

The coevolutionary mosaic of bat-betacoronaviruses spillover risk

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1 Spillover risk is not unidimensional. From the standpoint of an animal community, *i.e.* a pool of suitable
2 hosts, it is driven by a multiplicity of factors (Plowright et al. 2017). The global richness of hosts is one
3 such component commonly mentioned/analysed (see e.g. Anthony et al. 2017 for coronaviruses), but
4 there is an argument to be made that species who are not competent (or know) hosts of a specific virus
5 genus may not factor into this (Plowright et al. 2015), or that species who are assumed to share viruses at
6 different rates should be weighted accordingly (Albery et al. 2020). In mammals, key functional traits (for
7 which phylogeny is a reasonable proxy) are determinants of the spillover potential (Olival et al. 2017);
8 these include, notably, body mass and affinity for urban environments (Albery et al. 2022). Finally,
9 especially when the pool of potential hosts spans the entire globe, there may be local host pools that are
10 highly unique; not having been observed in other locations, these can act on the overall risk either by
11 providing novel contact opportunities, reflecting unique host-environment combinations (Engering et al.
12 2013), or facilitating rapid evolutionary changes in specialism of their pathogens (Agosta et al. 2010). In
13 the specific case of generalist pathogens, there is conceptual and empirical support to the idea that these
14 community- level mechanisms are even more important in driving the overall risk (Power and Mitchell
15 2004).

16 Bats are important reservoir hosts for different classes of microorganisms (Chu 2008, Donaldson 2010, Li
17 2010), some of which can threaten human health. Chiropters emerged around 64 million years ago and
18 are one of the most diverse mammalian orders, with an estimated richness of more than 14000 species
19 (Peixoto et al. 2018, Simmons and Cirranello 2020). They exhibit a broad variety of habitat use, behaviour,
20 and feeding strategies, resulting in their playing an essential role in the delivery of several ecosystem
21 services tied to important ecosystem-derived benefits (Kasso and Balakrishnan 2013). For example, over
22 two-thirds of bats are known to be either obligate or facultative insectivorous mammals, therefore playing
23 an important role in the regulation of insect pests that can affect crops (Williams-Guillén et al. 2008, Voigt
24 and Kingston 2016), and vectors of diseases that put a risk on human health (Gonsalves et al. 2013a, b).
25 Because bats are globally distributed and have a long evolutionary history, phylogeographic and
26 biogeographic approaches are required to shed light on the extant distribution of coevolutionary processes
27 between bats and the pathogens they carry. Not all areas in which bats, viruses, and human are
28 co-occurring are facing a risk of spillover towards human populations, and the areas in which this risk exist
29 may not be facing risks of the same nature and magnitude.

30 In this paper, we examine the biogeographic structure of bats-betacoronaviruses associations, based on a

31 curated dataset of known and recently discovered hosts. This work is important both as a description of
32 the bats-betacoronavirus complex, but also because more broadly, bats are known reservoirs for a variety
33 of emerging viruses and pathogens (Calisher et al. 2006, Melaun et al. 2014), making balancing the needs
34 for bat conservation and disease prevention a potentially difficult act and a source of human-wildlife
35 conflicts, especially in more densely populated areas (Stone et al. 2015, Rego et al. 2015). By drawing on
36 concepts from the Geographic Mosaic Theory of Coevolution (Thompson 2005), we turn these
37 associations into a spatially explicit additive mapping of zoonotic risk components, which reveals extreme
38 heterogeneity of risk at the global scale; furthermore, we identify the Amazon and South-Eastern Asia as
39 hotspots of phylogenetic distinctiveness of betacoronaviruses (Anthony et al. 2017); surprisingly, current
40 data suggest that viral sharing between hosts is high in the Amazon and low in South-Eastern Asia, which
41 has the potential to result in different evolutionary dynamics between these two regions.

42 Methods

43 Known betacoronavirus hosts

44 We downloaded the data on bats hosts of betacoronaviruses assembled by Becker et al. (2022) from
45 <https://www.viralemergence.org/betacov> on Apr. 2022, and filtered it to “known” hosts (established
46 before the emergence of SARS-CoV-2) and “novel” hosts (confirmed through sampling since the
47 emergence of SARS-CoV-2). The original database was assembled by a combination of data mining and
48 literature surveys, including automated alerts on the “bats” and “coronavirus” keywords to identify novel
49 empirical evidence of bats-betacoronaviruses associations.

50 Bats occurrences

51 We downloaded the rangemap of every extant bat species that was either classified as an empirically
52 documented host of beta-coronaviruses from the previous step, according to recent IUCN data (IUCN
53 2021). The range maps were subsequently rasterized using the rasterize function from GDAL (Rouault et
54 al. 2022) at a resolution of approximately **TK TP**. For every pixel in the resulting raster where at least one
55 bat host of betacoronavirus was present, we extract the species pool (list of all bat species), which was used
56 to calculate the following risk assessment components: phylogenetic diversity, bat compositional

57 uniqueness, and predicted viral sharing risk.

