

The coevolutionary mosaic of bat 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 Bat and betacoronavirus biogeography are broadly consistent

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

57 biogeography. However, host jumps at the family level or higher are relatively rare and significant events
58 in coronavirus evolutionary history;^{2,13} as a result, the mosaic of betacoronavirus phylogeography is
59 assembled from a set of overlapping smaller coevolutionary systems, superimposed in space and filtered
60 by the importance of different subgroups in local host communities. For example, the most speciose and
61 cosmopolitan family of bats, the vesper bats (Vespertilionidae), are considered the primary reservoir of
62 merbecoviruses;^{3,13} but in the Americas, where merbecoviruses are the only lineage present, they have
63 only been found in other bat taxa. At the coarsest scale, these heterogeneities are lost, and betacoronavirus
64 biogeography tracks the deep rifts in bat evolutionary history—but within broad regions, the component
65 coevolutionary systems may have very different dynamics.

66 **Hotspots of bat and betacoronavirus biodiversity are distinct**

67 Bats, the second most diverse groups of mammals, are found worldwide; gradients in their species
68 richness generally track broader patterns of mammal diversity, with a striking Neotropical hotspot
69 (especially in the Amazon basin) and a secondary hotspot centered in the southeast Asian peninsula.
70 These hotspots of bat diversity are generally presumed to be hotspots of viral adaptive radiation, and
71 therefore areas of concern for human health.^{2,14} However, the hotspots of known bat betacoronavirus
72 hosts show a distinct pattern, with primary hotspots (both in terms of size and higher values) of host
73 richness situated in southeast Asia, parts of southern Europe, and to a lesser extent parts of Africa in the
74 -25-0 range of latitudes (fig. 2; top). Although hundreds of species likely host undiscovered
75 betacoronaviruses, machine learning predictions have suggested that these undiscovered reservoirs should
76 follow the same diversity gradient.¹⁵ In principle, these hotspots of locally-diverse, virus-rich bat
77 communities should drive more adaptive diversification in their viruses.

78 [Figure 2 about here.]

79 However, we find that the global pattern of betacoronavirus phylogenetic distinctiveness is quite distinct
80 from both bat host richness and phylogenetic distinctiveness (fig. 2; bottom). In contrast to the sparsity of
81 Neotropical betacoronavirus hosts, South America has the most evolutionary distinct hosts *and* viruses,
82 followed by secondary hotspots in southeast Asia and the Rift Valley region have mostly distinct viruses.
83 Some degree of sampling bias may contribute to these patterns: for example, South-America is one of the
84 places where the fewest bat betacoronavirus sequences have been generated,^{2,14,16} resulting in a sparser

85 phylogenetic tree, and artificially inflating distinctiveness; conversely, disproportionate research effort in
86 eastern China¹⁷ may have led to a more complete inventory of the local diversity of coronaviruses, again
87 inflating these metrics relative to underlying patterns. Even accounting for these potential biases, though,
88 there is obvious heterogeneity in betacoronavirus evolutionary distinctiveness that is distinct from overall
89 bat diversity.

90 Overall, these patterns recapitulate the evolutionary history of both the order Chiroptera and the genus
91 *Betacoronavirus*. Horseshoe bats (Rhinolophidae) are both the reservoirs of the SARS-like viruses
92 (subgenus *Sarbecovirus*), the group of pandemic threats that have been of the greatest interest to
93 researchers¹³ (and so have been sampled most intensively).¹⁷ The hotspots of host richness and viral
94 diversity in southeast Asia—both of which are disproportionately high, considering the global landscape
95 of bat species richness—are almost entirely driven by viral adaptive radiation through host switching
96 within this clade^{3,15}. In contrast, the Neotropical hotspot of viral distinctiveness is driven by isolation by
97 host vicariance. Out of the four main groups of betacoronaviruses, only the subgenus *Merbecovirus*
98 (MERS-like viruses) has been found in animals in the Americas—an introduction that is generally
99 presumed to be ancient.³ While comparatively understudied, New World merbecoviruses have been found
100 in the ghost-faced bats (Mormoopidae), New World leaf-nosed bats (Phyllostomidae), and free-tailed bats
101 (Molossidae) (add cite: Olival 2020 PLoS Pathogens). The former two groups are endemic to the
102 Neotropics, while the explosive adaptive radiations of the latter two (and particularly the phyllostomids)
103 are responsible for the hotspot of bat diversity in the Amazon. Together, these clades of New World bats
104 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). 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 (cite Rulli et al 2021
150 Nature Food; cite Cui et al 2019 Nature Reviews Microbiology), and human population density and
151 connectivity^{1,20} (add: Muylaert 2022 Proc B; Hassell 2017 TREE) (fig. 5). Accounting for these factors,
152 most of South America and Europe are at comparatively lower risk, as—although densely
153 populated—settlements tend to be in areas with lower potential risk. Conversely, regions like Malaysia and
154 the northern coast of Australia have a high evolutionary risk component, but should represent a relatively
155 lower effective risk due to low human density. However, southeast Asia, the Indian subcontinent, and
156 scattered hotspots in sub-Saharan Africa are at high risk due to the overlap between human populations
157 and natural opportunities for cross-species transmission of betacoronaviruses.

