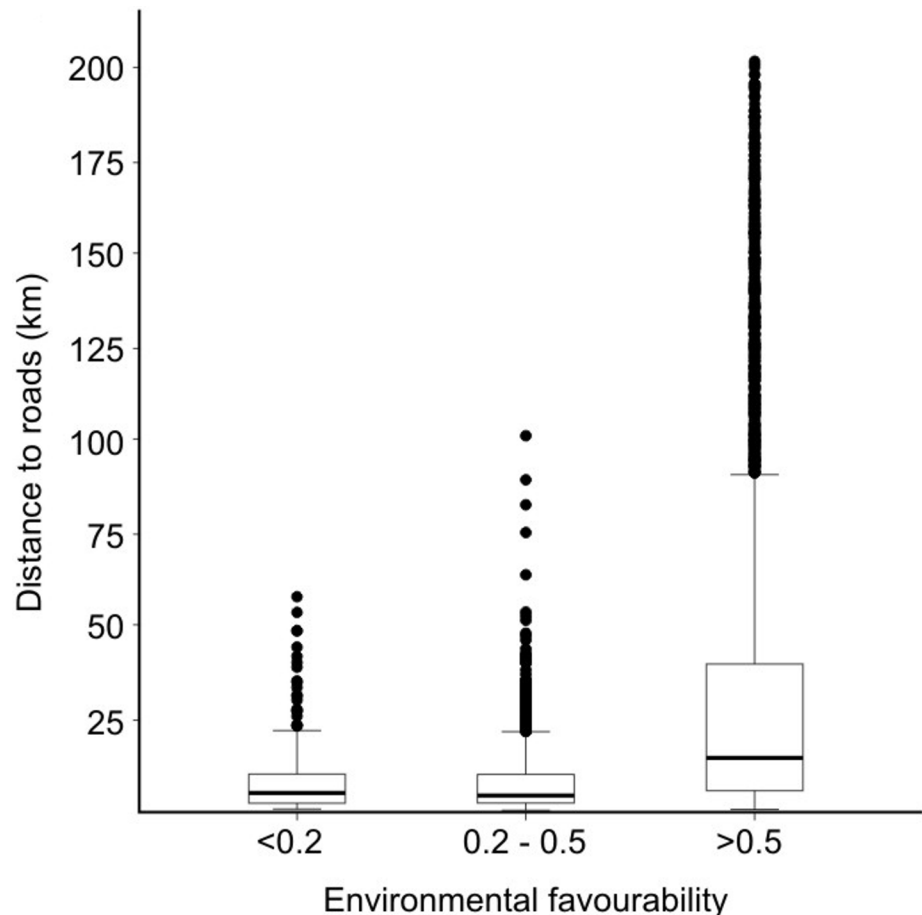


Fig 4. Box-plot showing relationships between favourability and distance to roads, within the areas recorded as Pygmy presences. Box upper limit: Q3; box lower limit: Q1; horizontal line: median; whisker limits: $Q1 - 1.5 \times (Q3 - Q1)$ and $Q3 + 1.5 \times (Q3 - Q1)$; points: outliers.

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Our model also indicated that *deciduous forests* were important for determining Pygmy presence, but this biome is limited to the east and the south of the Congo Basin. This region, primarily the east (Nord and Sud Kivu) and Southeastern DRC (North of the Katanga province), has experienced one of the most intensive sedentarisation processes among Pygmies [18]. In Katanga province, most Pygmy populations no longer live in the forest, but are confined to its margins; links to the forest have been nearly or completely severed along the shores of Lake Tanganyika, and conflicts over access to natural resources still occur [18]. In our model, marginal areas of the main rainforest block, i.e. *deciduous forests*, *woody savannas* and *non-intensive croplands*, are the main descriptors of Pygmy presence in the East and the South-east, as well as in the North of the Congo Basin. Our model was, thus, able to discriminate between the principal areas of Pygmy distribution and more marginal habitats.

One of the most significant variables in our model was the *distance to roads* (Table 1 and S3 Table). Distance to roads was significantly greater in those areas that were environmentally most favourable for Pygmies (Fig 4), especially in the central Congo Basin (see Fig 4 and S1 Fig). In contrast, Pygmy settlements in unfavourable areas were largely linked to roads (S5 Fig). This is the first quantitative indication that Pygmy settlements relocated to roadside areas are in environmentally suboptimal conditions compared to favourable areas determined by

our model. This observation is not surprising given that roads and other linear clearings can have an array of deleterious effects on tropical forests and their wildlife [43], and particularly in diminishing hunting resources [44]. From a socioeconomic point of view, Pygmy groups that have voluntarily moved away from less impacted forest areas have sought opportunities for work and trade [18], some of them owning fields [45]. Pygmy groups that have been relocated as part of official sedentarisation programs set up by governments may have failed to adjust to the new living conditions, often with severe consequences to their way of life [15,23,46]. Reasons for displacements may range from more indirect causes, such as deforestation for agriculture, logging or mining, to forced displacement under social evolutionary ones, which impose European development models which argue that indigenous groups and the protection of areas for nature conservation are incompatible [15, 23, 47].

Through our population-favourability analyses we estimated a population of around 900,000 Pygmies possible throughout all potential favourable areas in Central Africa, more than 60% in DRC. This figure cannot be verified against any available population census data since we extrapolate to areas outside the known distribution ranges of Pygmies. However, it is highly likely that Pygmy populations occur outside the polygons of distribution used for our study, as inferred from the latest Pygmy distribution map generated by the Rainforest Foundation-UK Mapping for Rights program [35].

Censuses are lacking for almost all groups, and estimations of the main Pygmy populations are generalisations from a few studied settlements or a direct extrapolation to areas presumed as occupied based on unclassified-maps. Thus, direct comparisons between our population estimates and published population figures are difficult, primarily because methods on how actual numbers were calculated for the latter are not explicitly described in the literature. The picture that emerges from published estimates for most groups is one denoting a wide spectrum of circumstances ranging from not more than 400 for the Bedzan in Cameroon, to around 50,000 for the Aka in CAR and ROC [7]. In most cases, the degree of fragmentation of all Pygmy groups is high, perhaps more clearly seen for the Bongo Pygmies where around 3,000 Pygmies may be distributed in about 43 subpopulations in Gabon [17]. More dramatically perhaps, our metapopulation estimate for all groups can be presumed to be relatively low, given the total area in which the close to one million estimated Pygmies are found. The metapopulation of Pygmy groups can be considered, at least in theory, to consist of several distinct populations together with areas of suitable habitat, which are currently unoccupied. Each population cycles in relative independence of the other populations and eventually goes extinct as a consequence of demographic or environmental stochasticity (fluctuations in population size due to random demographic events or to natural catastrophes); the smaller the population, the more prone it is to extinction. Although individual populations have finite life spans, the metapopulation as a whole is often stable because immigrants from one population (which may, for example, be experiencing a population boom) are likely to re-colonize habitat, which has been left open by the extinction of another population. Whether these subtleties of population exchanges are likely to happen to ensure the long-term viability of Pygmies throughout Central Africa is still unknown. Although much progress has been made in understanding dispersal and their implications on genetics of Pygmy groups, knowledge is insufficient at present to understand population connectivity or the impact of expansion of growing populations. On the contrary, the future of all Pygmy groups is severely compromised by threats of morbidity and mortality due to disease, discrimination and marginalisation, social alienation, and conflicts with extractive industries, agricultural expansion and occasionally conservation agendas. The latter may be a source of disagreement that could more easily be resolved, since the inclusion of indigenous peoples in conservation of lands can have more positive impacts on conservation outcomes than excluding them from decision-making [20]. Conservation of tropical

forests needs to integrate ecological and cultural components since neither is likely to survive without the other. Because the subsistence economies of indigenous forest peoples are based on the use of and access to natural resources, protection of these resources and of traditional practices for their use, management and conservation are essential to ensure their survival [48]. A number of conventions and similar instruments [49], specify that indigenous and tribal peoples have the right to participate in the use, management, protection, and conservation of natural resources, as well as the right to be asked for their free, prior and informed consent before natural resources on their territories are explored or exploited [50]. Enforcing these already existent instruments is fundamental to ensuring the survival of all Pygmy groups in Central Africa, and that of a unique set of human cultures.

Supporting Information

S1 Fig. Environmental favourability (F) model for Pygmies and correspondence with upper limit of potential population size (UPPS). Presence areas are delimited with a thick black line, and are derived from combining location data with extent-of-occurrence maps. Points indicate location data (grey coloured points had information about population size), which were surrounded with 20-km buffers representing a estimation of subsistence area. Slim black lines correspond to country boundaries. Grey lines represent the road network [Vector Map Level 0 at the Digital Chart of the World (DCW, <http://worldmap.harvard.edu>), updated in 2002].

(TIF)

S2 Fig. Variation partitioning diagram. The numbers specify how much of the variation in environmental favourability for Pygmies explained by the model was accounted for purely by habitat, climate and human factors, and which proportion was attributable to their shared effects (intersections). Values shown are the proportions of variation explained.

(TIF)

S3 Fig. Environmental favourability for Pygmies explained by the model. Favourability is plotted against the proportion of forest (i.e. the sum of *broadleaf evergreen/semideciduous*, *swamp* and *deciduous forests*) surface-area in the 35,340 0.1° x 0.1° cells that covered the study area. Green areas in the map represent forests. The blue line represent the lineal adjustment of these points ($R = 0.667$, $P_{35,340} < 0.001$).

(TIF)

S4 Fig. Mapped contribution of variables to the favourability model along the stepwise variable selection. Green: positive contribution; red: negative contribution.

(TIF)

S5 Fig. Two examples of Pygmy camp locations along the road network, outside the ecologically most favourable areas.

(TIF)

S1 File. Use of term Pygmy.

(DOC)

S1 Table. Pygmy-camp data sources.

(XLS)

S2 Table. Empirical data of territory sizes for Pygmy camps in various localities in Central Africa. Source: Hoare AL. 2007 *Resource rights and timber concessions: Integrating local peoples' land-use practices in forest management in the Congo Basin*. London: Rainforest

Foundation-UK.
(DOC)

S3 Table. Predictor-variable sources of the 34 predictor variables considered to build the environmental favourability model for Pygmies.

(DOC)

Acknowledgments

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Author Contributions

Conceived and designed the experiments: JEF JO RN. Performed the experiments: TB GMC MF FG BH SH JH MI KK JK JL NM AM BN AN DOE PP MR EGJS MT HY. Analyzed the data: JO MAF JEF RR JMV. Wrote the paper: JO JEF.

