

# The coevolutionary mosaic of bat betacoronavirus emergence risk

Norma R Forero-Muñoz<sup>1,2,‡</sup> Renata L. Muylaert<sup>3</sup> Stephanie N. Seifert<sup>4</sup> Gregory F. Albery<sup>5</sup> Daniel J. Becker<sup>6</sup> Colin J. Carlson<sup>7,8,9,‡</sup> **Timothée Poisot**<sup>1,2,‡</sup>

<sup>1</sup> Université de Montréal <sup>2</sup> Québec Centre for Biodiversity Sciences <sup>3</sup> Molecular Epidemiology and Public Health Laboratory, School of Veterinary Science, Massey University, New Zealand <sup>4</sup> Paul G. Allen School for Global Health, Washington State University, Pullman, WA, United States <sup>5</sup> Department of Biology, Georgetown University, Washington, DC, USA <sup>6</sup> Department of Biology, University of Oklahoma, Norman, OK, USA <sup>7</sup> Department of Biology, Georgetown University, Washington, DC,

<sup>8</sup> Center for Global Health Science and Security, Georgetown University Medical Center, Washington, DC, USA <sup>9</sup> Department of Microbiology and Immunology, Georgetown University Medical Center, Washington, DC, USA

‡ These authors contributed equally to the work

## Correspondance to:

Timothée Poisot — [timothee.poisot@umontreal.ca](mailto:timothee.poisot@umontreal.ca)

Pathogen evolution is one of the least predictable components of disease emergence, particularly in nature. Here, building on principles established by the geographic mosaic theory of coevolution, we develop a quantitative, spatially-explicit framework for mapping the evolutionary risk of viral emergence. Driven by interest in diseases like SARS, MERS, and COVID-19, we examine the global biogeography of bat-origin betacoronaviruses, and find that coevolutionary principles suggest geographies of risk that are distinct from the hotspots and coldspots of host richness. Further, our framework helps explain patterns like a unique pool of merbecoviruses in the Neotropics, a recently-discovered lineage of divergent nobecoviruses in Madagascar, and—most importantly—hotspots of diversification in southeast Asia, sub-Saharan Africa, and the Middle East that correspond to the site of previous zoonotic emergence events. Our framework may help identify hotspots of future risk that have also been previously overlooked, like west Africa and the Indian subcontinent, and may more broadly help researchers understand how host ecology shapes the evolution and diversity of pandemic threats.

1 Disease emergence is complex, and is driven not only by animal-human contact, but also by the  
2 underlying evolutionary dynamics in viral reservoirs.<sup>1</sup> Although host richness is often used as a superficial  
3 proxy for spillover risk,<sup>2,3</sup> these approaches oversimplify the relevant interspecific heterogeneity in  
4 immunology, behavior, and other traits, and therefore overlook unique host pools that allow for the rapid  
5 evolution of highly divergent viruses.<sup>4</sup> In the case of generalist pathogens like betacoronaviruses, there is  
6 conceptual and empirical support to the idea that these community-level mechanisms are even more  
7 important,<sup>5</sup> particularly given that cross-species transmission may, as a rule, structure viral evolution  
8 more than co-divergence with hosts.<sup>6</sup> This creates a disconnect between coevolutionary theory and most  
9 existing ecological frameworks for mapping spillover risk.

10 The geographic mosaic theory of coevolution (GMTC) attempts to explicitly connect microevolutionary  
11 dynamics to the macroecology and biogeography of symbiotic interactions.<sup>7</sup> The GMTC posits that  
12 coevolutionary processes among pairs<sup>8</sup> or complexes<sup>9</sup> of species are structured in space by the rippling  
13 effects of abiotic conditions onto evolutionary mechanisms, giving rise to fragmented systems with  
14 different ecologies over large spatial extents.<sup>10</sup> The GMTC predicts a spatial fragmentation of  
15 coevolutionary dynamics under the joint action of three processes:<sup>11</sup> coevolutionary hot- and coldspots,  
16 which appear when the intensity of *interaction* (in terms of reciprocal fitness consequences) varies  
17 spatially; selection mosaics, wherein the intensity of *selection* varies across space, driven by both the biotic  
18 complexity of the community (locally diverse hosts and viruses are more biotically complex) and the local  
19 favorability of the environment;<sup>12</sup> and trait remixing, which occurs when coevolutionary dynamics change  
20 when community-level *functional traits* change through meta-community dynamics.

21 Here, we apply the GMTC to explore and explain the global biogeography of betacoronaviruses, the group  
22 that includes SARS-CoV, MERS-CoV, and SARS-CoV-2. In their bat reservoirs, coronaviruses evolve  
23 through a mix of host jumps, recombination among disparate lineages, and, to a lesser degree,  
24 co-divergence with their hosts—<sup>2</sup>a mix of mechanisms that creates a complex and nonlinear relationship  
25 between host diversity and viral emergence. Working from a recently published database of bat hosts of  
26 betacoronaviruses, we test whether spatial structure in bat-betacoronavirus coevolution is identifiable at a  
27 global scale. Aiming to explain these patterns, we develop a generalized framework for applying the  
28 GMTC to host-virus interactions, with a specific emphasis on the potential to create independent  
29 coevolutionary dynamics (and therefore spatial fragmentation in risk) through heterogeneity. We develop  
30 a trivariate risk assessment system that connects each GMTC mechanism to a quantifiable aspect of

31 host-virus interactions: (i) viral sharing rates in host communities, representing the strength of potential  
32 interaction between viruses and any one host (i.e., places where viruses undergo constant host switching  
33 may be coevolutionary coldspots); (ii) the phylogenetic diversity of hosts, as a proxy for variation in the  
34 immunological mechanisms that antagonize viruses (i.e., the selection mosaic); and (iii) the local  
35 uniqueness of the bat community, representing the potential for viruses to be exposed to novel host traits  
36 (e.g., variation in receptor sequences). Together, we argue that these can be used to identify and map the  
37 evolutionary drivers that—in conjunction with transmission processes (e.g., viral prevalence in reservoirs  
38 and animal-human contact rates)—determine disease emergence risk.

## 39 Results and Discussion

### 40 Bat and betacoronavirus biogeography are broadly consistent

41 Most previous work has assumed that the presence or richness of key groups of bat hosts are predictive of  
42 coronavirus diversity.<sup>2,3</sup> Projecting bat and betacoronavirus phylogeny over space (fig. 1), we find support  
43 for the idea that bat community assembly is directly responsible for a global mosaic of viral evolution. The  
44 distinct groupings (represented by different colors, symbolizing positions in a subspace formed by the first  
45 two phylogenetic principal components) are essentially equivalent between the two groups, and can be  
46 coarsely delineated as (1) south and southeast Asia; (2) east Asia (including northern China), west Asia,  
47 and the Mediterranean coast; (3) Eurasia above a northing of 40; and (4) Africa and Latin America. In  
48 some cases, this diverges from expectations about coronavirus biogeography: for example, previous work  
49 has rarely flagged India as a region of interest, but for both bats and betacoronaviruses, the subcontinent  
50 falls into the same regions as the southeast Asian peninsula (and indeed, the region is home to known bat  
51 hosts of multiple betacoronavirus subgenera, including nobecoviruses, sarbecoviruses, and  
52 merbecoviruses).<sup>3</sup>

53 [Figure 1 about here.]

