

1 **Climate change impacts on the phylogenetic diversity of**  
2 **the world's terrestrial birds: more than species numbers**

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38 **Abstract**

39 Ongoing climate change is a major threat to biodiversity and impacts on species distributions and  
40 abundances are already evident. Heterogenous responses of species due to varying abiotic tolerances  
41 and dispersal abilities have the potential to further amplify or ameliorate these impacts through  
42 changes in species assemblages. Here we investigate the impacts of climate change on terrestrial bird  
43 distributions and, subsequently, on species richness as well as on different aspects of phylogenetic  
44 diversity of species assemblages across the globe. We go beyond previous work by disentangling the  
45 potential impacts on assemblage phylogenetic diversity of species gains vs. losses under climate  
46 change and compare the projected impacts to randomized assemblage changes.

47 We show that climate change might not only affect species numbers and composition of global species  
48 assemblages but could also have profound impacts on assemblage phylogenetic diversity, which,  
49 across extensive areas, differ significantly from random changes. Both the projected impacts on  
50 phylogenetic diversity and on phylogenetic structure vary greatly across the globe. Projected increases  
51 in the evolutionary history contained within species assemblages, associated with either increasing  
52 phylogenetic diversification or clustering, are most frequent at high northern latitudes. By contrast,  
53 projected declines in evolutionary history, associated with increasing phylogenetic over-dispersion or  
54 homogenisation, are projected across all continents.

55 The projected widespread changes in the phylogenetic structure of species assemblages show that  
56 changes in species richness do not fully reflect the potential threat from climate change to ecosystems.  
57 Our results indicate that the most severe changes to the phylogenetic diversity and structure of species  
58 assemblages are likely to be caused by species range shifts rather than range reductions and  
59 extinctions. Our findings highlight the importance of considering diverse measures in climate impact  
60 assessments and the value of integrating species-specific responses into assessments of entire  
61 community changes.

62

## 63 **Introduction**

64 Global warming has been identified as one of five main anthropogenic drivers of global biodiversity  
65 loss (IPBES, 2019; Secretariat of the Convention on Biological Diversity, 2020). Whilst global  
66 warming might not represent a major threat to many species currently (Tilman et al., 2017), it is  
67 projected to increasingly threaten biodiversity in the future (Broennimann et al., 2006; Engler et al.,  
68 2011; Foden et al., 2013; Thomas et al., 2004). First responses of species to climate change have  
69 already been reported (Chen et al., 2011; Higgins et al., 2014; Jonathan Lenoir et al., 2020; Radchuk et  
70 al., 2019), covering the three possible ways in which species can adapt to global warming, i.e. through  
71 changes in their phenology, physiology or by shifting their ranges (Bellard et al., 2012). In particular,  
72 changes in species abundance and distribution have already been observed in various taxa across the  
73 globe (Bowler et al., 2017; Maclean et al., 2008; Stephens et al., 2016; Thomas, 2010). Many of these  
74 observed range shifts have been towards higher latitudes and altitudes (Hickling et al., 2006; Parmesan  
75 et al., 1999; Walther et al., 2002), but species-specific range shifts in different directions also occur  
76 (Chen et al., 2011; Moritz et al., 2008; VanDerWal et al., 2013). These idiosyncratic range shifts have  
77 the potential to be especially problematic, since they will likely result in a reshuffling of species  
78 assemblages. Potential consequences could include changes to the competitive balance between  
79 species within these assemblages (Ockendon et al., 2014) and altered predator and prey densities  
80 (Harley, 2011) as well as changes to the trait composition of local assemblages (Barbet-Massin & Jetz,  
81 2015; Gallagher et al., 2013) and subsequently the provision of ecological functions (Pecl et al., 2017;  
82 Schleuning et al., 2020).

83 Compositional changes in species assemblages, caused by extinctions or range shifts, also have the  
84 potential to affect the underlying phylogenetic structure and diversity of the assemblage (Menéndez-  
85 Guerrero et al., 2020; Saladin et al., 2020). Such compositional changes can be assessed using  
86 different aspects of phylogenetic diversity. The total evolutionary diversity of a species assemblage is  
87 one such metric and measures the amount of evolutionary history that is stored within the assemblage  
88 (Flynn et al., 2011; Hardy & Senterre, 2007). Under the assumption that the evolutionary history of an  
89 assemblage indicates its evolutionary potential for adaptive change (Faith, 1992a; Forest et al., 2007),  
90 a loss of phylogenetic diversity could reduce the evolutionary potential of the assemblage, leaving it

91 increasingly vulnerable to environmental change (Faith & Richards, 2012). This aspect of  
92 phylogenetic diversity is frequently calculated using Faith's phylogenetic diversity (named Faith PD  
93 hereafter), which is the sum of the branch lengths of all species occurring within the assemblage back  
94 to their most recent common ancestor (Faith, 1992a). An alternative metric is the phylogenetic  
95 relatedness of the species assemblage, assessed using the mean phylogenetic distance (MPD). MPD is  
96 a measure of the deeper phylogenetic diversity of a species assemblage (Leprieur et al., 2016;  
97 Swenson & Umaña, 2014). It gives an indication of the average relatedness of the species in an  
98 assemblage. Under the assumption that closely related species have a tendency to share more similar  
99 traits than very distantly related species (Burns & Strauss, 2011), for example, an increase in the  
100 relatedness of species within an assemblage could imply a reduction in the diversity of traits present.  
101 This, in turn, could increase the vulnerability of an assemblage to environmental change (Faith, 1992a;  
102 Forest et al., 2007) but see (Jarzyna et al., 2020; Mazel et al., 2017).

103 Overall, MPD and Faith PD provide information on two very different aspects of the phylogenetic  
104 diversity of species assemblages; whilst the former measures the total standing evolutionary diversity  
105 across all species present (Barker, 2002), the latter measures the inverse of the average relatedness  
106 between all species pairs (Webb, 2000). Faith PD has often been found to be highly correlated to  
107 species richness for various taxa (Barker, 2002; Schipper et al., 2008), with some local exceptions  
108 where the correlation is less strong (Fritz & Rahbek, 2012; Voskamp et al., 2017). In contrast, MPD is  
109 independent of species richness (Fritz & Rahbek, 2012; Schipper et al., 2008). Since they differ  
110 mathematically, these measures have the potential to change independently of each other when species  
111 assemblages are changing (Tucker et al., 2017). Comparing these two measures when investigating  
112 temporal change in species assemblages yields additional information on the underlying phylogenetic  
113 changes that are taking place.

114 There are four potential directions in which the phylogenetic structure of species assemblages could  
115 shift when undergoing climate-induced compositional changes: a) MPD could increase whilst Faith  
116 PD decreases leading to increasing phylogenetic over-dispersion, i.e. increasingly distantly related  
117 species in an assemblage that represent lower values of evolutionary history; b) both MPD and Faith  
118 PD could decrease leading to increasing homogenisation; c) both MPD and Faith PD could increase

119 leading to increasing diversification; or d) MPD could decrease whilst Faith PD increases leading to  
120 increasing phylogenetic clustering of the species assemblage, i.e. increase in clusters of closely related  
121 species that represent high values of evolutionary history.

122 In addition to the spatial turnover in species, changes in species richness (i.e. the gain and loss of  
123 species into and from a species assemblage) could result in non-random changes to the phylogenetic  
124 structure of species assemblages. For instance, if extinction risk is clustered across the tree of life due  
125 to similarity in species traits that confer vulnerability, this can result in the loss of entire clades and  
126 families and subsequently a disproportionate amount of evolutionary history (Russell et al., 1998).  
127 Previous studies have found this clustered pattern in Red List extinction risk assessments of taxa that  
128 include mammals, angiosperms and birds (Bromham et al., 2012; Davies & Yessoufou, 2013; Fritz &  
129 Purvis, 2010; Vamosi & Wilson, 2008). By contrast, when looking at extinction risk based on climate  
130 change projections across Europe and South Africa for the same taxa, no phylogenetic signal was  
131 found (Pio et al., 2014; Thuiller et al., 2011).

132 Rather than assessing the impacts of extinction across a whole phylogeny, evaluating the spatial  
133 variation in impacts of global or local extinctions on the phylogenetic structure of species assemblages  
134 could reveal how local changes in species composition impact the local phylogenetic structure. It is  
135 possible that impacts of species loss under climate change on phylogenetic diversity do not differ from  
136 a random extinction process when assessed on a global scale, but still have a strong phylogenetic  
137 impact at the local scale, weeding out entire clades from species assemblages (Huang et al., 2012).  
138 Changes in the spatial patterns of phylogenetic diversity under climate change have been shown at a  
139 regional scale under different climate change projections, for mammals, angiosperms and birds  
140 (González-Orozco et al., 2016; Pio et al., 2014; Thuiller et al., 2011). However, a study investigating  
141 potential local changes in phylogenetic diversity as caused by the projected loss of plant, mammal or  
142 insect species across the Cape of South Africa under climate change, found little difference from a  
143 random extinction process in most places (Pio et al., 2014). It is not clear to what extent such findings  
144 hold true for other taxa and more broadly across the world. Furthermore, local phylogenetic diversity  
145 under climate change will not only be subject to change through species losses but also through  
146 species that newly arrive into an area. Identifying areas where changes in species richness lead to non-

147 random changes in phylogenetic diversity is important, since in those areas the projected changes in  
148 species richness will not reflect the entire range of impacts on the species community. For example,  
149 decreasing species richness could lead to significant homogenisation of assemblages or to significant  
150 phylogenetic over-dispersion, with very different implications for trait diversity and potential for  
151 changing competitive interactions and ecosystem function.

152 Here, we first (a) investigate how projected climate-induced range shifts and (local) species  
153 extinctions affect the spatial pattern of phylogenetic diversity for an entire taxon, the world's terrestrial  
154 bird species. Secondly, (b) we compare how the projected changes in each species assemblage differ  
155 from what would be expected at random given the projected local species richness change and, for the  
156 first time, disentangle non-random changes through species entering and leaving an assemblage.

157 Our hypotheses are that (a), due to the high correlation between species richness (SR) and  
158 Faith PD, spatial changes in SR will be largely reflected in the spatial changes in Faith PD, whilst  
159 changes in MPD will frequently differ from this pattern. In particular, we expect Faith PD (and hence  
160 SR) and MPD to behave differently in those areas of the world where highly directional range shifts  
161 are projected to occur. Such consistent directional shifts are expected by many species at the higher  
162 northern latitudes and due to collective shifts of species towards higher altitudes (Devictor et al., 2008;  
163 J Lenoir et al., 2008; Sekercioglu et al., 2008; Virkkala & Lehikoinen, 2014). These directional shifts  
164 could potentially select for species with similar traits, leading to increasing phylogenetic clustering;  
165 this process would be identified through an increase in SR and Faith PD at the higher northern  
166 latitudes and the higher altitudes (the receiving species assemblages), accompanied by a simultaneous  
167 reduction in MPD in these areas, through related species with similar traits coming into the  
168 assemblages.

169 Considering the potential for non-random changes of phylogenetic diversity across species  
170 assemblages, we test a second hypothesis that (b) changes through projected species loss are  
171 decoupled from changes through projected species gain within assemblages. For example, a given  
172 assemblage could lose significant phylogenetic diversity through species loss under climate change,  
173 but also gain significantly through species gain, so the overall change in phylogenetic diversity would  
174 be marginal, though the phylogenetic structure of the assemblage could change significantly. We

175 hypothesise that the increase in Faith PD in higher northern latitudes and higher altitudes should be  
176 lower than expected at random from the number of species gained, due to the increasing phylogenetic  
177 clustering. This clustering would also be expected to lead to significant declines in MPD (i.e.  
178 significant increase in average relatedness). Contrarily, a increase in Faith PD that is higher than  
179 expected from simply the gain of species into assemblages could occur in areas with less directional  
180 range shifts, i.e. in regions where species assemblages are more likely to be reshuffled rather than  
181 mostly gaining species. In these cases, significant changes in MPD could identify whether  
182 assemblages experience diversification (MPD increase) or phylogenetic clustering (MPD decrease). In  
183 contrast, non-random changes through the loss of species are harder to predict since they will depend  
184 on the unique evolutionary history a species brings to a local assemblage and which would be lost by  
185 its extinction or disappearance from the area. Areas that have a high number of species from ancient  
186 lineages, like montane areas in tropical Africa or the northern Andes (Fjeldså & Lovette, 1997; Hughes  
187 & Eastwood, 2006), are most likely to undergo a non-random decrease in Faith PD through a loss in  
188 species richness. In such regions, significant parallel decreases in MPD would indicate strong  
189 homogenisation, whereas significant increases in MPD would indicate increasing phylogenetic over-  
190 dispersion.

191

## 192 **Materials and Methods**

193 Species distribution and climatic data preparation, as well as the format for species distribution models  
194 (SDMs) and the design of the chosen dispersal buffer follow methods described in Hof et al (2018).  
195 Here, we provide an abridged summary of these methods (Hof et al., 2018), with full details in the  
196 supplementary material. The extent of our study is global, and focussed on all terrestrial areas  
197 excluding Antarctica.