158 [Figure 5 about here.]

159 Reassuringly, these predictions are validated by the sites where the three highly pathogenic coronavirus
160 are believed to have recently emerged. While available information puts the spillover of SARS-CoV-2 in a
161 live animal market in Wuhan, China, the ultimate origin of the virus is almost certainly in a Lineage 2
162 sarbecovirus from a southeast Asian horseshoe bat. Similarly, the SARS-CoV outbreak began in
163 Guangdong province in 2002, reaching humans through small carnivore bridge hosts, but was eventually
164 traced back to a set of likely progenitor viruses found in cave-dwelling horseshoe bats in Yunnan province
165 (cite Hu et al. 2017 PLoS Pathogens); nearby, antibody evidence has indicated human exposure to
166 SARS-like viruses.²¹ MERS-CoV was originally detected in Saudi Arabia, accompanied by a nearly
167 identical virus sequenced from an Egyptian tomb bat (*Taphozous perforatus*) (cite Memish et al. 2013
168 EID), but is widespread in camels in East Africa and the Middle East, and may have reached its bridge
169 host decades earlier than originally supposed (cite Muller et al 2014 EID); as a result, the geography of the

170 original bat-to-camel transmission is still widely regarded as uncertain. All of these are broadly consistent
171 with the risk factors we identify. Notably, India and west Africa are additional hotspots that have yet to
172 experience the emergence of a bat coronavirus into human populations, but may still be at
173 risk—particularly given known gaps in bat surveillance,¹⁷ and a dense population in both regions with
174 global connectivity. In any of these regions, surveillance on viral reservoirs can be paired with targeted
175 monitoring of high-risk human populations (i.e., those with regular wildlife contact)²² for maximum
176 impact.

177 Conclusion

178 Bats are important reservoir hosts for different classes of microorganisms, many of which a threat to
179 human health.^{23,24} Chiropterans emerged around 64 million years ago and are one of the most diverse
180 mammalian orders, with an estimated richness of more than 1400 species.^{25,26} They exhibit a broad variety
181 of habitat use, behaviour, and feeding strategies, putting them at key positions in the delivery and
182 provisioning of several ecosystem services, tied to important ecosystem-derived benefits to human.²⁷ For
183 example, bats are an essential component of many seed-dispersal networks.²⁸ Over two-thirds of bats are
184 know to be either obligate or facultative insectivores, therefore actively contributing for agricultural pest
185 control,^{29,30} and vectors of pathogens that put a risk on human health.^{31,32} Because bats are globally
186 distributed and have a long evolutionary history, phylogeographic and biogeographic approaches are
187 required to shed light on the contemporary distribution of coevolutionary processes between bats and the
188 pathogens they host. Not all areas in which bats, viruses, and human are co-occurring are facing a risk of
189 spillover towards human populations, and the areas in which this risk exist may not be facing risks of the
190 same nature and magnitude.

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

198 our framework identifies key differences between the regions. We find that Latin America is a hotspot of
199 both host and viral distinctiveness, suggesting that this branch of the bat-betacoronavirus complex may be
200 undergoing independent evolutionary dynamics from the rest of the global pool, but with limited potential
201 for viral diversification—a finding that is supported by previous work indicating a higher rate of
202 codivergence in Latin America.² In contrast, in southeast Asia, host richness and viral distinctiveness are
203 high but sharing is low; this suggests a different type of evolutionary dynamics that could generate high
204 local diversity of viruses through host switching and viral recombination (see e.g.,¹³ as well as the
205 discovery of recombinant viruses that share genetic material from both the SARS-CoV and SARS-CoV-2
206 branches of the Sarbecovirus lineage).³³ Both of these regions are priority areas for sampling, especially
207 given predictions that they contain many bat hosts of undiscovered betacoronaviruses.^{15,17} However, both
208 the evolutionary and ecological aspects of emergence risk are likely higher in southeast Asia—a fact that
209 will only become more relevant, as bats track shifting climates and exchange viruses with other species,
210 creating a hotspot of cross-species transmission unique to the region.³⁴

211 The diversity and diversification potential of bats responds to anthropogenic factors others than shifting
212 climates.³⁵ Land use changes could significantly decrease bat suitability, notably through effects on diet
213 and availability of habitats.³⁶ As our results establish that the diversification of bats betacoronaviruses
214 happens on top of processes affecting hosts, biogeographic variation in human population density and
215 anthropogenic disturbances may feed into co-evolutionary dynamics. Increase in humans-hosts contacts
216 also increase the risk of emergence of novel diseases,³⁷ so does the changes in landscape connectivity at
217 local/regional scales.³⁸ This represents a challenge for both conservation strategies and disease ecology:
218 some areas can a high emergence risk and more potential for the acquisition of zoonotic viruses through
219 bat-human encounters.³⁹ In particular, the challenge ahead lies in the need to quantify actual exposure
220 (and risk) accounting for several transmission scenarios, including both direct and indirect bat - human
221 interactions, and feeding back into the provision of ecosystem services by bats.

