Ebola spillover correlates with bat diversity

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Acknowledgements

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

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

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

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.

Key Words: 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 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).

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 group 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 spillover 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 spillover to humans (Plowright et al. 2015), we predicted that bat species richness would be a stronger predictor of outbreaks than human population density and 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 1990-2014 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 Systems (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,

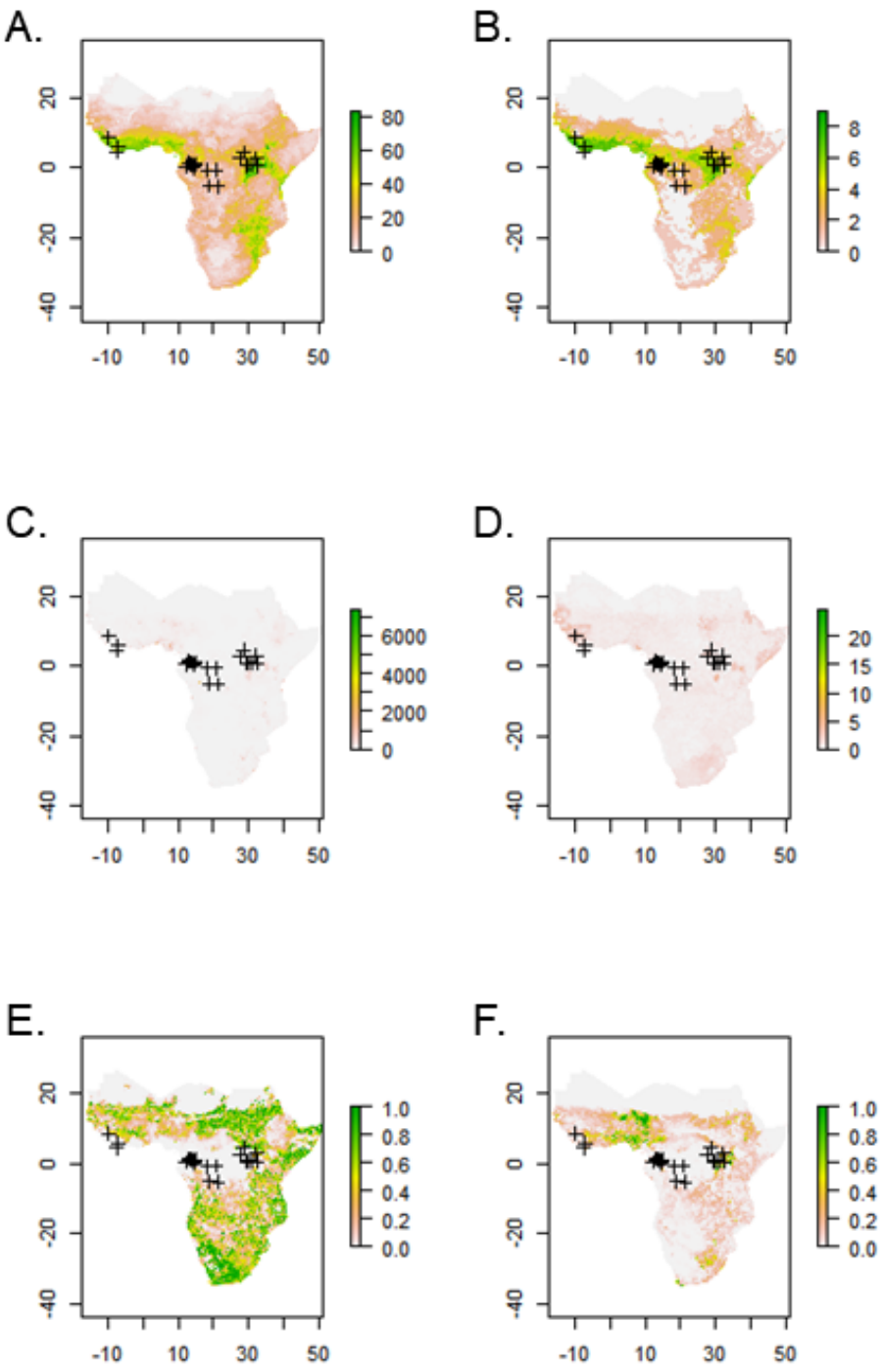

Figure 1. Maps showing distribution of A. Total bat species richness (number of species), B. Nycterid species richness (number of species), C. Human population density (individuals/km^2), D. Road density (km/km^2), E. Crop cover (proportion cover), and F. Pasture cover (proportion cover) . Crosses indicate locations of Ebola spillover to humans. The color gradient shows lowest values in gray and highest values in green.

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, 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 (Rulli et al. 2017), as the probability of contact with an infected host increases with population 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, b). 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 components 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 10-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 R. 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 number 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 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 GLM models 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).