54 Overall, these results suggest that the boundaries of bat and betacoronavirus biogeographic regions are  
55 largely consistent. This may be surprising, given that cross-species transmission may play a stronger role  
56 in coronavirus diversification than cospeciation—<sup>2</sup>a property that would theoretically allow for

57 substantial broad divergence in their biogeography. However, host jumps at the family level or higher are  
58 relatively rare and significant events in coronavirus evolutionary history;<sup>2,13</sup> as a result, the mosaic of  
59 betacoronavirus phylogeography is assembled from a set of overlapping smaller coevolutionary systems,  
60 superimposed in space and filtered by the importance of different subgroups in local host communities.  
61 For example, the most speciose and cosmopolitan family of bats, the vesper bats (Vespertilionidae), are  
62 considered the primary hosts of the subgenus *Merbecovirus* (MERS-like viruses);<sup>3,13</sup> but in the Americas,  
63 where merbecoviruses are the only lineage present, they have only been found in other bat taxa (e.g.,  
64 Molossidae, Phyllostomidae).<sup>14–17</sup> At the coarsest scale, these heterogeneities are lost, and betacoronavirus  
65 biogeography tracks the deep rifts in bat evolutionary history—but within broad regions, the component  
66 coevolutionary systems may have very different dynamics.

## 67 **Hotspots of bat and betacoronavirus biodiversity are distinct**

68 Bats, the second most diverse groups of mammals, are found worldwide; gradients in their species  
69 richness generally track broader patterns of mammal diversity, with a striking Neotropical hotspot  
70 (especially in the Amazon basin) and a secondary hotspot centered in Indochina. These hotspots of bat  
71 diversity are generally presumed to be hotspots of viral adaptive radiation, and therefore areas of concern  
72 for human health.<sup>2,18</sup> However, the hotspots of known bat betacoronavirus hosts show a distinct pattern,  
73 with primary hotspots (both in terms of area and higher values) of host richness situated in southeast  
74 Asia, parts of southern Europe, and to a lesser extent parts of Africa in the -25-0 range of latitudes (fig. 2;  
75 top). Although hundreds of species likely host undiscovered betacoronaviruses, machine learning  
76 predictions have suggested that these undiscovered reservoirs should follow the same diversity gradient.<sup>19</sup>  
77 In principle, these hotspots of locally-diverse, virus-rich bat communities should drive more adaptive  
78 diversification in their viruses.

79 [Figure 2 about here.]

80 However, we find that the global pattern of betacoronavirus phylogenetic distinctiveness is quite distinct  
81 from both bat host richness and phylogenetic distinctiveness (fig. 2; bottom). In contrast to the sparsity of  
82 Neotropical betacoronavirus hosts, South and Central America have the most evolutionary distinct hosts  
83 and viruses, followed by secondary hotspots in southeast Asia and the Rift Valley region have mostly  
84 distinct viruses. Some degree of sampling bias may contribute to these patterns: for example, the

85 Neotropics are one of the places where the fewest bat betacoronavirus sequences have been generated,<sup>20–22</sup>  
86 resulting in a sparser phylogenetic tree, and artificially inflating distinctiveness; conversely,  
87 disproportionate research effort in eastern China<sup>23</sup> may have led to a more complete inventory of the local  
88 diversity of coronaviruses, again inflating these metrics relative to underlying patterns. Even accounting  
89 for these potential biases, though, there is obvious heterogeneity in betacoronavirus evolutionary  
90 distinctiveness that is distinct from overall bat diversity.

91 Overall, these patterns recapitulate the evolutionary history of both the order Chiroptera and the genus  
92 *Betacoronavirus*. Horseshoe bats (Rhinolophidae) include the reservoirs of the SARS-like viruses  
93 (subgenus *Sarbecovirus*), the group of pandemic threats that have been of the greatest interest to  
94 researchers<sup>13</sup> (and so have been sampled most intensively).<sup>23</sup> The hotspots of host richness and viral  
95 diversity in southeast Asia—both of which are disproportionately high, considering the global landscape  
96 of bat species richness—are almost entirely driven by viral adaptive radiation through host switching  
97 within this clade<sup>3,19</sup>. In contrast, the Neotropical hotspot of viral distinctiveness is driven by isolation by  
98 host vicariance. Out of the four main groups of betacoronaviruses, only merbecoviruses have been found  
99 in animals in the Americas—an introduction that is generally presumed to be ancient.<sup>3,24</sup> While  
100 comparatively understudied, New World merbecoviruses have been found in the ghost-faced bats  
101 (Mormoopidae), Neotropical leaf-nosed bats (Phyllostomidae), and free-tailed bats (Molossidae).<sup>14–17</sup> The  
102 former two groups and a clade of the latter are endemic to the Neotropics, while the explosive adaptive  
103 radiations of the phyllostomids are responsible for the hotspot of bat diversity in the Amazon.<sup>25</sup> Together,  
104 these clades of New World bats play host to a distinct regime of betacoronavirus coevolution.

## 105 Coevolutionary regimes structure evolutionary potential for zoonotic emergence

106 The existence of well-defined cophylogenetic regions suggests that the bat-betacoronavirus system is  
107 spatially fragmented enough to create divergent coevolutionary trajectories; in turn, this coevolutionary  
108 mosaic may alter the risk of zoonotic emergence. These ideas are, respectively, supported by the existence  
109 of hotspots of viral uniqueness and the diverse origins of human betacoronaviruses. Together, this  
110 framework points to a predictable relationship between host community structure and coevolutionary  
111 pressure: phylogeographic structure in bat hosts (and their diverse immune strategies)<sup>26</sup> creates a  
112 landscape of selective pressure; the trajectory of viruses' coevolutionary response is, in turn, constrained  
113 by their opportunities for either specialization or diversification through host jumps and recombination.

114 Based on the geographic mosaic theory of coevolution, we developed a trivariate map of coevolutionary  
115 pressure (fig. 3): (1) *host phylogenetic diversity*: a high diversity of evolutionary histories should expose  
116 viruses to more variation in host immune traits; (2) *host community uniqueness*: exposure to greater host  
117 trait heterogeneity can drive viral diversification, and coevolving with more unique host communities  
118 should create more unique branches of viral evolution; and (3) propensity for *viral sharing*: frequent  
119 cross-species transmission may act as a buffer on selective pressure, while lower rates of exchange may  
120 enable more simultaneous trajectories of viral specialization to coexist within a given community. We  
121 combine global maps of all three to generate a map of coevolutionary regimes, where close colors  
122 represent similar risks, and paler pixels represent overall higher risk (see Methods). We find that these  
123 regions do not neatly overlap with those defined in fig. 1 or fig. 2, reinforcing the notion that local-scale  
124 coevolutionary mosaics can form within cophylogenetic regions.

125 [Figure 3 about here.]

126 The greatest evolutionary potential for zoonotic emergence exists where pathogen pools have a high  
127 genetic diversity and high propensity for cross-species transmission. In our framework, emergence risk is  
128 therefore maximized under higher phylogenetic diversity (viruses are exposed to different host clades),  
129 higher host uniqueness (viruses are experiencing novel, heterogeneous host traits combinations), and low  
130 to medium viral sharing (host-virus pairs can coevolve independently, but divergent viruses may still have  
131 opportunities for recombination). In fig. 3, this corresponds to yellow areas (dynamics dominated by low  
132 viral sharing, with equal contributions of selection mosaics and trait remixing; southeast Asia, and the  
133 Indian sub-continent), green-yellow areas (dynamics with low viral sharing but dominated by the  
134 selection mosaic effect of host diversity; sub-Saharan Africa), and red-yellow areas (dynamics with low  
135 viral sharing but dominated by trait remixing in host communities; the Middle East). Translating this axis  
136 of variation back into a univariate risk map (fig. 4) highlights that this evolutionary landscape has a  
137 striking correspondence to regions where zoonotic betacoronaviruses have previously emerged.

138 Compared to approaches that map emergence risk based only on the number of known bat hosts of  
139 betacoronaviruses, our framework suggests regions where high viral sharing dominates coevolutionary  
140 dynamics—such as Latin America, or Eurasia above a northing of 30—would pose less of a relative risk of  
141 zoonotic emergence. Nevertheless, areas of high host uniqueness coupled with high viral sharing  
142 (red-to-pink in fig. 3) could create hotspots facilitated by viral codivergence. Our framework identifies

143 Madagascar, where most bat species are endemic following evolutionary divergence from sister species in  
144 both African and Asian continents,<sup>27</sup> as one such hotspot; interestingly, a recent study<sup>28</sup> reported a novel  
145 and highly divergent lineage of nobecoviruses from Madagascar-endemic pteropid bat species (*Pteropus*  
146 *rufus* and *Rousettus madagascariensis*), again supporting the predictive power of the coevolutionary  
147 framework.

