

# The coevolutionary mosaic of bat betacoronavirus emergence risk

Norma Forero Rocio Munoz<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

<sup>‡</sup> These authors contributed equally to the work

## Correspondance to:

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

Driven by the need to understand the ecological factors involved in the emergence of *Betacoronavirus* (the genus causing SARS, MERS, and COVID-19 in human) through bat hosts, we develop an approach to the assessment of spillover risk based on the Geographic Mosaic Theory of Coevolution. In doing so, we provide a global mapping of the spillover risk posed by betacoronaviruses, reflecting the fact that this risk is best understood through the multi-faceted prism of ecological and evolutionary mechanisms. Our framework reveals that host richness alone, although a component of viral hazard, is not a sufficiently integrative predictor of risk. We offer alternative insights based on viral sharing, host compositional uniqueness, and host phylogenetic diversity and phylogeographic regions. By comparing our aggregated measure of risk to a proxy for human density, namely the proportion of each pixel that is covered by urban or built land, we provide a synthetic risk map, allowing the identification of hotspots where the bat-betacoronavirus interaction network may facilitate the emergence of novel viruses and their spillover into human populations.

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 the southeast Asian peninsula.  
71 These hotspots of bat diversity are generally presumed to be hotspots of viral adaptive radiation, and  
72 therefore areas of concern for human health.<sup>2,18</sup> However, the hotspots of known bat betacoronavirus  
73 hosts show a distinct pattern, with primary hotspots (both in terms of size and higher values) of host  
74 richness situated in southeast Asia, parts of southern Europe, and to a lesser extent parts of Africa in the  
75 -25-0 range of latitudes (fig. 2; top). Although hundreds of species likely host undiscovered  
76 betacoronaviruses, machine learning predictions have suggested that these undiscovered reservoirs should  
77 follow the same diversity gradient.<sup>19</sup> In principle, these hotspots of locally-diverse, virus-rich bat  
78 communities should drive more adaptive 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  
86 (cite2), resulting in a sparser phylogenetic tree, and artificially inflating distinctiveness; conversely,  
87 disproportionate research effort in eastern China<sup>20</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>20</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>3,21</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>22</sup> Together,  
104 these clades of New World bats play host to a distinct regime of betacoronavirus coevolution.

## 105 Coevolution-informed emergence risk is different in space

106 Both the diverse origins of betacoronavirus spillover events and the existence of well defined  
107 co-phylogenetic regions suggest that the system is spatially fragmented enough to create risks of  
108 emergence that are different in their amplitude and in the coevolutionary processes underlying them.  
109 Therefore, we turn to the Geographic Mosaic Theory of Coevolution to provide an assessment of risk  
110 accounting for these processes. In fig. 3, we overlapped three components of spillover risk: viral sharing  
111 (high viral sharing suggests slower, diffuse coevolution); host phylogenetic diversity (high diversity  
112 represents different evolutionary histories, suggesting more variation in immune strategies); host  
113 community uniqueness (high uniqueness suggests more potential for viruses to be exposed to novel host

traits). This approach leads to the definition of broad biogeographic regions of risk, where close colors represent similar risks, and paler pixels represent overall higher risk (see Methods). These regions do not neatly overlap with those defined in fig. 2 or fig. 1, reinforcing the notion that local-scale coevolutionary mosaics exist within co-phylogenetic regions.

[Figure 3 about here.]

Emergence risk is maximized under low viral sharing (host-virus pairs coevolve independently), high phylogenetic diversity (viruses are exposed to different host clades), and high host uniqueness (viruses are experiencing novel, heterogeneous host traits combinations). Under these conditions, very different betacoronaviruses could co-exist at the same place, yet evolve in independent ways. As betacoronaviruses often evolve (including host shifts) through recombination, the co-occurrence of sufficiently distinct viruses is a sufficient major driver of emergence, and the regions that meet these conditions therefore represent the higher risk. In fig. 3, this corresponds to yellow areas (dynamics dominated by low viral sharing, with equal contributions of selection mosaics and trait remixing; South-Eastern Asia, and the Indian sub-continent), green-yellow areas (dynamics with low viral sharing but dominated by the selection mosaic effect of host diversity; Africa below the Sahara desert), and would correspond to red-yellow areas (dynamics with low viral sharing but dominated by trait remixing in host communities; Middle-East). Indeed, these regions are broadly reflected in the risk map fig. 4.

