European Journal of Wildlife Research (2020) 66: 12
https://doi.org/10.1007/s10344-019-1346-7

ORIGINAL ARTICLE

Ebola spillover correlates with bat diversity

Julie Teresa Shapiro[1,2,3] · Adia R. Sovie[2] · Chelsey R. Faller[2,4] · Ara Monadjem[5,6] · Robert J. Fletcher Jr[1,2] · Robert A. McCleery[1,2,6]

Received: 23 May 2019 / Revised: 5 September 2019 / Accepted: 1 December 2019 / Published online: 3 January 2020

Abstract

Some of the world's deadliest diseases and greatest public health challenges are zoonoses from wildlife, such as Ebola (*Ebolavirus*). Due to the increasing number of cases in recent years, it has been widely hypothesized that increasing human population densities and anthropogenic disturbance largely explain outbreaks of Ebola virus disease in humans. While studies indicate that ebolaviruses are likely hosted by bats (Chiroptera), their role in outbreaks of the disease remains unclear. We tested whether bat species richness (total and within families), human population density, and anthropogenic disturbance explained the occurrence of Ebola virus disease spillovers within Africa using both generalized linear models and Maxent models. We demonstrate that spillover occurred in areas with high species richness of nycterid bats and low levels of both anthropogenic disturbance and human population density. Outbreaks of Ebola virus disease have devastating effects on people and communities and our results provide an important step toward understanding how and where Ebola virus disease may spill over to human populations.

Keywords Bats · Biodiversity · Chiroptera · Ebola · Emerging pathogens · Public health · Zoonotic disease

Introduction

Zoonotic diseases originating in wildlife, such as Ebola virus disease (*Ebolavirus*), pose great challenges to global public health. When these viruses "spill over" to humans, the effects can be devastating, as the Ebola virus disease outbreaks of 2013–2014 in West Africa (Elston et al. 2015; Spengler et al. 2016) and 2018–2019 in the Democratic Republic of the Congo (World Health Organization 2019) illustrate. While the first recorded outbreak of Ebola virus disease occurred in 1976 (Mylne et al. 2014), our understanding of how and why spillovers occur where they do is poor (Groseth et al. 2007; Alexander et al. 2015), although recent studies have made advances in this area (Rulli et al. 2017; Wilkinson et al. 2018). Furthermore, the role that putative reservoirs play in the spillover of Ebola virus disease is unclear (Leendertz et al. 2015; Leendertz 2016; Caron et al. 2018).

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10344-019-1346-7) contains supplementary material, which is available to authorized users.

✉ Julie Teresa Shapiro
julie.teresa.shapiro@gmail.com

[1] School of Natural Resources and Environment, University of Florida, 103 Black Hall, Gainesville, FL, USA

[2] Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL, USA

[3] Centre International de Recherche en Infectiologie, Institut national de la santé et de la recherche médicale, 46 Allée d'Italie, 69634 Lyon, France

[4] Conservation Management Institute, Virginia Polytechnic Institute and State University, 1900 Kraft Drive, Suite, Blacksburg, VA 250, USA

[5] Department of Biological Sciences, University of Eswatini, Private Bag 4, Kwaluseni, Eswatini

[6] Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield, Pretoria 0028, South Africa

Bats (order Chiroptera) are considered the most likely wild reservoir hosts of ebolaviruses (Leroy et al. 2005; Olival and Hayman 2014). There is still uncertainty and speculation that other species or species groups may ultimately prove to be the reservoir host(s) or complex of hosts (Leendertz et al. 2015; Leendertz 2016; Caron et al. 2018). Nevertheless, exposure to ebolaviruses has been detected via serology or PCR in 10 species in 3 families of bats in Africa (Leroy et al. 2005; Pourrut et al. 2009; Hayman et al. 2010, 2012; Ogawa et al. 2015; De Nys et al. 2018), and the full genome of a novel *Ebolavirus* species, *Bombali virus* (BOMV), has recently been isolated from bats, indicating that bats likely play an important role in the ecology of the virus even if other taxa are ultimately found to be the host reservoir (Caron et al. 2018). To date, pteropodid fruit bats have received the most attention as potential reservoir hosts of Ebola (Hayman et al. 2012; Pigott et al. 2014; Alexander et al. 2015; Leendertz et al. 2015), but serological studies have detected exposure to the virus at comparable rates in bats from other families (Pourrut et al. 2009; De Nys et al. 2018). Further, the recently described BOMV was detected in two species of molossid bat, *Chaerephon pumilus* and *Mops condylurus* (Goldstein et al. 2018), illustrating that there may be many as-yet-undetected non-pteropodid bats that host ebolaviruses.

Anthropogenic factors, such as high human population densities and disturbance, are thought to be major driving forces of Ebola virus disease spillover, particularly in light of the increasing number of outbreaks during recent decades of extensive growth and development (Muyembe-Tamfum et al. 2012; Changula et al. 2014). Human population density and disturbance may increase rates of contact with infected hosts or alter host ecology (Plowright et al. 2008, 2015; Bausch and Schwarz 2014; Alexander et al. 2015; Olivero et al. 2017; Rulli et al. 2017). However, the role of host diversity could also play a largely unexplored role in determining where ebolaviruses spill over. Zoonotic diseases have frequently emerged in areas of high biodiversity (Jones et al. 2008), and mammalian diversity appears to increase the general risk of zoonotic disease spillover (Allen et al. 2017). Finally, viruses with greater host diversity are more likely to spill over to people, and the incidence of these viruses may increase where many host species occur in sympatry (Olival et al. 2017).

Therefore, we compared the predictive power of bat diversity, human population density, and anthropogenic disturbance in predicting the location of Ebola virus disease spillovers to humans. Understanding the associations between the potential drivers and spillovers will give us a better understanding of the role that host diversity (a function of both biogeographic and ecological factors), compared with anthropogenic factors (a function of human activity), may play in Ebola virus disease spillovers. To do so, we used high resolution distribution maps of 172 African bat species. Due to the importance of reservoir hosts in constraining the presence of ebolaviruses and therefore its ability to spill over to humans (Plowright et al. 2015), we predicted that bat species richness would be a stronger predictor of outbreaks than human population density or anthropogenic disturbance.

Material and methods

Data compilation and spatial analysis

We identified the location of human Ebola virus disease outbreak points in sub-Saharan Africa, from 1990 to 2018 using the review by Mylne et al. (2014), other peer-reviewed articles, and reports from the World Health Organization and Centers for Disease Control and Prevention (Table S1). For each outbreak, we investigated the location of the initial spillover and assumed that subsequent cases were the result of human-to-human transmission (Gire et al. 2014).

We calculated potential bat species richness, human population density (individuals/km^2), road density (km/km^2), crop cover (proportion cover), and pasture cover (proportion cover) across Africa using Geographic Information System (Fig. 1). We only considered species richness of bats in our analysis because we wanted to understand the role of potential host diversity in spillover and there is compelling evidence for the role of bats as host reservoir (Leroy et al. 2005; Pourrut et al. 2009; Hayman et al. 2010, 2012). We only consider species richness because data sets for other measures, such as abundance or community composition, do not currently exist for African bat fauna (e.g., see Happold and Happold 2013). While multiple species of bat are suspected to be potential hosts of ebolaviruses due to serological exposure, relatively few species, especially outside the frugivorous pteropodid family, have been screened for it in tropical Africa. The newly described BOMV was detected in two species of molossid bats (Goldstein et al. 2018) from which other ebolaviruses had never before been detected, although they had survived experimental inoculation (Swanepoel 1996). Further, trait-based and phylogenetic analyses of ebolavirus hosts predict a wide range of potential hosts in several bat families (Han et al. 2016). These findings suggest that additional bat species could host the virus. Other mammals, such as primates and duikers, that may become infected by Ebola are considered dead-end hosts (Olival and Hayman 2014), and we therefore did not consider them in our analyses.