148 [Figure 4 about here.]

#### 149 **Human landscapes filter the geography of emergence risk**

150 The relationship between the underlying pathogen pool and emergence risk is mediated by both  
151 human-wildlife interfaces (the probability of spillover) and opportunities for onward horizontal  
152 transmission (the probability that spillovers become epidemics)<sup>1</sup>. As a proxy for both, we finally overlaid  
153 the risk component from the composite map (see above) with the proportion of built land, as a proxy for a  
154 mix of habitat disturbance, potential for bat synanthropy or contact with bridge hosts like livestock,<sup>29,30</sup>  
155 and human population density and connectivity<sup>1,31,32</sup> (fig. 5). Accounting for these factors, most of South  
156 America and Europe are at comparatively lower risk, as—although densely populated—settlements tend to  
157 be in areas with lower potential risk. Conversely, regions like Malaysia and the northern coast of Australia  
158 have a high evolutionary risk component, but should represent a relatively lower effective risk due to low  
159 human density. However, southeast Asia, the Indian subcontinent, and scattered hotspots in sub-Saharan  
160 Africa are at high risk due to the overlap between human populations and natural opportunities for  
161 cross-species transmission of betacoronaviruses.

162 [Figure 5 about here.]

163 Reassuringly, these predictions correspond to the geographic origins of the three bat-origin coronaviruses  
164 that have recently emerged in human populations. While available information puts the spillover of  
165 SARS-CoV-2 in a live animal market in Wuhan, China, the ultimate origin of the virus is almost certainly  
166 in a divergent lineage of sarbecoviruses from Indochina that was poorly characterized prior to the  
167 pandemic.<sup>20–22</sup> Similarly, the SARS-CoV outbreak began in Guangdong province in 2002, reaching  
168 humans through small carnivore bridge hosts, but was eventually traced back to a set of likely progenitor  
169 viruses found in cave-dwelling horseshoe bats in Yunnan province;<sup>33</sup> nearby, antibody evidence has

170 indicated human exposure to SARS-like viruses.<sup>34</sup> MERS-CoV was first detected in Jordan, but is  
171 widespread in camels in East Africa and the Middle East, and may have reached its bridge host decades  
172 earlier than originally supposed;<sup>35</sup> as a result, the geography of the original bat-to-camel transmission is  
173 still widely regarded as uncertain. All of these are broadly consistent with the risk factors we identify.  
174 Notably, India and west Africa are additional hotspots that have yet to experience the emergence of a bat  
175 coronavirus into human populations, but may still be at risk—particularly given known gaps in bat  
176 surveillance,<sup>23</sup> and a dense population in both regions with global connectivity. In any of these regions,  
177 surveillance on viral reservoirs can be paired with targeted monitoring of high-risk human populations  
178 (i.e., those with regular wildlife contact)<sup>36</sup> for maximum impact.

## 179 Conclusion

180 Bats emerged around 64 million years ago, and are one of the most diverse mammalian orders, with more  
181 than 1,400 estimated species.<sup>37,38</sup> They exhibit a broad variety of habitat use, behaviour, and feeding  
182 strategies, putting them at key positions in the delivery and provisioning of several ecosystem services, tied  
183 to important ecosystem-derived benefits to humans.<sup>39</sup> Over two-thirds of bats are known to be either  
184 obligate or facultative insectivores, therefore actively contributing for agricultural pest control,<sup>40,41</sup> and  
185 vectors of pathogens that put a risk on human health;<sup>42,43</sup> some other species are essential links in many  
186 seed-dispersal networks.<sup>44</sup> However, many of these species face a high risk of extinction, particularly given  
187 persecution and killings that sometimes follows from messaging about their role in disease emergence.

188 Areas where bats, viruses, and humans co-occur are not always hotspots of risk for human health; as such,  
189 developing more precise ways to map zoonotic hazards can help bats and humans coexist safely, and  
190 support the conservation of these important and unique animals.

191 Here, we propose a simple framework with broad explanatory power that helps contextualize discoveries  
192 like highly divergent nobecoviruses in Madagascar and the once-neglected adaptive radiation of  
193 sarbecoviruses in the Indochinese peninsula. In doing so, it advances ecological theory beyond the current  
194 state of the art for global maps of emergence risk. For example, previous studies that have used host  
195 richness as a proxy have predicted a high diversity of unsampled bat viruses,<sup>18</sup> bat coronaviruses,<sup>2</sup> and  
196 even specifically betacoronaviruses<sup>19</sup> in both the Amazon and southeast Asia. While we find that both  
197 regions are characterized by unique and diverse communities of both hosts and viruses, our framework is

198 able to identify key differences between the two systems. We find that the merbecovirus complex in Latin  
199 America has been a unique branch of evolution separate from the rest of the global pool, but with limited  
200 potential for viral diversification—a finding that is supported by previous work indicating a higher rate of  
201 codivergence in Latin America.<sup>2,45</sup> In contrast, in southeast Asia, host richness and viral distinctiveness  
202 are high but sharing is low; this suggests a different type of evolutionary dynamics that could generate  
203 high local diversity of viruses through host switching and viral recombination (see e.g.,<sup>13</sup> as well as the  
204 discovery of recombinant viruses with genetic material from both the SARS-CoV and SARS-CoV-2  
205 branches of the Sarbecovirus lineage).<sup>46</sup>

206 Both of these regions are priority areas for sampling, especially given predictions that they contain many  
207 bat hosts of undiscovered betacoronaviruses.<sup>19,23</sup> However, both the evolutionary and ecological aspects of  
208 emergence risk are higher in southeast Asia—a fact that will only become more relevant, as bats track  
209 shifting climates and exchange viruses with other species, creating a hotspot of elevated cross-species  
210 transmission unique to the region.<sup>31,47</sup> Bats—and the spillover of their viruses—are also sensitive to  
211 anthropogenic factors others than climate change, including deforestation and other kinds of habitat loss,  
212 increased stress, and greater contact with potential bridge hosts like domesticated species.<sup>29,48–50</sup> This  
213 represents a challenge for both conservation strategies and pandemic prevention,<sup>51</sup> but identifying areas at  
214 risk, and protecting the health of bats and ecosystems within those zones, can be a win-win intervention  
215 for both.<sup>52–54</sup>

216 **Acknowledgements:** We acknowledge that this study was conducted on land within the traditional  
217 unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and  
218 Omàmiwininiwak nations. This work was supported by funding to the Viral Emergence Research  
219 Initiative (VERENA) consortium including NSF BII 2021909 and a grant from Institut de Valorisation des  
220 Données (IVADO). This research was enabled in part by support provided by Calcul Québec  
221 ([www.calculquebec.ca](http://www.calculquebec.ca)) and Compute Canada ([www.computecanada.ca](http://www.computecanada.ca)). NF is funded by the NSERC  
222 BIOS<sup>2</sup> CREATE program. TP and NF are funded by the Courtois Foundation. RLM was supported by  
223 Bryce Carmine and Anne Carmine (née Percival), through the Massey University Foundation. DJB was  
224 supported by the National Institute of General Medical Sciences of the National Institutes of Health  
225 (P20GM134973).

226 **Methods**

227 **Known *Betacoronavirus* hosts**

228 We downloaded the data on bats hosts of *Betacoronavirus* from  
229 <https://www.viralemergence.org/betacov> on Apr. 2022,<sup>19</sup> and filtered it to “known” hosts (established  
230 before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling and competence  
231 assays since the initial data collection). The original database was assembled by a combination of data  
232 mining and literature surveys, including automated alerts on the “bats” and “coronavirus” keywords to  
233 identify novel empirical evidence of bats-betacoronaviruses associations; this yielded a total of 126 known  
234 hosts, 47 of which were novel hosts.

