

The coevolutionary mosaic of betacoronavirus emergence risk

Norma Forero Rocio Munoz^{1,2,‡} Renata L. Muylaert³ Stephanie N. Seifert⁴ Gregory F. Albery⁵

Daniel J. Becker⁶ Colin J. Carlson^{7,8,9,‡} [Timothée Poisot](#)^{1,2,‡}

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

⁸ Center for Global Health Science and Security, Georgetown University Medical Center, Washington, DC, USA ⁹ 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

Driven by the need to understand the ecological factors involved in the emergence of *Betacoronavirus* (the genus causing the 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 mechanism, giving rise to fragmented systems with
14 different structure and ecologically dynamics over large spatial extents.¹⁰ The GMTC predicts a spatial
15 fragmentation of coevolutionary dynamics under the joint action of three processes:¹¹ coevolutionary hot-
16 and coldspots, which appear when the intensity of *interaction* (in terms of reciprocal fitness consequences)
17 varies spatially; selection mosaics, wherein the intensity of *selection* varies across space, driven by both the
18 biotic complexity of the community (locally diverse hosts and viruses are more biotically complex) and the
19 local favorability of the environment;¹² and trait remixing, which occurs when coevolutionary dynamics
20 are driven by the arrival (or departure) of *functional traits*, through changes in community composition
21 due to invasions, meta-community dynamics, and dispersal.

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

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

40 Results and Discussion

41 Hotspots of host richness and viral diversification are distinct

42 Bats, the second most diverse group of mammals, are found worldwide; gradients in their species
43 richness generally track broader patterns of mammal diversity, with a striking Neotropical hotspot
44 (especially in the Amazon basin) and a secondary hotspot centered in the southeast Asian peninsula.
45 These hotspots of bat diversity are generally presumed to be hotspots of viral adaptive radiation, and
46 therefore areas of concern for human health.^{2,13} However, the hotspots of bat betacoronavirus reservoirs
47 show a distinct pattern, with primary hotspots (both in terms of size and higher values) of host richness
48 situated primarily southeast Asia, parts of southern Europe, and to a lesser extent parts of Africa in the
49 -25-0 range of latitudes (fig. 1; top). Although hundreds of species likely host undiscovered
50 betacoronaviruses, machine learning predictions have suggested that these undiscovered reservoirs should
51 follow the same diversity gradient.¹⁴ In principle, these hotspots of locally-diverse, virus-rich bat
52 communities should drive more adaptive diversification in their viruses.

53 [Figure 1 about here.]

54 However, we find that the global pattern of betacoronavirus phylogenetic distinctiveness is quite distinct
55 from both bat host richness and phylogenetic distinctiveness (fig. 1; bottom). In contrast to the sparsity of
56 Neotropical betacoronavirus hosts, South America has the most evolutionary distinct hosts *and* viruses,

57 followed by secondary hotspots in southeast Asia and the Rift Valley region have mostly distinct viruses.
58 Some degree of sampling bias may contribute to these patterns: for example, South-America is one of the
59 places where the fewest bat betacoronavirus sequences have been generated,^{2,13,15} resulting in a sparser
60 phylogenetic tree, and artificially inflating distinctiveness; conversely, disproportionate research effort in
61 eastern China¹⁶ may have led to a more complete inventory of the local diversity of coronaviruses, again
62 inflating these metrics relative to underlying patterns. Even accounting for these potential biases, though,
63 there is obvious heterogeneity in betacoronavirus evolutionary distinctiveness that is distinct from overall
64 bat diversity.

65 Overall, these patterns recapitulate the evolutionary history of both the order Chiroptera and the genus
66 *Betacoronavirus*. Horseshoe bats (Rhinolophidae) are both the reservoirs of the SARS-like viruses
67 (subgenus *Sarbecovirus*), the group of pandemic threats that have been of the greatest interest to
68 researchers¹⁷ (and so have been sampled most intensively).¹⁶ The hotspots of host richness and viral
69 diversity in southeast Asia—both of which are disproportionately high, considering the global landscape
70 of bat species richness—are almost entirely driven by viral adaptive radiation through host switching
71 within this clade^{3,14}. In contrast, the Neotropical hotspot of viral distinctiveness is driven by isolation by
72 host vicariance. Out of the four main groups of betacoronaviruses, only the subgenus *Merbecovirus*
73 (MERS-like viruses) has been found in animals in the Americas—an introduction that is generally
74 presumed to be ancient.³ While comparatively understudied, New World merbecoviruses have been found
75 in the ghost-faced bats (Mormoopidae), New World leaf-nosed bats (Phyllostomidae), and free-tailed bats
76 (Molossidae) (add cite: Olival 2020 PLoS Pathogens). The former two groups are endemic to the
77 Neotropics, while the explosive adaptive radiations of the latter two (and particularly the phyllostomids)
78 are responsible for the hotspot of bat diversity in the Amazon. Together, these clades of New World bats
79 play host to a distinct regime of betacoronavirus coevolution.

80 **Global biogeographic regions are consistent for bats and betacoronaviruses**

81 Most previous work has assumed that coronavirus biogeography is driven by coevolutionary regimes that
82 form at finer taxonomic scales, treating the presence or richness of key bat host groups as predictive of
83 these viruses' distribution.^{2,3} Projecting bat and betacoronavirus phylogeny over space (fig. 2), we find
84 further support for the idea that bat community assembly is directly responsible for spatial heterogeneity
85 in viral coevolutionary regimes. The distinct groupings (represented by different colors, symbolizing

86 positions in a subspace formed by the first two phylogenetic principal components) are essentially
87 equivalent between the two groups, and can be coarsely delineated as (1) south and southeast Asia, (2) east
88 Asia (including northern China), west Asia, and the Mediterranean coast; (3) Eurasia above a northing of
89 40; and (4) Africa and south America. In some cases, this diverges from expectations about coronavirus
90 biogeography: for example, previous work has rarely flagged India as a region of interest, but for both bats
91 and betacoronaviruses, the subcontinent falls into the same regions as the southeast Asian peninsula (and
92 indeed, the region is home to known bat hosts of nobecoviruses, sarbecoviruses, and merbecoviruses).³

93 [Figure 2 about here.]