Under this framework, other regions (where high viral sharing dominates the dynamics; see e.g. Latin America, Eurasia above a northing of 30) represent a lower risk of emergence. Nevertheless, areas of high host uniqueness coupled with high viral sharing (red-to-pink in fig. 3) could provide future hotspots of *Betacoronavirus* emergence risk through the sudden divergence of currently diffuse coevolutionary dynamics; this is a likely scenario knowing that can be facilitated by codivergence followed by recombination. Madagascar, where most bat species are endemic following evolutionary divergence from sister species in both African and Asian continents,<sup>23</sup> is one such potential future hotspot. Indeed, recent surveillance<sup>24</sup> has identified a novel *Betacoronavirus* (in the subgenus *Nobecovirus*) in Madagascar-endemic pteropid bat species (*Pteropus rufus*, *Rousettus madagascariensis*), emphasizing strong proof of principle in model predictions.

Our risk decomposition does not account for viral diversity or distinctiveness. Viral data acquisition is rarely disconnected from the acquisition of host data. There are more sources of information on hosts

143 than on viruses, allowing to develop a more robust host-centric perspective on risk. Any emergence risk  
144 estimate would benefit from viral traits related to e.g. ability to switch hosts or pathogenic potential. This  
145 is particularly true under recent findings that the diversification of bat coronaviruses is driven largely by  
146 host shifts (inter-genus or higher levels of cross-species transmission) and, to a lesser degree, cospeciation  
147 and sharing, representing intra-genus cross-species transmission.<sup>2</sup> This diversification is not an actual risk  
148 factor for emergence itself, but acts downstream of an emergence event by increasing the random chance  
149 of the emergence of a virus with the raw genomic components required to eventually infect humans.

150 [Figure 4 about here.]

## 151 Human landscapes filter the geography of emergence risk

152 The relationship between the underlying pathogen pool and emergence risk is mediated by both  
153 human-wildlife interfaces (the probability of spillover) and opportunities for onward transmission (the  
154 probability that spillovers become epidemics)<sup>1</sup>. As a proxy for both, we finally overlaid the risk component  
155 from the composite map (see above) with the proportion of built land, as a proxy for a mix of habitat  
156 disturbance, potential for bat synanthropy or contact with bridge hosts like livestock,<sup>25,26</sup> and human  
157 population density and connectivity<sup>1,27,28</sup> (fig. 5). Accounting for these factors, most of South America and  
158 Europe are at comparatively lower risk, as—although densely populated—settlements tend to be in areas  
159 with lower potential risk. Conversely, regions like Malaysia and the northern coast of Australia have a  
160 high evolutionary risk component, but should represent a relatively lower effective risk due to low human  
161 density. However, southeast Asia, the Indian subcontinent, and scattered hotspots in sub-Saharan Africa  
162 are at high risk due to the overlap between human populations and natural opportunities for cross-species  
163 transmission of betacoronaviruses.

164 [Figure 5 about here.]