222 **Acknowledgements:** We acknowledge that this study was conducted on land within the traditional
223 unceded territory of the Saint Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and
224 Omàmiwininiwak nations. This work was supported by funding to the Viral Emergence Research
225 Initiative (VERENA) consortium including NSF BII 2021909 and a grant from Institut de Valorisation des
226 Données (IVADO). This research was enabled in part by support provided by Calcul Québec
227 (www.calculquebec.ca) and Compute Canada (www.computecanada.ca). NF is funded by the NSERC

228 BIOS² CREATE program. TP and NF are funded by the Courtois Foundation. RLM was supported by
229 Bryce Carmine and Anne Carmine (née Percival), through the Massey University Foundation. DJB was
230 supported by the National Institute of General Medical Sciences of the National Institutes of Health
231 (P20GM134973).

232 **Methods**

233 **Known *Betacoronavirus* hosts**

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

241 **Bat occurrences**

242 We downloaded the rangemap of every current bat species that was classified as an empirically
243 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data.⁴⁰ The range
244 maps were subsequently rasterized using the rasterize function from GDAL⁴¹ at a resolution of
245 approximately 100kmx100km. For every pixel in the resulting raster where at least one bat host of
246 *Betacoronavirus* was present, we extract the species pool (list of all known bat hosts), which was used to
247 calculate the following risk assessment components: bat phylogenetic diversity, bat compositional
248 uniqueness, and predicted viral sharing risk.

249 **Bat phylogenetic diversity**

250 For every pixel, we measured Faith’s Phylogenetic Diversity⁴² based on a recent synthetic tree with robust
251 time calibration, covering about 6000 mammalian species.⁴³ Faith’s PD measures the sum of unique
252 branches from an arbitrary root to a set of tips, and comparatively larger values indicate a more
253 phylogenetic diverse species pool. We measured phylogenetic diversity starting from the root of the entire
254 tree (and not from Chiroptera); this bears no consequences on the resulting values, since all branches
255 leading up to Chiroptera are only counted one per species pool, and (as we explain when describing the
256 assembly of the composite risk map), all individual risk components are ranged in [0,1]. This measure
257 incorporates a richness component, which we chose not to correct for; the interpretation of the

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

260 **Bat compositional uniqueness**

261 For every species pool, we measured its Local Contribution to Beta-Diversity;⁴⁴ LCBD works from a
262 species-data matrix (traditionally noted as \mathbf{Y}), where species are rows and sites are columns, and a value of
263 1 indicates occurrence. We extracted the \mathbf{Y} matrix assuming that every pixel represents a unique location,
264 and following best practices⁴⁵ transformed it using Hellinger's distance to account for unequal bat
265 richness at different pixels. The correction of raw community data is particularly important for two
266 reasons: first, it prevents the artifact of richer sites having higher importance; second, it removes the effect
267 of overall species richness, which is already incorporated in the phylogenetic diversity component. High
268 values of LCBD indicate that the pixel has a community that is on average more dissimilar in species
269 composition than what is expected knowing the entire matrix, i.e. a more unique community. Recent
270 results by⁴⁶ shows that LCBD measures are robust with regards to spatial scale, and are therefore
271 applicable at the global scale.

272 **Viral sharing between hosts**

273 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a
274 previously published generalized additive mixed model of virus sharing by a tensor function of
275 phylogenetic distance and geographic range overlap across mammals.⁴⁷ This network stores pairwise
276 values of viral community similarity. To project viral sharing values into a single value for every pixel, we
277 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant
278 bat assemblage is likely to be proficient at exchanging viruses.

279 **Composite risk map**

280 To visualize the aggregated risk at the global scale, we combine the three individual risk components
281 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model.⁴⁸ In
282 this approach, every risk component gets assigned a component in the RGB color model (phylogenetic
283 diversity is green, compositional uniqueness is red, and viral sharing is blue). In order to achieve a valid

284 RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no
285 phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for
286 each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the
287 risk as colors diverge towards combinations of values for three risk components. Out of the possible
288 combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic
289 diversity and low viral sharing,⁴⁹ in that this allows multiple independent host-virus coevolutionary
290 dynamics to take place in the same location. In the colorimetric space, this corresponds to yellow – because
291 the HSV space is more amenable to calculations for feature extraction,⁵⁰ we measured the risk level by
292 calculating the angular distance of the hue of each pixel to a reference value of 60 (yellow), and weighted
293 this risk level by the value component. Specifically, given a pixel with colorimetric coordinates (h, s, v) , its
294 ranged weighted risk value is