94 Overall, these results suggest that, although there are unique hotspots of viral adaptive radiation,
95 biogeographic regions are mostly consistent between bats and their viruses. This may be surprising, given
96 that cospeciation plays a minor role in coronavirus diversification,² which could theoretically allow for
97 broad divergence in their biogeography. However, host jumps at the family level or higher are relatively
98 rare and significant events in coronavirus evolutionary history;^{2,17} as a result, the mosaic of
99 betacoronavirus phylogeography is assembled from a set of overlapping smaller coevolutionary systems,
100 superimposed in space and filtered by the importance of different subgroups in local host communities.
101 For example, the most speciose and cosmopolitan family of bats, the vesper bats (Vespertilionidae), are
102 considered the primary reservoir of merbecoviruses;^{3,17} but in the Americas, where merbecoviruses are
103 the only lineage present, they have only been found in other bat taxa. At the coarsest scale, these
104 heterogeneities are lost, and betacoronavirus biogeography tracks the deep rifts in bat evolutionary
105 history—but within broad regions, the component coevolutionary systems may have very different
106 dynamics.

107 **Coevolution-informed emergence risk is different in space**

108 As host richness, joint distinctiveness, or phylogeographic structure suggest that the bat-betacoronaviruses
109 complex is globally fragmented enough to give rise to both different levels of risk (as evidenced by the
110 spatial location of spillover events) and different types of co-evolutionary dynamics, we turn to the
111 Geographic Mosaic Theory of Coevolution to provide a measure of risk accounting for multiple processes.
112 In fig. 3, we overlapped three components of spillover risk: viral sharing, *i.e.* the chance that two bats will
113 share viruses overall; Local Contribution to Beta Diversity, *i.e.* the fact that a bat community is

114 compositionally unique compared to the average compositional similarity across the entire system; finally,
115 host phylogenetic diversity, *i.e.* how dispersed the bats in a location are within the tree of life. This
116 approach leads to the definition of broad biogeographic regions of risk, where the same color represents
117 the same type of risk. By way of contrast to figures fig. 1 and fig. 2, these regions do not necessarily
118 overlap with previous spatial partitions of the bat-betacoronaviruses complex.

119 [Figure 3 about here.]

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

138 [Figure 4 about here.]

139 From another perspective, areas of high host uniqueness and virus sharing (red-to-pink) could provide
140 hotspots of *Betacoronavirus* risk through mixing of unique viruses (via codivergence) and in turn
141 recombination. Under our framework, such a hotspot was identified in Madagascar, where most bat

142 species are endemic following evolutionary divergence from sister species in both African and Asian
143 continents.¹⁸ Recent surveillance¹⁹ has identified a novel *Betacoronavirus* (in the subgenus *Nobecovirus*) in
144 Madagascar-endemic pteropid bat species (*Pteropus rufus*, *Rousettus madagascariensis*), emphasizing
145 strong proof of principle in model predictions.

146 **Human occupancy drives different levels of effective risk globally**

147 Based on the previous result, we extracted the risk component from the composite map (see Methods), to
148 provide a single measure of risk varying between 0 and 1. This measure is presented in fig. 4. As this map
149 represents the potential risk, it must be weighed by the potential for contacts with humans. As a proxy for
150 this measure, we used the proportion of build/urban land from the EarthEnv dataset: this is a reasonable
151 proxy for the density of humans per unit area, which increases the probability of pathogen spread more
152 widely.²⁰ Since human activity is required to amplify the frequency of virus encounters and thus create
153 areas of viral amplification, mapping the potential risk against measures of land use is required to generate
154 a more actionable assessment of risk. This map is presented in fig. 5. Most of South America and Europe
155 are at comparatively lower risk, as although densely populated, settlements tend to be in areas with lower
156 potential risk. Regions like Malaysia and the North coast of Australia have a high risk component, but
157 should represent a relatively lower effective risk due to low human density. However, this mapping reveals
158 that South-East Asia, the Indian subcontinent, and parts of sub-Saharan Africa, are at high risk due to the
159 overlap between built areas and bat communities representing more opportunities for cross-species
160 transmission of betacoronaviruses. In looking for the origins of SARS in China,²¹ present serological
161 evidence that strongest human-animal contact results in higher risk of virus exposure, regardless of the
162 animal species, but that different types of contact had different impacts. Ideally, finer-grained information
163 about human activity (rather than human presence through anthropisation) could allow to partition this
164 risk further, albeit at the cost of more hypotheses required to estimate the amount of risk represented by
165 each activity. Our map of purported high risk/diversitifcation potential (Madagascar, South-America)
166 overlay with sampling gaps for *Betacoronavirus*,¹⁶ stressing the need for spatially targeted monitoring and
167 discovery.

168 [Figure 5 about here.]

169 PUT THIS SOMEWHERE: Available information describing the spillover of zoonotic betacoronaviruses of

170 bat origin where data was available before and up through the COVID-19 pandemic puts spillover events
171 of SARS-CoV-2 in Wuhan, China; SARS-CoV in Guangdong, China based on the presence of closest
172 known viruses circulating in nature, and a nearby location where serological (antibody) evidence has
173 indicated human exposure to SARS-like viruses;²² MERS-CoV in Saudi Arabia based on index cases
174 available from a recently-published compendium of cases.²³ For the latest event, most if not all index cases
175 are presumed to be camel-to-human transmission, and the precise origin point (if it exists) of MERS-CoV
176 in bats is uncertain. Recent recombinant canine coronavirus spillover events in Haiti²⁴ and Europe²⁵ are
177 not relevant here, as bats' involvement in these cycles of transmission have been supposed to be
178 non-existent. These index cases fall within different phylogeographic bioregions (fig. 2), which further
179 highlight the issue that different host-virus sub-systems may lead to widespread emergence.

