

1 Climate change will drive novel cross-species

2 viral transmission

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Abstract

15 Between 10,000 and 600,000 species of mammal virus are estimated to have the
16 potential to spread in human populations, but the vast majority are currently cir-
17 culating in wildlife, largely undescribed and undetected by disease outbreak surveil-
18 lance^{1,2,3}. In addition, changing climate and land use drive geographic range shifts
19 in wildlife, producing novel species assemblages and opportunities for viral sharing
20 between previously isolated species^{4,5}. In some cases, this will inevitably facilitate
21 spillover into humans^{6,7}—a possible mechanistic link between global environmental
22 change and emerging zoonotic disease⁸. Here, we map potential hotspots of viral
23 sharing, using a phylogeographic model of the mammal-virus network, and projec-
24 tions of geographic range shifts for 3,870 mammal species under climate change and
25 land use scenarios for the year 2070. Shifting mammal species are predicted to ag-
26 gregate at high elevations, in biodiversity hotspots, and in areas of high human pop-
27 ulation density in Asia and Africa, sharing novel viruses between 3,000 and 13,000
28 times. Counter to expectations, holding warming under 2°C within the century
29 does not reduce new viral sharing, due to greater range expansions—highlighting
30 the need to invest in surveillance even in a low-warming future. Most projected vi-
31 ral sharing is driven by diverse hyperreservoirs (rodents and bats) and large-bodied
32 predators (carnivores). Because of their unique dispersal capacity, bats account for
33 the majority of novel viral sharing, and are likely to share viruses along evolutionary
34 pathways that could facilitate future emergence in humans. Our findings highlight
35 the urgent need to pair viral surveillance and discovery efforts with biodiversity
36 surveys tracking range shifts, especially in tropical countries that harbor the most
37 emerging zoonoses.

³⁸ Main Text

³⁹ In the face of rapid environmental change, survival for many species depends on moving
⁴⁰ to track shifting climates. Even in a best case scenario, many species are projected
⁴¹ to shift a hundred kilometers or more in the next century^{9,10}. In the process, many
⁴² animals will bring their parasites and pathogens into new environments^{4,11}, creating new
⁴³ evolutionary opportunities for host jumps⁸. Most conceptual frameworks for cross-species
⁴⁴ transmission revolve around how these host jumps facilitate the spillover of new zoonotic
⁴⁵ pathogens into humans^{12,13,14}, but viral evolution is an undirected process¹⁵, in which
⁴⁶ humans are only one of over 5,000 mammal species with over 12 million possible pairwise
⁴⁷ combinations¹⁶. Despite their indisputable significance, zoonotic emergence events are
⁴⁸ just the tip of the iceberg; almost all cross-species transmission events will occur among
⁴⁹ wild mammals, largely undetected and mostly inconsequential for public health.

⁵⁰ Of the millions of possible pairwise viral exchanges, the vast majority are biologically
⁵¹ implausible, as host species' geographic ranges currently do not overlap. However, as
⁵² ranges shift, a small fraction of possible interactions will occur, of which a subset will
⁵³ lead to viral establishment in a novel host. Which subset results in establishment de-
⁵⁴pends on *opportunity* and *compatibility*^{14,17,18}, analogous to exposure and susceptibility
⁵⁵ within populations, and both dimensions pose an important predictive challenge. The
⁵⁶ ability of species to track shifting habitats in a changing climate will determine which
⁵⁷ pairs of species encounter each other for the first time^{4,19}. Habitat selection and be-
⁵⁸havioral differences can further limit contact, even if species are nominally sympatric¹⁹.
⁵⁹ Some viruses may spread environmentally between spatially-proximate species with no
⁶⁰ direct behavioral contact²⁰, but generally, sharing is more likely among species with more
⁶¹ ecological overlap²¹. Even among species in close contact, most spillovers are still a dead
⁶² end; progressively smaller subsets of viruses can infect novel host cells, proliferate, and
⁶³ transmit onward in a new host¹⁸. Their ability to do so is determined by compatibility
⁶⁴ between viral structures, host cell receptors, and host immunity⁶. Because closely related
⁶⁵ species share both ecological and immunological traits through identity by descent, phy-
⁶⁶logeny is a strong predictor of pathogen sharing^{17,22}, as well as susceptibility to invasion
⁶⁷ by new viruses^{23,24,25}. In a changing world, these factors should continue to mediate the
⁶⁸ impact of ecosystem turnover on the mammalian virome.

⁶⁹ Although several studies have mapped current hotspots of emerging diseases^{3,26,27},
⁷⁰ few have modeled them in the context of global change. With the global reassortment
⁷¹ of animal biodiversity, it is unknown whether bats and rodents will still play a central
⁷² role in viral emergence^{3,28} (ED Figure 1), or whether hotspots of viral emergence will
⁷³ stay in tropical rainforests^{27,29} which currently harbor most undiscovered viruses^{3,30}.
⁷⁴ Here, by projecting geographic range shifts and applying fundamental biological rules

75 for cross-species transmission, we predicted how and where global change could create
76 novel opportunities for viral sharing. We built species distribution models for 3,870
77 mammal species, and projected geographic range shifts based on four paired scenarios
78 of climate change (representative concentration pathways, RCPs) and land use change
79 (shared socioeconomic pathways, SSPs) by 2070. We treated dispersal potential as an
80 additional layer of biological realism, inferring these limits for species based on allomet-
81 ric scaling³¹, and compared predictions with and without dispersal constraints. We used
82 these projections to identify where novel range overlap among unfamiliar species (“first
83 encounters”) could happen, and used a recently-developed model to predict the proba-
84 bility of viral sharing based on geographic overlap and host phylogenetic similarity¹⁷.
85 (ED Figure 2) This model framework allows powerful inference based on the ~1% of
86 the global mammalian virome that has been described^{1,3,17}. Using this approach, we
87 tested the hypothesis that environmental change should drive biotic homogenization of
88 mammal communities, exposing mammals to novel viruses, and altering the structure of
89 mammal-virus interactions.

90 Most mammals are projected to undergo rapid range shifts in the next half century¹⁰.
91 If range shifts can keep pace with the velocity of climate change³², we predict that the
92 vast majority of mammal species (89%–98%) will overlap with at least one unfamiliar
93 species somewhere in their future range, regardless of emissions scenario. At the global
94 level, community turnover would permit almost 300,000 novel species interactions (ED
95 Figure 3). These “first encounters” between mammal species will occur everywhere in the
96 world, but are concentrated in tropical Africa and southeast Asia (ED Figure 4). This
97 result was surprising, and counter to our expectation that species might aggregate at
98 higher latitudes, given that most research has focused on poleward range shifts^{33,34,35},
99 and previous work has anticipated a link between climate change, range shifts, and
100 parasite host-switching in the Arctic^{36,37}. However, our findings show that communities
101 tend to shift along latitudinal gradients together, with species rarely encountering new
102 conspecifics³⁸. In contrast, species will track thermal optima along elevational gradients
103 and aggregate in novel combinations in mountain ranges, especially in tropical areas with
104 the highest baseline diversity, matching prior predictions³⁹.

105 This global re-organization of mammal assemblages is projected to dramatically im-
106 pact the structure of the mammalian virome. Accounting for geographic opportunity
107 and phylogenetic compatibility, we projected that a total of 279,427 first encounters in
108 RCP 2.6 would lead to nearly 12,000 novel sharing events. Assuming that spillover will
109 be localized to areas of novel host overlap, we mapped expected viral sharing events, and
110 found again that most sharing should occur in high-elevation, species-rich ecosystems
111 in Africa and Asia (Figure 1A). If species survive a changing climate by aggregating in
112 high elevation refugia, this suggests emerging viruses may be an increasing problem for

113 their conservation^{40,41}. Across scenarios, the spatial signal of expected sharing events is
114 nearly identical, and dominated more by the extent of range shifts than by underlying
115 community phylogenetic structure (ED Figure 5); at least in our framework, opportunity
116 drives spatial patterns more than compatibility.

117 Species' dispersal capacity is likely to constrain range shifts, and therefore to limit
118 novel viral exchange. We limited the dispersal potential of flightless species further to the
119 restrictions placed on the SDM projections, based on an established allometric scaling
120 with body size, trophic rank, and generation time⁴². Dispersal limits caused significant
121 reductions in range expansions across all scenarios, especially warmer ones, and therefore
122 drove a reduction in novel interactions. Even in RCP 2.6 (the mildest scenario), limiting
123 dispersal reduced the number of first encounters by 60%, and reduced the associated viral
124 sharing events by 69%—to a still-staggering 3,600–3,800 projected viral sharing events.
125 Because trophic position and body size determine dispersal capacity, carnivores account
126 for a disproportionate number of first encounters, while ungulates and rodents have
127 slightly fewer first encounters than expected at random (ED Figure 6) Spatial patterns
128 also changed dramatically when dispersal constraints were added, with the majority of
129 first encounters and cross-species viral transmission events occurring in southeast Asia
130 (Figure 1B, ED Figures 4, 5). This viral sharing hotspot is driven disproportionately
131 by bats, because their dispersal was left unconstrained; we made this choice given their
132 exclusion from the original study³¹, genetic evidence that flight allows bats—and their
133 viruses—to circulate at continental levels^{43,44}, and data suggesting that bat distributions
134 are already undergoing disproportionately rapid shifts⁴⁵. Bats account for 87% of first
135 encounters after constraining dispersal, and dominate the spatial pattern, with most of
136 their first encounters restricted to southeast Asia (Figure 2).