235 **Bat occurrences**

236 We downloaded the rangemap of every current bat species that was classified as an empirically  
237 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data.<sup>55</sup> The range  
238 maps were subsequently rasterized using the rasterize function from GDAL<sup>56</sup> at a resolution of  
239 approximately 100kmx100km at the equator. For every pixel in the resulting raster where at least one bat  
240 host of *Betacoronavirus* was present, we extract the species pool (list of all known bat hosts), which was  
241 used to calculate the following risk assessment components: bat phylogenetic diversity, bat compositional  
242 uniqueness, and predicted viral sharing risk.

243 **Bat phylogenetic diversity**

244 For every pixel, we measured Faith’s Phylogenetic Diversity<sup>57</sup> based on a recent synthetic tree with robust  
245 time calibration, covering about 6000 mammalian species.<sup>58</sup> Faith’s PD measures the sum of unique  
246 branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more  
247 phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire  
248 tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches  
249 leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the  
250 assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure  
251 incorporates a richness component, which we chose not to correct for; the interpretation of the

252 phylogenetic diversity is therefore a weighted species richness, that accounts for phylogenetic  
253 over/under-dispersal in some places.

## 254 **Bat compositional uniqueness**

255 For every species pool, we measured its Local Contribution to Beta-Diversity;<sup>59</sup> LCBD works from a  
256 species-data matrix (traditionally noted as  $\mathbf{Y}$ ), where species are rows and sites are columns, and a value of  
257 1 indicates occurrence. We extracted the  $\mathbf{Y}$  matrix assuming that every pixel represents a unique location,  
258 and following best practices<sup>60</sup> transformed it using Hellinger's distance to account for unequal bat  
259 richness at different pixels. The correction of raw community data is particularly important for two  
260 reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the effect  
261 of overall species richness, which is already incorporated in the phylogenetic diversity component. High  
262 values of LCBD indicate that the pixel has a community that is on average more dissimilar in species  
263 composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent  
264 results by<sup>61</sup> shows that LCBD measures are robust with regards to spatial scale, and are therefore  
265 applicable at the global scale.

## 266 **Viral sharing between hosts**

267 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a  
268 previously published generalized additive mixed model of virus sharing by a tensor function of  
269 phylogenetic distance and geographic range overlap across mammals.<sup>62</sup> This network stores pairwise  
270 values of viral community similarity. To project viral sharing values into a single value for every pixel, we  
271 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant  
272 bat assemblage is likely to be proficient at exchanging viruses.

## 273 **Composite risk map**

274 To visualize the aggregated risk at the global scale, we combine the three individual risk components  
275 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model.<sup>63</sup> In  
276 this approach, every risk component gets assigned a component in the RGB color model (phylogenetic  
277 diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid

278 RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no  
279 phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for  
280 each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the  
281 risk as colors diverge towards combinations of values for three risk components. Out of the possible  
282 combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic  
283 diversity and low viral sharing,<sup>64</sup> in that this allows multiple independent host-virus coevolutionary  
284 dynamics to take place in the same location. In the colorimetric space, this corresponds to yellow – because  
285 the HSV space is more amenable to calculations for feature extraction,<sup>65</sup> we measured the risk level by  
286 calculating the angular distance of the hue of each pixel to a reference value of 60 (yellow), and weighted  
287 this risk level by the value component. Specifically, given a pixel with colorimetric coordinates  $(h, s, v)$ , its  
288 ranged weighted risk value is

$$v \times \left[ 1 - \frac{|\text{atan}(\cos(\text{rad}(h)), \sin(\text{rad}(h))) - X|}{2\pi} \right],$$

289 where  $X$  is  $\text{atan}(\cos(\text{rad}(60)), \sin(\text{rad}(60)))$ , a constant approximately equal to 0.5235.

## 290 Viral phyogeography and evolutionary diversification

291 To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed  
292 betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data  
293 from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR  
294 betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR  
295 sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated  
296 to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained  
297 words indicating recombinant or laboratory strains including “patent”, “mutant”, “GFP”, and  
298 “recombinant”. We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East  
299 respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus  
300 RdRp sequences were then aligned using MAFFT<sup>66</sup> v1.4.0 (Algorithm FFT-NS-2, Scoring matrix 200PAM /  
301 k=2, gap open penalty 1.53m offset value 0.123) and a maximum likelihood tree reconstructed in  
302 IQ-TREE<sup>67</sup> v1.6.12 with ModelFinder<sup>68</sup> ultrafast bootstrap approximation<sup>69</sup> with a general time reversible  
303 model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of nucleotide

304 substitution (GTR+F+R5).

305 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat  
306 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the  
307 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary  
308 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary  
309 distinctiveness<sup>70</sup> for each of the viruses in the tree, then averaged these at the bat species level, projected  
310 these values onto their geographic distributions, and averaged across every bat found in a given pixel. As  
311 such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral  
312 community believed to be associated with a particular subset of bats present.

### 313 **Co-distribution of hosts and viral hotspots**

314 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the  
315 biogeography of their hosts. To test this idea, we loosely adapted a method from,<sup>71,72</sup> who proposed a  
316 phylogenetic method for the delineation of animal biogeographic regions. In their original method, a  
317 distance matrix - where each row or column represents a geographic raster’s grid cell, and the dissimilarity  
318 values are the “beta diversity similarity” of their community assemble - undergoes non-metric  
319 multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a  
320 four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we  
321 measure the phylogenetic distance between the different viruses in the betacoronaviruses tree by using the  
322 cophenetic function in ape;<sup>73</sup> subsequently, we take a principal components analysis of that distance  
323 matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional  
324 space. We then take the first two principal components and, as with the evolutionary distinctiveness  
325 analysis, aggregated these to a mean host value and projected them using a four-color bivariate map.

326 **References**

- 327 1.
- 328 Plowright, R. K. *et al.* Pathways to zoonotic spillover. *Nature Reviews Microbiology* **15**, 502–510 (2017).
- 329 2.
- 330 Anthony, S. J. *et al.* Global patterns in coronavirus diversity. *Virus Evolution* **3**, (2017).
- 331 3.
- 332 Ruiz-Aravena, M. *et al.* Ecology, evolution and spillover of coronaviruses from bats. *Nature Reviews Microbiology* **20**, 299–314 (2022).
- 333 4.
- 334 Agosta, S. J., Janz, N. & Brooks, D. R. How specialists can be generalists: Resolving the ‘parasite paradox’ and implications for emerging infectious disease. *Zoologia (Curitiba)* **27**, 151–162 (2010).
- 335 5.
- 336 Power, A. G. & Mitchell, C. E. Pathogen Spillover in Disease Epidemics. *The American Naturalist* **164**, S79–S89 (2004).
- 337 6.
- 338 Geoghegan, J. L., Duchêne, S. & Holmes, E. C. Comparative analysis estimates the relative frequencies of co-divergence and cross-species transmission within viral families. *PLOS Pathogens* **13**, e1006215 (2017).
- 339 7.
- 340 Thompson, J. N. *The Geographic Mosaic of Coevolution*. (University Of Chicago Press, 2005).
- 341 8.
- 342 Thompson, J. N. *The Coevolutionary Process*. (University Of Chicago Press, 1994).
- 343 9.
- 344 Janzen, D. H. When is it Coevolution? *Evolution* **34**, 611–612 (1980).
- 345 10.
- 346 Price, P. W. *Macroevolutionary Theory on Macroecological Patterns*. (Cambridge University Press, 2002).  
doi:[10.1017/CBO9780511615030](https://doi.org/10.1017/CBO9780511615030).
- 347 11.
- 348 Gomulkiewicz, R. *et al.* Dos and don’ts of testing the geographic mosaic theory of coevolution. *Heredity* **98**, 249–258 (2007).

