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PREDICTIVE REVIEW

Human activities link fruit bat presence to Ebola virus disease outbreaks

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African rainforests, biogeography, deforestation, emerging infectious diseases, favourability modelling, Pteropodidae, zoonosis

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[†] Our friend and colleague Siv Aina Leendertz died in July 2018. She made a vast contribution to the ecology of wildlife disease, and will be missed by many. We dedicate this paper to her.

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ABSTRACT

1. A significant link between forest loss and fragmentation and outbreaks of Ebola virus disease (EVD) in humans has been documented. Deforestation may alter the natural circulation of viruses and change the composition, abundance, behaviour and possibly viral exposure of reservoir species. This in turn might increase contact between infected animals and humans.
2. Fruit bats of the family Pteropodidae have been suspected as reservoirs of the Ebola virus. At present, the only evidence associating fruit bats with EVD is the presence of seropositive individuals in eight species and polymerase chain reaction-positive individuals in three of these.
3. Our study investigates whether human activities can increase African fruit bat geographical ranges and whether this influence overlaps geographically with EVD outbreaks that, in turn, are favoured by deforestation.
4. We use species observation records for the 20 fruit bat species found in favourable areas for the Ebola virus to determine factors affecting the bats' range inside the predicted Ebola virus area. We do this by employing a hypothetico-deductive approach based on favourability modelling.
5. We show that the range of some fruit bat species is linked to human activities within the favourable areas for the Ebola virus. More specifically, the areas where human activities favour the presence of five fruit bat species

overlap with the areas where EVD outbreaks in humans were themselves favoured by deforestation. These five species are as follows: *Eidolon helvum*, *Epomops franqueti*, *Megaloglossus woermanni*, *Micropteropus pusillus* and *Rousettus aegyptiacus*. Of these five, all but *Megaloglossus woermanni* have recorded seropositive individuals. For the remaining 15 bat species, we found no biogeographical support for the hypothesis that positive human influence on fruit bats could be associated with EVD outbreaks in deforested areas within the tropical forest biome in West and Central Africa.

6. Our work is a useful first step allowing further investigation of the networks and pathways that may lead to an EVD outbreak. The modelling framework we employ here can be used for other emerging infectious diseases.

INTRODUCTION

Environmental changes caused by humans can drive the emergence of infectious diseases throughout the world (Daszak et al. 2000, Rogalski et al. 2017). In the case of the Ebola virus disease (EVD), a zoonosis caused by *Ebolavirus* spp. (family Filoviridae) that is often fatal in humans, a significant link between forest loss and fragmentation and disease outbreaks in humans, has been documented (Rulli et al. 2017, Olivero et al. 2017b). Details of how deforestation affects viral spillover are yet to be discovered, but it is likely that the reduction in forest cover may alter the natural circulation of viruses as well as changing the composition, abundance, behaviour and possibly viral exposure of reservoir species (such as bats; Smith & Wang 2013, Maganga et al. 2014). This in turn may increase contact between infected animals and humans (Castro & Michalski 2014, Leendertz 2016, Loveridge et al. 2016).

Although there is no definitive proof that fruit bats are the main drivers of human EVD outbreaks (Leendertz et al. 2016), there is evidence that these bats are intermittently and, in certain geographical areas, briefly infected with the Ebola virus (Leendertz 2016). Amongst the 20 fruit bat species of the family Pteropodidae in Africa (Almeida et al. 2016), *Ebolavirus* antibodies have been detected in eight, suggesting that these taxa may somehow be involved in the life cycle of the filoviruses (Leroy et al. 2005, Pourrut et al. 2009, Hayman et al. 2012, Olival et al. 2017). Of the eight bat species, the African straw-coloured fruit bat *Eidolon helvum* is a migrant or nomadic species and the little collared fruit bat *Myonycteris torquata* and Veldkamp's dwarf epauletted fruit bat *Nanonycteris veldkampii* undertake seasonal movements (Wolton et al. 1982, Thomas 1983), whereas others may be affected by seasonal changes in food availability (e.g. the Gambian epauletted fruit bat *Epomophorus gambianus*, Franquet's epauletted fruit bat *Epomops franqueti* and the hammer-headed fruit bat *Hypsignathus monstrosus*; Happold & Happold 2013). Because these bat species travel large distances annually in search of better environmental conditions (e.g. food and shelter) and could be involved in the spread of Ebola virus in Africa, the use of predictive tools is fundamental to assess which ecological conditions are significantly associated with the use of different habitats, including human-modified ones (Peel et al. 2013, Fiorillo et al. 2018).

