

The coevolutionary mosaic of *Betacoronavirus* spillover risk from bat hosts

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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 reservoir 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 system may originate novel viruses in humans.

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 (Plowright et al. 2017). Although host richness is
3 often used as a superficial proxy for spillover risk (Anthony et al. 2017, Ruiz-Aravena et al. 2022), these
4 approaches oversimplify the relevant interspecific heterogeneity in immunology, behavior, and other
5 traits, and therefore overlook unique host pools that allow for the rapid evolution of highly divergent
6 viruses (Agosta et al. 2010). In the case of generalist pathogens like betacoronaviruses, there is conceptual
7 and empirical support to the idea that these community-level mechanisms are even more important
8 (Power and Mitchell 2004). This creates a disconnect between coevolutionary theory and existing
9 ecological frameworks for mapping spillover risk.

10 The Geographic Mosaic Theory of Coevolution (GMTC; Thompson 2005) attempts to explicitly connect
11 microevolutionary dynamics to the macroecology and biogeography of symbiotic interactions. The GMTC
12 posits that coevolutionary processes among pairs (Thompson 1994) or complexes (Janzen 1980) of species
13 are structured in space by the rippling effects of abiotic conditions onto evolutionary mechanism, giving
14 rise to fragmented systems with different structure and ecologically dynamics over large spatial extents
15 (see e.g. Price 2002). The GMTC predicts a spatial fragmentation of coevolutionary dynamics under the
16 joint action of three processes (see notably Gomulkiewicz et al. 2007): coevolutionary hot- and coldspots,
17 which appear when the intensity of *interaction* (in terms of reciprocal fitness consequences) varies
18 spatially; selection mosaics, wherein the intensity of *selection* varies across space, driven by both the biotic
19 complexity of the community (locally diverse hosts and viruses are more biotically complex) and the local
20 favorability of the environment (**Thrall2007?**); and trait remixing, which occurs when coevolutionary
21 dynamics are driven by the arrival (or departure) of *functional traits*, through changes in community
22 composition due to invasions, meta-community dynamics, and dispersal.

23 Here, we apply the GMTC to explore and explain the global biogeography of betacoronaviruses, the group
24 that includes SARS-CoV, MERS-CoV, and SARS-CoV-2. Working from a recently published database of
25 bat hosts of betacoronaviruses, we develop the first global maps of both host and virus evolutionary
26 distinctiveness and biogeographic regions for this system. Aiming to explain these patterns, we develop a
27 generalized framework for applying the GMTC to host-virus interactions, with a specific emphasis on the
28 potential to create independent coevolutionary dynamics (and therefore spatial fragmentation in risk)
29 through heterogeneity. We develop a trivariate risk assessment system that connects each GMTC
30 mechanism to a quantifiable aspect of host-virus interactions: (i) viral sharing rates in host communities,

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

39 **Host richness does not predict virus distinctiveness**

40 Bats, the second most diverse groups of mammals, are found worldwide and serve as the main animal
41 reservoir for different strains of betacoronaviruses (Drexler et al. 2014). This has attracted attention to
42 areas where high diversity of bats, and therefore presumably high diversity of betacoronaviruses, can be an
43 important issue for human health (Calisher et al. 2006, Moratelli and Calisher 2015). By overlaying the
44 IUCN range maps for confirmed bat hosts of betacoronaviruses [fig. 1; top], we see that the the main
45 hotspots (both in terms of size and higher values) of host richness are primarily South-Eastern Asia, parts
46 of Southern Europe, and to a lesser extent parts of Africa in the -25-0 range of latitudes. The description of
47 host richness is an important first step towards understanding risk, as previous research (Anthony et al.
48 2017, Mollentze and Streicker 2020) states that locally diverse bat communities could maintain more
49 viruses and hence, a higher probability of having a pathogen that could represent a risk for human health.

50 [Figure 1 about here.]

51 Nevertheless, locally diverse and virus-rich bat communities could represent an increased risk of spillover
52 under climate change through the creation of novel interactions (Carlson et al. 2022), and therefore the
53 diversity of *Betacoronavirus* strains should similarly be ccounted for. In fig. 1 (bottom), we contrast the
54 evolutionary distinctiveness of bats and viruses – this reveals a slightly different portrait than bat richness
55 alone. Chiropterans can be classified, from a macro-evolutionary standpoint, as Yangochiroptera and
56 Yinpterochiroptera elsewhere (Teeling et al. 2005, Springer 2013). Specifically, we would expect that the
57 so-called “New World” group of bats, being more evolutionary distinct, would also have evolutionary
58 distinct viruses. Indeed fig. 1 (bottom) reveals it to be the case, and this region harbors a distinct