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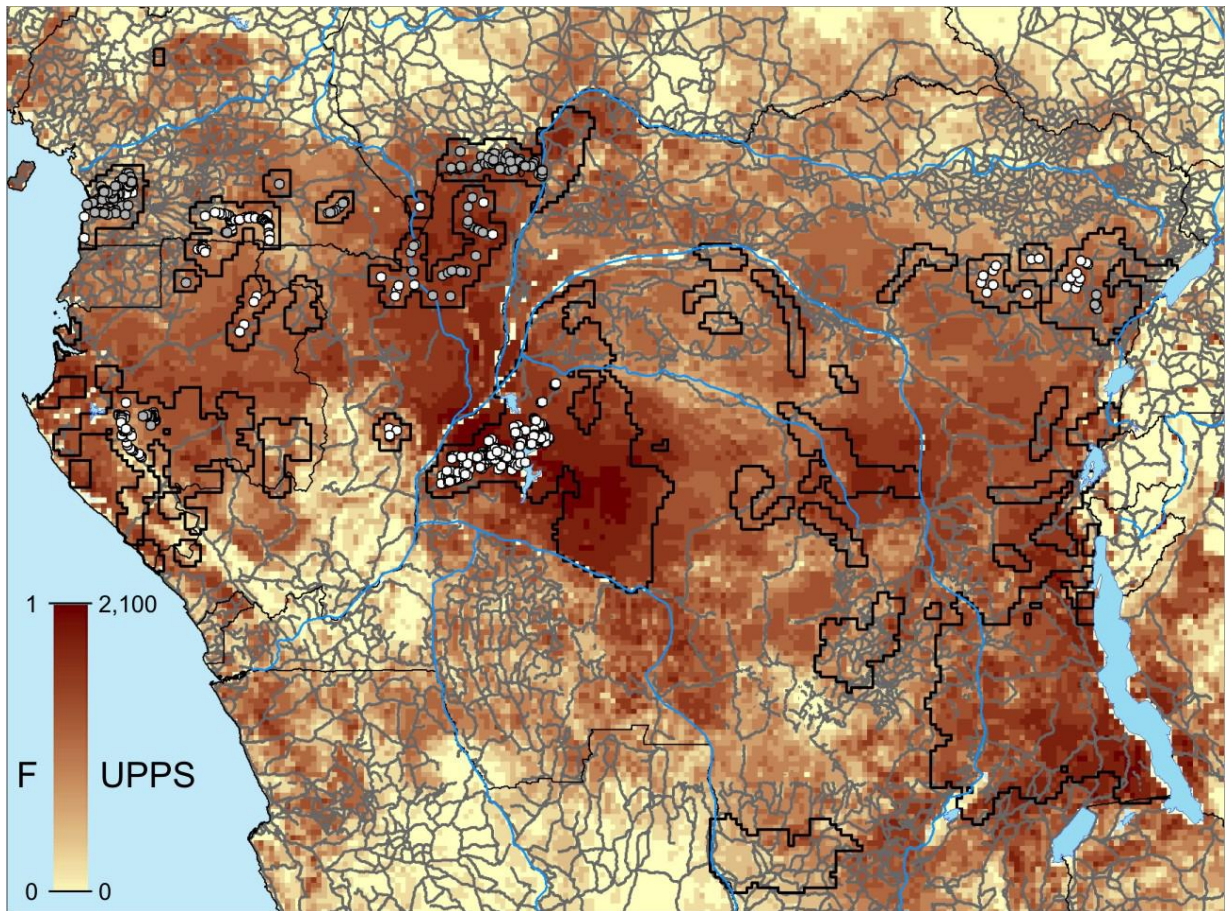
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SUPPORTING INFORMATION

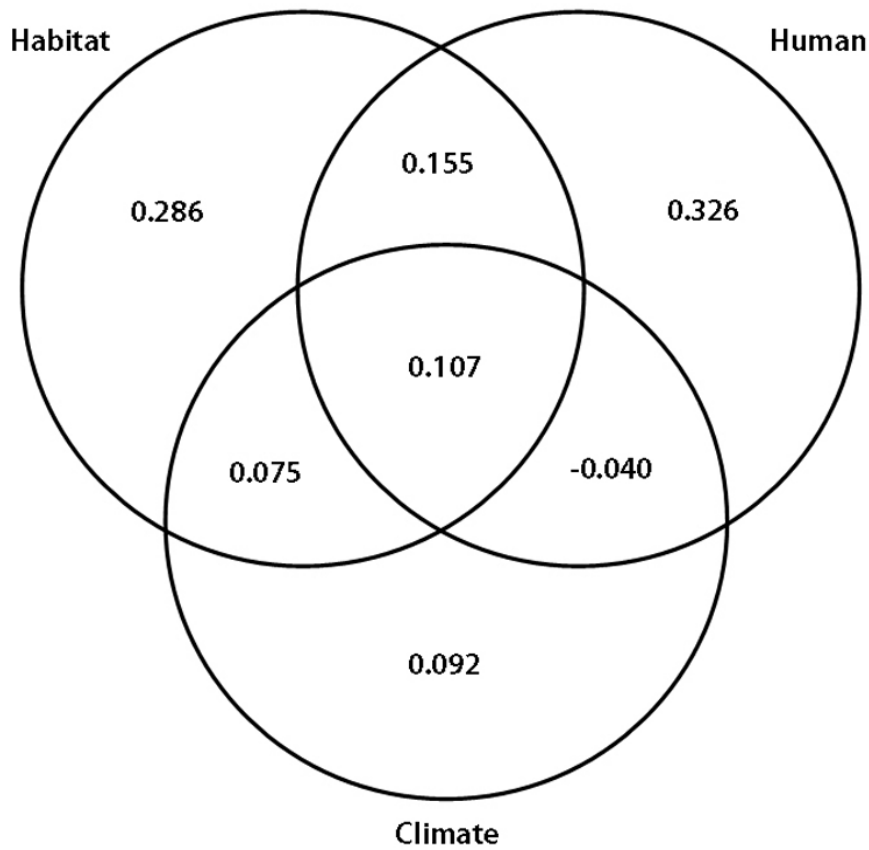
S1 Fig. Environmental favourability (F) model for Pygmies and correspondence with upper limit of potential population size (UPPS).

Presence areas are delimited with a thick black line, and are derived from combining location data with extent-of-occurrence maps. Points indicate location data (grey coloured points had information about population size), which were surrounded with 20-km buffers representing a estimation of subsistence area. Slim black lines correspond to country boundaries. Grey lines represent the road network [Vector Map Level 0 at the Digital Chart of the World (DCW, <http://worldmap.harvard.edu>), updated in 2002].



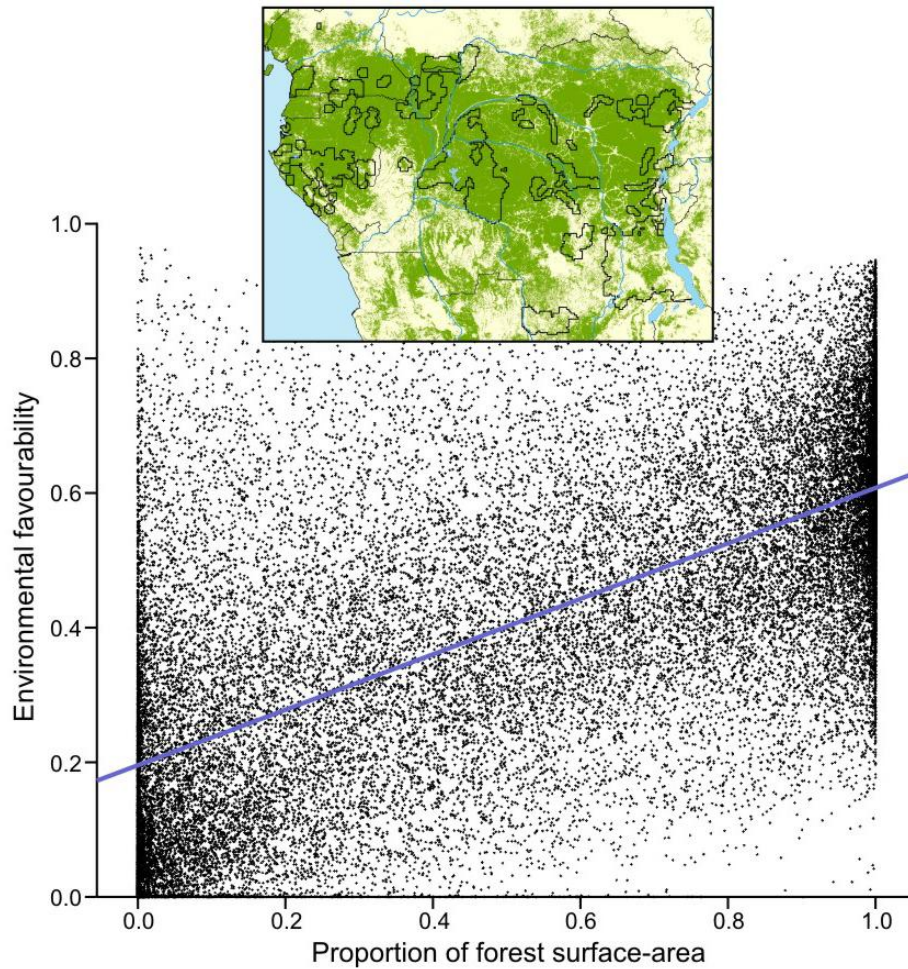
S2 Fig. Variation partitioning diagram.

The numbers specify how much of the variation in environmental favourability for Pygmies explained by the model was accounted for purely by habitat, climate and human factors, and which proportion was attributable to their shared effects (intersections). Values shown are the proportions of variation explained.