180 Conclusion

181 Bats are important reservoir hosts for different classes of microorganisms, many of which a threat to
182 human health.^{26,27} Chiropterans emerged around 64 million years ago and are one of the most diverse
183 mammalian orders, with an estimated richness of more than 1400 species.^{28,29} They exhibit a broad variety
184 of habitat use, behaviour, and feeding strategies, putting them at key positions in the delivery and
185 provisioning of several ecosystem services, tied to important ecosystem-derived benefits to human.³⁰ For
186 example, bats are an essential component of many seed-dispersal networks.³¹ Over two-thirds of bats are
187 know to be either obligate or facultative insectivores, therefore actively contributing for agricultural pest
188 control,^{32,33} and vectors of pathogens that put a risk on human health.^{34,35} Because bats are globally
189 distributed and have a long evolutionary history, phylogeographic and biogeographic approaches are
190 required to shed light on the contemporary distribution of coevolutionary processes between bats and the
191 pathogens they host. Not all areas in which bats, viruses, and human are co-occurring are facing a risk of
192 spillover towards human populations, and the areas in which this risk exist may not be facing risks of the
193 same nature and magnitude.

194 Here, we propose a simple framework with broad explanatory power that helps contextualize discoveries
195 like highly divergent nobecoviruses in Madagascar and the previously-neglected adaptive radiation of
196 sarbecoviruses outside of southern China and throughout southeast Asia. In doing so, it advances
197 ecological theory beyond the current state of the art for global maps of emergence risk. For example,

198 previous studies that have used host richness as proxy have predicted a high diversity of unsampled bat
199 viruses,¹³ bat coronaviruses,² and even specifically betacoronaviruses¹⁴ in both the Amazon and southeast
200 Asia. While we find that both regions are characterized by highly divergent host and viral communities,
201 our framework identifies key differences between the regions. We find that Latin America is a hotspot of
202 both host and viral distinctiveness, suggesting that this branch of the bat-betacoronavirus complex may be
203 undergoing independent evolutionary dynamics from the rest of the global pool, but with limited potential
204 for viral diversification—a finding that is supported by previous work indicating a higher rate of
205 codivergence in Latin America.² In contrast, in southeast Asia, host richness and viral distinctiveness are
206 high but sharing is low; this suggests a different type of evolutionary dynamics that could generate high
207 local diversity of viruses through host switching and viral recombination (see e.g.,¹⁷ as well as the
208 discovery of recombinant viruses that share genetic material from both the SARS-CoV and SARS-CoV-2
209 branches of the Sarbecovirus lineage).³⁶ Both of these regions are priority areas for sampling, especially
210 given predictions that they contain many bat hosts of undiscovered betacoronaviruses.^{14,16} However, both
211 the evolutionary and ecological aspects of emergence risk are likely higher in southeast Asia—a fact that
212 will only become more relevant, as bats track shifting climates and exchange viruses with other species,
213 creating a hotspot of cross-species transmission unique to the region.³⁷

214 The diversity and diversification potential of bats responds to anthropogenic factors others than shifting
215 climates.³⁸ Land use changes could significantly decrease bat suitability, notably through effects on diet
216 and availability of habitats.³⁹ As our results establish that the diversification of bats betacoronaviruses
217 happens on top of processes affecting hosts, biogeographic variation in human population density and
218 anthropogenic disturbances may feed into co-evolutionary dynamics. Increase in humans-hosts contacts
219 also increase the risk of emergence of novel diseases,⁴⁰ so does the changes in landscape connectivity at
220 local/regional scales.⁴¹ This represents a challenge for both conservation strategies and disease ecology:
221 some areas can a high emergence risk and more potential for the acquisition of zoonotic viruses through
222 bat-human encounters.⁴² In particular, the challenge ahead lies in the need to quantify actual exposure
223 (and risk) accounting for several transmission scenarios, including both direct and indirect bat - human
224 interactions, and feeding back into the provision of ecosystem services by bats.

225 **Acknowledgements:** We acknowledge that this study was conducted on land within the traditional
226 unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and
227 Omàmiwininiwak nations. This work was supported by funding to the Viral Emergence Research

228 Initiative (VERENA) consortium including NSF BII 2021909 and a grant from Institut de Valorisation des
229 Données (IVADO). This research was enabled in part by support provided by Calcul Québec
230 (www.calculquebec.ca) and Compute Canada (www.computecanada.ca). NF is funded by the NSERC
231 BIOS² CREATE program. TP and NF are funded by the Courtois Foundation. RLM was supported by
232 Bryce Carmine and Anne Carmine (née Percival), through the Massey University Foundation. DJB was
233 supported by the National Institute of General Medical Sciences of the National Institutes of Health
234 (P20GM134973).

235 **Methods**

236 **Known *Betacoronavirus* hosts**

237 We downloaded the data on bats hosts of *Betacoronavirus* from
238 <https://www.viralemergence.org/betacov> on Apr. 2022,¹⁴ and filtered it to “known” hosts (established
239 before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling and competence
240 assays since the initial data collection). The original database was assembled by a combination of data
241 mining and literature surveys, including automated alerts on the “bats” and “coronavirus” keywords to
242 identify novel empirical evidence of bats-betacoronaviruses associations; this yielded a total of 126 known
243 hosts, 47 of which were novel hosts.

