

39 **Summary**

40 *Bacillus anthracis* is a spore-forming, Gram-positive bacterium responsible for anthrax, an acute
41 and commonly lethal infection that most significantly affects grazing livestock, wild ungulates
42 and other herbivorous mammals, but also poses a serious threat to human health^{1,2}. The
43 geographic extent of *B. anthracis* endemism is still poorly understood, despite multi-decade
44 research on anthrax epizootic and epidemic dynamics around the world^{3,4}. Several biogeographic
45 studies have focused on modeling environmental suitability for anthrax at local or national
46 scales⁵⁻⁹, but many countries have limited or inadequate surveillance systems, even within
47 known endemic regions. Here we compile an extensive global occurrence dataset for *B.*
48 *anthracis*, drawing on confirmed human, livestock, and wildlife anthrax outbreaks. With these
49 records, we use boosted regression trees^{10,11} to produce the first map of the global distribution of
50 *B. anthracis* as a proxy for anthrax risk. Variable contributions to the model support pre-existing
51 hypotheses that environmental suitability for *B. anthracis* depends most strongly on soil
52 characteristics such as pH that affect spore persistence, and the extent of seasonal fluctuations in
53 vegetation, which plays a key role in transmission for herbivores^{12,13}. We apply the global model
54 to estimate that 1.83 billion people (95% credible interval: 0.59—4.16 billion) live within
55 regions of anthrax risk, but most of that population faces little occupational exposure to anthrax.
56 More informatively, a global total of 63.8 million rural poor livestock keepers (95% CI: 17.5—
57 168.6 million) and 1.1 billion livestock (95% CI: 0.4—2.3 billion) live within vulnerable regions.
58 Human risk is concentrated in rural areas, and human and livestock vulnerability are both
59 concentrated in rainfed systems throughout arid and temperate land across Eurasia, Africa, and
60 North America. We conclude by mapping where anthrax risk overlaps with vulnerable wild
61 ungulate populations, and therefore could disrupt sensitive conservation efforts for species like
62 bison, pronghorn, and saiga that coincide with anthrax-prone, mixed-agricultural landscapes.

63 Anthrax is a zoonotic disease caused by the Gram-positive bacterium *Bacillus anthracis*, a
64 generalist soil-transmitted pathogen found on every inhabited continent¹⁴, and several islands
65 including Haiti and parts of the Philippines and Indonesia. Worldwide, an estimated 20,000 to
66 100,000 cases of anthrax occur annually, mostly in poor rural areas¹⁵. In clinical presentations of
67 anthrax, case fatality rates are a function of exposure pathway. Respiratory exposure from spore
68 inhalation is important in the context of bioterrorism, but is highly uncommon, and accounts for a
69 negligible fraction of the global burden of anthrax cases. Cutaneous exposure to *B. anthracis*
70 accounts for the majority of human cases worldwide, and typically presents with low mortality;
71 gastrointestinal exposure accounts for the remainder and presents with intermediate to high
72 fatality rates. Cutaneous and gastrointestinal cases of anthrax are most commonly caused by
73 handling and slaughtering infected livestock, or butchering and eating contaminated meat;
74 untreated gastrointestinal cases likely account for most human mortality from anthrax.¹⁴⁻¹⁶

75 Human mortality from anthrax is driven by ecological dynamics at the wildlife-livestock
76 interface¹⁷. In nature, the enzootic cycle of anthrax is characterized by a combination of long-
77 term spore persistence in soil, and an obligate-lethal transmission route, primary in herbivorous
78 mammals^{1,2,14}. Both wild herbivores and livestock are gastrointestinally exposed to *B. anthracis*
79 spores from soil while grazing, become infected, and usually return spores to the soil when they
80 die and decompose¹³. Because domesticated and wild herbivores frequently share grazing
81 grounds, wildlife epizootics can lead to downstream infections in livestock and humans. In some
82 regions, anthrax is hyperendemic, and cases follow regular seasonal trends; in other regions, the
83 disease re-emerges in major epidemics after years or decades without a single case¹.
84 Environmental persistence facilitates these unusual dynamics; under optimal conditions, *B.*
85 *anthracis* spores are able to persist in the soil for long periods (i.e. decades). Alkaline, calcium-
86 rich soils are believed to facilitate sporulation, and therefore drive landscape-level patterns of
87 persistence; these patterns are usually hypothesized to drive the distribution of *B. anthracis* up to
88 the continental scale^{2,14}.

89 Global variation in anthrax endemism and outbreak intensity has been previously
90 characterized at extremely coarse scales^{3,18}, but anthrax is a neglected disease, and its global
91 distribution is still poorly characterized. In total, roughly a dozen studies have used ecological
92 niche models to develop regional (usually national-level) maps of suitability for *B. anthracis* (see
93 **Table S1**). These regional mapping efforts are a critical part of the public health planning

94 process⁴, but are primarily conducted in isolation, and the results of these studies have yet to be
95 consolidated and synthesized. Furthermore, cross-validation of regional models has only been
96 recently attempted¹⁹, and indicates either limitations in model transferability, or possible genetic
97 or ecological differences underlying distributional patterns of different regions; either way, this
98 highlights the limitations preventing regional models from being scaled up to a global estimate.
99 Moreover, the distribution of anthrax has yet to be modelled in several broad regions where it is
100 nevertheless pervasive, especially Western Europe, the Middle East, and South America. Cryptic
101 persistence of *B. anthracis* spores in the soil makes mapping efforts especially challenging, as
102 suitable and endemic regions could go years or potentially decades without a recorded outbreak.

