

Updates to the zoonotic niche map of Ebola virus disease in Africa

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Abstract As the outbreak of Ebola virus disease (EVD) in West Africa is now contained, attention is turning from control to future outbreak prediction and prevention. Building on a previously published zoonotic niche map (Pigott *et al.*, 2014), this study incorporates new human and animal occurrence data and expands upon the way in which potential bat EVD reservoir species are incorporated. This update demonstrates the potential for incorporating and updating data used to generate the predicted suitability map. A new data portal for sharing such maps is discussed. This output represents the most up-to-date estimate of the extent of EVD zoonotic risk in Africa. These maps can assist in strengthening surveillance and response capacity to contain viral haemorrhagic fevers.

DOI: 10.7554/eLife.16412.001

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Competing interest: See page 10

Funding: See page 10

Received: 30 March 2016

Accepted: 20 June 2016

Published: 14 July 2016

Reviewing editor: Mark Jit, London School of Hygiene & Tropical Medicine, and Public Health England, United Kingdom

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Introduction

Since the index case in 2013, the West African Ebola epidemic has killed more than 11,000 people (World Health Organization, 2016) and exposed national and international inadequacies in pandemic preparedness and response (Moon *et al.*, 2015). In 2014 a zoonotic niche map for Ebola virus disease (EVD) was produced (Pigott *et al.*, 2014) in part to assess the expected geographical extent of spillover risk. This research was then expanded to explore how changes in demography and international connectivity may have facilitated the establishment and rapid subsequent spread of the epidemic (Bogoch *et al.*, 2015). The West African outbreak of EVD has again highlighted key information gaps that exist with respect to the broader epidemiology of Ebola virus, particularly concerning viral persistence in reservoirs (Funk and Piot, 2014; Mari Saez *et al.*, 2015; Leendertz, 2016), and prompted a variety of questions concerning the role bats play in transmission (Leendertz *et al.*, 2016). Identifying reservoirs of zoonotic disease is a complex process (Viana *et al.*, 2014; Haydon *et al.*, 2002) and whilst considerable sampling effort has been undertaken over the years (Kuhn, 2008; Leirs *et al.*, 1999), isolation of Ebolavirus from living animals has been rare (Leroy *et al.*, 2005). The original eLife study only incorporated the three bat species found to be RNA-positive (Leroy *et al.*, 2005). Whilst this remains currently the best evidence for an animal reservoir species, it is important to consider that other sampling efforts may by chance represent false negatives, particularly if infection is rare.

Consequently, to contribute to these broader discussions, the original paper (Pigott *et al.*, 2014) was updated with new occurrence data and expanded to consider a wider range of potential bat reservoir species. Bats remained the priority mammalian order given the previous viral isolation and the repeated anecdotal implications in previous outbreaks (Leroy *et al.*, 2009; Mari Saez *et al.*, 2015). Since there are a large number of bat species found in Africa, we defined three groupings, based upon the strength of evidence supporting their potential Ebola reservoir status. As a result, not only were the original three RNA-positive bats included (Leroy *et al.*, 2005), but also those species with serological evidence of EVD infection (Olival and Hayman, 2014) and those identified through trait-based machine learning approaches as being similar to species already reporting filoviral infection (Han *et al.*, 2016).

Results

Six additional records of EVD were incorporated into the disease occurrence database: one human outbreak in the Democratic Republic of Congo (Maganga *et al.*, 2014); two reports of infections in animals in Zambia (Ogawa *et al.*, 2015); and three animal infections in Central African Republic (Morvan *et al.*, 1999) (Figure 1). Of these new occurrences, two in southern Central African Republic are found in areas predicted to be at-risk by the previous model (Pigott *et al.*, 2014), with the index case from the Democratic Republic of Congo located in close proximity (<10 km) to at-risk areas. The occurrences in Zambia and northern Central African Republic lie, respectively, to the south and north of previously predicted at-risk regions.

Figure 2 depicts the three new consolidated bat distributions. The revised distribution of the Group 1 bats (*i.e.* those found to have been Ebolavirus RNA positive) is broadly consistent with that published in the original paper except that the peripheries of Central Africa are now predicted to be environmentally suitable for these bats, as well as some parts of East Africa, particularly Tanzania, Mozambique and Madagascar. The Group 2 and Group 3 bat species are predicted to be distributed across much of Africa stretching from West to East Sub-Saharan Africa, as well as much of the coastline of the continent.

The revised niche map, incorporating the updated bat covariates and disease occurrence database, is presented in Figure 3. The map shows the predicted areas of environmental suitability for zoonotic Ebola virus transmission to be consistent with previous attempts, but the relative environmental suitability within this distribution differs from the previous estimates. Figure 3—figure supplement 1 demonstrates that Cameroon, Gabon, Republic of Congo and mainland Equatorial Guinea are now predicted to be more environmentally suitable than in the previous analysis. The regions of Central Africa (particularly Gabon and the Republic of Congo) identified as being most environmentally suitable for zoonotic EVD transmission in the previous analysis remain so in this analysis. The revised number of predicted at-risk countries, determined by thresholding the map by a probability that captures 95% of the occurrence dataset, is 23 (Table 1).

The similar AUC values (0.85 ± 0.04 compared to 0.8236 ± 0.080) between the previous and current iterations suggest that the updated model fits the new occurrence dataset as well as the previous model fitted the older dataset. Mean enhanced vegetation index (EVI) remains the highest relative predictor covariate for zoonotic EVD transmission while the relative importance of Group 1 bat distributions moved from being the fifth most important to the second. Mean night-time land surface temperature (LST), elevation and mean daytime LST complete the top five predictors (Table 2).

When separate bat layers were used in the model, as opposed to the consolidated covariates, the predictions were geographically similar (Figure 3—figure supplement 2) however, four bat species were identified as explaining more of the variation than the rest; *Hypsignathus monstrosus*, *Epomops franqueti* (from both of which Ebolavirus RNA has been isolated), *Otomops martiensseni* and *Epomophorus labiatus* (both from Group 3). The explanatory power of this model (evaluated using AUC) was comparable to the model results described above ($AUC = 0.819 \pm 0.080$).