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

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

296 **Viral phyogeography and evolutionary diversification**

297 To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed
298 betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data
299 from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR
300 betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR
301 sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated
302 to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained
303 words indicating recombinant or laboratory strains including “patent”, “mutant”, “GFP”, and
304 “recombinant”. We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East
305 respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus
306 RdRp sequences were then aligned using MAFFT⁵¹ v1.4.0 (Algorithm FFT-NS-2, Scoring matrix 200PAM /
307 k=2, gap open penalty 1.53m offset value 0.123) and a maximum likelihood tree reconstructed in
308 IQ-TREE⁵² v1.6.12 with ModelFinder⁵³ ultrafast bootstrap approximation⁵⁴ with a general time reversible
309 model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of nucleotide

310 substitution (GTR+F+R5).

311 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat
312 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the
313 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary
314 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary
315 distinctiveness⁵⁵ for each of the viruses in the tree, then averaged these at the bat species level, projected
316 these values onto their geographic distributions, and averaged across every bat found in a given pixel. As
317 such, this can be thought of as a map of the mean evolutionary distinctiveness of the known viral
318 community believed to be associated with a particular subset of bats present.

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

320 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the
321 biogeography of their hosts. To test this idea, we loosely adapted a method from,^{56,57} who proposed a
322 phylogenetic method for the delineation of animal biogeographic regions. In their original method, a
323 distance matrix - where each row or column represents a geographic raster’s grid cell, and the dissimilarity
324 values are the “beta diversity similarity” of their community assemble - undergoes non-metric
325 multidimensional scaling (NMDS); the first two axes of the NMDS are projected geographically using a
326 four-color bivariate map. Here, we build on this idea with an entirely novel methodology. First, we
327 measure the phylogenetic distance between the different viruses in the betacoronaviruses tree by using the
328 cophenetic function in ape;⁵⁸ subsequently, we take a principal components analysis of that distance
329 matrix (readily interchangeable for NMDS in this case) to project the viral tree into an n-dimensional
330 space. We then take the first two principal components and, as with the evolutionary distinctiveness
331 analysis, aggregated these to a mean host value and projected them using a four-color bivariate map.

332 **References**

- 333 1.
- 334 Plowright, R. K. *et al.* Pathways to zoonotic spillover. *Nature Reviews Microbiology* **15**, 502–510 (2017).
- 335 2.
- 336 Anthony, S. J. *et al.* Global patterns in coronavirus diversity. *Virus Evolution* **3**, (2017).
- 337 3.
- 338 Ruiz-Aravena, M. *et al.* Ecology, evolution and spillover of coronaviruses from bats. *Nature Reviews Microbiology* **20**, 299–314 (2022).
- 339 4.
- 340 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).
- 341 5.
- 342 Power, A. G. & Mitchell, C. E. Pathogen Spillover in Disease Epidemics. *The American Naturalist* **164**, S79–S89 (2004).
- 343 6.
- 344 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).
- 345 7.
- 346 Thompson, J. N. *The Geographic Mosaic of Coevolution*. (University Of Chicago Press, 2005).
- 347 8.
- 348 Thompson, J. N. *The Coevolutionary Process*. (University Of Chicago Press, 1994).
- 349 9.
- 350 Janzen, D. H. When is it Coevolution? *Evolution* **34**, 611–612 (1980).
- 351 10.
- 352 Price, P. W. *Macroevolutionary Theory on Macroecological Patterns*. (Cambridge University Press, 2002).
doi:[10.1017/CBO9780511615030](https://doi.org/10.1017/CBO9780511615030).
- 353 11.
- 354 Gomulkiewicz, R. *et al.* Dos and don’ts of testing the geographic mosaic theory of coevolution. *Heredity* **98**, 249–258 (2007).

- 355 12.
- 356 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).
- 357 13.
- 358 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).
- 359 14.
- 360 Olival, K. J. *et al.* Host and viral traits predict zoonotic spillover from mammals. *Nature* **546**, 646–650 (2017).
- 361 15.
- 362 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).
- 363 16.
- 364 Allen, T. *et al.* Global hotspots and correlates of emerging zoonotic diseases. *Nature Communications* **8**,
(2017).
- 365 17.
- 366 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).
- 367 18.
- 368 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).
- 369 19.
- 370 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).
- 371 20.
- 372 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).
- 373 21.
- 374 Wang, N. *et al.* Serological Evidence of Bat SARS-Related Coronavirus Infection in Humans, China.
Virologica Sinica **33**, 104–107 (2018).
- 375 22.
- 376 Xu, R.-H. *et al.* Epidemiologic Clues to SARS Origin in China. *Emerging Infectious Diseases* **10**, 1030–1037
(2004).