244 **Bat occurrences**

245 We downloaded the rangemap of every current bat species that was classified as an empirically
246 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data.⁴³ The range
247 maps were subsequently rasterized using the rasterize function from GDAL⁴⁴ at a resolution of
248 approximately 100kmx100km. For every pixel in the resulting raster where at least one bat host of
249 *Betacoronavirus* was present, we extract the species pool (list of all known bat hosts), which was used to
250 calculate the following risk assessment components: bat phylogenetic diversity, bat compositional
251 uniqueness, and predicted viral sharing risk.

252 **Bat phylogenetic diversity**

253 For every pixel, we measured Faith’s Phylogenetic Diversity⁴⁵ based on a recent synthetic tree with robust
254 time calibration, covering about 6000 mammalian species.⁴⁶ Faith’s PD measures the sum of unique
255 branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more
256 phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire
257 tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches
258 leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the
259 assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure
260 incorporates a richness component, which we chose not to correct for; the interpretation of the

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

263 **Bat compositional uniqueness**

264 For every species pool, we measured its Local Contribution to Beta-Diversity;⁴⁷ LCBD works from a
265 species-data matrix (traditionally noted as \mathbf{Y}), where species are rows and sites are columns, and a value of
266 1 indicates occurrence. We extracted the \mathbf{Y} matrix assuming that every pixel represents a unique location,
267 and following best practices⁴⁸ transformed it using Hellinger's distance to account for unequal bat
268 richness at different pixels. The correction of raw community data is particularly important for two
269 reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the effect
270 of overall species richness, which is already incorporated in the phylogenetic diversity component. High
271 values of LCBD indicate that the pixel has a community that is on average more dissimilar in species
272 composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent
273 results by⁴⁹ shows that LCBD measures are robust with regards to spatial scale, and are therefore
274 applicable at the global scale.

275 **Viral sharing between hosts**

276 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a
277 previously published generalized additive mixed model of virus sharing by a tensor function of
278 phylogenetic distance and geographic range overlap across mammals.⁵⁰ This network stores pairwise
279 values of viral community similarity. To project viral sharing values into a single value for every pixel, we
280 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant
281 bat assemblage is likely to be proficient at exchanging viruses.

282 **Composite risk map**

283 To visualize the aggregated risk at the global scale, we combine the three individual risk components
284 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model.⁵¹ In
285 this approach, every risk component gets assigned a component in the RGB color model (phylogenetic
286 diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid

287 RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no
288 phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for
289 each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the
290 risk as colors diverge towards combinations of values for three risk components. Out of the possible
291 combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic
292 diversity and low viral sharing,⁵² in that this allows multiple independent host-virus coevolutionary
293 dynamics to take place in the same location. In the colorimetric space, this corresponds to yellow – because
294 the HSV space is more amenable to calculations for feature extraction,⁵³ we measured the risk level by
295 calculating the angular distance of the hue of each pixel to a reference value of 60 (yellow), and weighted
296 this risk level by the value component. Specifically, given a pixel with colorimetric coordinates (h, s, v) , its
297 ranged weighted risk value is

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

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

299 **Viral phyogeography and evolutionary diversification**

300 To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed
301 betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data
302 from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR
303 betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR
304 sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated
305 to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained
306 words indicating recombinant or laboratory strains including “patent”, “mutant”, “GFP”, and
307 “recombinant”. We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East
308 respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus
309 RdRp sequences were then aligned using MAFFT⁵⁴ v1.4.0 (Algorithm FFT-NS-2, Scoring matrix 200PAM /
310 k=2, gap open penalty 1.53m offset value 0.123) and a maximum likelihood tree reconstructed in
311 IQ-TREE⁵⁵ v1.6.12 with ModelFinder⁵⁶ ultrafast bootstrap approximation⁵⁷ with a general time reversible
312 model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of nucleotide

313 substitution (GTR+F+R5).

314 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat
315 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the
316 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary
317 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary
318 distinctiveness⁵⁸ for each of the viruses in the tree, then averaged these at the bat species level, projected
319 these values onto their geographic distributions, and averaged across every bat found in a given pixel. As
320 such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral
321 community believed to be associated with a particular subset of bats present.

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

323 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the
324 biogeography of their hosts. To test this idea, we loosely adapted a method from,^{59,60} who proposed a
325 phylogenetic method for the delineation of animal biogeographic regions. In their original method, a
326 distance matrix - where each row or column represents a geographic raster’s grid cell, and the dissimilarity
327 values are the “beta diversity similarity” of their community assemble - undergoes non-metric
328 multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a
329 four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we
330 measure the phylogenetic distance between the different viruses in the betacoronaviruses tree by using the
331 cophenetic function in ape;⁶¹ subsequently, we take a principal components analysis of that distance
332 matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional
333 space. We then take the first two principal components and, as with the evolutionary distinctiveness
334 analysis, aggregated these to a mean host value and projected them using a four-color bivariate map.