Though direct human activities, for example hunting, have clear negative impacts on bat populations (Kamins et al. 2011), a range of human-induced environmental changes positively influence tropical bat abundance and increase species' geographical ranges (Meyer et al. 2015). Many tropical frugivorous bat species are favourably affected by moderate forest fragmentation (Delaval & Charles-Dominique 2006, Klingbeil & Willig 2009), low-intensity selective logging (Clarke et al. 2005, Castro & Michalski 2014), secondary forest and succession (Muscarella & Fleming 2007), agroforestry (Williams-Guillén & Perfecto 2010, Castro-Luna & Galindo-González 2012) and agriculture (Medellín et al. 2000, Luskin 2010). More specifically, fruit bat populations respond positively to increased availability of new agricultural food sources (Luskin 2010), but this response has not been confirmed for tropical bats outside Asia and South America (Klingbeil & Willig 2009, Luskin 2010, Williams-Guillén & Perfecto 2010). In Africa, evidence exists to show that the distributions of *Eidolon helvum* and the Egyptian rousette *Rousettus aegyptiacus* largely reflect human-induced changes (Lang & Chapin 1917, Centeno-Cuadros et al. 2017). *Eidolon helvum* is reputed to have spread across the continent in the early 20th century due to the expansion of non-indigenous fruit cultivation (Lang & Chapin 1917), whilst the foraging behaviour of *Rousettus aegyptiacus* in the Middle East is influenced by agriculture (Centeno-Cuadros et al. 2017).

Using biogeographical records for sub-Saharan African fruit bats, we assessed whether fruit bat species' range sizes are positively affected by human activities, i.e. sources of pressures on the environment such as deforestation, human population density, transport infrastructure, numbers of livestock and agriculture (Appendix S1). We also determined whether fruit bat ranges are linked to EVD outbreaks, which have been shown to be favoured by deforestation (Olivero et al. 2017b). To achieve these two aims, we adopted a hypothetico-deductive approach based on predictive model testing, an approach we considered more suitable than purely mechanistic methods due to the dearth of empirical information. Modelling approaches such as ours have been used to understand viral dynamics and emergence by providing insights into pattern–process relationships (Hayman 2016). In the context of pathogeography, spatial models can be used to describe the ecological determinants of pathogen richness and epidemiological processes (Olivero et al. 2017a, Murray et al. 2018).

In this paper, we present a testable and falsifiable hypothesis: human influence on fruit bats is linked to EVD outbreaks in deforested areas. For this hypothesis to be supported, we propose three observable predictions: 1) within the Ebola virus area, human activities contribute significantly to explaining favourable areas for the presence of fruit bats; 2) if this happens, the contribution involves an increase of favourability for bat presence in at least some areas; and 3) EVD outbreak sites linked to forest loss overlap significantly with the areas mentioned in prediction 2. These three predictions must be fulfilled; otherwise, the hypothesis will be rejected. Stronger links between human activities, Ebola outbreaks and bat species would be corroborated if these associations appeared significant for taxa that are serologically positive for the Ebola virus.

METHODS

Geographical context

The geographical context for our analyses was the area where environmental conditions are favourable for the presence of Ebola virus in the wild, as mapped by Olivero et al. (2017a). This map resulted from a model that included climate (i.e. annual temperature range), the presence of terra-firme rainforest and certain mammalian chorotypes in West and Central Africa. We refer to this area as to ‘the Ebola virus area’.