Discussion

This research advance integrates new data as well as a more thorough consideration of the bat species that act as a reservoir for the virus in order to update our modelled estimate of the zoonotic

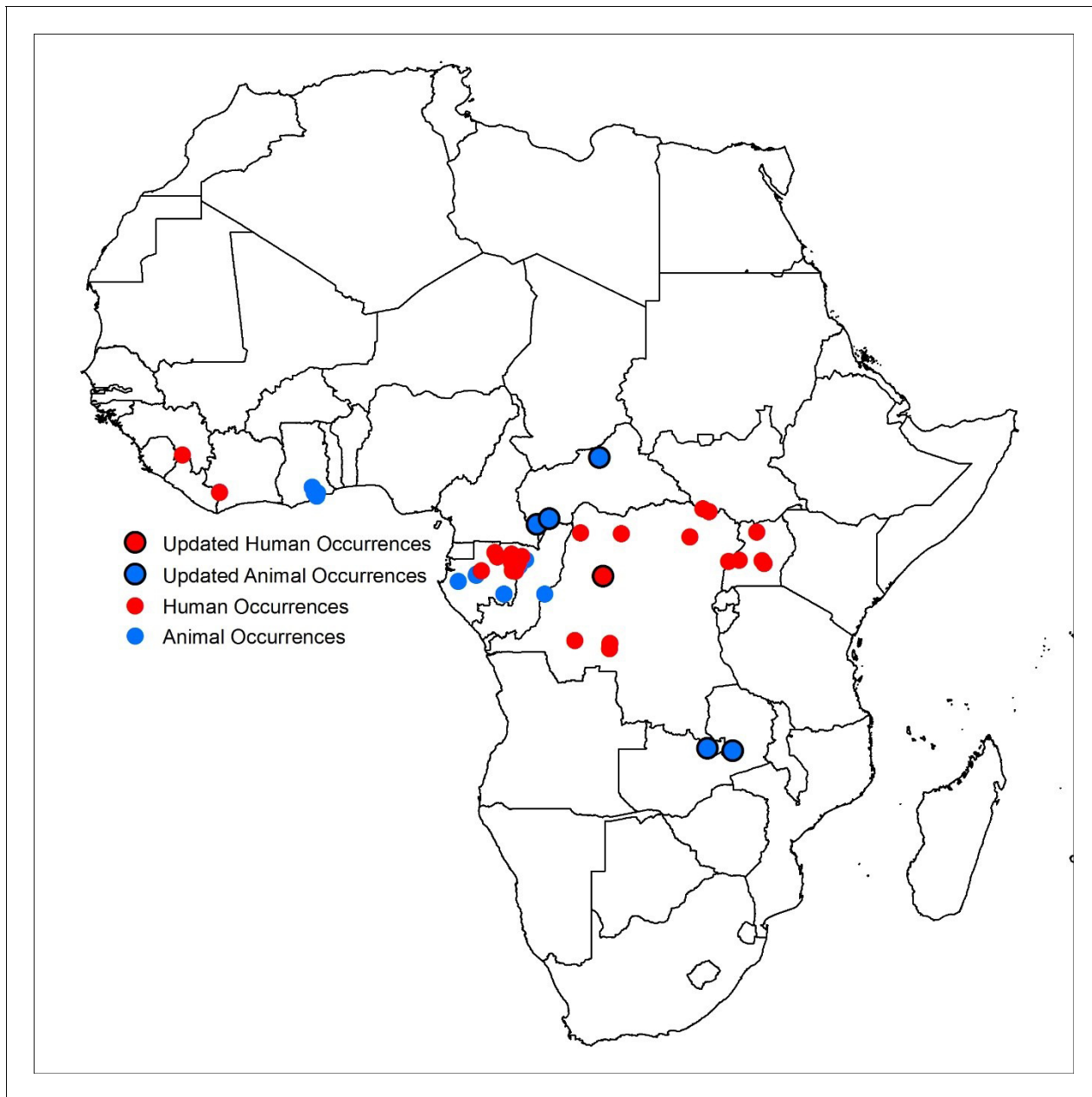


Figure 1. Updated Ebola virus disease occurrence database. Human index cases are represented by red circles, animal occurrences in blue. New occurrence information is indicated by the black circle. The coordinates of polygon centroids are displayed for occurrences defined by an area greater than 5 km x 5 km.

DOI: [10.7554/eLife.16412.002](https://doi.org/10.7554/eLife.16412.002)

niche of EVD. The area estimated to be at potential risk of zoonotic EVD transmission has now expanded to include Kenya and the influence of additional bat species demonstrates that continued focus should be placed on rigorously identifying reservoir species and the role they play in sustaining viral transmission ([Leendertz, 2016](#)). The fact that *O. martiensseni* and *E. labiatus* contribute explanatory power to the model, in comparison with their distributions on the eastern and southern periphery of reported cases of EVD ([Figure 2—figure supplement 3](#)) suggests that different regions of the continent may support transmission cycles with differing reservoir species. This, coupled with the potential for each of the pathogenic species of *Ebolavirus* potentially having differing distributions ([Peterson et al., 2004](#)), cannot currently be explored more rigorously due to insufficient data.

