

The coevolutionary mosaic of bat betacoronavirus emergence risk

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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.¹ Although host richness is often used as a superficial
3 proxy for spillover risk,^{2,3} 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.⁴ 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,⁵ particularly given that cross-species transmission may, as a rule, structure viral evolution
8 more than co-divergence with hosts.⁶ 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.⁷ The GMTC posits that
12 coevolutionary processes among pairs⁸ or complexes⁹ 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.¹⁰ The GMTC predicts a spatial fragmentation of
15 coevolutionary dynamics under the joint action of three processes:¹¹ 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;¹² 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—²a 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.^{2,3} 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).³

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—²a 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;^{2,13} 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);^{3,13} 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) (refs1). At the coarsest scale, these heterogeneities are lost, and
65 betacoronavirus biogeography tracks the deep rifts in bat evolutionary history—but within broad regions,
66 the component 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.^{2,14} 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.¹⁵ 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 China¹⁶ 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 researchers¹³ (and so have been sampled most intensively).¹⁶ 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^{3,15}. 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.^{3,17} 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) (refs3).
102 The 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 (refs4).
104 Together, 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 As host richness, joint distinctiveness, or phylogeographic structure suggest that the bat-betacoronaviruses
107 complex is globally fragmented enough to give rise to both different levels of risk (as evidenced by the
108 spatial location of spillover events) and different types of co-evolutionary dynamics, we turn to the
109 Geographic Mosaic Theory of Coevolution to provide a measure of risk accounting for multiple processes.
110 In fig. 3, we overlapped three components of spillover risk: viral sharing, i.e. the chance that two bats will
111 share viruses overall; Local Contribution to Beta Diversity, i.e. the fact that a bat community is
112 compositionally unique compared to the average compositional similarity across the entire system; finally,
113 host phylogenetic diversity, i.e. how dispersed the bats in a location are within the tree of life. This

114 approach leads to the definition of broad biogeographic regions of risk, where the same color represents
115 the same type of risk. By way of contrast to figures fig. 2 and fig. 1, these regions do not necessarily
116 overlap with previous spatial partitions of the bat-betacoronaviruses complex.

117 [Figure 3 about here.]

118 From the perspective of spillover risk, the most important combination of factors is a high phylogenetic
119 diversity of hosts with low viral sharing; this, essentially, means that very different betacoronaviruses
120 could co-exist within the same place. This is particularly the case given that betacoronaviruses often
121 evolve and even achieve host shifts through recombination, which requires the co-occurrence of
122 sufficiently distinct viruses to be a major driver of emergence. In fig. 3, this corresponds to yellow to pale
123 green areas, which are essentially limited to South-Eastern Asia, and to some part of Sub-Saharan Africa.
124 Adopting a geographic mosaic theory perspective on risk, other regions of the world are of lesser concern
125 (fig. 4). Our risk decomposition does not account for viral diversity or distinctiveness. The simple
126 rationale behind it is that the acquisition of viral data is rarely disconnected from the acquisition of host
127 data. There are more sources of information on hosts than on viruses, allowing to develop a host-centric
128 perspective on risk (although this estimate would be more accurate with viral traits related to e.g. ability to
129 switch hosts or pathogenic potential). Areas with high bat diversity and high turnover *may* facilitate the
130 evolutionary radiation of viruses, matching previous findings that the diversification of bat coronaviruses
131 is driven largely by host shifts (inter-genus or higher levels of cross-species transmission) and, to a lesser
132 degree, cospeciation and sharing, representing intra-genus cross-species transmission.² This
133 diversification is not an actual risk factor for spillover itself, but acts downstream of a spillover event by
134 increasing the random chance of the emergence of a virus with the raw genomic components required for
135 the potential to infect humans.

136 [Figure 4 about here.]

137 From another perspective, areas of high host uniqueness and virus sharing (red-to-pink) could provide
138 hotspots of *Betacoronavirus* risk through mixing of unique viruses (via codivergence) and in turn
139 recombination. Under our framework, such a hotspot was identified in Madagascar, where most bat
140 species are endemic following evolutionary divergence from sister species in both African and Asian
141 continents.¹⁸ Recent surveillance¹⁹ has identified a novel *Betacoronavirus* (in the subgenus *Nobecovirus*) in

142 Madagascar-endemic pteropid bat species (*Pteropus rufus*, *Rousettus madagascariensis*), emphasizing
143 strong proof of principle in model predictions.