- 349 12.
- 350 Thrall, P. H., Hochberg, M. E., Burdon, J. J. & Bever, J. D. Coevolution of symbiotic mutualists and parasites  
in a community context. *Trends in Ecology & Evolution* **22**, 120–126 (2007).
- 351 13.
- 352 Latinne, A. *et al.* Origin and cross-species transmission of bat coronaviruses in China. *bioRxiv: The Preprint  
Server for Biology* 2020.05.31.116061 (2020) doi:[10.1101/2020.05.31.116061](https://doi.org/10.1101/2020.05.31.116061).
- 353 14.
- 354 Anthony, S. J. *et al.* Coronaviruses in bats from Mexico. *The Journal of General Virology* **94**, 1028–1038  
(2013).
- 355 15.
- 356 Góes, L. G. B. *et al.* Novel Bat Coronaviruses, Brazil and Mexico. *Emerging Infectious Diseases* **19**, 1711–1713  
(2013).
- 357 16.
- 358 Góes, L. G. B. *et al.* Genetic diversity of bats coronaviruses in the Atlantic Forest hotspot biome, Brazil.  
*Infection, Genetics and Evolution: Journal of Molecular Epidemiology and Evolutionary Genetics in Infectious  
Diseases* **44**, 510–513 (2016).
- 359 17.
- 360 Brandão, P. E. *et al.* A coronavirus detected in the vampire bat Desmodus rotundus. *Brazilian Journal of  
Infectious Diseases* **12**, 466–468 (2008).
- 361 18.
- 362 Olival, K. J. *et al.* Host and viral traits predict zoonotic spillover from mammals. *Nature* **546**, 646–650 (2017).
- 363 19.
- 364 Becker, D. J. *et al.* Optimising predictive models to prioritise viral discovery in zoonotic reservoirs. *The  
Lancet Microbe* (2022) doi:[10.1016/S2666-5247\(21\)00245-7](https://doi.org/10.1016/S2666-5247(21)00245-7).
- 365 20.
- 366 Worobey, M. *et al.* The Huanan market was the epicenter of SARS-CoV-2 emergence. *Zenodo* (2022)  
doi:[10.5281/zenodo.6299600](https://doi.org/10.5281/zenodo.6299600).
- 367 21.
- 368 Temmam, S. *et al.* Bat coronaviruses related to SARS-CoV-2 and infectious for human cells. *Nature* **604**,  
330–336 (2022).
- 369 22.
- 370 Boni, M. F. *et al.* Evolutionary origins of the SARS-CoV-2 sarbecovirus lineage responsible for the COVID-  
19 pandemic. *Nature microbiology* **5**, 1408–1417 (2020).

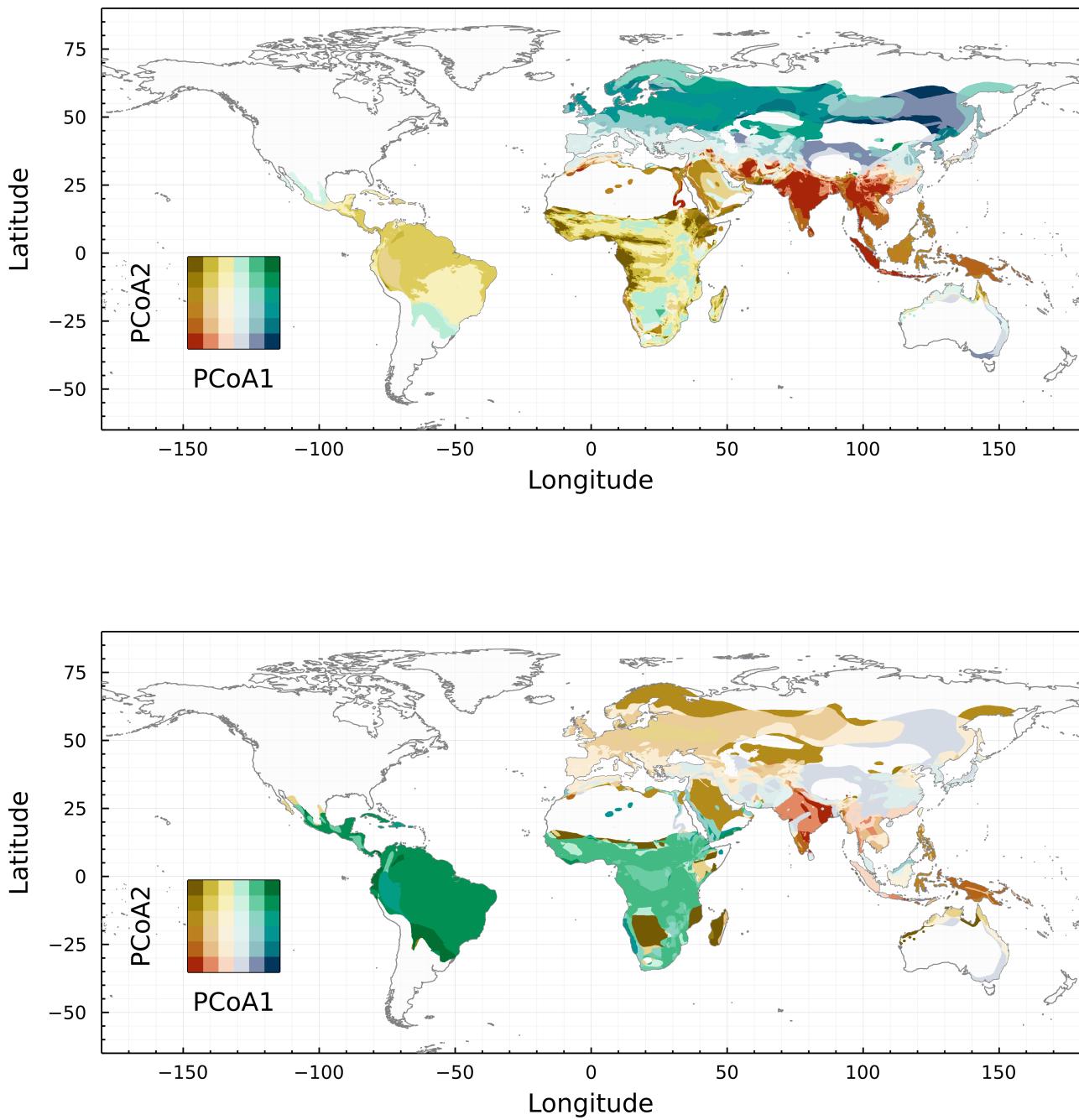
- 371 23.
- 372 Cohen, L. E., Fagre, A. C., Chen, B., Carlson, C. J. & Becker, D. J. Sampling strategies and pre-pandemic  
surveillance gaps for bat coronaviruses. 2022.06.15.496296 (2022) doi:[10.1101/2022.06.15.496296](https://doi.org/10.1101/2022.06.15.496296).
- 373 24.
- 374 Olival, K. J. *et al.* Possibility for reverse zoonotic transmission of SARS-CoV-2 to free-ranging wildlife: A  
case study of bats. *PLoS pathogens* **16**, e1008758 (2020).
- 375 25.
- 376 Ammerman, L. K., Lee, D. N. & Tipps, T. M. First molecular phylogenetic insights into the evolution of free-  
tailed bats in the subfamily Molossinae (Molossidae, Chiroptera). *Journal of Mammalogy* **93**, 12–28 (2012).
- 377 26.
- 378 Banerjee, A. *et al.* Novel Insights Into Immune Systems of Bats. *Frontiers in Immunology* **11**, 26 (2020).
- 379 27.
- 380 Shi, J. J. *et al.* A Deep Divergence Time between Sister Species of Eidolon (Pteropodidae) with Evidence for  
Widespread Panmixia. *Acta Chiropterologica* **16**, 279–292 (2014).
- 381 28.
- 382 Kettenburg, G. *et al.* Full Genome Nobcovirus Sequences From Malagasy Fruit Bats Define a Unique  
Evolutionary History for This Coronavirus Clade. *Frontiers in Public Health* **10**, (2022).
- 383 29.
- 384 Rulli, M. C., D’Odorico, P., Galli, N. & Hayman, D. T. Land-use change and the livestock revolution increase  
the risk of zoonotic coronavirus transmission from rhinolophid bats. *Nature Food* **2**, 409–416 (2021).
- 385 30.
- 386 Cui, J., Li, F. & Shi, Z.-L. Origin and evolution of pathogenic coronaviruses. *Nature Reviews Microbiology*  
**17**, 181–192 (2019).
- 387 31.
- 388 Muylaert, R. L. *et al.* Present and future distribution of bat hosts of sarbecoviruses: Implications for  
conservation and public health. *Proceedings of the Royal Society B: Biological Sciences* **289**, 20220397 (2022).
- 389 32.
- 390 Hassell, J. M., Begon, M., Ward, M. J. & Fèvre, E. M. Urbanization and disease emergence: Dynamics at the  
wildlife–livestock–human interface. *Trends in ecology & evolution* **32**, 55–67 (2017).
- 391 33.
- 392 Hu, B. *et al.* Discovery of a rich gene pool of bat SARS-related coronaviruses provides new insights into the  
origin of SARS coronavirus. *PLoS pathogens* **13**, e1006698 (2017).