We measured human population density (people/km^2) because greater human population densities are generally hypothesized to increase the risk of zoonotic disease spillover (Mahy and Brown 2000; Weiss and McMichael 2004; Jones et al. 2008) and specifically may increase the risk of Ebola virus disease spillover (Rulli et al. 2017), as the probability of contact with an infected host increases with population

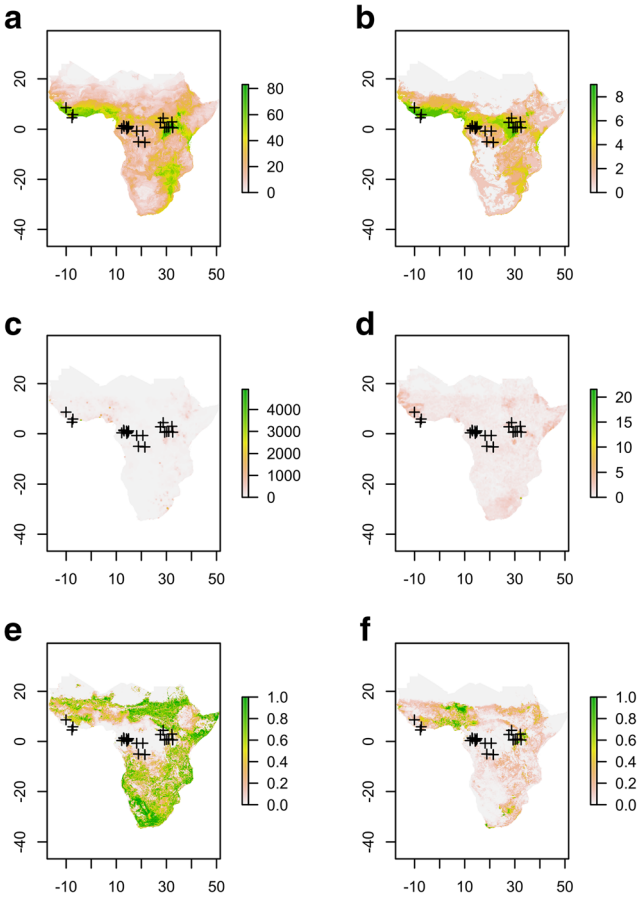

Fig. 1 Maps showing distribution of (a) total bat species richness (number of species), (b) nycterid species richness (number of species), (c) human population density (individuals/km^2), (d) road density (km/km^2), (e) crop cover (proportion cover), and (f) pasture cover (proportion cover). Crosses indicate locations of Ebola virus disease spillover to humans. The color gradient shows lowest values in gray and highest values in green

density. We used the Gridded Population of the World (GPW) version 3 for the year 2000 to measure human population density (Center for International Earth Science Information Network 2005; Balk et al. 2006). This data set was intended to be used to assess the number of people at risk of infectious disease throughout the world. It is based on the highest resolution census data available for each country. The census data from irregularly shaped administrative areas were then converted to regularly shaped grids (Balk et al. 2006).

Anthropogenic disturbance is hypothesized to increase the risk of zoonotic disease spillover, including Ebola virus disease (Bausch and Schwarz 2014; Olivero et al. 2017; Rulli et al. 2017) especially in remote areas (Wolfe et al. 2005). We measured road density (km/km^2), crop cover (proportion cover) and pasture cover (proportion cover) as proxies for disturbance. We used road density because it is considered a strong indicator of anthropogenic disturbance (Gill et al. 1996; Forman and Alexander 1998; Sanderson et al. 2002). In addition to serving as a proxy for disturbance, roads also facilitate the movement of people into and across these remote areas, increasing both contact with potential disease vectors and facilitating the spread of diseases among people after the initial spillover event (Patz et al. 2004; Wolfe et al. 2005). We also measured crop and pasture cover because these are two of the principle forms of land cover change in sub-Saharan Africa (Ellis and Ramankutty 2008; Ramankutty et al. 2008; Brink and Eva 2009) and are not captured by increased density of roads.

We used the Global Roads Open Access Data Set (gROADS) (Center for International Earth Science Information Network 2013) to measure road density. This data set is based on merging existing global and country-level data sets of roads, filling gaps, and adjusting topology using Google Earth imagery (Center for International Earth Science Information Network 2013). We used the Global Agricultural Lands data sets for both crop cover and pasture cover (Ramankutty et al. 2008, 2010a, 2010b). Both of these data sets were based on remote-sensing imagery from multiple satellites, as well as census data at multiple spatial scales (Ramankutty et al. 2008). We obtained the population density, road density, crop cover, and pasture cover data sets from the Socioeconomic Data and Applications Center (http://sedac.ciesin.columbia.edu/).

To test if diversity of the bat community was correlated with the probability of Ebolavirus disease outbreaks, we determined the bat species richness across sub-Saharan Africa. To do so, we compiled distributions for all bat species for which ≥ 5 records exist in Africa (n = 172) based on data taken from literature, which included 14,145 unique locality-species records (see Monadjem et al. 2018). These records are based on museum specimens that have been reported in > 140 publications (all cited in Monadjem et al. 2018). For each species, we used Maxent (Phillips et al. 2006) to model the predicted suitable habitat space under present climatic conditions. We ran models at a resolution of approximately 5 km (2.5 arc min) using all 19 BIOCLIM variables from the WorldClim database (Hijmans et al. 2005), as bioclimatic conditions are important for determining bat species' distributions (McCain 2007; Rebelo et al. 2010), as well as altitude (Hijmans et al. 2005), altitudinal roughness, and ecoregions as classified by Olson et al. (2001) (Monadjem et al. 2010, 2018). Because the use of highly correlated layers may lead to model over-fitting, we also ran these Maxent models after removing redundant BioClim variables with a principal component analysis (PCA) in R version 3.0.1 (R Core Team 2013) using the package FactoMineR (Lê et al. 2008). (See Table S2 for list of final BioClim variables included in these Maxent models.) We divided occurrence data into training and testing sets for a ten-fold cross-validation, testing each model on identical withheld data via the area under the receiver operating characteristic curve (AUC) test statistic. Each model was set to use auto

features for the analyses based on the number of records for each species (Phillips and Dudík 2008).

Using predictions from presence-only Maxent models to quantify species richness based on "stacked" distribution models (S-SDM) requires truncating probabilities to 0/1 data. We selected species-specific thresholds that maximized the sum of sensitivity and specificity, which has been argued to be an appropriate technique for presence-only data (Liu et al. 2013). With this information, we then summed 0/1 data to quantify species richness of all bat species considered as well as species richness of ten different bat families. We did this to determine if some families might have more influence in explaining spillover events than others. Ebolaviruses have been detected in ten species in three different families (Table S3). However, only a limited number of species have been screened, and it is still unclear which species or families are the most likely reservoir hosts. We also summed the richness of all non-pteropodid species, to determine the influence of dietary niche (insectivorous vs. frugivorous) in explaining spillover events. (All frugivorous species in the study area are in the pteropodid family.)

Statistical analysis

To understand the relationships between bat species richness, human population density, anthropogenic disturbance, and the probability of spillover events, we compared outbreak locations to 10,000 background (random) locations throughout sub-Saharan Africa. We generated random points using the function "sampleRandom" in the package raster (Hijmans and van Etten 2012) in the program R (R Core Team 2013). We chose the number of random points to represent the continuous nature of the variables throughout the study area (Renner et al. 2015). We ran models with different numbers of background points, starting with 100,000, 50,000, and then in decreasing increments of 10,000 background points until reaching 10,000. We observed no difference in standard errors between models using any of the different quantities of background points and therefore used 10,000 background points (Renner et al. 2015). We evaluated bat diversity, human population density, road density, crop cover, and pasture cover at a scale of 25 km for every outbreak and background point. Twenty-five km^2 was the finest spatial resolution we could obtain for where actual spillover events occurred based on descriptions of the index case and that person's movements prior to showing symptoms.