335 **References**

- 336 1.
- 337 Plowright, R. K. *et al.* Pathways to zoonotic spillover. *Nature Reviews Microbiology* **15**, 502–510 (2017).
- 338 2.
- 339 Anthony, S. J. *et al.* Global patterns in coronavirus diversity. *Virus Evolution* **3**, (2017).
- 340 3.
- 341 Ruiz-Aravena, M. *et al.* Ecology, evolution and spillover of coronaviruses from bats. *Nature Reviews Microbiology* **20**, 299–314 (2022).
- 342 4.
- 343 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).
- 344 5.
- 345 Power, A. G. & Mitchell, C. E. Pathogen Spillover in Disease Epidemics. *The American Naturalist* **164**, S79–S89 (2004).
- 346 6.
- 347 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).
- 348 7.
- 349 Thompson, J. N. *The Geographic Mosaic of Coevolution*. (University Of Chicago Press, 2005).
- 350 8.
- 351 Thompson, J. N. *The Coevolutionary Process*. (University Of Chicago Press, 1994).
- 352 9.
- 353 Janzen, D. H. When is it Coevolution? *Evolution* **34**, 611–612 (1980).
- 354 10.
- 355 Price, P. W. *Macroevolutionary Theory on Macroecological Patterns*. (Cambridge University Press, 2002).
doi:[10.1017/CBO9780511615030](https://doi.org/10.1017/CBO9780511615030).
- 356 11.
- 357 Gomulkiewicz, R. *et al.* Dos and don’ts of testing the geographic mosaic theory of coevolution. *Heredity* **98**, 249–258 (2007).

- 358 12.
- 359 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).
- 360 13.
- 361 Olival, K. J. *et al.* Host and viral traits predict zoonotic spillover from mammals. *Nature* **546**, 646–650 (2017).
- 362 14.
- 363 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).
- 364 15.
- 365 Allen, T. *et al.* Global hotspots and correlates of emerging zoonotic diseases. *Nature Communications* **8**,
(2017).
- 366 16.
- 367 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).
- 368 17.
- 369 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).
- 370 18.
- 371 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).
- 372 19.
- 373 Kettenburg, G. *et al.* Full Genome Nobecovirus Sequences From Malagasy Fruit Bats Define a Unique
Evolutionary History for This Coronavirus Clade. *Frontiers in Public Health* **10**, (2022).
- 374 20.
- 375 Hazarie, S., Soriano-Paños, D., Arenas, A., Gómez-Gardeñes, J. & Ghoshal, G. Interplay between population
density and mobility in determining the spread of epidemics in cities. *Communications Physics* **4**, 191 (2021).
- 376 21.
- 377 Xu, R.-H. *et al.* Epidemiologic Clues to SARS Origin in China. *Emerging Infectious Diseases* **10**, 1030–1037
(2004).
- 378 22.
- 379 Wang, N. *et al.* Serological Evidence of Bat SARS-Related Coronavirus Infection in Humans, China.
Virologica Sinica **33**, 104–107 (2018).

- 380 23.
- 381 Ramshaw, R. E. *et al.* A database of geopositioned Middle East Respiratory Syndrome Coronavirus
occurrences. *Scientific Data* **6**, 318 (2019).
- 382 24.
- 383 Lednicky, J. A. *et al.* Isolation of a Novel Recombinant Canine Coronavirus from a Visitor to Haiti: Further
Evidence of Transmission of Coronaviruses of Zoonotic Origin to Humans. *Clinical Infectious Diseases: An
Official Publication of the Infectious Diseases Society of America* ciab924 (2021) doi:[10.1093/cid/ciab924](https://doi.org/10.1093/cid/ciab924).
- 384 25.
- 385 Vlasova, A. N. *et al.* Animal alphacoronaviruses found in human patients with acute respiratory illness in
different countries. *Emerging Microbes & Infections* **11**, 699–702 (2022).
- 386 26.
- 387 Letko, M., Seifert, S. N., Olival, K. J., Plowright, R. K. & Munster, V. J. Bat-borne virus diversity, spillover
and emergence. *Nature Reviews Microbiology* **18**, 461–471 (2020).
- 388 27.
- 389 Van Brussel, K. & Holmes, E. C. Zoonotic disease and virome diversity in bats. *Current Opinion in Virology*
52, 192–202 (2022).
- 390 28.
- 391 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).
- 392 29.
- 393 Simmons, N. B. & Cirranello, A. L. Bat Species of the World: A taxonomic and geographic database. <https://batnames.org/> (2020).
- 394 30.
- 395 Kasso, M. & Balakrishnan, M. Ecological and Economic Importance of Bats (Order Chiroptera). *ISRN
Biodiversity* **2013**, e187415 (2013).
- 396 31.
- 397 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).
- 398 32.
- 399 *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).
- 400 33.
- 401 Williams-Guillén, K., Perfecto, I. & Vandermeer, J. Bats Limit Insects in a Neotropical Agroforestry System.
Science **320**, 70–70 (2008).

- 402 34.
- 403 Gonsalves, L., Bicknell, B., Law, B., Webb, C. & Monamy, V. Mosquito Consumption by Insectivorous Bats:
Does Size Matter? *PLOS ONE* **8**, e77183 (2013).
- 404 35.
- 405 Gonsalves, L., Lamb, S., Webb, C., Law, B. & Monamy, V. Do mosquitoes influence bat activity in coastal
habitats? *Wildlife Research* **40**, 10–24 (2013).
- 406 36.
- 407 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).
- 408 37.
- 409 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).
- 410 38.
- 411 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).
- 412 39.
- 413 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).
- 414 40.
- 415 Johnson, C. K. *et al.* Global shifts in mammalian population trends reveal key predictors of virus spillover
risk. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20192736 (2020).
- 416 41.
- 417 Gryseels, S. *et al.* When Viruses Don't Go Viral: The Importance of Host Phylogeographic Structure in the
Spatial Spread of Arenaviruses. *PLOS Pathogens* **13**, e1006073 (2017).
- 418 42.
- 419 Amman, B. R. *et al.* Investigating the role of bats in emerging zoonoses: Balancing ecology, conservation and
public health interest. (FAO, 2011).
- 420 43.
- 421 IUCN. The IUCN Red List of Threatened Species. <https://www.iucnredlist.org> (2021).
- 422 44.
- 423 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).