- 393 34.
- 394 Wang, N. *et al.* Serological Evidence of Bat SARS-Related Coronavirus Infection in Humans, China. *Virologica Sinica* **33**, 104–107 (2018).
- 395 35.
- 396 Müller, M. A. *et al.* MERS coronavirus neutralizing antibodies in camels, Eastern Africa, 1983–1997. *Emerging infectious diseases* **20**, 2093 (2014).
- 397 36.
- 398 Xu, R.-H. *et al.* Epidemiologic Clues to SARS Origin in China. *Emerging Infectious Diseases* **10**, 1030–1037 (2004).
- 399 37.
- 400 Peixoto, F. P., Braga, P. H. P. & Mendes, P. A synthesis of ecological and evolutionary determinants of bat diversity across spatial scales. *BMC ecology* **18**, 18 (2018).
- 401 38.
- 402 Simmons, N. B. & Cirranello, A. L. Bat Species of the World: A taxonomic and geographic database. <https:////batnames.org/> (2020).
- 403 39.
- 404 Kasso, M. & Balakrishnan, M. Ecological and Economic Importance of Bats (Order Chiroptera). *ISRN Biodiversity* **2013**, e187415 (2013).
- 405 40.
- 406 *Bats in the Anthropocene: Conservation of Bats in a Changing World.* (Springer International Publishing, 2016). doi:[10.1007/978-3-319-25220-9](https://doi.org/10.1007/978-3-319-25220-9).
- 407 41.
- 408 Williams-Guillén, K., Perfecto, I. & Vandermeer, J. Bats Limit Insects in a Neotropical Agroforestry System. *Science* **320**, 70–70 (2008).
- 409 42.
- 410 Gonsalves, L., Bicknell, B., Law, B., Webb, C. & Monamy, V. Mosquito Consumption by Insectivorous Bats: Does Size Matter? *PLOS ONE* **8**, e77183 (2013).
- 411 43.
- 412 Gonsalves, L., Lamb, S., Webb, C., Law, B. & Monamy, V. Do mosquitoes influence bat activity in coastal habitats? *Wildlife Research* **40**, 10–24 (2013).
- 413 44.
- 414 Mello, M. A. R. *et al.* The Missing Part of Seed Dispersal Networks: Structure and Robustness of Bat-Fruit Interactions. *PLOS ONE* **6**, e17395 (2011).

- 415 45.
- 416 Caraballo, D. A. Cross-Species Transmission of Bat Coronaviruses in the Americas: Contrasting Patterns  
between Alphacoronavirus and Betacoronavirus. *Microbiology Spectrum* **0**, e01411–22 (2022).
- 417 46.
- 418 Wu, Z. *et al.* A comprehensive survey of bat sarbecoviruses across China for the origin tracing of SARS-CoV  
and SARS-CoV-2. (2021) doi:[10.21203/rs.3.rs-885194/v1](https://doi.org/10.21203/rs.3.rs-885194/v1).
- 419 47.
- 420 Carlson, C. J. *et al.* Climate change increases cross-species viral transmission risk. *Nature* 1–1 (2022)  
doi:[10.1038/s41586-022-04788-w](https://doi.org/10.1038/s41586-022-04788-w).
- 421 48.
- 422 Alves, D. M. C. C., Diniz-Filho, J. A. F., da Silva e Souza, K., Gouveia, S. F. & Villalobos, F. Geographic  
variation in the relationship between large-scale environmental determinants and bat species richness.  
*Basic and Applied Ecology* **27**, 1–8 (2018).
- 423 49.
- 424 Treitler, J. T., Heim, O., Tschapka, M. & Jung, K. The effect of local land use and loss of forests on bats and  
nocturnal insects. *Ecology and Evolution* **6**, 4289–4297 (2016).
- 425 50.
- 426 Mendenhall, C. D., Karp, D. S., Meyer, C. F. J., Hadly, E. A. & Daily, G. C. Predicting biodiversity change  
and averting collapse in agricultural landscapes. *Nature* **509**, 213–217 (2014).
- 427 51.
- 428 Amman, B. R. *et al.* Investigating the role of bats in emerging zoonoses: Balancing ecology, conservation and  
public health interest. (FAO, 2011).
- 429 52.
- 430 Hopkins, S. R. *et al.* How to identify win-win interventions that benefit human health and conservation.  
*Nature Sustainability* **4**, 298–304 (2021).
- 431 53.
- 432 Plowright, R. K. *et al.* Land use-induced spillover: A call to action to safeguard environmental, animal, and  
human health. *The Lancet Planetary Health* **5**, e237–e245 (2021).
- 433 54.
- 434 OHLEP *et al.* One Health: A new definition for a sustainable and healthy future. *PLOS Pathogens* **18**,  
e1010537 (2022).
- 435 55.
- 436 IUCN. The IUCN Red List of Threatened Species. <https://www.iucnredlist.org> (2021).

- 437 56.
- 438 Rouault, E. et al. *GDAL/OGR Geospatial Data Abstraction software Library*. (Zenodo, 2022).  
doi:[10.5281/ZENODO.5884351](https://doi.org/10.5281/ZENODO.5884351).
- 439 57.
- 440 Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1–10 (1992).
- 441 58.
- 442 Upham, N. S., Esselstyn, J. A. & Jetz, W. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology* **17**, e3000494 (2019).
- 443 59.
- 444 Legendre, P. & De Cáceres, M. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters* **16**, 951–963 (2013).
- 445 60.
- 446 Legendre, P. & Condit, R. Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama. *Forest Ecosystems* **6**, 7 (2019).
- 447 61.
- 448 Dansereau, G., Legendre, P. & Poisot, T. Evaluating ecological uniqueness over broad spatial extents using species distribution modelling. *Oikos* **n/a**, e09063 (2022).
- 449 62.
- 450 Albery, G. F., Eskew, E. A., Ross, N. & Olival, K. J. Predicting the global mammalian viral sharing network using phylogeography. *Nature Communications* **11**, 2260 (2020).
- 451 63.
- 452 Seekell, D. A., Lapierre, J.-F. & Cheruvilil, K. S. A geography of lake carbon cycling. *Limnology and Oceanography Letters* **3**, 49–56 (2018).
- 453 64.
- 454 Gomulkiewicz, R., Thompson, J. N., Holt, R. D., Nuismer, S. L. & Hochberg, M. E. Hot Spots, Cold Spots, and the Geographic Mosaic Theory of Coevolution. *The American Naturalist* **156**, 156–174 (2000).
- 455 65.
- 456 Keke, S., Peng, Z. & Guohui, L. Study on skin color image segmentation used by Fuzzy-c-means arithmetic. in *2010 Seventh International Conference on Fuzzy Systems and Knowledge Discovery* vol. 2 612–615 (2010).
- 457 66.
- 458 Katoh, K. & Standley, D. M. MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution* **30**, 772–780 (2013).