165 Reassuringly, these predictions correspond to the geographic origins of the three bat-origin coronaviruses  
166 that have recently emerged in human populations. While available information puts the spillover of  
167 SARS-CoV-2 in a live animal market in Wuhan, China, the ultimate origin of the virus is almost certainly  
168 in a divergent lineage of sarbecoviruses from the Indochinese peninsula that was poorly characterized  
169 prior to the pandemic.<sup>29–31</sup> Similarly, the SARS-CoV outbreak began in Guangdong province in 2002,

reaching humans through small carnivore bridge hosts, but was eventually traced back to a set of likely progenitor viruses found in cave-dwelling horseshoe bats in Yunnan province;<sup>32</sup> nearby, antibody evidence has indicated human exposure to SARS-like viruses.<sup>33</sup> MERS-CoV was originally detected in Saudi Arabia, accompanied by a nearly identical virus sequenced from an Egyptian tomb bat (*Taphozous perforatus*),<sup>34</sup> but is widespread in camels in East Africa and the Middle East, and may have reached its bridge host decades earlier than originally supposed;<sup>35</sup> as a result, the geography of the original bat-to-camel transmission is still widely regarded as uncertain. All of these are broadly consistent with the risk factors we identify. Notably, India and west Africa are additional hotspots that have yet to experience the emergence of a bat coronavirus into human populations, but may still be at risk—particularly given known gaps in bat surveillance,<sup>20</sup> and a dense population in both regions with global connectivity. In any of these regions, surveillance on viral reservoirs can be paired with targeted monitoring of high-risk human populations (i.e., those with regular wildlife contact)<sup>36</sup> for maximum impact.

## Conclusion

Bats are important reservoir hosts for different classes of microorganisms, many of which a threat to human health.<sup>37,38</sup> Chiropters emerged around 64 million years ago and are one of the most diverse mammalian orders, with an estimated richness of more than 1400 species.<sup>39,40</sup> They exhibit a broad variety of habitat use, behaviour, and feeding strategies, putting them at key positions in the delivery and provisioning of several ecosystem services, tied to important ecosystem-derived benefits to human.<sup>41</sup> For example, bats are an essential component of many seed-dispersal networks.<sup>42</sup> Over two-thirds of bats are known to be either obligate or facultative insectivores, therefore actively contributing for agricultural pest control,<sup>43,44</sup> and vectors of pathogens that put a risk on human health.<sup>45,46</sup> Because bats are globally distributed and have a long evolutionary history, phylogeographic and biogeographic approaches are required to shed light on the contemporary distribution of coevolutionary processes between bats and the pathogens they host. Not all areas in which bats, viruses, and human are co-occurring are facing a risk of spillover towards human populations, and the areas in which this risk exist may not be facing risks of the same nature and magnitude.

Here, we propose a simple framework with broad explanatory power that helps contextualize discoveries like highly divergent nobecoviruses in Madagascar and the previously-neglected adaptive radiation of

198 sarbecoviruses outside of southern China and throughout southeast Asia. In doing so, it advances  
199 ecological theory beyond the current state of the art for global maps of emergence risk. For example,  
200 previous studies that have used host richness as proxy have predicted a high diversity of unsampled bat  
201 viruses,<sup>18</sup> bat coronaviruses,<sup>2</sup> and even specifically betacoronaviruses<sup>19</sup> in both the Amazon and southeast  
202 Asia. While we find that both regions are characterized by highly divergent host and viral communities,  
203 our framework identifies key differences between the regions. We find that Latin America is a hotspot of  
204 both host and viral distinctiveness, suggesting that this branch of the bat-betacoronavirus complex may be  
205 undergoing independent evolutionary dynamics from the rest of the global pool, but with limited potential  
206 for viral diversification—a finding that is supported by previous work indicating a higher rate of  
207 codivergence in Latin America.<sup>2</sup> In contrast, in southeast Asia, host richness and viral distinctiveness are  
208 high but sharing is low; this suggests a different type of evolutionary dynamics that could generate high  
209 local diversity of viruses through host switching and viral recombination (see e.g.,<sup>13</sup> as well as the  
210 discovery of recombinant viruses that share genetic material from both the SARS-CoV and SARS-CoV-2  
211 branches of the Sarbecovirus lineage).<sup>47</sup> Both of these regions are priority areas for sampling, especially  
212 given predictions that they contain many bat hosts of undiscovered betacoronaviruses.<sup>19,20</sup> However, both  
213 the evolutionary and ecological aspects of emergence risk are likely higher in southeast Asia—a fact that  
214 will only become more relevant, as bats track shifting climates and exchange viruses with other species,  
215 creating a hotspot of cross-species transmission unique to the region.<sup>48</sup>