103 This study consolidates clinical and ecological research on enzootic and epidemic anthrax
104 reports, compiling the largest global database of anthrax occurrences on record to map the global
105 suitability for *Bacillus anthracis* persistence. A total of 5,108 records were compiled describing
106 the global distribution of anthrax across 70 countries (**Figure 1**). Here we used a subset of 2,310
107 of these data points to describe the global distribution and eco-epidemiology of *Bacillus*
108 *anthracis*, exploring the relationship of anthrax outbreaks to environmental factors including soil
109 characteristics and climate, via boosted regression trees (BRTs) as a tool for species distribution
110 modelling. These maps provide a proxy for anthrax risk. We apply this global anthrax model to
111 provide a first estimate of the global human and livestock populations at risk from anthrax. We
112 compare the distribution of anthrax to that of critically threatened wildlife populations, and
113 identify areas where additional or new surveillance is needed to anticipate and prevent rare, but
114 likely catastrophic, threats to wildlife conservation efforts.

115 Our global ensemble distribution model (**Figure 2**) performed very well on validation
116 data (mean AUC = 0.9244), and regionally matches the well-established distribution of anthrax
117 in China²⁰, Kazakhstan²¹, North America⁵, and Australia⁸, suggesting that it appropriately
118 captures the global range of *Bacillus anthracis*. These four regions, along with a band of
119 suitability in sub-Saharan Africa around roughly 15° S, represent the most geographically-
120 expansive zones of anthrax endemicity, and hotspots of human vulnerability. However, our study
121 also shows that perhaps the majority of the European continent, and a substantial part of the
122 Anatolian peninsula and surrounding region, are also highly suitable for *B. anthracis*. In some
123 cases, high risk areas match hyperendemic areas, such as Turkey and South Africa; but in other
124 cases (e.g., in Ethiopia), predicted areas of suitability were more limited than expected in

125 countries with a high anthrax burden. This may reflect sampling limitations in these areas, but
126 also likely reflects regional variation in anthrax control. Where food safety practices prevent
127 exposure and livestock vaccinations are affordable, high anthrax suitability may not translate into
128 high case burdens (supported by the vaccination data in the **Supporting Information**);
129 conversely, anthrax morbidity and mortality are usually exacerbated by limited local knowledge
130 about anthrax, limited access to healthcare, and conflicting pressures like food insecurity that
131 force local populations to handle and eat contaminated meat.

132 Globally, we find an estimated 1.8 billion people live within anthrax-suitable areas, the
133 vast majority of whom live in rural areas in Africa, Europe and Asia (**Table 1**). However, most
134 of that population probably has no occupational exposure to infected animals, and direct
135 exposure from the soil has rarely been reported for human cases; in those few reported cases
136 patients had compromised immune systems and unknown or unusual exposure²². For a more
137 informative perspective on risk, we estimate that a total of 63.8 million rural poor livestock
138 keepers live in anthrax-affected areas (95% credible interval: 17.5—168.6 million; **Table 1**),
139 again primarily in Africa and Eurasia. Globally, we found that areas of anthrax risk contain 1.1
140 billion livestock (95% CI: 404 million—2.3 billion; **Table 2**), including 320 million sheep (95%
141 CI: 138—622 million), 294.9 million pigs (95% CI: 103—583 million), 268.1 million cattle
142 (95% CI: 87.4—639 million), 211.2 million goats (95% CI: 74.8—453 million), and 0.6 million
143 buffalo (95% CI: 0.16—1.6 million). Although arid and semi-arid ecosystems were a significant
144 source of vulnerable livestock across production systems (especially for cattle), the single most
145 significant across all four groups was rainfed mixed crop/livestock systems in temperate-
146 highland ecosystems, due to the disproportionate contribution from East Asia, especially China
147 (Table 1).

148 Most livestock at risk of anthrax are unvaccinated in any given year. Per reported data, an
149 average of 212.8 million live attenuated vaccines for anthrax are manufactured every year (2005-
150 2016) outside the United States (which reports no data but is also a major manufacturer); on
151 average, 198.2 million doses are used for livestock every year. Compared to the 1.1 billion
152 livestock at risk, vaccine coverage is patchy and regionally-variable; roughly 90% of cattle,
153 sheep, and goats are annually vaccinated in Eastern Europe and Central Asia, due to a strong
154 legacy of mass vaccination campaigns in the former Soviet Union. On the other hand,
155 vaccination rates are alarmingly low in sub-Saharan Africa (0-6%), East Asia (0-5%) and South

156 Asia (< 1%), where more than half of the livestock at risk and 48.5 million rural poor livestock
157 keepers are located. In these regions, livestock vaccination is commonly used reactively after a
158 major outbreak, rather than as a preventative measure^{5,23}; improving proactive vaccination in
159 under-vaccinated, hyperendemic countries (in particular Afghanistan, Bangladesh, Ethiopia,
160 South Africa, Turkey, and Zimbabwe) could help bring anthrax outbreaks under control²⁴.
161 Vaccination may also be less effective than usual for the 31 million livestock and 4.6 million
162 poor livestock keepers in West Africa, where an endemic lineage of *B. anthracis* shares an
163 anthrose-deficiency mutation that has been hypothesized to lead to a vaccine escape²⁵. Education
164 campaigns may be more cost-effective than mass vaccination, which is both cost-prohibitive and
165 logistically-challenging in inaccessible rural areas. However, livestock keepers may continue to
166 sell contaminated meat to recoup financial losses (which also contributes to underreporting); this
167 has increased cases urban settings²⁶. In cases of extreme food insecurity, poor populations may
168 eat anthrax-infected meat despite understanding the risks.