58 **Bats phyogeography**

59 For every pixel, we measured Faith's Phylogenetic Diversity (Faith 1992) based on a recent synthetic tree
60 with robust time calibration, covering about 6000 mammalian species (Upham et al. 2019). Faith's PD
61 measures the sum of unique branches from an arbitrary root to a set of tips, and comparatively larger
62 values indicate a more phylogenetic diverse species pool. We measured phylogenetic diversity starting
63 from the root of the entire tree (and not from Chiroptera); this bears no consequences on the resulting
64 values, since all branches leading up to Chiroptera are only counted one per species pool, and (as we
65 explain when describing the assembly of the composite risk map), all individual risk components are
66 ranged in [0,1]. This measure incorporates a richness component, which we chose not to correct for; the
67 interpretation of the phylogenetic diversity is therefore a weighted species richness, that accounts for
68 phylogenetic over/under-dispersal in some places.

69 **Bats compositional uniqueness**

70 For every species pool, we measured its Local Contribution to Beta-Diversity (Legendre and De Cáceres
71 2013); LCBD works from a species-data matrix (traditionally noted as \mathbf{Y}), where species are rows and sites
72 are columns, and a value of 1 indicates occurrence. We extracted the \mathbf{Y} matrix assuming that every pixel
73 represents a unique location, and following best practices (Legendre and Condit 2019) transformed it
74 using Hellinger's distance to account for unequal bat richness at different pixels. The correction of raw
75 community data is particularly important for two reasons: first, it prevents the artifact of richer sites
76 having higher importance; second, it removes the effect of overall species richness, which is already
77 incorporated in the phylogenetic diversity component. High values of LCBD indicate that the pixel has a
78 community that is on average more dissimilar in species composition than what is expected knowing the
79 entire matrix, i.e. a more unique community. Recent results by Dansereau et al. (2022) shows that LCBD
80 measures are robust with regards to spatial scale, and are therefore applicable at the global scale.

81 **Viral sharing between hosts**

82 For all bat hosts of betacoronaviruses, we extracted their predicted viral sharing network (Albery et al.
83 2020). This network stores pairwise values of viral community similarity. To project viral sharing values
84 into a single value for every pixel, we averaged the pairwise scores. High values of the average sharing
85 propensity means that this specific extant bat assemblage is likely to be proficient at exchanging viruses.

86 **Composite risk map**

87 To visualize the aggregated risk at the global scale, we combine the three individual risk components
88 (phylogenetic diversity, compositional uniqueness, and viral sharing) using an additive color model
89 (Seekell et al. 2018). In this approach, every risk component gets assigned a component in the RGB color
90 model (phylogenetic diversity is green, compositional uniqueness is red, and viral sharing is blue). In
91 order to achieve a valid RGB measure, all components are re-scaled to the [0,1] interval, so that a pixel
92 with no sharing, no phylogenetic diversity, and no compositional uniqueness is black, and a pixel with
93 maximal values for each is white. This additive model conveys both the intensity of the overall risk, but
94 also the nature of the risk as colors diverge towards combinations of values for three risk components. Out
95 of the possible combinations, the most risky in terms of rapid diversification and spillover potential is high
96 phylogenetic diversity and low viral sharing (Gomulkiewicz et al. 2000, Cavender-Bares et al. 2009), in
97 that this allows multiple independent host-virus coevolutionary dynamics to take place in the same
98 location. In the colorimetric space, this corresponds to yellow – because the HSV space is more amenable
99 to calculations for feature extraction (see e.g. Keke et al. 2010), we measured the risk level by calculating
100 the angular distance of the hue of each pixel to a reference value of 60, and weighted this risk level by the
101 value component. Specifically, given a pixel with colorimetric coordinates (h, s, v) , its ranged weighted
102 risk value is

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

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

104 **Viral phylogeography and evolutionary diversification**

105 We used the following query to pull all betacoronavirus sequence data from the GenBank Nucleotide
106 database except SARS-CoV-2; (“Betacoronavirus”[Organism] OR betacoronavirus[All Fields]) NOT
107 (“Severe acute respiratory syndrome coronavirus 2”[Organism] OR sars-cov-2[All Fields]). We added a
108 single representative sequence for SARS-CoV-2 and manually curated to remove sequences without the
109 RNA-dependent RNA polymerase (RdRp) sequence or that contained words indicating recombinant or
110 laboratory strains including “patent,” “mutant,” “GFP,” and “recombinant.” We filtered over-represented
111 taxa including betacoronavirus 1, hCoV-OC43, Middle East respiratory syndrome coronavirus, Murine
112 hepatitis virus, and hCoV-HKU1. Curated betacoronavirus RdRp sequences were then aligned using
113 MAFFT v 1.4.0 (**Katoh and Standley 2013**, parameters in text?) and a maximum likelihood tree
114 reconstructed in IQ-TREE v 1.6.12 (Nguyen et al. 2015) with ModelFinder (Kalyaanamoorthy et al. 2017)
115 ultrafast bootstrap approximation (Hoang et al. 2018) and the following parameters (**STEPH WILL ADD**,
116 parameters in text?).