59 bat-betacoronaviruses complex. This can be explained by the fact that Yangochiroptera, although not
60 limited to the western hemisphere, contain the highly diverse adaptive radiation in the Phyllostomidae
61 (Villalobos and Arita 2010), which is restricted to the western hemisphere. By contrast, South-Eastern
62 Asia has a lot of non-evolutionary distinct bats, who nevertheless hosted evolutionary-distinct viruses.
63 It is noteworthy that outside of South America, viral evolutionary distinctiveness does not accurately track
64 host diversity, with some areas having over-distinct viruses (eastern China but, oddly, not the rest of
65 southeast Asia). There are a number of likely explanations. First, given the richness of bats in southeast
66 Asia, many betacoronaviruses likely remain to be discovered in this region. Indeed, global predictions by
67 Becker et al. (2022) highlight that southeast Asia is a likely hotspot of unconfirmed hosts of
68 betacoronaviruses, which would likely result in additional viral discoveries. This idea is unsurprising
69 given the growing realization, especially since the emergence of SARS-CoV-2, that unique lineages of
70 similar viruses are widespread in bats but still mostly undescribed. The most distinct
71 bats-betacoronaviruses complex is found in South America, a region with a comparatively lower number
72 of hosts; this matches with the isolation through variance of the host group, and may highlight a different
73 co-evolutionary dynamic. Alternatively, this distinctiveness hotspot may be a product of under-sampling:
74 South-America is one of the places where the fewest *Betacoronavirus* sequences have been discovered
75 (Anthony et al. 2017, Olival et al. 2017, Allen et al. 2017), resulting in sparser phylogenetic tree, thereby
76 artificially inflating distinctiveness. Adding more viruses would bring the distinctiveness of known
77 sequences down. Finally, South-America is the range of Phyllostomidae, a group of bats that underwent
78 explosive diversification events (Villalobos and Arita 2010), which may drive the emergence of multiple
79 viral lineages.

80 The phylogeographic regions of hosts and their viruses overlap

81 Despite the difference in evolutionary distinctiveness globally, there are reasons to expect that the
82 phylogeography of bats and betacoronaviruses should show some degree of congruence (Letko et al. 2020,
83 Van Brussel and Holmes 2022). In particular, this should be the case if viruses can circulate among hosts
84 and co-evolve with local hosts communities, making their evolutionary process more than a byproduct of
85 host evolution. High density of hosts sharing the same virus (albeit possibly different strains) can drive or
86 result from evolution of the bat antiviral immune system, resulting in spatially distinct immunological
87 responses, as evidenced in several bat species (Banerjee et al. 2020). Immune characteristics that allow

88 bats to be better adapted to infection by emerging viruses (Gorbunova et al. 2020, Irving et al. 2021), in
89 addition to being hardcoded in their genome (Jebb et al. 2020), may be related to a wide variety of diets
90 (Banerjee et al. 2020, Moreno Santillán et al. 2021), themselves likely to be driven by spatial effects,
91 especially at the local scale – bats, indeed, occupy a variety of environments, and therefore display a
92 variety of adaptations to these environments (Muylaert et al. 2022).

93 [Figure 2 about here.]

94 In fig. 2, we show a projection of the phylogeographic signal of bats (top) and viruses (bottom) in space;
95 the distinct groupings (represented by different colors symbolizing positions in the subspace formed by
96 the first two axes of the PCoA) are essentially equivalent between the two groups, and can be coarsely
97 delineated as southeast Asia, Eurasia above a northing of 25, and Africa and south America. These results
98 suggest that, although the evolutionary distinctiveness of the bat-betacoronaviruses complex varies
99 spatially, the system shows an important degree of spatial consistency, with a reduced number of
100 bioregions. Available information describing the spillover of zoonotic betacoronaviruses of bat origin
101 where data was available before and up through the COVID-19 pandemic puts spillover events of
102 SARS-CoV-2 in Wuhan, China; SARS-CoV in Guangdong, China based on the presence of closest known
103 viruses circulating in nature, and a nearby location where serological (antibody) evidence has indicated
104 human exposure to SARS-like viruses (Wang et al. 2018); MERS-CoV in Saudi Arabia based on index cases
105 available from a recently-published compendium of cases (Ramshaw et al. 2019). For the latest event,
106 most if not all index cases are presumed to be camel-to-human transmission, and the precise origin point
107 (if it exists) of MERS-CoV in bats is uncertain. Recent recombinant canine coronavirus spillover events in
108 Haiti (Lednicky et al. 2021) and Europe (Vlasova et al. 2022) are not relevant here, as bats' involvement in
109 these cycles of transmission have been supposed to be non-existent. These index cases fall within different
110 phylogeographic bioregions (fig. 2), which further highlight the issue that different host-virus sub-systems
111 may lead to widespread emergence.