### 198 **Species data**

199 We obtained expert range maps for 9882 terrestrial bird species from BirdLife International (Birdlife  
200 International and NatureServe, 2015), considering only areas where a species was resident or  
201 occurring regularly during the breeding season. Non-breeding distributions were excluded from the  
202 analysis, because the climatic requirements of a species during the breeding season are most crucial  
203 for its survival and the non-breeding distributions of migratory species are less well known (Eyres et  
204 al., 2017; Howard et al., 2020).

### 205 **Climate data**

206 We calculated the 19 bioclimatic variables, as described by Hijmans *et al.* (Hijmans et al., 2005),  
207 using the merged and bias-corrected meteorological forcing datasets Earth2Observe, WFDEI and  
208 ERA-Interim as provided by ISIMIP (Lange, 2016). As baseline period we used 1980 – 2009 (centred  
209 around 1995). For future projections we used the climate data provided by ISIMIP2b (Frieler et al.,  
210 2017), which comprises data from each of four different general circulation models (GCMs), i.e.  
211 MIROC5, GFDL-ESM2M, HadGEM2-ES and IPSL-CM5A-LR, for a medium warming scenario  
212 (RCP 6.0) (but see Fig. S2 to S5 and Table S2 and S3, for equivalent results based on a low warming  
213 scenario (RCP 2.6)). As a future timeframe we used end-of-century projections (2065 – 2095, centred  
214 around 2080). All climate data were provided on a 0.5° x 0.5° latitude–longitude grid.

### 215 **Species distribution models (SDMs)**

216 We used two types of SDMs, generalized additive models (GAM, (Hastie & Tibshirani, 1990; Wood,  
217 2006)) and boosted regression trees (GBM, (Ridgeway, 2007)), to derive the relationship between a  
218 species' current range extent and the bioclimatic variables, following the methods in Hof et al (2018).  
219 To prepare the projected species distributions for the phylogenetic analysis, we followed the common



220 practice of applying thresholds to transfer the projected suitability values into binary presence-absence  
221 data (Freeman & Moisen, 2008). We applied species-specific thresholds that maximized the fit to the  
222 current data, using the true skill statistic (MaxTSS) (Allouche et al., 2006). Incorporating species'  
223 dispersal ability into future projections is vital, since the assumption of unlimited dispersal is likely to  
224 lead to unrealistic projections (Araújo et al., 2006; Berg et al., 2010; Travis et al., 2013). However,  
225 empirical natal dispersal data are available for only a very small proportion of the global terrestrial  
226 bird species (Paradis et al., 1998). Therefore, we restricted the projected future distribution of each  
227 species using estimated dispersal buffers. This approach follows previous studies that evaluated the  
228 impact of various dispersal buffers (Barbet-Massin & Jetz, 2015; Zurell et al., 2018) on projected  
229 changes in species richness, but instead of applying a constant buffer distance across all species, we  
230 applied species-specific dispersal buffers. The size of the buffer was calculated as  $\frac{d}{2}$ , where d equals  
231 the diameter of the largest range polygon of a species (see Hof et al., 2018 for a comparison of the  
232 impact of varying sizes of dispersal buffers on species richness; and Fig. S5 to S7 and Table S4 and S5  
233 for impacts on the projected phylogenetic measures using a more restricted dispersal assumption).

#### 234 **Phylogenetic data**

235 For the phylogenetic analysis we used the first full species-level phylogeny of extant birds (Jetz et al.,  
236 2012). We compiled a consensus tree using 150 randomly sampled trees out of the 10,000 possible  
237 tree topologies provided. For the analysis we chose the tree topologies based on the Hackett taxonomic  
238 backbone, which is the more recent of the two high-level avian topologies (Hackett et al., 2008),  
239 employed by Jetz et al. (2012). The maximum clade credibility tree topology was calculated using  
240 BEAST v1.8.4 (Drummond & Rambaut, 2007), applying the 50% majority rule and using median  
241 node heights. We matched the taxonomy used by Jetz et al. (2012) with the BirdLife version 5.0  
242 taxonomy (Birdlife International and NatureServe, 2015), resolving all conflicting species, which  
243 resulted in a final combined dataset on the breeding range and phylogeny for 8768 species.

#### 244 **Projected spatial patterns in phylogenetic diversity metrics**

245 To extract potential changes in species richness (SR), Faith PD as well as the mean pairwise distance  
246 (MPD), we derived current and future species assemblages for each grid cell globally based on the  
247 projected species distributions.

248 *Change in SR* was simply calculated as the proportional change between the number of species  
249 projected to occur in a grid cell currently and in the future.

250 *Change in Faith PD* was calculated Faith PD for the species projected to occur in a grid cell, for both  
251 time periods, following the methods of Faith (Faith, 1992a). Faith PD is one of the most commonly  
252 used measures to calculate phylogenetic diversity (Cadotte et al., 2010). It summarizes how much of a  
253 phylogenetic tree is represented in a community by adding all branch lengths that connect the species  
254 within the community (Faith, 1992a). Change in Faith PD was then calculated as the proportional  
255 change between the current and future Faith PD value of a grid cell.

256 *Change in MPD* was calculated as the mean of all branch lengths that connect each pair of species  
257 within a community (Clarke & Warwick, 1998; Kembel et al., 2010; Webb et al., 2002). It gives an  
258 indication of how closely related individuals are, on average, within a community (Tucker et al.,  
259 2017). Subsequently, change in MPD was again calculated as the proportional change between the  
260 current and future MPD value of a grid cell.

#### 261 **Projected non-random changes in phylogenetic assemblage structure**

262 We evaluated whether the projected changes in Faith PD and mean pairwise distance (MPD) were  
263 different from what could be expected if the species that moved in or out of an area were randomly  
264 distributed across the phylogeny. These randomizations are necessary because the structure of the  
265 phylogeny determines the possible extent of projected changes in Faith PD and MPD given a  
266 particular species assemblage and number of species moving in or out (May, 1990; Purvis et al.,  
267 2000). We decomposed the net change in SR in a given assemblage (grid cell) into the species  
268 persisting under climate change, the species projected to be lost (through extinction or emigration),  
269 and the species projected to be gained (through colonisation) under climate change (Fig. 1).

270 Random changes in both phylogenetic measures of a species assemblage (grid cell), through species  
271 loss, were calculated using the list of species projected to be currently present in the assemblage. The  
272 same number of species as projected to be lost (by the SDMs) from the assemblage was then  
273 repeatedly (1000 times) dropped from the current species assemblage at random, and both  
274 phylogenetic measures were recalculated each time (Fig. 1a). The change in Faith PD or MPD was  
275 then calculated as Faith PD<sub>remaining</sub> *minus* Faith PD<sub>current</sub> or MPD<sub>remaining</sub> *minus* MPD<sub>current</sub>, respectively

276 (Fig. 1a). Finally, based on the 1000 repeats we calculated a two-sided p-value as the proportion of  
277 random values that were smaller or larger than the observed value. This p-value indicates if there was  
278 a significant difference between the projected change in the phylogenetic measures and the changes  
279 based on random species removals.

280 When projecting potential changes to species assemblages under climate change, there will not only be  
281 species that are lost from the assemblage, but also species that are gained by the assemblage (Fig. 1b).  
282 To calculate if the change in both phylogenetic measures, based on species projected to be gained by  
283 the assemblage (colonising the assemblage), was different from what one would expect if species  
284 would have been gained at random, we again compared the lists of species IDs projected to occur in  
285 the assemblage currently and in future. We extracted the number of species that are projected to be  
286 gained by the assemblage (grid cell) and then, using this number, we randomly added new species to  
287 those that were projected to remain in the assemblage under climate change, using a species pool  
288 defined based on estimated species' dispersal abilities as explained in more detail below (Fig. 1b). The  
289 change in Faith PD or MPD was then calculated as  $\text{Faith PD}_{(\text{remaining} + \text{gain})} \text{ minus } \text{Faith PD}_{\text{remaining}}$  or  
290  $\text{MPD}_{(\text{remaining} + \text{gain})} \text{ minus } \text{MPD}_{\text{remaining}}$ , respectively. Again, we calculated a two sided p-value indicating  
291 if there was a significant difference between the projected change and the random change in both  
292 phylogenetic measures based on random species being gained by the assemblage.

293 Drawing random species to be gained by an assemblage (grid cell) from a species pool containing the  
294 whole list of terrestrial birds included in the analysis (8269 globally distributed species) would yield  
295 highly unlikely results, because many species would be unable to move into the area due to climate or  
296 habitat requirements, dispersal ability or dispersal barriers. To produce more realistic projections, we  
297 created assemblage-specific (grid cell-specific) species pools to draw the species from (Fig. 1b). To  
298 create these species pools we used the estimated species-specific dispersal buffers we applied for the  
299 projections (see SDM methods). For each species assemblage we extracted the mean estimated  
300 dispersal distance across all species occurring within the assemblage, to have an estimate on how far  
301 birds are projected to disperse within this area. We then used this mean distance to create a buffer  
302 around the species assemblage (grid cell). The species pool for an individual assemblage subsequently  
303 contained all the species that occurred within this buffer. We used these assemblage-specific dispersal

304 buffers because the average natal dispersal distance varies globally, with on average much shorter  
305 dispersal distances in the tropics (Janzen, 1967; Salisbury et al., 2012).

306

307 The final dataset containing the species assemblage values needed to run the analysis and create the  
308 plots can be found on Zenodo (10.5281/zenodo.4262462). The R code for the analysis is provided on

309 GitHub ([https://github.com/AlkeVoskamp/Climate\\_change\\_PD\\_MPD.git](https://github.com/AlkeVoskamp/Climate_change_PD_MPD.git)). *BOTH WILL BE MADE*

310 *PUBLIC UPON ACCEPTANCE*

311

312 **Results**

313 **Projected spatial patterns in phylogenetic diversity metrics**

314 The projected changes in species richness (SR) within assemblages (grid cells) do not differ greatly  
315 across continents but do differ within them (Fig. 2a). These SR changes are spatially highly correlated  
316 with projected changes in Faith PD across the globe (Fig. 2b). Although proportional losses in both SR  
317 and Faith PD are likely to be most extreme in species-poor regions (e.g. deserts of Middle East,  
318 Sahara, Australia and southern Africa), we also project high proportional losses in some of the very  
319 species-rich regions of the world (Fig. 2d and 2e). Across the species-rich regions the proportional  
320 changes in Faith PD and SR are especially severe in parts of South America, such as the Amazon  
321 region, Uruguay and northern Argentina, as well as on New Guinea, but assemblages with losses up to  
322 30 % can be found across all continents (Fig 2d and 2e). Assemblages with a projected proportional  
323 gain in both measures are especially widespread at high northern latitudes across the Nearctic and  
324 Palearctic realm (Fig 2d and 2e).

325 The projected changes in mean phylogenetic distance (MPD) differ substantially from the projected  
326 changes in SR (Fig. 2c) and Faith PD. Looking at the same areas described above for changes in SR  
327 and PD, we find, that assemblages for which we project a decrease in MPD are widespread across the  
328 northern Nearctic and Palearctic (Fig. 2f), whereas assemblages projected to experience an increase in  
329 MPD are located in the southern parts of the Amazon, Uruguay and northern Argentina as well as New  
330 Guinea. Overall, the spatial patterns of projected change in MPD are often opposite to those in Faith  
331 PD and SR (Fig. 2d-f). An example for this opposite trend in the three indicators are the changes  
332 projected across Europe. Increases in Faith PD (and gains in SR) are mainly projected in the northern  
333 parts, across the UK and Scandinavia, whereas decreases are projected to be widespread across  
334 mainland Europe including Spain (Fig. 2g-h). On the contrary, Scandinavia and the UK are projected  
335 to experience decreases in MPD, whereas increases are scattered across mainland Europe including  
336 Spain (Fig. 2i).

337 Overall, when looking at projected changes in the two phylogenetic structure metrics (Fig. 2), we find  
338 that Faith PD and MPD are changing into opposite directions in approximately 60% of the global  
339 terrestrial area (Table 1). Exploring the correlation and divergence between Faith PD and MPD further

340 (Fig. 3, Table 1), we find that 30% of the global species assemblages (grid cells) are projected to  
341 experience an increase in MPD and a decrease in Faith PD, i.e. a loss in average relatedness and a loss  
342 in standing evolutionary history, leading to increasing phylogenetic over-dispersion of these species  
343 assemblages. In 15% of the species assemblages globally, both MPD and Faith PD decrease, leading  
344 to increasing relatedness and decreasing evolutionary history, i.e. an increasing homogenisation of  
345 these species assemblages. Further, 29% of the species assemblages experience a decrease in MPD  
346 and an increase in Faith PD, indicating increasing relatedness and evolutionary history which leads to  
347 phylogenetic clustering of the species assemblages. Finally, 26% of the species assemblages are  
348 experiencing increases of both MPD and Faith PD, indicating losses of relatedness and gains in  
349 evolutionary history that translate to overall increasing diversification of these species assemblages  
350 under global warming.