Bat distribution data

We compiled a georeferenced location data base for the 20 currently recognised African fruit bat species, of 12 genera (*Casinycteris*, *Eidolon*, *Epomophorus*, *Epomops*, *Hypsignathus*, *Lissonycteris*, *Megaloglossus*, *Micropteropus*, *Myonycteris*, *Nanonycteris*, *Rousettus* and *Scotonycteris*), whose distributions partially or entirely overlap with the Ebola virus area (Appendix S3). This data base was built using species range maps (Bergmans 1988, 1989, 1990, 1994, 1997) containing bat presence records at a 0.5° × 0.5° spatial resolution, and based on museum specimens. Using bat distributions since the 1980s is appropriate, as this matches the period during which Ebola virus outbreaks in Africa have been recorded. We revised Bergmans’ taxonomy following the Integrated Taxonomic Information System (www.itis.gov, recovered on 15/02/2019), which resulted in 20 species (see Appendix S2). Although Woermann’s long-tongued fruit bat *Megaloglossus woermanni* is currently split in the Integrated Taxonomic Information System into *Megaloglossus woermanni* and *Megaloglossus azagnyi* (Nesi et al. 2013), we decided to be conservative based on the note in the International Union for Conservation of Nature’s Red List (www.iucnredlist.org) that suggests that the two *Megaloglossus* species are thought to be allopatric but the exact limits of their ranges are not currently known. We also updated our data base by including presence data up to 2016 from the Global Biodiversity Information Facility (http://www.gbif.org/), filtered for reliability by ensuring overlap with the International Union for Conservation of Nature’s range maps and geographical affinity with Bergmans’ data. Occurrence data with ambiguous information in terms of coordinate precision and taxonomical attribution were rejected. Bergmans’ and filtered Global Biodiversity Information Facility presences were finally transferred to a single 0.5° × 0.5°-polygon shapefile using ArcGIS 10.3 (http://desktop.arcgis.com/en/).

Favourability modelling

We modelled the spatial distribution of each of the 20 bat species within the Ebola virus area. The models were developed at a 0.5° × 0.5° spatial resolution, based on the presence and the absence of recorded occurrences in every grid, and according to a set of predictor variables including environment (i.e. climate, topography and ecosystem types), spatial autocorrelation (trend-surface according to Legendre 1993), as well as socio-economic descriptors potentially driving human-induced habitat changes (i.e. non-intact forest, agriculture, livestock density, urbanisation, human population density). Besides, this 0.5° × 0.5° grid approach prevented autocorrelation that could result from spatial dependence amongst very close observations (i.e. within areas of approximately 2500 km^2; Legendre & Legendre 1998). Descriptors defining vegetation and land uses were expressed as proportions of every 0.5° × 0.5° grid occupied by each land-cover type; mean variable values in each grid were calculated for the rest of the descriptors (see Appendix S1). These values were computed using ArcGIS 10.3 (http://desktop.arcgis.com/en/).

All models were constructed using the Favourability Function (Real et al. 2006, Acevedo & Real 2012), which is defined by Equation 1:

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}} \quad (1)$$

where F is a favourability value for each 0.5° × 0.5° grid, ranging from 0 to 1; P is the probability of occurrence of a species, according to the set of predictor variables included in the model; n_1 is the number of recorded presences of the species, and n_0 is the number of recorded absences. P was calculated using logistic regression according to Equation 2 (i.e. based on presence/absence as the dependent variable), with the IBM-SPSS Statistics 23 software:

$$P = \frac{e^y}{1 + e^y} \quad (2)$$

where e is the base of Napierian logarithms and y is a linear combination of predictor variables. We chose this generalised linear model approach to minimise overfitting with respect to presences, as the absence of recorded occurrences at a given grid cell could mean either real absences or pseudoabsences of individuals of the target species. Generalised linear models are flexible enough to detect non-linear responses of the species to the environment, but also constrained enough to avoid modelling stochastic variation in species distributions (Olivero et al. 2016). A forward stepwise procedure was performed in order to avoid the inclusion of redundant variables in y. The stepwise selection identifies the most significant model with only one predictor, for which we used Rao's score test; then adds new variables, one at a time, only if the variable can contribute significantly to improving the model of the previous step. The model parameterisation was fitted by iterative log-likelihood maximisation. A chi-square test was used to evaluate the model's goodness-of-fit, and the contribution of every predictor variable in the model was assessed using Wald tests. All models were also evaluated according to their classification (sensitivity, specificity, correct classification rate and kappa; Fielding & Bell 1997) and discrimination capacities (area under the Receiving Operating Characteristics, ROC curve; Lobo et al. 2008).

Before the stepwise variable selection, Benjamini and Hochberg's (1995) false discovery rate control method was used to avoid type I errors resulting from the large number of variables considered. We also prevented excessive multicollinearity by not including highly correlated variables (Spearman's correlation coefficient >0.8) in the model.