112 **Coevolution-informed spillover risk is different in space**

113 As host richness, joint distinctiveness, or phylogeographic structure suggest that the bat-betacoronaviruses
114 complex is globally fragmented enough to give rise to both different levels of risk (as evidenced by the
115 spatial location of spillover events) and different types of co-evolutionary dynamics, we turn to the

116 Geographic Mosaic Theory of Coevolution (Thompson 2005) to provide a measure of risk accounting for
117 multiple processes. In fig. 3, we overlapped three components of spillover risk: viral sharing, *i.e.* the
118 chance that two bats will share viruses overall; Local Contribution to Beta Diversity, *i.e.* the fact that a bat
119 community is compositionally unique compared to the average compositional similarity across the entire
120 system; finally, host phylogenetic diversity, *i.e.* how dispersed the bats in a location are within the tree of
121 life. This approach leads to the definition of broad biogeographic regions of risk, where the same color
122 represents the same type of risk. By way of contrast to figures fig. 1 and fig. 2, these regions do not
123 necessarily overlap with previous spatial partitions of the bat-betacoronaviruses complex.

124 [Figure 3 about here.]

125 From the perspective of spillover risk, the most important combination of factors is a high phylogenetic
126 diversity of hosts with low viral sharing; this, essentially, means that very different betacoronaviruses
127 could co-exist within the same place. This is particularly the case given that betacoronaviruses often
128 evolve and even achieve host shifts through recombination, which requires the co-occurrence of
129 sufficiently distinct viruses to be a major driver of emergence. In fig. 3, this corresponds to yellow to pale
130 green areas, which are essentially limited to South-Eastern Asia, and to some part of Sub-Saharan Africa.
131 Adopting a geographic mosaic theory perspective on risk, other regions of the world are of lesser concern
132 fig. 4. Our risk decomposition does not account for viral diversity or distinctiveness. The simple rationale
133 behind it is that the acquisition of viral data is rarely disconnected from the acquisition of host data. There
134 are more sources of information on hosts than on viruses, allowing to develop a host-centric perspective
135 on risk (although this estimate would be more accurate with viral traits related to e.g. ability to switch hosts
136 or pathogenic potential). Areas with high bat diversity and high turnover *may* facilitate the evolutionary
137 radiation of viruses, matching previous findings that the diversification of bat coronaviruses is driven
138 largely by host shifts (inter-genus or higher levels of cross-species transmission) and, to a lesser degree,
139 cospeciation and sharing (intra-genus cross-species transmission; Anthony et al. 2017). This
140 diversification is not an actual risk factor for spillover itself, but acts downstream of a spillover event by
141 increasing the random chance of the emergence of a virus with the raw genomic components required for
142 the potential to infect humans.

143 [Figure 4 about here.]

144 From another perspective, areas of high host uniqueness and virus sharing (red-to-pink) could provide
145 hotspots of *Betacoronavirus* risk through mixing of unique viruses (via codivergence) and in turn
146 recombination. Under our framework, such a hotspot was identified in Madagascar, where most bat
147 species are endemic following evolutionary divergence from sister species in both African and Asian
148 continents (e.g. Shi et al. 2014). Recent surveillance (Kettenburg et al. 2022) has identified a novel
149 *Betacoronavirus* (in the subgenus *Nobecovirus*) in Madagascar-endemic pteropid bat species (*Pteropus*
150 *rufus*, *Rousettus madagascariensis*), emphasizing strong proof of principle in model predictions.

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

152 Based on the previous result, we extracted the risk component from the composite map (see Methods), to
153 provide a single measure of risk varying between 0 and 1. This measure is presented in fig. 4. As this map
154 represents the potential risk, it must be weighed by the potential for contacts with humans. As a proxy for
155 this measure, we used the proportion of build/urban land from the EarthEnv dataset: this is a reasonable
156 proxy for the density of humans per unit area, which increases the probability of pathogen spread more
157 widely (Hazarie et al. 2021). Since human activity is required to amplify the frequency of virus encounters
158 and thus create areas of viral amplification, mapping the potential risk against measures of land use is
159 required to generate a more actionable assessment of risk. This map is presented in fig. 5. Most of South
160 America and Europe are at comparatively lower risk, as although densely populated, settlements tend to
161 be in areas with lower potential risk. Regions like Malaysia and the North coast of Australia have a high
162 risk component, but should represent a relatively lower effective risk due to low human density. However,
163 this mapping reveals that South-East Asia, the Indian subcontinent, and parts of sub-Saharan Africa, are
164 at high risk due to the overlap between built areas and bat communities representing more opportunities
165 for cross-species transmission of betacoronaviruses. In looking for the origins of SARS in China, Xu et al.
166 (2004) present serological evidence that strongest human-animal contact results in higher risk of virus
167 exposure, regardless of the animal species, but that different types of contact had different impacts. Ideally,
168 finer-grained information about human activity (rather than human presence through anthropisation)
169 could allow to partition this risk further, albeit at the cost of more hypotheses required to estimate the
170 amount of risk represented by each activity. Our map of risk overlays with recent results from Cohen et al.
171 (2022) – areas of purported high risk/diversitification potential (Madagascar, South-America) overlay with
172 sampling gaps for *Betacoronavirus*, stressing the need for spatially targeted monitoring and discovery.