144 **Human landscapes filter the geography of emergence risk**

145 The relationship between the underlying pathogen pool and emergence risk is mediated by both
146 human-wildlife interfaces (the probability of spillover) and opportunities for onward transmission (the
147 probability that spillovers become epidemics)¹. As a proxy for both, we finally overlaid the risk component
148 from the composite map (see above) with the proportion of built land, as a proxy for a mix of habitat
149 disturbance, potential for bat synanthropy or contact with bridge hosts like livestock,^{20,21} and human
150 population density and connectivity^{1,22,23} (fig. 5). Accounting for these factors, most of South America and
151 Europe are at comparatively lower risk, as—although densely populated—settlements tend to be in areas
152 with lower potential risk. Conversely, regions like Malaysia and the northern coast of Australia have a
153 high evolutionary risk component, but should represent a relatively lower effective risk due to low human
154 density. However, southeast Asia, the Indian subcontinent, and scattered hotspots in sub-Saharan Africa
155 are at high risk due to the overlap between human populations and natural opportunities for cross-species
156 transmission of betacoronaviruses.

157 [Figure 5 about here.]

158 Reassuringly, these predictions correspond to the geographic origins of the three bat-origin coronaviruses
159 that have recently emerged in human populations. While available information puts the spillover of
160 SARS-CoV-2 in a live animal market in Wuhan, China, the ultimate origin of the virus is almost certainly
161 in a divergent lineage of sarbecoviruses from the Indochinese peninsula that was poorly characterized
162 prior to the pandemic.^{24–26} Similarly, the SARS-CoV outbreak began in Guangdong province in 2002,
163 reaching humans through small carnivore bridge hosts, but was eventually traced back to a set of likely
164 progenitor viruses found in cave-dwelling horseshoe bats in Yunnan province;²⁷ nearby, antibody
165 evidence has indicated human exposure to SARS-like viruses.²⁸ MERS-CoV was originally detected in
166 Saudi Arabia, accompanied by a nearly identical virus sequenced from an Egyptian tomb bat (*Taphozous*
167 *perforatus*)²⁹, but is widespread in camels in East Africa and the Middle East, and may have reached its
168 bridge host decades earlier than originally supposed;³⁰ as a result, the geography of the original
169 bat-to-camel transmission is still widely regarded as uncertain. All of these are broadly consistent with the

170 risk factors we identify. Notably, India and west Africa are additional hotspots that have yet to experience
171 the emergence of a bat coronavirus into human populations, but may still be at risk—particularly given
172 known gaps in bat surveillance,¹⁶ and a dense population in both regions with global connectivity. In any
173 of these regions, surveillance on viral reservoirs can be paired with targeted monitoring of high-risk
174 human populations (i.e., those with regular wildlife contact)³¹ for maximum impact.

175 Conclusion

176 Bats are important reservoir hosts for different classes of microorganisms, many of which a threat to
177 human health.^{32,33} Chiropterans emerged around 64 million years ago and are one of the most diverse
178 mammalian orders, with an estimated richness of more than 1400 species.^{34,35} They exhibit a broad variety
179 of habitat use, behaviour, and feeding strategies, putting them at key positions in the delivery and
180 provisioning of several ecosystem services, tied to important ecosystem-derived benefits to human.³⁶ For
181 example, bats are an essential component of many seed-dispersal networks.³⁷ Over two-thirds of bats are
182 know to be either obligate or facultative insectivores, therefore actively contributing for agricultural pest
183 control,^{38,39} and vectors of pathogens that put a risk on human health.^{40,41} Because bats are globally
184 distributed and have a long evolutionary history, phylogeographic and biogeographic approaches are
185 required to shed light on the contemporary distribution of coevolutionary processes between bats and the
186 pathogens they host. Not all areas in which bats, viruses, and human are co-occurring are facing a risk of
187 spillover towards human populations, and the areas in which this risk exist may not be facing risks of the
188 same nature and magnitude.