Contribution of human activities to the explanation of fruit bat distributions

We employed variation partitioning analysis (Borcard et al. 1992) within every favourability model (FM), according to the approach proposed by Muñoz and Real (2006), to quantify the contribution (both positive and negative) of human activities relative to other factors. First, we defined the following concepts: the 'pure effect' of human activities is the contribution of this factor to the FM (i.e. to explaining favourability for the presence of the species) that is not influenced by covariation with non-human variables; the 'shared effect' by human and other variables is the intersection of the contributions made by both factors; the 'apparent effect' of a given factor is its total contribution to the FM, considering both its pure and shared effects. Then, for each species, we produced a new model (NHM) considering only the non-human variables included in the FM. We estimated the apparent effect of non-human variables using the square of Spearman's correlation coefficient (R^2) between FM and NHM: R^2_{NHM}. Finally, the pure effect of human activities was assessed by subtracting the apparent effect of non-human variables from the total variation within the FM (i.e. from 1):

$$\text{Pure effect of human activities} = 1 - R^2_{\mathrm{NHM}} \quad (3)$$

Local sampling bias, representing a greater chance of observing a species in accessible (and thus probably human-modified) areas, was reduced because presences, predictor variables, and the models themselves were built on a 0.5° × 0.5° resolution (i.e. on around 2500-km^2 squares). Nevertheless, to test whether the effects of this bias still persisted at this resolution, we repeated all the models, this time constraining the model training extent to squares where bat observations have effectively occurred (n = 1331 squares), that is squares that have been visited by samplers. In this way, we verified, for every species, whether the human footprint still showed positive and significant relations with bat presence in a model training extent in which we controlled for this bias. When the human contribution in one of these models was null, we rejected the information provided by the corresponding model for the whole study area. In the remaining cases, trends in human contributions defined by both model sets were compared by using the Spearman's rank correlation coefficient.

Overlap between EVD outbreaks and areas where human activities could influence fruit bat distributions

We mapped those geographical expanses where the presence of a given fruit bat species could be favoured by human activities using ArcGIS 10.3. These areas were defined by a ≥ 0.1 positive difference between FM favourability values and NHM favourability values for each 0.5° × 0.5° grid cell.

We estimated the overlap between 1) the areas where the presence of a fruit bat species could be favoured by human activities and 2) two different sets of locations associated with EVD outbreaks in humans. The latter included all EVD cases recorded between 1976 and 2014 ($n = 40$; Olivero et al. 2017a; Appendix S3), as well as outbreak locations significantly linked to deforestation events after 2006 ($n = 7$; Olivero et al. 2017b; Appendix S3). The overlap was the proportion of outbreak sites occurring within that area. The degrees of overlap between both sets of outbreak locations were compared using the chi-square test for comparison of proportions (Snedecor & Cochran 1967).

RESULTS

Of the 20 fruit bat species considered in our analyses, we obtained significant models for 16 species (all models' goodness-of-fit had $P < 0.01$, Appendix S2). The four species without significant models were the golden short-palated fruit bat *Casinycteris argynnis*, the Campo-Ma'an fruit bat *Casinycteris campomaanensis*, Sanborn's epauletted fruit bat *Epomophorus grandis* and Hayman's lesser epauletted fruit bat *Micropteropus intermedius*. The three latter species are very rare and known only from very few localities.

Most significant models had excellent discrimination capacities (mean area under the ROC curve = 0.879, standard deviation, SD = 0.073) and provided correct classification for more than 75% of presences and absences (mean correct classification rate = 0.784, SD = 0.082). Kappa, which considers the chance of random correct classifications, always produced positive values (mean Kappa = 0.247, SD = 0.108). For these 16 species, human activities contributed (both positive and negatively) a mean of 29% (SD = 27) in explaining favourable areas for the presence of bat species (Fig. 1). The model for only one species, the little epauletted fruit bat *Epomophorus labiatus*, showed no influence of human activities. Considering the remaining 15 cases, the human contribution in models focused on the whole study area was significantly correlated with the contribution indicated by the models restricted to visited grids ($R = 0.510$, $P < 0.05$), suggesting that there was no sampling bias towards human-modified