We evaluated the associations of bat species richness, population density, and anthropogenic disturbance with Ebola virus disease outbreaks using species distribution models. Modeling frameworks that focus on presence-only or presence-background data, including certain specifications of Maxent and generalized linear models (Phillips et al. 2006; Elith et al. 2006), approximate the inhomogeneous point process model (IPPM) (Renner et al. 2015). Here we use GLMs and Maxent, specifying them to approximate the inhomogeneous point process model. Generalized linear models (GLMs) are widely used in ecological modeling (Austin 2002) and have been applied to disease ecology (e.g., Luis et al. 2013; Morand et al. 2013). Maxent is a widely used modeling approach that tends to perform well, in terms of model predictions, relative to other common modeling approaches (Phillips et al. 2006; Elith et al. 2006). We fit GLMs as infinitely weighted logistic regression to approximate the IPPM with a binomial distribution, with weights set to 1 for presence points and 10^6 for background points as described by Renner et al. (2015). In order to use Maxent as an IPPM, we ensured that duplicates within grid cells were not removed. In addition, we only considered linear, quadratic, and hinge features in modeling (Renner et al. 2015).

We initially ran both the GLM and Maxent models with five variables: total bat species richness, human population density, road density, crop cover, and pasture cover. Before running the models, we checked for correlation between these five variables using the "layerStats" function in the R package raster (Hijmans and van Etten 2012). Correlation for all pairs was < 0.27, including population density and road density ($r = 0.22$) (Table S4). For the GLM, we examined the 95% confidence intervals on the estimates of each variable. We then ran separate GLMs using only variables from the first model whose 95% confidence interval did not include 0. We also ran GLMs with the species richness of each individual family as the explanatory variable. For comparison, we also ran models with a single variable from the initial model (human population density, road density, crop cover, and pasture cover). We then identified the most parsimonious model using Akaike information criterion corrected for small samples sizes (AICc) (Table 1). We considered the model with the lowest AICc the best model and considered models within 2 units as competing models (Burnham and Anderson 2002).

For the Maxent model, the initial model also included total bat species richness, human population density, road density, crop cover, and pasture cover. We evaluated the percent contribution of each variable. We then ran a second model that included the variables that contributed > 5% to the initial model and also added the richness of each individual bat family and insectivorous bat richness. We then again evaluated the percent contribution of each variable to the model (Table 2).

We assessed predictive accuracy of the top GLM and Maxent models using fourfold cross-validation with an equal number of presence points in each fold and report the area under the curve (AUC), sensitivity, specificity, the true skill statistic (TSS), and kappa (Hanley and McNeil 1982; Allouche et al. 2006). For the GLM, we used the mean model prediction from all folds as the threshold when calculating

Table 1 Model selection results for generalized linear models. We also show the intercept, degrees of freedom (df), log likelihood, Akaike information criterion corrected for small sample size (AICc), delta AICc, and model weights for each GLM. "+" indicates additive terms

Model	(Intercept)	df	LogLik	AICc	Delta	Weight
Nycterid richness + pasture	−20.3	3	−438.6	883.1	0.0	0.92
Pteropodid richness + pasture	−20.0	3	−441.3	888.7	5.52	0.06
Bat richness + pasture	−20.0	3	−443.1	892.2	9.12	0.01
Vespertilionid richness + pasture	−19.8	3	−443.8	893.6	10.47	0
Insectivorous bat richness + pasture	−19.9	3	−443.8	893.7	10.53	0
Molossid bat richness + pasture	−19.7	3	−444.5	895.0	11.88	0
Rhinopomatid richness + pasture	−19.0	3	−445.1	896.1	13.00	0
Bat richness + human population density + road density + crop + pasture	−20.0	6	−442.3	896.7	13.52	0
Hipposiderid richness + pasture	−19.5	3	−447.0	900.1	16.94	0
Emballonurid richness + pasture	−19.5	3	−447.5	901.0	17.91	0
Rhinolophid richness + pasture	−19.4	3	−448.0	902.0	18.83	0
Pasture	−19.2	2	−449.1	902.3	19.13	0
Miniopterid richness + pasture	−19.3	3	−448.3	902.7	19.54	0
Megadermatid richness + pasture	−19.2	3	−448.8	903.5	20.38	0
Road density	−20.1	2	−460.0	923.9	40.81	0
Population density	−20.0	2	−460.2	924.5	41.33	0
Crop	−19.9	2	−460.3	924.6	41.51	0

sensitivity and specificity because the probabilities were small. For the Maxent model, the optimal threshold was based on maximizing sensitivity and specificity. We ran all models in the program R (R Core Team 2013), using the base package for GLMs and the package dismo for Maxent models (Hijmans et al. 2013).

Results

We identified 22 spillover events of Ebola virus disease from 1990 to 2018 (Table S1). Across sub-Saharan Africa, human population density ranged from 0 to 3114.4 people/km^2, and road density ranged from 0.0 to 23.6 km/km^2. Both proportion

Table 2 Variable contribution for Maxent models including the percent contribution and permutation importance

Model	Variable	Percent contribution	Permutation importance
Simple Maxent	Pasture	56.9	52.7
	Bat richness	32.8	40.2
	Population density	7.8	6.3
	Crop	2.6	0.7
	Road density	0.0	0.1
Maxent with bat families	Nycterid richness	51.2	57.5
	Pasture	35.0	17.7
	Population density	4.9	5.3
	Rhinopomatid richness	3.0	13.7
	Emballonurid richness	2.5	0.6
	Hipposiderid richness	1.5	1.3
	Molossid richness	0.9	0.4
	Insectivorous bat richness	0.5	2.6
	Rhinolophid richness	0.2	0.4
	Vespertilionid richness	0.2	0.5
	Pteropodid richness	0.1	0.0
	Megadermatid richness	0.0	0.0
	Bat richness	0.0	0.0
	Miniopterid richness	0.0	0.0

crop cover and proportion pasture cover ranged from 0.0 to 1.0. Bat species richness ranged from 0 to 79 species (Fig. 1).

The initial GLM , which included total bat species richness, human population density, road density, crop cover, and pasture cover, identified bat species richness and pasture cover as the best predictors, with bat richness having a positive effect on the relative probability of spillover ($\beta = 0.04 \pm 0.01$, 95% confidence interval: 0.02–0.06), while pasture cover had a negative effect ($\beta = -6.69 \pm 2.58$, 95% CI: −13.09 – −2.86) (Fig. 2). These were the only predictors in the model whose 95% confidence intervals did not include 0 (crop cover, -1.77 ± 1.78, 95% CI: −6.30 – 1.01; human population density, -0.0002 ± 0.002, 95% CI: −0.006 – 0.001; road density, -0.13 ± 0.30, 95% CI: −0.57 – 0.65).

Next, we ran separate models with only bat species richness and pasture cover; the richness of each bat family and pasture cover; and insectivorous bat species richness and pasture cover. Model selection of GLMs showed that the model with nycterid bat species richness was the top model ($\beta = 0.39 \pm 0.09$, 95% confidence interval: 0.22–0.56) (Table 3; Fig. 2). There were no competing models: model weight was 0.92, and ΔAICc between the nycterid richness model and the next-best model (pteropodid richness) was 5.52. The nycterid richness model also had relatively high predictive accuracy (AUC = 0.86; TSS = 0.75) (Table 3).