216 The diversity and diversification potential of bats responds to anthropogenic factors others than shifting  
217 climates.<sup>49</sup> Land use changes could significantly decrease bat suitability, notably through effects on diet  
218 and availability of habitats.<sup>50</sup> As our results establish that the diversification of bats betacoronaviruses  
219 happens on top of processes affecting hosts, biogeographic variation in human population density and  
220 anthropogenic disturbances may feed into co-evolutionary dynamics. Increase in humans-hosts contacts  
221 also increase the risk of emergence of novel diseases,<sup>51</sup> so does the changes in landscape connectivity at  
222 local/regional scales.<sup>52</sup> This represents a challenge for both conservation strategies and disease ecology:  
223 some areas can a high emergence risk and more potential for the acquisition of zoonotic viruses through  
224 bat-human encounters.<sup>53</sup> In particular, the challenge ahead lies in the need to quantify actual exposure  
225 (and risk) accounting for several transmission scenarios, including both direct and indirect bat - human  
226 interactions, and feeding back into the provision of ecosystem services by bats.

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237 **Methods**

238 **Known *Betacoronavirus* hosts**

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

246 **Bat occurrences**

247 We downloaded the rangemap of every current bat species that was classified as an empirically  
248 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data.<sup>54</sup> The range  
249 maps were subsequently rasterized using the rasterize function from GDAL<sup>55</sup> at a resolution of  
250 approximately 100kmx100km. For every pixel in the resulting raster where at least one bat host of  
251 *Betacoronavirus* was present, we extract the species pool (list of all known bat hosts), which was used to  
252 calculate the following risk assessment components: bat phylogenetic diversity, bat compositional  
253 uniqueness, and predicted viral sharing risk.

254 **Bat phylogenetic diversity**

255 For every pixel, we measured Faith’s Phylogenetic Diversity<sup>56</sup> based on a recent synthetic tree with robust  
256 time calibration, covering about 6000 mammalian species.<sup>57</sup> Faith’s PD measures the sum of unique  
257 branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more  
258 phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire  
259 tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches  
260 leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the  
261 assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure  
262 incorporates a richness component, which we chose not to correct for; the interpretation of the

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

## 265 **Bat compositional uniqueness**

266 For every species pool, we measured its Local Contribution to Beta-Diversity;<sup>58</sup> LCBD works from a  
267 species-data matrix (traditionally noted as  $\mathbf{Y}$ ), where species are rows and sites are columns, and a value of  
268 1 indicates occurrence. We extracted the  $\mathbf{Y}$  matrix assuming that every pixel represents a unique location,  
269 and following best practices<sup>59</sup> transformed it using Hellinger's distance to account for unequal bat  
270 richness at different pixels. The correction of raw community data is particularly important for two  
271 reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the effect  
272 of overall species richness, which is already incorporated in the phylogenetic diversity component. High  
273 values of LCBD indicate that the pixel has a community that is on average more dissimilar in species  
274 composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent  
275 results by<sup>60</sup> shows that LCBD measures are robust with regards to spatial scale, and are therefore  
276 applicable at the global scale.

## 277 **Viral sharing between hosts**

278 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a  
279 previously published generalized additive mixed model of virus sharing by a tensor function of  
280 phylogenetic distance and geographic range overlap across mammals.<sup>61</sup> This network stores pairwise  
281 values of viral community similarity. To project viral sharing values into a single value for every pixel, we  
282 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant  
283 bat assemblage is likely to be proficient at exchanging viruses.