169 Although risk is most commonly measured at the human-agriculture interface, anthrax
170 also has a major ecological impact; while *B. anthracis* is a stable part of some savannah
171 ecosystems, epizootics in other regions can have catastrophic impacts on wildlife
172 populations^{14,27}. We note that several ungulate species could probably benefit from improved
173 epizootic surveillance, given range overlap with anthrax and limited coverage by protected areas,
174 which are a foundation of anthrax surveillance and control for most wildlife (**Table 3**).²⁸ Saiga
175 antelope (*Saiga tatarica*) in particular have a significant overlap with anthrax outside of
176 protected parts of their range, and the recent mass die-off of a third of the entire population of
177 saiga in three weeks highlights the vulnerability of threatened ungulates to sudden, disease-
178 induced population crashes. The anthrax vaccine may be used by conservationists in special
179 cases (e.g. with cheetahs and rhinoceros²⁹), but the lack of an oral anthrax vaccine makes mass
180 vaccination more impractical for wildlife than for livestock, making surveillance all the more
181 important.

182 Our study has proposed the first global map of *B. anthracis* suitability as a proxy for
183 anthrax risk, and while this is a major step forward, several important directions remain to make
184 these models actionable for public health practitioners. Although some estimates have been
185 proposed for the annual global burden of anthrax, these estimates range by several orders of
186 magnitude. Most regional assessments, especially in rural Africa, agree that anthrax cases are

187 severely underreported despite mandatory reporting. Similar studies to ours have used suitability
188 maps to extrapolate global case burden for diseases like dengue fever or melioidosis
189 (*Burkholderia pseudomallei*)^{11,30}; however, this approach seems inadequate for anthrax, given
190 that human incidence is just as strongly determined by anthrax dynamics in wildlife, local
191 agricultural intensity, knowledge about anthrax transmission, access to healthcare and
192 vaccination, and complicating factors like food insecurity. At national and local levels, One
193 Health approaches to surveillance have had promising results, but a more globally-coordinated
194 network among these programs might help address some of the major data gaps.

195 Our work also sets a foundation for investigating how climate change will impact the
196 distribution and burden of anthrax. Published work suggests anthrax suitability may decrease in
197 parts of Kazakhstan and the southern United States in a changing climate, but other work
198 anticipates warming-driven emergence at higher latitudes^{31,32}. Our study includes recent records
199 from the Yamalo-Nenets area of Russia, where outbreaks in reindeer have led to massive
200 economic losses and threaten the livelihood of traditional pastoralists. However, our model made
201 limited predictions of suitability in the sub-Arctic in current climates. Even though anthrax cases
202 are regularly reported throughout Sweden, northern Russia, and other cold, high-latitude
203 countries, high-latitude outbreaks are proportionally under-represented in our database (and are
204 often poorly documented). Persistence at higher latitudes may also be better predicted by a
205 slightly different set of climatic constraints on persistence. A recently-published model trained
206 on high-latitude cases in the Northern Hemisphere seems to under-predict known areas of
207 endemism in warmer climates, possibly supporting this explanation³². Feedback between local
208 modelling efforts and updated global consensus mapping will improve our overall understanding
209 of what drives different anthrax dynamics, and the likely impact of climate change.

210 Finally, we observe increasing interest, by microbiologists and ecologists alike, in the
211 closely related “anthrax-like” *Bacillus cereus* biovar. *anthracis*. Whereas *Bacillus cereus* is a
212 typically non-pathogenic soil bacterium, the pathogenic *B. cereus* biovar. *anthracis* (*Bcbva*)
213 carries variants of the pXO1 and pXO2 plasmids that allow capsule production, which are both
214 required for full virulence in *B. anthracis*. A recent study in Taï National Park in Cote D’Ivoire
215 showed that *Bcbva* accounted for 40% of wildlife mortality in a 26-year survey, and could
216 potentially drive the local extinction of chimpanzees in the Taï Forest within the next century.³³
217 The geographic distribution of *Bcbva* is still unknown, and it is plausible that different climatic

218 and environmental factors determine the spatial patterns of its transmission; though improved
219 diagnostics will be necessary to differentiate the role of the two pathogens in anthrax infections
220 beyond Taï National Park. Mapping *Bcbva* across West Africa may be an important next step for
221 measuring the threat of anthrax and anthrax-like disease to wildlife conservation (and,
222 potentially, to human health down the road).