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

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

126 Subsequently, we tested the hypothesis that the biogeography of bat betacoronaviruses should track the
127 biogeography of their hosts. To test this idea, we loosely adapted a method from (Kreft and Jetz 2007,
128 2010), who proposed a phylogenetic method for the delineation of animal biogeographic regions. In their
129 original method, a distance matrix - where each row or column represents a geographic raster’s grid cell,
130 and the dissimilarity values are the “beta diversity similarity” of their community assemble - undergoes
131 non-metric multidimensional scaling (NMDS); the first two axes of the NMDS are projected

132 geographically using a four-color bivariate map. Here, we build on this idea with an entirely novel
133 methodology. First, we measure the phylogenetic distance between the different viruses in the
134 betacoronavirus tree by using the cophenetic function in ape (Paradis and Schliep 2019); subsequently, we
135 take a principal components analysis of that distance matrix (readily interchangeable for NMDS in this
136 case) to project the viral tree into an n-dimensional space. We then take the first two principal
137 components and, as with the evolutionary distinctiveness analysis, aggregated these to a mean host value
138 and projected them using a four-color bivariate map.

139 Results and discussion

140 Host distribution

141 Bats are found worldwide and are one of the most diverse groups among mammals (Moratelli & Calisher,
142 2015), and one of the main animal reservoir for different strains of betacoronaviruses (Drexler et al. 2014).
143 This has attracted attention to areas where high diversity of bats, and therefore presumably high diversity
144 of betacoronaviruses, can be an important issue for human health (Calisher et al. 2006, Moratelli and
145 Calisher 2015). Accordingly, we collected the IUCN rangemaps for known hosts of betacoronaviruses, to
146 illustrate where hotspots of host diversity are. These results are presented in Fig xx.a. As per our current
147 knowledge of which bats are hosts of betacoronaviruses, these hotspots are primarily South-East Asia,
148 parts of Europe, and to a lesser extent sub-saharan Africa. Even the subset of chiroptera that are hosts of
149 betacoronaviruses fits the evolutionary timeline of the group. Chiropterans can be classified as
150 Microchiroptera and macrochiroptera, where macrochiroptera have an older history from an evolutionary
151 perspective compared to microchiroptera (Teeling et al. 2005, Springer 2013).

152 [Figure 1 about here.]

153 South-East Asia has a high diversity of bats (**Kingston, 2010**), and our results show that part of that
154 diversity includes betacoronavirus hosts. High density of hosts sharing the same virus (albeit possibly
155 different strains) calls into question the evolution of the bat antiviral immune system and its co-evolution
156 with viruses, which may result in distinct immunological responses in different areas, as evidenced in
157 other bat species (Banerjee et al. 2020). Immune characteristics that allow bats to be better adapted to

158 infection by emerging viruses (Gorbunova et al., 2020; Irving et al., 2021) may be related to a wide variety
159 of diets (Jones et al., 2022; Moreno Santillán et al., 2021; Banerjee et al., 2020; Schneeberger et al., 2013).
160 Considering whether viruses easily adapted to multiple hosts have lower virulence on these hosts, or
161 lower ability to jump to hosts with different immune characteristics, should yield valuable additional
162 predictors for the total risk of spillover. Previous research (**Anthony et al., 2017; Mollentze & Streicker,**
163 **2020**) states that locally diverse bat communities could maintain more viruses and hence, a higher
164 probability of having a pathogen that could represent a risk for human health; locally diverse, virus-rich
165 bats communities could represent an increased risk of spillover under climate change (**Ice ice berg berg**).
166 This probability involves multiple factors, among which the relatedness of hosts (which can make the
167 jumps easier (**Longdon et al., 2011; Mollentze et al., 2020; Wolfe et al., 2007**), and the overall tendency
168 of hosts within a locality to share viruses, which may limit viral diversity because of within-host
169 competition (Leeks et al., 2018; Sallinen et al., 2020). All things considered, the richness of known
170 betacoronaviruses hosts is not a sufficient predictor of spillover risk.

171 **Viral evolutionary distinctiveness**

172 Higher host diversity may not result in a higher viral diversity, for example if all hosts share the same
173 viruses, or share closely evolutionarily related strains. For this reason, we quantified and mapped the
174 evolutionary distinctiveness of betacoronaviruses, based on their position in a molecular phylogeny. Viral
175 evolutionary distinctiveness largely tracks host diversity, particularly in southern China but, oddly, not
176 throughout the rest of southeast Asia. This indicates, perhaps, that many distinctive viruses remain to be
177 discovered in this region (an idea that is unsurprising given the growing realization, around the
178 emergence of SARS-CoV-2, that a unique lineage of similar viruses are widespread in bats but still mostly
179 undescribed). The most distinct betacoronaviruses are found in South America, a region with a
180 comparatively lower number of hosts; this suggests that the South American bat-betacoronavirus complex
181 has been more isolated, and is probably undergoing a different co-evolutionary dynamic. Alternatively,
182 this distinctiveness hotspot may be a product of under-sampling: South-America is one of the places
183 where the fewest betacoronaviruses have been discovered (Anthony et al. 2017), and adding more viruses
184 would bring the distinctiveness of known sequences down. Previous work has suggested the Americas
185 may be a hotspot of both undiscovered bat viruses in general (Olival et al. 2017, Allen et al. 2017) and
186 coronavirus specifically (Anthony et al. 2017), though not necessarily betacoronaviruses, and particularly

187 not those in clades with notable zoonotic potential.

188 [Figure 2 about here.]