174 **Conclusion**

175 Bats are important reservoir hosts for different classes of microorganisms, many of which a threat to
176 human health (Letko et al. 2020, Van Brussel and Holmes 2022). Chiropterans emerged around 64 million
177 years ago and are one of the most diverse mammalian orders, with an estimated richness of more than
178 1400 species (Peixoto et al. 2018, Simmons and Cirranello 2020). They exhibit a broad variety of habitat
179 use, behaviour, and feeding strategies, putting them at key positions in the delivery and provisioning of
180 several ecosystem services, tied to important ecosystem-derived benefits to human (Kasso and
181 Balakrishnan 2013). For example, bats are an essential component of many seed-dispersal networks
182 (Mello et al. 2011). Over two-thirds of bats are know to be either obligate or facultative insectivores,
183 therefore actively contributing for agricultural pest control (Williams-Guillén et al. 2008, Voigt and
184 Kingston 2016), and vectors of pathogens that put a risk on human health (Gonsalves et al. 2013a, b).
185 Because bats are globally distributed and have a long evolutionary history, phylogeographic and
186 biogeographic approaches are required to shed light on the contemporary distribution of coevolutionary
187 processes between bats and the pathogens they host. Not all areas in which bats, viruses, and human are
188 co-occurring are facing a risk of spillover towards human populations, and the areas in which this risk exist
189 may not be facing risks of the same nature and magnitude.

190 RELOCATE: Indeed, it only assumes the action of well described evolutionary mechanisms. The benefit
191 of this approach is to provide the potential for a more dynamic and nuanced understanding of risk: not
192 only on ecological timescales, but also by providing clues about which areas can change over
193 micro-evolutionary timescales.

194 Our study focuses largely on the biogeography of hosts. Specifically, we identify the Amazon and
195 South-Eastern Asia as hotspots where the phylogenetic distinctiveness of *Betacoronavirus* is the highest
196 (Anthony et al. 2017); surprisingly, current data suggest that viral sharing between hosts is high in the
197 Amazon and low in South-Eastern Asia, which has the potential to result in different evolutionary
198 dynamics between these two regions, hinting at different futures for their viral communities. This work is
199 important both as a description of the bats-betacoronaviruses complex, but also because more broadly,
200 bats are known reservoirs for a variety of emerging viruses and other pathogens (Calisher et al. 2006,

201 Melaun et al. 2014), making balancing the needs for bat conservation and disease prevention most likely
202 very difficult and a source of human-wildlife conflicts, especially in more densely populated areas (Stone
203 et al. 2015, Rego et al. 2015).

204 Yet, we know that viruses with high host plasticity, that is, the ability of a given virus to adapt to various
205 taxonomic orders and ecological groups (Kreuder Johnson et al. 2015), are more likely to amplify viral
206 spillover, followed by secondary human-to-human transmission, and geographical spread (Hazarie et al.
207 2021). High viral host plasticity is an especially important trait for RNA viruses like betacoronaviruses
208 (Haddad et al. 2021). Indeed, our analysis of viral sequences reveals that Latin America is a hotspot of
209 viral distinctiveness, suggesting that this part of the bats-betacoronaviruses complex may be undergoing
210 independent evolutionary dynamics (related species sharing viruses that are different from the rest of the
211 global pool). The other hotspot of viral distinctiveness is S.E. Asia, in which richness is high but sharing is
212 low; this suggests a different type of evolutionary dynamics (unrelated viruses coevolving with
213 evolutionarily distinct hosts, generating high diversity locally, see e.g. Latinne et al. 2020). Both of these
214 areas should be priority areas for sampling, especially since Becker et al. (2022) advance that they harbor
215 undiscovered hosts of beta-coronaviruses. This diversity of hosts, and the mechanisms by which the
216 exchange of viruses occurs between species, is largely affected by the local environmental conditions and
217 environmental change.

218 There are several factors that drive changes in the diversity of bats (Alves et al. 2018), but human
219 activities' effects on the ecosystem (like modifications of land use) could significantly decrease it.
220 Therefore, it can be suggested that changes in the diversity of betacovs in bats are linked to their
221 biogeographic variation, and human population density and other anthropogenic factors are decisive
222 moderators for its implications in public health. With the increase of contact between humans and
223 potential hosts, we also increase the risk of emergence of novel diseases (Johnson et al. 2020), as previous
224 studies on RNA viruses suggest the importance of host phylogeography at the time of virus dispersal
225 (Gryseels et al. 2017). One of these scenarios where interaction between bats and humans can occur can
226 be seed dispersal in tropical agroecosystems. It opens the discussion of whether the fruits thrown by bats
227 not only disperse seeds but could also be a source of indirect interaction between viruses of bat origin and
228 humans (Deshpande et al. 2022). This represents a challenge for conservation strategies and disease
229 ecology since some areas can have both potential for the acquisition of zoonotic viruses and bat-human
230 interactions; in particular, the challenge lies in the fact that actual exposure must then be quantified

231 accounting for several transmission scenarios, including both direct and indirect bat - human interaction.