### 351 **Projected non-random changes in phylogenetic assemblage structure**

352 We identify areas where the projected changes in each phylogenetic diversity metric, i.e. Faith PD and  
353 MPD, are higher or lower than we would expect from the projected changes in SR, by randomising the  
354 identity of species that were gained by or lost from a species assemblage. Focussing only on the areas  
355 where the projected changes differ significantly from what would be expected at random, based on the  
356 two-sided p-value, we find that areas where the decrease in Faith PD (through the loss in SR) was  
357 significantly less than expected from randomized species moving out of the assemblage occur on all  
358 continents but are most frequent in the northern Palearctic and Nearctic (Fig. 4a). In these areas,  
359 assemblages are projected to lose species through climate change that represent unusually low  
360 amounts of evolutionary history. In contrast, areas with a significantly stronger decrease in Faith PD  
361 than we would expect at random (through the loss of species) also occur on all continents but are most  
362 common in central South America and southern African regions (Fig. 4a). These areas are therefore  
363 projected to lose species that represent disproportionately high amounts of evolutionary history in their  
364 respective assemblages.

365 Focussing on the increases, we find that areas with significantly lower increases in Faith PD than  
366 would be expected through equivalent random species gains are most frequent at high northern  
367 latitudes, stretching across the entire Nearctic and Palearctic realm, but also across parts of South

368 America and Australia (Fig. 4b). This category of significantly lower increase in Faith PD is the most  
369 widespread in extent, indicating that not only are more areas projected to gain more species than lose  
370 them (cf. Fig. 2d), but also that the species gains in these areas do not lead to the expected increases in  
371 evolutionary history in a large part of the world. Areas with a significantly higher increase in Faith PD  
372 than expected by chance (through the gain in SR) are much less common and are mainly located in  
373 northern Africa, northern central America and the eastern half of South America (Fig. 4b). These areas  
374 are projected to gain species that represent unusually high amounts of evolutionary history, potentially  
375 making those assemblages more diverse and increasing their evolutionary potential.

376 For the changes in MPD, we find areas where the projected loss in SR leads to significantly lower  
377 declines in MPD than equivalent random losses occur globally, but are generally most extensive in the  
378 Nearctic and Palearctic realm (Fig. 4c). In these areas, mean relatedness either decreases or does not  
379 increase as much as expected from the projected species loss, indicating that assemblages are projected  
380 to lose species that were significantly less closely related to remaining species than expected under  
381 random loss. In contrast, the projected loss in SR leads to a significantly stronger decrease in MPD  
382 than expected at random in Northern Africa, Arabia and the Middle East, but also to significant but  
383 less strong decreases across the Americas as well as in southern Africa and west Siberia (Fig. 4c). In  
384 these areas average relatedness of species within assemblages either increases significantly more, or  
385 declines significantly less, than expected under random species loss; this suggests that the species  
386 projected to be lost are disproportionately more closely related to the remaining species.

387 Similar to the projected changes in Faith PD, the non-random changes in MPD are much stronger from  
388 species gain under climate change (Fig. 4d) than from species loss (Fig. 4c). Areas where the increase  
389 in SR leads to significantly less increase in MPD than expected from equivalent random species  
390 additions are nearly completely restricted to the Nearctic realm as well as the northern Himalayas and  
391 Qinghai-Tibet Plateau (Fig. 4d). In these areas, assemblages tend to gain species that are significantly  
392 more closely related to existing species than expected at random. Areas where the increase in MPD is  
393 significantly higher than would be expected by an equivalent gain in random species are widespread  
394 across most continents (Fig. 4d), indicating that average relatedness across most of the world

395 decreases through species projected to be gained under climate change, i.e. that assemblages gain  
396 species that are more distantly related to existing species than expected at random.

397 When comparing the significant non-random increases vs. decreases in phylogenetic diversity within  
398 each assemblage, we find that there are numerous assemblages where projected significant changes in  
399 phylogenetic structure overlap, e.g. stronger decreases than expected from random species loss and, at  
400 the same time, weaker increases than expected from random species gain (Table 2). Projected future  
401 changes in Faith PD that differ significantly from equivalent random species losses or gains overlap  
402 most in assemblages that show a stronger decrease and coinciding stronger increase of evolutionary  
403 history than expected, i.e. these assemblages will lose more phylogenetic diversity than if species were  
404 lost randomly and simultaneously gain more phylogenetic diversity than if species were gained  
405 randomly (>14% of global assemblages; Table 2, second row). This indicates that particularly high  
406 proportions of assemblages in most continents (in South America, Africa, North America and Europe)  
407 are projected to experience species reshuffling through both species losses and gains. Our results are  
408 similar for MPD, where >14% of global assemblages are projected to decrease significantly more than  
409 under random species loss and simultaneously increase significantly less than under random species  
410 loss, indicating that the species losses and gains will both cause an unusually strong increase in net  
411 relatedness of species in these assemblages (Table 2, second row; particularly in South America,  
412 Africa, North America, and Asia). For Faith PD, the only other category of coinciding significantly  
413 non-random changes is that of simultaneous stronger decrease and weaker increase (Table 2, first  
414 row), indicating that >10% of assemblages in Europe and North America are projected to experience  
415 unusually strong decreases in Faith PD and therefore lose significant amounts of evolutionary history  
416 through both species losses and gains. For MPD, a vast majority of assemblages does not experience  
417 any of the overlap categories, with the exceptions of the above-mentioned ones, although nearly 10%  
418 of European assemblages are projected to experience simultaneous stronger increases and stronger  
419 decreases in relatedness than expected under random species loss and gain (Table 2, third row). This  
420 further corroborates the results for Faith PD, indicating that a high proportion of assemblages in  
421 Europe stand to experience major species reshuffling.

422



423 **Discussion**

424 We found that the projected impacts of climate change not only affected the amount of evolutionary  
425 history stored within species assemblages but also had significant impact on the phylogenetic structure  
426 of species communities. The independent changes in the two phylogenetic diversity measures, Faith  
427 PD and MPD, resulted in four main directions in which the phylogenetic structures of species  
428 communities can change. The frequency with which these structural changes occurred showed a  
429 latitudinal gradient, with increases in the amount of evolutionary history contained within species  
430 assemblages, associated with either increasing phylogenetic diversification or clustering, being most  
431 frequent at high northern latitudes. By contrast, declining evolutionary history, associated with  
432 increasing phylogenetic over-dispersion or homogenisation, occurred across all continents. Overall,  
433 the projected changes in Faith PD and MPD differed significantly from what we would expect if  
434 random species were being gained or lost across large areas of the globe, indicating that the  
435 phylogenetic assemblage structure might be changed completely in the future through local species  
436 loss and gain that is strongly selective in terms of phylogeny.

437 **Projected spatial patterns in phylogenetic diversity metrics**

438 As expected, our results showed that the spatial patterns of proportional changes in species richness  
439 (SR) and Faith PD are highly correlated on a global scale (Fig. 2b), thus the projected losses as well as  
440 gains in assemblage SR is largely reflected in their decreases and increases in Faith PD (Figure 1). By  
441 contrast, the changes in mean phylogenetic distance (MPD) are independent from the changes in SR  
442 and Faith PD and frequently show an opposite pattern. These striking differences are corroborated by  
443 the strong spatial patterns in those changes that are significantly non-random (Fig 4, Table 2,  
444 supplementary discussion).

445 Focussing on the example of Europe (Figure 2), the increase in Faith PD in combination with the  
446 simultaneous decrease in MPD across the UK and Scandinavia indicates that, although these areas  
447 tend to gain species, the projected future assemblages might comprise more closely related species in  
448 the future than currently. The projected gains in species in these areas are in line with already observed  
449 northwards shifts of terrestrial bird species (Thomas & Lennon, 1999; Virkkala et al., 2014). The  
450 projected simultaneous decrease in MPD in these areas supports the idea that species responses to

451 climate change might in some cases be linked to species traits, with species that have similar traits  
452 showing similar responses (Leach et al., 2015; Mason et al., 2019). If these traits are clustered across  
453 the phylogeny, which is the case for some traits (Barnagaud et al., 2014; Böhning-Gaese & Oberrath,  
454 1999); but see (Khaliq et al., 2015; Losos, 2008)), this could explain the projected gain in species  
455 richness and increase in Faith PD as well as the simultaneous increase in relatedness within northern  
456 species assemblages.

457 A decrease in Faith PD (and loss of species) in combination with a simultaneous increase in MPD is  
458 projected to occur widely across mainland Europe and is especially widespread across Spain (Figure  
459 2), indicating that future species assemblages in these areas are projected to be less related despite the  
460 overall decrease in species numbers. Focussing on Spain, one possible explanation for these changes  
461 could be that species which currently have their breeding grounds limited to northern Africa are  
462 projected to move into Spain under climate change (Barbet-Massin et al., 2010; Guitierrez, 2001),  
463 potentially adding species to the assemblages in Spain that are very different from currently occurring  
464 species. These interpretations made for the example of Europe can be made for other regions in a  
465 similar fashion. In general, our results show that it is important to consider additional biodiversity  
466 indices to the usual SR metrics to evaluate potential impacts of the redistribution of species under  
467 climate change; in this case, even though the changes in SR are mostly matched by the change in Faith  
468 PD, the mismatch with MPD shows that different aspects of biodiversity of a species assemblage can  
469 be affected in different ways.

470 The extinction of species from, and introduction of species into species assemblages can lead to  
471 phylogenetic restructuring (Winter et al., 2009). For example, it is well supported that anthropogenic  
472 impacts such as habitat alteration or species invasions into assemblages can lead not only to taxonomic  
473 but also phylogenetic homogenisation of species communities, through mechanisms of extinction and  
474 replacement (McKinney & Lockwood, 1999; Nowakowski et al., 2018; Olden et al., 2018).  
475 Interpreting what changes to the phylogenetic structure of species assemblages could mean in  
476 conservation terms is difficult. Generally, more phylogenetically diverse communities have been  
477 associated with higher ecosystem stability (Cadotte et al., 2012) and the continuity of ecological  
478 functions and services (Cadotte et al., 2011). Furthermore, species assemblages with a higher

479 phylogenetic diversity are thought to be more resilient to ecological disturbance (Faith, 1992a).  
480 Therefore, those assemblages that maintain a high Faith PD or experience an increase in Faith PD  
481 could be less vulnerable and continue to contribute to the delivery of ecosystem services relative to  
482 assemblages where PD declines (Faith et al., 2010). A decrease in MPD that leads to increased  
483 clustering within species assemblages might also be problematic. As closely related species frequently  
484 share similar traits, clustering could increase competition between species within an assemblage  
485 (Procheş et al., 2008). Overall, our analysis shows that species range shifts under climate change are  
486 not only affecting species numbers but are likely to impact the phylogenetic structure of species  
487 assemblages in ways that could affect the stability of communities and also the future provision of  
488 ecosystem services and ultimately human wellbeing (Faith et al., 2010; Srivastava et al., 2012).  
489 Looking at the potential impacts of climate change on the phylogenetic structure of species  
490 assemblages in more detail we showed that the species assemblages are projected to change into each  
491 of four possible directions (Figure 3). We classified these four different directions into four types of  
492 potential changes to the phylogenetic structure of species assemblages, which are predominant in  
493 different parts of the world (Figure 3). Firstly, we interpreted those assemblages that are undergoing a  
494 projected loss in Faith PD with a simultaneous gain in MPD as experiencing increasing phylogenetic  
495 over-dispersion, meaning there will be fewer species that are very distantly related (Cavender-Bares  
496 et al., 2004; Webb et al., 2002). Phylogenetic over-dispersion can often be observed in ecological  
497 communities that are thought to have evolved under competitive exclusion (Cooper et al., 2008;  
498 Dehling et al., 2014; Emerson & Gillespie, 2008; Slingsby et al., 2006). For the projections under  
499 climate change, this pattern might be largely driven by the loss of species from assemblages, since the  
500 increase in phylogenetic over-dispersion occurs widely in species rich, tropical areas that are also  
501 projected to undergo high species losses (Fig. 1d and 2b).  
502 Second, we interpreted those assemblages with a projected loss of MPD and gain in Faith PD as  
503 experiencing increasing phylogenetic clustering, meaning that they are gaining species but these are  
504 mostly related to each other or to the species already occurring in the assemblage. Phylogenetic  
505 clustering has been observed in species assemblages that evolved under environmental filtering, which  
506 selected for species that are able to cope with the same conditions (Asefa et al., 2017; Emerson &

507 Gillespie, 2008); but see (Cadotte & Tucker, 2017; Kraft et al., 2015). Under our climate change  
508 projections this type of compositional change is mainly found at high northern latitudes as well as  
509 along the southern Andes and the Tibetan plateau (Fig. 3b). This is in line with our hypothesis that  
510 uniform responses across species, like highly directional range shifts (such as widespread shifts  
511 towards higher latitudes and altitudes; (Devictor et al., 2008; J Lenoir et al., 2008; Sekercioglu et al.,  
512 2008; Virkkala & Lehikoinen, 2014)) might select for species with similar traits and subsequently  
513 increase phylogenetic clustering.