189 **Geographic Mosaic of bat-betacoronavirus risk**

190 In order to turn the hypotheses based on the Geographic Mosaic Theory of Coevolution into a measure of
191 risk, we overlapped three components of spillover risk: viral sharing, *i.e.* the chance that two bats will
192 share viruses overall; Local Contribution to Beta Diversity, *i.e.* the fact that a bat community is
193 compositionally unique compared to the average compositional similarity across the entire system; finally,
194 the phylogenetic diversity, *i.e.* how dispersed the bats in a location are within the tree of life. These results
195 are presented using an additive color mapping in Figure xx, and lead to the definition of broad
196 biogeographic regions of risk, where the same color represents the same type of risk. Pairwise maps of the
197 three components are present in supplementary materials.

198 [Figure 3 about here.]

199 From the perspective of spillover risk, the most important combination of factors is a high phylogenetic
200 diversity of hosts with low viral sharing; this, essentially, means that very different betacoronavirus could
201 co-exist within the same place. This is particularly the case given that betacoronaviruses often evolve and
202 even achieve host shifts through recombination, which requires the co-occurrence of sufficiently distinct
203 viruses to be a major driver of emergence. In Fig. xx, this corresponds to yellow to pale green areas, which
204 are essentially limited to South-Eastern Asia, and to some part of Sub-Saharan Africa. Adopting a
205 geographic mosaic theory perspective on risk, other regions of the world are of lesser concern.

206 [Figure 4 about here.]

207 Available data on bat betacoronavirus spillover into humans (TP overlay on the figure) is limited and
208 circumstantial at best for these purposes, but our risk maps suggest that the areas predicted by prior
209 expectations about host biogeography correspond loosely to those where previous emergence events have
210 been recorded. Areas with high bat diversity and high turnover may facilitate the evolutionary radiation of
211 viruses, matching previous findings that the diversification of bat coronaviruses is driven largely by host

212 shifts (inter-genus or higher levels of cross-species transmission) and, to a lesser degree, cospeciation and
213 sharing (intra-genus cross-species transmission; Anthony et al. 2017). This diversification - while not an
214 actual risk factor for spillover itself - likely increases the random chance of a virus with the raw genomic
215 components required for the potential to infect humans.

216 **Global distribution of spillover risk**

217 Based on the previous result, we extracted the yellow component of the risk map (TP add methods), to
218 provide a single measure of risk varying between 0 and 1. This measure is presented in Fig. xxA. However,
219 this maps the potential risk, which must be weighed by the potential for contacts with humans. As a proxy
220 for this measure, we used the proportion of build/urban land from the EarthEnv dataset: this is a
221 reasonable proxy for the density of humans per unit area, which increases the probability of pathogen
222 spread more widely (Hazarie et al., 2021). Since human activity is required to amplify the frequency of
223 virus encounters and thus create areas of viral amplification, mapping the potential risk against measures
224 of land use is required to generate a more actionable assessment of risk. This map is presented in Fig. xxB.
225 Most of South America and Europe are at low risk, as although densely populated, settlements tend to be
226 in areas with lower potential risk. However, this mapping reveals that South-East Asia, the Indian
227 subcontinent, and parts of sub-Saharan Africa, are at high risk due to the overlap between built areas and
228 bat communities representing more opportunities for cross-species transmission of betacoronaviruses.

229 [Figure 5 about here.]

230 Finally, we provide a summary visualization of what available information describes the spillover of
231 zoonotic betacoronaviruses of bat origin where data was available before and up through the COVID-19
232 pandemic. The SARS-CoV-2 outbreak was georeferenced to the initial case cluster in Wuhan, China;
233 SARS-CoV was georeferenced based on the cave with the closest known viruses circulating in nature (Hu
234 et al. 2017 PLoS Pathogens), and a nearby location where serological (antibody) evidence has indicated
235 human exposure to SARS-like viruses (Wang et al. 2018 Virologica Sinica). For MERS-CoV, we presented
236 the index cases available from a recently-published compendium of MERS-CoV cases (Ramshaw et
237 al. 2019); these are largely if not all presumed to be camel-to-human transmission, and the precise origin
238 point of MERS-CoV in bats is uncertain. Not shown is a recent case of a recombinant canine coronavirus
239 that showed the ability to infect humans, both because this study was published after the beginning of the

240 COVID-19 pandemic and because bats' involvement in this cycle of transmission has been marginal to
241 non-existent.

242 Our study focuses largely on the biogeography of hosts. Yet, we know that viruses with high host
243 plasticity, that is, the ability of a given virus to adapt to various taxonomic orders and ecological groups
244 (Kreuder Johnson et al., 2015); are more likely to amplify viral spillover, followed by secondary
245 human-to-human transmission, and geographical spread (Hazarie et al., 2021). High viral host plasticity is
246 an especially important trait for RNA viruses such as betacov (Kreuder Johnson et al., 2015; Haddad et al.,
247 2021). Indeed, our analysis of viral sequences reveals that Latin America is a hotspot of viral
248 distinctiveness, suggesting that this part of the bats-betacov system may be undergoing independent
249 evolutionary dynamics (related species sharing viruses that are different from the rest of the global pool).
250 The other hotspot of viral distinctiveness is S.E. Asia, in which richness is high but sharing is low; this
251 suggests a different type of evolutionary dynamics (unrelated viruses coevolving with evolutionarily
252 distinct hosts, generating high diversity locally).