189 Here, we propose a simple framework with broad explanatory power that helps contextualize discoveries
190 like highly divergent nobecoviruses in Madagascar and the previously-neglected adaptive radiation of
191 sarbecoviruses outside of southern China and throughout southeast Asia. In doing so, it advances
192 ecological theory beyond the current state of the art for global maps of emergence risk. For example,
193 previous studies that have used host richness as proxy have predicted a high diversity of unsampled bat
194 viruses,¹⁴ bat coronaviruses,² and even specifically betacoronaviruses¹⁵ in both the Amazon and southeast
195 Asia. While we find that both regions are characterized by highly divergent host and viral communities,
196 our framework identifies key differences between the regions. We find that Latin America is a hotspot of
197 both host and viral distinctiveness, suggesting that this branch of the bat-betacoronavirus complex may be

198 undergoing independent evolutionary dynamics from the rest of the global pool, but with limited potential
199 for viral diversification—a finding that is supported by previous work indicating a higher rate of
200 codivergence in Latin America.² In contrast, in southeast Asia, host richness and viral distinctiveness are
201 high but sharing is low; this suggests a different type of evolutionary dynamics that could generate high
202 local diversity of viruses through host switching and viral recombination (see e.g.,¹³ as well as the
203 discovery of recombinant viruses that share genetic material from both the SARS-CoV and SARS-CoV-2
204 branches of the Sarbecovirus lineage).⁴² Both of these regions are priority areas for sampling, especially
205 given predictions that they contain many bat hosts of undiscovered betacoronaviruses.^{15,16} However, both
206 the evolutionary and ecological aspects of emergence risk are likely higher in southeast Asia—a fact that
207 will only become more relevant, as bats track shifting climates and exchange viruses with other species,
208 creating a hotspot of cross-species transmission unique to the region.⁴³

209 The diversity and diversification potential of bats responds to anthropogenic factors others than shifting
210 climates.⁴⁴ Land use changes could significantly decrease bat suitability, notably through effects on diet
211 and availability of habitats.⁴⁵ As our results establish that the diversification of bats betacoronaviruses
212 happens on top of processes affecting hosts, biogeographic variation in human population density and
213 anthropogenic disturbances may feed into co-evolutionary dynamics. Increase in humans-hosts contacts
214 also increase the risk of emergence of novel diseases,⁴⁶ so does the changes in landscape connectivity at
215 local/regional scales.⁴⁷ This represents a challenge for both conservation strategies and disease ecology:
216 some areas can a high emergence risk and more potential for the acquisition of zoonotic viruses through
217 bat-human encounters.⁴⁸ In particular, the challenge ahead lies in the need to quantify actual exposure
218 (and risk) accounting for several transmission scenarios, including both direct and indirect bat - human
219 interactions, and feeding back into the provision of ecosystem services by bats.

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230 **Methods**

231 **Known *Betacoronavirus* hosts**

232 We downloaded the data on bats hosts of *Betacoronavirus* from
233 <https://www.viralemergence.org/betacov> on Apr. 2022,¹⁵ and filtered it to “known” hosts (established
234 before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling and competence
235 assays since the initial data collection). The original database was assembled by a combination of data
236 mining and literature surveys, including automated alerts on the “bats” and “coronavirus” keywords to
237 identify novel empirical evidence of bats-betacoronaviruses associations; this yielded a total of 126 known
238 hosts, 47 of which were novel hosts.

239 **Bat occurrences**

240 We downloaded the rangemap of every current bat species that was classified as an empirically
241 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data.⁴⁹ The range
242 maps were subsequently rasterized using the rasterize function from GDAL⁵⁰ at a resolution of
243 approximately 100kmx100km. For every pixel in the resulting raster where at least one bat host of
244 *Betacoronavirus* was present, we extract the species pool (list of all known bat hosts), which was used to
245 calculate the following risk assessment components: bat phylogenetic diversity, bat compositional
246 uniqueness, and predicted viral sharing risk.