514 Third, we interpreted species assemblages with a projected loss in both MPD and Faith PD as  
515 undergoing an overall increase in phylogenetic homogenisation, meaning that they are also  
516 experiencing a loss in Faith PD (and hence evolutionary history) whilst the overall relatedness  
517 between species slightly decreases, leaving the assemblage with fewer and more closely related  
518 species than before. Phylogenetic homogenisation is often observed in species communities that have  
519 undergone anthropogenic disturbance, like habitat conversion through urbanisation or agricultural  
520 expansion or intensification (Liang et al., 2019; Sol et al., 2017). Under the climate change projections  
521 utilized here, phylogenetic homogenisation occurs least frequently (Table 1), mainly across Eastern  
522 Europe (Fig. 3b), and is characterized by relatively small changes in all three measures SR, Faith PD  
523 and MPD (Fig. 3a). That we do not see drastic losses here could be due to the high mobility of many  
524 bird species. Looking at the impacts for other, less mobile, taxa or assuming a no-dispersal scenario  
525 would likely increase the number of assemblages in this group due to potentially higher extinction  
526 (Foden et al., 2013).

527 Finally and fourth, we interpreted those assemblages with a projected increase in both MPD and Faith  
528 PD as undergoing increasing diversification, meaning that the assemblages are becoming overall more  
529 phylogenetically rich with an increase in evolutionary history and a decrease in the overall relatedness  
530 of the species. These increases are mostly projected into currently species poor regions such as parts of  
531 the North American, European and Asian Taiga and some of the world's deserts, such as the Saharan,  
532 Arabian, Australian and Kalahari deserts (Fig. 3b). This distribution is probably due to the fact that in  
533 species-poor regions, the addition of even just one species is highly likely to increase phylogenetic  
534 diversity for simple mathematical reasons.

### 535 **Projected non-random changes in phylogenetic assemblage structure**

536 The magnitude in which phylogenetic diversity is changing depends on the structure of the  
537 phylogenetic tree (Cadotte & Davies, 2016; Heard & Mooers, 2000; Vellend et al., 2011) and, for  
538 Faith PD, can mirror or deviate from the taxonomic diversity (Frishkoff et al., 2014). In contrast to  
539 earlier studies that projected global extinction risk from climate change to be evenly distributed across  
540 the phylogeny for some taxa (Pio et al., 2014; Thuiller et al., 2011), we show that projected changes in  
541 the phylogenetic diversity of species assemblages under climate change can differ significantly from  
542 equivalent random changes to the species pool (Fig. 4). Looking at the decreases in Faith PD and  
543 MPD through the loss of species, we project that for terrestrial bird species there are substantial areas  
544 across the globe where phylogenetic diversity decreases or increases more than expected at random.  
545 Especially for Faith PD, the non-random decreases might be connected to the local loss of ancient  
546 lineages, since assemblages where Faith PD decreases more than expected at random are mostly  
547 located in tropical Africa and South America which host higher numbers of ancient lineages (Procheş  
548 et al., 2015; Voskamp et al., 2017). By contrast, assemblages where Faith PD decreases less than  
549 expected at random are mostly located at high northern latitudes which are known to host fewer  
550 ancient lineages (Procheş et al., 2015). Our findings conflict somewhat with a study that investigated  
551 non-random declines in Faith PD under climate change in various mammal, plant and insect families  
552 in the Floristic Cape Region of South Africa and found that the observed decline differed little from  
553 random simulations (Pio et al., 2014). This difference in the results might reflect variation between  
554 taxa, or the fact that the latter analysis was conducted in a biodiversity hotspot that is rich in endemics  
555 and old lineages (Cape floristic region has over 1500 plant genera, 30% of which occur nowhere else  
556 globally), but is more likely due to the scale of the analysis.

557 Importantly, aside from investigating potential non-random declines in phylogenetic diversity, we  
558 used novel methods to disentangle the impacts of projected assemblage gains and losses under climate  
559 change. We found that, in particular, the impacts of assemblage gains differ significantly from random  
560 across large areas globally. Our results show that identifying areas where the changes in phylogenetic  
561 diversity differ from random is important, since they could be more widespread than previously

562 assumed, and our analyses highlight where projected richness changes might not fully reflect the risk  
563 that climate change poses to communities.

564 When disentangling the impacts of species loss and gain, we identified areas in the world where the  
565 impacts of species losses and gains on the phylogenetic diversity of the assemblages are causing  
566 changes in the same direction. The outcome could be positive, where the PD or MPD increases,  
567 through species entering an assemblage, are significantly higher than expected whilst the PD or MPD  
568 decreases, through species being lost from the same assemblage, are significantly lower than expected.  
569 Or the outcome could be negative, with lower PD or MPD gains than expected based on species gains  
570 and greater PD or MPD declines than expected based on species losses. For such assemblages, the  
571 overall changes in phylogenetic diversity will be clearly positive or negative. By contrast, there are  
572 also situations where the loss and gain of species have different implications for the assemblage  
573 phylogenetic diversity, highlighting the utility of a multi-metric approach to studying impacts. For  
574 example, in such areas the species gains can lead to a greater PD or MPD than expected but, at the  
575 same time, species losses lead to lower PD or MPD than expected (or vice versa). In such  
576 assemblages, the net change in PD or MPD might be close to zero, but the underlying changes in the  
577 species composition, are nonetheless high, indicating greater shifts in assemblage composition than  
578 would be apparent if gains and losses of species were not separately assessed. Our results show that  
579 disentangling the impacts of species gains and losses can aid understanding of how assemblage  
580 phylogenetic diversity might be impacted by climate change, and that important aspects of this impact  
581 might be masked if only considering overall phylogenetic diversity change or if only focussing on  
582 losses.

### 583 **Data limitations and model uncertainties**

584 There are several data-related and methodological caveats that need to be considered when interpreting  
585 the results of this study. Firstly, we were gridding species distribution range maps at a  $0.5^\circ \times 0.5^\circ$  grid  
586 (circa 55x55 km) resolution. Aside from the debate around the utility of range maps for SDMs (Herkt  
587 et al., 2017), the coarse resolution of the resultant distribution data and the associated climate data  
588 used in the modelling may lead to potential misinterpretation of the finer-scale relationships between  
589 species occurrences and climate. However, our global assessment for all bird species could only be

590 conducted at this scale due to a paucity of more highly resolved occurrence data, as is common with  
591 almost all similar global analyses. Consequently, our study is useful in outlining broad trends in  
592 potential assemblage changes but should not be extended to infer locality- or species-specific  
593 responses.

594 Additionally, our projections of species' current and future ranges are solely based on the climatic  
595 niche of a species. Both changes in land cover and land-use as well as biotic interactions will have an  
596 impact on the future ranges of the modelled species (Engelhardt et al., 2020; Godsoe & Harmon, 2012;  
597 Sirami et al., 2017). Furthermore, biotic interactions will also have an impact on the likelihood of the  
598 future establishment of species (Mitchell et al., 2006). Whilst some promising modelling approaches  
599 incorporate biotic interactions into SDMs (Kissling et al., 2012), this is still a major challenge (Zurell  
600 et al., 2020), especially when working on a global scale and considering entire higher taxa. Similarly,  
601 our ability to integrate land-use and climate change remains limited (Sirami et al., 2017). Although  
602 there have been advances in the understanding of species-specific habitat suitability (Methorst et al.,  
603 2017; Rondinini et al., 2011) and efforts to derive links between land-use change and biodiversity loss  
604 (Newbold et al., 2014, 2015), obtaining biologically relevant data at the scale of this study remains a  
605 challenge. Nevertheless, despite these sources of uncertainties, we believe our method is robust and  
606 highlights broad geographic trends in potential phylogenetic change as well as identifying ways in  
607 which both heterogeneous and homogenous responses of species to climate change could impact the  
608 phylogenetic structure of species assemblages.

### 609 **Implications for conservation**

610 The value and practicability of using phylogenetic diversity indices for conservation purposes has  
611 been widely discussed (Winter et al., 2012). Phylogenetic measures can add valuable information for  
612 conservation planning (Pollock et al., 2015, 2017), and the preservation of phylogenetic diversity  
613 could be key to the resilience of communities to environmental change (Faith, 1992a, 1992b). Among  
614 the different actions planned to reduce biodiversity loss and reach the 2050 Vision on Biodiversity,  
615 climate change action plays a significant role (Secretariat of the Convention on Biological Diversity,  
616 2020). Although no phylogenetic signal in climate change vulnerability had been identified prior to  
617 this study, our results showing strong heterogeneity in assemblage-level changes reinforce the utility

618 of phylogenetic indices for climate impact studies. Whilst our results should not be interpreted at a  
619 local scale, they do highlight the implications that climate change induced range shifts could have on  
620 the phylogenetic diversity of species assemblages. The widespread projected changes to phylogenetic  
621 diversity we demonstrate, indicate a potential for strong changes to the diversity of species' traits and  
622 attributes important for maintaining functioning ecosystems. They thus emphasise the need to  
623 minimise future climate change although, for the conservation of biodiversity, climate change  
624 mitigation strategies must run alongside reductions in other drivers of biodiversity loss (Leclère et al.,  
625 2020).

626

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629

### 630 **Author contributions**

631 AV and SGW conceived the initial idea. AV, SAF and CH designed the study. AV analyzed the data  
632 with input from SAF, CH, MFB and SGW. AV wrote the manuscript with comments from all  
633 contributing authors.

634

### 635 **Conflict of interest**

636 The authors declare no conflict of interest.

637



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1095 **Fig. 1:** Methods used to compare the projected changes in Faith PD (called PD in the flow diagram)  
1096 and mean phylogenetic distance (MPD) of a species assemblage (grid cell), based on species that are  
1097 projected to be lost from (a) and gained into (b) the assemblage, with the expected changes in Faith  
1098 PD/MPD based on the same number of species being lost and gained at random. In this example, we  
1099 assume that a) there were 10 species in the assemblage initially and we project 7 species to remain in  
1100 the assemblage (with 3 species projected to emigrate or go extinct). To calculate the expectation for  
1101 random species loss, we then drop 3 random species from the list of ten species 1000 times, i.e. the  
1102 species pool is just the focal assemblage in this case. We then recalculate the two metrics of  
1103 phylogenetic assemblage structure for each random assemblage, and compare this expected change  
1104 under random species loss to the projected change in the two metrics. Then, we assume that b) seven  
1105 species remain in the assemblage and two species are projected to be gained to the assemblage. To  
1106 calculate the expectation for random species gain, we draw 2 random species from the species pool  
1107 1000 times, where the colonist species are drawn randomly from a pool of candidate species that occur  
1108 within a colonisable distance of the focal assemblage; the mean dispersal ability for each species is  
1109 estimated as half the value of the longest range diameter (D). We then recalculate the two metrics of  
1110 phylogenetic assemblage structure for each random assemblage, and compare this expected change  
1111 under random species gain to the projected change in the two metrics.

1112

1113 **Fig. 2:** Projected changes in species richness (SR), Faith's phylogenetic diversity (Faith PD) and  
1114 mean phylogenetic distance (MPD) under a medium emission scenario (RCP6.0) and a medium  
1115 dispersal scenario by 2080. (a) shows the percentage change in SR against absolute change in SR; (b)  
1116 the percentage change in Faith PD against percentage change in SR; (c) the percentage change in MPD  
1117 against percentage change in SR (d) the spatial distribution of percentage change in SR; (e) the spatial  
1118 distribution of percentage change in Faith PD and (f) the spatial distribution of percentage change in  
1119 MPD. The percentage change for all three measures is shown in detail for Europe (g – i). Red indicates  
1120 a negative change (e.g. loss in species richness, Faith PD or MPD), blue indicates a positive change  
1121 (e.g. gain in species richness, Faith PD or MPD).

1122

1123 **Fig. 3:** Comparison of the direction of projected changes in phylogenetic assemblage structure as  
1124 indicated by mean phylogenetic distance (MPD) versus by Faith's phylogenetic diversity (Faith PD)  
1125 under a medium emission scenario (RCP 6.0) assuming a medium dispersal scenario by 2080. The  
1126 scatterplot (a) shows percentage change in MPD against percentage change in Faith PD, divided into  
1127 four categories of change using the median along each axis. The map (b) shows the spatial distribution  
1128 of the species assemblages falling into one of these four categories, and the bar chart (c) shows the  
1129 number of assemblages per category across different continents. The four defined categories are: grid  
1130 cells with a projected gain in MPD and loss in Faith PD leading to increasing phylogenetic  
1131 overdispersion of these species assemblages (blue); grid cells with a projected loss in both MPD and  
1132 Faith PD, leading to increasing homogenisation of these species assemblages (purple); grid cells with  
1133 a projected loss of MPD and gain in Faith PD, indicating increasing phylogenetic clustering of these  
1134 species assemblages (red); and grid cells with a projected gain in both MPD and Faith PD, indicating  
1135 increasing diversification within these species assemblages (yellow).