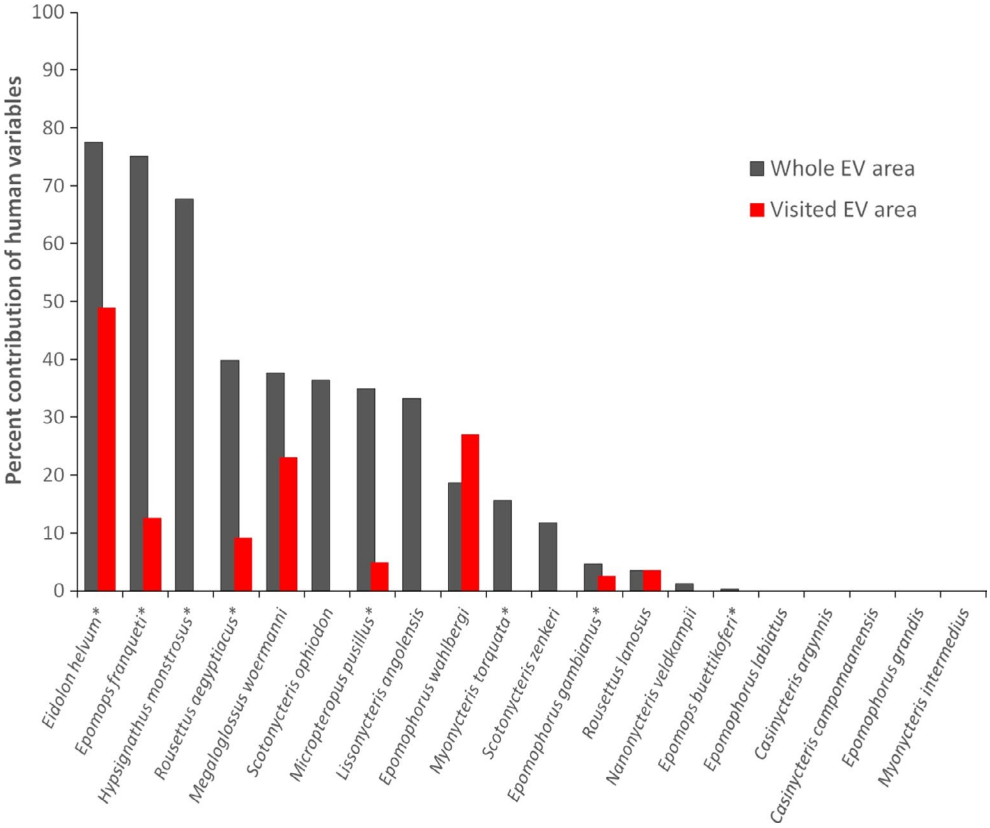

Fig. 1. Contribution (%, both positive and negative) of human variables in explaining favourable conditions for the presence of fruit bats in the whole Ebola virus area as determined by Olivero et al. (2017a), and within this area, in the squares where bat observations have occurred effectively (i.e. in the 'visited' Ebola virus area). Asterisks indicate species serologically linked to the Ebola virus. [Colour figure can be viewed at wileyonlinelibrary.com]

areas in these cases. However, for seven species, models restricted to visited grids attributed no influence to human activities: *Hypsignathus monstrosus*, the Angolan soft-furred fruit bat *Lissonycteris angolensis*, *Myonycteris torquata*, Büttikofer's epauletted fruit bat *Epomops buettikoferi*, Pohle's fruit bat *Scotonycteris ophiodon*, Zenker's fruit bat *Scotonycteris zenkeri* and *Nanonycteris veldkampii* (Fig. 1). So for these species, we cannot affirm that the contribution of human activities suggested by their models in the Ebola virus area was not due to sampling bias. These seven species were thus excluded from the remaining analyses.

In the models for the eight remaining species, the concentration of humans (i.e. shorter distance to populated localities and high rural population density) was positively linked to favourable conditions for the presence of seven species; and infrastructures (i.e. shorter distance to roads and rail-roads) were positively linked to favourable conditions for the presence of three species (Appendix S2). Agriculture, represented by the density of croplands, was positively related to favourable conditions for the presence of three species, whilst the percentage of non-intact forests characterised the favourable conditions for the presence of two species. High livestock concentration was relevant in explaining the favourable conditions for the presence of two species.