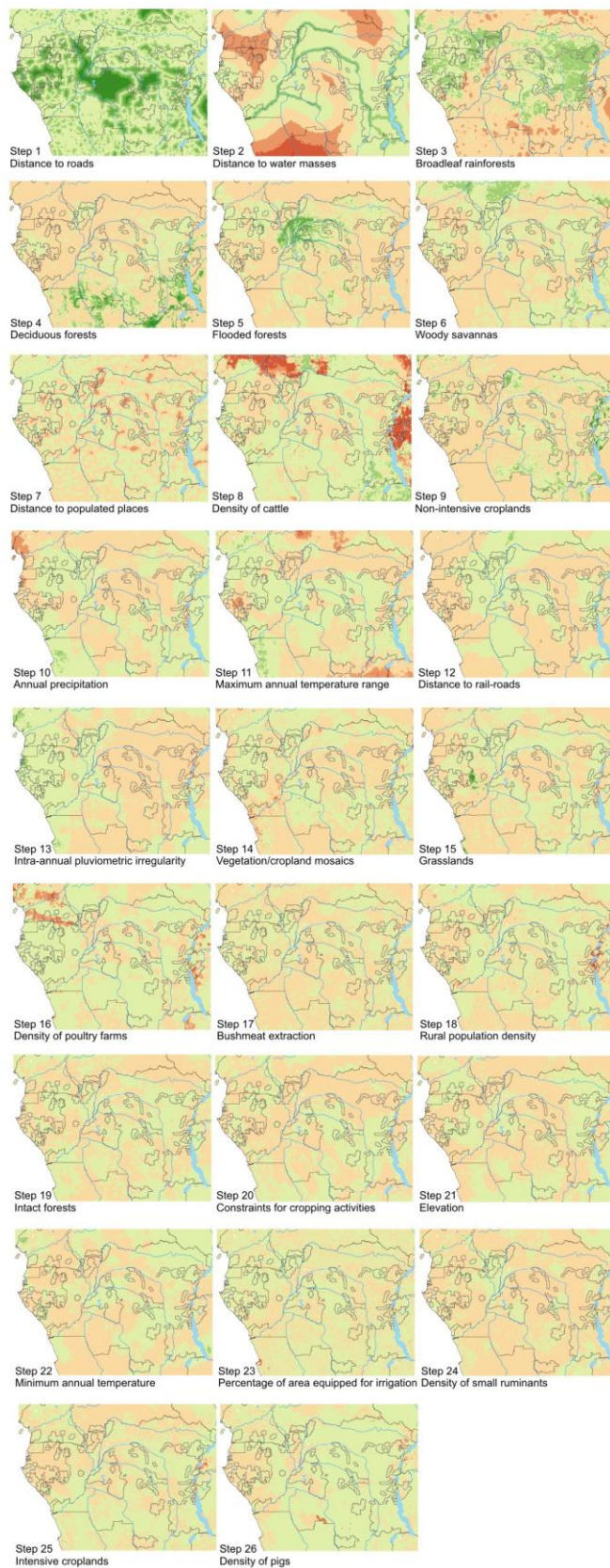
S3 Fig. Environmental favourability for Pygmies explained by the model.

Favourability is plotted against the proportion of forest (i.e. the sum of *broadleaf evergreen/semideciduous*, *swamp* and *deciduous forests*) surface-area in the 35,340 $0.1^\circ \times 0.1^\circ$ cells that covered the study area. Green areas in the map represent forests. The blue line represent the lineal adjustment of these points ($R = 0.667$, $P_{35,340} < 0.001$).

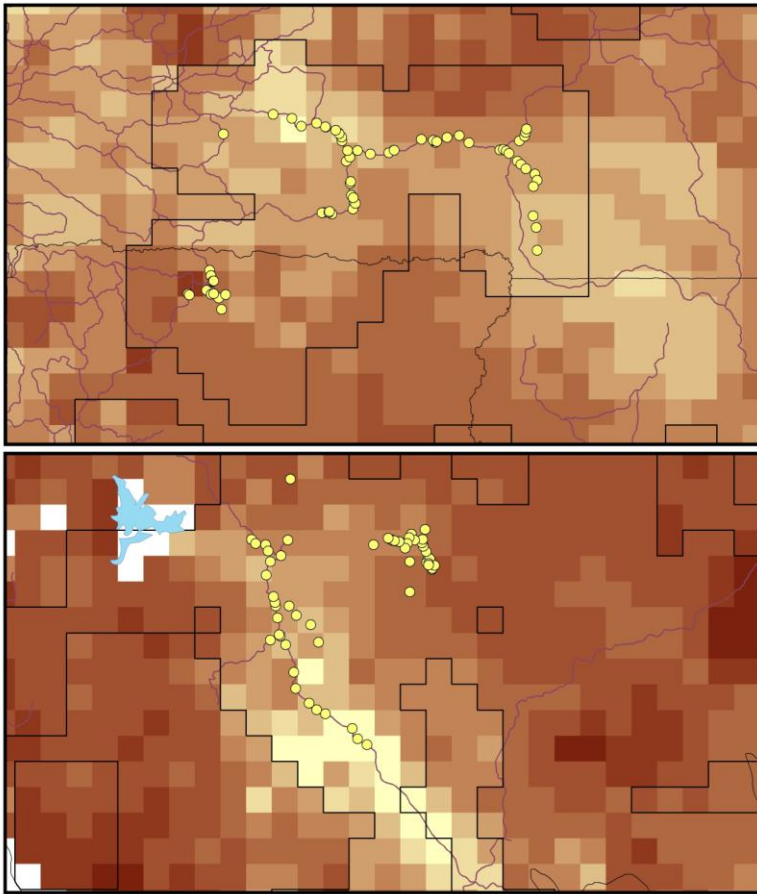


S4 Fig. Mapped contribution of variables to the favourability model along the stepwise variable selection.

Green: positive contribution; red: negative contribution.



S5 Fig. Two examples of Pygmy camp locations along the road network, outside the ecologically most favourable areas.



S1 File

Use of the Term Pygmy

Although numerous alternative terms to Pygmy have been used to refer the rainforest hunter-gatherers of the Congo Basin, none have been agreed upon by academics or the people themselves to replace it. Although some academics and Central African government officers feel the term Pygmy is derogatory or does not adequately represent the people, the term Pygmy *sensu lato*, to refer to all hunter-gatherer groups in Central Africa, is widely used by a broad group of people in Europe, Japan, the United States and Africa. Moreover, International and local NGOs use the term in their titles or literature e.g. *Pygmy Survival Alliance*, *Forest Peoples' Programme*, *Survival International*, *Rainforest Foundation*, *Reseau Recherches Actions Concertees Pygmees*, *Centre d'Accompagnement des Autochtones Pygmees et Minoritaires Vulnerables* and *the Association for the Development of Pygmy Peoples of Gabon*. Congo Basin conservation groups, such as World Wildlife Fund and Wildlife Conservation Society and international human rights groups working in the region, such as UNICEF and Integrated Regional Information Networks (IRIN), also regularly use the term Pygmy in their literature.

In our study, we consider all groups under the umbrella of Pygmy as expressing an equivalent spatial relationship between their presence and their immediate environment. In so doing, we do not ignore the fact that various 'Pygmy' groups express distinct cultures and in some case ethnicity from other 'Pygmy' groups, and is not meant in any way a disrespect to the various ethnicities. Although it is likely that there may be cultural reasons for geographical location and distribution, we argue that the ecological setting is a primary driver in humans in choosing localities to live in. Ichikawa (2014)14:332-3 – 'The forest plants and animals provide the people with the basis for their cultural identity. Their life and culture cannot be maintained without the forest in its entirety ... The destruction of the forest would result in the deterioration of a culture that is heavily dependent on, and in very significant ways a part of, the Congo Basin rainforest.'

Background

Pygmy groups consider themselves, and are judged by their farming neighbours, as the aboriginal people of the Central African forests (Köhler and Lewis 2002). They identify closely with the forest, expressed in the BaYaka saying "A Pygmy loves the forest as she loves her own body" (Lewis 2009), dependent to varying degrees on wild products from the rainforest ecosystem. The archaeological presence of autochthonous Pygmy people in the Congo River Basin is not clear, but recent genetic studies suggest ancestral groups may have entered the forest >50,000 YBP (Patin et al. 2009; Verdu et al. 2009; Verdu 2014). These groups are distributed discontinuously across nine different African countries [Angola, the Democratic Republic of the Congo (DRC), the Republic of Congo (ROC), the Central African Republic (CAR), Cameroon, Gabon, Rwanda, Burundi, Uganda]. Pygmies were also found in Equatorial Guinea (locally known as the Bayele though part of the Kola group of Pygmies from Cameroon), but are now limited to a single extended family in Ayamiken, Northeastern Rio Muni, Equatorial Guinea (Appiah and Gates 2010). Diverse ethnolinguistic Pygmy communities are often hunter-

gatherers or former hunter-gatherers, with variable access to wild forest resources today. They trade with neighbouring farmers to acquire cultivated foods and other material items; it is today rare for groups to live isolated in the deep forest without access to agricultural products, though some still do (Lewis 2005). Despite the great diversity of situations Pygmy groups share some remarkable similarities. In particular, an egalitarian social organization bound up in a matrix with other key cultural practices; some of these as spending at least 4 months a year hunting and gathering in the forest; strongly identifying with and preferring forest life; contrasting the “forest world” to the “village world”; having economies based on demand-sharing; practicing important rituals associated with elephant hunting; having intimate parent-child relations; and diverse relationships with neighbouring farming groups (Hewlett 1996). Most Pygmy groups are mobile within a delimited territory or group of territories to which they have affiliations through clan or marriage relations, moving between places for both social and nutritional reasons. Recent legislation in some countries has recognized the rights of autochthones (indigenous or first peoples) (Republique du Congo 2011). However despite such provisions under law, in all countries where Pygmies are found, they are increasingly marginalised, and threatened by disease, displacement, forced sedentarisation, and deforestation (ohenjo et al. 2006; Wodon et al. 2012).

Data Availability

Data associated with the environmental favourability model has been uploaded as part of the supporting materials. Due to ethical restrictions, primary data, including the coordinates of Pygmy settlements in Central Africa, are not deposited publicly. For further enquiries contact J. E. Fa (jfa949@gmail.com), Division of Biology and Conservation Ecology, School of Science and the Environment, Manchester Metropolitan University, Manchester M1 5GD, UK.

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S1 Table. Pygmy-camp data sources

Settlement Number	Country	Name	Region	Population Size	Group	Data Source
1	Cameroon	Zoulabot Ancien	East			1
2	Cameroon	Malea Ancien	Est (Boumba/Ngoko)		Baka	2
3	Cameroon	Balé	Centre		Baka	3
4	Cameroon	Bandevouri	Sud		Baka	3
5	Cameroon	Bellay Bas	Sud		Baka	3
6	Cameroon	Bellay Haut I	Sud		Baka	3
7	Cameroon	Bellay Haut II	Sud		Baka	3
8	Cameroon	Bibira	Sud		Baka	3
9	Cameroon	Bidjouka II	Sud		Baka	3
10	Cameroon	Bidjouka II'	Sud		Baka	3
11	Cameroon	Bidou, Bivuo	Sud		Baka	3
12	Cameroon	Bilolo I	Sud		Baka	3
13	Cameroon	Bindiansa	Sud		Baka	3
14	Cameroon	Bissiang	Sud		Baka	3
15	Cameroon	Bodi	Centre		Baka	3
16	Cameroon	Ebobissé I	Sud		Baka	3
17	Cameroon	Ebobissé II	Sud		Baka	3
18	Cameroon	Gwap	Sud		Baka	3
19	Cameroon	Kwa	Sud		Baka	3
20	Cameroon	Kwambo	Sud		Baka	3
21	Cameroon	Labtol	Centre		Baka	3
22	Cameroon	Lambi	Sud		Baka	3