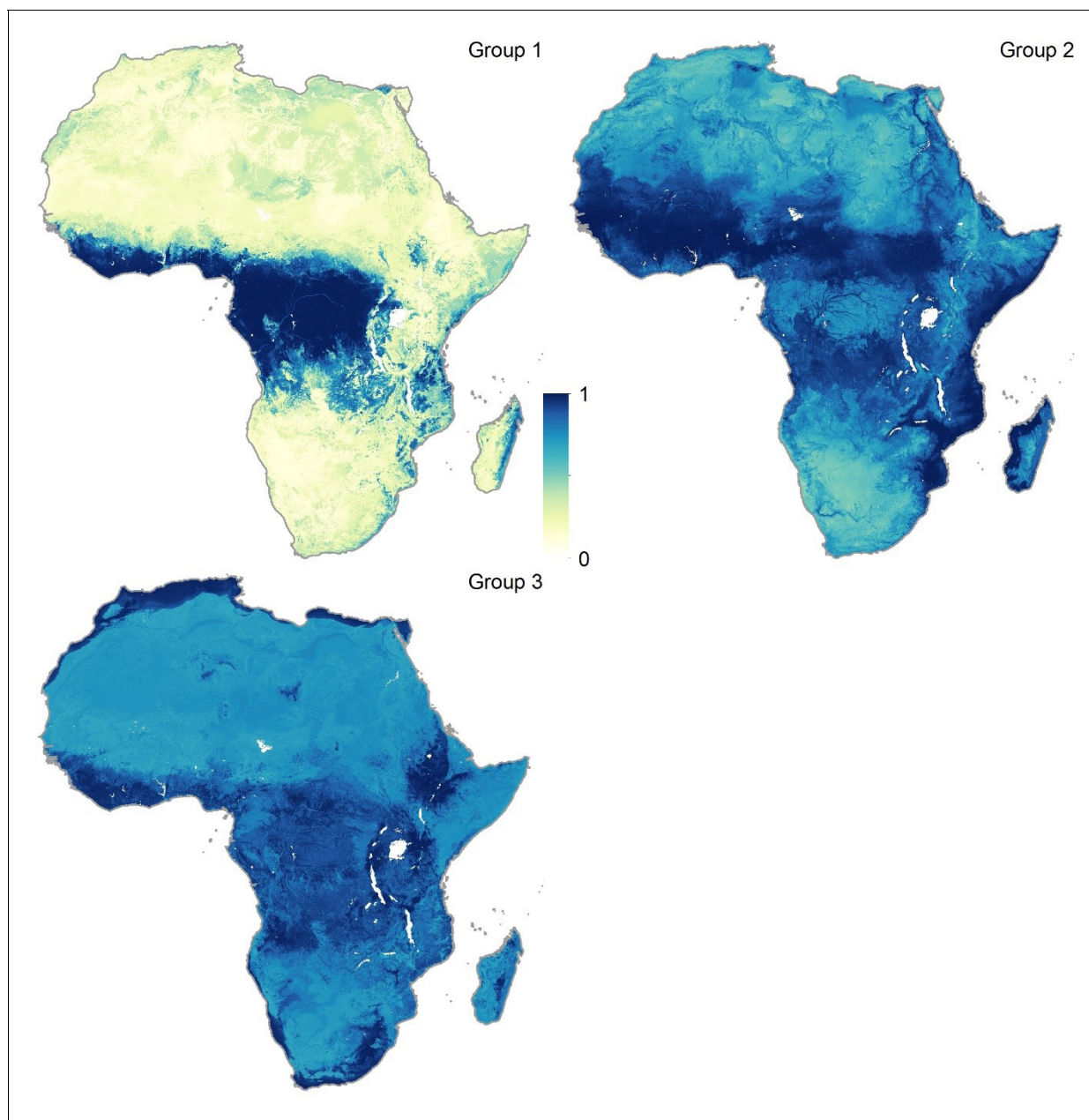


Figure 2. Combined suitability surfaces for each of the potential reservoir bat groupings. For each layer the species specific suitability maps were combined to produce a surface approximating the probability that any bat species in that group may be present. Regions in blue (1) are most environmentally similar to locations reporting bat records. Areas in yellow (0) are the least environmentally similar. The top left panel depicts Group 1, top right Group 2 and bottom left Group 3 bats.

DOI: [10.7554/eLife.16412.003](https://doi.org/10.7554/eLife.16412.003)

The following figure supplements are available for figure 2:

Figure supplement 1. Group 1 bat distributions.

DOI: [10.7554/eLife.16412.004](https://doi.org/10.7554/eLife.16412.004)

Figure supplement 2. Group 2 bat distributions.

DOI: [10.7554/eLife.16412.005](https://doi.org/10.7554/eLife.16412.005)

Figure supplement 3. Group 3 bat distributions.

DOI: [10.7554/eLife.16412.006](https://doi.org/10.7554/eLife.16412.006)