- 377 23.
- 378 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).
- 379 24.
- 380 Van Brussel, K. & Holmes, E. C. Zoonotic disease and virome diversity in bats. *Current Opinion in Virology*
52, 192–202 (2022).
- 381 25.
- 382 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).
- 383 26.
- 384 Simmons, N. B. & Cirranello, A. L. Bat Species of the World: A taxonomic and geographic database. <https://batnames.org/> (2020).
- 385 27.
- 386 Kasso, M. & Balakrishnan, M. Ecological and Economic Importance of Bats (Order Chiroptera). *ISRN
Biodiversity* **2013**, e187415 (2013).
- 387 28.
- 388 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).
- 389 29.
- 390 *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).
- 391 30.
- 392 Williams-Guillén, K., Perfecto, I. & Vandermeer, J. Bats Limit Insects in a Neotropical Agroforestry System.
Science **320**, 70–70 (2008).
- 393 31.
- 394 Gonsalves, L., Bicknell, B., Law, B., Webb, C. & Monamy, V. Mosquito Consumption by Insectivorous Bats:
Does Size Matter? *PLOS ONE* **8**, e77183 (2013).
- 395 32.
- 396 Gonsalves, L., Lamb, S., Webb, C., Law, B. & Monamy, V. Do mosquitoes influence bat activity in coastal
habitats? *Wildlife Research* **40**, 10–24 (2013).
- 397 33.
- 398 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).

- 399 34.
- 400 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).
- 401 35.
- 402 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).
- 403 36.
- 404 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).
- 405 37.
- 406 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).
- 407 38.
- 408 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).
- 409 39.
- 410 Amman, B. R. *et al.* *Investigating the role of bats in emerging zoonoses: Balancing ecology, conservation and
public health interest.* (FAO, 2011).
- 411 40.
- 412 IUCN. The IUCN Red List of Threatened Species. <https://www.iucnredlist.org> (2021).
- 413 41.
- 414 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).
- 415 42.
- 416 Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61**, 1–10 (1992).
- 417 43.
- 418 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).
- 419 44.
- 420 Legendre, P. & De Cáceres, M. Beta diversity as the variance of community data: Dissimilarity coefficients
and partitioning. *Ecology Letters* **16**, 951–963 (2013).

- 421 45.
- 422 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).
- 423 46.
- 424 Dansereau, G., Legendre, P. & Poisot, T. Evaluating ecological uniqueness over broad spatial extents using
species distribution modelling. *Oikos* **n/a**, e09063 (2022).
- 425 47.
- 426 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).
- 427 48.
- 428 Seekell, D. A., Lapierre, J.-F. & Cheruvelil, K. S. A geography of lake carbon cycling. *Limnology and
Oceanography Letters* **3**, 49–56 (2018).
- 429 49.
- 430 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).
- 431 50.
- 432 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).
- 433 51.
- 434 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).
- 435 52.
- 436 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).
- 437 53.
- 438 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).
- 439 54.
- 440 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).
- 441 55.
- 442 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).

- 443 56.
- 444 Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *Proceedings of the National
Academy of Sciences* **104**, 5925–5930 (2007).
- 445 57.
- 446 Kreft, H. & Jetz, W. A framework for delineating biogeographical regions based on species distributions.
Journal of Biogeography **37**, 2029–2053 (2010).
- 447 58.
- 448 Paradis, E. & Schliep, K. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in
R. Bioinformatics **35**, 526–528 (2019).