247 **Bat phylogenetic diversity**

248 For every pixel, we measured Faith’s Phylogenetic Diversity⁵¹ based on a recent synthetic tree with robust
249 time calibration, covering about 6000 mammalian species.⁵² Faith’s PD measures the sum of unique
250 branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more
251 phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire
252 tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches
253 leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the
254 assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure
255 incorporates a richness component, which we chose not to correct for; the interpretation of the

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

258 **Bat compositional uniqueness**

259 For every species pool, we measured its Local Contribution to Beta-Diversity;⁵³ LCBD works from a
260 species-data matrix (traditionally noted as \mathbf{Y}), where species are rows and sites are columns, and a value of
261 1 indicates occurrence. We extracted the \mathbf{Y} matrix assuming that every pixel represents a unique location,
262 and following best practices⁵⁴ transformed it using Hellinger's distance to account for unequal bat
263 richness at different pixels. The correction of raw community data is particularly important for two
264 reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the effect
265 of overall species richness, which is already incorporated in the phylogenetic diversity component. High
266 values of LCBD indicate that the pixel has a community that is on average more dissimilar in species
267 composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent
268 results by⁵⁵ shows that LCBD measures are robust with regards to spatial scale, and are therefore
269 applicable at the global scale.

270 **Viral sharing between hosts**

271 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a
272 previously published generalized additive mixed model of virus sharing by a tensor function of
273 phylogenetic distance and geographic range overlap across mammals.⁵⁶ This network stores pairwise
274 values of viral community similarity. To project viral sharing values into a single value for every pixel, we
275 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant
276 bat assemblage is likely to be proficient at exchanging viruses.

277 **Composite risk map**

278 To visualize the aggregated risk at the global scale, we combine the three individual risk components
279 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model.⁵⁷ In
280 this approach, every risk component gets assigned a component in the RGB color model (phylogenetic
281 diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid

282 RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no
283 phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for
284 each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the
285 risk as colors diverge towards combinations of values for three risk components. Out of the possible
286 combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic
287 diversity and low viral sharing,⁵⁸ in that this allows multiple independent host-virus coevolutionary
288 dynamics to take place in the same location. In the colorimetric space, this corresponds to yellow – because
289 the HSV space is more amenable to calculations for feature extraction,⁵⁹ we measured the risk level by
290 calculating the angular distance of the hue of each pixel to a reference value of 60 (yellow), and weighted
291 this risk level by the value component. Specifically, given a pixel with colorimetric coordinates (h, s, v) , its
292 ranged weighted risk value is

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

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

294 **Viral phyogeography and evolutionary diversification**

295 To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed
296 betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data
297 from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR
298 betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR
299 sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated
300 to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained
301 words indicating recombinant or laboratory strains including “patent”, “mutant”, “GFP”, and
302 “recombinant”. We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East
303 respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus
304 RdRp sequences were then aligned using MAFFT⁶⁰ v1.4.0 (Algorithm FFT-NS-2, Scoring matrix 200PAM /
305 k=2, gap open penalty 1.53m offset value 0.123) and a maximum likelihood tree reconstructed in
306 IQ-TREE⁶¹ v1.6.12 with ModelFinder⁶² ultrafast bootstrap approximation⁶³ with a general time reversible
307 model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of nucleotide

308 substitution (GTR+F+R5).

309 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat
310 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the
311 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary
312 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary
313 distinctiveness⁶⁴ for each of the viruses in the tree, then averaged these at the bat species level, projected
314 these values onto their geographic distributions, and averaged across every bat found in a given pixel. As
315 such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral
316 community believed to be associated with a particular subset of bats present.

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

318 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the
319 biogeography of their hosts. To test this idea, we loosely adapted a method from,^{65,66} who proposed a
320 phylogenetic method for the delineation of animal biogeographic regions. In their original method, a
321 distance matrix - where each row or column represents a geographic raster’s grid cell, and the dissimilarity
322 values are the “beta diversity similarity” of their community assemble - undergoes non-metric
323 multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a
324 four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we
325 measure the phylogenetic distance between the different viruses in the betacoronaviruses tree by using the
326 cophenetic function in ape;⁶⁷ subsequently, we take a principal components analysis of that distance
327 matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional
328 space. We then take the first two principal components and, as with the evolutionary distinctiveness
329 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.