223

224

Methods

225

226 Occurrence & Pseudoabsence Data

227 We assembled a global occurrence database for *Bacillus anthracis* out of a combination of (i)
228 outbreak data collected in the field by the authors or their extended team of collaborators, (ii)
229 national passive surveillance and reporting infrastructures, (iii) online records from ProMed
230 Mail, and (iv) georeferenced records or (v) digitized maps from peer-reviewed publications
231 documenting anthrax outbreaks. Our final database of 5,018 unique records spanning 70
232 countries and more than a century (1914 – 2018), thinned to 2,310 distinct localities after
233 removing uncertain sightings and thinning to a single point per unique 10 arcminute (~20 km at
234 the equator) cell, to correct for sampling bias³⁴. For background environmental data, a total
235 dataset of 10,000 pseudoabsences were randomly generated from countries where anthrax
236 occurrence records were collected, an upper sample commonly used for similar disease
237 distribution mapping studies³⁵. Of these 10,000, an equal 1:1 sample was randomly selected to
238 match the presence points in submodels, as is recommended for boosted regression tree
239 models³⁶.

240

241 Environmental Predictors

242 Global layers of environmental predictors were selected based on successful variables used in
243 previously published anthrax distribution modelling studies at regional scales^{5,21,37}, as well as
244 from other distribution modelling studies on soil-borne pathogens³⁰. Climate data were taken
245 from version 1.4 of the WorldClim dataset, which includes nineteen bioclimatic variables
246 characterizing average and seasonal trends in temperature and precipitation³⁸. In addition to
247 climate data, we included layers describing elevation, soil, and two vegetation indices.
248 Elevational data was taken from the Global Multi-resolution Terrain Elevation Data
249 (GMTED2010) dataset provided by the US Geological Service. Soil layers were taken from the
250 Global Soil Information Facilities (GSIF) SoilGrids database at 250 m resolution; four layers
251 were included: soil pH, and the predicted soil content of sand, humult, and calcic vertisols at a
252 depth of 0-5 cm³⁹. The mean and amplitude of the normalized difference vegetation index
253 (NDVI) were taken from the Trypanosomiasis & Land Use in Africa (TALA) dataset⁴⁰. To

254 prevent overfitting and reduce correlation among predictor variables, the variable set was
255 reduced down using an automated procedure within the boosted regression tree implementation.

256

257 **Distribution Modelling**

258 Boosted regression trees (BRTs) are currently considered a best practices method for modelling
259 the global distribution of infectious diseases^{11,41}, including other soil-transmitted pathogens like
260 *Burkholderia pseudomallei*³⁰. In our study, BRTs were implemented using the ‘gbm’ package in
261 R to develop a global species distribution model for *Bacillus anthracis*. Automated variable set
262 reduction procedures selected a total of seventeen predictor layers: ten bioclimatic variables, two
263 vegetation indices, elevation, and four soil variables. Presence, absence, and environmental data
264 were run through the ‘gbm.step’ procedure on default settings (tree complexity = 4, learning rate
265 = 0.005), following the established template of other studies. A total of 500 submodels were run;
266 for each, presence points were bootstrapped, and pseudoabsences were randomly selected from
267 the total 10,000 to achieve a 1:1 ratio³⁶. Separate from the internal cross-validation (75%-25%
268 split) of the BRT procedure, both presence and pseudoabsence points were split into an 80%
269 training and 20% test dataset in each submodel, and model AUC was evaluated based on the
270 independent test dataset. A final average model was calculated across the 500 submodels, and the
271 5th and 95th percentile were retained for use in the population at risk analyses. Models performed
272 very well on the withheld test data (mean submodel AUC = 0.9244).

273

274 **Estimation of Human and Livestock Populations-at-Risk**

275 We estimated the vulnerability of human and livestock populations by overlaying population
276 datasets with maps of anthrax-suitable areas⁴². We mapped global anthrax suitability by
277 dichotomizing model predictions with a threshold of 0.565 for suitable versus unsuitable
278 predictions, with the threshold selected to maximize the true skill statistic (which weights
279 sensitivity and specificity equally) of mean predictions across the entire dataset of all sightings
280 and pseudoabsences. We estimated global population at risk using human population counts for
281 2015 from the Gridded Population of the World (GPW) dataset, version 4.0. We dichotomized
282 “urban” and “rural” areas using the Global Human Built-up and Settlement Extent (HBASE)
283 Dataset, version 1.0. We further split “urban” areas into urban and peri-urban based on the GPW
284 population dataset, where we used a density under 1,000 persons per km² as the threshold for

285 classification as peri-urban. To measure possible occupational exposure, we used a global dataset
286 of rural poor livestock keeper density.⁴³ Finally, we estimated the number of livestock (cattle,
287 sheep, goats, and swine) using a database of global livestock density at a spatial resolution of
288 ~1km x 1km (<http://www.livestock.geo-wiki.org/>).⁴⁴ Those livestock populations at risk were
289 further stratified by each of the livestock production zones using the livestock production
290 systems data version 5 (<http://www.livestock.geo-wiki.org/>).⁴³⁻⁴⁵ For all human and livestock
291 analyses, we obtained vulnerability estimates by overlaying population counts with dichotomized
292 anthrax suitable areas from the BRT models; 95% credibility intervals were calculated by using
293 the 5% (lower) and 95% (upper) bounds of the averaged BRT model prediction, in place of the
294 mean prediction.⁴²