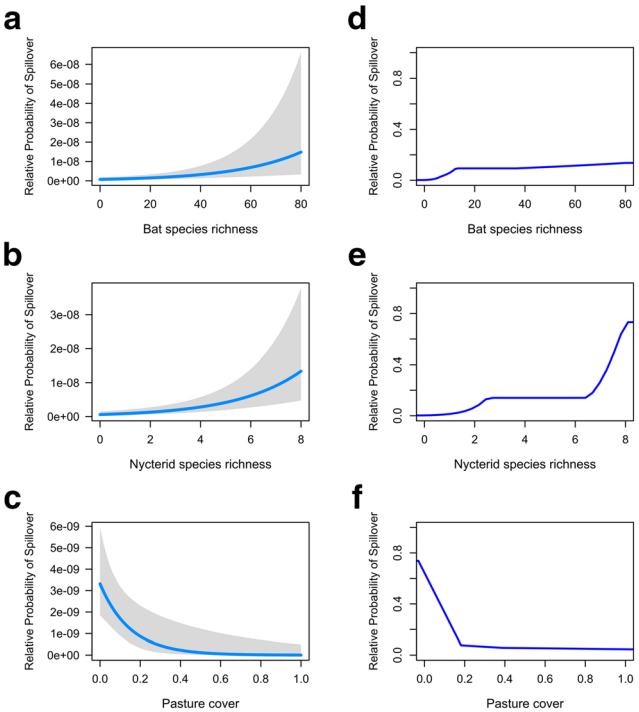

Fig. 2 Response of relative probability of Ebola virus disease spillover according to generalized linear models (GLM) (a, b, c) and Maxent models (d, e, f) to total bat species richness, nycterid species richness, and pasture cover. Predictions are shown in solid lines. For GLMs, 95% confidence intervals are shown in gray shading

In the initial Maxent model, pasture cover, which was negatively associated with spillover, had the greatest contribution at 56.9% while bat species richness contributed, 32.8%, with a positive association. Human population density contributed 7.8% and was negatively associated with spillovers, and road density contributed 0%. Similarly, permutation importance was highest for pasture cover (52.7%), followed by bat richness (40.2%), human population density (6.3%), road density (0.7%), and crop cover (0.1%) (Table 2). In the next Maxent model (which included total bat species richness, the richness of each bat family, the richness of insectivorous bats, pasture cover, and human population density), nycterid bat richness made the highest contribution at 51.2%. Pasture cover contributed 35.0% and was negatively associated with spillovers. All other variables combined contributed only 13.8%, with each variable contributing < 5%. Nycterid bats also had the highest permutation importance at 57.5%, followed by pasture cover (17.7%) (Table 2). This Maxent model also had relatively high predictive accuracy (AUC = 0.82, TSS = 0.65) (Table 3).

Discussion

Our models consistently showed that Ebola virus disease spillovers were associated with areas of high bat richness and reduced pasture cover. The only association we found with anthropogenic disturbance was a negative relationship with pasture cover, indicating that spillovers are more likely to occur where pasture cover is low. Neither human population density, road density, nor crop cover was a strong predictor of spillover events in any models (Table 1, Table 2). Among specific bat families, we found that spillover was associated with areas of high nycterid species richness. The GLM including nycterid richness had a model weight over 0.9, and nycterid richness made the greatest contribution by far in the Maxent model. The richness of other bat families made only marginal contributions. Our models had high predictive accuracy comparable to previous studies (Pigott et al. 2014, 2016).

Increasing human population densities and anthropogenic disturbance have been widely cited as major drivers of zoonotic disease spillover in general (Daszak 2000; Daszak et al. 2001; Jones et al. 2008; Plowright et al. 2015; Brierley et al. 2016). These factors have also been suggested as potential drivers of Ebola virus disease spillovers (Daszak 2000), including the 2013–2014 outbreak (Bausch and Schwarz 2014; Changula et al. 2014; Laporta and Laporta 2014; Alexander et al. 2015; Olivero et al. 2017), and have frequently been referred to in popular media reports (Wilkinson and Leach 2015). Rulli et al. (2017) found that within West and Central Africa, outbreaks occurred in areas with higher human population density and forest fragmentation (although not complete loss), compared to average levels in the region. On the other

Table 3 Top models for Ebola virus disease spillover based on generalized linear and Maxent models, showing the area under the curve (AUC), sensitivity, specificity, and true skill statistic (TSS) for both model types. Beta (β), 95% confidence interval (CI), and *p* values are shown for the GLM only

Model	Best model	AUC	Sensitivity	Specificity	TSS	Kappa	β	95% CI	P
GLM	Nycterid richness + pasture	0.86	0.95	0.80	0.75	0.02	0.39 −5.53	0.22–0.56 −11.56 – −1.96	< 0.001 0.02
Maxent	Bat families	0.82	0.82	0.83	0.65	0.02	–	–	–

hand, our analysis shows that at the continental scale, even relatively remote areas with low population densities and little anthropogenic disturbance may still have an elevated risk of Ebola virus disease spillover if potential bat species richness is high. This discrepancy may be due to the difference in spatial scale between this study and Rulli et al. (2017) (continental vs. regional). While locations where Ebola virus disease spillover occurred may have higher population density than other areas in the region, these are not large cities or population centers. Modeling by Wilkinson et al. (2018) also indicates that many areas at high risk of Ebola virus disease spillover have low human population density.

In addition, our study used covariate data from a single point in time, while Rulli et al. (2017) analyzed the amount of fragmentation from the year 2000 to the year of each outbreak. It is possible that considering population growth or changes in crop and pasture cover over time might alter our findings. Nevertheless, population density and connectivity can clearly affect the size and scope of an epidemic once human-to-human transmission has begun (Pigott et al. 2014; Alexander et al. 2015).

Other types of local disturbance that we could not measure could play a role in spillover. For example, culling of bats has been shown to increase the prevalence of the related filovirus Marburg virus (MARV) in bat hosts (Amman et al. 2014), which could then lead to increased risks of spillover to humans (Plowright et al. 2015, 2017). Similar mechanisms could potentially lead to spillover of ebolaviruses.

The association between high bat diversity and Ebola virus disease spillover to humans may be due to the fact that the virus appears able to infect a wide range of bat species (Swanepoel 1996; Leroy et al. 2005; Pourrut et al. 2009; Hayman et al. 2010, 2012), which means that areas of high bat diversity provide many potential hosts for the virus. In general, viruses with broad host breadth appear to have higher potential to spill over and infect humans (Olival et al. 2017). Therefore, ebolaviruses may persist where potential bat host diversity is higher and perhaps incidentally spill over to people in these areas.

To date, most research linking bats to ebolaviruses has focused on pteropodid fruit bats (Leendertz et al. 2015), the first live wild animals in which ebolaviruses were detected (Leroy et al. 2005). Ebolaviruses have not yet been detected in nycterid bats: only one study reports testing them for the virus (Leirs et al. 1999), while an additional study reports testing them for MARV (Swanepoel et al. 2007). Both studies examined only one species (*Nycteris hispida*) of the 15 nycterid species that occur on the continent. Further research on this family could clarify whether nycterid bats do in fact play a role in Ebola virus disease spillover to humans.

Some researchers have pointed to bushmeat as a possible mechanism of spillover, either through the direct consumption of bats or more commonly through the consumption of putative intermediate hosts, such as primates or duikers (Boumandouki et al. 2005; Nkoghe et al. 2005, 2011a; Leroy et al. 2009; Kamins et al. 2011; Alexander et al. 2015). While pteropodid fruit bats are the most commonly consumed bats (Mickleburgh et al. 2009; Kamins et al. 2011), other species, including nycterids, are also eaten, although far less frequently (Anti et al. 2015; Mildenstein et al. 2016). Given the long history and widespread consumption of bushmeat, it has been argued that spillovers of Ebola virus disease would be more frequent if bushmeat consumption was the primary mechanism (Wilkinson and Leach 2015). However, if consumption of a less commonly hunted group, such as the nycterids, is a driver, this could help explain the relative rarity of spillover events. It must also be noted that spillover may not always lead to widespread epidemics; recent evidence suggests that exposure to ebolaviruses may be common in some regions (Becquart et al. 2010; Nkoghe et al. 2011b; Mulangu et al. 2018) and some infections may be misdiagnosed as other febrile illnesses (Schoepp et al. 2014) or not detected or reported at all, especially when the initial cluster of cases is small (Glennon et al. 2019).