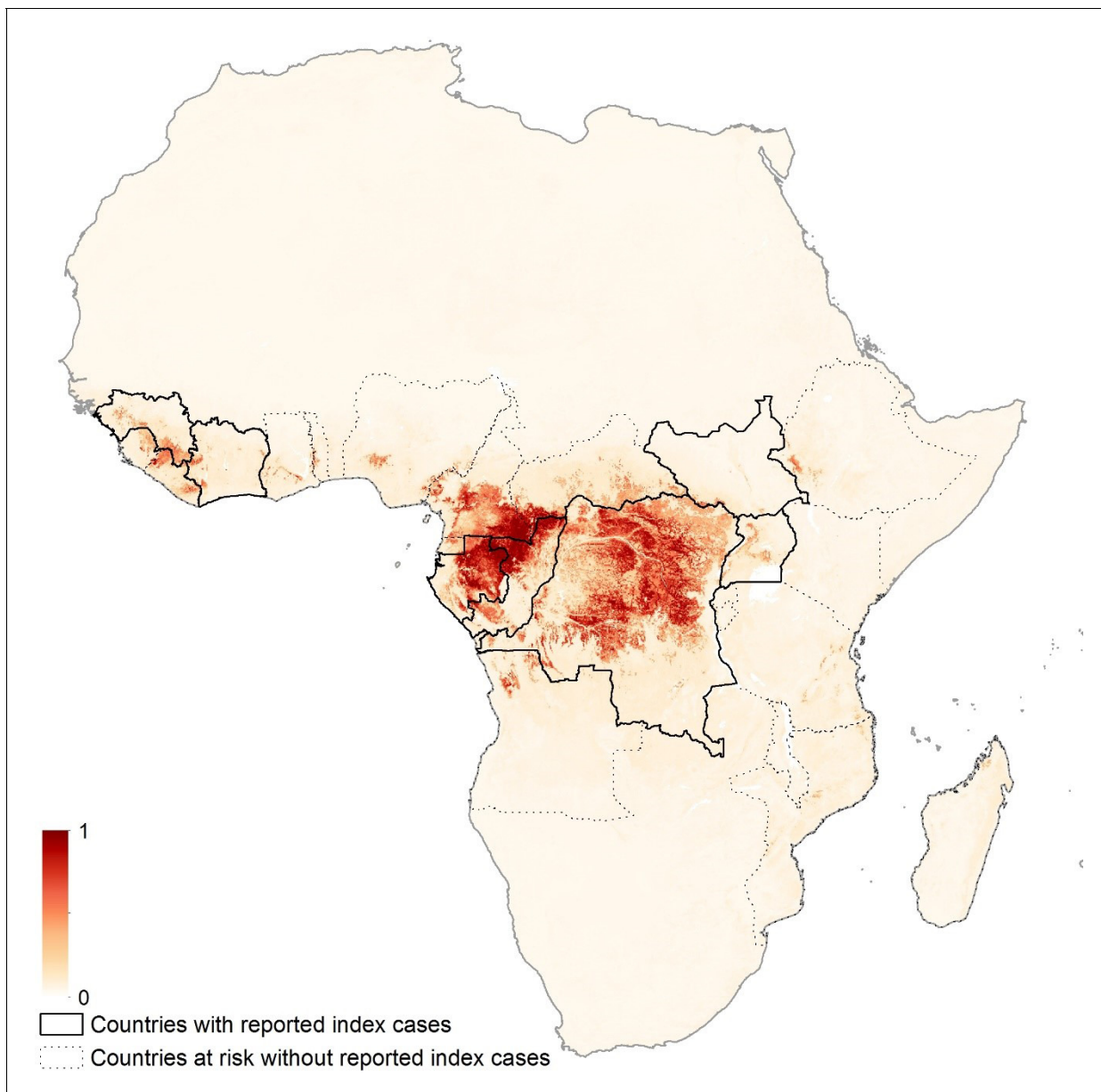


Figure 3. Updated map showing areas most environmentally suitable for the zoonotic transmission of Ebola virus. Areas closer to dark red (1) are most environmentally similar to locations reporting Ebola virus occurrences; areas in light yellow (0) are least similar. Countries with borders outlined are those which are predicted to contain at-risk areas for zoonotic transmission based on a thresholding approach. Output displayed generated from model using the three consolidated bat covariates.

DOI: [10.7554/eLife.16412.007](https://doi.org/10.7554/eLife.16412.007)

The following figure supplements are available for figure 3:

Figure supplement 1. Absolute differences between previous and revised maps.

DOI: [10.7554/eLife.16412.008](https://doi.org/10.7554/eLife.16412.008)

Figure supplement 2. Zoonotic niche map based upon inclusion of individual bat covariate layers.

DOI: [10.7554/eLife.16412.009](https://doi.org/10.7554/eLife.16412.009)

As with the original publication, it must be reiterated that environmental suitability does not inevitably lead to spillover events. Currently absolute human population residing in at-risk pixels is used as a proxy for spillover likelihood, however, a variety of factors will influence the outbreak risk within each location (*Plowright et al., 2015*) and only by including covariates that consider human behaviour (*Woldehanna and Zimicki, 2015*), patterns of susceptibility in other animals (*Walsh et al.,*

Table 1. National populations at risk.

	Country	Population-at-risk (in 100,000s)
Countries previously reporting index cases	Democratic Republic of the Congo	170.18
	Uganda	21.58
	Guinea	17.61
	Côte d'Ivoire	4.08
	Gabon	3.65
	South Sudan	1.80
	Republic of Congo	1.07
Countries with no reported index cases	Nigeria	29.13
	Cameroon	22.90
	Central African Republic	7.62
	Liberia	5.88
	Ghana	4.04
	Sierra Leone	3.94
	Angola	3.25
	Togo	1.78
	Ethiopia	1.75
	Equatorial Guinea	1.22
	Tanzania	1.18
	Burundi	1.07
	Mozambique	0.55
	Madagascar	<0.1
	Kenya	<0.1
	Malawi	<0.1

DOI: 10.7554/eLife.16412.010

2007; 2009), impacts of land use change (Rosales-Chilama et al., 2015) and within-host viral dynamics (Amman et al., 2012; Hayman, 2015) can an approximation of spillover risk be defined.

These updates demonstrate the ease and speed with which new data and covariate considerations can be incorporated within existing empirical models (Kraemer et al., 2016). As the wider discussion on EVD turns to focus on strategies to prevent or contain future spillover events as well as developing long-term in-country containment capacities (Currie et al., 2016), it is hoped that maps

Table 2. Comparison of previous and revised niche models.

	Revised niche map (with summary bat layers)	Revised niche map (with individual bat layers)	Previous eLife niche map (Pigott et al., 2014)
AUC	0.8236 ± 0.08	0.8195 ± 0.08	0.85 ± 0.04
Occurrences	n = 57 (animals), n = 31 (humans)	n = 57 (animals), n = 31 (humans)	n = 51 (animals), n = 30 (humans)
Ranked relative contributions	EVI mean (0.55)	EVI mean (0.46)	EVI mean (0.65)
	Group 1 bat distribution (0.18)	Hypsignathus monstrosus (0.15)	Elevation (0.12)
	LST mean (night) (0.08)	Epomops franqueti (0.08)	LST mean (night) (0.08)
	Elevation (0.06)	Otomops martiensseni (0.06)	PET mean (0.06)
	LST mean (day) (0.04)	Epomophorus labiatus (0.04)	Bat distribution (0.04)

DOI: 10.7554/eLife.16412.011

such as these convey the heterogeneities in spillover risk that exist within Africa. To better enable researchers and policymakers to consider EVD preparedness and necessary contingencies, a new online tool has been developed which allows users to interrogate the revised maps in more detail, in areas of specific interest (<http://vizhub.healthdata.org/ebola>). As part of this tool, the zoonotic niche output and Group 1 bat layers are now available, along with filters for identifying at-risk countries and locations of previous index cases from outbreaks.

Geographic datasets such as these provide context to broader discussions as our aspirations transition from controlling outbreaks to mitigating the risk of future spillover events prioritised by their potential for more widespread epidemics. Such data are particularly important for determining where best to investigate the frequency of potentially transmissible contacts between reservoir and susceptible species and humans. Previous niche maps served as an important impetus in the search for potential reservoirs (*Peterson et al., 2004*) and these iterations can continue to inform such work. As researchers and policy makers seek to resolve outstanding questions about EVD epidemiology, it is hoped that the continued updating and dissemination of this information can contribute to this discussion.

Materials and methods

Updating the occurrence database

Since the previous publication, an outbreak of EVD occurred in humans in the Democratic Republic of the Congo (*Maganga et al., 2014*). The outbreak is thought to have originated in Inkanamongo, a village near Boende, Équateur province and resulted in 66 probable and confirmed cases and 49 probable and confirmed deaths (*Rosello et al., 2015*). A polygon of radius 10 km centered on the town of Boende was included to capture the location of the index case, increasing the database of assumed independent animal-to-human spillover events to 31 as part of 24 distinct reported outbreaks (*Mylne et al., 2014*).