Table 1. Model selection results for generalized linear models. We also show the intercept, degrees of freedom (df), loglikelihood, 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

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).

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

We assessed predictive accuracy of the top GLM and Maxent models using 4-fold 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 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 program R (R Core Team 2013), using the base package for GLM models and package dismo for Maxent model (Hijmans et al. 2013).

Results

We identified 22 spillover events of Ebola virus disease from 1990 – 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 crop cover and proportion pasture cover ranged from 0.0 – 1.0. Bat species richness ranged from 0 – 79 species (Fig. 1).

The initial GLM model, 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 GLM's 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).

Table 3. Top models for Ebola 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	-	-	-

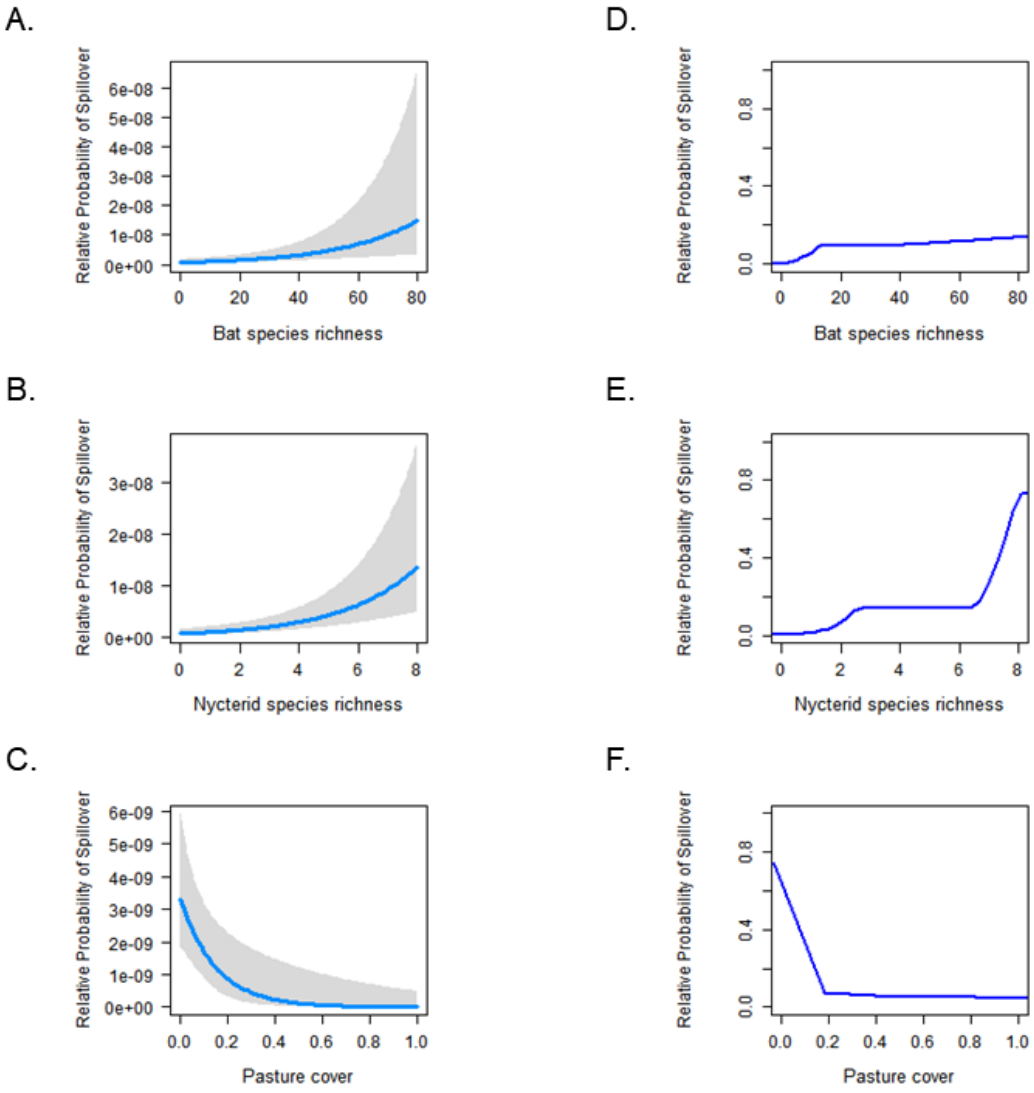

Figure 2. Response of relative probability of Ebola spillover according to generalized linear models (GLM) (A, B, C) and Maxent models (D, E, F) to total bat species richness, nycterid species richness, and pasture cover. Predictions are shown in solid lines. For GLMs, 95% confidence intervals are shown 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 pasture (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 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. Modelling 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 spillover and infect humans (Olival et al. 2017). Therefore, ebolaviruses may persist where potential bat host diversity is higher and perhaps incidentally spillover 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 bats 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 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 coinhabiting 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 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).

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