- 459 67.
- 460 Nguyen, L.-T., Schmidt, H. A., von Haeseler, A. & Minh, B. Q. IQ-TREE: A Fast and Effective Stochastic  
Algorithm for Estimating Maximum-Likelihood Phylogenies. *Molecular Biology and Evolution* **32**, 268–274  
(2015).
- 461 68.
- 462 Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A. & Jermiin, L. S. ModelFinder: Fast model  
selection for accurate phylogenetic estimates. *Nature Methods* **14**, 587–589 (2017).
- 463 69.
- 464 Hoang, D. T., Chernomor, O., von Haeseler, A., Minh, B. Q. & Vinh, L. S. UFBoot2: Improving the Ultrafast  
Bootstrap Approximation. *Molecular Biology and Evolution* **35**, 518–522 (2018).
- 465 70.
- 466 Isaac, N. J. B., Turvey, S. T., Collen, B., Waterman, C. & Baillie, J. E. M. Mammals on the EDGE: Conservation  
Priorities Based on Threat and Phylogeny. *PLOS ONE* **2**, e296 (2007).
- 467 71.
- 468 Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *Proceedings of the National  
Academy of Sciences* **104**, 5925–5930 (2007).
- 469 72.
- 470 Kreft, H. & Jetz, W. A framework for delineating biogeographical regions based on species distributions.  
*Journal of Biogeography* **37**, 2029–2053 (2010).
- 471 73.
- 472 Paradis, E. & Schliep, K. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in  
R. *Bioinformatics* **35**, 526–528 (2019).



**Figure 1: Bat and betacoronavirus biogeographic regions.** Phylogeography of bats (top) and viruses (bottom) is categorized based on analysis of bat distributions paired with bat or virus phylogeny. The different colors show tendencies to separate alongside the first two components of a PCoA. Note that the PCoA for the bats and viruses are independent, and so cannot be compared directly – that being said, the regions can be compared across maps.

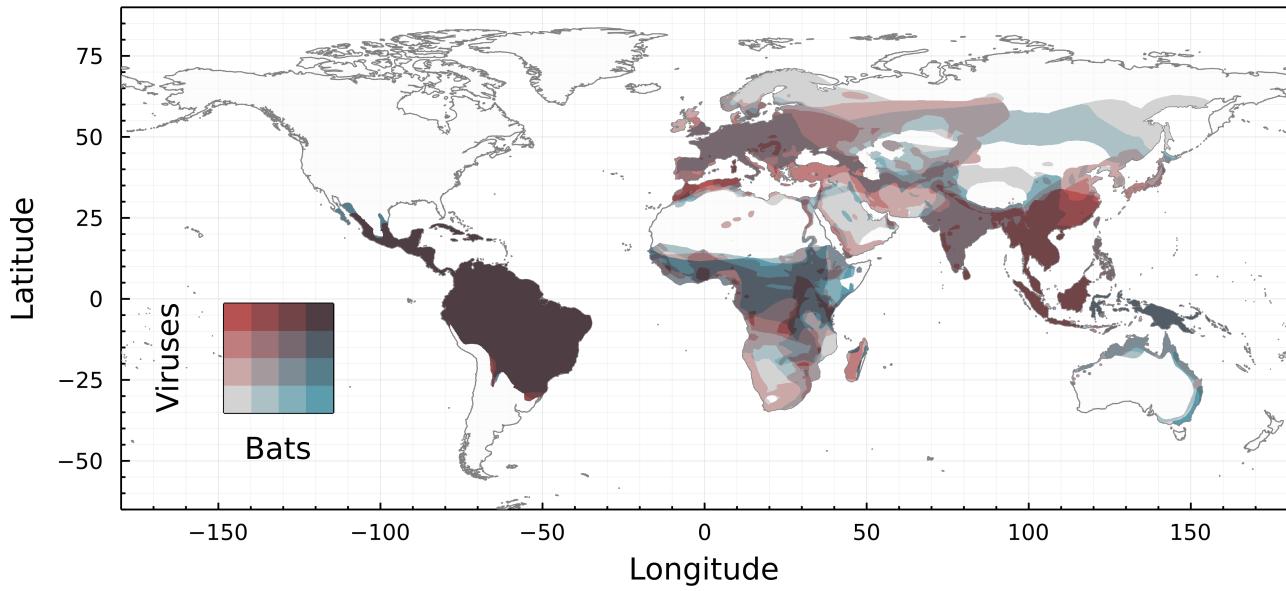
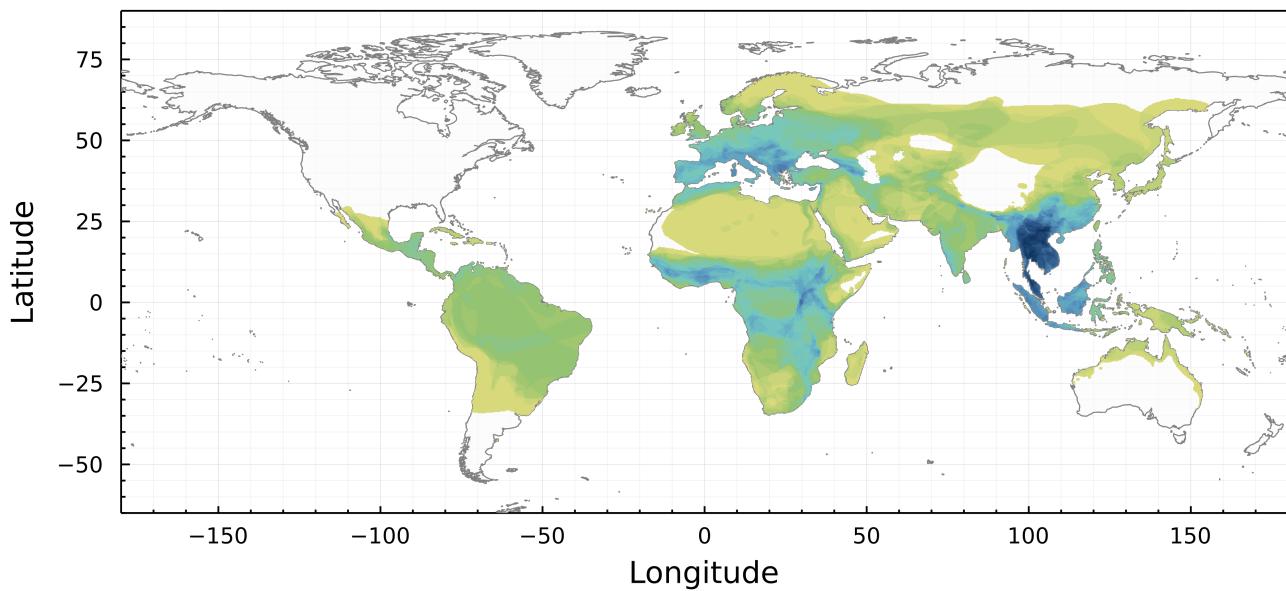


Figure 2: **Bat and betacoronavirus diversity.** Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red).