23	Cameroon	Log Ndiga	Sud		Baka	3
24	Cameroon	Malandi I + II	Sud		Baka	3
25	Cameroon	Manguengues	Centre		Baka	3
26	Cameroon	Mbikiliki	Sud		Baka	3
27	Cameroon	Melen	Sud		Baka	3
28	Cameroon	Memel II	Sud		Baka	3
29	Cameroon	Memel II'	Sud		Baka	3
30	Cameroon	Milongo I	Centre		Baka	3
31	Cameroon	Milongo II	Centre		Baka	3
32	Cameroon	Minbiti	Sud		Baka	3
33	Cameroon	Nazareth	Sud		Baka	3
34	Cameroon	Ngoyang	Sud		Baka	3
35	Cameroon	Ngoyang, chefferie	Sud		Baka	3
36	Cameroon	Njangsang, Nkolo I	Sud		Baka	3
37	Cameroon	Nkolo	Sud		Baka	3
38	Cameroon	Pfoulngangang	Sud		Baka	3
39	Cameroon	Song Mahi, Accusé	Sud		Baka	3
40	Cameroon	Song Mahi, Simono	Sud		Baka	3
41	Cameroon	Song Makasso, Nkolo I	Sud		Baka	3
42	Cameroon	Song Mataa	Centre		Baka	3
43	Cameroon	Song Mbogyamb, Nkolo	Sud		Baka	3
44	Cameroon	Zok	Sud		Baka	3
45	Cameroon	Nkolenyeng	Sud		Baka	4
46	Cameroon	Nomedjoh	Est		Baka	4
47	Cameroon	DM1-Meyos Obam	Sud (Dja-et-Lobo)		Baka	5
48	Cameroon	DM2-Adjap (Djoum)	Sud (Dja-et-Lobo)		Baka	5
49	Cameroon	DM3-Ando'o	Sud (Dja-et-Lobo)		Baka	5
50	Cameroon	DM4-Minko'o Messeng	Sud (Dja-et-Lobo)		Baka	5

51	Cameroon	DM5-Kondou	Sud (Dja-et-Lobo)		Baka	5
52	Cameroon	DO1-Nkan	Sud (Dja-et-Lobo)		Baka	5
53	Cameroon	DO2-Minko'o	Sud (Dja-et-Lobo)		Baka	5
54	Cameroon	DO3-Mfem	Sud (Dja-et-Lobo)		Baka	5
55	Cameroon	DO4-Bindoumba	Sud (Dja-et-Lobo)		Baka	5
56	Cameroon	DO5-Mebane (I, II y III)	Sud (Dja-et-Lobo)		Baka	5
57	Cameroon	DO6-Mbonhate	Sud (Dja-et-Lobo)		Baka	5
58	Cameroon	DO7-Okweng	Sud (Dja-et-Lobo)		Baka	5
59	Cameroon	DO8-Nkolenyeng	Sud (Dja-et-Lobo)		Baka	5
60	Cameroon	DS1-Abing (Djoum)	Sud (Dja-et-Lobo)		Baka	5
61	Cameroon	DS2-Keka Abengue (Kenga Peke)	Sud (Dja-et-Lobo)		Baka	5
62	Cameroon	DS3-Koungou	Sud (Dja-et-Lobo)		Baka	5
63	Cameroon	DS4-Mveng	Sud (Dja-et-Lobo)		Baka	5
64	Cameroon	DS5-Nyabibete	Sud (Dja-et-Lobo)		Baka	5
65	Cameroon	DS6-Melen Boulou	Sud (Dja-et-Lobo)		Baka	5
66	Cameroon	DS7-Akom Ndong	Sud (Dja-et-Lobo)		Baka	5
67	Cameroon	DS8-Ngomebae	Sud (Dja-et-Lobo)		Baka	5
68	Cameroon	DS9-Alouma	Sud (Dja-et-Lobo)		Baka	5
69	Cameroon	MA1-Abing (Mintom)	Sud (Dja-et-Lobo)		Baka	5
70	Cameroon	MA2-Meyos	Sud (Dja-et-Lobo)		Baka	5
71	Cameroon	MA3-Bemba I	Sud (Dja-et-Lobo)		Baka	5
72	Cameroon	MA4-Bemba II	Sud (Dja-et-Lobo)		Baka	5
73	Cameroon	MC10-Nkolfon	Sud (Dja-et-Lobo)		Baka	5
74	Cameroon	MC11-Lele	Sud (Dja-et-Lobo)		Baka	5
75	Cameroon	MC1-Odoumou	Sud (Dja-et-Lobo)		Baka	5
76	Cameroon	MC2-Assok	Sud (Dja-et-Lobo)		Baka	5
77	Cameroon	MC3-Akom	Sud (Dja-et-Lobo)		Baka	5

78	Cameroon	MC4-Mekom	Sud (Dja-et-Lobo)		Baka	5
79	Cameroon	MC5-Belle Ville	Sud (Dja-et-Lobo)		Baka	5
80	Cameroon	MC6-Nkolkoumou	Sud (Dja-et-Lobo)		Baka	5
81	Cameroon	MC7-Melen	Sud (Dja-et-Lobo)		Baka	5
82	Cameroon	MC8-Bite	Sud (Dja-et-Lobo)		Baka	5
83	Cameroon	MC9-Mboutokon	Sud (Dja-et-Lobo)		Baka	5
84	Cameroon	MV1-Projet Baka	Sud (Dja-et-Lobo)		Baka	5
85	Cameroon	MV2-Doum	Sud (Dja-et-Lobo)		Baka	5
86	Cameroon	MV3-Adjap	Sud (Dja-et-Lobo)		Baka	5
87	Cameroon	MV4-Mekoto	Sud (Dja-et-Lobo)		Baka	5
88	Cameroon	OO1-Elom	Sud (Dja-et-Lobo)		Baka	5
89	Cameroon	Ambpiah	Sud		Bakola	6
90	Cameroon	Angoua Nvoule	Sud		Bakola	6
91	Cameroon	Antande	Sud		Bakola	6
92	Cameroon	Bandevouri	Sud		Bakola	6
93	Cameroon	Basili	Sud		Bakola	6
94	Cameroon	Bidou	Sud		Bakola	6
95	Cameroon	Bikouale	Sud		Bakola	6
96	Cameroon	Bilolo	Sud		Bakola	6
97	Cameroon	Bingambilli	Sud		Bakola	6
98	Cameroon	Binzambo I & II	Sud		Bakola	6
99	Cameroon	Bokoui	Sud		Bakola	6
100	Cameroon	Fu`Ur Ngi`Ur	Sud		Bakola	6
101	Cameroon	Gianggo	Sud		Bakola	6
102	Cameroon	Kota babi	Sud		Bakola	6
103	Cameroon	Kour Mintoum	Sud		Bakola	6
104	Cameroon	Koutaba	Sud		Bakola	6
105	Cameroon	Log	Sud		Bakola	6

106	Cameroon	Maboulo	Sud		Bakola	6
107	Cameroon	Madoula (Makoure)	Sud		Bakola	6
108	Cameroon	Malandi	Sud		Bakola	6
109	Cameroon	Malang Si	Sud		Bakola	6
110	Cameroon	Maschouh	Sud		Bakola	6
111	Cameroon	Matsindi Bouo	Sud		Bakola	6
112	Cameroon	Mbango Bitouer	Sud		Bakola	6
113	Cameroon	Mbpango	Sud		Bakola	6
114	Cameroon	Mfangala	Sud		Bakola	6
115	Cameroon	Minbiti	Sud		Bakola	6
116	Cameroon	Minkwa Milundi	Sud		Bakola	6
117	Cameroon	Mougo BandÚ	Sud		Bakola	6
118	Cameroon	Mougo Liang	Sud		Bakola	6
119	Cameroon	Mvounde	Sud		Bakola	6
120	Cameroon	Ndiga	Sud		Bakola	6
121	Cameroon	Ndtouah I	Sud		Bakola	6
122	Cameroon	Ndtouah II	Sud		Bakola	6
123	Cameroon	Ngo Manguéle	Sud		Bakola	6
124	Cameroon	Ngongo	Sud		Bakola	6
125	Cameroon	Ngouombi	Sud		Bakola	6
126	Cameroon	Nkollo Centre I & II	Sud		Bakola	6
127	Cameroon	Nkouah Noumba	Sud		Bakola	6
128	Cameroon	NkouamboundÚ	Sud		Bakola	6
129	Cameroon	Nkouli (Zouli I & II)	Sud		Bakola	6
130	Cameroon	Nkouong Guio	Sud		Bakola	6
131	Cameroon	Nobonzouondi I	Sud		Bakola	6
132	Cameroon	Nobonzouondi II	Sud		Bakola	6
133	Cameroon	Nobonzouondi III	Sud		Bakola	6

134	Cameroon	Oding Otoh	Sud		Bakola	6
135	Cameroon	Pfoulnganga	Sud		Bakola	6
136	Cameroon	Poutmekop (Bella Bas)	Sud		Bakola	6
137	Cameroon	Song Bikim	Sud		Bakola	6
138	Cameroon	Song Makasso	Sud		Bakola	6
139	Cameroon	Sum Mimbo	Sud		Bakola	6
140	Cameroon	Gribe	East		Bakola	7
141	Central African Republic	Bakourba	Lobaye		Aka, Bayaka	8
142	Central African Republic	Gbangouma	Lobaye		Aka, Bayaka	8
143	Central African Republic	Machado 2	Lobaye		Aka, Bayaka	8
144	Central African Republic	Mobi	Lobaye		Aka, Bayaka	8
145	Central African Republic	Sibouanga	Lobaye		Aka, Bayaka	8
146	Central African Republic	Sogba	Lobaye		Aka, Bayaka	8
147	Central African Republic	Bakota	Lobaye	320	Aka, Bayaka	8
148	Central African Republic	Bouze	Lobaye	802	Aka, Bayaka	8
149	Central African Republic	Gbokoulou	Lobaye	380	Aka, Bayaka	8
150	Central African Republic	Ibata	Lobaye	205	Aka, Bayaka	8
151	Central African	Kengua I	Lobaye	606	Aka, Bayaka	8

	Republic					
152	Central African Republic	Kengua II	Lobaye	225	Aka, Bayaka	8
153	Central African Republic	Kpidi-Croisement	Lobaye	235	Aka, Bayaka	8
154	Central African Republic	Kpidi-Mitterand	Lobaye	267	Aka, Bayaka	8
155	Central African Republic	Loko-Ville	Lobaye	705	Aka, Bayaka	8
156	Central African Republic	Massenguela	Lobaye	180	Aka, Bayaka	8
157	Central African Republic	Moale	Sangha Mbaéré	435	Aka, Bayaka	8
158	Central African Republic	Moboma	Lobaye	345	Aka, Bayaka	8
159	Central African Republic	Moloukou	Lobaye	508	Aka, Bayaka	8
160	Central African Republic	Monguenza	Lobaye	345	Aka, Bayaka	8
161	Central African Republic	Ngoundou	Lobaye	350	Aka, Bayaka	8
162	Central African Republic	Bakourba	Lobaye		Aka, Bayaka	8
163	Central African Republic	Belou	Lobaye		Aka, Bayaka	8
164	Central African Republic	Bokarakombo	Lobaye		Aka, Bayaka	8
165	Central African Republic	Bomolet	Lobaye		Aka, Bayaka	8