## 284 **Composite risk map**

285 To visualize the aggregated risk at the global scale, we combine the three individual risk components  
286 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model.<sup>62</sup> In  
287 this approach, every risk component gets assigned a component in the RGB color model (phylogenetic  
288 diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid

289 RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no  
290 phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for  
291 each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the  
292 risk as colors diverge towards combinations of values for three risk components. Out of the possible  
293 combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic  
294 diversity and low viral sharing,<sup>63</sup> in that this allows multiple independent host-virus coevolutionary  
295 dynamics to take place in the same location. In the colorimetric space, this corresponds to yellow – because  
296 the HSV space is more amenable to calculations for feature extraction,<sup>64</sup> we measured the risk level by  
297 calculating the angular distance of the hue of each pixel to a reference value of 60 (yellow), and weighted  
298 this risk level by the value component. Specifically, given a pixel with colorimetric coordinates  $(h, s, v)$ , its  
299 ranged weighted risk value is

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

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

### 301 **Viral phyogeography and evolutionary diversification**

302 To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed  
303 betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data  
304 from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR  
305 betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR  
306 sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated  
307 to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained  
308 words indicating recombinant or laboratory strains including “patent”, “mutant”, “GFP”, and  
309 “recombinant”. We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East  
310 respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus  
311 RdRp sequences were then aligned using MAFFT<sup>65</sup> v1.4.0 (Algorithm FFT-NS-2, Scoring matrix 200PAM /  
312 k=2, gap open penalty 1.53m offset value 0.123) and a maximum likelihood tree reconstructed in  
313 IQ-TREE<sup>66</sup> v1.6.12 with ModelFinder<sup>67</sup> ultrafast bootstrap approximation<sup>68</sup> with a general time reversible  
314 model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of nucleotide

315 substitution (GTR+F+R5).

316 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat  
317 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the  
318 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary  
319 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary  
320 distinctiveness<sup>69</sup> for each of the viruses in the tree, then averaged these at the bat species level, projected  
321 these values onto their geographic distributions, and averaged across every bat found in a given pixel. As  
322 such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral  
323 community believed to be associated with a particular subset of bats present.

324 **Co-distribution of hosts and viral hotspots**

325 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the  
326 biogeography of their hosts. To test this idea, we loosely adapted a method from,<sup>70,71</sup> who proposed a  
327 phylogenetic method for the delineation of animal biogeographic regions. In their original method, a  
328 distance matrix - where each row or column represents a geographic raster’s grid cell, and the dissimilarity  
329 values are the “beta diversity similarity” of their community assemble - undergoes non-metric  
330 multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a  
331 four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we  
332 measure the phylogenetic distance between the different viruses in the betacoronaviruses tree by using the  
333 cophenetic function in ape;<sup>72</sup> subsequently, we take a principal components analysis of that distance  
334 matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional  
335 space. We then take the first two principal components and, as with the evolutionary distinctiveness  
336 analysis, aggregated these to a mean host value and projected them using a four-color bivariate map.

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Figure 1: Phylogeographic regions of bats (top) and viruses (bottom) based on the joint analysis of their occurrence and phylogenetic relatedness. 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.