1136

1137 **Fig.4:** The significance and direction of projected changes in Faith's phylogenetic diversity (Faith PD)  
1138 and mean phylogenetic distance (MPD) of species assemblages (grid cells), through species that are  
1139 projected to be lost from (a and c) and gained into (b and d) assemblages, in comparison to expected  
1140 changes if species were lost and gained at random. Difference values for species being lost from an  
1141 assemblage are calculated as shown in Fig 1. For the maps of change in Faith PD/MPD through  
1142 species being lost from an assemblage (a and c), red indicates that the loss of Faith PD/MPD caused  
1143 by the species that are projected to be lost from the assemblage is significantly higher than what would  
1144 be expected if the same number of random species would be lost; blue indicates that the loss is  
1145 significantly lower than what would be expected if random species would be lost (significance is  
1146 derived using a two-sided p-value  $< 0.05$  or  $> 0.95$ ). For the maps of change in Faith PD/MPD  
1147 through species being gained into an assemblage (b and d), red indicates that the gain in Faith  
1148 PD/MPD through the species projected to be gained into the assemblage is significantly lower than  
1149 what would be expected if the same number of random species would be gained into the assemblage,  
1150 blue indicates that the gain is significantly higher than what would be expected if random species

1151 would be gained. A gain or loss in Faith PD signifies a significant increase or decrease in total  
1152 evolutionary history represented, respectively; a gain or loss in MPD signifies a significant decrease or  
1153 increase in average relatedness, respectively. White areas in each map have no significant changes  
1154 compared to random species gain or loss. Results are shown for a medium emission scenario (RCP6.0)  
1155 and a medium dispersal scenario by 2080.

1156

1157 **Table 1:** The overall terrestrial area, globally and per continent, that falls into the four different  
1158 categories of combined change in two phylogenetic structure metrics, Faith's phylogenetic diversity  
1159 (Faith PD) and mean phylogenetic distance (MPD) (as shown in Fig. 3): increasing homogenisation  
1160 (loss of PD and MPD); Increasing clustering (gain in PD and loss of MPD); Increasing over-dispersion  
1161 (loss of PD and gain in MPD) and Increasing diversification (gain in PD and MPD). The area extent is  
1162 given in km<sup>2</sup> as well as in the percentage of the total terrestrial area, per continent and globally. The  
1163 extent of the area projected to fall into the four different categories is derived assuming a medium  
1164 emission scenario (RCP6.0) and a medium dispersal scenario by 2080.

1165

1166 **Table 2:** Combined projected changes in Faith's phylogenetic diversity (Faith PD) and mean  
1167 phylogenetic distance (MPD), indicating the proportions of those assemblages across the globe where  
1168 each measure changes significantly compared to both, a randomized gain and a randomized loss of  
1169 species (as shown in Fig. 4). The area extent is given in km<sup>2</sup> as well as in terms of percentage of the  
1170 total global land mass; percentage values above 10% are printed in bold. The extent of the area  
1171 projected to fall into the four different combinations is derived assuming a medium emission scenario  
1172 (RCP6.0) and a medium dispersal scenario by 2080.

1173 Table 1

	Increasing homogenisation		Increasing clustering		Increasing over-dispersion		Increasing diversification	
	<i>Area in km<sup>2</sup></i>	<i>%</i>	<i>Area in km<sup>2</sup></i>	<i>%</i>	<i>Area in km<sup>2</sup></i>	<i>%</i>	<i>Area in km<sup>2</sup></i>	<i>%</i>
<b>Africa</b>	4,321,971	15	5,572,879	19	13,159,337	44	6,813,364	23
<b>Asia</b>	4,928,362	17	6,055,430	29	12,751,917	42	7,307,249	23
<b>Australia</b>	2,345,390	28	1,830,899	22	2,834,075	33	1,467,003	18
<b>Europe</b>	3,223,093	12	7,390,459	37	2,937,947	10	9,160,714	41
<b>North America</b>	2,969,140	12	7,371,192	41	7,060,167	23	5,383,293	25
<b>South America</b>	1,603,745	9	3,829,585	22	9,151,380	52	3,015,050	17
<b>Global km<sup>2</sup></b>	19,391,701		32,050,444		47,894,823		33,146,674	
<b>Global %</b>	14		29		31		27	

1174 **Table 2**

1175

Combinations of significantly non-random changes	Continent	Faith PD		MPD	
		Area in km <sup>2</sup>	%	Area in km <sup>2</sup>	%
<b>More decrease than under random species loss</b> <b>AND</b> <b>Less increase than under random species gain</b>	<i>Africa</i>	617,294	2.01	95,040	0.30
	<i>Asia</i>	1,018,127	3.54	95,338	0.28
	<i>Australia</i>	49,022	0.55	9,979	0.13
	<i>Europe</i>	2,542,569	<b>10.97</b>	6,202	0.03
	<i>North America</i>	2,444,568	<b>10.24</b>	623,843	0.05
	<i>South America</i>	562,389	3.07	8,958	0.05
	<i>Global</i>	7,233,968	6.41	839,360	0.80
<b>More decrease than under random species loss</b> <b>AND</b> <b>More increase than under random species gain</b>	<i>Africa</i>	5,242,431	<b>17.32</b>	5,594,644	<b>18.25</b>
	<i>Asia</i>	3,115,838	9.96	4,477,026	<b>14.17</b>
	<i>Australia</i>	445,208	5.17	776,455	8.85
	<i>Europe</i>	2,908,113	<b>12.34</b>	1,816,491	7.48
	<i>North America</i>	3,955,785	<b>16.53</b>	3,647,676	<b>16.23</b>
	<i>South America</i>	4,963,732	<b>27.18</b>	3,876,950	<b>21.82</b>
	<i>Global</i>	20,631,107	<b>14.76</b>	20,189,242	<b>14.17</b>
<b>Less decrease than under random species loss</b> <b>AND</b> <b>More increase than random species gain</b>	<i>Africa</i>	964,809	3.33	644,903	2.22
	<i>Asia</i>	879,000	2.79	1,766,252	5.81
	<i>Australia</i>	240,567	2.83	176,295	2.15
	<i>Europe</i>	1,332,718	7.06	2,314,457	<b>9.82</b>
	<i>North America</i>	373,769	1.79	986,123	4.50
	<i>South America</i>	344,488	2.04	389,379	2.14
	<i>Global</i>	4,135,350	3.65	6,277,408	5.34
<b>Less decrease than under random species loss</b> <b>AND</b> <b>Less increase than under random species gain</b>	<i>Africa</i>	91,834	0.32	9,050	0.03
	<i>Asia</i>	356,260	1.19	508,642	1.6
	<i>Australia</i>	13,936	0.16	0	0
	<i>Europe</i>	1,228,379	6.61	63,660	0.30
	<i>North America</i>	231,209	1.12	185,502	0.78
	<i>South America</i>	97,367	0.55	18,408	0.10
	<i>Global</i>	2,018,983	2.25	785,262	0.59

1176 **Supplementary material**

1177 **Figure S1:** Map of the distribution of the species that had to be excluded from the analysis due to  
1178 limited range extent or low model performance

1179 **Figure S2:** *Adapted figure 2:* Projected changes in SR Faith PD and MPD for RCP 2.6 under a  
1180 medium dispersal scenario

1181 **Figure S3:** *Adapted figure 3:* Comparison of phylogenetic assemblage structure for RCP 2.6 under a  
1182 medium dispersal scenario

1183 **Figure S4:** *Adapted figure 4:* Projected changes in Faith's phylogenetic diversity (Faith PD) and mean  
1184 phylogenetic distance (MPD) of species assemblages for RCP 2.6 under a medium dispersal scenario

1185 **Figure S5:** *Adapted figure 2:* Projected changes in SR Faith PD and MPD for RCP 6.0 under a low  
1186 dispersal scenario

1187 **Figure S6:** *Adapted figure 3:* Comparison of phylogenetic assemblage structure for RCP 6.0 under a  
1188 low dispersal scenario

1189 **Figure S7:** *Adapted figure 4:* Projected changes in Faith's phylogenetic diversity (Faith PD) and mean  
1190 phylogenetic distance (MPD) of species assemblages for RCP 6.0 under a low dispersal scenario

1191 **Table S1:** Species numbers included in the different steps of the analysis

1192 **Table S2:** *Adapted table 1:* The overall terrestrial area, globally and per continent, that falls into the  
1193 four different change categories for RCP 2.6 under a medium dispersal scenario

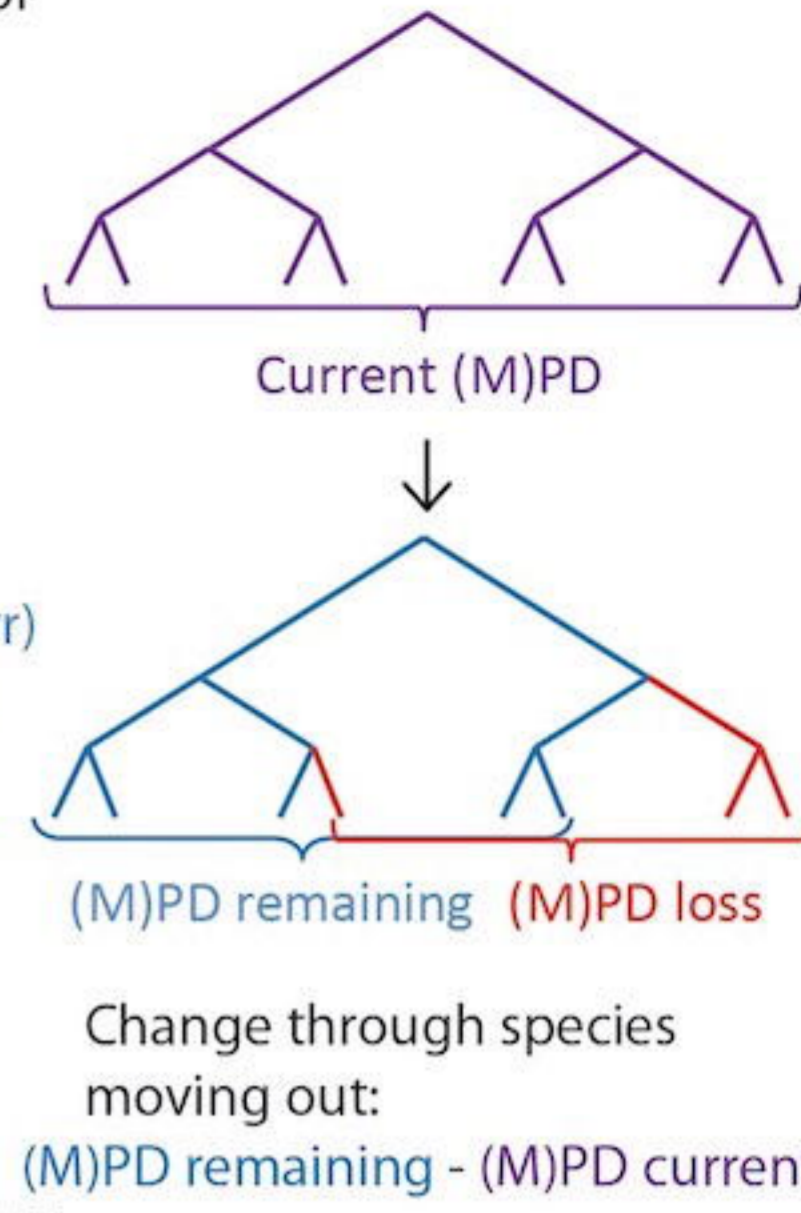
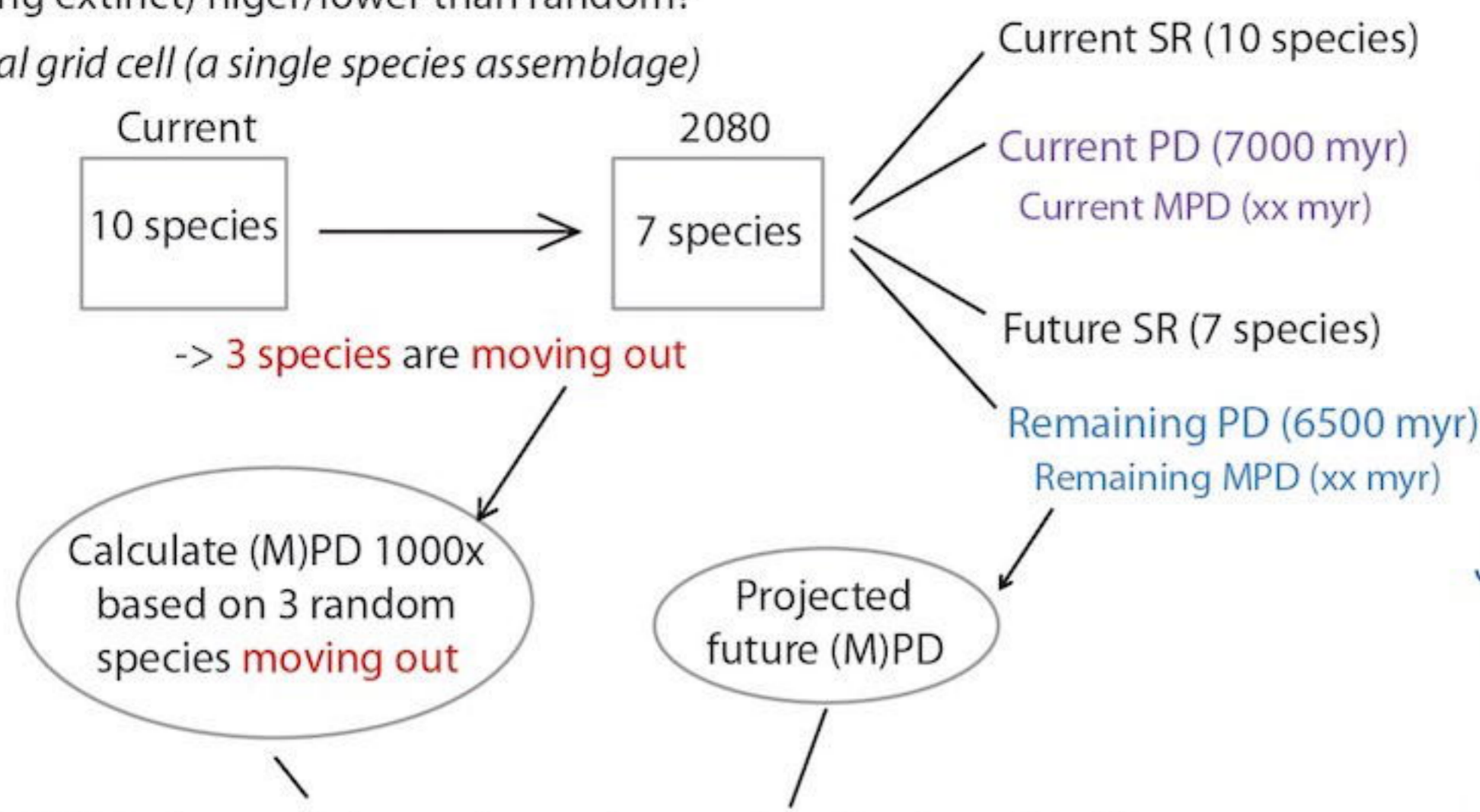
1194 **Table S3:** *Adapted table 2:* Combined projected changes in Faith's phylogenetic diversity and mean  
1195 phylogenetic distance for RCP 2.6 under a medium dispersal scenario