	Republic					
166	Central African Republic	Bondayo 2	Lobaye		Aka, Bayaka	8
167	Central African Republic	Bossindo 2	Lobaye		Aka, Bayaka	8
168	Central African Republic	Botto	Lobaye		Aka, Bayaka	8
169	Central African Republic	Boyoba	Lobaye		Aka, Bayaka	8
170	Central African Republic	Gbangouma	Lobaye		Aka, Bayaka	8
171	Central African Republic	Gbokia	Lobaye		Aka, Bayaka	8
172	Central African Republic	IbenguÚ	Lobaye		Aka, Bayaka	8
173	Central African Republic	Ibola/Carriere	Lobaye		Aka, Bayaka	8
174	Central African Republic	Ikoumba	Lobaye		Aka, Bayaka	8
175	Central African Republic	Kaza/ZomÚa	Lobaye		Aka, Bayaka	8
176	Central African Republic	Kpetene	Lobaye		Aka, Bayaka	8
177	Central African Republic	Kpotolo	Lobaye		Aka, Bayaka	8
178	Central African Republic	Lhoko	Lobaye		Aka, Bayaka	8
179	Central African Republic	Loko-centre	Lobaye		Aka, Bayaka	8

	Republic					
180	Central African Republic	LokombÚ	Lobaye		Aka, Bayaka	8
181	Central African Republic	Machado2	Lobaye		Aka, Bayaka	8
182	Central African Republic	Mangoussa	Lobaye		Aka, Bayaka	8
183	Central African Republic	Mbangoma	Lobaye		Aka, Bayaka	8
184	Central African Republic	Mbeko	Lobaye		Aka, Bayaka	8
185	Central African Republic	Mete 2	Lobaye		Aka, Bayaka	8
186	Central African Republic	Mobi	Lobaye		Aka, Bayaka	8
187	Central African Republic	Mokinda	Lobaye		Aka, Bayaka	8
188	Central African Republic	Mombembe	Lobaye		Aka, Bayaka	8
189	Central African Republic	MossÚbou	Lobaye		Aka, Bayaka	8
190	Central African Republic	Motomato	Lobaye		Aka, Bayaka	8
191	Central African Republic	Ngongo	Lobaye		Aka, Bayaka	8
192	Central African Republic	Ngotogbe	Lobaye		Aka, Bayaka	8
193	Central African Republic	Petri	Lobaye		Aka, Bayaka	8

	Republic					
194	Central African Republic	PK 6	Lobaye		Aka, Bayaka	8
195	Central African Republic	Route Manguier	Lobaye		Aka, Bayaka	8
196	Central African Republic	Safa-kokombet	Lobaye		Aka, Bayaka	8
197	Central African Republic	Sagbado	Lobaye		Aka, Bayaka	8
198	Central African Republic	Sakoungou	Lobaye		Aka, Bayaka	8
199	Central African Republic	Sibouanga	Lobaye		Aka, Bayaka	8
200	Central African Republic	Sipo	Lobaye		Aka, Bayaka	8
201	Central African Republic	Siriri	Lobaye		Aka, Bayaka	8
202	Central African Republic	Sogba	Lobaye		Aka, Bayaka	8
203	Central African Republic	Tomoki	Lobaye		Aka, Bayaka	8
204	Central African Republic	Toukoulou	Lobaye		Aka, Bayaka	8
205	Central African Republic	Wana-Pont	Lobaye		Aka, Bayaka	8
206	Central African Republic	Wele-wele	Lobaye		Aka, Bayaka	8
207	Central African	Bayanga	Sangha Mbaéré			9

	Republic					
208	Democratic Republic of Congo	Alipanda	Province Orientale (Haut-Uele)		Mbuti	10
209	Democratic Republic of Congo	Andelifou	Province Orientale (Ituri)		Mbuti	10
210	Democratic Republic of Congo	Angbetima	Province Orientale (Ituri)		Mbuti	10
211	Democratic Republic of Congo	Apa Kengetu	Province Orientale (Ituri)		Mbuti	10
212	Democratic Republic of Congo	Apa Mutelepu	Province Orientale (Ituri)		Mbuti	10
213	Democratic Republic of Congo	Apa Njaro	Province Orientale (Ituri)		Mbuti	10
214	Democratic Republic of Congo	Babama	Province Orientale (Ituri)		Mbuti	10
215	Democratic Republic of Congo	Bafwabenje	Province Orientale (Tshopo)		Mbuti	10
216	Democratic Republic of Congo	Bafwabwane	Province Orientale (Tshopo)		Mbuti	10
217	Democratic Republic of Congo	Bafwaguda	Province Orientale (Tshopo)		Mbuti	10
218	Democratic Republic of Congo	Bafwamane	Province Orientale (Tshopo)		Mbuti	10
219	Democratic Republic of Congo	Bafwamate	Province Orientale (Tshopo)		Mbuti	10
220	Democratic Republic of Congo	Bafwamiti	Province Orientale (Ituri)		Mbuti	10
221	Democratic	Bataka	Province Orientale		Mbuti	10

	Republic of Congo		(Ituri)			
222	Democratic Republic of Congo	Bingo	Province Orientale (Haut-Uele)		Mbuti	10
223	Democratic Republic of Congo	Eboyo	Province Orientale (Ituri)		Mbuti	10
224	Democratic Republic of Congo	Lubeye	Province Orientale (Ituri)		Mbuti	10
225	Democratic Republic of Congo	Makongo Tudu	Province Orientale (Ituri)		Mbuti	10
226	Democratic Republic of Congo	Amalutu	Province Orientale (Ituri)		Mbuti	11
227	Democratic Republic of Congo	Apekel-2	Province Orientale (Ituri)		Mbuti	11
228	Democratic Republic of Congo	Apekele 1	Province Orientale (Ituri)		Mbuti	11
229	Democratic Republic of Congo	Bujumbra	Province Orientale (Ituri)		Mbuti	11
230	Democratic Republic of Congo	Katala-Kalonge	Province Orientale (Ituri)		Mbuti	11
231	Democratic Republic of Congo	Mahuaka	Province Orientale (Ituri)		Mbuti	11
232	Democratic Republic of Congo	Mawanbo	Province Orientale (Ituri)		Mbuti	11
233	Democratic Republic of Congo	Sayu	Province Orientale (Ituri)		Mbuti	11
234	Democratic Republic of Congo	Sengule	Province Orientale (Ituri)		Mbuti	11
235	Democratic	Tabia	Province Orientale		Mbuti	11

	Republic of Congo		(Ituri)			
236	Democratic Republic of Congo	Teturi	Province Orientale (Ituri)		Mbuti	11
237	Democratic Republic of Congo	Teturi 2	Province Orientale (Ituri)		Mbuti	11
238	Gabon	Bikourou	Ngounié (Tsamba-Magotsi-west)		Babongo	12
239	Gabon	Boulongou Boua Ngagni	Ngounié (Tsamba-Magotsi-west)		Babongo	12
240	Gabon	Chantier Bordamur	Ngounié (Tsamba-Magotsi-east)		Babongo	12
241	Gabon	Chantier Bordamur Ikoye	Ngounié (Tsamba-Magotsi-west)		Babongo	12
242	Gabon	Digha	Ngounié (Tsamba-Magotsi-east)		Babongo	12
243	Gabon	Dikouka	Ngounié (Tsamba-Magotsi-east)		Babongo	12
244	Gabon	Ditounga (campement)	Ngounié (Tsamba-Magotsi-west)		Babongo	12
245	Gabon	Divanga	Ngounié (Tsamba-Magotsi-east)		Babongo	12
246	Gabon	Divinde	Ngounié (Tsamba-Magotsi-east)		Babongo	12
247	Gabon	Doubou	Ngounié (Tsamba-Magotsi-west)		Babongo	12
248	Gabon	Ekanga	Ngounié (Tsamba-Magotsi-west)		Babongo	12
249	Gabon	Evouta 1	Ngounié (Tsamba-		Babongo	12

			Magotsi-east)			
250	Gabon	Evouta 2	Ngounié (Tsamba-Magotsi-east)		Babongo	12
251	Gabon	Ghughouba	Ngounié (Tsamba-Magotsi-east)		Babongo	12
252	Gabon	Grand Odavo	Ngounié (Tsamba-Magotsi-west)		Babongo	12
253	Gabon	Guiamba	Ngounié (Tsamba-Magotsi-west)		Babongo	12
254	Gabon	Guidouma	Ngounié (Tsamba-Magotsi-west)		Babongo	12
255	Gabon	Iboundji	Ngounié (Tsamba Magotsi)		Babongo	12
256	Gabon	Ikobey	Ngounié (Tsamba-Magotsi-west)		Babongo	12
257	Gabon	Kessi	Ngounié (Tsamba-Magotsi-west)		Babongo	12
258	Gabon	Konagua et Ndougou	Ngounié (Tsamba-Magotsi-west)		Babongo	12
259	Gabon	Mandilou 1	Ngounié (Tsamba-Magotsi-west)		Babongo	12
260	Gabon	Mandilou 2	Ngounié (Tsamba-Magotsi-west)		Babongo	12
261	Gabon	Mboukou	Ngounié (Tsamba-Magotsi-west)		Babongo	12
262	Gabon	Mikanda (campement)	Ngounié (Tsamba-Magotsi-west)		Babongo	12
263	Gabon	Mimongo 2	Ngounié (Tsamba-		Babongo	12

			Magotsi-east)			
264	Gabon	Mimongo village 1	Ngounié (Tsamba-Magotsi-east)		Babongo	12
265	Gabon	Moukabou	Ngounié (Tsamba-Magotsi-west)		Babongo	12
266	Gabon	Moulandoufoulala	Ngounié (Tsamba-Magotsi-west)		Babongo	12
267	Gabon	Mourimatsiengui	Ngounié (Tsamba-Magotsi-west)		Babongo	12
268	Gabon	Mutamba Sane Fumu	Ngounié (Tsamba-Magotsi-west)		Babongo	12
269	Gabon	Ningui	Ngounié (Tsamba-Magotsi-west)		Babongo	12
270	Gabon	Nyoye 1	Ngounié (Tsamba-Magotsi-east)		Babongo	12
271	Gabon	Nyoye 2	Ngounié (Tsamba-Magotsi-east)		Babongo	12
272	Gabon	Nzemba	Ngounié (Tsamba-Magotsi-west)		Babongo	12
273	Gabon	Oghoubi	Ngounié (Tsamba-Magotsi-east)		Babongo	12
274	Gabon	Ossimba	Ngounié (Tsamba-Magotsi-east)		Babongo	12
275	Gabon	Oyenano	Ngounié (Tsamba-Magotsi-west)		Babongo	12
276	Gabon	Petit Odavo	Ngounié (Tsamba-Magotsi-west)		Babongo	12
277	Gabon	Rembo	Ngounié (Tsamba-		Babongo	12