137 Bats' unique capacity for flight could be an important and previously unconsidered
138 link between climate-driven range shifts and future changes in the mammal virome.
139 Even non-migratory bats can regularly travel hundreds of kilometers within a lifetime,
140 far exceeding what small mammals might be able to cover in 50 years; half of all bat
141 population genetic studies have failed to find any evidence for isolation by distance⁴⁶.
142 This unique dispersal capacity has inevitable epidemiological implications, with recent
143 evidence suggesting that continental panmixia may be common for zoonotic reservoirs,
144 and allow viral circulation at comparable scales^{43,44,47}. We found that a staggering
145 number of studies have also identified ongoing rapid range expansions in bat species
146 around the world^{45,48,49,50,51,52,53,54,55}, with little mention in the broader climate change
147 or emerging disease literature. If flight does allow bats to undergo more rapid range
148 shifts than other mammals, we expect they should drive the majority of novel cross-
149 species viral transmission, and likely bring zoonotic viruses into new regions. This could
150 add an important new dimension to ongoing debate about whether bats are “special”

151 due to their higher viral richness, higher proportion of zoonotic viruses, and potentially
152 unique immune adaptations^{3,56,57,58,59}.

153 More broadly, climate-driven changes in the mammalian virome are likely to cascade
154 in future emergence of zoonotic viruses. Among the tens of thousands of expected viral
155 host jumps, some of the highest-risk zoonoses or potential zoonoses are likely to find
156 new hosts. This may pose a threat to human health down the road: the same general
157 rules for cross-species transmission explain spillover patterns for emerging zoonoses^{60,61},
158 and the viral species that make successful jumps across wildlife species have the highest
159 propensity for zoonotic emergence^{3,7,28}. Just as simian immunodeficiency virus emer-
160 gence in chimpanzees and gorillas facilitated the origin of HIV, or SARS-CoV spillover
161 into civets allowed a bat virus to reach humans, these wildlife-to-wildlife host jumps may
162 be evolutionary stepping stones for the ~10,000 to 600,000 potentially zoonotic viruses
163 that are currently circulating in mammal hosts¹.

164 To illustrate this problem, we constructed a sub-network of 13 possible Zaire ebolavirus
165 hosts in Africa, and projected possible first encounters involving these species (Figure
166 3A-C). We project these 13 species to encounter 3,604 new mammals in RCP 2.6, with
167 a modest reduction to 2,586 species by dispersal limits. These first encounters are pre-
168 dicted to produce 87 new viral sharing events that might include ZEBOV, and which
169 cover a much broader part of Africa than the current zoonotic niche of Ebola⁶². Hu-
170 man spillover risk aside, this could expose several new wildlife species to a deadly virus,
171 historically responsible for sizable primate die-offs⁶³. Moreover, for zoonoses like Zaire
172 ebolavirus without known reservoirs, future host jumps would only complicate urgent
173 efforts to trace the source of spillover and anticipate future emergences^{64,65}. Ebola is
174 far from unique: with 5,762–11,122 first encounters between bats and primates alone
175 leading to an expected 57–181 new viral sharing events across scenarios (Figure 3D),
176 many potential zoonoses are likely to experience new evolutionary opportunities because
177 of climate change.

178 Future hotspots of novel assemblages and viral evolution are projected to coincide
179 areas of high human population density, further increasing vulnerability to potential
180 zoonoses. First encounters are disproportionately likely to occur in areas that are pro-
181 jected to be either human settled or used as cropland, and surprisingly less likely to
182 occur in forests, which current literature highlights as producing most emerging diseases
183 (Figure 4)²⁷. This finding is consistent for bats and non-bats, and may be an accident
184 of geography, but more likely represents the tendency of human settlements to aggre-
185 gate on continental edges and around biodiversity hotspots⁶⁶. Regardless of mechanism,
186 we predict that tropical hotspots of novel viral sharing will broadly coincide with high
187 population density areas in 2070, especially in the Sahel, the Ethiopian highlands and
188 the Rift Valley, India, eastern China, Indonesia, and the Philippines (Figure 4). Some

189 European population centers also land in these hotspots; recent emergences in this re-
190 gion like Usutu virus⁶⁷ highlight that these populations can still be vulnerable, despite
191 greater surveillance and healthcare access. If range-shifting mammals create ecological
192 release for undiscovered zoonoses, populations in these areas are likely to be the most
193 vulnerable.

194 Whereas most studies agree that climate change mitigation through reducing green-
195 house gas emissions will prevent extinctions and minimize harmful ecosystem impacts,
196 our results suggest that mitigation cannot reduce the likelihood of climate-driven viral
197 sharing. Instead, the mildest, slowest scenarios for biotic homogenization appear likely
198 to produce the most cross-species viral transmission: when climate velocity is lowest,
199 species can successfully track shifting climate optima, leading to more range expansion,
200 and more first encounters. Accounting for dispersal limits, species gained an average
201 of 75% range in the mildest pathway (RCP 2.6); in comparison, only 28% of species
202 experienced a net expansion in the most extreme pathway (RCP 8.5), for an average of
203 21% range gain. (ED Figure 3A) In fact, in the warmest scenario, up to 326 species lost
204 their entire range, with 168 attributable to dispersal limits alone. As a result, there were
205 5% fewer first encounters in RCP 8.5 compared to RCP 2.6, and unexpectedly, a 2%
206 reduction in the connectivity of the future global sharing network. (ED Figure 3B,D)
207 Overall, our results indicate that a mild perturbation of the climate system could create
208 thousands of new eco-evolutionary opportunities for viruses. We caution that this does
209 not imply a possible upside to catastrophic warming, which will be accompanied by mass
210 defaunation, devastating disease emergence, and unprecedented levels of human displace-
211 ment and global instability. Rather, our results highlight the urgency of better wildlife
212 surveillance systems and health infrastructure as a form of climate change adaptation,
213 even if mitigation efforts are successful and global temperatures stay under +2°C.

214 Our study establishes a macroecological link between climate change and cross-species
215 viral transmission. In practice, the patterns we describe are likely to be complicated by
216 several ecological factors, including the temperature sensitivity of viral host jumps⁶⁸;
217 the possibility that defaunation especially at low elevations might interact with disease
218 prevalence through biodiversity dilution and amplification effects, not captured by our
219 models⁶⁹; or temporal heterogeneity in exposure (hosts might exchange viruses in passing
220 but not overlap by 2070, especially in warmer scenarios). Future work can also expand
221 the scope of our findings to other host-parasite systems; our novel approach, which
222 combines viral sharing models with massive species distribution modeling pipelines, is
223 readily applied to other datasets. Birds have the best documented virome after mammals,
224 and changing migration targets in a warming world may be especially important targets
225 for prediction. With amphibians facing disproportionately high extinction rates due
226 to a global fungal panzootic, and emerging threats like ranavirus causing conservation

227 concern, viral exchange among amphibians may be especially important information for
228 conservation practitioners⁷⁰. Finally, marine mammals are an important target given
229 their exclusion here, especially after a recent study implicating reduced Arctic sea ice in
230 viral sharing among sympatric pinnipeds and sea otters—a result that may be the first
231 proof of concept for our proposed climate-disease link⁷¹.

232 Because hotspots of cross-species transmission are predictable, our study provides
233 the first template for how surveillance could target *future* hotspots of viral emergence in
234 wildlife. In the next decade alone, over a billion dollars could be spent on a proposed
235 global effort to identify zoonotic threats before they spread from wildlife reservoirs into
236 human populations². These efforts are being undertaken during the greatest period
237 of global ecological change recorded in human history, and in a practical sense, the
238 rapid movement of species and formation of no-analog communities poses an unexpected
239 challenge for virological research. While several studies have addressed how range shifts
240 in zoonotic reservoirs might expose humans to novel viruses, few have considered the fact
241 that most new exposures will be among mammal species. Tracking spillover into humans
242 is paramount, but so is tracking of viral sharing in wildlife, and targeting surveillance in
243 hotspots of future sharing may help researchers identify host jumps early on.

244 Methods

245 In this study, we develop global maps for terrestrial mammals that model their eco-
246 logical niche as a function of climate and habitat use. We project these into paired
247 climate-land use futures for 2070, with dispersal limitations set by biological constraints
248 for each species. We predict the probability of viral sharing among species pairs us-
249 ing a model of the mammalian viral sharing network that is trained on phylogenetic
250 relatedness and current geographic range overlaps. With that model, we map the pro-
251 jected hotspots of new viral sharing in different futures. All analysis code is available at
252 github.com/cjcarlson/iceberg.

253 Mapping species distributions

254 We developed species distribution models for a total of 3,870 species in this study, divided
255 into two modeling pipelines based on data availability (ED Figures 8, 9).

256 Data Collection

257 We scraped the Global Biodiversity Informatics Facility (GBIF) for mammal occurrence
258 records, and developed species distribution models for all 3,870 species with at least 3
259 unique terrestrial presence records on a 25 km by 25 km grid (one unique point per grid
260 cell). This grain was chosen based on the availability of future land use projections (see
261 below). Spatial and environmental outliers were removed based on Grubb outlier tests
262 (p-value of 1e-3)⁷².