295

296 **Delineating Wildlife at Risk**

297 We identified ungulate species of interest based on species of conservation concern with known
298 range overlap with anthrax, and measured the degree of range overlap with our global *B.*
299 *anthracis* model, as a proxy for anthrax exposure. We selected seven candidate species of
300 interest: pronghorn (*Antilocapra americana*), roan (*Hippotragus equinus*), saiga (*Saiga tatarica*),
301 moose (*Alces alces*), reindeer (*Rangifer tarandus*), wild yak (*Bos mutus*), and bison (*Bison*
302 *bison*). Of the seven, saiga are most threatened, and are listed on the IUCN red list as critically
303 endangered. Yak are listed as vulnerable; bison are listed as near threatened; and pronghorn,
304 roan, and moose are listed as least concern. We use the Global Protected Areas Database and
305 official IUCN range maps, though we note that these range maps tend to overestimate ranges and
306 can be misleading for conservation work⁴⁶. (At least for saiga, we note that telemetry studies are
307 currently underway to reassess the boundaries of the species' range.)

308

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Author Contributions

319 CJC, ITK and JKB conceived of the study. JKB, MEHJ, ITK, and CJC collected and
320 georeferenced data. CJC, ITK and JKB designed the models, and CJC ran models and analyses.
321 NR contributed R code. All authors contributed to the writing and editing of the draft, and
322 approved the study before submission.

323 **Literature Cited**

- 324 1. Hugh-Jones, M. & De Vos, V. Anthrax and wildlife. *Rev. Sci. Tech.-Off. Int. Epizoot.* **21**, 359–384 (2002).
- 325 2. Hugh-Jones, M. & Blackburn, J. The ecology of *Bacillus anthracis*. *Mol. Aspects Med.* **30**, 356–367 (2009).
- 326 3. Coleman, M. E., Thran, B., Morse, S. S., Hugh-Jones, M. & Massulik, S. Inhalation anthrax: Dose response and
327 risk analysis. *Biosecurity Bioterrorism Biodefense Strategy Pract. Sci.* **6**, 147–160 (2008).
- 328 4. Blackburn, J. K., Kracalik, I. T. & Fair, J. M. Applying Science: Opportunities to Inform Disease Management
329 Policy with Cooperative Research within a One Health Framework. *Front. Public Health* **3**, (2015).
- 330 5. Blackburn, J. K., McNyset, K. M., Curtis, A. & Hugh-Jones, M. E. Modeling the geographic distribution of
331 *Bacillus anthracis*, the causative agent of anthrax disease, for the contiguous United States using predictive
332 ecologic niche modeling. *Am. J. Trop. Med. Hyg.* **77**, 1103–1110 (2007).
- 333 6. Aikembayev, A. M. *et al.* Historical distribution and molecular diversity of *Bacillus anthracis*, Kazakhstan.
334 *Emerg. Infect. Dis.* **16**, 789 (2010).
- 335 7. Zhang, W.-Y. *et al.* Spatiotemporal clustering analysis and risk assessments of human cutaneous anthrax in
336 China, 2005–2012. *PloS One* **10**, e0133736 (2015).
- 337 8. Barro, A. S. *et al.* Redefining the Australian anthrax belt: Modeling the ecological niche and predicting the
338 geographic distribution of *Bacillus anthracis*. *PLoS Negl Trop Dis* **10**, e0004689 (2016).
- 339 9. Blackburn, J. K. *et al.* *Bacillus anthracis* diversity and geographic potential across Nigeria, Cameroon and Chad:
340 further support of a novel West African lineage. *PLoS Negl Trop Dis* **9**, e0003931 (2015).
- 341 10. Elith, J., Leathwick, J. R. & Hastie, T. A working guide to boosted regression trees. *J. Anim. Ecol.* **77**, 802–813
342 (2008).
- 343 11. Bhatt, S. *et al.* The global distribution and burden of dengue. *Nature* **496**, 504–507 (2013).
- 344 12. Blackburn, J. K. & Goodin, D. G. Differentiation of springtime vegetation indices associated with summer
345 anthrax epizootics in west Texas, USA, deer. *J. Wildl. Dis.* **49**, 699–703 (2013).
- 346 13. Turner, W. C. *et al.* Fatal attraction: vegetation responses to nutrient inputs attract herbivores to infectious
347 anthrax carcass sites. *Proc. R. Soc. Lond. B Biol. Sci.* **281**, 20141785 (2014).
- 348 14. Carlson, C. J. *et al.* Spores and soil from six sides: interdisciplinarity and the environmental biology of anthrax
349 (*Bacillus anthracis*). *Biol. Rev.* in press (2018).
- 350 15. Swartz, M. N. Recognition and management of anthrax—an update. *N. Engl. J. Med.* **345**, 1621–1626 (2001).