			Magotsi-west)			
278	Gabon	Sale Diambou	Ngounié (Tsamba-Magotsi-west)		Babongo	12
279	Gabon	Sindara	Ngounié (Tsamba-Magotsi-west)		Babongo	12
280	Gabon	Tranquille	Ngounié (Tsamba-Magotsi-east)		Babongo	12
281	Gabon	Waka	Ngounié (Tsamba-Magotsi-west)		Babongo	12
282	Gabon	Yombi 1	Ngounié (Tsamba-Magotsi-west)		Babongo	12
283	Gabon	Yombi 2	Ngounié (Tsamba-Magotsi-west)		Babongo	12
284	Gabon	Bitouga	Woleu-Ntem	< 80	Baka	3
285	Gabon	Doumassi	Woleu-Ntem	< 100	Baka	3
286	Gabon	Esseng	Woleu-Ntem	< 160	Baka	3
287	Gabon	Etogo	Woleu-Ntem	< 80	Baka	3
288	Gabon	Mbounane Ville	Woleu-Ntem		Baka	3
289	Gabon	MfÚfÚlam	Woleu-Ntem		Baka	3
290	Gabon	Nkoakom	Woleu-Ntem	< 80	Baka	3
291	Gabon	Ovang-Alene	Woleu-Ntem	< 80	Baka	3
292	Gabon	Zangaville	Woleu-Ntem	< 40	Baka	3
293	Gabon	Mimbang	Woleu-Ntem	< 80	Baka	3
294	Gabon	Ayos	Woleu-Ntem	< 20 non permanent	Baka	3
295	Gabon	Boutoumbi	Ngounié (Ogoulou)		Babongo	
296	Republic of Congo	Bangui-Motaba	Likouala	399	Mbendjele	9
297	Republic of Congo	Berandjokou	Likouala	1137	Mbendjele	9
298	Republic of Congo	Bomassa	Sangha	95	BaNgombe	9

299	Republic of Congo	Djello	Likouala	170	Mbendjele	9
300	Republic of Congo	Gatongo	Sangha	148	Mbendjele	9
301	Republic of Congo	Gbakgbali	Sangha	60	Mbendjele	9
302	Republic of Congo	Ibamba	Likouala	249	Mbendjele	9
303	Republic of Congo	Ikelemba	Likouala	249	Mbendjele	9
304	Republic of Congo	Kabo	Sangha	95	Mbendjele	9
305	Republic of Congo	Linganga-Makao	Likouala	580	Mbendjele	9
306	Republic of Congo	Manfouete	Likouala		Mbendjele	9
307	Republic of Congo	Mbandza	Likouala	943	Mbendjele	9
308	Republic of Congo	Mboua	Likouala	491	Mbendjele	9
309	Republic of Congo	Minganga	Likouala	450	Mbendjele	9
310	Republic of Congo	Mobangi/Bene y Mobangi	Likouala	491	Mbendjele	9
311	Republic of Congo	Mompoutou	Likouala		Mbendjele	9
312	Republic of Congo	Ngandzikolo	Sangha	128	Mbendjele	9
313	Republic of Congo	Seke-Beye	Likouala	182	Mbendjele	9
314	Republic of Congo	Toukoulaka	Likouala	170	Mbendjele	9
315	Republic of Congo	Linganga-Makaou	Likouala		Mbendjele	13
316	Republic of Congo	Likombo	Likouala		Mbendjele	14
317	Republic of Congo	Makao-Linganga	Likouala		Mbendjele	14
318	Republic of Congo	Minganga	Sangha/Likouala		Longa	14
319	Republic of Congo	Minganga	Sangha/Likouala		Enoko	14
320	Republic of Congo	Minganga	Sangha/Likouala		Mbaya	14
321	Republic of Congo	Ndjube	Likouala		Mbendjele	14
322	Republic of Congo	Sombo	Likouala		Mbendjele	14
323	Republic of Congo	Zingo	Likouala		Mbendjele	14
324	Republic of Congo	Gouga	Likouala		Mbendjele	8
325	Republic of Congo	Ndobo	Likouala		Mbendjele	8
326	Cameroon	Adjap	Sud			15

327	Cameroon	Akanga	Sud			15
328	Cameroon	Akom I	Sud	22		15
329	Cameroon	Akonetse	Sud			15
330	Cameroon	Ako'ozam	Sud			15
331	Cameroon	Ako-ozam	Sud	45		15
332	Cameroon	Alop	Sud			15
333	Cameroon	Ambier	Sud			15
334	Cameroon	Ando'o	Sud			15
335	Cameroon	Awomo	Sud	35		15
336	Cameroon	Awoule	Sud	10		15
337	Cameroon	Bazili	Sud			15
338	Cameroon	Biabonga	Sud			15
339	Cameroon	Bibia	Sud			15
340	Cameroon	Bibondi	Sud			15
341	Cameroon	Bidjoka	Sud			15
342	Cameroon	Bidoumba	Sud			15
343	Cameroon	Bifoum	Sud			15
344	Cameroon	Bikala	Sud			15
345	Cameroon	Bikoualo	Sud	28		15
346	Cameroon	Bingambo	Sud			15
347	Cameroon	Bipindi rurale	Sud			15
348	Cameroon	Bipindi village	Sud			15
349	Cameroon	BISSONO	Sud			15
350	Cameroon	Bissono	Sud	20		15
351	Cameroon	Bitombo	Sud	10		15
352	Cameroon	Bokwi	Sud	25		15
353	Cameroon	Bomlafenda	Sud	35		15
354	Cameroon	Bongwana	Sud			15

355	Cameroon	DJOMOKO	Est			15
356	Cameroon	DjouzÚ	Sud			15
357	Cameroon	Ebimimbang	Sud			15
358	Cameroon	Ekom	Sud			15
359	Cameroon	GOUONEPOUM ANCIEN	Est			15
360	Cameroon	Grand Zambi	Sud			15
361	Cameroon	GRIBE(Dingwa)	Est			15
362	Cameroon	GRIBE(Nkoual)	Est			15
363	Cameroon	Kouambo	Sud			15
364	Cameroon	Koutababik	Sud			15
365	Cameroon	Kwambo	Sud			15
366	Cameroon	Lambi	Sud			15
367	Cameroon	Log-diga	Sud	17		15
368	Cameroon	Loundabele	Sud	16		15
369	Cameroon	Mabolo	Sud	53		15
370	Cameroon	Madensi	Sud			15
371	Cameroon	Madoungou	Sud			15
372	Cameroon	Makordjong	Sud	36		15
373	Cameroon	MALLEA ANCIEN	Est			15
374	Cameroon	Mandtoua	Sud	26		15
375	Cameroon	Mashouer-mashouer	Sud	63		15
376	Cameroon	Mebane	Sud			15
377	Cameroon	Mebia'a	Sud	27		15
378	Cameroon	Mefane	Sud	74		15
379	Cameroon	Melen	Sud			15
380	Cameroon	Mfem	Sud			15
381	Cameroon	Miatta	Sud			15
382	Cameroon	Minfombo	Sud			15

383	Cameroon	Mingoh	Sud			15
384	Cameroon	Mingo'o	Sud	185		15
385	Cameroon	Minko'omesseng	Sud			15
386	Cameroon	Molombo	Sud		Bayaka, Bilo	15
387	Cameroon	MouguÚ	Sud			15
388	Cameroon	MoungouÚ	Sud			15
389	Cameroon	Mpomlep	Sud			15
390	Cameroon	Mveng	Sud			15
391	Cameroon	Naantande	Sud	24		15
392	Cameroon	Ndabagyeli	Sud			15
393	Cameroon	Ndabiang	Sud	13		15
394	Cameroon	Ndamayo	Sud	24	Bayaka, Bilo	15
395	Cameroon	Ndtoua	Sud			15
396	Cameroon	Ndtoua route	Sud	18		15
397	Cameroon	Nezam	Sud			15
398	Cameroon	Ngato ancien	Est			15
399	Cameroon	Ngola	Sud			15
400	Cameroon	Ngom	Sud			15
401	Cameroon	Ngovayang I	Sud			15
402	Cameroon	Ngovayang II	Sud			15
403	Cameroon	Ngovayang III	Sud			15
404	Cameroon	Ngwap	Sud			15
405	Cameroon	Nkolekuk	Sud			15
406	Cameroon	Nkolenyeng (Oding)	Sud			15
407	Cameroon	Nkolo	Sud			15
408	Cameroon	Nkolo 2	Sud			15
409	Cameroon	Nkondoum	Sud	10		15
410	Cameroon	Nkon'ouvoumba	Sud	88		15

411	Cameroon	NKO'O ASSENG	Sud			15
412	Cameroon	Nkoulekouk	Sud	32		15
413	Cameroon	nsong Bikim	Sud			15
414	Cameroon	Nsong Mayi	Sud			15
415	Cameroon	NyabibÚtÚ	Sud			15
416	Cameroon	Nyabitande	Sud	13		15
417	Cameroon	Nyaminkoum	Sud			15
418	Cameroon	Nyanit	Sud	4		15
419	Cameroon	Nzambi	Sud			15
420	Cameroon	Nzock	Sud			15
421	Cameroon	Okpweng	Sud			15
422	Cameroon	Sa'ah	Sud	35		15
423	Cameroon	SOM ANCIEN	Est			15
424	Cameroon	Yanebote	Sud	26		15
425	Cameroon	Zoulabot ancien	Est			15
426	Central African Republic	Gbadane	Lobaye	50		15
427	Central African Republic	Lokombe	Lobaye	86		15
428	Central African Republic	Londo	Sangha Mbaéré	711		15
429	Central African Republic	Mbakoro	Sangha Mbaéré	294		15
430	Central African Republic	Moale	Sangha Mbaéré	500		15
431	Central African Republic	Moloukou	Lobaye	1300		15
432	Central African	Ndele	Sangha Mbaéré	422		15