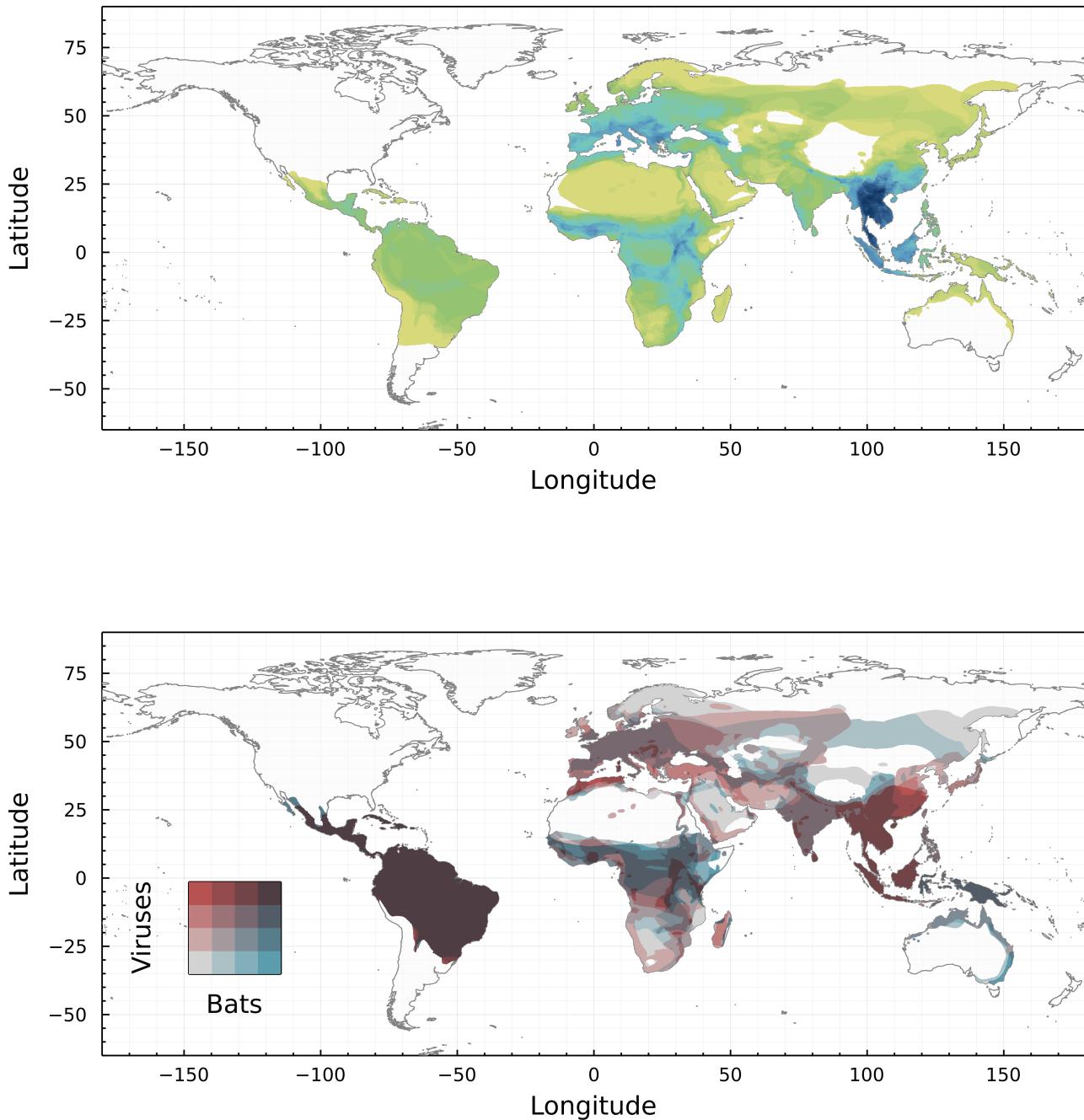


Figure 2: Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red).