263 Poisson point process models

264 For 3,088 species with at least 10 unique presence records, Poisson point process models
265 (closely related to Maxent) were fit using regularized downweighted Poisson regression⁷³
266 with 20,000 background points fit with the R package `glmnet`^{74,75,74}. The spatial do-
267 main of predictions was chosen based on the continent(s) where a species occurred in
268 their IUCN range map. We trained species distribution models on current climate data
269 using the WorldClim 2 data set⁷⁶, using mean annual temperature, mean diurnal temper-
270 ature range, annual precipitation, precipitation seasonality, and precipitation in warmest
271 quarter/ (precipitation in warmest quarter + precipitation in coldest quarter). These
272 predictors were chosen based on having global correlations <0.7 among one another.
273 These candidate predictors were further filtered on a species-by-species basis, retaining
274 the maximum number of predictors with correlation <0.7 within the domain where the
275 model was fit.

Models were fit with 5-fold cross validation, where folds were assigned based on spatial clusters to remove the influence of spatial autocorrelation on cross-validation performance statistics. Linear (all species), quadratic (species with >100 records), and product (species with >200 records) features were used. The regularization parameter was determined based on 5-fold cross-validation with each fold, choosing a value 1 standard deviation below the minimum deviance⁷⁷. This resulted in five models per species which were then combined in an unweighted ensemble. Continuous predictions of the ensemble were converted to binary presence/absence predictions by choosing a threshold based on the 5th percentile of the ensemble predictions at training presence locations.

When models were projected into the future, we limited extrapolation to 1 standard deviation beyond the data range of presence locations for each predictor. This decision balances a small amount of extrapolation based on patterns in a species niche with limiting the influence of monotonically increasing marginal responses, which can lead to statistically unsupported (and likely biologically unrealistic) responses to climate.

Range bagging models

For an additional 783 rare species (3 to 9 unique points on the 25 km grid), we produced species distribution models with a simpler range bagging algorithm, a stochastic hull-based method that can estimate climate niches from an ensemble of underfit models^{78,79}, and is therefore well suited for smaller datasets. From the full collection of presence observations and environmental variables range-bagging proceeds by randomly sampling a subset of presences (proportion p) and a subset of environmental variables (d). From these, a convex hull around the subset of points is generated in environmental space. The hull is then projected onto the landscape with a location considered part of the species range if its environmental conditions fall within the estimate hull. The subsampling is replicated N times, generating N ‘votes’ for each cell on the landscape. One can then choose a threshold for the number of votes required to consider the cell as part of the species’ range to generate the binary map used in our downstream analyses. Based on general guidelines in⁷⁸ we chose $p = 0.33$, $d = 2$, and $N = 100$. We then chose the voting threshold to be 0.165 ($=0.33/2$) because this implies that the cell is part of the range at least half the time for each subsample. Upon visual inspection, this generally lead to predictions that were very conservative about inferring that unsampled locations were part of a species distribution. The same environmental predictors and ecoregion-based domain selection rules were used for range bagging models as were used for the point process models discussed above. This hull-based approach is particularly valuable for poorly sampled species which may suffer from sampling bias because bias within niche limits has little effect on range estimates.

312 **Model validation**

313 PPM models performed well, with a mean test AUC under 5 fold cross-validation (using
314 spatial clustering to reduce inflation) of 0.77 (s.d. 0.13). The mean partial AUC eval-
315 uated over a range of sensitivity relevant for SDM (0.8-0.95) was 0.8 (s.d. 0.08). The
316 mean sensitivity of binary maps used to assess range overlap (based on the 5% training
317 threshold used to make a binary map) was 0.89 (s.d. 0.08). Range bagging models were
318 difficult to meaningfully evaluate because they were based on extremely small sample
319 sizes (3-9). The mean training AUC (we did not perform cross-validation due to small
320 sample size) was 0.96 (s.d. 0.09). The binary maps had perfect sensitivity (1) because
321 the threshold used to make them was chosen sufficiently low to include the handful of
322 known presences for each species. One way to assess how much we inferred the range
323 for these species is to quantify how much of the range was estimated based on our mod-
324 els, based on the number of (10km) cells predicted to be part of the species range even
325 when it was not observed there. The mean number of cells inferred to contain a presence
326 was 253 (s.d. 448); however, the distribution is highly right skewed with a median of
327 94. This indicates that the range bagging models were typically relatively conservative
328 about inferring ranges for poorly sampled species.

329 **Habitat range and land use**

330 We used the Land Use Harmonization version 2.0 (LUH2) gridded dataset to capture
331 global patterns in land cover for the present and future⁸⁰. These data are derived from
332 an integrative assessment model that pairs land use scenarios with representative con-
333 centration pathways. For the current models, we used historical land-use maps (LUH2
334 v2h), which are intended for use over the period 850 to 2015 C.E.⁸¹. To capture species'
335 habitat preference, we collated data for all 3,870 mammal species from the IUCN Habitat
336 Classification Scheme version 3.1. We then mapped 104 unique IUCN habitat classifi-
337 cations onto the eight land use types present in the LUH dataset. For 962 species, no
338 habitat data was available, or no correspondence existed between a land type in the IUCN
339 scheme and our land use data; for these species, land use filters were not used. Filtering
340 based on habitat was done conservatively: species were allowed in current and future
341 ranges to exist in a pixel if any non-zero percent was assigned a suitable habitat type;
342 almost all pixels contain multiple habitats. In some scenarios, human settlements cover
343 at least some of a pixel for most of the world, allowing synanthropic species to persist
344 throughout most of their climatically-suitable range. For those with habitat data, the
345 average reduction in range from habitat filtering was 7.6% of pixels.

346 Refining the dataset

347 Of the 3,870 species for which we generated distribution models, 103 were aquatic mam-
348 mals (cetaceans, sirenians, pinnipeds, and sea otters), and 382 were not present in the
349 mammalian supertree that we used for phylogenetic data⁸². These species were ex-
350 cluded. Aquatic species were removed using a two-filter approach, by cross-referencing
351 with Pantheria⁸³. These results were verified by checking no species only had marine
352 habitat use types (see ‘Habitat range and land use’). We also excluded 246 monotremes
353 and marsupials because the shape of the supertree prevented us from fitting satisfactory
354 GAMM smooths to the phylogeny effect, leaving 3,139 non-marine Eutherian mammals
355 with associated phylogenetic data.

356 Predicting future species distributions

357 We modeled a total of 16 possible futures, produced by four paired climate-land use
358 change pathways and two optional filters on species ranges (habitat preferences and dis-
359 persal limits). The full matrix of possible scenarios captures a combination of scenario
360 uncertainty about global change and epistemological uncertainty about how best to pre-
361 dict species’ range shifts. By filtering possible future distributions based on climate, land
362 use, and dispersal constraints, we aimed to maximize realism; our predictions were con-
363 gruent with extensive prior literature on climate- and land use-driven range loss^{84,85,86}.

364 Climate and land use futures

365 Species distribution models were projected for 2070 using climate models, and then spa-
366 tially filtered by land use projections. Climate and land-use future pathways are coupled
367 by the Land Use Harmonization 2.0 integrative assessment model^{87,81}, such that every
368 future has a representative concentration pathway (RCP) for climate and a shared so-
369 cioeconomic pathway (SSP) for land use. For climate we used the HadGEM2 Earth
370 System Model projections for 2070, with the four standard RCPs: 2.6, 4.5, 6.0, and 8.5
371 (where the values represent added W/m² of solar radiation by the end of the century
372 due to greenhouse gas emissions). These were respectively paired with SSP 1 (“Sustain-
373 ability”); SSP 2 (“Middle of the Road”); SSP 4 (“Inequality”); and SSP 5 (“Fossil-Fueled
374 Development”).

375 These pairings can be thought of as a gradient of scenarios of global change with differ-
376 ent levels of severity and sustainability. Not all scenarios are possible; the four we selected
377 are drawn as some of the most representative from an underlying “scenario matrix” that
378 includes every possible parameterization, some of which are entirely incompatible⁸⁸. (For
379 example, in the vast majority of integrative assessment models, decarbonization cannot

380 be achieved fast enough in the SSP 5 scenario to achieve RCP 2.6.) As pairs, SSP-RCP
381 narratives can be merged to create overall narratives about how global change could look.
382 For example, in SSP 1-RCP 2.6, a global transition to renewable energy and mitigation of
383 climate change corresponds to sustainable population growth and economic development.
384 Driven by international cooperation on climate agreements, afforestation and bioenergy
385 cropland become major land uses, while tropical deforestation is strongly reduced. In
386 contrast, in SSP 5-RCP 8.5, business-as-usual development leads to catastrophic levels
387 of warming, unsustainable population growth and increasing poverty, and massive land
388 conversion^{89,90}.

389 **Limiting dispersal capacity**

390 Not all species can disperse to all environments, and not all species have equal disper-
391 sal capacity—in ways likely to covary with viral sharing properties. We follow a rule
392 proposed by Schloss *et al.*³¹, who described an approximate formula for mammal range
393 shift capacity based on body mass and trophic position. For carnivores, the maximum
394 distance traveled in a generation is given as $D = 40.7M^{0.81}$, where D is distance in kilo-
395 meters and M is body mass in kilograms. For herbivores and omnivores, the maximum
396 is estimated as $D = 3.31M^{0.65}$.

397 We used mammalian diet data from the EltonTraits database⁹¹, and used the same
398 cutoff as Schloss to identify carnivores as any species with 10% or less plants in their
399 diet. We used body mass data from EltonTraits in the Schloss formula to estimate
400 maximum generational dispersal, and converted estimates to annual maximum dispersal
401 rates by dividing by generation length, as previously estimated by another comprehensive
402 mammal dataset⁹². We multiply by 50 years and use the resulting distance as a buffer
403 around the original range map, and constrain possible range shifts within that buffer. For
404 420 species with missing data in one of the required sources, we interpolated dispersal
405 distance based on the closest relative in our supertree with a dispersal velocity estimate.