253 Conclusion

254 Driven by the need to understand the ecological factors involved in the emergence of viral pathogens, we
255 spatially mapped bat-betacoronavirus interactions worldwide, using (i) a database of known betacov
256 hosts(Becker et al., 2020), and (ii) range maps for the hosts according to IUCN (IUCN 2021). To reflect the
257 fact that the risk posed by viruses has many ecological origins, we quantified the phylogenetic diversity of
258 hosts, their compositional uniqueness, and the expected viral sharing. Because these components of risk
259 matter when contrasted to human density, we compared them to a proxy, namely the proportion of each
260 pixel that is covered by urban or built land. This provides a synthetic risk map, allowing to identifying of
261 hotspots where the bat-betacoronavirus system may originate viruses in humans. SE Asia is one of the
262 regions with the highest risk since, according to our results, several of its conditions could increase the
263 risk of transmission of the virus.

264 Species richness, therefore, is not a sufficient measure of viral risk. This is exemplified in our results,
265 where both South America and South-Eastern Asia have a high species richness of betacov hosts, but only
266 the latter region has a high risk. Specifically, because previous studies propose that Asia is important
267 when it comes to understanding the evolutionary origin of various mammalian taxa (Beard C K, 1988).

268 There are several factors that drive changes in the diversity of bats (Alves et al., 2018), but human
269 activities' effects on the ecosystem (like modifications of land use) could significantly decrease it.
270 Therefore, it can be suggested that changes in the diversity of betacovs in bats are linked to their
271 biogeographic variation, and human population density and other anthropogenic factors are decisive
272 moderators for its implications in public health. With the increase of contact between humans and
273 potential hosts, we also increase the risk of emergence of novel diseases (Johnson et al., 2020), as previous
274 studies on RNA viruses suggest the importance of host phylogeography at the time of virus dispersal
275 (Gryseels et al., 2017).

276 This diversity of hosts and how the exchange of viruses occurs between species, is largely affected by the
277 different environmental changes, as the case of sarbecovirus bats reservoirs (Muylaert et al., 2021) where
278 they are affected by the area of the cave or the alteration of the forest, which could result in modifications
279 of host distribution. Additionally, our results highlight the importance of Asia as a betacov hotspot, which
280 is consistent with recent studies (Muylaert et al., 2021), where projections on this area suggest that new
281 future events of sarbecovirus viral exchange might be easily spread among species or humans.

282 One of these scenarios where interaction between bats and humans can occur can be seed dispersal in
283 tropical agroecosystems. It opens the discussion of whether the fruits thrown by bats not only disperse
284 seeds but could also be a source of indirect interaction between viruses of bat origin and humans
285 (Deshpande et al., 2022). This represents a challenge for conservation strategies and disease ecology since
286 we have areas with potential zoonotic viruses and bat-human interaction. However, it must still be taken
287 into account the quantification of real exposure from several scenarios, where there can be directly or
288 indirectly bat - human interaction.