- 351 16. World Health Organization and International Office of Epizootics (last). *Anthrax in humans and animals*. (World
352 Health Organization, 2008).
- 353 17. Alexander, K. A., Lewis, B. L., Marathe, M., Eubank, S. & Blackburn, J. K. Modeling of wildlife-associated
354 zoonoses: applications and caveats. *Vector-Borne Zoonotic Dis.* **12**, 1005–1018 (2012).
- 355 18. Shadomy, S. *et al.* Anthrax outbreaks: a warning for improved prevention, control and heightened awareness.
356 *Emerg. Prev. Syst. EMPRES Watch* **37**, (2016).
- 357 19. Mullins, J. C. *et al.* Ecological niche modeling of *Bacillus anthracis* on three continents: evidence for genetic-
358 ecological divergence? *PLoS One* **8**, e72451 (2013).
- 359 20. Chen, W.-J. *et al.* Mapping the Distribution of Anthrax in Mainland China, 2005–2013. *PLoS Negl Trop Dis* **10**,
360 e0004637 (2016).
- 361 21. Mullins, J. *et al.* Ecological Niche Modelling of the *Bacillus anthracis* A1. a sub-lineage in Kazakhstan. *BMC*
362 *Ecol.* **11**, 32 (2011).
- 363 22. Griffith, J. *et al.* Investigation of inhalation anthrax case, United States. *Emerg. Infect. Dis.* **20**, 280 (2014).
- 364 23. Kracalik, I. *et al.* Changing patterns of human anthrax in Azerbaijan during the post-Soviet and preemptive
365 livestock vaccination eras. *PLoS Negl. Trop. Dis.* **8**, e2985 (2014).
- 366 24. Blackburn, J. K., Kracalik, I. T. & Fair, J. M. Applying Science: Opportunities to Inform Disease Management
367 Policy with Cooperative Research within a One Health Framework. *Front. Public Health* **3**, (2015).
- 368 25. Blackburn, J. K. *et al.* *Bacillus anthracis* diversity and geographic potential across Nigeria, Cameroon and Chad:
369 further support of a novel West African lineage. *PLoS Negl Trop Dis* **9**, e0003931 (2015).
- 370 26. Kracalik, I., Malania, L., Imnadze, P. & Blackburn, J. K. Human Anthrax Transmission at the Urban–Rural
371 Interface, Georgia. *Am. J. Trop. Med. Hyg.* **93**, 1156–1159 (2015).
- 372 27. Hampson, K. *et al.* Predictability of anthrax infection in the Serengeti, Tanzania. *J. Appl. Ecol.* **48**, 1333–1344
373 (2011).
- 374 28. Clegg, S. Preparedness for anthrax epizootics in wildlife areas. (2006).
- 375 29. Turnbull, P. *et al.* Vaccine-induced protection against anthrax in cheetah (*Acinonyx jubatus*) and black
376 rhinoceros (*Diceros bicornis*). *Vaccine* **22**, 3340–3347 (2004).
- 377 30. Limmathurotsakul, D. *et al.* Predicted global distribution of *Burkholderia pseudomallei* and burden of
378 melioidosis. *Nat. Microbiol.* **1**, 15008 (2016).

- 379 31. Blackburn, J. K. Integrating geographic information systems and ecological niche modeling into disease ecology:
380 a case study of *Bacillus anthracis* in the United States and Mexico. in *Emerging and Endemic Pathogens* 59–88
381 (Springer, 2010).
- 382 32. Walsh, M. G., de Smalen, A. W. & Mor, S. Climatic influence on the anthrax niche in warming northern
383 latitudes. *Sci. Rep.* **8**, 9269 (2018).
- 384 33. Hoffmann, C. *et al.* Persistent anthrax as a major driver of wildlife mortality in a tropical rainforest. *Nature* **548**,
385 82–86 (2017).
- 386 34. Boria, R. A., Olson, L. E., Goodman, S. M. & Anderson, R. P. Spatial filtering to reduce sampling bias can
387 improve the performance of ecological niche models. *Ecol. Model.* **275**, 73–77 (2014).
- 388 35. Nsoesie, E. O. *et al.* Global distribution and environmental suitability for chikungunya virus, 1952 to 2015. *Euro*
389 *Surveill. Bull. Eur. Sur Mal. Transm. Eur. Commun. Dis. Bull.* **21**, (2016).
- 390 36. Barbet-Massin, M., Jiguet, F., Albert, C. H. & Thuiller, W. Selecting pseudo-absences for species distribution
391 models: how, where and how many? *Methods Ecol. Evol.* **3**, 327–338 (2012).
- 392 37. Barro, A. S. *et al.* Redefining the Australian anthrax belt: Modeling the ecological niche and predicting the
393 geographic distribution of *Bacillus anthracis*. *PLoS Negl Trop Dis* **10**, e0004689 (2016).
- 394 38. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate
395 surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
- 396 39. Hengl, T. *et al.* SoilGrids250m: Global gridded soil information based on machine learning. *PLoS One* **12**,
397 e0169748 (2017).
- 398 40. Hay, S., Tatem, A., Graham, A., Goetz, S. & Rogers, D. Global environmental data for mapping infectious
399 disease distribution. *Adv. Parasitol.* **62**, 37–77 (2006).
- 400 41. Messina, J. P. *et al.* The global distribution of Crimean-Congo hemorrhagic fever. *Trans. R. Soc. Trop. Med.*
401 *Hyg.* trv050 (2015).
- 402 42. Kracalik, I. T. *et al.* Modeling the environmental suitability of anthrax in Ghana and estimating populations at
403 risk: Implications for vaccination and control. *PLoS Negl. Trop. Dis.* **11**, e0005885 (2017).
- 404 43. *Global livestock production systems.* (Food and Agriculture Organization of the United Nations, 2011).
- 405 44. Robinson, T. P. *et al.* Mapping the Global Distribution of Livestock. *PLoS ONE* **9**, e96084 (2014).
- 406 45. Thornton, P. *Mapping poverty and livestock in the developing world.* (ILRI (aka ILCA and ILRAD), 2002).