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240 **Methods**

241 **Known *Betacoronavirus* hosts**

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

249 **Bat occurrences**

250 We downloaded the rangemap of every current bat species that was classified as an empirically
251 documented host of *Betacoronavirus* from the previous step, according to recent IUCN data (IUCN 2021).
252 The range maps were subsequently rasterized using the rasterize function from GDAL (Rouault et al.
253 2022) at a resolution of approximately 100kmx100km. For every pixel in the resulting raster where at least
254 one bat host of *Betacoronavirus* was present, we extract the species pool (list of all competent bat hosts),
255 which was used to calculate the following risk assessment components: bat phylogenetic diversity, bat
256 compositional uniqueness, and predicted viral sharing risk.

257 **Bat phylogenetic diversity**

258 For every pixel, we measured Faith’s Phylogenetic Diversity (Faith 1992) based on a recent synthetic tree
259 with robust time calibration, covering about 6000 mammalian species (Upham et al. 2019). Faith’s PD
260 measures the sum of unique branches from an arbitrary root to a set of tips, and comparatively larger
261 values indicate a more phylogenetic diverse species pool. We measured phylogenetic diversity starting
262 from the root of the entire tree (and not from Chiroptera); this bears no consequences on the resulting
263 values, since all branches leading up to Chiroptera are only counted one per species pool, and (as we
264 explain when describing the assembly of the composite risk map), all individual risk components are
265 ranged in [0,1]. This measure incorporates a richness component, which we chose not to correct for; the

266 interpretation of the phylogenetic diversity is therefore a weighted species richness, that accounts for
267 phylogenetic over/under-dispersal in some places.

268 **Bat compositional uniqueness**

269 For every species pool, we measured its Local Contribution to Beta-Diversity (Legendre and De Cáceres
270 2013); LCBD works from a species-data matrix (traditionally noted as \mathbf{Y}), where species are rows and sites
271 are columns, and a value of 1 indicates occurrence. We extracted the \mathbf{Y} matrix assuming that every pixel
272 represents a unique location, and following best practices (Legendre and Condit 2019) transformed it
273 using Hellinger's distance to account for unequal bat richness at different pixels. The correction of raw
274 community data is particularly important for two reasons: first, it prevents the artifact of richer sites
275 having higher importance; second, it removes the effect of overall species richness, which is already
276 incorporated in the phylogenetic diversity component. High values of LCBD indicate that the pixel has a
277 community that is on average more dissimilar in species composition than what is expected knowing the
278 entire matrix, i.e. a more unique community. Recent results by Dansereau et al. (2022) shows that LCBD
279 measures are robust with regards to spatial scale, and are therefore applicable at the global scale.

280 **Viral sharing between hosts**

281 For all bat hosts of *Betacoronavirus*, we extracted their predicted viral sharing network, generated from a
282 previously published generalized additive mixed model of virus sharing by a tensor function of
283 phylogenetic distance and geographic range overlap (Albery et al. 2020). This network stores pairwise
284 values of viral community similarity. To project viral sharing values into a single value for every pixel, we
285 averaged the pairwise scores. High values of the average sharing propensity means that this specific extant
286 bat assemblage is likely to be proficient at exchanging viruses.

287 **Composite risk map**

288 To visualize the aggregated risk at the global scale, we combine the three individual risk components
289 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model
290 (Seekell et al. 2018). In this approach, every risk component gets assigned a component in the RGB color
291 model (phylogenetic diversity is green, compositional uniqueness is red, and viral sharing is blue). In

order to achieve a valid RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel with no sharing, no phylogenetic diversity, and no compositional uniqueness is black, and a pixel with maximal values for each is white. This additive model conveys both the intensity of the overall risk, but also the nature of the risk as colors diverge towards combinations of values for three risk components. Out of the possible combinations, the most risky in terms of rapid diversification and spillover potential is high phylogenetic diversity and low viral sharing (Gomulkiewicz et al. 2000, Cavender-Bares et al. 2009), in that this allows multiple independent host-virus coevolutionary dynamics to take place in the same location. In the colorimetric space, this correspond to yellow – because the HSV space is more amenable to calculations for feature extraction (see e.g. Keke et al. 2010), we measured the risk level by calculating the angular distance of the hue of each pixel to a reference value of 60, and weighted this risk level by the value component. Specifically, given a pixel with colorimetric coordinates (h, s, v) , its ranged weighted risk value is

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

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

305 **Viral phyogeography and evolutionary diversification**

To next represent phyogeography of betacoronaviruses in bats, we aggregated and analyzed betacoronavirus sequence data. We used the following query to pull all *Betacoronavirus* sequence data from the GenBank Nucleotide database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR betacoronavirus[All Fields]) NOT (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR sars-cov-2[All Fields]). We added a single representative sequence for SARS-CoV-2 and manually curated to remove sequences without the RNA-dependent RNA polymerase (RdRp) sequence or that contained words indicating recombinant or laboratory strains including “patent,” “mutant,” “GFP,” and “recombinant.” We filtered over-represented taxa including betacoronavirus 1, hCoV-OC43, Middle East respiratory syndrome coronavirus, Murine hepatitis virus, and hCoV-HKU1. Curated betacoronavirus RdRp sequences were then aligned using MAFFT v 1.4.0 [Katoh and Standley (2013); Algorithm FFT-NS-2, Scoring matrix 200PAM / k=2, gap open penalty 1.53m offset value 0.123] and a maximum likelihood tree reconstructed in IQ-TREE v 1.6.12 (Nguyen et al. 2015) with ModelFinder

318 (Kalyaanamoorthy et al. 2017) ultrafast bootstrap approximation (Hoang et al. 2018) with a general time
319 reversible model with empirical base frequencies and the 5-discrete-rate-category FreeRaye model of
320 nucleotide substitution (GTR+F+R5).