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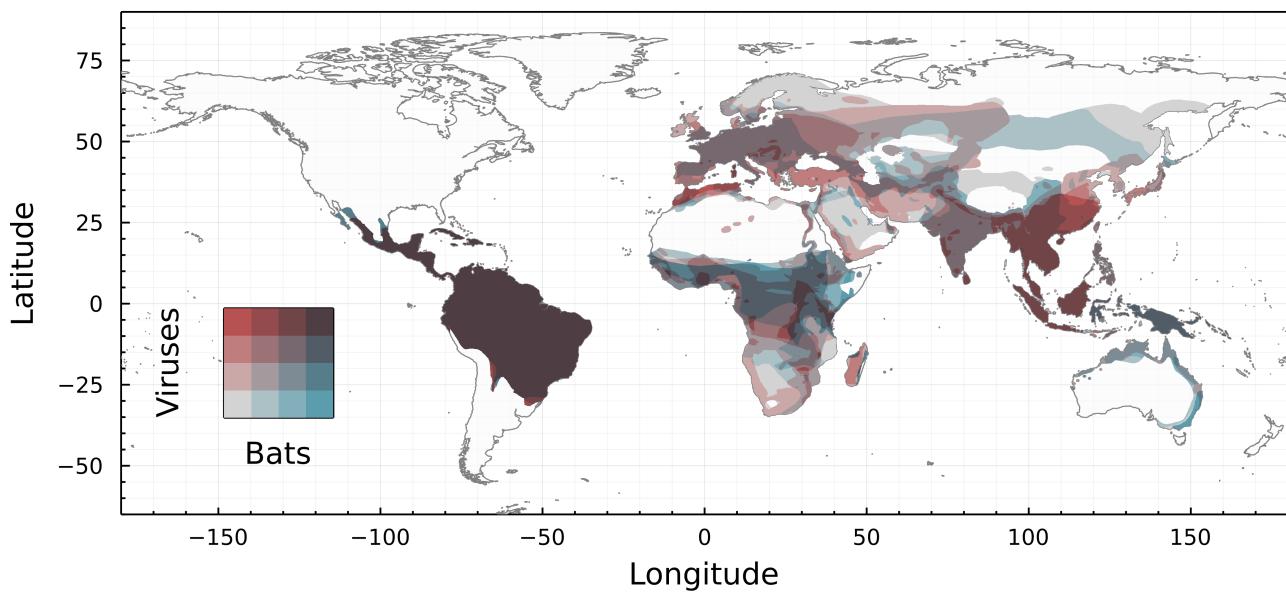
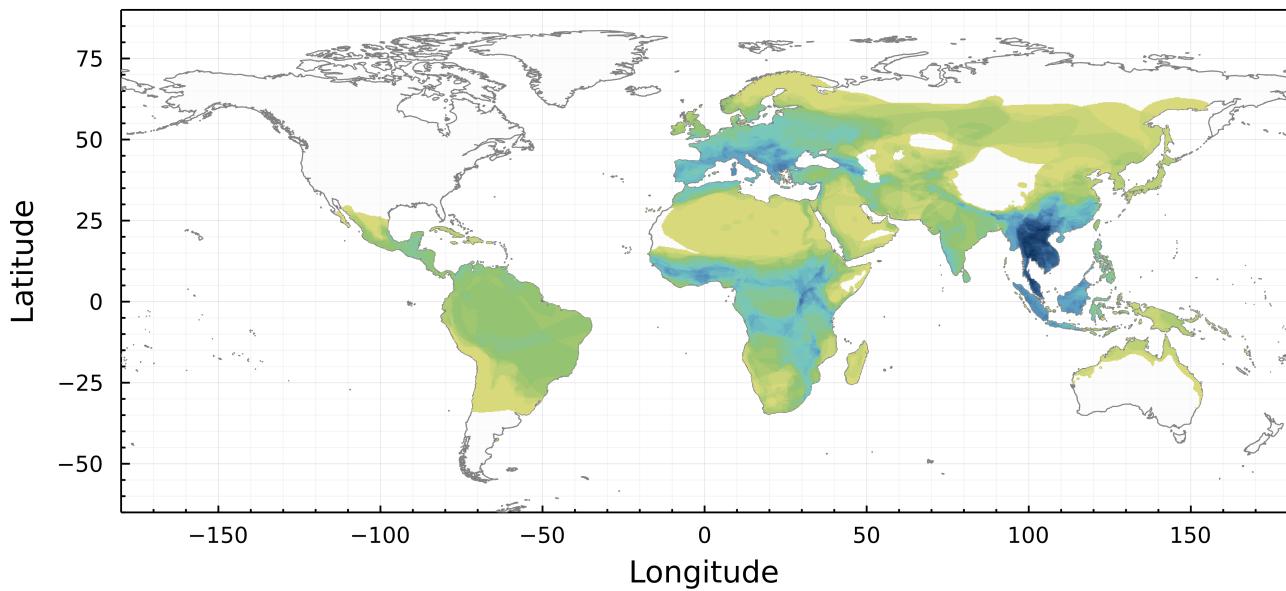