When all the recorded EVD outbreaks (Appendix S3) were included in the analysis, the proportion of overlap between outbreak locations and areas where human activities could influence fruit bat presence positively ranged from 0 to 0.5 (mean proportion = 0.28; *n* = 40; Table 1, Appendix S4). In contrast, when only those cases that were significantly linked to deforestation between 2001 and 2014 were considered (Olivero et al. 2017b; Appendix S3), proportions ranged from 0 to 0.86 (mean proportion = 0.62; *n* = 7). For five bat species, the degree of overlap for outbreaks linked to forest loss was significantly higher than the overlap for all EVD outbreaks between 1976 and 2014 (Table 1): *Eidolon helvum*, *Epomops franqueti*, *Megaloglossus woermanni*, Peters's lesser epauletted fruit bat *Micropteropus pusillus* and *Rousettus aegyptiacus* (Fig. 2). Amongst the species not excluded due to possible sampling bias, these five were attributed the highest influence to human activities (≥35%). All of them except *Megaloglossus woermanni* have been serologically linked to the Ebola virus, and polymerase chain reaction-positive individuals have been also found of *Epomops franqueti* (Leroy et al. 2005).

DISCUSSION

For five out of the 20 bat species considered in our study, we provide biogeographical support for the hypothesis that positive human influence on fruit bats could be associated with EVD outbreaks in deforested areas within the tropical forest biome in West and Central Africa; this biome is described as favourable for the occurrence of Ebola virus in the wild by Olivero et al. (2017a). The five species are as follows: *Eidolon helvum*, *Epomops franqueti*, *Megaloglossus woermanni*, *Micropteropus pusillus* and *Rousettus aegyptiacus*. For *Eidolon helvum* and *Epomops franqueti* in particular, humans have a strong effect: human variables contribute as much as 78% and 40% in explaining favourable areas for their presence respectively, both positively and negatively. This result strengthens observations made for these species (Lang & Chapin 1917, Centeno-Cuadros et al. 2017), which suggests that the expansion of cultivated fruits provides an ample year-round food supply for them. In the case of *Eidolon helvum*, its large-scale mobility allows it to exploit seasonal local fruiting peaks over large areas, as indicated by Thomas (1983). Moreover, roosting opportunities provided by parks and other urban

Table 1. Proportion of the Ebola virus disease (EVD) outbreak locations that overlap with areas where human activities favour the presence of each species of fruit bat. Proportions are shown for all locations, and separately for those linked to forest loss (Olivero et al. 2017a). When the forest-loss-outbreak proportion was higher than the all-outbreak proportion, a chi-square test was used for comparison between them. Results for species not subject to sampling bias are shown; ^{EV} indicates species in which seropositive individuals have been recorded. *Significant difference between proportions ($P < 0.05$).

Fruit bat species	Proportion of EVD outbreak locations in which bats are favoured by humans (all 40 EVD outbreaks between 1976 and 2014)	Proportion of EVD outbreak locations in which bats are favoured by humans (7 EVD outbreaks linked to forest loss)	χ^2
Eidolon helvum^{EV}	0.38	0.86	2.55*
Epomophorus gambianus^{EV}	0.03	0.14	1.02
Epomophorus wahlbergi	0.30	0.57	1.35
Epomops franqueti^{EV}	0.33	0.86	2.80*
Megaloglossus woermanni	0.50	0.86	1.96*
Micropteropus pusillus^{EV}	0.40	0.86	2.45*
Rousettus aegyptiacus^{EV}	0.33	0.86	2.81*
Rousettus lanosus	0.00	0.00	–