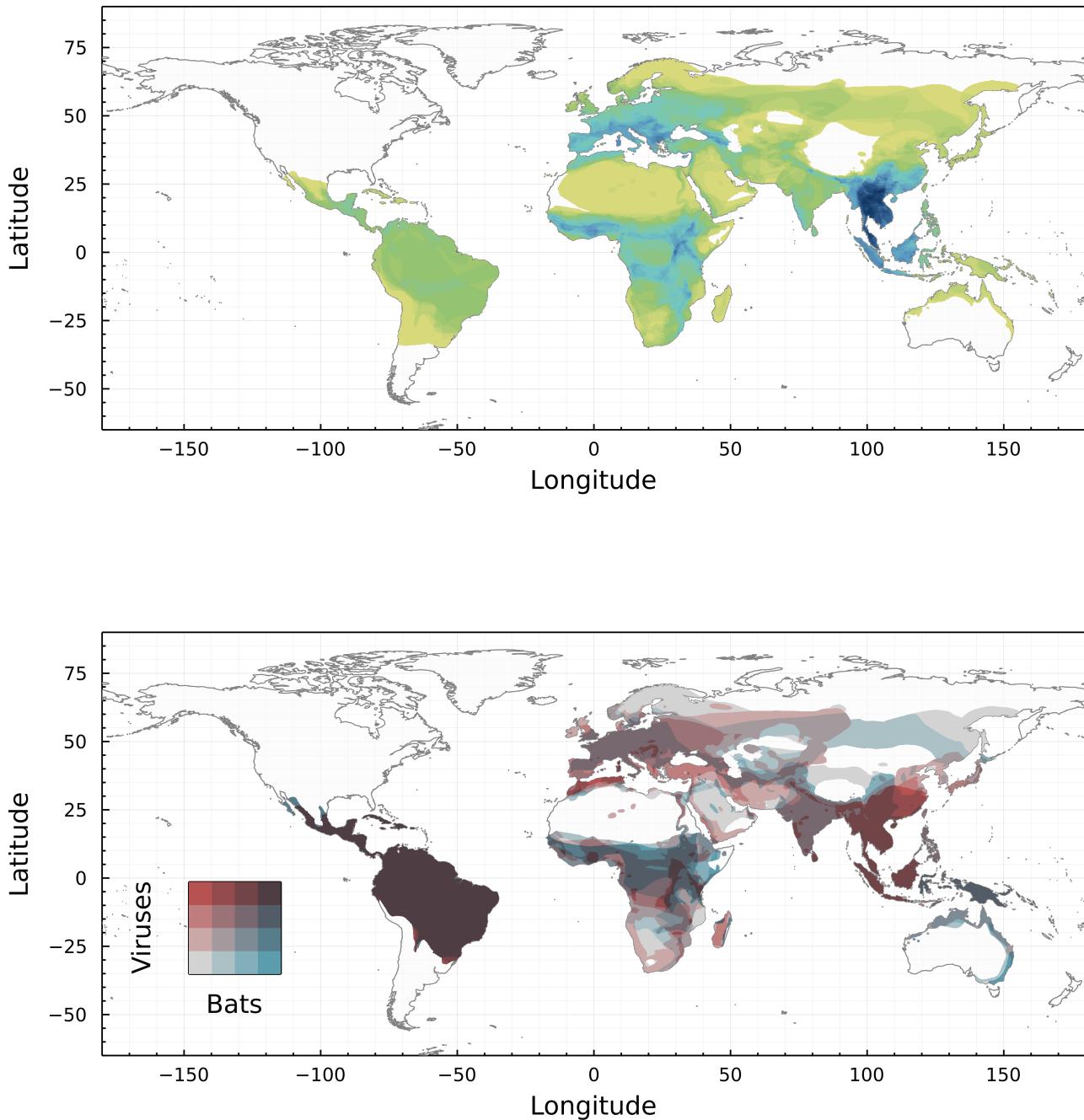


Figure 2: Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red).