Humans may also come into contact with bats in other contexts apart from bushmeat. Many bat species, including nycterids, roost in man-made structures, such as abandoned houses, tunnels, or culverts (Fenton and Thomas 1980; Fenton et al. 1993; Monadjem 2005; Monadjem et al. 2010). In some areas, people may frequently enter caves in which bats roost and are familiar with nycterid bats (Anti et al. 2015). Several transmissions of MARV have been linked to entering caves where the bat species *Rousettus aegyptiacus*, known to host MARV, roosts (Fujita et al. 2009; Adjemian et al. 2011). Similar contact between people and nycterid bats could also occur in either natural caves or anthropogenic structures in

which they roost. Alternatively, nycterid bats, which typically roost in caves or hollow trees, may interact in their roosting sites with obligate cave-dwelling pteropodids such as *R. aegyptiacus* and *Myonycteris angolensis* (Monadjem et al. 2010). Transmission of ebolaviruses may therefore follow a complicated pathway that starts with bats co-inhabiting the same roosts.

It is possible that nycterid diversity is associated with Ebolavirus disease spillover because these bats could also interact with intermediate hosts, such as primates or ungulates, from whom spillover to humans then occurs (Leroy et al. 2004; Olival and Hayman 2014; Alexander et al. 2015). In addition to caves or anthropogenic structures, some nycterids may roost in the abandoned burrows of other animals, such as aardvarks (Monadjem et al. 2009) or in vegetation (Rosevear 1965). Using these types of roosts may lead other animals to have contact with ebolaviruses if nycterid bats secrete the virus in feces, urine, or saliva. However, since ebolaviruses have not yet been detected in nycterid bats, this is highly speculative.

Our study does not incorporate bat abundance because data on bat population sizes across Africa do not currently exist (Happold and Happold 2013). While abundance could play a role in the prevalence of the virus as well as rates of contact with humans (Plowright et al. 2015, 2017), studies of rodent-borne zoonotic diseases show little or no effect of host abundance on spillover to humans (Davis et al. 2005). Nevertheless, further localized studies on bat diversity, abundance, community composition, and prevalence of ebolaviruses near spillover locations and across a gradient of biodiversity could provide more evidence of how these factors affect ebolavirus prevalence, transmission between bats, and spillover to humans.

Bat species richness is correlated with species richness of mammals in general (Schipper et al. 2008) as well as with other taxa (Willig et al. 2003). Thus, it is possible that the pattern of Ebola virus disease outbreaks is linked to the diversity of taxa other than bats (or nycterids). These other taxa could include intermediate hosts from which humans can then be infected with Ebola virus disease, such as primates or ungulates (Leroy et al. 2004; Olival and Hayman 2014), which could confound our results. It has also been suggested that insects could play a role in the ecology of ebolaviruses (Leendertz 2016; Dutto et al. 2016; Caron et al. 2018), and a recent study suggested that even fruit bats could acquire viruses from arthropods (Bennett et al. 2019). However, most current evidence still supports bats, not other wildlife, as reservoir hosts (Olival and Hayman 2014).

It is also possible that areas of high nycterid richness may coincide with some other geographic or environmental characteristic that explains Ebola virus disease spillover. Nycterid species are insectivorous and often forage in riparian areas (Fenton et al. 1990, 1993; Monadjem et al. 2010). Leendertz (2016) proposed a potential connection between riparian habitats and ebolaviruses, possibly through yet-unknown aquatic or semi-aquatic invertebrate hosts which may also be prey for insectivorous bat species, such as nycterids. Therefore, areas of high nycterid richness could indicate areas with extensive riparian habitats that are home to a still-undiscovered host or areas where interspecies transmission occurs.

While much uncertainty surrounds the ecology of ebolaviruses, monitoring of bats and other taxa in these areas of high nycterid richness might help isolate mechanisms of spillover and prevent future epidemics. Such research should also support the protection of bat populations and their habitats, which could prevent future spillover events (Schneeberger and Voigt 2016). Further education on the benefits bats bring can also temper the fear that reporting on bat-borne disease may provoke (Schneeberger and Voigt 2016; López-Baucells et al. 2018). Despite their ability to host diverse viruses, bats also provide essential ecosystem services, such as insect population control, seed dispersal, and pollination, that benefit both people and the ecosystems we inhabit (Kunz et al. 2011; Ghanem and Voigt 2012; Schneeberger and Voigt 2016).

Our results show that Ebola virus disease outbreaks occurred in areas of high bat species richness, in particular areas with high richness of nycterid bats, while human population density and anthropogenic disturbance could not explain where spillover occurs. Thus far, studies analyzing patterns of Ebola virus disease outbreaks, predicting areas of future outbreak risk, or determining the zoonotic niche of the virus typically only consider a small subset of bat species and have not considered this family (Pigott et al. 2014, 2016; Alexander et al. 2015). Hence, we suggest that studies of the ecology and epidemiology of these viruses should be expanded to encompass more species of bats, including nycterids (Leendertz 2016).

Acknowledgments We thank Kathleen Alexander for her helpful suggestions for this manuscript and Kok Ben Toh for helping debug code.

Funding information This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138 (JTS).

Compliance with ethical standards

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

References

Adjemian J, Farnon EC, Tschioko F et al (2011) Outbreak of Marburg hemorrhagic fever among miners in Kamwenge and Ibanda districts, Uganda, 2007. J Infect Dis 204:S796–S799. https://doi.org/10.1093/infdis/jir312

Alexander KA, Sanderson CE, Marathe M, Lewis BL, Rivers CM, Shaman J, Drake JM, Lofgren E, Dato VM, Eisenberg MC, Eubank S (2015) What factors might have led to the emergence of Ebola in West Africa? PLoS Negl Trop Dis 9:e0003652. https://doi.org/10.1371/journal.pntd.0003652

Allen T, Murray KA, Zambrana-Torrelio C, Morse SS, Rondinini C, di Marco M, Breit N, Olival KJ, Daszak P (2017) Global hotspots and correlates of emerging zoonotic diseases. Nat Commun 8:1124. https://doi.org/10.1038/s41467-017-00923-8

Allouche O, Tsoar A, Kadom R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Amman BR, Nyakarahuka L, McElroy AK, Dodd KA, Sealy TK, Schuh AJ, Shoemaker TR, Balinandi S, Atimnedi P, Kaboyo W, Nichol ST, Towner JS (2014) Marburgvirus resurgence in Kitaka Mine bat population after extermination attempts, Uganda. Emerg Infect Dis 20: 1761–1764. https://doi.org/10.3201/eid2010.140696

Anti P, Owusu M, Agbenyega O, Annan A, Badu EK, Nkrumah EE, Tschapka M, Oppong S, Adu-Sarkodie Y, Drosten C (2015) Human-bat interactions in rural West Africa. Emerg Infect Dis 21: 1418–1421. https://doi.org/10.3201/eid2108.142015

Austin M (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol Model 157:101–118. https://doi.org/10.1016/S0304-3800(02)00205-3

Balk DL, Deichmann U, Yetman G, Pozzi F, Hay SI, Nelson A (2006) Determining global population distribution: methods, applications and data. Adv Parasitol 62:119–156. https://doi.org/10.1016/S0065-308X(05)62004-0

Bausch DG, Schwarz L (2014) Outbreak of Ebola virus disease in Guinea: where ecology meets economy. PLoS Negl Trop Dis 8: e3056. https://doi.org/10.1371/journal.pntd.0003056

Becquart P, Wauquier N, Mahlakõiv T, Nkoghe D, Padilla C, Souris M, Ollomo B, Gonzalez JP, de Lamballerie X, Kazanji M, Leroy EM (2010) High prevalence of both humoral and cellular immunity to Zaire Ebolavirus among rural populations in Gabon. PLoS One 5: e9126. https://doi.org/10.1371/journal.pone.0009126

Bennett AJ, Bushmaker T, Cameron K, Ondzie A, Niama FR, Parra HJ, Mombouli JV, Olson SH, Munster VJ, Goldberg TL (2019) Diverse RNA viruses of arthropod origin in the blood of fruit bats suggest a link between bat and arthropod viromes. Virology 528:64–72. https://doi.org/10.1016/J.VIROL.2018.12.009

Boumandouki P, Formenty P, Epelboin A et al (2005) Prise en charge des malades et des défunts lors de l'épidémie de fièvre hémorragique due au virus Ebola d'octobre à décembre 2003 au Congo. Bull Soc Pathol Exot 98:218–223