321 We first tested the hypothesis that hotspots of viral diversification would track hotspots of bat
322 diversification. To do so, we plotted the number of known bat hosts (specifically only those included in the
323 phylogeny, so there was a 1:1 correspondence between data sources) against the “mean evolutionary
324 distinctiveness” of the associated viruses. To calculate this, we derived the fair proportions evolutionary
325 distinctiveness (Isaac et al. 2007) for each of the viruses in the tree, then averaged these at the bat species
326 level, projected these values onto their geographic distributions, and averaged across every bat found in a
327 given pixel. As such, this can be thought of as a map of the mean evolutionary distinctiveness of the
328 known viral community believed to be associated with a particular subset of bats present.

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

330 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the
331 biogeography of their hosts. To test this idea, we loosely adapted a method from (Kreft and Jetz 2007,
332 2010), who proposed a phylogenetic method for the delineation of animal biogeographic regions. In their
333 original method, a distance matrix - where each row or column represents a geographic raster’s grid cell,
334 and the dissimilarity values are the “beta diversity similarity” of their community assemble - undergoes
335 non-metric multidimensional scaling (NMDS); the first two axes of the NMDS are projected
336 geographically using a four-color bivariate map. Here, we build on this idea with an entirely novel
337 methodology. First, we measure the phylogenetic distance between the different viruses in the
338 betacoronaviruses tree by using the cophenetic function in ape (Paradis and Schliep 2019); subsequently,
339 we take a principal components analysis of that distance matrix (readily interchangeable for NMDS in this
340 case) to project the viral tree into an n-dimensional space. We then take the first two principal
341 components and, as with the evolutionary distinctiveness analysis, aggregated these to a mean host value
342 and projected them using a four-color bivariate map.

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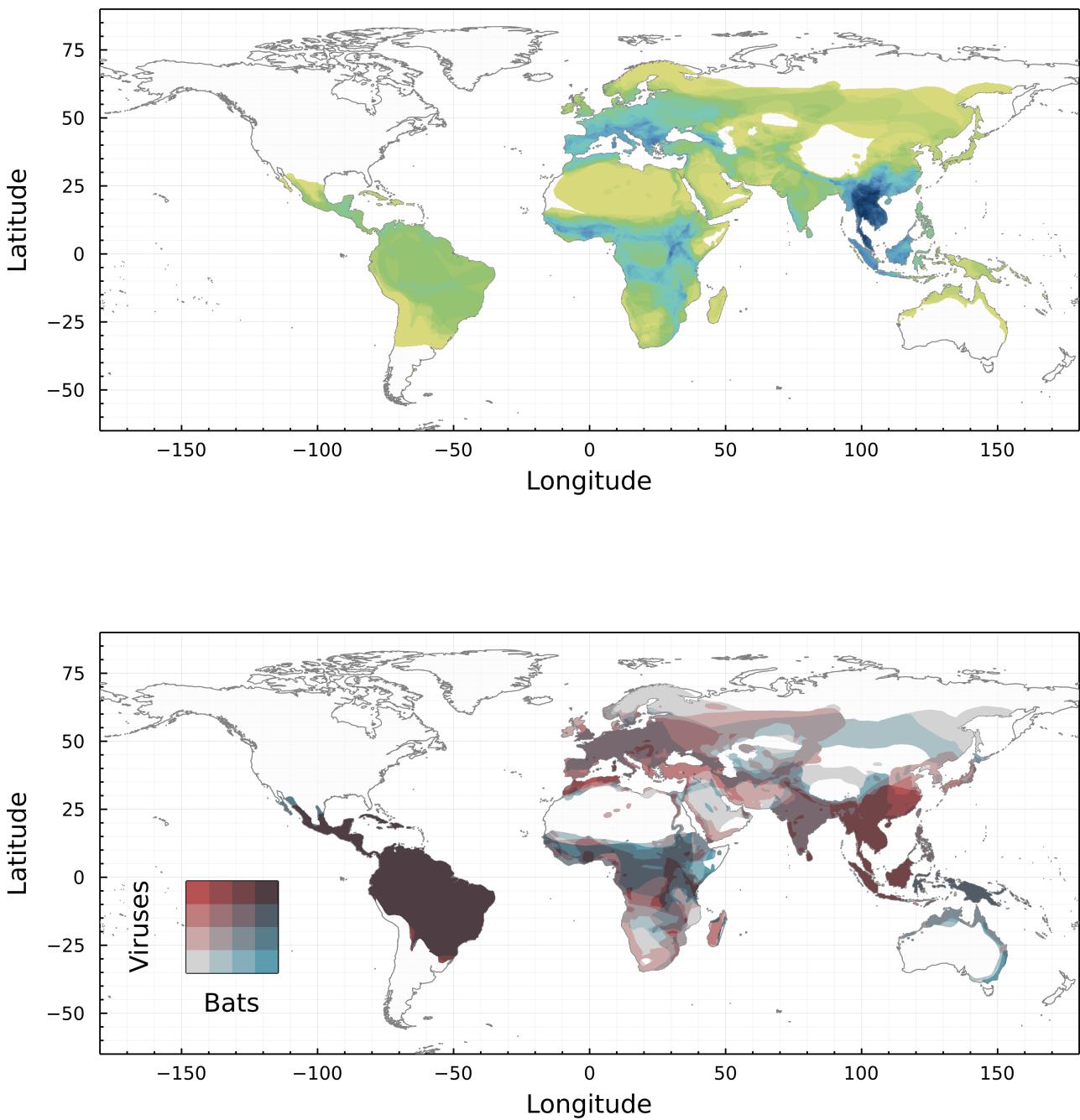