407 46. Ramesh, V., Gopalakrishna, T., Barve, S. & Melnick, D. J. IUCN greatly underestimates threat levels of endemic
408 birds in the Western Ghats. *Biol. Conserv.* **210**, 205–221 (2017).

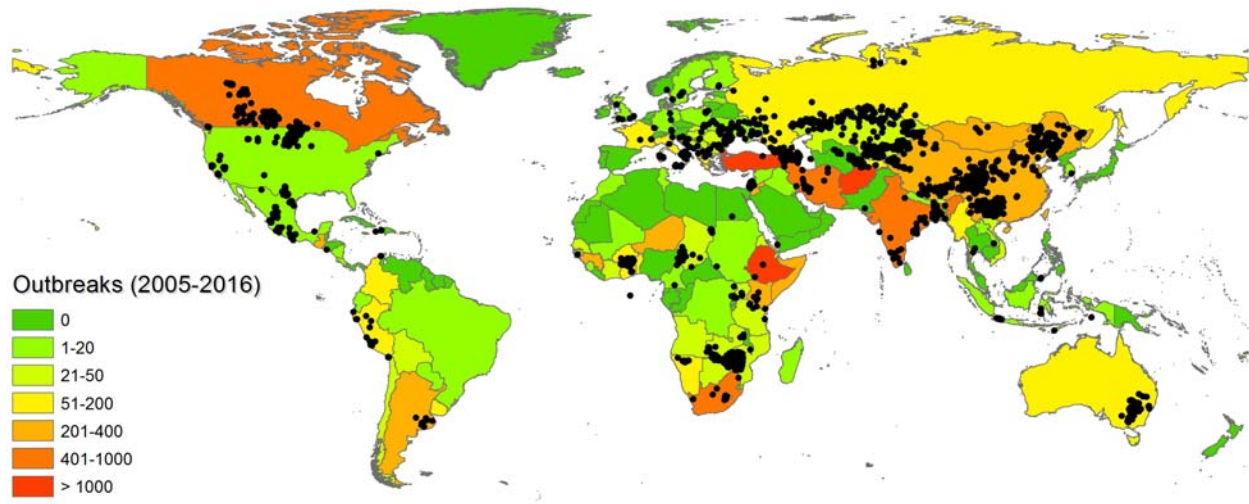
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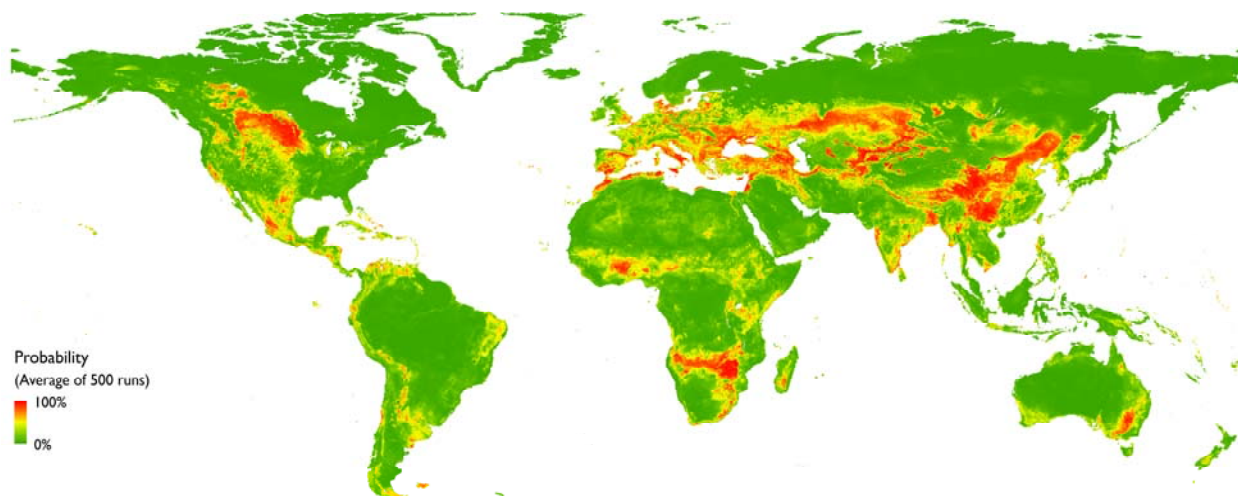
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Figures

412 **Figure 1.** Global database of anthrax occurrences (points), versus outbreaks of anthrax by
413 country (Jan. 2005-Aug. 2016; data digitized from United Nations Food & Agriculture
414 Organization report).