406 Qualified by the downsides of assuming full dispersal⁹³, we excluded bats from the
407 assumed scaling of dispersal limitations. The original study by Schloss *et al.*³¹ chose
408 to omit bats entirely, and subsequent work has not proposed any alternative formula.
409 Moreover, the Schloss formula performs notably poorly for bats: for example, it would
410 assign the largest bat in our study, the Indian flying fox (*Pteropus giganteus*), a disper-
411 sal capacity lower than that of the gray dwarf hamster (*Cricetus migratorius*). Bats
412 were instead given full dispersal in all scenarios: given significant evidence that some bat
413 species regularly cover continental distances^{43,44}, and that isolation by distance is uncom-
414 mon within many bats' ranges⁴⁶, we felt this was a defensible assumption for modeling
415 purposes. Moving forward, the rapid range shifts already observed in many bat species

416 (see main text) could provide an empirical reference point to fit a new allometric scaling
417 curve (after standardizing those results for the studies' many different methodologies).
418 A different set of functional traits likely govern the scaling of bat dispersal, chiefly the
419 aspect ratio (length:width) of wings, which is a strong predictor of population genetic
420 differentiation⁴⁶. Migratory status would also be important to include as a predictor
421 although here, we exclude information on long-distance migration for all species (due to
422 a lack of any real framework for adding that information to species distribution models
423 in the literature).

424 **Explaining spatial patterns**

425 To explore the geography of novel assemblages, we used linear models which predicted the
426 number of first encounters (novel overlap of species pairs) at the 25km level ($N = 258,539$
427 grid cells). Explanatory variables included: richness (number of species inhabiting the
428 grid cell in our predicted current ranges for the given scenario); elevation in meters (de-
429 rived from the US Geological Service Global Multi-resolution Terrain Elevation Data
430 2010 dataset); and the predominant land cover type for the grid cell. We simplified
431 the classification scheme for land use types into five categories for these models (human
432 settlement, cropland, rangeland and pasture, forest, and unforested wildland), and as-
433 signed pixels a single land use type based on the maximum probability from the land
434 use scenarios. We fitted a model for each scenario and pair of biological assumptions;
435 because of the large effect bats had on the overall pattern, we retrained these models on
436 subsets of encounters with and without a bat species involved. To help model fitting, we
437 log(x+1)-transformed the response variable (number of overlaps in the pixel) and both
438 continuous explanatory variables (meters of elevation above the lowest point and species
439 richness). Because some elevation values were lower than 0 (i.e., below sea level), we
440 treated elevation as meters above the lowest terrestrial point rather than meters above
441 sea level to allow us to log-transform the data.

442 **Viral sharing models**

443 **Generalized Additive Mixed Models**

444 We used a previously-published model of the phylogeography of viral sharing patterns
445 to make predictions of future viral sharing¹⁷. This model was based on an analysis of
446 510 viruses shared between 682 mammal species³, and predicted the probability that a
447 pair of mammal species will share a virus given their geographic range overlap and phy-
448 logenetic relatedness. The original study uncovered strong, nonlinear effects of spatial
449 overlap and phylogenetic similarity in determining viral sharing probability, and simu-

450 lating the unobserved global network using these effect estimates capitulated multiple
451 macroecological patterns of viral sharing.

452 In the original study, a Generalized Additive Mixed Model (GAMM) was used to
453 predict virus sharing as a binary variable, based on (1) geographic range overlap; (2) phy-
454 logenetic similarity; and (3) species identity as a multi-membership random effect. The
455 phylogeographic explanatory variables were obtained from two broadly available, low-
456 resolution data sources: pairwise phylogenetic similarity was derived from a mammalian
457 supertree previously modified for host-pathogen studies^{82,3}, with similarity defined as
458 the inverse of the cumulative branch length between two species, scaled to between 0
459 and 1. Geographic overlap was defined as the area of overlap between two species' IUCN
460 range maps, divided by their cumulative range size⁹⁴.

461 We first retrained the GAMMs from¹⁷ on the pairwise overlap matrix of species distri-
462 bution models generated for this study, so that present predictions would be comparable
463 with future distributions. Of the 3,139 species in our reduced dataset, 544 had viral
464 records in our viral sharing dataset and shared with at least one other mammal, and
465 were used to retrain the GAMM from¹⁷. To check the performance of the GAMM, we
466 predicted sharing patterns with a) only random effects, b) only fixed effects, and c) with
467 both. Although species-level random effects had a mean effect of ~ 0, excluding them en-
468 tirely resulted in a substantial underestimation of the mean viral sharing rates across the
469 network (mean sharing ≈ 0.02 compared to ≈ 0.06). Therefore to ensure that the model
470 recapitulated traits of the observed network, we simulated 1,000 binary sharing networks
471 when predicting with only fixed effects, randomly drawing species-level random effects
472 in each iteration. The mean sharing value across these iterations closely approximated
473 observed sharing probability (~ 0.06).

474 **Model validation and limits**

475 Compared to the current viral sharing matrix, the model performs well with only fixed
476 effects ($AUC = 0.80$) and extremely well with both fixed and random effects ($AUC =$
477 0.93). The model explained a very similar proportion of the deviance in viral sharing to
478 that in Albery *et al.*¹⁷ (44.5% and 44.8% respectively).

479 In practice, several unpredictable but confounding factors could affect the reliability
480 of this model as a forecasting tool, including temperature sensitivity of viral evolution in
481 host jumps⁶⁸, or increased susceptibility of animals with poorer health in lower-quality
482 habitat or unfavorable climates. Moreover, once viruses can produce an infection, their
483 ability to transmit *within* a new species is an evolutionary race between mutation and
484 recombination rates in viral genomes, host innate and adaptive immunity, virulence-
485 related mortality, and legacy constraints of coevolution with prior hosts and vectors^{60,61}.

486 But data cataloging these precise factors are hardly comprehensive for the hundreds of
487 zoonotic viruses, let alone for the thousands of undescribed viruses in wildlife. Moreover,
488 horizontal transmission is not necessary for spillover potential to be considered significant;
489 for example, viruses like rabies or West Nile virus are not transmitted within human
490 populations but humans are still noteworthy hosts.

491 **Mapping opportunities for sharing**

492 We used the GAMM effect estimates to predict viral sharing patterns across the 3,139
493 mammals with associated geographic range and phylogenetic data, for both the present
494 and future scenarios. By comparing current and future sharing probabilities for each of
495 the four global change scenarios, we estimated which geographic and taxonomic patterns
496 of viral sharing would likely emerge. We separately examined patterns of richness, pat-
497 tterns of sharing probability, and their change (i.e., future sharing probability - current
498 sharing probability, giving the expected probability of a novel sharing event).

499 A subset of the mammals in our dataset were predicted to encounter each other for the
500 first time during range shifts. For each of these pairwise first encounters, we extracted the
501 area of overlap in every future scenario, and assigned each overlap a probability of sharing
502 from the mean GAMM predictions and mapped the mean and cumulative probability of
503 a new sharing event happening in a given geographic pixel.

504 **Case study on Zaire ebolavirus**

505 For a case study in possible significant cross-species transmission, we compiled a list
506 of known hosts of Zaire ebolavirus (ZEBOV), a zoonosis with high host breadth that
507 has been known to cause wildlife die-offs, but has no known definitive reservoir. Hosts
508 were taken from two sources: the training dataset on host-virus associations³, and an
509 additional dataset of filovirus testing in bats³⁰. In the latter case, any bats that have
510 been reported antibody positive or PCR-positive for ZEBOV were included. A total
511 of 13 current “known hosts” in Africa were used to predict current possible hosts, and
512 first encounters in all scenarios. We restricted our analysis to Africa because there is
513 no published evidence that Zaire ebolavirus actively circulates outside Africa; although
514 some bat species outside Africa have tested positive for antibodies to ZEBOV, this is
515 likely due to cross-reactivity with other undiscovered filoviruses^{95,96,30}.

516 **Overlap with human populations**

517 To examine the possibility that hotspots of cross-species transmission would overlap with
518 human populations, we used SEDAC’s global population projections version 1.0 for the

519 year 2070⁹⁷. We aggregated these to native resolution, for each of the four SSP paired
520 with the native RCP/SSP pairing for the species distribution models. In Figure 4 we
521 present the population projections for SSP 1, which pairs with RCP 2.6.

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532 Author Contributions

533 CJC and GFA conceived the study. CM, CJC, and CHT developed species distribution
534 models; GFA, EAE, KJO, and NR developed the generalized additive models. CJC, GFA,
535 and CMZ integrated the predictions of species distributions and viral sharing patterns
536 and designed visualizations. All authors contributed to the writing of the manuscript.