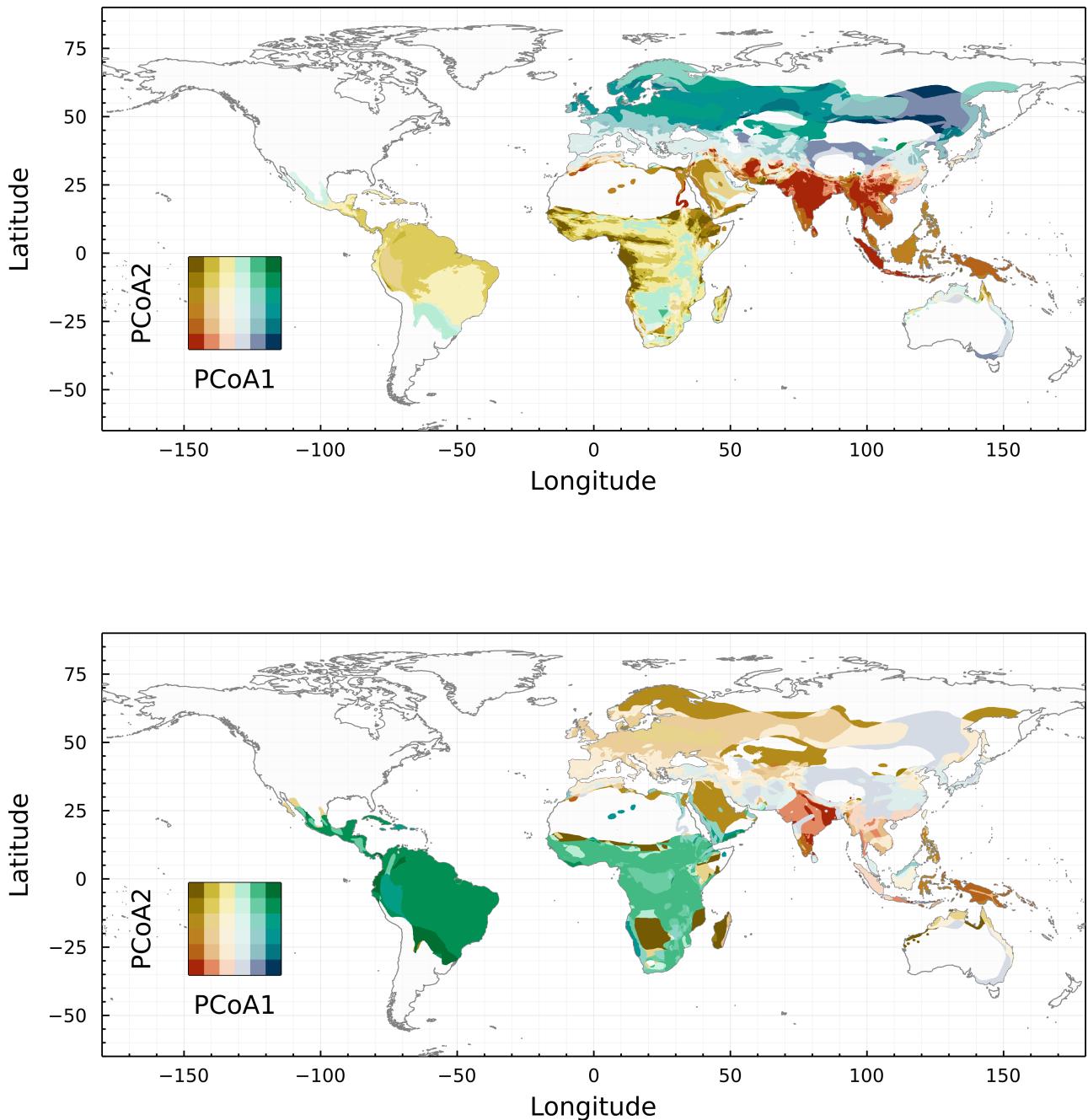


Figure 1: Phylogeographic regions of bats (top) and viruses (bottom) based on the joint analysis of their occurrence and phylogenetic relatedness. The different colors show tendencies to separate alongside the first two components of a PCoA. Note that the PCoA for the bats and viruses are independent, and so cannot be compared directly – that being said, the regions can be compared across maps.