In addition, a re-analysis of the literature available on infections in animal species was completed on 7th October 2015. Due to the poor differential capacity of immunological tests to discriminate Ebola virus from other viruses we retained the following inclusion criteria for the database; for susceptible species mortality events linked to Ebolavirus by any diagnostic methodology or PCR-positive diagnosis of Ebolavirus were included. Inclusion criteria for potential bat reservoir species were either PCR-positivity or serological evidence suggesting Ebolavirus infection. Serological studies were included without fatal outcomes (unlike with susceptible species) due to the hypothesised asymptomatic nature of infection in the reservoir hosts. As a result of these inclusion criteria, studies with serological detection of Ebolavirus in healthy non-Chiropteran species were excluded, such as surveys in dogs (*Allela et al., 2005*).

In total six new records of EVD occurrence in animals were identified and included within the database to increase the total to 57. These records were obtained from two research articles. The first of these assessed Ebolavirus load in a variety of mammal species and identified PCR-positivity in a number of small mammals across three sites in Central African Republic (*Morvan et al., 1999*). In total, four separate occurrences, consisting of three different species, were identified as being PCR positive: a member of the *Praomys* complex, Peter's mouse (*Mus setulosus*) and the greater forest shrew (*Sylvisorex ollula*). The second study investigated serological responses in straw-coloured fruit bats (*Eidolon helvum*) caught in two districts in Zambia (*Ogawa et al., 2015*). Specific latitudes and longitudes of the study sites were supplied for the Central African Republic study and were used to generate point occurrences. For the Zambian study it was necessary to use administrative data representing the two districts where the bats were caught (Serenje and Ndola districts).

Expanding potential bat reservoir species

Potential bat reservoir species were stratified into three groupings based upon the strength of evidence suggesting their reservoir status (*Table 3*). Group 1 contained the three species of bat from which Ebolavirus RNA has been detected and therefore have the strongest evidence to support potential reservoir status (*Leroy et al., 2005*). Group 2 species are those that, using a variety of serological tests, have been reported to be Ebolavirus seropositive, suggesting potential reservoir status. A previous review (*Olival and Hayman, 2014*), identified nine species as seropositive for

Table 3. Final bats included in analysis classified by evidence grouping.

Grouping	Bat	Occurrences
Group 1	Franquet's epauletted fruit bat (<i>Epomops franqueti</i>)	442
	Hammerheaded fruit bat (<i>Hypsignathus monstrosus</i>)	254
	Little collared fruit bat (<i>Myonycteris torquata</i>)	107
Group 2	Angolan free-tailed bat (<i>Tadarida condylura</i> , formerly <i>Mops condylurus</i>)	179
	Egyptian fruit bat (<i>Rousettus aegyptiacus</i>)	177
	Gambian epauletted fruit bat (<i>Epomophorus gambianus</i>)	166
	Peter's dwarf epauletted fruit bat (<i>Micropteropus pusillus</i>)	208
	Straw-coloured fruit bat (<i>Eidolon helvum</i>)	282
Group 3	Buettikofer's epauletted fruit bat (<i>Epomops buettikoferi</i>)	50
	Common bent-wing bat (<i>Miniopterus schreibersii</i>)	31
	Eloquent horseshoe bat (<i>Rhinolophus eloquens</i>)	61
	Ethiopian epauletted fruit bat (<i>Epomophorus labiatus</i>)	187
	Giant leaf-nosed bat (<i>Hipposideros gigas</i>)	21
	Greater long-fingered bat (<i>Miniopterus inflatus</i>)	56
	Large-eared free-tailed bat (<i>Otomops martiensseni</i>)	33

DOI: [10.7554/eLife.16412.012](https://doi.org/10.7554/eLife.16412.012)

Ebolavirus. This was reduced to five species after the removal of the three species already categorised in Group 1 and Leschenault's Rousette, *Rousettus leschenaultii*, which is not found in Africa.

Finally, Group 3 species were identified via generalized boosted regression analysis, which discriminates the bats reported to be filovirus-positive by learning trait patterns that distinguish them from all other bat species (Han et al., 2016). Generalized boosted regression (Elith et al., 2008) was applied to traits describing all bat species, including life history, physiological, ecological, morphological and demographic variables collected from numerous published sources. In addition to traits, the filovirus status of each bat species was assigned as a binary score (0 – not currently known to be positive for any filoviruses; 1 – published evidence). This analysis produces a rank list of all bat species according to their probability of being a filovirus carrier on the basis of their trait similarities with known filovirus-positive bat species. Bats found in the 90th percentile of likely filovirus carriers were initially considered, and then filtered to include only those which have home ranges in Africa (Schipper et al., 2008). As per the original publication, occurrence records were extracted from the Global Biodiversity Information Facility (GBIF). Species for which there were fewer than 20 unique GBIF records in Africa were dropped from the analysis due to data paucity. Table 3 reports the bat species and corresponding numbers of occurrences included in the analysis.

For Group 1 species, occurrence records were supplemented by searching PubMed and Web of Knowledge for additional reports. A literature review was completed on the 8th September 2015 using the following sets of keywords:

- '*Hypsignathus monstrosus*' or 'hammer-headed bat' or 'hammer headed bat' or 'hammer-headed bat' or 'big-lipped bat' or 'big lipped bat' or '*Hypsignathus labrosus*' or '*Hypsignathus macrocephalus*'
- '*Myonycteris torquata*' or 'little collared fruit bat' or '*Myonycteris collaris*' or '*Myonycteris leptodon*' or '*Myonycteris wroughtoni*'
- '*Epomops franqueti*' or "Franquet's epauletted fruit bat" or '*Epomops comptus*' or '*Epomops strepitans*'

A total of 34 articles were identified for inclusion, from which 564 additional occurrences were sourced.

All bat species were modelled separately using boosted regression trees (Elith *et al.*, 2008) utilising the same modelling procedure as outlined in the original article except that 100, rather than 50, bootstrap models were fitted. This resulted in 15 individual environmental suitability maps for bat species (see **Figure 2—figure supplements 1, 2 and 3**), as well as three consolidated bat layers combining the environmental suitability maps for the bats within each of the three groupings (**Figure 2**).