537

Figures

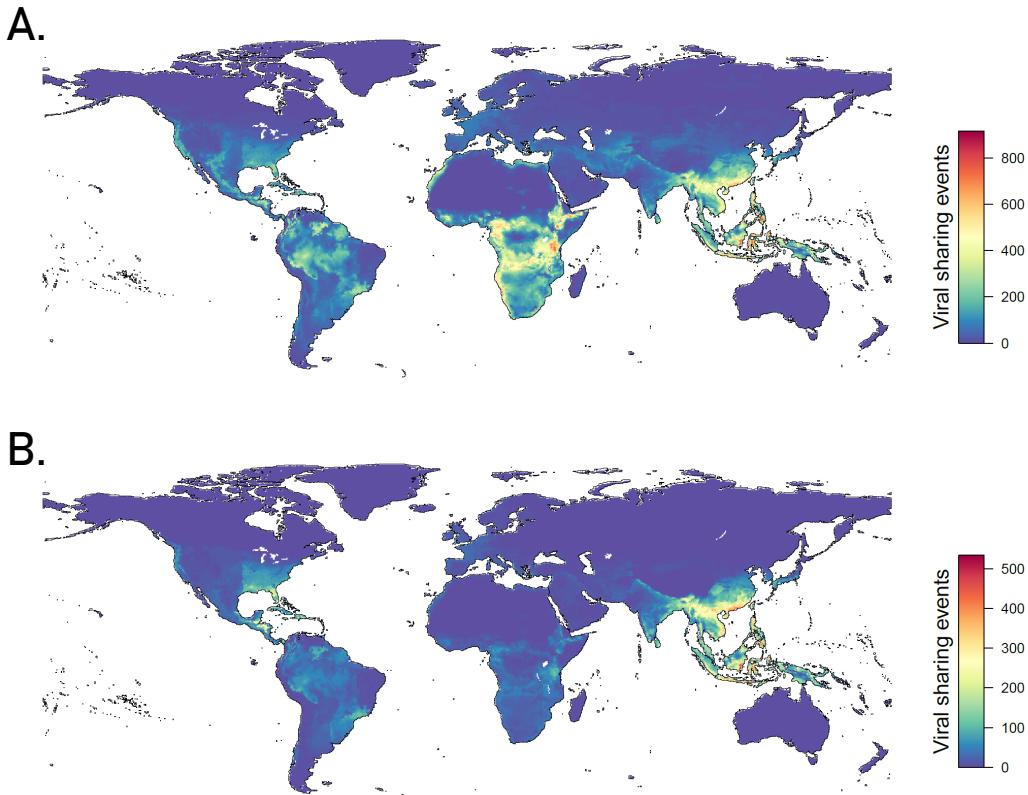


Figure 1: Climate change will drive novel viral sharing among mammal species.
The projected number of novel viral sharing events among mammal species in 2070 based on host species geographic range shifts from climate change (RCP 2.6) and land-use change (SSP 1), without dispersal limits (A) and with dispersal limitation (B).

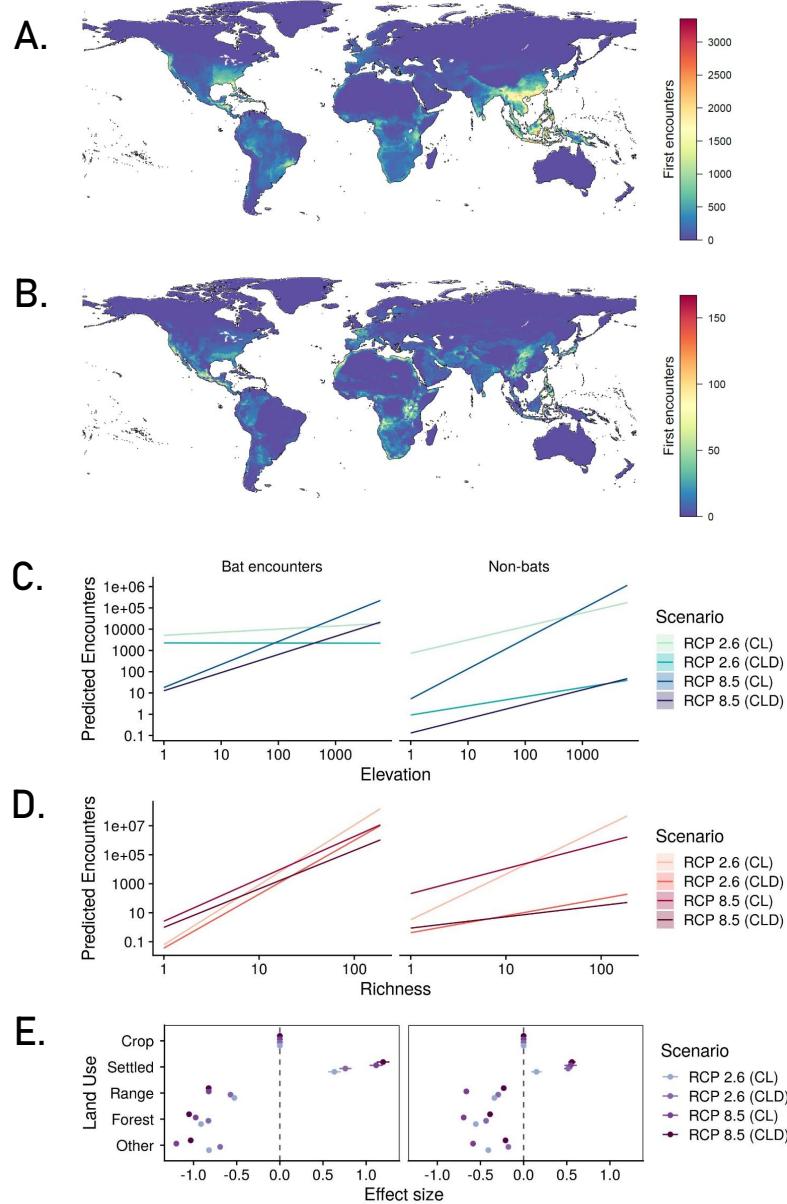


Figure 2: Bats disproportionately drive future novel viral sharing. The spatial pattern of first encounters differs among range-shifting mammal pairs including bat-bat and bat-nonbat encounters (A) and only encounters among non-bats (B). Using a linear model, we show that elevation (C), species richness (D), and land use (E) together explain 57.7% of deviance in new overlaps for bats, and 25.8% for non-bats. Slopes for the elevation effect were generally steeply positive: a \log_{10} -increase in elevation was associated with between a 0.4-1.41 \log_{10} -increase in first encounters.

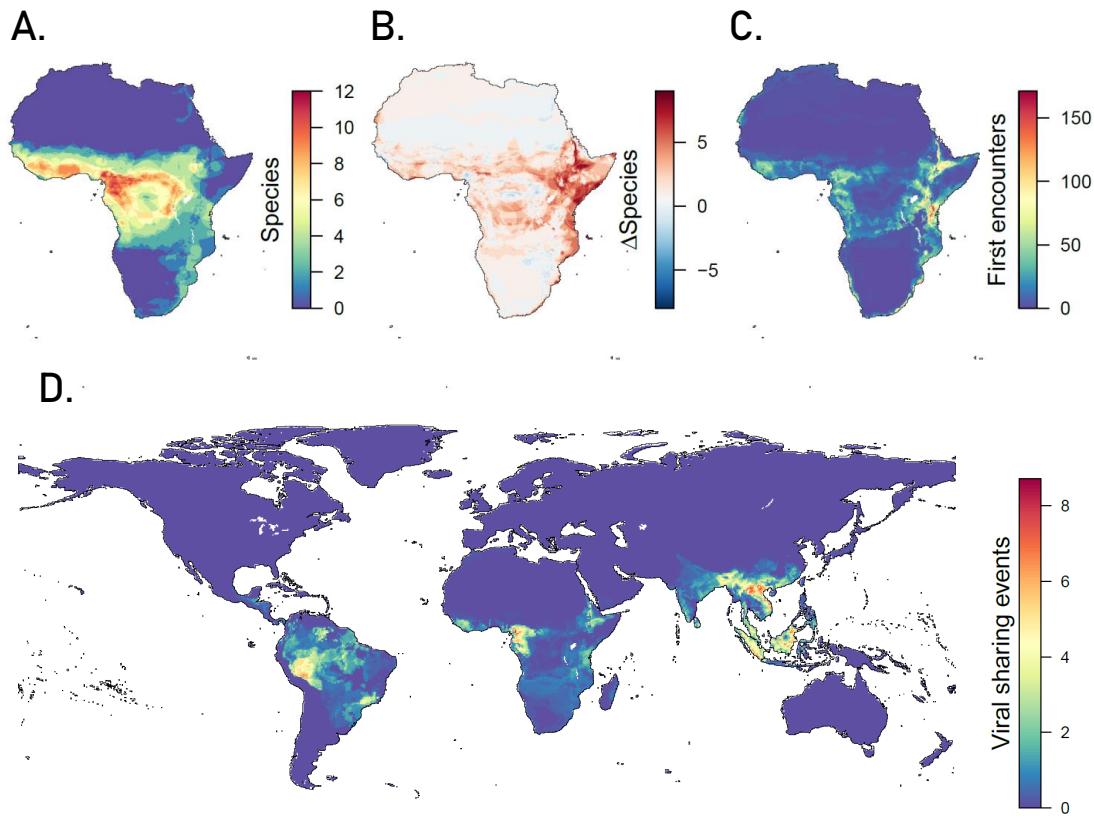


Figure 3: **Range expansions will expose naive hosts to zoonotic reservoirs.** (A) The predicted distribution of known African hosts of Zaire ebolavirus. (B) The change in richness of these hosts as a result of range shifts. (C) Projected first encounters with non-Ebola hosts. (D) Bat-primate first encounters are projected to occur globally, producing novel sharing events.