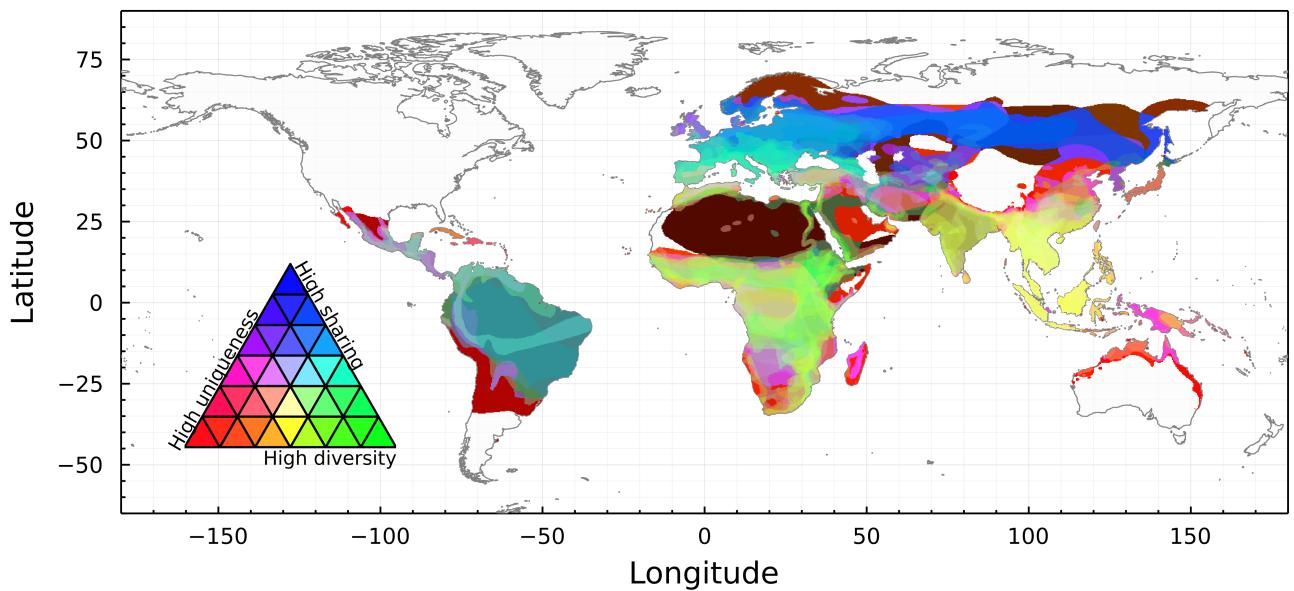


Figure 3: Trivariate additive mapping of the components of risk in the red/green/blue, where high virus sharing is encoded in the blue channel, host phylogenetic diversity in the green channel, and compositional uniqueness in the red channel. The main driver of emergence risk (possibility of spatially overlapped but coevolutionarily independent host-viral dynamics) corresponds to low viral sharing, *i.e.* pixels around yellow. Pixels in the yellow-green space (Africa) correspond to areas where, despite the potential for viral diversification, coevolutionary dynamics are likely to currently be dominated by the effect of host phylogenetic diversity.