- 424 45.
- 425 Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1–10 (1992).
- 426 46.
- 427 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).
- 428 47.
- 429 Legendre, P. & De Cáceres, M. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. *Ecology Letters* **16**, 951–963 (2013).
- 430 48.
- 431 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).
- 432 49.
- 433 Dansereau, G., Legendre, P. & Poisot, T. Evaluating ecological uniqueness over broad spatial extents using species distribution modelling. *Oikos* **n/a**, e09063 (2022).
- 434 50.
- 435 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).
- 436 51.
- 437 Seekell, D. A., Lapierre, J.-F. & Cheruvellil, K. S. A geography of lake carbon cycling. *Limnology and Oceanography Letters* **3**, 49–56 (2018).
- 438 52.
- 439 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).
- 440 53.
- 441 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).
- 442 54.
- 443 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).
- 444 55.
- 445 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).

- 446 56.
- 447 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).
- 448 57.
- 449 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).
- 450 58.
- 451 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).
- 452 59.
- 453 Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *Proceedings of the National
Academy of Sciences* **104**, 5925–5930 (2007).
- 454 60.
- 455 Kreft, H. & Jetz, W. A framework for delineating biogeographical regions based on species distributions.
Journal of Biogeography **37**, 2029–2053 (2010).
- 456 61.
- 457 Paradis, E. & Schliep, K. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in
R. *Bioinformatics* **35**, 526–528 (2019).

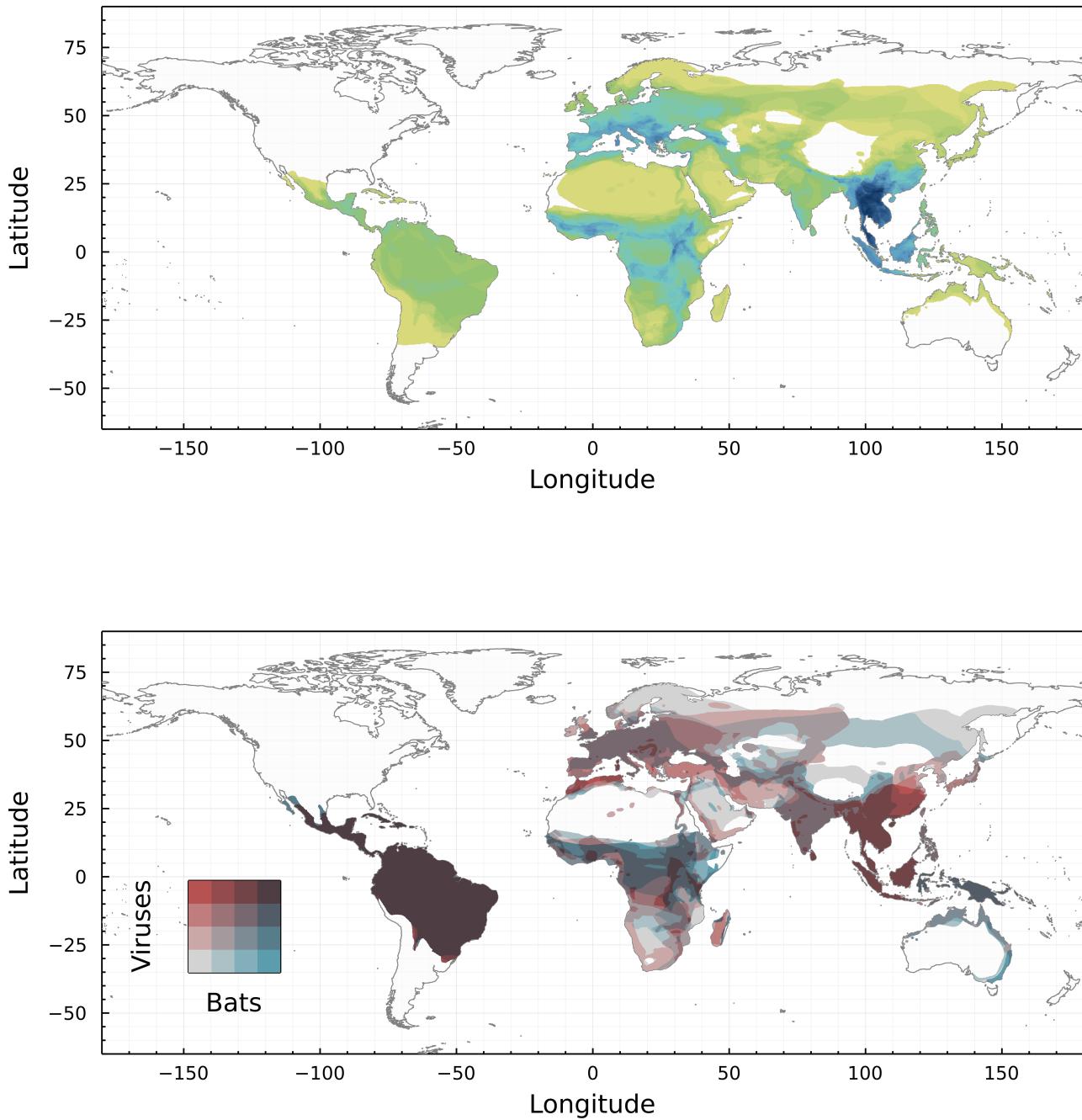


Figure 1: Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red).