Figure 1: Top panel: relative diversity of known bat hosts of betacoronaviruses. This map shows that the region with the largest number of possible hosts is South-Eastern Asia. Bottom panel: congruence between the evolutionary distinctiveness of the hosts (grey to blue) and the viruses (grey to red). By contrast to the richness map, this reveals that South America has the most evolutionary distinct hosts *and* viruses, whereas South-Eastern Asia and the Rift Valley region have mostly distinct viruses. This is congruent with known results about New World bats being evolutionary distinct, and suggests that they similarly have distinct viruses.



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.

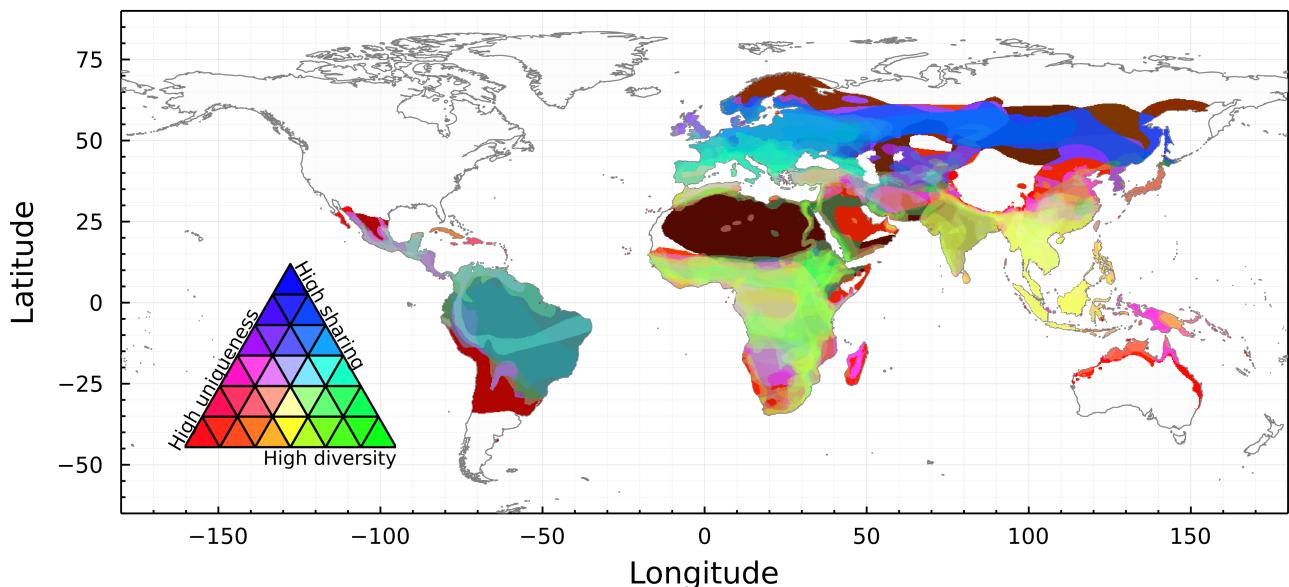


Figure 3: Trivariate additive mapping of the components of risk in the red/green/blue, where high virus sharing is encoded in the blue channel, host phylogenetic diversity in the green channel, and compositional uniqueness in the red channel. A pixel that would maximize all measures (highest possible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