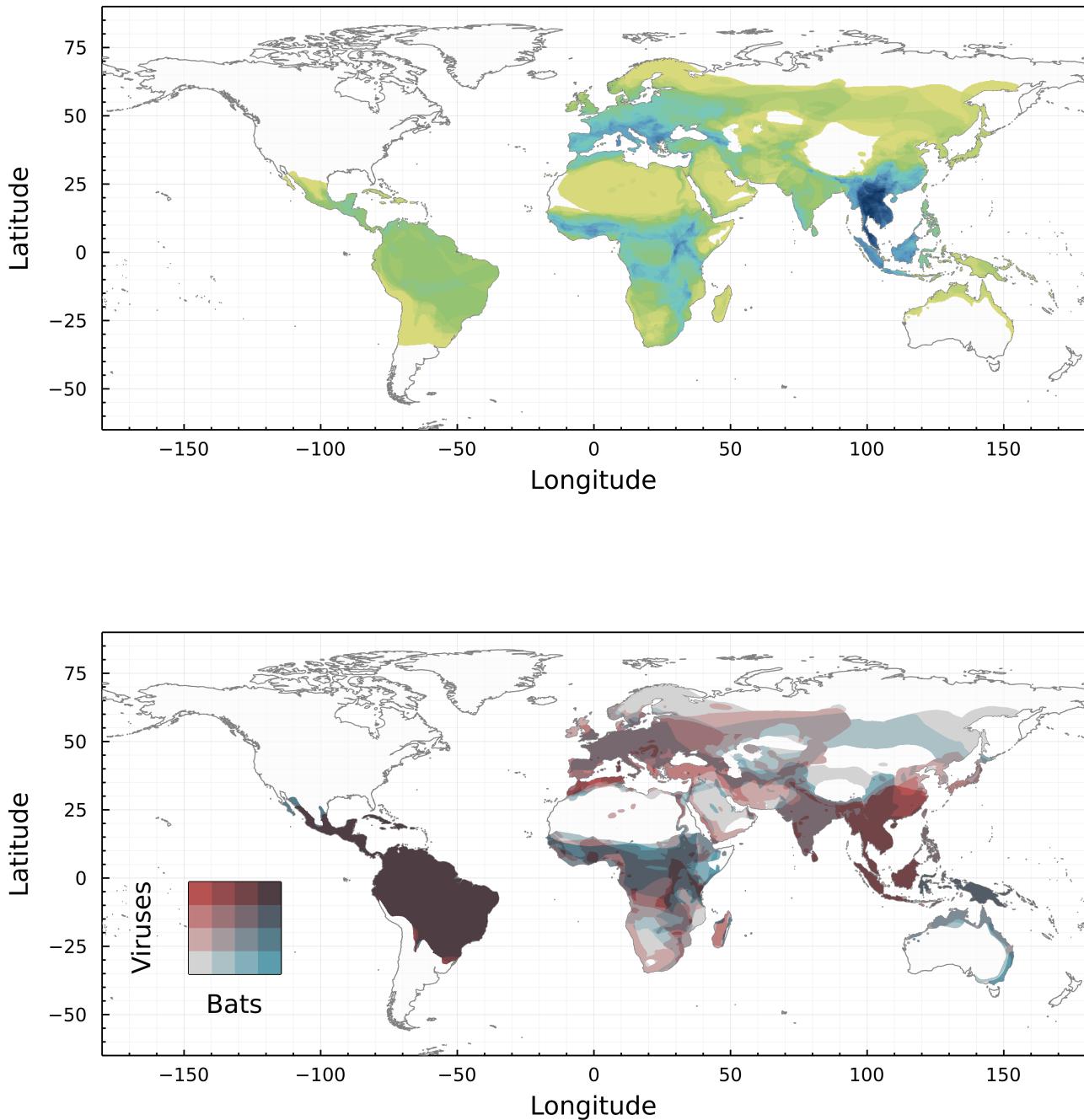


Figure 2: Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red).

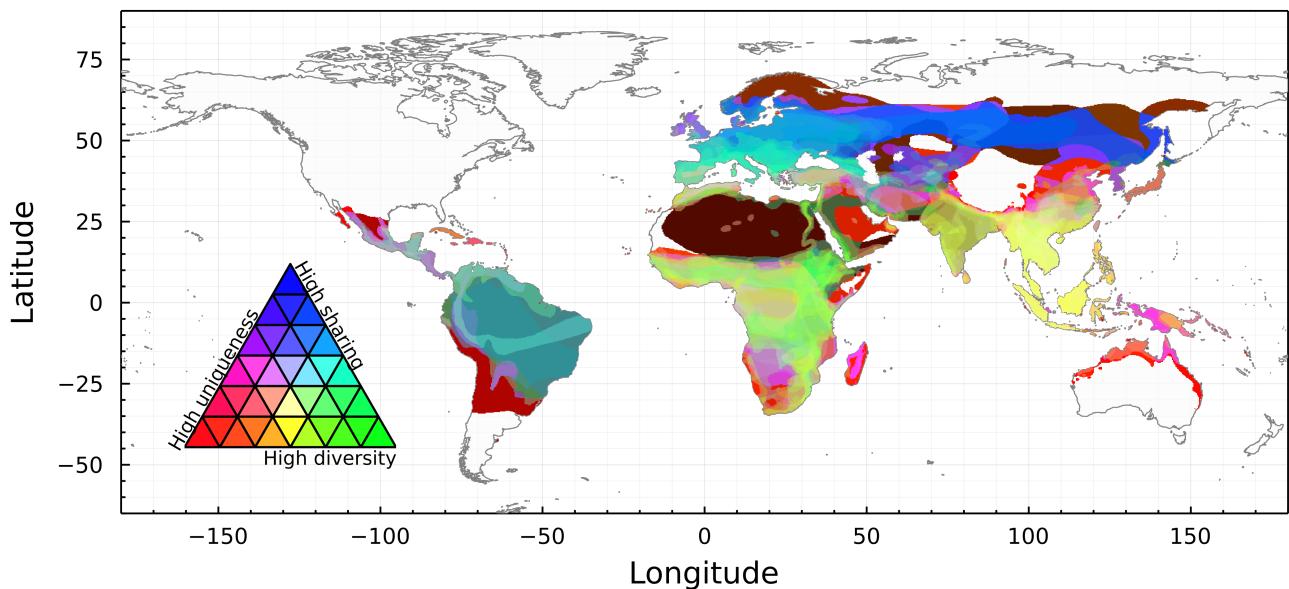


Figure 3: Trivariate additive mapping of the components of risk in the red/green/blue, where high virus sharing is encoded in the blue channel, host phylogenetic diversity in the green channel, and compositional uniqueness in the red channel. A pixel that would maximize all measures (highest possible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