1196 **Table S4:** *Adapted table 1:* The overall terrestrial area, globally and per continent, that falls into the  
1197 four different change categories for RCP 6.0 under a low dispersal scenario

1198 **Table S5:** *Adapted table 2:* Combined projected changes in Faith's phylogenetic diversity and mean  
1199 phylogenetic distance for RCP 6.0 under a low dispersal scenario

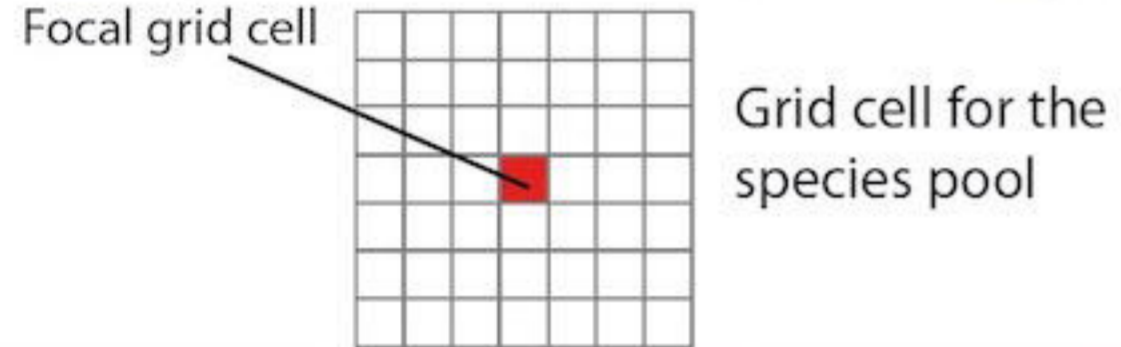
a) Is projected (M)PD change (through species **moving out** of a species assemblage or going extinct) higher/lower than random?

Focal grid cell (a single species assemblage)



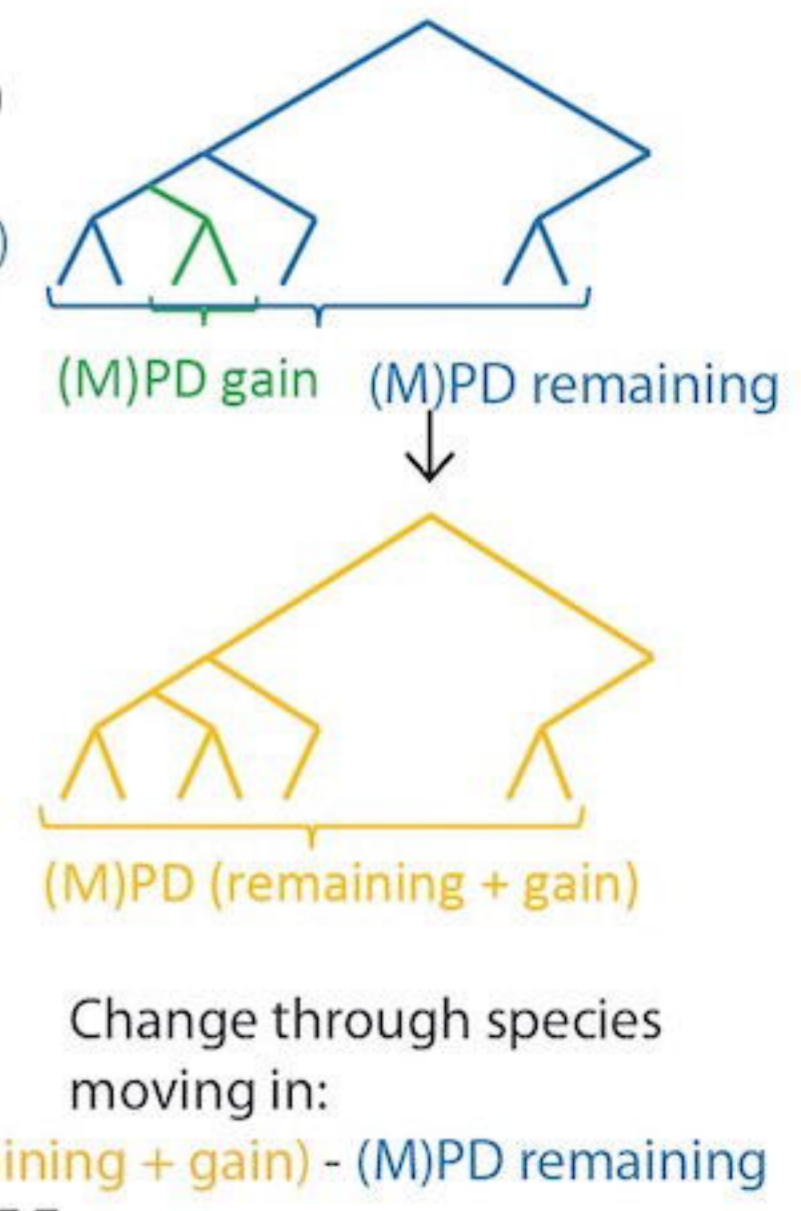
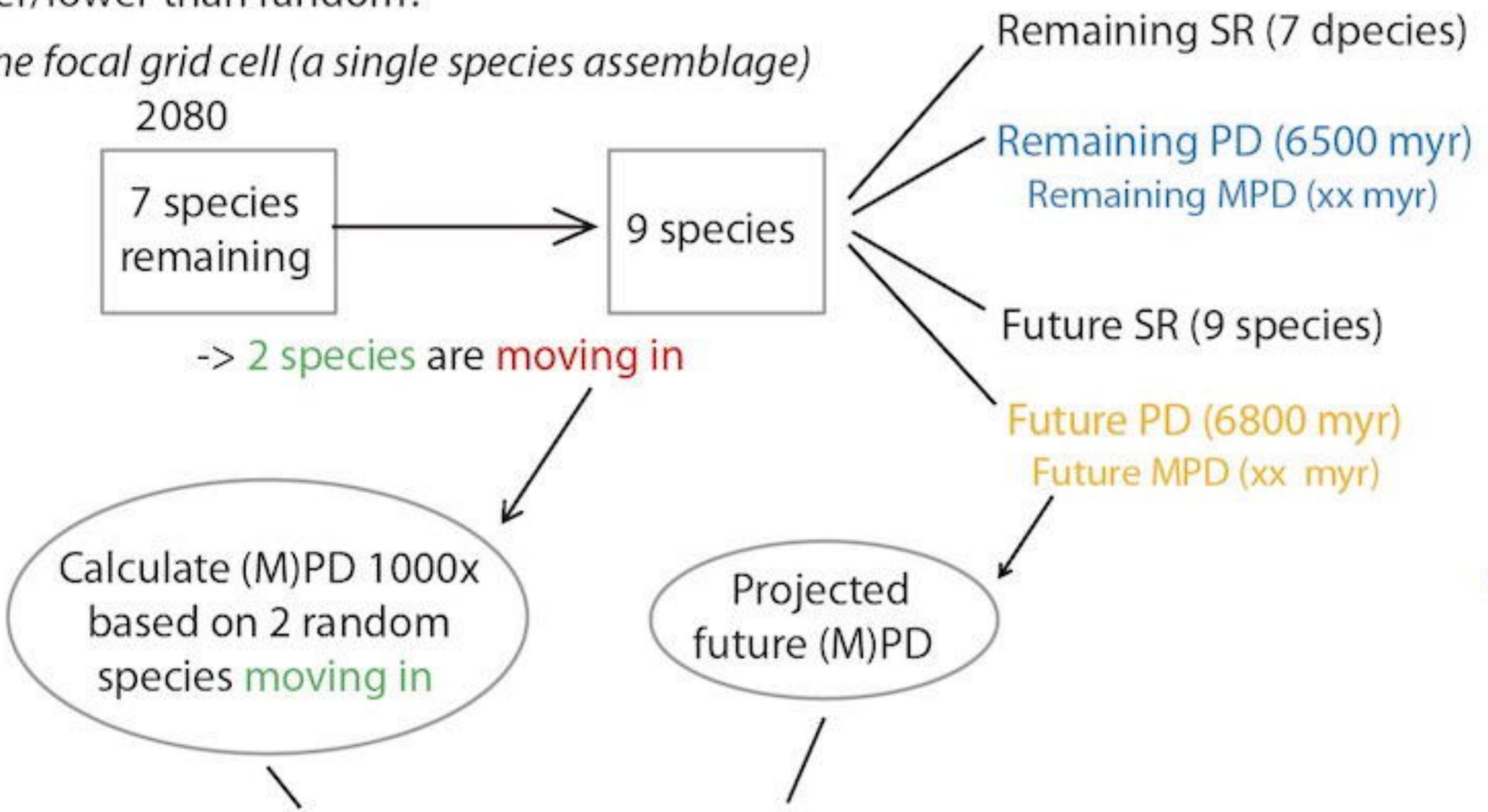
Is (M)PD change higher or lower than random for the grid cell?