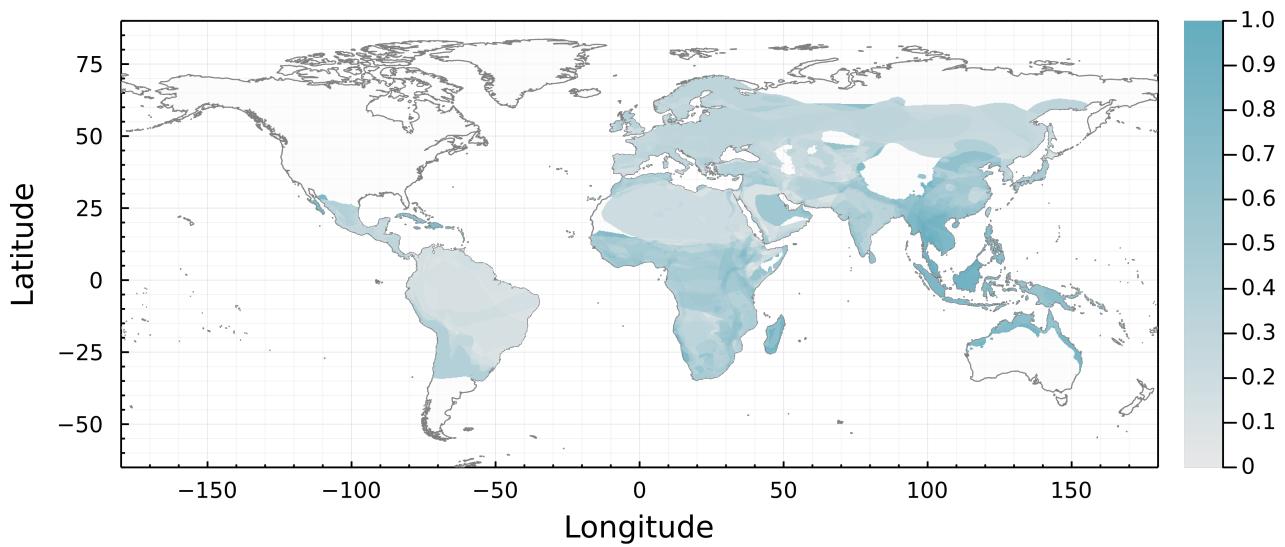


Figure 4: Extraction of a measure of *Betacoronavirus* spillover risk from bat hosts based on the colorimetric space from fig. 3. The risk is a composite measure of the color value and angular distance to the yellow hue, as defined in the methods, ranged in the unit space. Based on this analyses, regions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

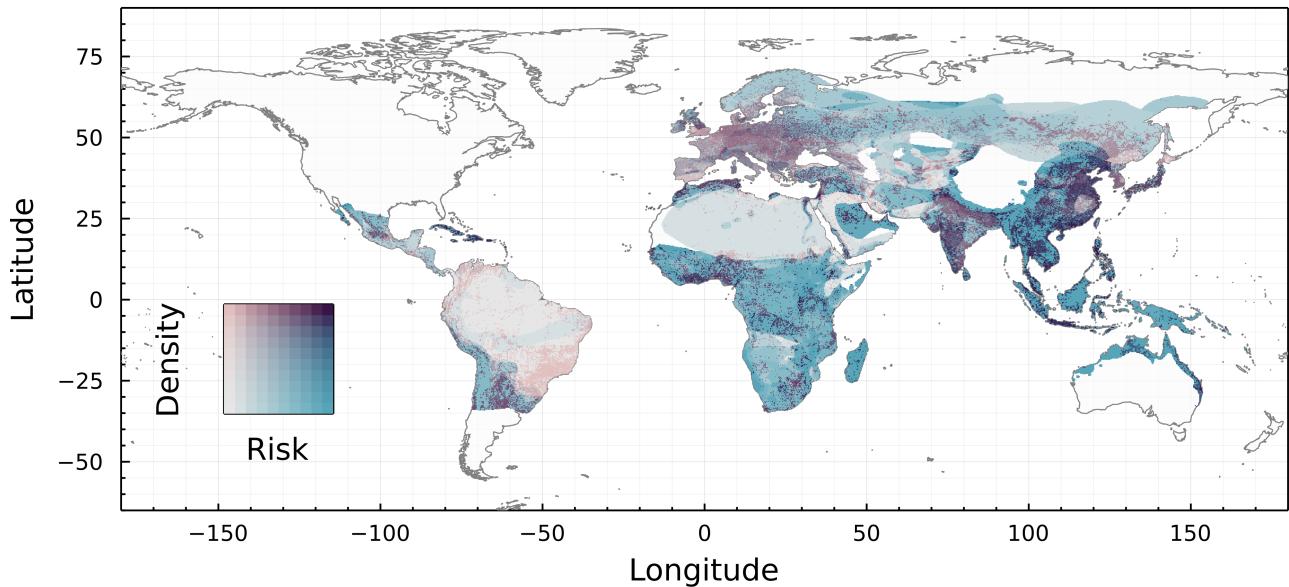


Figure 5: Overlap of the percent of each pixel occupied by urbanized structures, representing the degree of settlement, on the spillover risk map (where the risk comes only from wildlife, and ignores multi-hosts chains of transmissions including non-bats hosts). Darker pixels correspond to more risk,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