Brierley L, Vonhof MJ, Olival KJ, Daszak P, Jones KE (2016) Quantifying global drivers of zoonotic bat viruses: a process-based perspective. Am Nat 187:E53–E64. https://doi.org/10.1086/684391

Brink AB, Eva HD (2009) Monitoring 25 years of land cover change dynamics in Africa: a sample based remote sensing approach. Appl Geogr 29:501–512. https://doi.org/10.1016/j.apgeog.2008.10.004

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York

Caron A, Bourgarel M, Cappelle J et al (2018) Ebola virus maintenance: if not (only) bats, what else? Viruses 10:549. https://doi.org/10.3390/v10100549

Center for International Earth Science Information Network (2005) Population Count Grid, v3: Gridded Population of the World (GPW), v3 | SEDAC. http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-count. Accessed 13 Oct 2015

Center for International Earth Science Information Network (2013) Global Roads Open Access Data Set (gROADS), v1: Global Roads | SEDAC. http://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1. Accessed 13 Oct 2015

Changula K, Kajihara M, Mweene AS, Takada A (2014) Ebola and Marburg virus diseases in Africa: increased risk of outbreaks in previously unaffected areas? Microbiol Immunol 58:483–491. https://doi.org/10.1111/1348-0421.12181

Daszak P (2000) Emerging infectious diseases of wildlife– threats to biodiversity and human health. Science 287(80):443–449. https://doi.org/10.1126/science.287.5452.443

Daszak P, Cunningham AAA, Hyatt ADD (2001) Anthropogenic environmental change and the emergence of infectious diseases in wildlife. Acta Trop 78:103–116. https://doi.org/10.1016/s0001-706x(00)00179-0

Davis S, Calvet E, Leirs H (2005) Fluctuating rodent populations and risk to humans from rodent-borne zoonoses. Vector Borne Zoonotic Dis 5:305–314

De Nys HM, Kingebeni PM, Keita AK et al (2018) Survey of Ebola viruses in frugivorous and insectivorous bats in Guinea, Cameroon, and the Democratic Republic of the Congo, 2015–2017. Emerg Infect Dis 24:2228–2240. https://doi.org/10.3201/eid2412.180740

Dutto M, Bertero M, Petrosillo N, Pombi M, Otranto D (2016) Ebola virus and arthropods: a literature review and entomological consideration on the vector role. Bull Soc Pathol Exot 109:244–247. https://doi.org/10.1007/s13149-016-0525-y

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elston JWT, Moosa AJ, Moses F et al (2015) Impact of the Ebola outbreak on health systems and population health in Sierra Leone. J Public Health (Bangkok) 38:673–678. https://doi.org/10.1093/pubmed/fdv158

Fenton MB, Thomas DW (1980) Dry-season overlap in activity patterns, habitat use, and prey selection by sympatric African insectivorous bats. Biotropica 12:81–90. https://doi.org/10.2307/2387723

Fenton MB, Swanepoel CM, Brigham RM et al (1990) Foraging behavior and prey selection by large slit-faced bats (Nycteris grandis; Chiroptera: Nycteridae). Biotropica 22:2–8

Fenton MB, Rautenbach IL, Chipese D et al (1993) Variation in foraging behaviour, habitat use, and diet of large slit-faced bats (*Nycteris grandis*). Z Säugetierkd 58:65–74

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29:207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Fujita N, Miller A, Miller G et al (2009) Imported case of Marburg hemorrhagic fever - Colorado, 2008. Morb Mortal Wkly Rep 58: 1377–1381

Ghanem SJ, Voigt CC (2012) Increasing awareness of ecosystem services provided by bats. Adv. Study Behav. 44: 279–302. https://doi.org/10.1016/B978-0-12-394288-3.00007-1

Gill JA, Sutherland WJ, Watkinson AR (1996) A method to quantify the effects of human disturbance on animal populations. J Appl Ecol 33: 786–792. https://doi.org/10.2307/2404948

Gire SK, Goba A, Andersen KG, Sealfon RSG, Park DJ, Kanneh L, Jalloh S, Momoh M, Fullah M, Dudas G, Wohl S, Moses LM, Yozwiak NL, Winnicki S, Matranga CB, Malboeuf CM, Qu J, Gladden AD, Schaffner SF, Yang X, Jiang PP, Nekoui M, Colubri A, Coomber MR, Fonnie M, Moigboi A, Gbakie M, Kamara FK, Tucker V, Konuwa E, Saffa S, Sellu J, Jalloh AA, Kovoma A, Koninga J, Mustapha I, Kargbo K, Foday M, Yillah M, Kanneh F, Robert W, Massally JLB, Chapman SB, Bochicchio J, Murphy C, Nusbaum C, Young C, Birren BW, Grant DS, Scheiffelin JS, Lander ES, Happi C, Gevao SM, Gnirke A, Rambaut A, Garry RF, Khan SH, Sabeti PC (2014) Genomic surveillance elucidates Ebola virus origin and transmission during the 2014 outbreak. Science 345 (6202):1369-1372

Glennon EE, Jephcott FL, Restif O, Wood JLN (2019) Estimating undetected Ebola spillovers. PLoS Negl Trop Dis 13:e0007428. https://doi.org/10.1371/journal.pntd.0007428

Goldstein T, Anthony SJ, Gbakima A, Bird BH, Bangura J, Tremeau-Bravard A, Belaganahalli MN, Wells HL, Dhanota JK, Liang E, Grodus M, Jangra RK, DeJesus V, Lasso G, Smith BR, Jambai A, Kamara BO, Kamara S, Bangura W, Monagin C, Shapira S, Johnson CK, Saylors K, Rubin EM, Chandran K, Lipkin WI, Mazet JAK (2018) The discovery of Bombali virus adds further support for bats as hosts of ebolaviruses. Nat Microbiol 3:1084–1089. https://doi.org/10.1038/s41564-018-0227-2

Groseth A, Feldmann H, Strong JE (2007) The ecology of Ebola virus. Trends Microbiol 15:408–416. https://doi.org/10.1016/j.tim.2007.08.001

Han BA, Schmidt JP, Alexander LW, Bowden SE, Hayman DT, Drake JM (2016) Undiscovered bat hosts of filoviruses. PLoS Negl Trop Dis 10:e0004815. https://doi.org/10.1371/journal.pntd.0004815

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29–36. https://doi.org/10.1148/radiology.143.1.7063747

Happold M, Happold DCD (eds) (2013) Mammals of Africa, vol IV. Hedgehogs, Shrews and Bats. Bloomsbury Publishing, London

Hayman DTS, Emmerich P, Yu M, Wang LF, Suu-Ire R, Fooks AR, Cunningham AA, Wood JL (2010) Long-term survival of an urban fruit bat seropositive for Ebola and Lagos bat viruses. PLoS One 5:e11978. https://doi.org/10.1371/journal.pone.0011978

Hayman DTS, Yu M, Crameri G, Wang LF, Suu-Ire R, Wood JL, Cunningham AA (2012) Ebola virus antibodies in fruit bats, Ghana, West Africa. Emerg Infect Dis 18:1207–1209. https://doi.org/10.3201/eid1807.111654

Hijmans RJ, van Etten J (2012) Raster: geographic analysis and modeling with raster data. R Package Version 2:0–12. http://cran.r-project.org/package=raster

Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. https://doi.org/10.1002/joc.1276

Hijmans RJ, Phillips S, Leathwick J, Elith J (2013) Package "dismo": species distribution modeling

Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P (2008) Global trends in emerging infectious diseases. Nature 451:990–993. https://doi.org/10.1038/nature06536

Kamins AO, Restif O, Ntiamoa-Baidu Y, Suu-Ire R, Hayman DT, Cunningham AA, Wood JL, Rowcliffe JM (2011) Uncovering the fruit bat bushmeat commodity chain and the true extent of fruit bat hunting in Ghana, West Africa. Biol Conserv 144:3000–3008. https://doi.org/10.1016/j.biocon.2011.09.003

Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH (2011) Ecosystem services provided by bats. Ann N Y Acad Sci 1223:1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

Laporta GZ, Laporta GZ (2014) Landscape fragmentation and Ebola outbreaks. Mem Inst Oswaldo Cruz 109:1088–1088. https://doi.org/10.1590/0074-0276140417

Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25:1–18. https://doi.org/10.18637/jss.v025.i01

Leendertz SAJ (2016) Testing new hypotheses regarding Ebolavirus reservoirs. Viruses 8:3–8. https://doi.org/10.3390/v8020030

Leendertz SAJ, Gogarten JF, Düx A et al (2015) Assessing the evidence supporting fruit bats as the primary reservoirs for Ebola viruses. Ecohealth 13:18–25. https://doi.org/10.1007/s10393-015-1053-0

Leirs H, Mills JN, Krebs JW et al (1999) Search for the Ebola virus reservoir in Kikwit, Democratic Republic of the Congo: reflections on a vertebrate collection. J Infect Dis 179:S155–S163. https://doi.org/10.1086/514299

Leroy EM, Rouquet P, Formenty P, Souquière S, Kilbourne A, Froment JM, Bermejo M, Smit S, Karesh W, Swanepoel R, Zaki SR, Rollin PE (2004) Multiple Ebola virus transmission events and rapid decline of central African wildlife. Science 303:387–390. https://doi.org/10.1126/science.1092528

Leroy EM, Kumulungui B, Pourrut X, Rouquet P, Hassanin A, Yaba P, Délicat A, Paweska JT, Gonzalez JP, Swanepoel R (2005) Fruit bats as reservoirs of Ebola virus. Nature 438:575–576. https://doi.org/10.1038/438575a

Leroy EM, Epelboin A, Mondonge V, Pourrut X, Gonzalez JP, Muyembe-Tamfum JJ, Formenty P (2009) Human Ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. Vector Borne Zoonotic Dis 9:723–728. https://doi.org/10.1089/vbz.2008.0167

Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. J Biogeogr 40:778–789. https://doi.org/10.1111/jbi.12058

López-Baucells A, Rocha R, Fernández-Llamazares Á (2018) When bats go viral: negative framings in virological research imperil bat conservation. Mammal Rev 48:62–66. https://doi.org/10.1111/mam.12110

Luis AD, Hayman DTS, O'Shea TJ et al (2013) A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? Proc R Soc B 280:20122753. https://doi.org/10.1098/rspb.2012.2753

Mahy BWJ, Brown CC (2000) Emerging zoonoses: crossing the species barrier. Rev Sci Tech 19:33–40

McCain CM (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Glob Ecol Biogeogr 16:1–13. https://doi.org/10.1111/j.1466-8238.2006.00263.x

Mickleburgh S, Waylen K, Racey P (2009) Bats as bushmeat: a global review. Oryx 43:217–234. https://doi.org/10.1017/S0030605308000938

Mildenstein T, Tanshi I, Racey PA (2016) Exploitation of bats for Bushmeat and medicine. In: Voigt C, Kingston T (eds) Bats in the Anthropocene: conservation of bats in a changing world. Springer International Publishing, Cham, pp 325–375

Monadjem A (2005) Survival and roost-site selection in the African bat *Nycteris thebaica* (Chiroptera: Nycteridae) in Swaziland. Belg J Zool 135:103–107

Monadjem A, Reside A, Cornut J, Perrin MR (2009) Roost selection and home range of an African insectivorous bat Nycteris thebaica (Chiroptera, Nycteridae). Mammalia 73:353–359. https://doi.org/10.1515/mamm.2009.056

Monadjem A, Taylor PJ, Cotterill FPD, Schoeman MC (2010) Bats of southern and Central Africa: a biogeographic and taxonomic synthesis. Wits University Press, Johannesburg

Monadjem A, Taylor PJ, Conenna I, Schoeman MC (2018) Species richness patterns and functional traits of the bat fauna of arid southern Africa. Hystrix. https://doi.org/10.4404/hystrix-00016-2017

Morand S, Owers KA, Waret-Szkuta A, McIntyre KM, Baylis M (2013) Climate variability and outbreaks of infectious diseases in Europe. Sci Rep 3:888–900. https://doi.org/10.1038/srep01774

Mulangu S, Alfonso VH, Hoff NA, Doshi RH, Mulembakani P, Kisalu NK, Okitolonda-Wemakoy E, Kebela BI, Marcus H, Shiloach J, Phue JN, Wright LL, Muyembe-Tamfum JJ, Sullivan NJ, Rimoin AW (2018) Serologic evidence of Ebolavirus infection in a population with no history of outbreaks in the Democratic Republic of the Congo. J Infect Dis 217:529–537. https://doi.org/10.1093/infdis/jix619

Muyembe-Tamfum JJ, Mulangu S, Masumu J et al (2012) Ebola virus outbreaks in Africa: past and present. Onderstepoort J Vet Res 79:1–8. https://doi.org/10.4102/ojvr.v79i2.451

Mylne A, Brady OJ, Huang Z, Pigott DM, Golding N, Kraemer MUG, Hay SI (2014) A comprehensive database of the geographic spread of past human Ebola outbreaks. Sci Data 1:140042–140010. https://doi.org/10.1038/sdata.2014.42

Nkoghe D, Formenty P, Leroy EM et al (2005) Plusieurs épidémies de fièvre hémorragique due au virus Ebola au Gabon, d'octobre 2001 à avril 2002. Bull Soc Pathol Exot 98:224–229

Nkoghe D, Kone ML, Yada A, Leroy E (2011a) A limited outbreak of Ebola haemorrhagic fever in Etoumbi, Republic of Congo, 2005. Trans R Soc Trop Med Hyg 105:466–472. https://doi.org/10.1016/j.trstmh.2011.04.011

Nkoghe D, Padilla C, Becquart P et al (2011b) Risk factors for Zaire Ebolavirus-specific IgG in rural Gabonese populations. J Infect Dis 204:S768–S775. https://doi.org/10.1093/infdis/jir344

Ogawa H, Miyamoto H, Nakayama E et al (2015) Seroepidemiological prevalence of multiple species of filoviruses in fruit bats (*Eidolon helvum*) migrating in Africa. J Infect Dis 212(Suppl):S101–S108. https://doi.org/10.1093/infdis/jiv063

Olival KJ, Hayman DTS (2014) Filoviruses in bats: current knowledge and future directions. Viruses 6:1759–1788. https://doi.org/10.3390/v6041759

Olival KJ, Hosseini PR, Zambrana-Torrelio C, Ross N, Bogich TL, Daszak P (2017) Host and viral traits predict zoonotic spillover from mammals. Nature 546:646–650. https://doi.org/10.1038/nature22975

Olivero J, Fa JE, Real R, Márquez AL, Farfán MA, Vargas JM, Gaveau D, Salim MA, Park D, Suter J, King S, Leendertz SA, Sheil D, Nasi R (2017) Recent loss of closed forests is associated with Ebola virus disease outbreaks. Sci Rep 7:14291. https://doi.org/10.1038/s41598-017-14727-9

Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. Bioscience 51:933–938. https://doi.org/10.1641/0006-3568(2001)051[0933:teotwa]2.0.co;2

Patz JA, Daszak P, Tabor GM, Aguirre AA, Pearl M, Epstein J, Wolfe ND, Kilpatrick AM, Foufopoulos J, Molyneux D, Bradley DJ, Working Group on Land Use Change and Disease Emergence (2004) Unhealthy landscapes: policy recommendations on land use change and infectious disease emergence. Environ Health Perspect 112:1092–1098. https://doi.org/10.1289/EHP.6877

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Pigott DM, Golding N, Mylne A, Huang Z, Henry AJ, Weiss DJ, Brady OJ, Kraemer MU, Smith DL, Moyes CL, Bhatt S, Gething PW, Horby PW, Bogoch II, Brownstein JS, Mekaru SR, Tatem AJ, Khan K, Hay SI (2014) Mapping the zoonotic niche of Ebola virus disease in Africa. Elife 3:e04395. https://doi.org/10.7554/eLife.04395