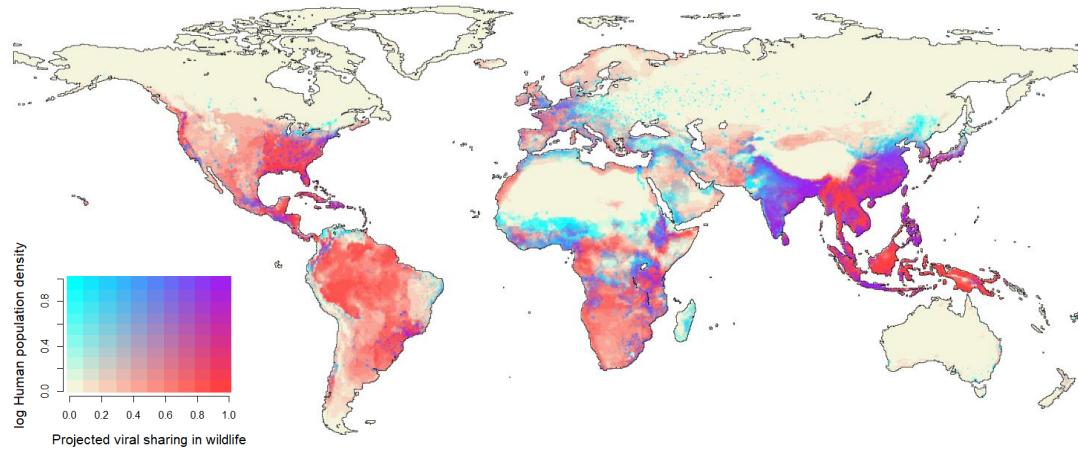
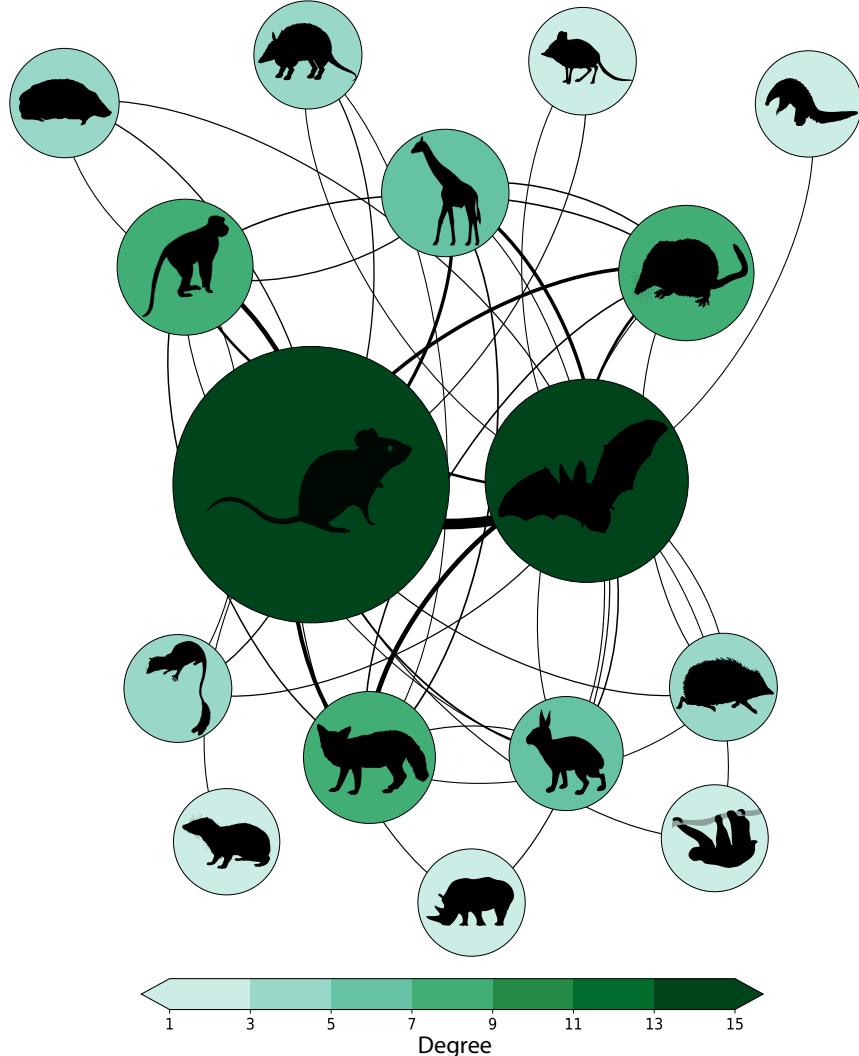
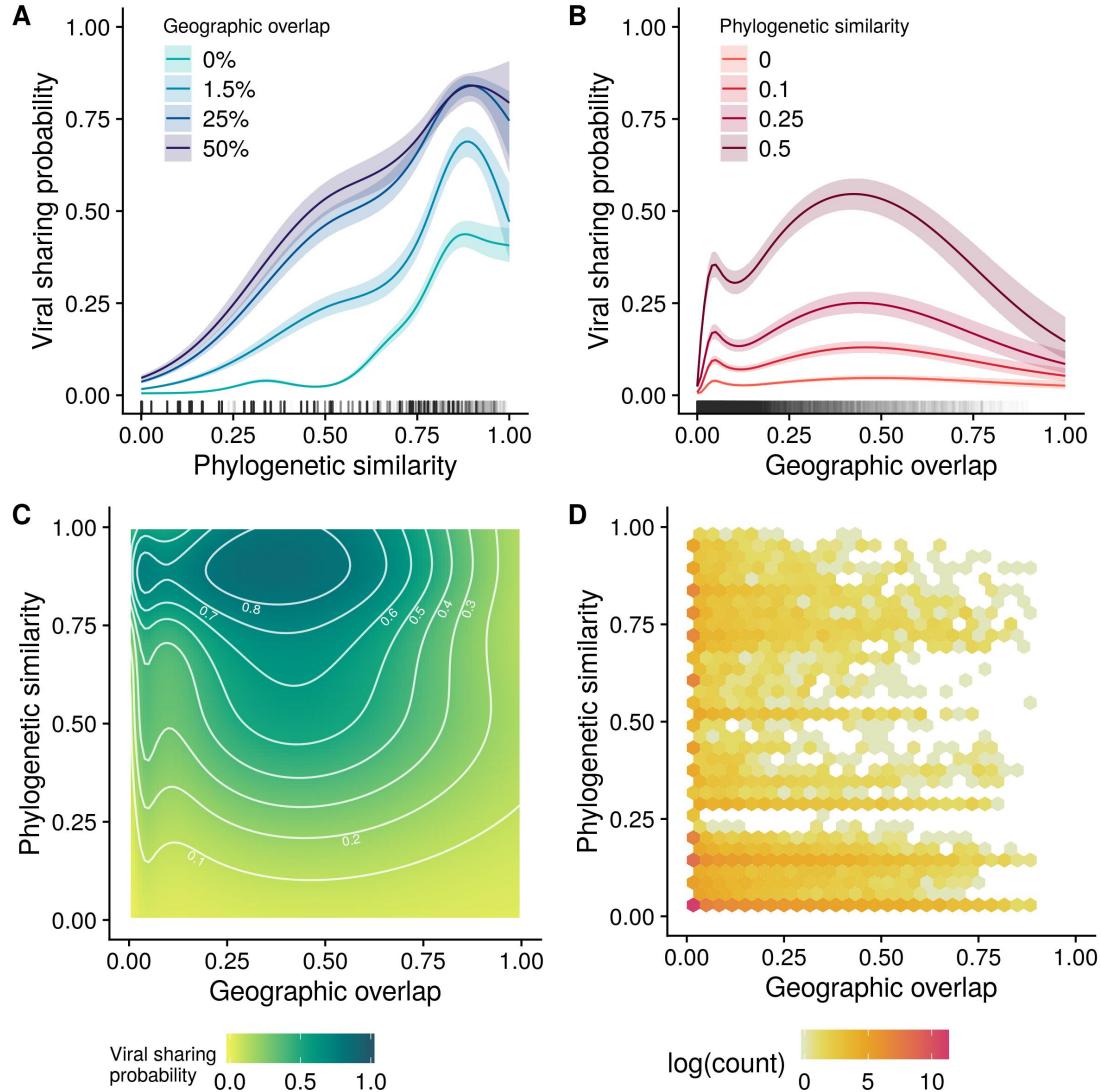