	Republic					
433	Central African Republic	Ngola	Lobaye	800		15
434	Central African Republic	Ngoundi	Sangha Mbaéré	270		15
435	Democratic Republic of Congo	Bakumo	Bandundu			15
436	Democratic Republic of Congo	Banjow Moke	Bandundu			15
437	Democratic Republic of Congo	Banjow Monene	Bandundu			15
438	Democratic Republic of Congo	Basimba	Bandundu			15
439	Democratic Republic of Congo	Beenge	Bandundu			15
440	Democratic Republic of Congo	Bekamba (Pygme)	Equateur			15
441	Democratic Republic of Congo	Bekeli	Equateur			15
442	Democratic Republic of Congo	Bekonge	Bandundu			15
443	Democratic Republic of Congo	Bekungu	Bandundu			15
444	Democratic Republic of Congo	Bekungu	Bandundu			15
445	Democratic Republic of Congo	Belombo	Bandundu			15
446	Democratic	Benye	Bandundu			15

	Republic of Congo					
447	Democratic Republic of Congo	Besako	Bandundu			15
448	Democratic Republic of Congo	Besau	Bandundu			15
449	Democratic Republic of Congo	Betumbe	Bandundu			15
450	Democratic Republic of Congo	Betumbe	Bandundu			15
451	Democratic Republic of Congo	Bikonda	Bandundu			15
452	Democratic Republic of Congo	Bilobi	Bandundu			15
453	Democratic Republic of Congo	Bilonalona	Bandundu			15
454	Democratic Republic of Congo	Bipomi	Bandundu			15
455	Democratic Republic of Congo	Boala	Equateur			15
456	Democratic Republic of Congo	Bobala	Bandundu			15
457	Democratic Republic of Congo	Bobilia	Equateur			15
458	Democratic Republic of Congo	Bokama	Bandundu			15
459	Democratic Republic of Congo	Bokokosikili	Bandundu			15
460	Democratic	Bokoli	Bandundu			15

	Republic of Congo					
461	Democratic Republic of Congo	Bokote	Bandundu			15
462	Democratic Republic of Congo	Bongemba	Equateur			15
463	Democratic Republic of Congo	Bongende	Bandundu			15
464	Democratic Republic of Congo	Bongo II	Bandundu			15
465	Democratic Republic of Congo	Bongo III	Bandundu			15
466	Democratic Republic of Congo	Bonkange	Bandundu			15
467	Democratic Republic of Congo	Boondo	Bandundu			15
468	Democratic Republic of Congo	Boongo I	Bandundu			15
469	Democratic Republic of Congo	Boota	Equateur			15
470	Democratic Republic of Congo	Bosando	Bandundu			15
471	Democratic Republic of Congo	Bosango	Bandundu			15
472	Democratic Republic of Congo	Bosele	Bandundu			15
473	Democratic Republic of Congo	Bosoli	Bandundu			15
474	Democratic	Bosoli III	Bandundu			15

	Republic of Congo					
475	Democratic Republic of Congo	Botangeli	Bandundu			15
476	Democratic Republic of Congo	Botendo	Equateur			15
477	Democratic Republic of Congo	Botongomba	Bandundu			15
478	Democratic Republic of Congo	Bowa	Bandundu			15
479	Democratic Republic of Congo	Bowa PA	Bandundu			15
480	Democratic Republic of Congo	Bowolo Mpinga	Bandundu			15
481	Democratic Republic of Congo	Boyamba	Bandundu			15
482	Democratic Republic of Congo	Boyanga	Bandundu			15
483	Democratic Republic of Congo	Bwenzey	Bandundu			15
484	Democratic Republic of Congo	Edua	Bandundu			15
485	Democratic Republic of Congo	Ekodi	Bandundu			15
486	Democratic Republic of Congo	Elenge	Bandundu			15
487	Democratic Republic of Congo	Elole	Bandundu			15
488	Democratic	Epokenkaso	Bandundu			15

	Republic of Congo				
489	Democratic Republic of Congo	Epoko funga	Bandundu		15
490	Democratic Republic of Congo	Eteyi	Bandundu		15
491	Democratic Republic of Congo	Gbado	Bandundu		15
492	Democratic Republic of Congo	Ibamba	Bandundu		15
493	Democratic Republic of Congo	Ibanda	Bandundu		15
494	Democratic Republic of Congo	Ibata	Bandundu		15
495	Democratic Republic of Congo	IBEKE	Bandundu		15
496	Democratic Republic of Congo	Ikenze	Bandundu		15
497	Democratic Republic of Congo	Ikongo P.A	Bandundu		15
498	Democratic Republic of Congo	Ikonya Moke	Bandundu		15
499	Democratic Republic of Congo	Ikonya monene	Bandundu		15
500	Democratic Republic of Congo	Ikumu	Bandundu		15
501	Democratic Republic of Congo	Ikuye	Bandundu		15
502	Democratic	Ilanga II	Bandundu		15

	Republic of Congo					
503	Democratic Republic of Congo	Ilengi	Bandundu			15
504	Democratic Republic of Congo	Ilobo	Bandundu			15
505	Democratic Republic of Congo	Ilombe	Bandundu			15
506	Democratic Republic of Congo	Ilungu	Bandundu			15
507	Democratic Republic of Congo	Inongo	Bandundu			15
508	Democratic Republic of Congo	Ipanga	Bandundu			15
509	Democratic Republic of Congo	Isangi	Bandundu			15
510	Democratic Republic of Congo	Isobi	Bandundu			15
511	Democratic Republic of Congo	Isoko	Bandundu			15
512	Democratic Republic of Congo	Isongo	Bandundu			15
513	Democratic Republic of Congo	Itebe	Bandundu			15
514	Democratic Republic of Congo	Itito	Bandundu			15
515	Democratic Republic of Congo	Iyanza	Bandundu			15
516	Democratic	Iyombo	Bandundu			15

	Republic of Congo					
517	Democratic Republic of Congo	Kalina	Bandundu			15
518	Democratic Republic of Congo	Kama II	Bandundu			15
519	Democratic Republic of Congo	Kapanda	Bandundu			15
520	Democratic Republic of Congo	Katindambo	Bandundu			15
521	Democratic Republic of Congo	Koloti	Bandundu			15
522	Democratic Republic of Congo	Kundo	Bandundu			15
523	Democratic Republic of Congo	Kutu moke	Bandundu			15
524	Democratic Republic of Congo	Lobongo	Bandundu			15
525	Democratic Republic of Congo	Lodimo	Bandundu			15
526	Democratic Republic of Congo	Loile	Bandundu			15
527	Democratic Republic of Congo	Lokanga	Bandundu			15
528	Democratic Republic of Congo	Lokembe	Bandundu		Bayaka, Bilo	15
529	Democratic Republic of Congo	Lombe	Bandundu		Bayaka, Bilo	15
530	Democratic	Lonio	Bandundu			15

	Republic of Congo					
531	Democratic Republic of Congo	Lunda	Bandundu			15
532	Democratic Republic of Congo	Maliba	Bandundu			15
533	Democratic Republic of Congo	Malondo	Bandundu			15
534	Democratic Republic of Congo	Mankakiti	Bandundu			15
535	Democratic Republic of Congo	Mankoka	Bandundu			15
536	Democratic Republic of Congo	Masobe	Bandundu			15
537	Democratic Republic of Congo	Mbaki	Bandundu		Bayaka, Bilo	15
538	Democratic Republic of Congo	Mbala	Bandundu			15
539	Democratic Republic of Congo	Mbange	Bandundu			15
540	Democratic Republic of Congo	Mbelo	Bandundu			15
541	Democratic Republic of Congo	Mbongo	Bandundu			15
542	Democratic Republic of Congo	Mbuse Mpoto	Bandundu			15
543	Democratic Republic of Congo	Mekiri	Bandundu			15
544	Democratic	Mfwaki	Bandundu			15

	Republic of Congo					
545	Democratic Republic of Congo	Minyanya	Bandundu		Bayaka, Bilo	15
546	Democratic Republic of Congo	Molende	Bandundu			15
547	Democratic Republic of Congo	Molokiesambo	Bandundu			15
548	Democratic Republic of Congo	Mongalo	Bandundu			15
549	Democratic Republic of Congo	Mongempongo	Bandundu			15
550	Democratic Republic of Congo	Motoko	Bandundu			15
551	Democratic Republic of Congo	Mpa 2	Bandundu			15
552	Democratic Republic of Congo	Mpaha	Bandundu			15
553	Democratic Republic of Congo	Mpaha1	Bandundu			15
554	Democratic Republic of Congo	Mpamole	Bandundu			15
555	Democratic Republic of Congo	Mpenda	Equateur			15
556	Democratic Republic of Congo	Mpenge	Bandundu			15
557	Democratic Republic of Congo	Mpili	Bandundu			15
558	Democratic	Mpisse	Bandundu			15

	Republic of Congo					
559	Democratic Republic of Congo	Mpite	Bandundu			15
560	Democratic Republic of Congo	Mpole	Bandundu			15
561	Democratic Republic of Congo	Mponde	Bandundu			15
562	Democratic Republic of Congo	Mponde I	Bandundu			15
563	Democratic Republic of Congo	Mponde II	Bandundu			15
564	Democratic Republic of Congo	Mponde IV	Bandundu			15
565	Democratic Republic of Congo	Mpongoboli	Bandundu			15
566	Democratic Republic of Congo	Mpulungu	Bandundu			15
567	Democratic Republic of Congo	Nbange	Bandundu			15
568	Democratic Republic of Congo	Ndonga	Bandundu			15
569	Democratic Republic of Congo	Ndongese	Bandundu			15
570	Democratic Republic of Congo	Ndongiele	Bandundu			15
571	Democratic Republic of Congo	Nfwa	Bandundu			15
572	Democratic	Nganda Malebo	Bandundu			15

	Republic of Congo					
573	Democratic Republic of Congo	Ngelo	Bandundu			15
574	Democratic Republic of Congo	Ngembo	Bandundu			15
575	Democratic Republic of Congo	Ngombe	Equateur			15
576	Democratic Republic of Congo	Ngomelenge PA	Bandundu			15
577	Democratic Republic of Congo	Ngomo	Bandundu			15
578	Democratic Republic of Congo	Ngongo	Bandundu			15
579	Democratic Republic of Congo	Nianganga	Bandundu			15
580	Democratic Republic of Congo	Nkala	Bandundu			15
581	Democratic Republic of Congo	Nkanta	Bandundu			15
582	Democratic Republic of Congo	Nkata	Bandundu			15
583	Democratic Republic of Congo	Nkile	Bandundu			15
584	Democratic Republic of Congo	Nkole	Bandundu			15
585	Democratic Republic of Congo	Nkombe	Bandundu			15
586	Democratic	Nkongoli	Equateur			15