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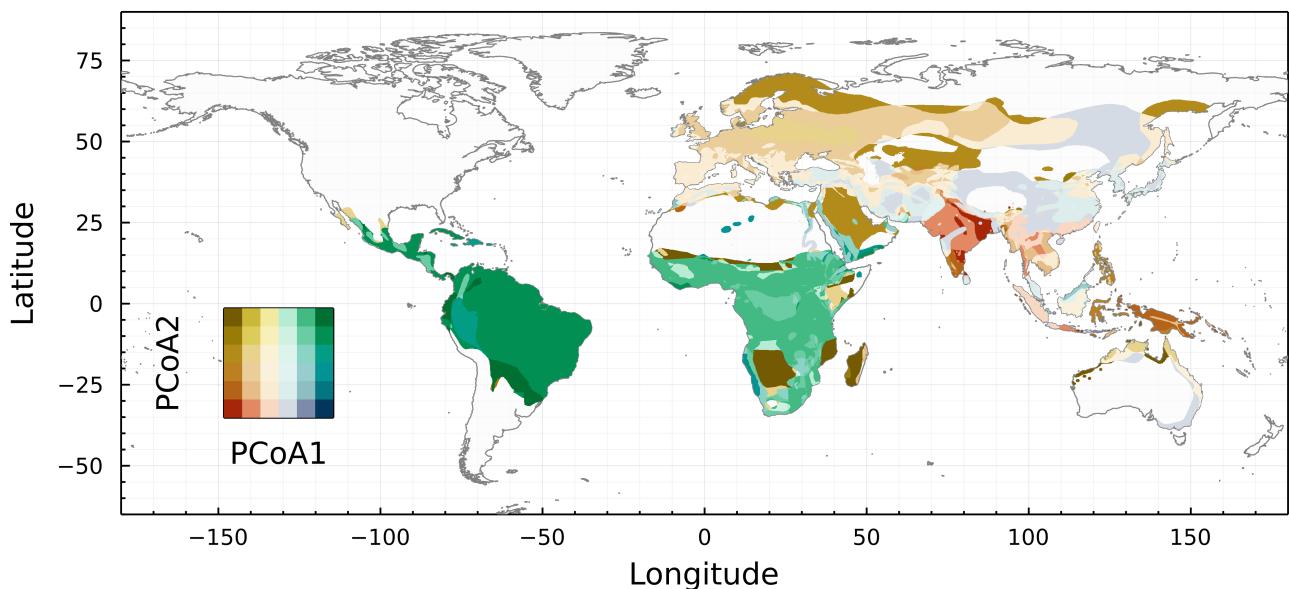
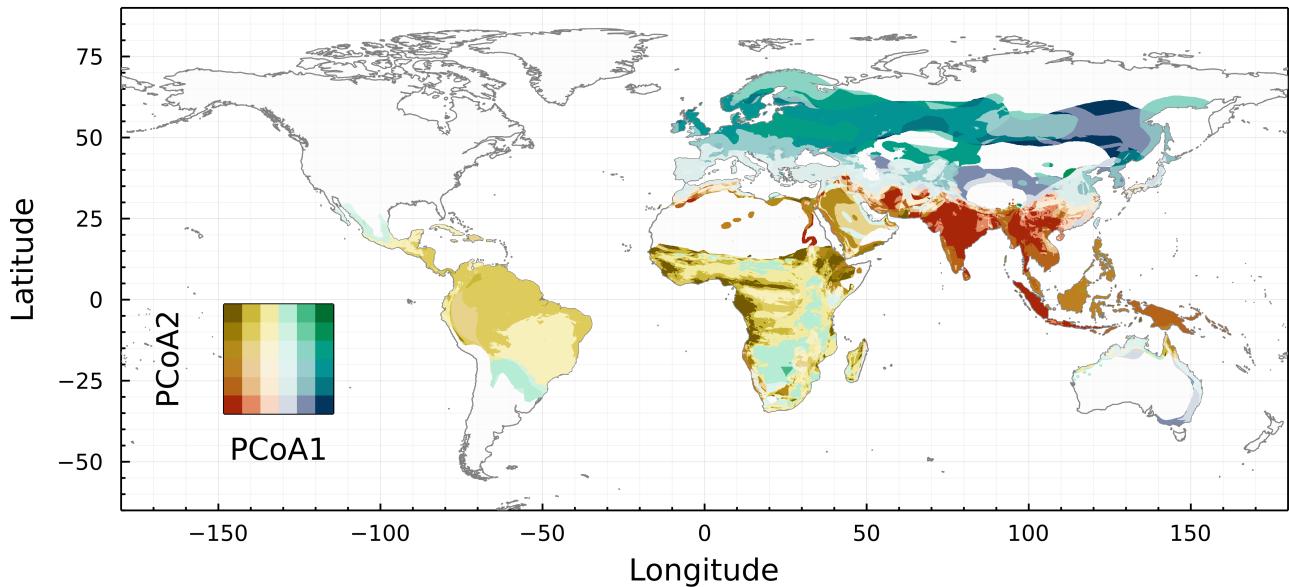


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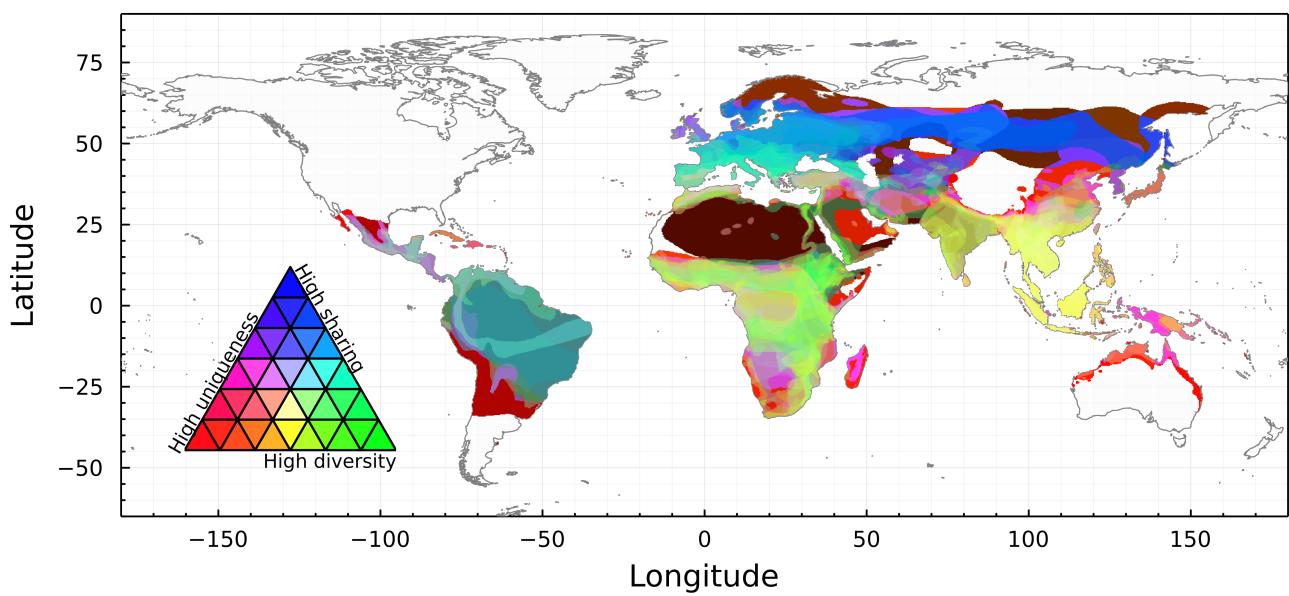