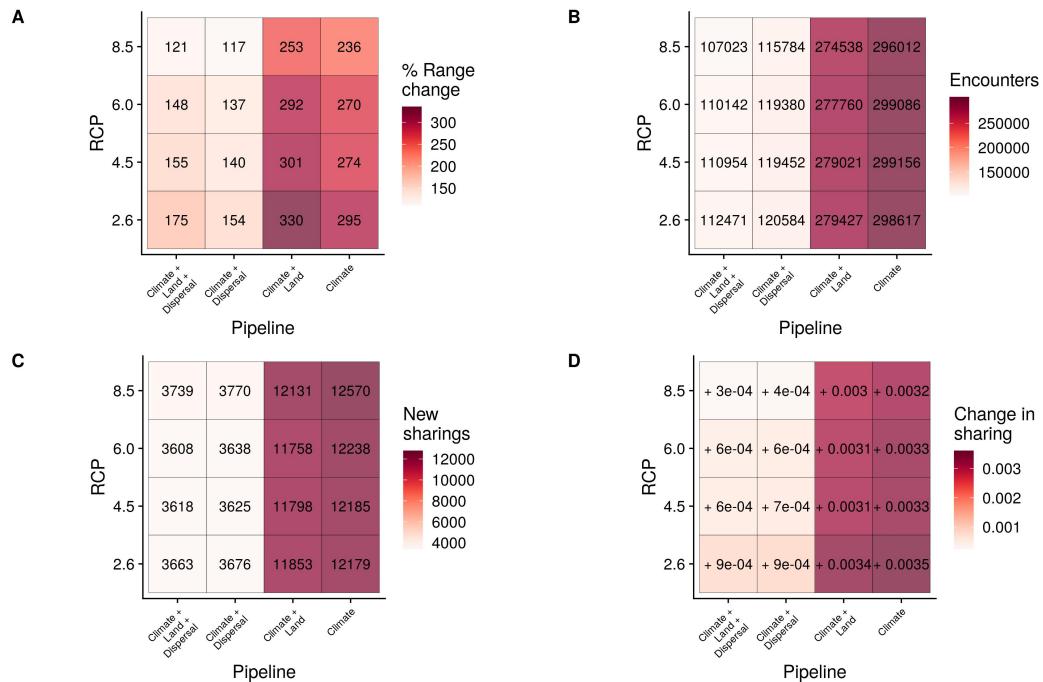
Figure 4: Novel viral sharing events coincide with population centers. In 2070 (RCP 2.6; climate only), human population centers in equatorial Africa, south China and southeast Asia will overlap with projected hotspots of cross-species viral transmission in wildlife. (Both variables are linearly rescaled to 0 to 1.)



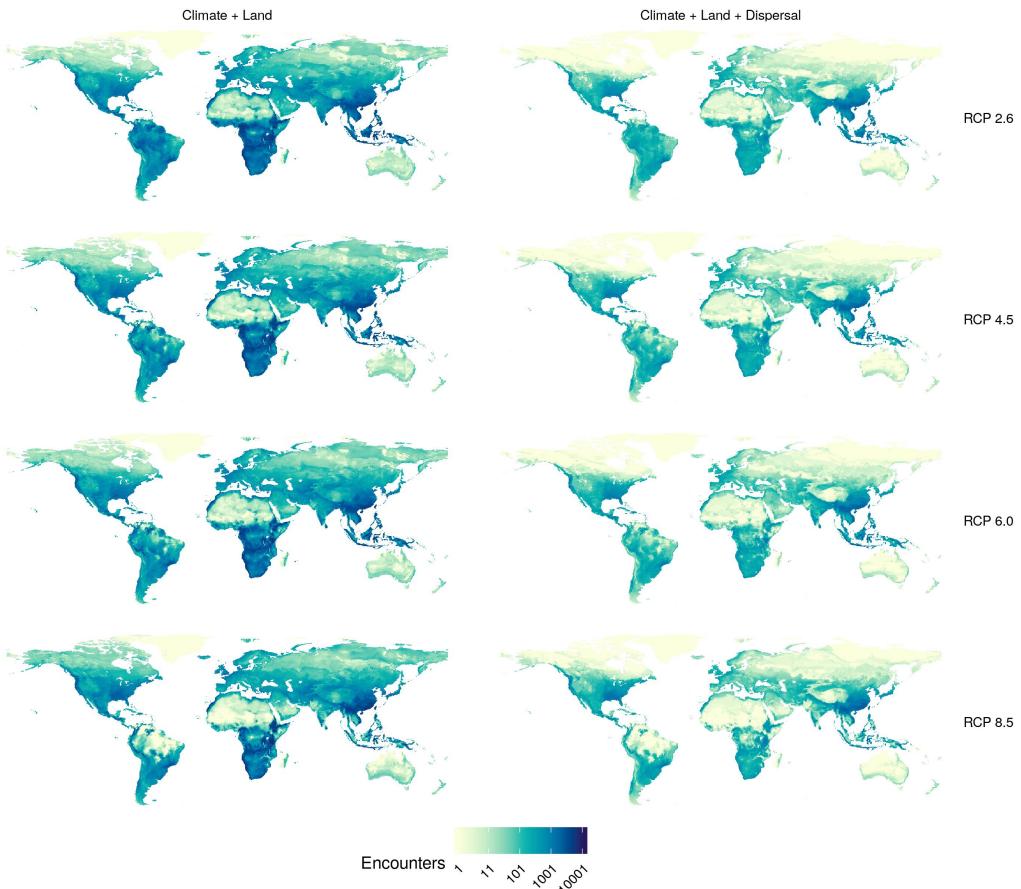
Extended Data Figure 1: **The mammal-virus network.** The present-day viral sharing network by mammal order inferred from modeled pairwise predictions of viral sharing probabilities. Edge width denotes the expected number of shared viruses (the sum of pairwise species-species viral sharing probabilities), with most sharing existing among the most speciose and closely-related groups. Edges shown in the network are the top 25% of links. Nodes are sized by total number of species in that order in the host-virus association dataset, color is scaled by degree.



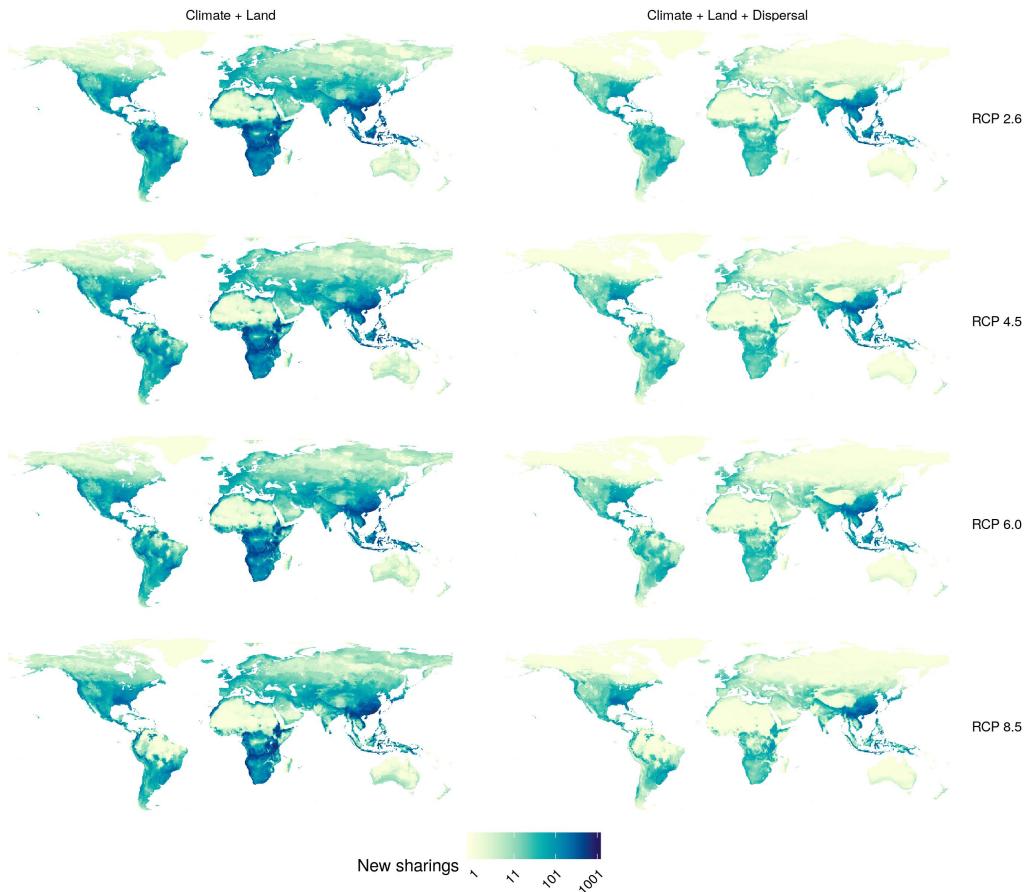
Extended Data Figure 2: **Predicted phylogeographic structure of viral sharing.** Phylogeographic prediction of viral sharing using a generalized additive mixed model. Viral sharing increases as a function of phylogenetic similarity (A) and geographic overlap (B), fit together as a tensor interaction (C). White contour lines denote 10% increments of sharing probability. Declines at high values of overlap may be an artefact of model structure and low sampling in the upper levels of geographic overlap, shown in a hexagonal bin chart for raw data (D).