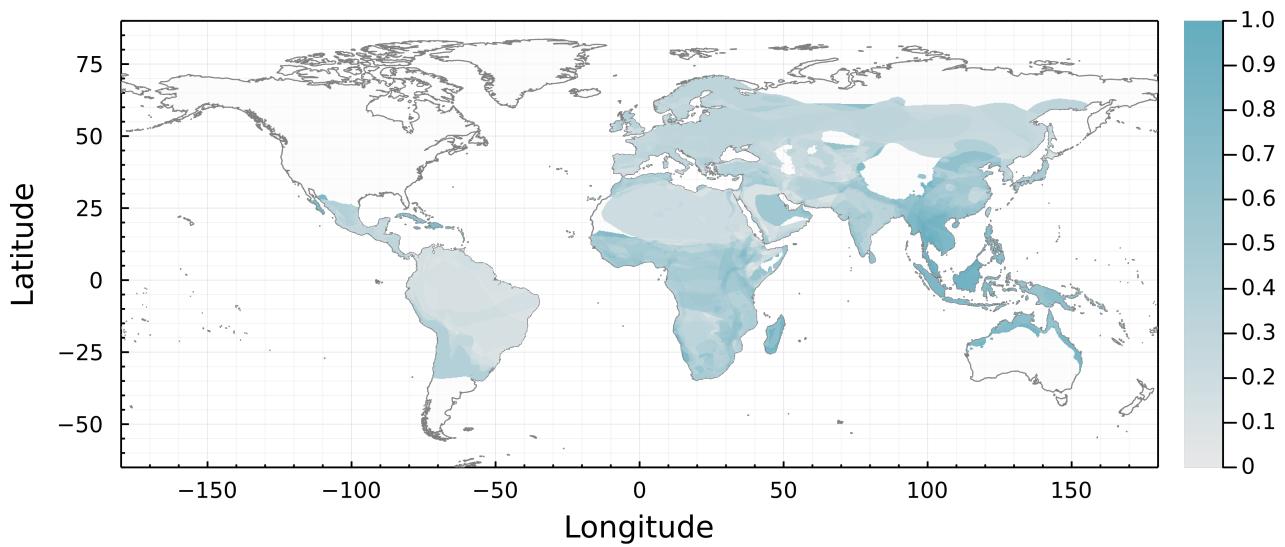


Figure 4: Extraction of a measure of *Betacoronavirus* spillover risk from bat hosts based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on this analyses, regions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

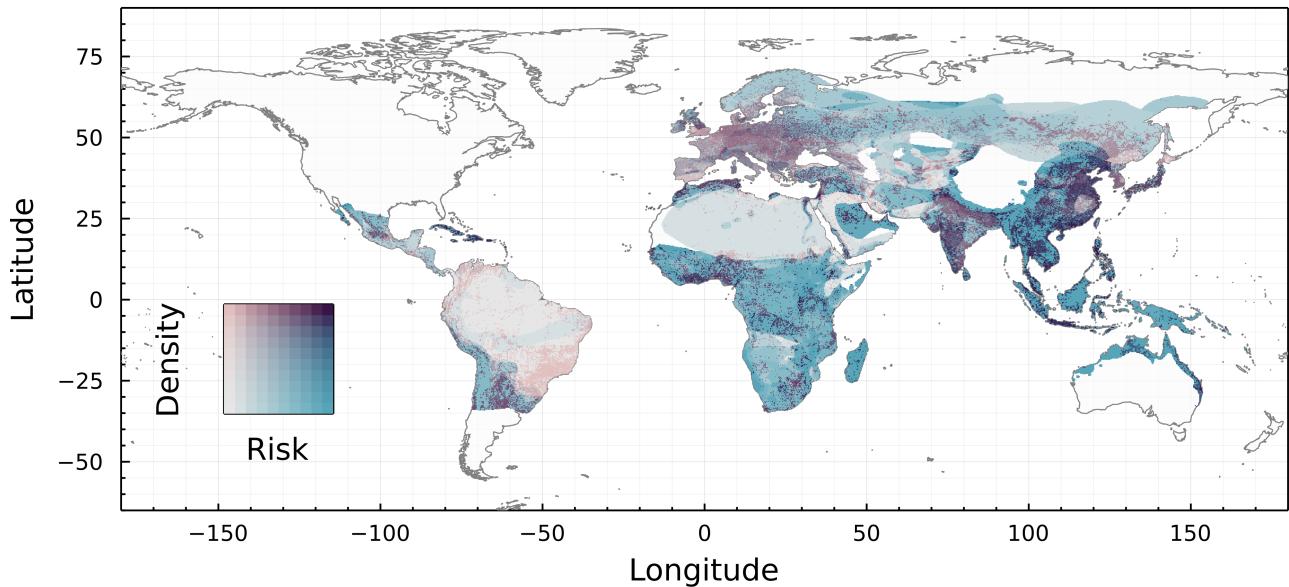


Figure 5: Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk,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