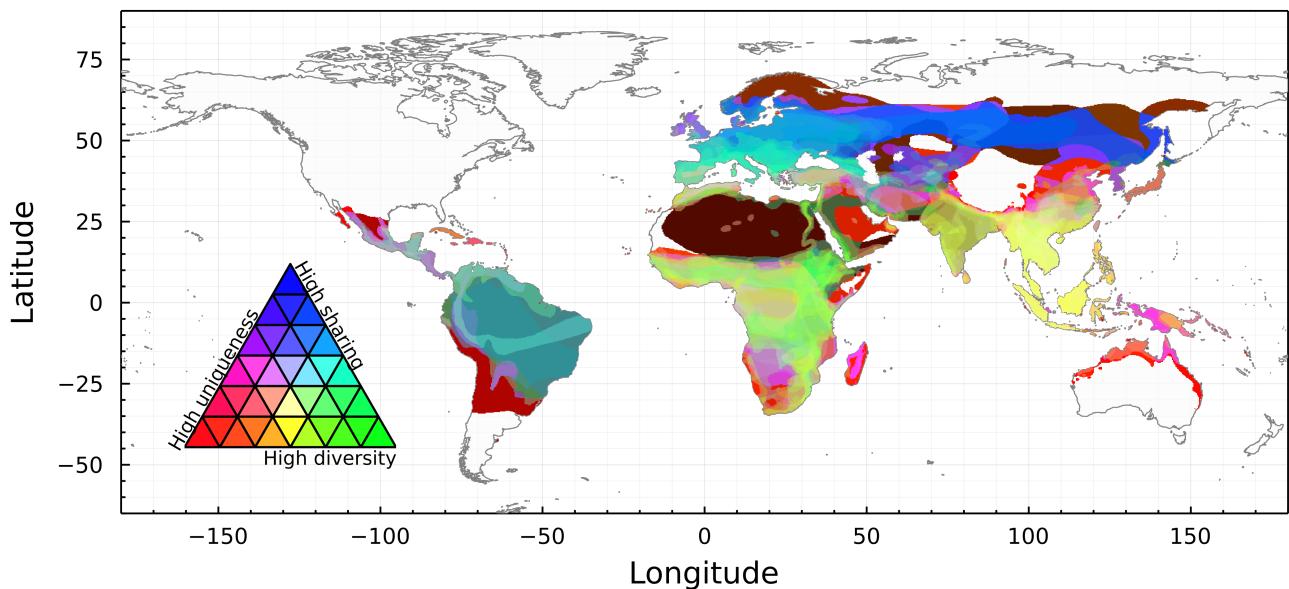


Figure 3: **Trivariate additive mapping of the components of risk.** Viral sharing runs from yellow (low) to blue (high); host phylogenetic diversity runs from pink (low) to high (green); and host compositional uniqueness runs from cyan (low) to red (high). The GMTC suggests that the highest evolutionary potential for emergence exists in unique and diverse host communities with low viral sharing, *i.e.* pixels around yellow. All components within bat host ranges are scaled in brightness so that a pixel with no sharing, no phylogenetic diversity, and no compositional uniqueness would be black, and a pixel with maximal values for each would be white.

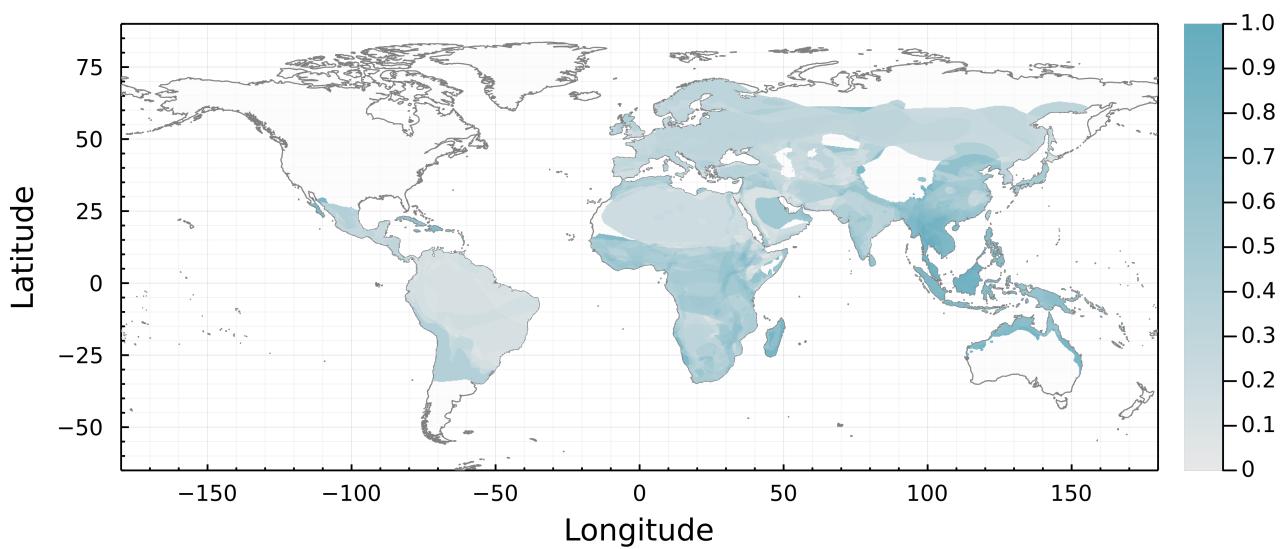


Figure 4: **Evolutionary potential for zoonotic emergence of bat-origin betacoronaviruses.** Risk is a composite measure of the color value and angular distance to the yellow hue in fig. 3 (see Methods).

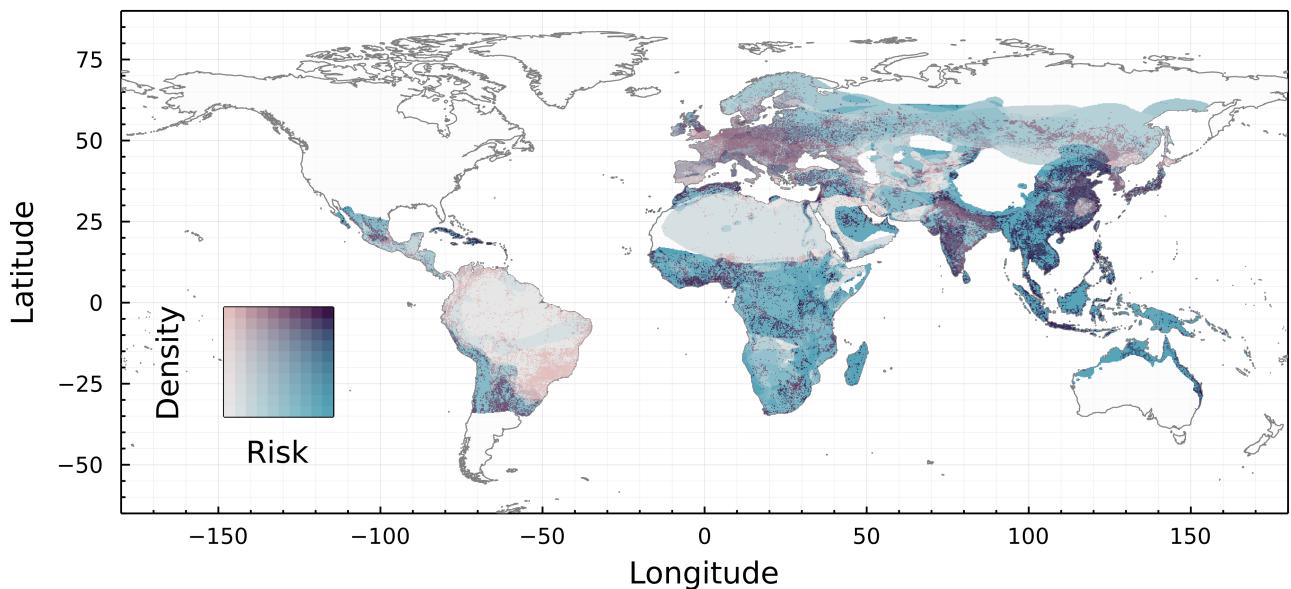


Figure 5: **Overlap between evolutionary potential and ecological opportunity for zoonotic emergence.** Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk, in that the GMTC-derived risk of fig. 4 is high *and* the pixel is densely occupied by human populations.