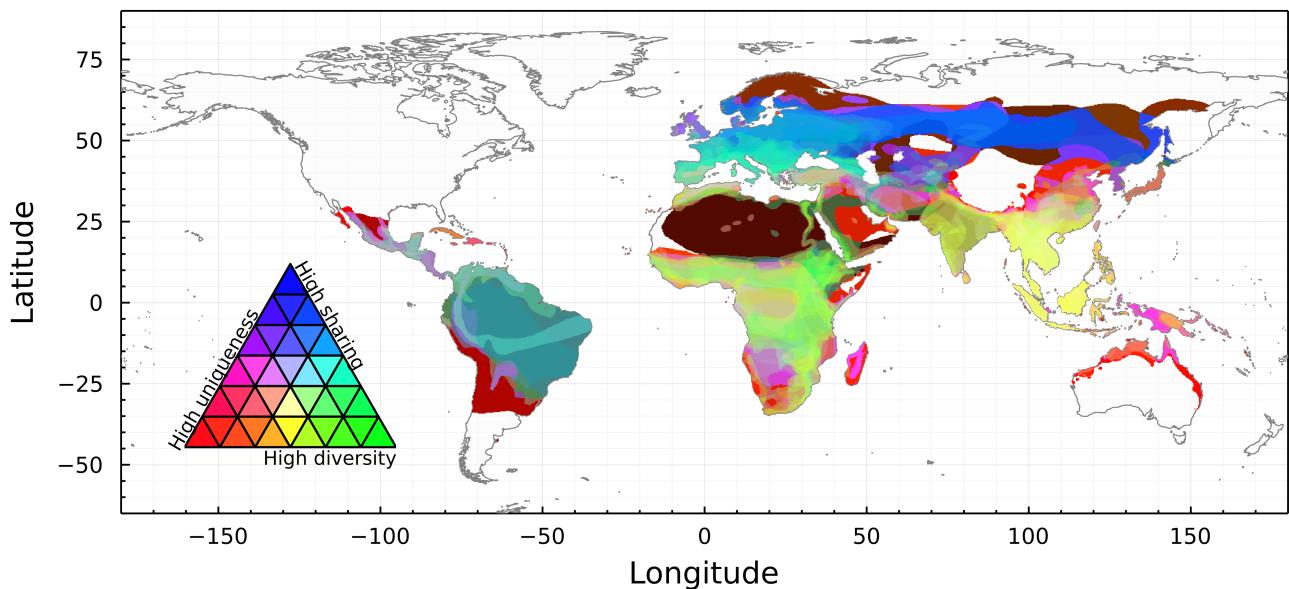


Figure 3: Trivariate additive mapping of the components of risk in the red/green/blue, where high virus sharing is encoded in the blue channel, host phylogenetic diversity in the green channel, and compositional uniqueness in the red channel. A pixel that would maximize all measures (highest possible risk) would be a pure white (specifically $\text{RGB}(1.0, 1.0, 1.0)$), and a pixel with the lowest possible values would be pure black (specifically $\text{RGB}(0.0, 0.0, 0.0)$). Therefore, lighter values (the sum of the three channels gets closer to 3) indicate higher risk, and the color indicates the proportional distribution of the factors making up the total risk.