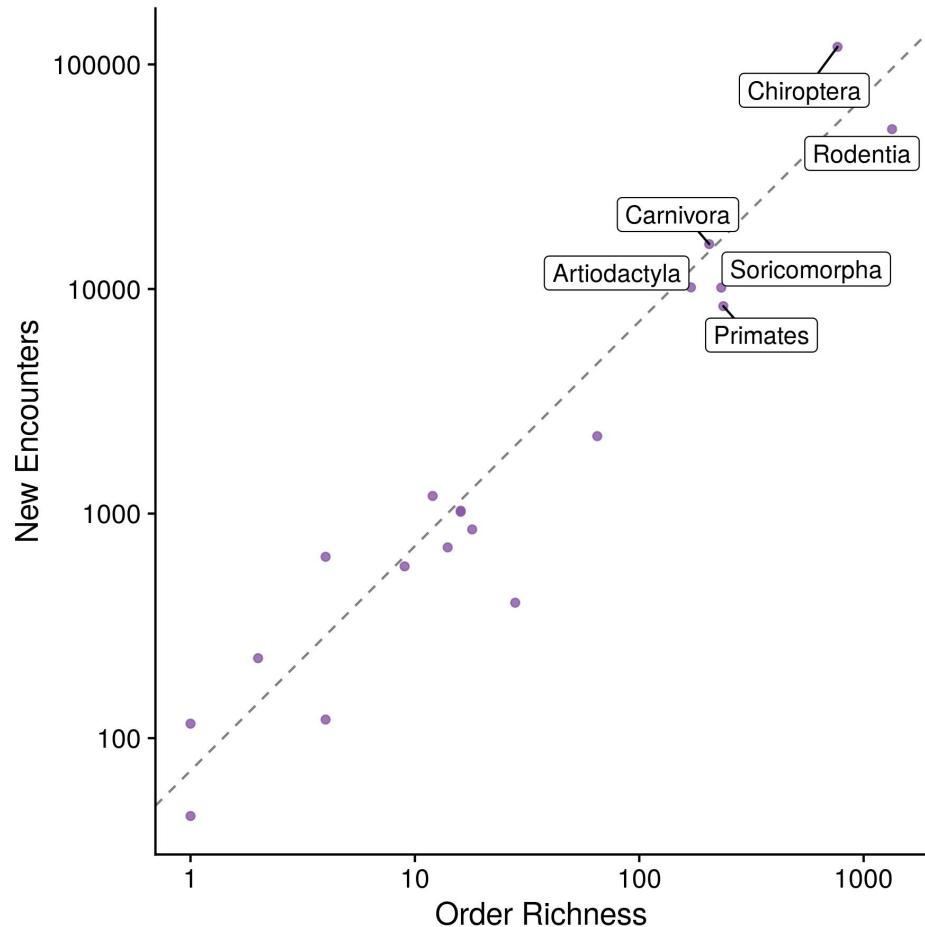
Extended Data Figure 3: **Outcomes by model formulation and climate change scenario.** Heatmaps displaying predicted changes across model formulations. (A) Range expansions were highest in non-dispersal-limited scenarios and in milder RCPs. (B) The number of predicted first encounters was higher in non-dispersal-limited scenarios and in milder RCPs. (C) The number of expected new viral sharing events was higher in non-dispersal-limited scenarios and in more severe RCPs. (D) The overall change in sharing probability (connectance) across the viral sharing network between the present day and the future scenarios; absolute change is minimal but positive across all scenarios, being greatest in non-dispersal-limited scenarios and in milder RCPs.



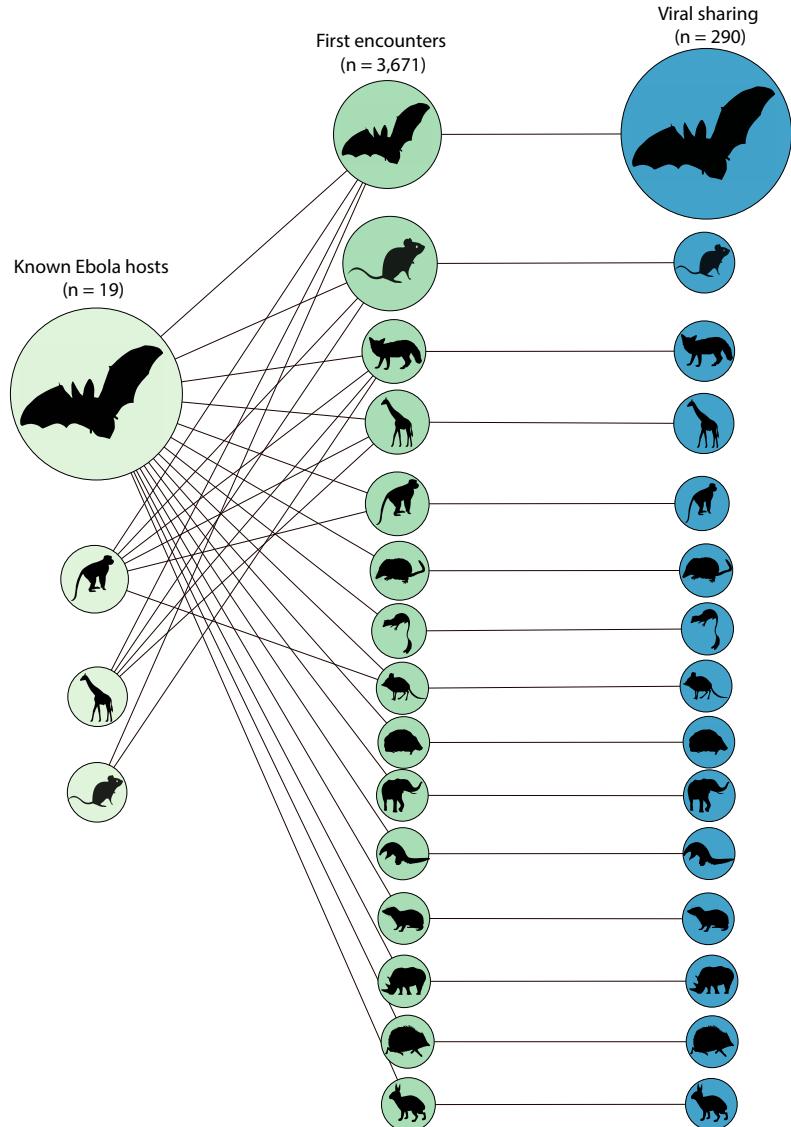
Extended Data Figure 4: **Geographic distribution of first encounters.** Predictions were carried out for four representative concentration pathways (RCPs), accounting for climate change and land use change, without (left) and with dispersal limits (right). Darker colours correspond to greater numbers of first encounters in the pixel.



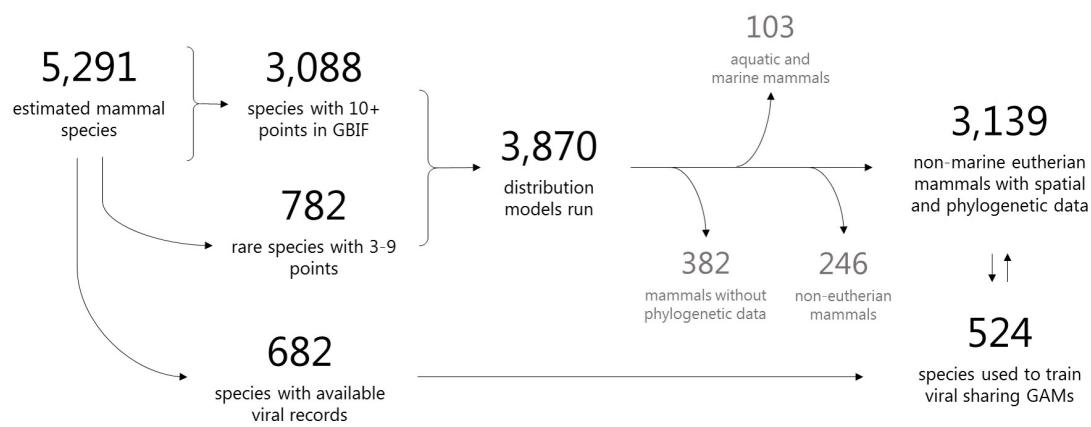
Extended Data Figure 5: Geographic distribution of expected viral sharing events from first encounters. Predictions were carried out for future distributions for four representative concentration pathways (RCPs), accounting for climate change and land use change, without (left) and with dispersal limits (right). Darker colours correspond to greater numbers of new viral sharing events in the pixel. Probability of new viral sharing was calculated by subtracting the species pair's present sharing probability from their sharing probability that our viral sharing GAMMs predicted. This probability was projected across the species pair's range intersection, and then summed across all novel species pairs in each pixel.



Extended Data Figure 6: **Order-level heterogeneity in first encounters.** Dispersal stratifies the number of first encounters (RCP 2.6 with all range filters), where some orders have more than expected at random, based on the mean number of first encounters and order size (line).



Extended Data Figure 7: **Projected viral sharing from suspected Ebola reservoirs is dominated by bats.** Node size is proportional to (left) the number of suspected Ebola host species in each order, which connect to (middle) first encounters with potentially naive host species; and (right) the number of projected viral sharing events in each receiving group. (Node size denotes proportions out of 100% within each column total.) While Ebola hosts will encounter a much wider taxonomic range of mammal groups than current reservoirs, the vast majority of viral sharing will occur disproportionately in bats.



Extended Data Figure 8: **Data processing workflow.** Summary of species inclusion across the modeling pipeline for species distributions and viral sharing models. The final analyses in the main text use 3,139 species of Eutherian mammals across all scenarios.



Extended Data Figure 9: Species distribution modeling workflow for a single species. A focal species (the European red deer, *Cervus elaphus*) is displayed as an illustrative example. The present day climate prediction (top left) was clipped to the same continent according to the IUCN distribution (top right). This was then clipped according to *Cervus elaphus* land use (second row, left). The known dispersal distance of the red deer was used to buffer the climate distribution (second row, right). The future distribution predictions (RCP 2.6 shown as an example) are displayed in the bottom four panels, for each of the four pipelines: only climate (third row, left); climate + dispersal clip (third row, right); climate + land use clip (bottom row, left) and climate + land use + dispersal clip (bottom row, right). The four distributions clearly display the limiting effect of the dispersal filter (bottom right panels) in reducing the probability of novel species interactions (bottom left panels). The land use clip had little effect on this species as the entire distribution area was habitable for the red deer.

538

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