Pigott DM, Millear AI, Earl L et al (2016) Updates to the zoonotic niche map of Ebola virus disease in Africa. Elife 5:e16412. https://doi.org/10.7554/eLife.16412

Plowright RK, Field HE, Smith C, Divljan A, Palmer C, Tabor G, Daszak P, Foley JE (2008) Reproduction and nutritional stress are risk factors for Hendra virus infection in little red flying foxes (*Pteropus scapulatus*). Proc R Soc B 275:861–869. https://doi.org/10.1098/rspb.2007.1260

Plowright RK, Eby P, Hudson PJ, Smith IL, Westcott D, Bryden WL, Middleton D, Reid PA, McFarlane R, Martin G, Tabor GM, Skerratt LF, Anderson DL, Crameri G, Quammen D, Jordan D, Freeman P, Wang LF, Epstein JH, Marsh GA, Kung NY, McCallum H (2015) Ecological dynamics of emerging bat virus spillover. Proc R Soc B 282:20142124. https://doi.org/10.1098/rspb.2014.2124

Plowright RK, Parrish CR, McCallum H, Hudson PJ, Ko AI, Graham AL, Lloyd-Smith JO (2017) Pathways to zoonotic spillover. Nat Rev Microbiol 15:502–510. https://doi.org/10.1038/nrmicro.2017.45

Pourrut X, Souris M, Towner JS, Rollin PE, Nichol ST, Gonzalez JP, Leroy E (2009) Large serological survey showing cocirculation of Ebola and Marburg viruses in Gabonese bat populations, and a high seroprevalence of both viruses in *Rousettus aegyptiacus*. BMC Infect Dis 9:159. https://doi.org/10.1186/1471-2334-9-159

R Core Team (2013) R: A language and environment for statistical computing

Ramankutty E (2008) Putting people in the map: anthropogenic biomes of the world. Front Ecol Environ 6:439–447. https://doi.org/10.1890/070062

Ramankutty N, Evan AT, Monfreda C, Foley JA (2008) Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Glob Biogeochem Cycles 22:GB1003. https://doi.org/10.1029/2007GB002952

Ramankutty N, Evan AT, Monfreda C, Foley JA (2010a) Global Agricultural Lands: Croplands, 2000

Ramankutty N, Evan AT, Monfreda C, Foley JA (2010b) Global Agricultural Lands: Pastures, 2000

Rebelo H, Tarraso P, Jones G (2010) Predicted impact of climate change on European bats in relation to their biogeographic patterns. Glob Chang Biol 16:561–576. https://doi.org/10.1111/j.1365-2486.2009.02021.x

Renner IW, Elith J, Baddeley A et al (2015) Point process models for presence-only analysis. Methods Ecol Evol 6:366–379. https://doi.org/10.1111/2041-210X.12352

Rosevear DR (1965) The bats of West Africa. British Museum (Natural History), London

Rulli MC, Santini M, Hayman DTS, D'Odorico P (2017) The nexus between forest fragmentation in Africa and Ebola virus disease outbreaks. Sci Rep 7:41613. https://doi.org/10.1038/srep41613

Sanderson EW, Jaiteh M, Levy MA et al (2002) The human footprint and the last of the wild. Bioscience 52:891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V, Lamoreux J, Rodrigues AS, Stuart SN, Temple HJ, Baillie J, Boitani L, Lacher te Jr, Mittermeier RA, Smith AT, Absolon D, Aguiar JM, Amori G, Bakkour N, Baldi R, Berridge RJ, Bielby J, Black PA, Blanc JJ, Brooks TM, Burton JA, Butynski TM, Catullo G, Chapman R, Cokeliss Z, Collen B, Conroy J, Cooke JG, da Fonseca GA, Derocher AE, Dublin HT, Duckworth JW, Emmons L, Emslie RH, Festa-Bianchet M, Foster M, Foster S, Garshelis DL, Gates C, Gimenez-Dixon M, Gonzalez S, Gonzalez-Maya JF, Good TC, Hammerson G, Hammond PS, Happold D, Happold M, Hare J, Harris RB, Hawkins CE, Haywood M, Heaney LR, Hedges S, Helgen KM, Hilton-Taylor C, Hussain SA, Ishii N, Jefferson TA, Jenkins RK, Johnston CH, Keith M, Kingdon J, Knox DH, Kovacs KM, Langhammer P, Leus K, Lewison R, Lichtenstein G, Lowry LF, Macavoy Z, Mace GM, Mallon DP, Masi M, McKnight M, Medellín RA, Medici P, Mills G, Moehlman PD, Molur S, Mora A, Nowell K, Oates JF, Olech W, Oliver WR, Oprea M, Patterson BD, Perrin WF, Polidoro BA, Pollock C, Powel A, Protas Y, Racey P, Ragle J, Ramani P, Rathbun G, Reeves RR, Reilly SB, Reynolds JE 3rd, Rondinini C, Rosell-Ambal RG, Rulli M, Rylands AB, Savini S, Schank CJ, Sechrest W, Self-Sullivan C, Shoemaker A, Sillero-Zubiri C, de Silva N, Smith DE, Srinivasulu C, Stephenson PJ, van Strien N, Talukdar BK, Taylor BL, Timmins R, Tirira DG, Tognelli MF, Tsytsulina K, Veiga LM, Vié JC, Williamson EA, Wyatt SA, Xie Y, Young BE (2008) The status of the world's land and marine mammals: diversity, threat and knowledge. Science 322:225–230

Schneeberger K, Voigt CC (2016) Zoonotic viruses and conservation of bats. In: Kingston T, Voigt C (eds) Bats in the Anthropocene: conservation of bats in a changing world. Springer International Publishing, Cham, pp 263–292

Schoepp RJ, Rossi CA, Khan SH, Goba A, Fair JN (2014) Undiagnosed acute viral febrile illnesses, Sierra Leone. Emerg Infect Dis 20: 1176–1182. https://doi.org/10.3201/eid2007.131265

Spengler JR, Ervin ED, Towner JS, Rollin PE, Nichol ST (2016) Perspectives on West Africa Ebola virus disease outbreak, 2013-2016. Emerg Infect Dis 22:956–963. https://doi.org/10.3201/eid2206.160021

Swanepoel R (1996) Experimental inoculation of plants and animals with Ebola virus. Emerg Infect Dis 2:321–325. https://doi.org/10.3201/eid0204.960407

Swanepoel R, Smit SB, Rollin PE, Formenty P, Leman PA, Kemp A, Burt FJ, Grobbelaar AA, Croft J, Bausch DG, Zeller H, Leirs H, Braack LE, Libande ML, Zaki S, Nichol ST, Ksiazek TG, Paweska JT, International Scientific and Technical Committee for Marburg Hemorrhagic Fever Control in the Democratic Republic of Congo (2007) Studies of reservoir hosts for Marburg virus. Emerg Infect Dis 13:1847–1851. https://doi.org/10.3201/eid1312.071115

Weiss RA, McMichael AJ (2004) Social and environmental risk factors in the emergence of infectious diseases. Nat Med 10:S70–S76. https://doi.org/10.1038/nm1150

Wilkinson A, Leach M (2015) Briefing: Ebola-myths, realities, and structural violence. Afr Aff 114:136–148. https://doi.org/10.1093/afraf/adu080

Wilkinson DA, Marshall JC, French NP, Hayman DTS (2018) Habitat fragmentation, biodiversity loss and the risk of novel infectious disease emergence. J R Soc Interface 15:20180403. https://doi.org/10.1098/rsif.2018.0403

Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

Wolfe ND, Daszak P, Kilpatrick AM, Burke DS (2005) Bushmeat hunting, deforestation, and prediction of zoonotic disease emergence. Emerg Infect Dis 11:1822–1827

World Health Organization (2019) Ebola virus disease – Democratic Republic of the Congo