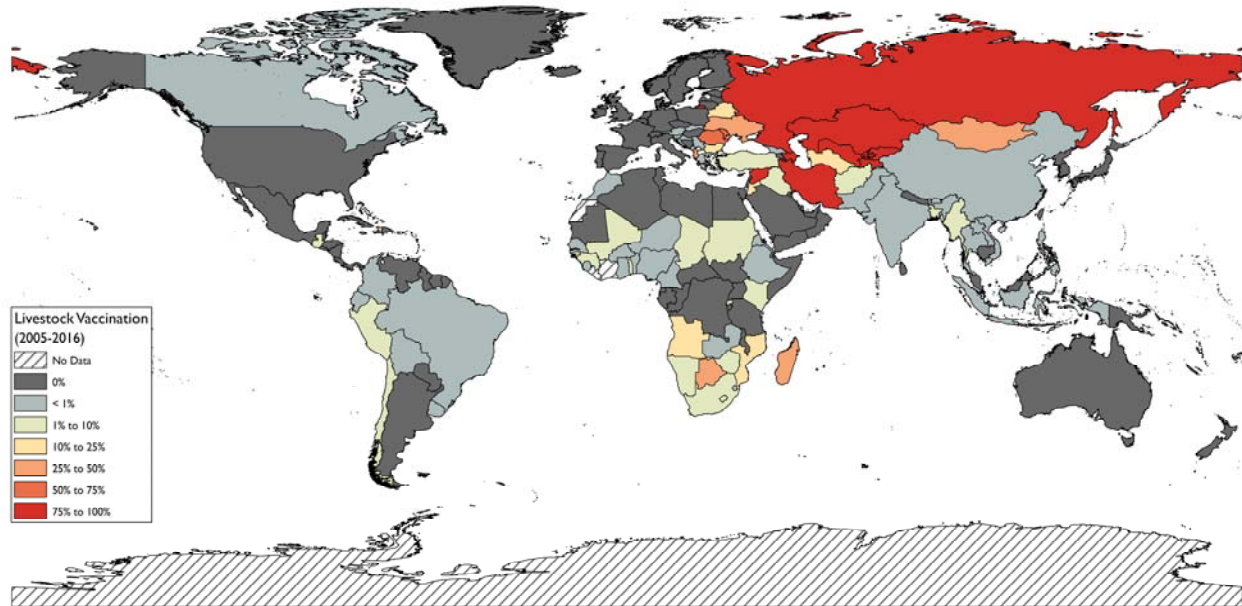
416 **Figure 2.** Global environmental suitability (probability of occurrence) for *Bacillus anthracis*
417 modelled by an ensemble of 500 boosted regression trees.
418



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420

421 **Figure 3.** Average vaccination rates for all livestock (cattle, sheep, goats, buffalo, and pigs)
422 reported to WAHIS over the interval 2005-2016, as a function of doses administered and
423 reported livestock populations at risk, excluding years with no reported vaccination.



424

425

Tables.

426

427 **Table 1.** Population at risk (in millions) by region, land use, and occupational exposure.

Region	Poor livestock keepers	Rural	Peri-urban	Urban	Total
East Asia and the Pacific	5.7	458.5	15.0	162.4	635.9
South Asia	26.6	345.0	1.9	55.1	401.9
Western and Central Europe	0.26	125.3	14.0	79.6	218.8
North Africa and the Middle East	6.6	152.9	6.1	51.7	210.7
Eastern Europe and Central Asia	5.6	112.7	3.4	26.5	142.7
Sub-Saharan Africa	16.2	84.2	1.5	16.6	102.3
Latin America and the Caribbean	2.9	38.1	2.6	42.0	82.7
North America	< 0.1	5.6	3.6	21.5	30.8
Australia and Oceania	< 0.1	0.74	0.24	0.7	1.76
World Total	63.8	1,323.1	48.4	456.1	1,827.5

428

429 **Table 2.** Estimated global livestock at risk (by millions), by species & region.

Region	Cattle	Pigs	Goats	Sheep	Buffalo	Total
East Asia and the Pacific	63.2	190.9	79.9	108.1	0.24	442.4
South Asia	61.6	1.8	72.5	18.7	0.33	154.8
Western and Central Europe	22.2	60.9	7.5	42.2	< 0.1	132.8
North Africa and the Middle East	15.8	0.2	13.4	65.2	< 0.1	94.6
Eastern Europe and Central Asia	26.6	12.0	8.9	40.4	< 0.1	87.8
Sub-Saharan Africa	30.5	5.3	22.4	14.5	0	72.8
Latin America and the Caribbean	21.9	8.0	5.7	8.1	0	43.7
North America	23.0	15.2	0.45	0.29	0	39.0
Australia and Oceania	3.1	0.61	0.47	22.7	0	26.9
World Total	268.1	294.9	211.2	320.1	0.58	1,094.9

430

431 **Table 3.** Overlap between wildlife species of concern and the global distribution of anthrax,
432 including overlap with the protected areas database.

Wildlife Species	Geographic Overlap	Anthrax suitable area overlap with protected areas	IUCN Red List Status
Bison (<i>Bison bison</i>)	32.2%	64.6%	NT
Pronghorn (<i>Antilocapra americana</i>)	26.6%	3.9%	LC
Roan (<i>Hippotragus equinus</i>)	23.9%	30.5%	LC
Saiga (<i>Saiga tatarica</i>)	17.5%	2.8%	CE (A2acd)
Moose (<i>Alces alces</i>)	6.0%	9.9%	LC
Reindeer (<i>Rangifer tarandus</i>)	1.6%	14.9%	LC
Yak (<i>Bos mutus</i>)	0.7%	0%	VU (C10)

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