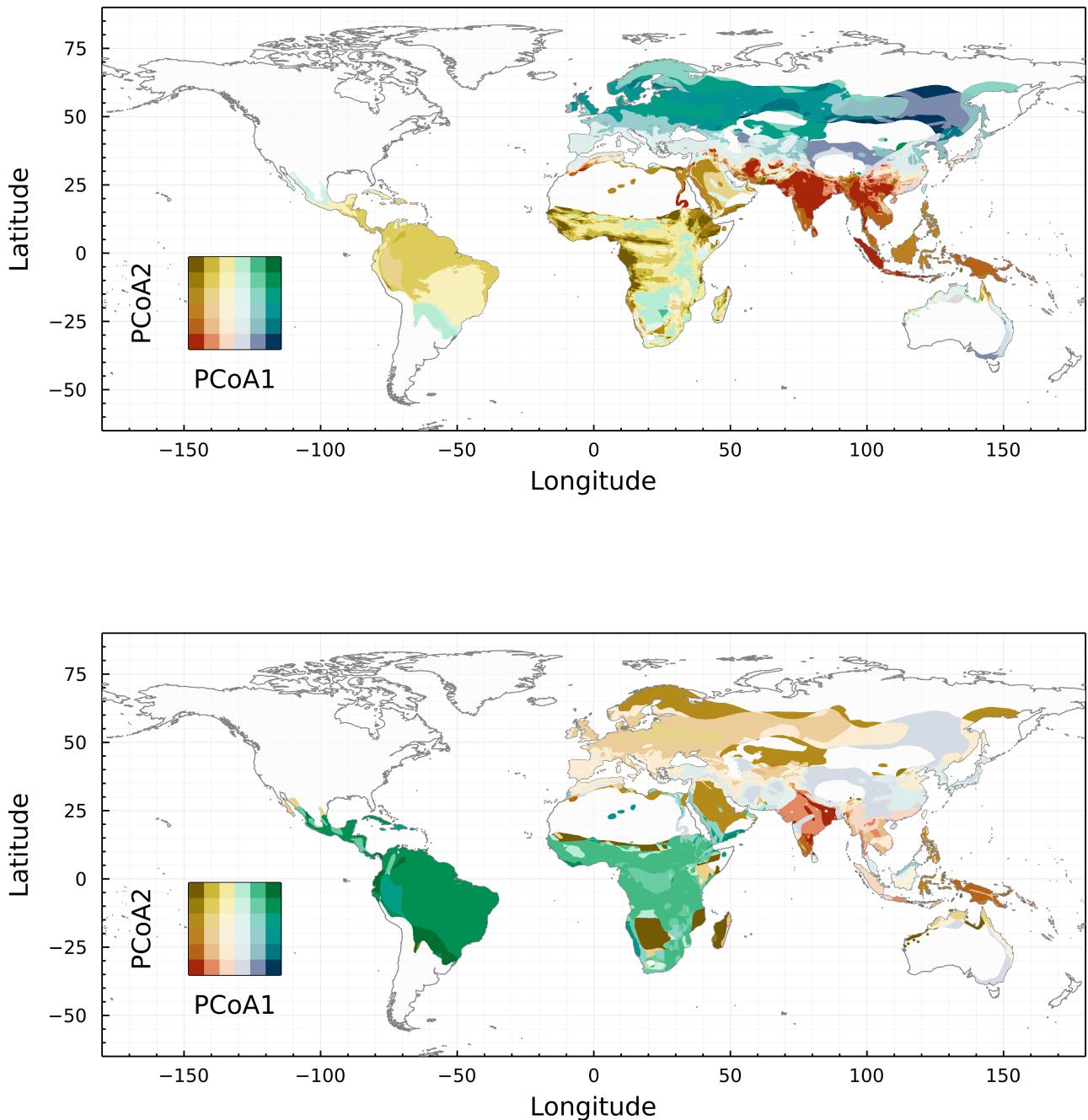


Figure 2: Phylogeographic regions of bats (top) and viruses (bottom) based on the joint analysis of their occurrence and phylogenetic relatedness. The different colors show tendencies to separate alongside the first two components of a PCoA. Note that the PCoA for the bats and viruses are independent, and so cannot be compared directly – that being said, the regions can be compared across maps.

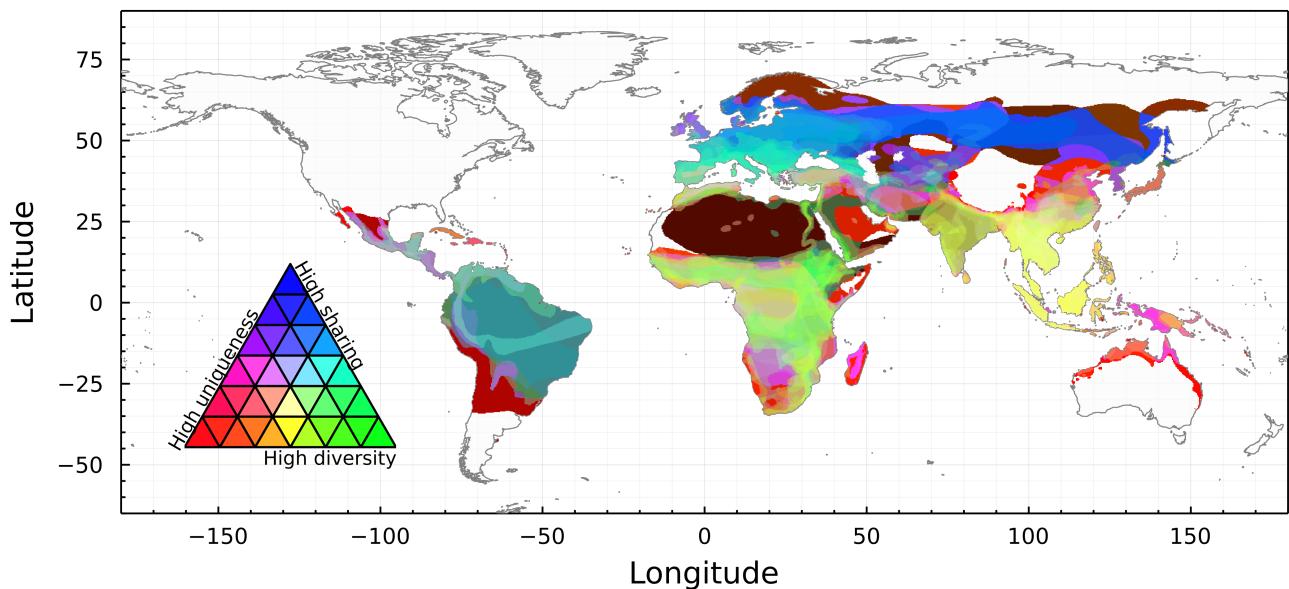


Figure 3: Trivariate additive mapping of the components of risk in the red/green/blue, where high virus sharing is encoded in the blue channel, host phylogenetic diversity in the green channel, and compositional uniqueness in the red channel. A pixel that would maximize all measures (highest possible 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.