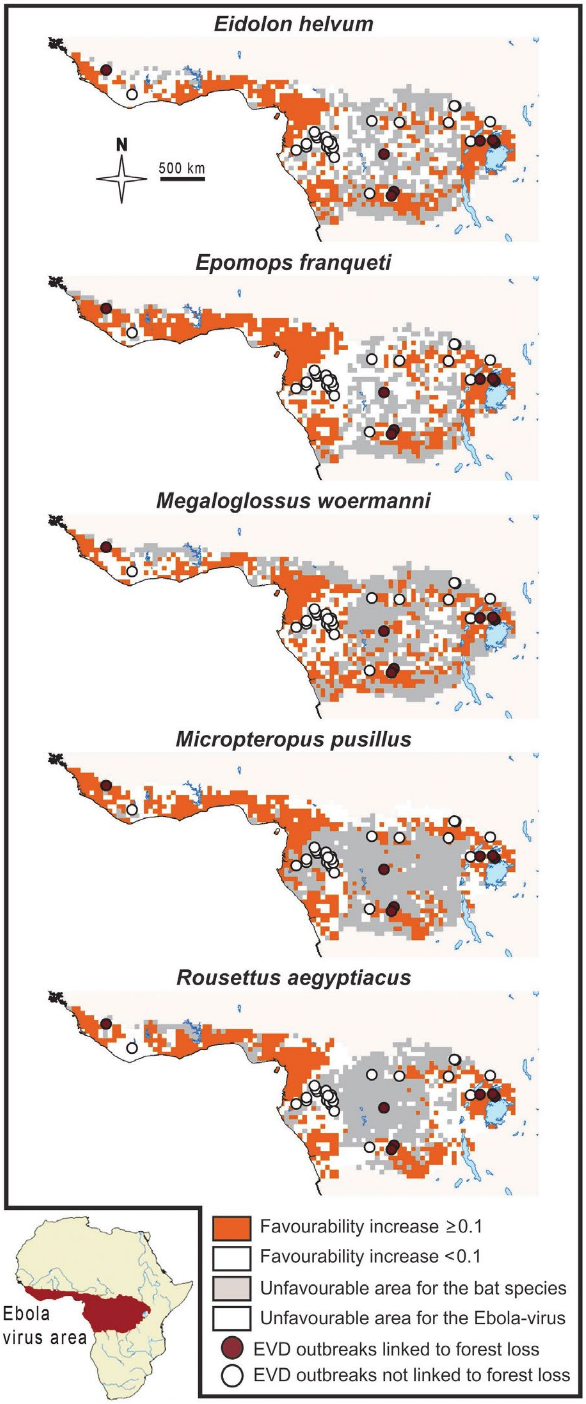

Fig. 2. Maps of geographical areas in Africa where bat presence is favoured by human activities (i.e. favourability increases when human variables are considered) in the Ebola virus area (Olivero et al. 2017a) and overlap with Ebola virus disease (EVD) outbreaks. EVD cases linked and not linked to deforestation (Olivero et al. 2017b) are shown. A map is shown for each of the five bat species for which the degree of overlap for outbreaks linked to forest loss was significantly higher than the overlap for all EVD outbreaks between 1976 and 2014 (Table 1). [Colour figure can be viewed at wileyonlinelibrary.com]

environments allow large concentrations of these bats to form (Happold & Happold 2013, Peel et al. 2017).

The insights that can be derived from a better understanding of the human-fruit bat associations we present here are fundamental to helping scientists determine the anthropogenic settings that may trigger the Ebola virus to jump from wildlife to humans. Our biogeographical analysis supports the hypothesis that some African fruit bat distributions are significantly linked to human activities throughout the region where the Ebola virus occurs. More specifically, we show that the positive human influence on four of the fruit bat species that have been serologically linked to the Ebola virus overlaps with areas where EVD outbreaks were favoured by deforestation. The implications of these relationships for Ebola virus transmission must be taken seriously in order to determine how Ebola virus may spread in deforested areas. It is now critical to comprehend the networks and pathways that may lead to an EVD outbreak. The perception that bats can cause disease in humans may help raise awareness in cultures that use bat products, perhaps resulting in interventions such as temporal restrictions on hunting or selling (Kamins et al. 2015). Nevertheless, negative attitudes that may threaten populations of these animals (e.g. by uncontrolled culling of fruit bats) must be avoided (Guyton & Brook 2015). The loss of bats will in turn affect the ecosystem services they provide (Kunz et al. 2011) and may even increase pathogen prevalence and enhance disease transmission to humans (Streicker et al. 2012, Amman et al. 2014).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Predictor variables used to build favourability models for fruit bat species.

Appendix S2. Favourability models for fruit bat species distribution in the Ebola virus area.

Appendix S3. List of 40 confirmed outbreaks of EVD (events of zoonotic transmission of EVD to humans) between 1976 and 2014.

Appendix S4. A. Presence records, within the Ebola virus area, for the 15 fruit bat species with significant favourability models that are partially explained by human activities in this geographical context. B. Maps of favourability models. C. Maps of geographical areas where bat presence is favoured by human activities, and overlap with EVD outbreaks.