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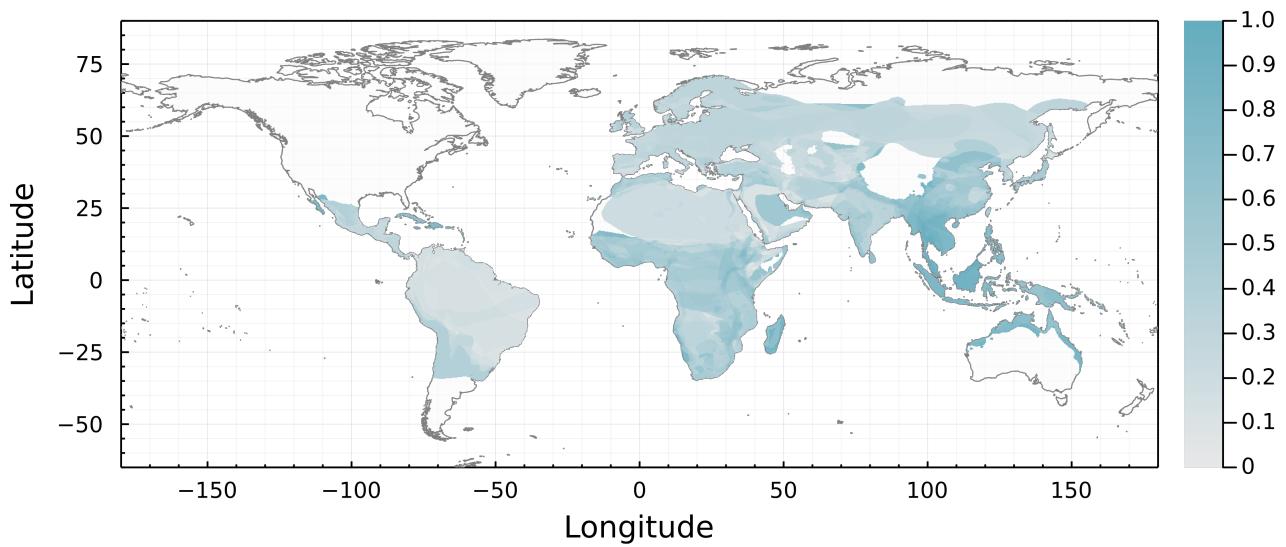


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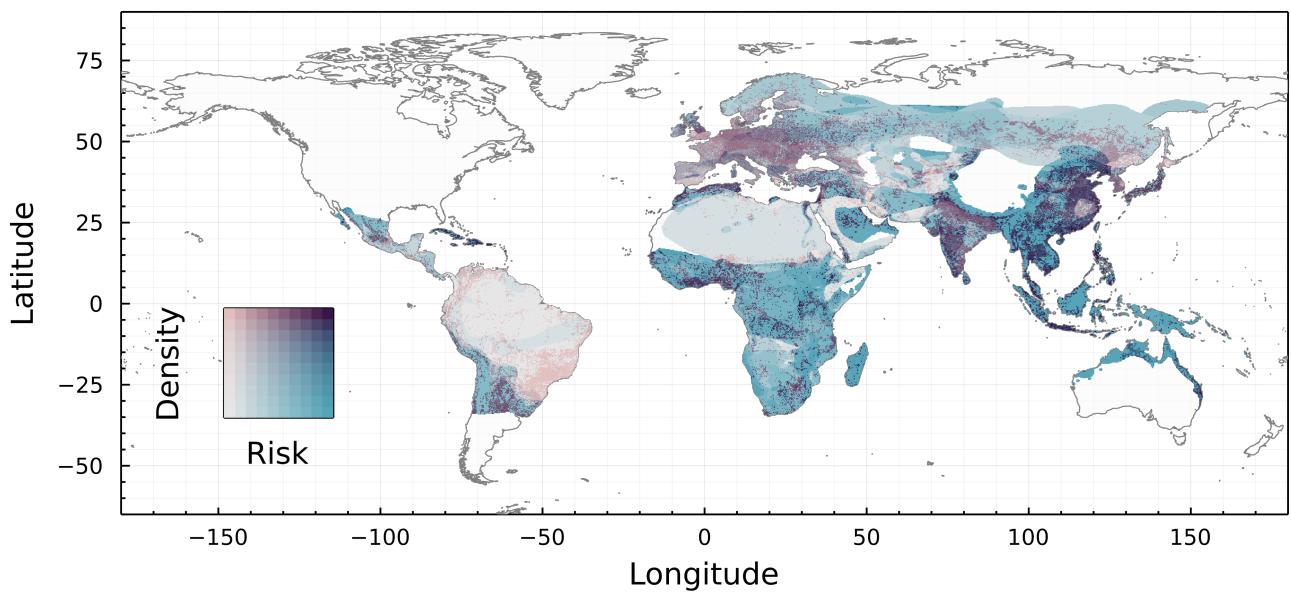


Figure 5: This is the legend of the figure...