Revising the predicted zoonotic niche map

A species distribution model, specifically a boosted regression trees approach (Elith *et al.*, 2008), was implemented. The model generates regression trees based upon binary splits of linked covariates, which are iteratively improved upon by boosting. The regression trees are capable of characterising complex environmental interactions and correlations since each tree is built from a hierarchy of multiple nodes, each based upon different successive binary splits of the covariates. The model extracts environmental information for each reported occurrence of Ebolavirus to define an optimal relationship between presence of the disease and environmental factors. Predictive performance is improved by including a comparison background dataset that acts as a hypothesised environmental negative control (Phillips *et al.*, 2009). As per the previous analysis, this dataset was generated by randomly sampling across Africa biased towards areas of high population density. By including human population density in this way, some potential sampling biases present in human index case reporting can be mitigated as cases are more likely to be reported in more populous areas. The boosted regression trees were re-run using the same parameters and covariates (elevation, mean evapotranspiration rate, and mean and range measures of enhanced vegetation index, daytime land surface temperature (LST), and night-time LST) as the previous publication except for the inclusion of the new occurrence data outlined above and the new bat layers. Two model iterations were run: one with the three consolidated bat layers (i.e. Groups 1, 2 and 3) and the other with all the bat species layers considered separately.

Estimating populations at risk

The continuous suitability surface was converted into a binary at-risk versus not-at-risk surface by determining a threshold value that included 95% of the estimated suitability values of pixels with reported human index cases (Pigott *et al.*, 2015). For sites represented by a specific latitude and longitude the suitability score was taken from the corresponding pixel; for polygon estimates covering a number of cells, the mean suitability was taken across all pixels covered by the polygon.

Whilst not included directly as a covariate in the modelling process, human population layers were assessed in at-risk locations as a potential proxy for spillover frequency. The populations living within the gridded cells thought to be at-risk of potential Ebolavirus transmission from zoonotic sources were calculated using an updated contemporary gridded estimate of population (WorldPop Project, 2015).

Acknowledgements

This work was funded by a grant from The Paul G. Allen Family Foundation (#11878) to SIH which also provided funding for DMP, AIM, LE and CM. BAH acknowledges support from the National Institute of General Medical Sciences of the National Institutes of Health (#U01GM110744). FMS is funded by the Rhodes Trust. OJB is funded by the Bill & Melinda Gates Foundation (#OPP1119467). MUGK is funded by the German Academic Exchange Service (DAAD) through a graduate scholarship. CLM and NG acknowledge support from the Bill & Melinda Gates Foundation (#OPP1053338).

PWG is a Career Development Fellow (#K00669X) jointly funded by the UK Medical Research Council (MRC) and the UK Department for International Development (DFID) under the MRC/DFID Concordat agreement and receives support from the Bill & Melinda Gates Foundation (#OPP1068048, #OPP1106023) which also supports DJW and SB. SIH is also funded by a Senior Research Fellowship from the Wellcome Trust (#095066) and grants from the Bill & Melinda Gates Foundation (#OPP1093011, #OPP1132415). DMP and BAH also acknowledge the support for a collaborative meeting from the RAPIDD program of the Science & Technology Directorate. SIH also acknowledges a grant from the Research for Health in Humanitarian Crises (R2HC) Programme, managed by ELHRA (#13468) and funded equally by the Wellcome Trust and DFID, which also supported NG and MUGK.

Additional information

Competing interests

SIH: Reviewing editor, *eLife*. The other authors declare that no competing interests exist.

Funding

Funder	Grant reference number	Author
Paul G. Allen Family Foundation	11878	David M Pigott Anoushka I Millear Lucas Earl Chloe Morozoff Simon I Hay
Science and Technology Directorate	RAPIDD program	David M Pigott Barbara A Han
National Institute of General Medical Sciences	U01GM110744	Barbara A Han
Rhodes Scholarships		Freya M Shearer
Bill and Melinda Gates Foundation	OPP1068048	Daniel J Weiss Samir Bhatt Peter W Gething
Bill and Melinda Gates Foundation	OPP1106023	Daniel J Weiss Samir Bhatt Peter W Gething
Bill and Melinda Gates Foundation	OPP1119467	Oliver J Brady
German Academic Exchange Service London	Graduate Scholarship	Moritz UG Kraemer
Research for Health in Humanitarian Crises (R2HC) Programme	ELHRA (#13468)	Moritz UG Kraemer Nick Golding Simon I Hay
Wellcome Trust		Moritz UG Kraemer Nick Golding
Department for International Development		Moritz UG Kraemer Nick Golding
Bill and Melinda Gates Foundation	OPP1053338	Catherine L Moyes Nick Golding
Medical Research Council	MRC/DFID Concordat agreement	Peter W Gething
Department for International Development	MRC/DFID Concordat agreement	Peter W Gething
Wellcome Trust	Senior Research Fellowship #095066	Simon I Hay
Bill and Melinda Gates Foundation	OPP1093011	Simon I Hay

Bill and Melinda Gates
Foundation

OPP1132415

Simon I Hay

The funders had no role in study design, data collection and interpretation, or the decision to submit the work for publication.

Author contributions

DMP, SIH, Conception and design, Acquisition of data, Analysis and interpretation of data, Drafting or revising the article; AIM, BAH, Acquisition of data, Analysis and interpretation of data, Drafting or revising the article; LE, CM, FMS, OJB, MUGK, Analysis and interpretation of data, Drafting or revising the article; DJW, Acquisition of data, Drafting or revising the article; CLM, NG, Conception and design, Analysis and interpretation of data, Drafting or revising the article; SB, PWG, Conception and design, Drafting or revising the article

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Additional files

Major datasets

The following dataset was generated:

Author(s)	Year	Dataset title	Dataset URL	Database, license, and accessibility information
David M Pigott, Anoushka I Millear, Lucas Earl, Chloe Morozoff, Barbara A Han, Freya M Shearer, Daniel J Weiss, Oliver J Brady, Moritz UG Kraemer, Catherine L Moyes, Samir Bhatt, Peter W Gething, Nick Golding, Simon I Hay	2016	eLife Advances - Updates to the zoonotic niche map of Ebola virus disease in Africa	http://dx.doi.org/10.6084/m9.figshare.c.3267965.v1	Publicly available at figshare (https://figshare.com/)