	Republic of Congo					
587	Democratic Republic of Congo	Nkoso	Bandundu			15
588	Democratic Republic of Congo	Nkoso	Bandundu			15
589	Democratic Republic of Congo	Nkoy	Bandundu			15
590	Democratic Republic of Congo	Nkuku	Bandundu			15
591	Democratic Republic of Congo	Nsangando	Bandundu			15
592	Democratic Republic of Congo	Nsaw	Bandundu			15
593	Democratic Republic of Congo	Nsele	Bandundu			15
594	Democratic Republic of Congo	Nsele	Bandundu			15
595	Democratic Republic of Congo	Nselenge	Bandundu			15
596	Democratic Republic of Congo	Nsingi	Bandundu			15
597	Democratic Republic of Congo	Nsombele	Bandundu			15
598	Democratic Republic of Congo	Nsondia	Bandundu			15
599	Democratic Republic of Congo	Ntande Ngomo	Bandundu			15
600	Democratic	Ntandembelo	Bandundu			15

	Republic of Congo					
601	Democratic Republic of Congo	Ntanga	Bandundu			15
602	Democratic Republic of Congo	Ntikokoli	Bandundu			15
603	Democratic Republic of Congo	Ntomba	Bandundu			15
604	Democratic Republic of Congo	Ntumbe	Bandundu			15
605	Democratic Republic of Congo	Okanisaka	Bandundu			15
606	Democratic Republic of Congo	Okobamwe	Bandundu			15
607	Democratic Republic of Congo	Pokolo	Bandundu			15
608	Democratic Republic of Congo	Sala Ozwa	Bandundu			15
609	Democratic Republic of Congo	Sanga	Bandundu			15
610	Democratic Republic of Congo	Tambola Malembe	Bandundu			15
611	Democratic Republic of Congo	Tomba	Bandundu			15
612	Democratic Republic of Congo	Walonga	Bandundu			15
613	Democratic Republic of Congo	Wando	Bandundu			15
614	Democratic	Wanya	Bandundu			15

	Republic of Congo					
615	Democratic Republic of Congo	Wenge	Bandundu			15
616	Democratic Republic of Congo	Weti	Equateur			15
617	Democratic Republic of Congo	Winangomo	Bandundu			15
618	Democratic Republic of Congo	Zali Mboka	Bandundu			15
619	Democratic Republic of Congo		Equateur			15
620	Democratic Republic of Congo		Equateur			15
621	Democratic Republic of Congo		Equateur			15
622	Gabon	Adjap	Ogooué-Ivindo	< 100	Baka	15
623	Gabon	Bitouga	Woleu-Ntem			15
624	Gabon	Divangha	Ngounié			15
625	Gabon	Divinde	Ngounié			15
626	Gabon	Doumassi	Woleu-Ntem			15
627	Gabon	Egoubha	Ngounié			15
628	Gabon	Elarmitang	Woleu-Ntem	< 100	Baka	15
629	Gabon	EpassendjP	Ogooué-Ivindo	< 100	Baka	15
630	Gabon	Eto'o	Woleu-Ntem			15
631	Gabon	Evouta	Ngounié			15
632	Gabon	Loa Loa	Ogooué-Ivindo			15
633	Gabon	Mayibouth1	Ogooué-Ivindo			15
634	Gabon	Mbolo 3	Ogooué-Ivindo			15

635	Gabon	Mekob	Ogooué-Ivindo	< 80	Baka	15
636	Gabon	Mimongo	Ngounié			15
637	Gabon	Mokoko	Ngounié			15
638	Gabon	Motombi	Ngounié			15
639	Gabon	Ndoughou	Ngounié			15
640	Gabon	Nioye 1	Ngounié			15
641	Gabon	Nioye 2	Ngounié			15
642	Gabon	Ossimba	Ngounié			15
643	Gabon	Sogha	Ngounié			15
644	Gabon	Tchibanga	Ngounié			15
645	Gabon	Tranquille	Ngounié			15
646	Republic of Congo	Assengue	Plateaux		Twa	15
647	Republic of Congo	Epounou	Plateaux			15
648	Republic of Congo	Ibangui	Plateaux			15
649	Republic of Congo	Inga	Plateaux			15
650	Republic of Congo	Ngombe	Sangha			15
651	Republic of Congo	Ngombe carrefour	Sangha			15
652	Republic of Congo	Ouessou - mbila	Sangha			15
653	Republic of Congo	Poulani	Sangha			15
654	Republic of Congo	Zoulabout	Sangha			15

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S2 Table. Empirical data of territory sizes for Pygmy camps in various localities in Central Africa (Source: Hoare AL. 2007 *Resource rights and timber concessions: Integrating local peoples' land-use practices in forest management in the Congo Basin*. London: Rainforest Foundation-UK).

Pygmy group	Size of territory (km ²)	Region / district	Observations
Mbuti	120-150	Ituri (DRC)	
Mbuti	150-300	Tetri region, Ituri (DRC)	Including overlapping areas
Mbuti	160-170	Tetri region, Ituri (DRC)	Not included overlapping areas
Aka	400	Lobaye (CAR)	
Aka	150	Likouala (NE Congo)	Hunting areas
Aka	70	Likouala (NE Congo)	Gathering areas
Mbendjele	4,831	Berandjokou (N Congo)	
Mbendjele	5,964	Linganga-Makao (Congo)	
Mbendjele	214	Seke-Beye (Congo)	
Mbendjele	910	Bangui-Motaba (Likouala, Congo)	
Mbendjele	2,239	Mbandza (Congo)	
Mbendjele	3,970	Minganga (Congo)	
Mbendjele	1,189	Ngandzikolo (N Congo)	
Mbendjele	1,495	Gatongo (Congo)	
Mbendjele	1,738	Mobangi Bene & Mobangi Mboua (Congo)	
Mbendjele	872	Toukoulaka Djello (Congo)	
Mbendjele	3,736	Ibamba-Ikelemba (Congo)	
Mbendjele & Nbombé Baka	265	Bomassa-Kabo (N Congo)	
Not specified	520	E Cameroon	Hunting areas
Not specified	81	Mbomo (Congo)	Hunting areas
Not specified	110	Ikela (DRC)	Hunting areas
Not specified	15	Ikela (DRC)	Hunting areas
Not specified	400	NE Gabon	Hunting areas
Not specified	211	Kompia (Cameroon)	Hunting areas
Not specified	160	Kompia (Cameroon)	Hunting areas
Not specified	355	Kompia (Cameroon)	Hunting areas
Not specified	300	Kompia (Cameroon)	Hunting areas
Not specified	452	CAR	Hunting areas
Not specified	130	CAR	Hunting areas

S3 Table. Predictor-variable sources of the 34 predictor variables considered to build the environmental favourability model for Pygmies.

Predictor variables	Source
Climate:	
<ul style="list-style-type: none"> – <i>Maximum annual temperature</i> – <i>Minimum annual temperature</i> – <i>Maximum annual temperature range</i> – <i>Annual precipitation</i> – <i>Intra-annual pluviometric irregularity</i> (i.e. annual variation coefficient of monthly precipitation) 	WorldClim (http://www.worldclim.org)
Topography:	
<ul style="list-style-type: none"> – <i>Elevation</i> – <i>Slope</i> 	GTOPO30 (US Geological Survey 1996)
Hydrography:	
<ul style="list-style-type: none"> – <i>Distance to water masses</i> (i.e. lakes delimited as in http://www.natureearthdata.com, and main river courses with water flow accumulation > 10⁶ cells, according to HydroSHEDS) – <i>Distance to minor rivers</i> (with water flow accumulation between 10⁴ and 10⁶ cells) 	Hydrologically conditioned DEM of HydroSHEDS (http://hydrosheds.cr.usgs.gov)
Ecosystem types:	
<ul style="list-style-type: none"> – <i>Broadleaf evergreen/semideciduous rainforests</i> (GC class 40) – <i>Swamp forests</i> (GC class 160) – <i>Deciduous forests</i> (GC class 50) – <i>Woody savannas</i> (GC classes 60 and 120) – <i>Shrublands</i> (GC classes 110 and 130) 	GlobCover (GC) Land Cover version 2.2 database for 2005-2006 (Bicheron et al. 2008)

<ul style="list-style-type: none"> – <i>Grasslands</i> (GC class 140) – <i>Deserts</i> (GC class 200) 	
<ul style="list-style-type: none"> – <i>Intact forest</i> 	World Intact Forest Landscapes (IFL) Map in the year 2005 (Potapov et al. 2008)
Human concentration:	
<ul style="list-style-type: none"> – <i>Rural population density</i> 	LandScan™ 2008 High Resolution Global Population Data Set (copyrighted by UT-Battelle, LLC, operator of Oak Ridge National Laboratory), excluding any areas less than 2-km far from urban areas (as delimited by the MODIS 500-m Map of Global Urban Extent for 2001-2002 (Schneider et al. 2009; 2010)
<ul style="list-style-type: none"> – <i>Distance to populated places</i> 	Administrative Centres & Populated Places shapefile at the Relational World Database II (RWDB2) updated in 2000 (http://www.fao.org/geonetwork)
Infrastructures:	
<ul style="list-style-type: none"> – <i>Distance to roads</i> – <i>Distance to rail-roads</i> 	Vector Map Level 0 at the Digital Chart of the World (DCW, http://worldmap.harvard.edu), updated in 2002
Agriculture:	
<ul style="list-style-type: none"> – <i>Intensive croplands</i> (GC class 14, including lands exclusively devoted to cropping) – <i>Cropland (>50%)/vegetation mosaics</i> (GC class 20) – <i>Vegetation (>50%)/cropland mosaics</i> (GC class 30) 	GlobCover (GC) Land Cover version 2.2 database for 2005-2006 (Bicheron et al. 2008)

<ul style="list-style-type: none"> – <i>Non-intensive croplands</i> – <i>Global climate, soil and terrain slope constraints for cropping activities</i> 	Food Insecurity, Poverty and Environment Global GIS Database (FGGD Digital Atlas for the year 2000) (FAO & IIASA 2007)
<ul style="list-style-type: none"> – <i>Percentage of area equipped for irrigation</i> 	Global Map of Irrigation Areas (version 4.0.1) around the year 2000 (http://www.fao.org/nr/water)
Livestock:	
<ul style="list-style-type: none"> – <i>Pasture and browse</i> 	Food Insecurity, Poverty and Environment Global GIS Database (FGGD Digital Atlas for the year 2000) (FAO & IIASA 2007)
<ul style="list-style-type: none"> – <i>Density of poultry farms</i> – <i>Density of pigs</i> – <i>Density of cattle</i> – <i>Density of small ruminants (sheep, goats)</i> 	FAO's Gridded Livestock of the World maps, derived from national data from 1992 to 2003 (Robinson <i>et al.</i> 2007)
Nature conservation policies:	
<ul style="list-style-type: none"> – <i>Distance from protected areas</i> 	World Database on Protected Areas (WDPA) (UNEP-WCMC 2012)
Exploitation of fauna:	
<ul style="list-style-type: none"> – <i>Bushmeat extraction</i> 	Fa <i>et al.</i> (2015)

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