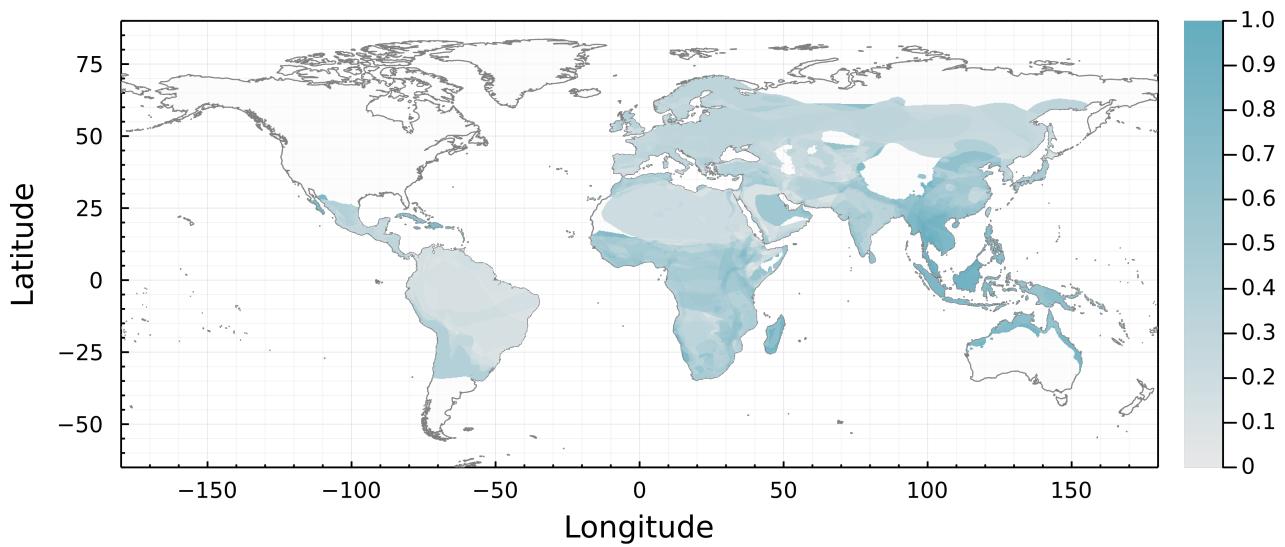


Figure 4: Extraction of a measure of *Betacoronavirus* spillover risk from bat hosts based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on this analyses, regions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

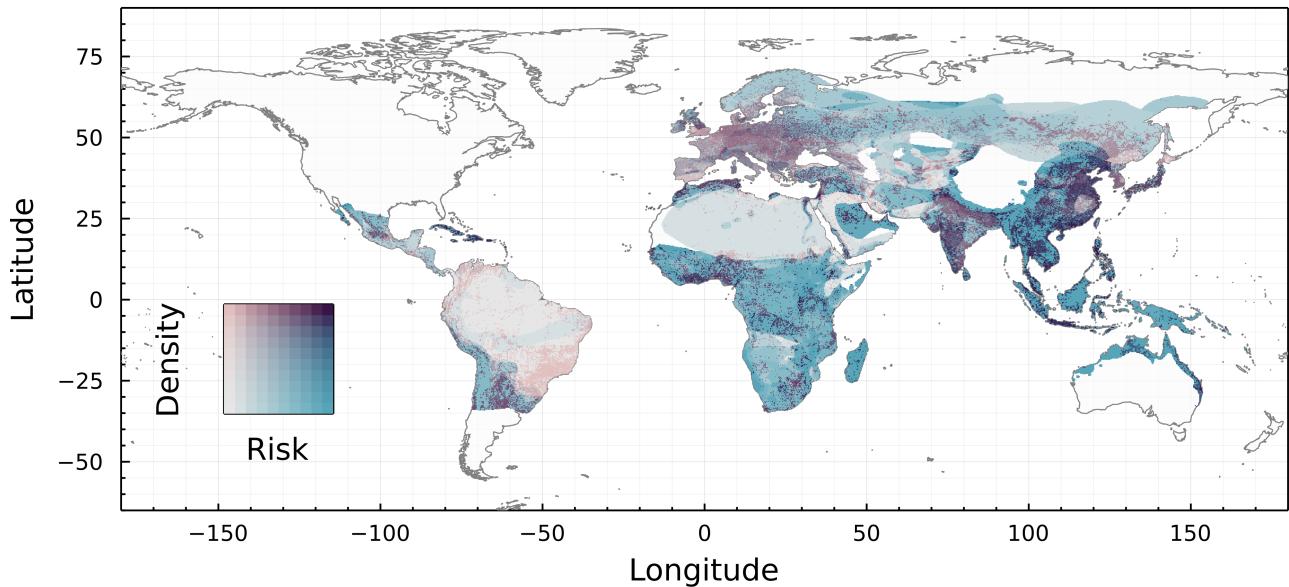


Figure 5: Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk,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