References

- Allela L, Boury O, Pouillot R, Délicat A, Yaba P, Kumulungui B, Rouquet P, Gonzalez JP, Leroy EM. 2005. Ebola virus antibody prevalence in dogs and human risk. *Emerging Infectious Diseases* **11**:385–390. doi: [10.3201/eid1103.040981](https://doi.org/10.3201/eid1103.040981)
- Amman BR, Carroll SA, Reed ZD, Sealy TK, Balinandi S, Swanepoel R, Kemp A, Erickson BR, Comer JA, Campbell S, Cannon DL, Khristova ML, Atimnedi P, Paddock CD, Crockett RJ, Flietstra TD, Warfield KL, Unfer R, Katongole-Mbidde E, Downing R, et al. 2012. Seasonal pulses of Marburg virus circulation in juvenile *Rousettus aegyptiacus* bats coincide with periods of increased risk of human infection. *PLoS Pathogens* **8**: e1002877. doi: [10.1371/journal.ppat.1002877](https://doi.org/10.1371/journal.ppat.1002877)
- Bogoch II, Creatore MI, Cetron MS, Brownstein JS, Pesik N, Miniota J, Tam T, Hu W, Nicolucci A, Ahmed S, Yoon JW, Berry I, Hay SI, Anema A, Tatem AJ, MacFadden D, German M, Khan K. 2015. Assessment of the potential for international dissemination of Ebola virus via commercial air travel during the 2014 west African outbreak. *The Lancet* **385**:29–35. doi: [10.1016/S0140-6736\(14\)61828-6](https://doi.org/10.1016/S0140-6736(14)61828-6)
- Currie J, Grenfell B, Farrar J. 2016. Infectious diseases. Beyond Ebola. *Science* **351**:815–816. doi: [10.1126/science.aad8521](https://doi.org/10.1126/science.aad8521)
- Elith J, Leathwick JR, Hastie T. 2008. A working guide to boosted regression trees. *Journal of Animal Ecology* **77**:802–813. doi: [10.1111/j.1365-2656.2008.01390.x](https://doi.org/10.1111/j.1365-2656.2008.01390.x)
- Funk S, Piot P. 2014. Mapping Ebola in wild animals for better disease control. *eLife* **3**:e04565. doi: [10.7554/eLife.04565](https://doi.org/10.7554/eLife.04565)

- Han BA, Schmidt JP, Alexander LW, Bowden SE, Hayman DTS, Drake JM. 2016. Undiscovered bat hosts of filoviruses. *PLoS Neglected Tropical Diseases* **10**:e0004815. doi: [10.1371/journal.pntd.0004815](https://doi.org/10.1371/journal.pntd.0004815)
- Haydon DT, Cleaveland S, Taylor LH, Laurenson MK. 2002. Identifying reservoirs of infection: a conceptual and practical challenge. *Emerging Infectious Diseases* **8**:1468–1473. doi: [10.3201/eid0812.010317](https://doi.org/10.3201/eid0812.010317)
- Hayman DT. 2015. Biannual birth pulses allow filoviruses to persist in bat populations. *Proceedings of the Royal Society B* **282**:20142591. doi: [10.1098/rspb.2014.2591](https://doi.org/10.1098/rspb.2014.2591)
- Kraemer MU, Hay SI, Pigott DM, Smith DL, Wint GR, Golding N. 2016. Progress and challenges in infectious disease cartography. *Trends in Parasitology* **32**:19–29. doi: [10.1016/j.pt.2015.09.006](https://doi.org/10.1016/j.pt.2015.09.006)
- Kuhn JH. 2008. Filoviruses. A compendium of 40 years of epidemiological, clinical, and laboratory studies. *Archives of Virology. Supplementum* **20**:13–360.
- Leendertz S. 2016. Testing new hypotheses regarding ebolavirus reservoirs. *Viruses* **8**:30. doi: [10.3390/v8020030](https://doi.org/10.3390/v8020030)
- Leendertz SA, Gogarten JF, Dux A, Calvignac-Spencer S, Leendertz FH. 2016. Assessing the evidence supporting fruit bats as the primary reservoirs for Ebola viruses. *EcoHealth* **13**:18–25. doi: [10.1007/s10393-015-1053-0](https://doi.org/10.1007/s10393-015-1053-0)
- Leirs H, Mills JN, Krebs JW, Childs JE, Akaibe D, Woollen N, Ludwig G, Peters CJ, Ksiazek TG. 1999. Search for the Ebola virus reservoir in Kikwit, Democratic Republic of the Congo: reflections on a vertebrate collection. *Journal of Infectious Diseases* **179** Suppl 1:S155–163. doi: [10.1086/514299](https://doi.org/10.1086/514299)
- 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 and Zoonotic Diseases* **9**:723–728. doi: [10.1089/vbz.2008.0167](https://doi.org/10.1089/vbz.2008.0167)
- 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. doi: [10.1038/438575a](https://doi.org/10.1038/438575a)
- Maganga GD, Kapetshi J, Berthet N, Kebela Ilunga B, Kabange F, Mbala Kengebeni P, Mondonge V, Muyembe JJ, Bertherat E, Briand S, Cabore J, Epelboin A, Formenty P, Kobinger G, González-Angulo L, Labouba I, Manuguerra JC, Okwo-Bele JM, Dye C, Leroy EM. 2014. Ebola virus disease in the Democratic Republic of Congo. *New England Journal of Medicine* **371**:2083–2091. doi: [10.1056/NEJMoa1411099](https://doi.org/10.1056/NEJMoa1411099)
- Mari Saez A, Weiss S, Nowak K, Lapeyre V, Zimmermann F, Dux A, Kuhl HS, Kaba M, Regnaut S, Merkel K, Sachse A, Thiesen U, Villanyi L, Boesch C, Dabrowski PW, Radonic A, Nitsche A, Leendertz SAJ, Petterson S, Becker S, et al. 2015. Investigating the zoonotic origin of the West African Ebola epidemic. *EMBO Molecular Medicine* **7**:17–23. doi: [10.15252/emmm.201404792](https://doi.org/10.15252/emmm.201404792)
- Moon S, Sridhar D, Pate MA, Jha AK, Clinton C, Delaunay S, Edwin V, Fallah M, Fidler DP, Garrett L, Goosby E, Gostin LO, Heymann DL, Lee K, Leung GM, Morrison JS, Saavedra J, Tanner M, Leigh JA, Hawkins B, et al. 2015. Will Ebola change the game? Ten essential reforms before the next pandemic. The report of the harvard-LSHTM independent panel on the global response to Ebola. *The Lancet* **386**:2204–2221. doi: [10.1016/S0140-6736\(15\)00946-0](https://doi.org/10.1016/S0140-6736(15)00946-0)
- Morvan JM, Deubel V, Gounon P, Nakouné E, Barrière P, Murri S, Perpète O, Selekon B, Coudrier D, Gautier-Hion A, Colyn M, Volekhov V. 1999. Identification of Ebola virus sequences present as RNA or DNA in organs of terrestrial small mammals of the Central African Republic. *Microbes and Infection* **1**:1193–1201. doi: [10.1016/S1286-4579\(99\)00242-7](https://doi.org/10.1016/S1286-4579(99)00242-7)
- 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. *Scientific Data* **1**:140042. doi: [10.1038/sdata.2014.42](https://doi.org/10.1038/sdata.2014.42)
- Ogawa H, Miyamoto H, Nakayama E, Yoshida R, Nakamura I, Sawa H, Ishii A, Thomas Y, Nakagawa E, Matsuno K, Kajihara M, Maruyama J, Nao N, Muramatsu M, Kuroda M, Simulundu E, Changula K, Hang'ombe B, Namangala B, Nambota A, et al. 2015. Seroepidemiological prevalence of multiple species of filoviruses in fruit bats (*Eidolon helvum*) migrating in Africa. *Journal of Infectious Diseases* **212** Suppl 2:S101–108. doi: [10.1093/infdis/jiv063](https://doi.org/10.1093/infdis/jiv063)
- Olival KJ, Hayman DT. 2014. Filoviruses in bats: current knowledge and future directions. *Viruses* **6**:1759–1788. doi: [10.3390/v6041759](https://doi.org/10.3390/v6041759)
- Peterson AT, Bauer JT, Mills JN. 2004. Ecologic and geographic distribution of filovirus disease. *Emerging Infectious Diseases* **10**:40–47. doi: [10.3201/eid1001.030125](https://doi.org/10.3201/eid1001.030125)
- Peterson AT, Carroll DS, Mills JN, Johnson KM. 2004. Potential mammalian filovirus reservoirs. *Emerging Infectious Diseases* **10**:2073–2081. doi: [10.3201/eid1012.040346](https://doi.org/10.3201/eid1012.040346)
- Phillips SJ, Dudik M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* **19**:181–197. doi: [10.1890/07-2153.1](https://doi.org/10.1890/07-2153.1)
- Pigott DM, Golding N, Mylne A, Huang Z, Henry AJ, Weiss DJ, Brady OJ, Kraemer MUG, 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. doi: [10.7554/eLife.04395](https://doi.org/10.7554/eLife.04395)
- Pigott DM, Golding N, Mylne A, Huang Z, Weiss DJ, Brady OJ, Kraemer MU, Hay SI. 2015. Mapping the zoonotic niche of Marburg virus disease in Africa. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **109**:366–378. doi: [10.1093/trstmh/trv024](https://doi.org/10.1093/trstmh/trv024)
- Plowright RK, Eby P, Hudson PJ, Smith IL, Westcott D, Bryden WL, Middleton D, Reid PA, McFarlane RA, Martin G, Tabor GM, Skerratt LF, Anderson DL, Crameri G, Quammen D, Jordan D, Freeman P, Wang LF, Epstein JH, Marsh GA, et al. 2015. Ecological dynamics of emerging bat virus spillover. *Proceedings of the Royal Society B* **282**:20142124. doi: [10.1098/rspb.2014.2124](https://doi.org/10.1098/rspb.2014.2124)
- Rosales-Chilama M, Gongora RE, Valderrama L, Jojoa J, Alexander N, Rubiano LC, Cossio A, Adams ER, Saravia NG, Gomez MA. 2015. Parasitological Confirmation and Analysis of Leishmania Diversity in Asymptomatic and