Species pool for randomisation procedure (**species moving out**)



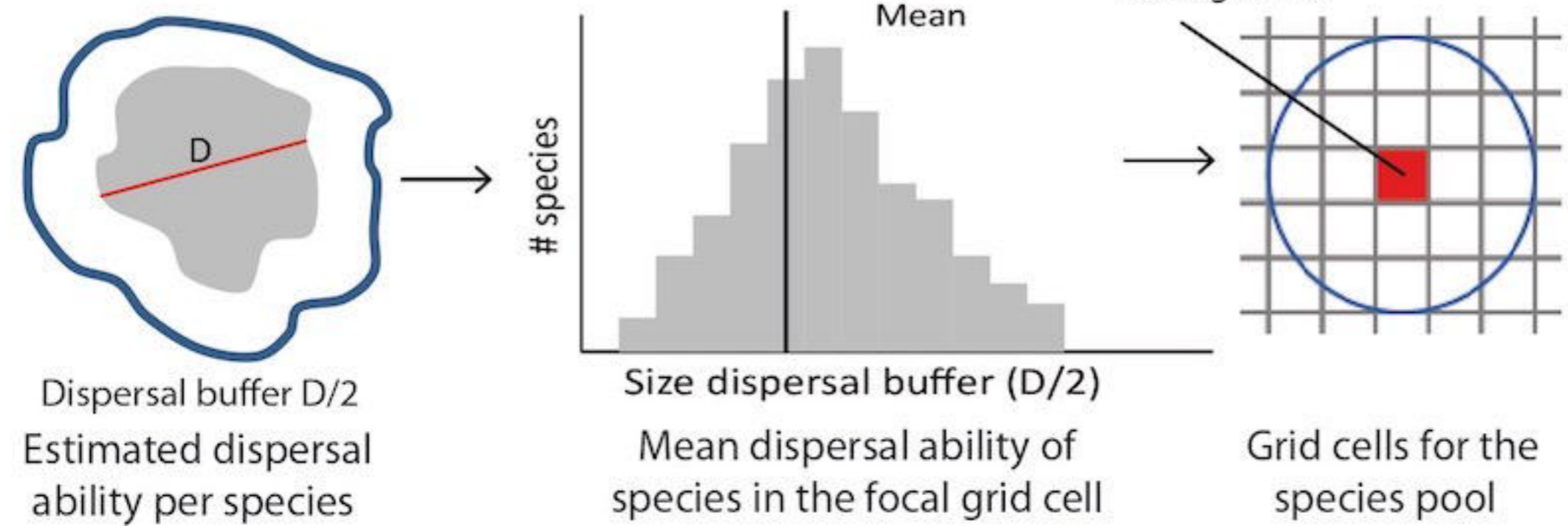
b) Is projected (M)PD change (through species **moving in** to a species assemblage) higher/lower than random?

Same focal grid cell (a single species assemblage)



Is (M)PD change higher or lower than random for the grid cell?

Species pool for randomisation procedure (**species moving in**)



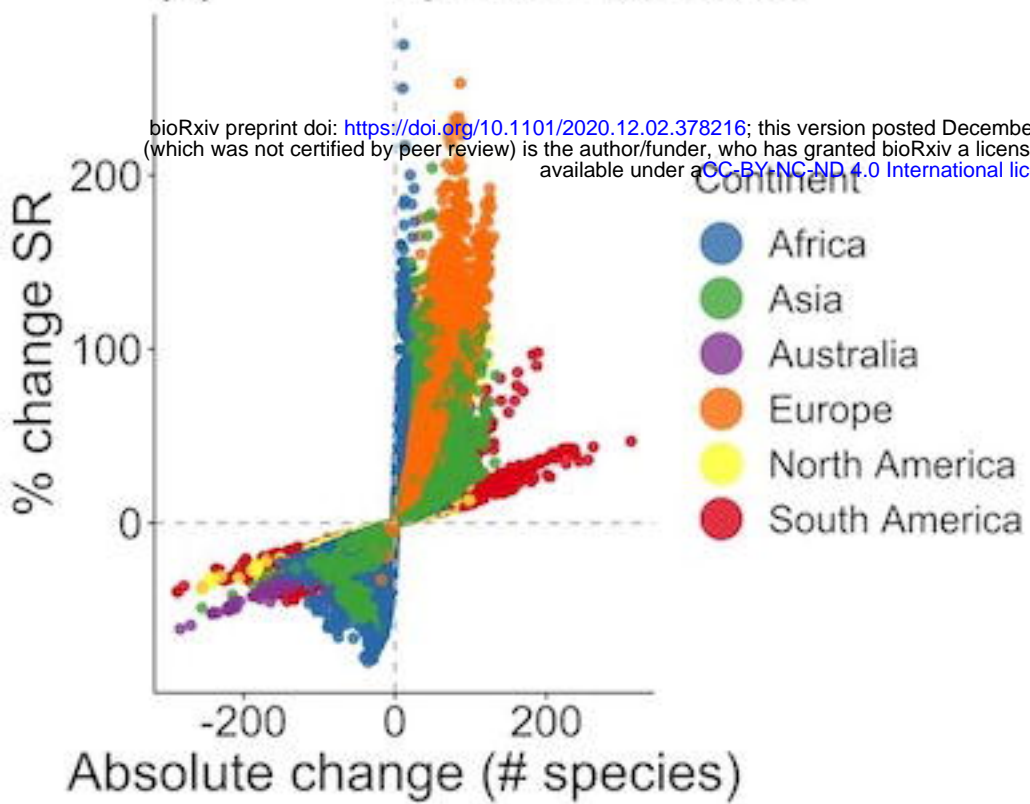
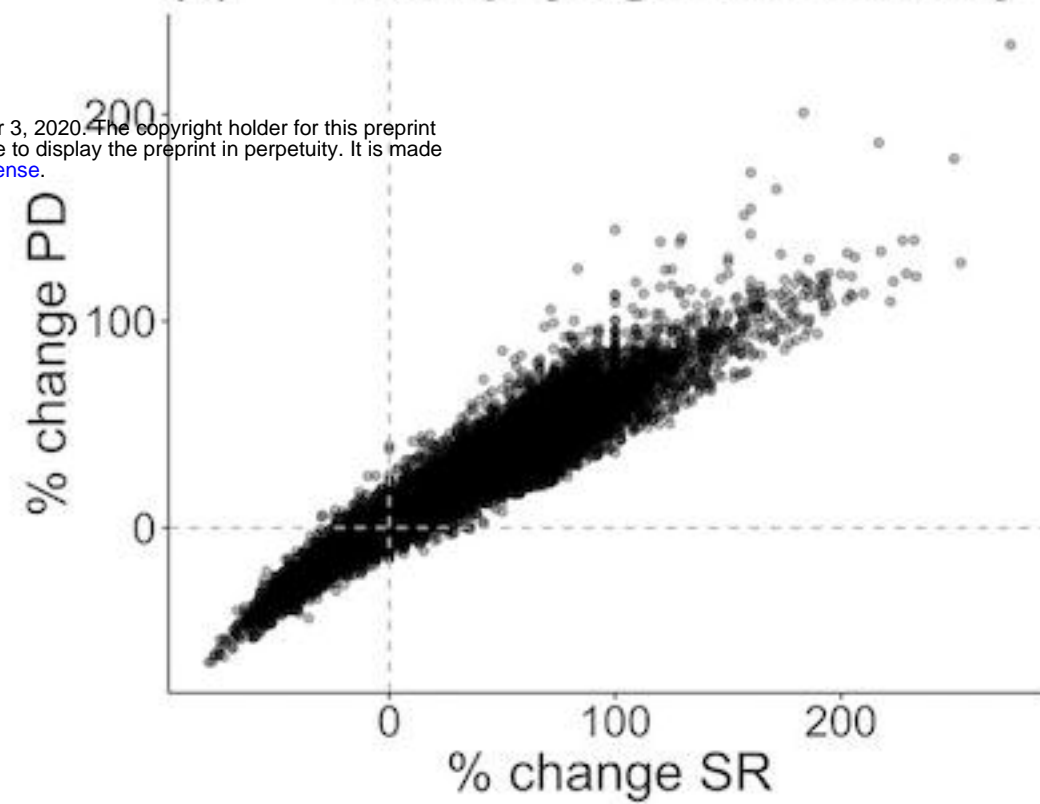
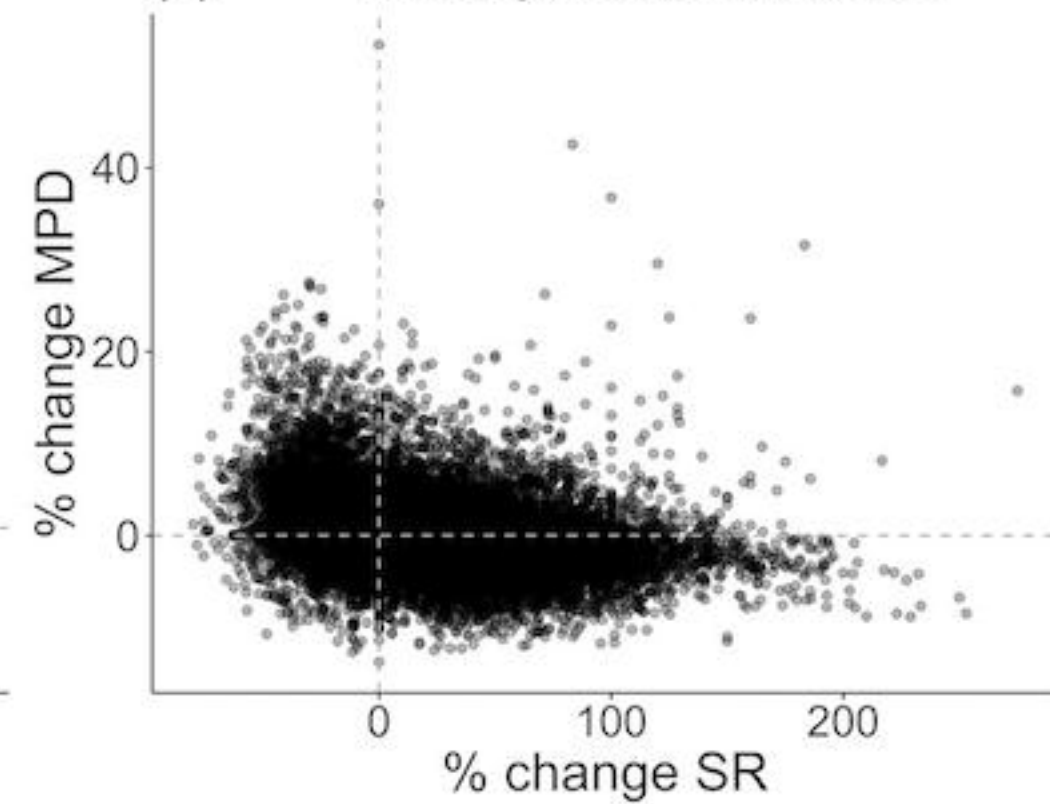
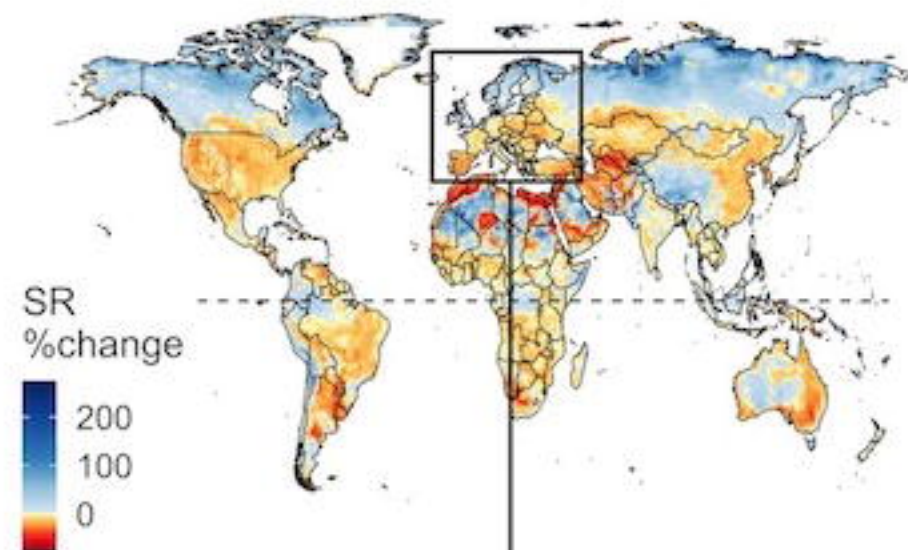
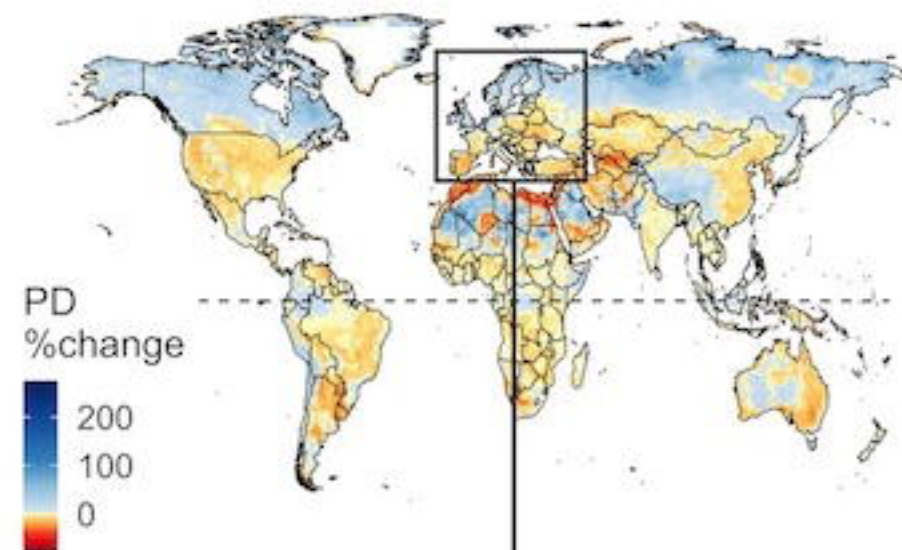
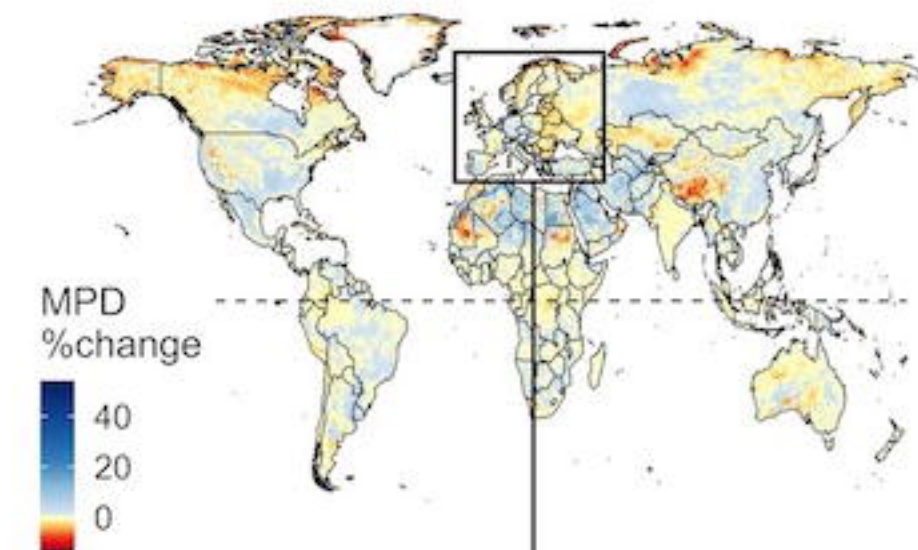
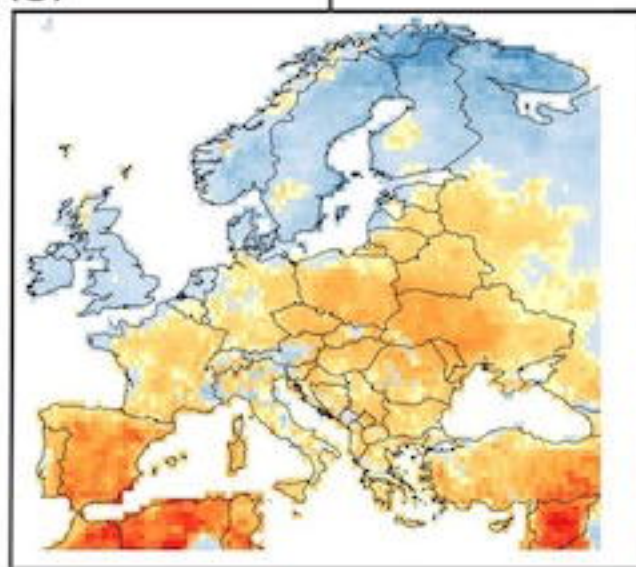
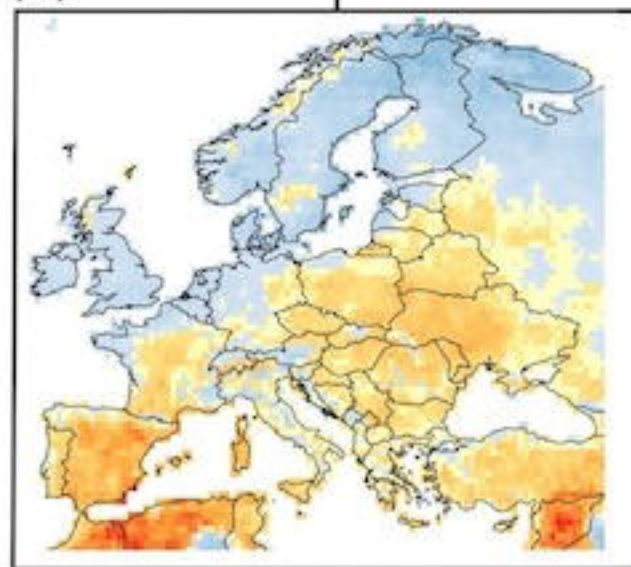
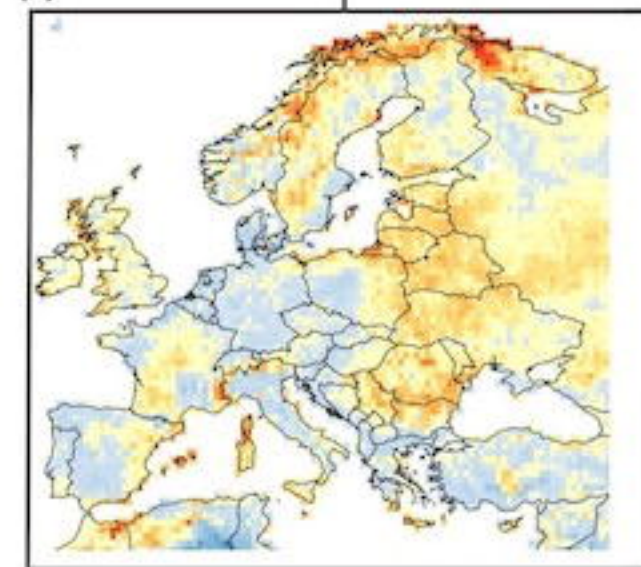
Dispersal buffer D/2  
Estimated dispersal ability per species