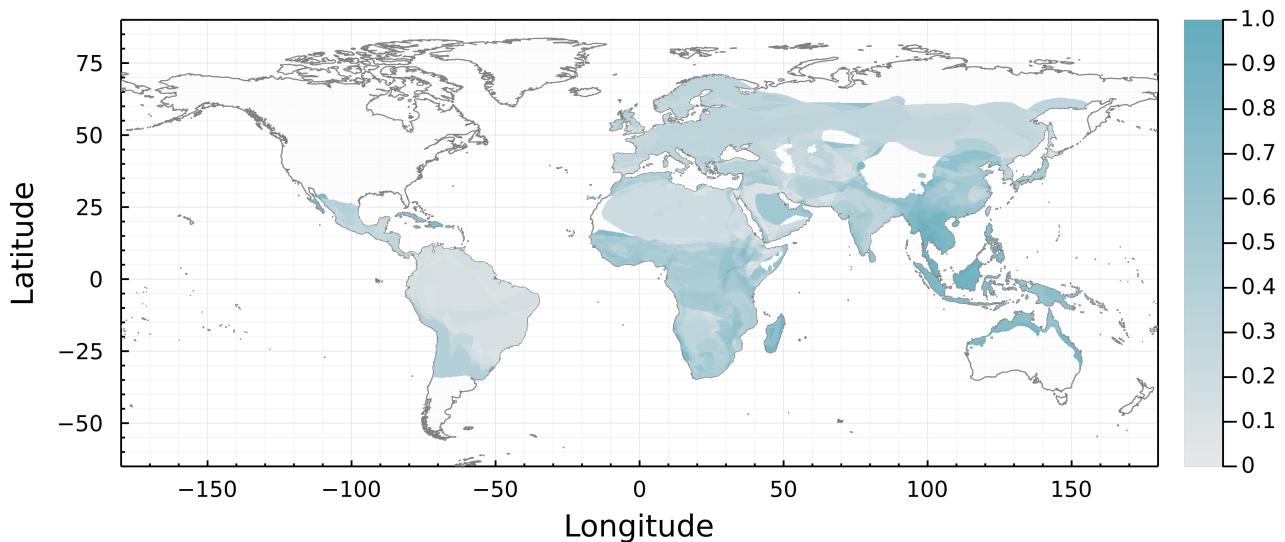


Figure 4: Extraction of a measure of *Betacoronavirus* emergence risk from bat hosts based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on these analyses, South-Eastern Asia, Madagascar, the Middle-East, and Africa below the Sahara desert have the highest relative risk of emergence.

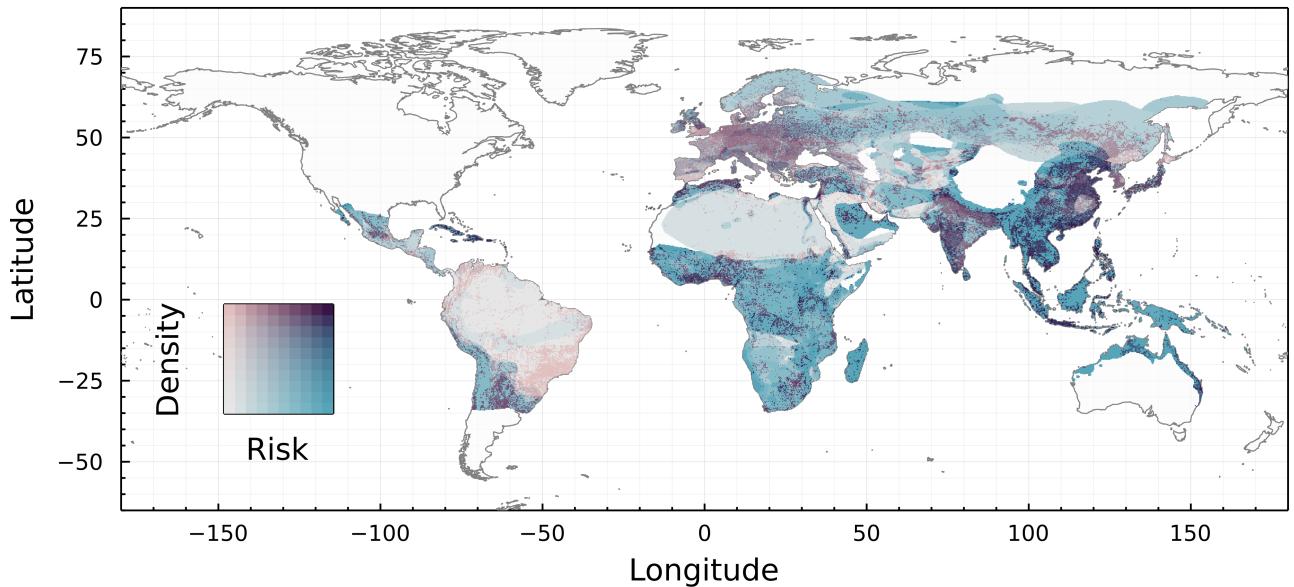


Figure 5: Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk, in that the GMTC-derived risk of fig. 4 is high *and* the pixel is densely occupied by human populations. This approach increases the relative risk of several regions in Africa, and highlights the risk in India, southeast China, and the Arabian peninsula where areas of high to moderate risk overlap with areas of denser population.