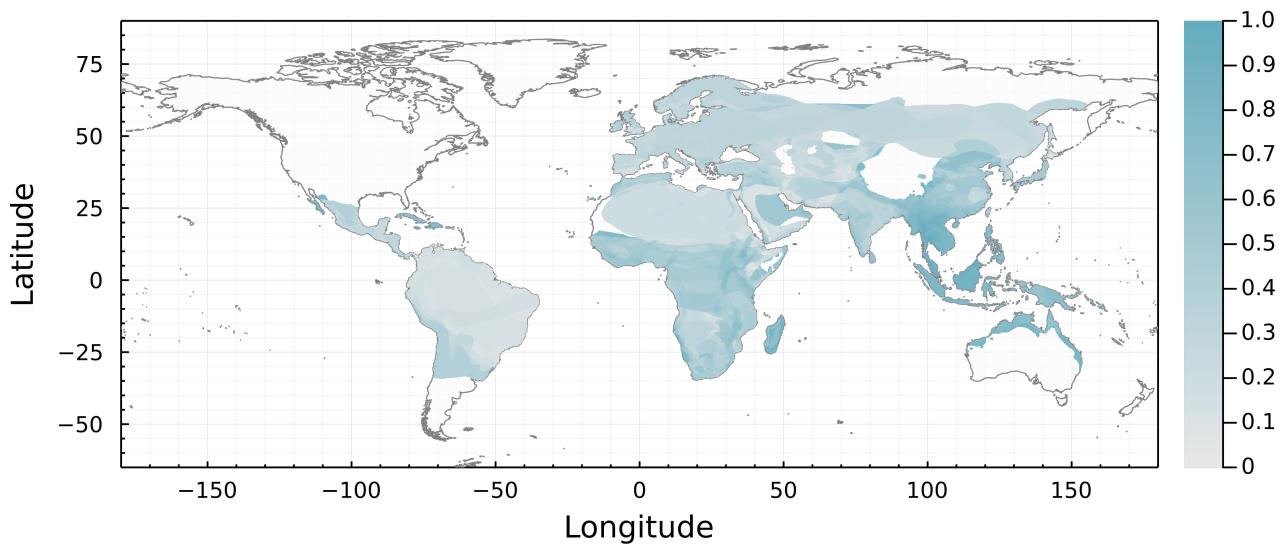


Figure 4: Extraction of a measure of *Betacoronavirus* spillover risk from bat hosts based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on this analyses, regions at high risk of spillover are southeast Asia and Madagascar.

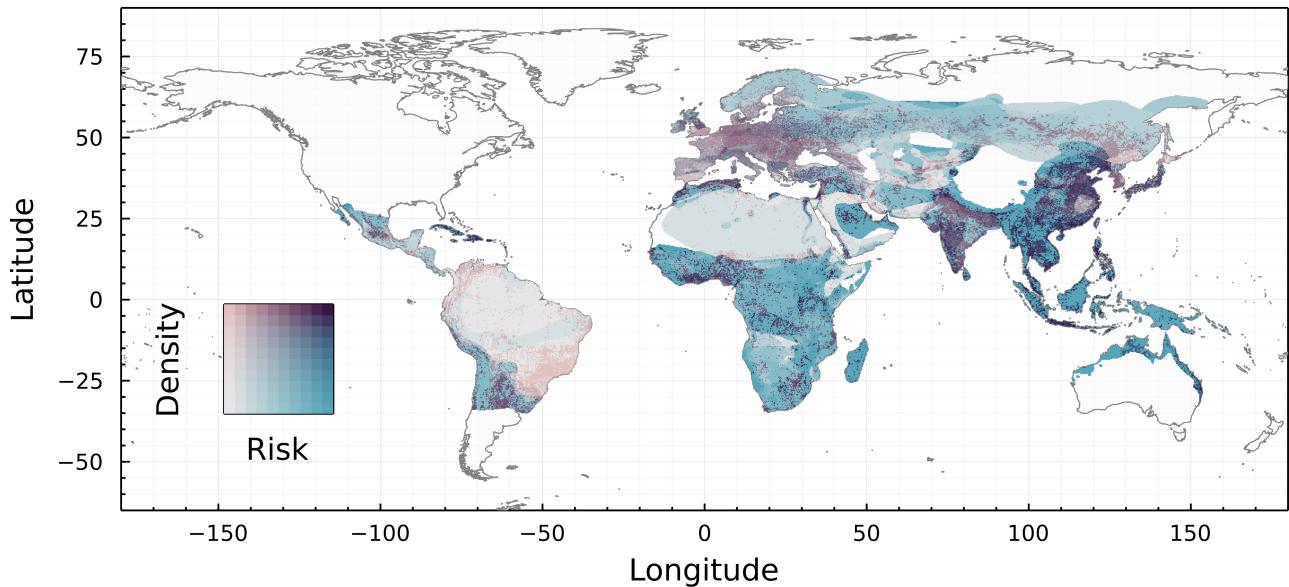


Figure 5: Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk, 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.