- Subclinical Infection following Resolution of Cutaneous Leishmaniasis. *PLoS Neglected Tropical Diseases* **9**: e0003652. doi: [10.1371/journal.pntd.0004273](https://doi.org/10.1371/journal.pntd.0004273)
- Rosello A**, Mossoko M, Flasche S, Van Hoek AJ, Mbala P, Camacho A, Funk S, Kucharski A, Ilunga BK, Edmunds WJ, Piot P, Baguelin M, Tamfum JJ. 2015. Ebola virus disease in the Democratic Republic of the Congo, 1976–2014. *eLife* **4**:e09015. doi: [10.7554/eLife.09015](https://doi.org/10.7554/eLife.09015)
- 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, Mittermeier RA, Smith AT, Absolon D, Aguiar JM, Amori G, Bakkour N, Baldi R, et al. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* **322**:225–230. doi: [10.1126/science.1165115](https://doi.org/10.1126/science.1165115)
- Toledo J**, George L, Martinez E, Lazaro A, Han WW, Coelho GE, Runge Ranzinger S, Horstick O, Han BA. 2016. Relevance of Non-communicable Comorbidities for the Development of the Severe Forms of Dengue: A Systematic Literature Review. *PLoS Neglected Tropical Diseases* **10**:e0004284. doi: [10.1371/journal.pntd.0004284](https://doi.org/10.1371/journal.pntd.0004284)
- Viana M**, Mancy R, Biek R, Cleaveland S, Cross PC, Lloyd-Smith JO, Haydon DT. 2014. Assembling evidence for identifying reservoirs of infection. *Trends in Ecology & Evolution* **29**:270–279. doi: [10.1016/j.tree.2014.03.002](https://doi.org/10.1016/j.tree.2014.03.002)
- Walsh PD**, Bermejo M, Rodriguez-Teijeiro JD. 2009. Disease avoidance and the evolution of primate social connectivity. In: *Primate Parasite Ecology: The Dynamics and Study of Host-Parasite Relationships*. 183–197.
- Walsh PD**, Breuer T, Sanz C, Morgan D, Doran-Sheehy D. 2007. Potential for Ebola transmission between gorilla and chimpanzee social groups. *American Naturalist* **169**:684–689. doi: [10.1086/513494](https://doi.org/10.1086/513494)
- Woldehanna S**, Zimicki S. 2015. An expanded one health model: integrating social science and one health to inform study of the human-animal interface. *Social Science & Medicine* **129**:87–95. doi: [10.1016/j.socscimed.2014.10.059](https://doi.org/10.1016/j.socscimed.2014.10.059)
- World Health Organization**. 2016. Ebola situation reports. Available at <http://www.who.int/csr/disease/ebola/en/>. Accessed March 14, 2016.
- WorldPop Project**. 2015. Gridded population surface of Africa. Available at <http://www.worldpop.org.uk/>. Accessed November 6, 2015.