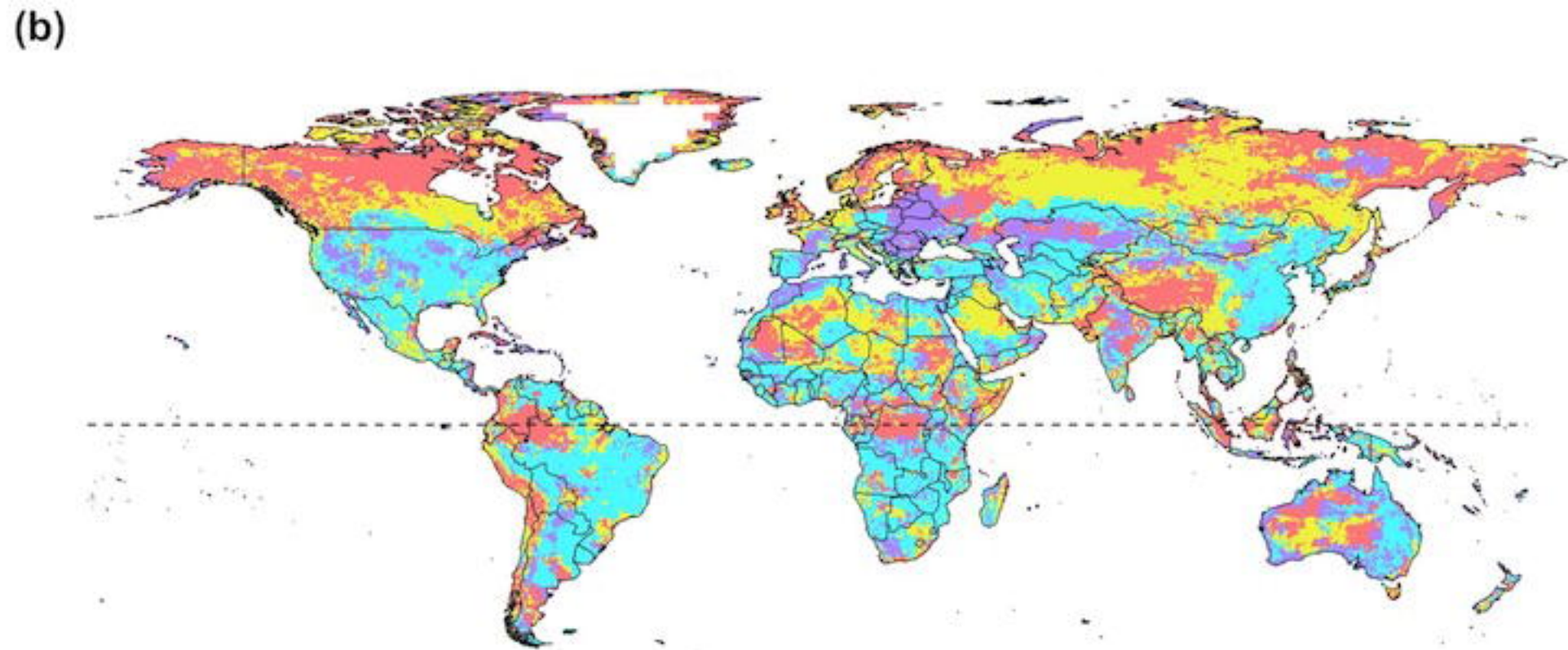
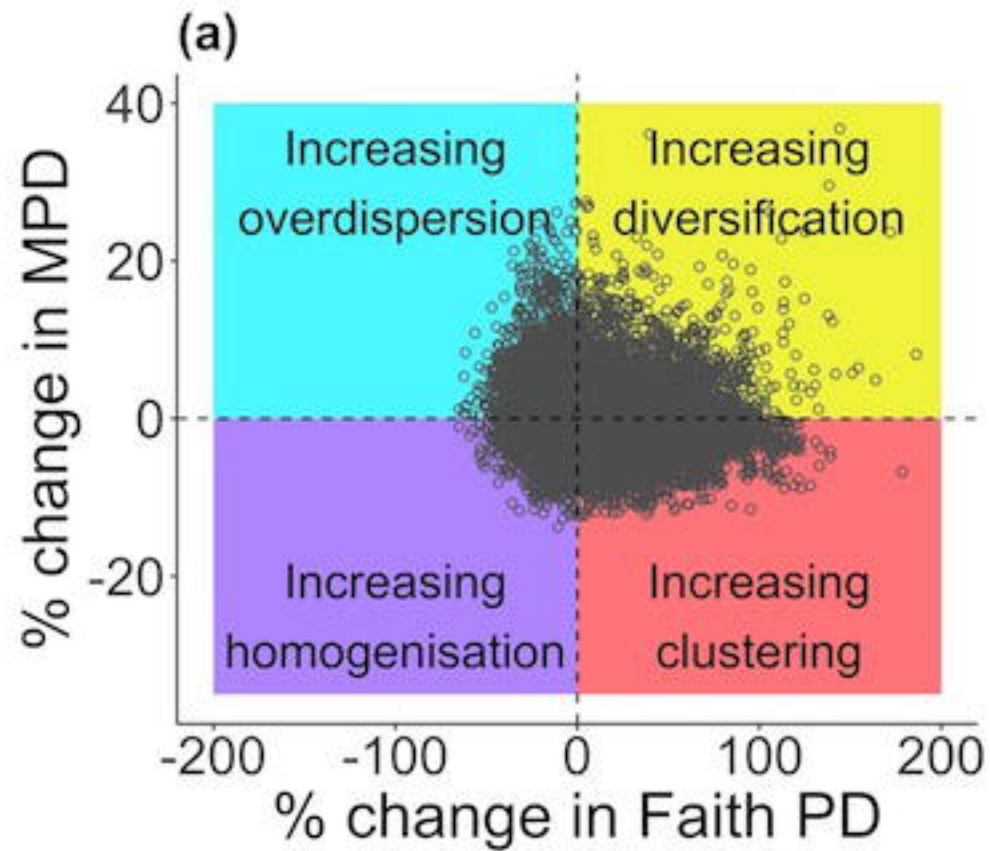
Mean  
# species  
Size dispersal buffer (D/2)  
Mean dispersal ability of species in the focal grid cell

Focal grid cell  
Grid cells for the species pool

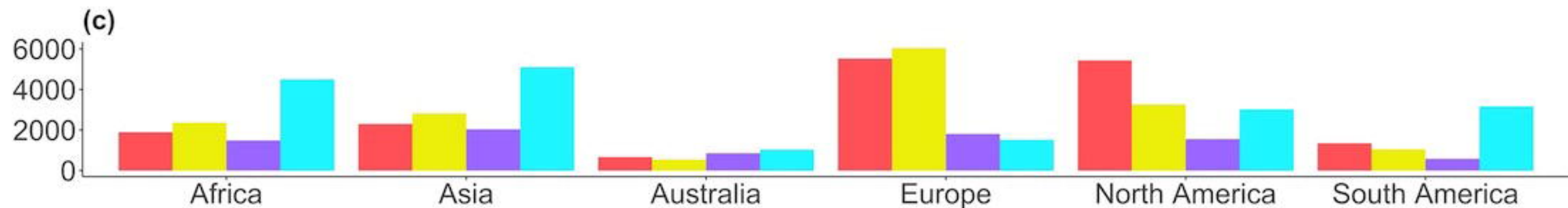
bioRxiv preprint doi: <https://doi.org/10.1101/2020.12.02.378216>; this version posted December 3, 2020. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.



**(a) Species richness****(b) Faith phylogenetic diversity****(c) Mean pairwise distance****(d)****(e)****(f)****(g)****(h)****(i)**

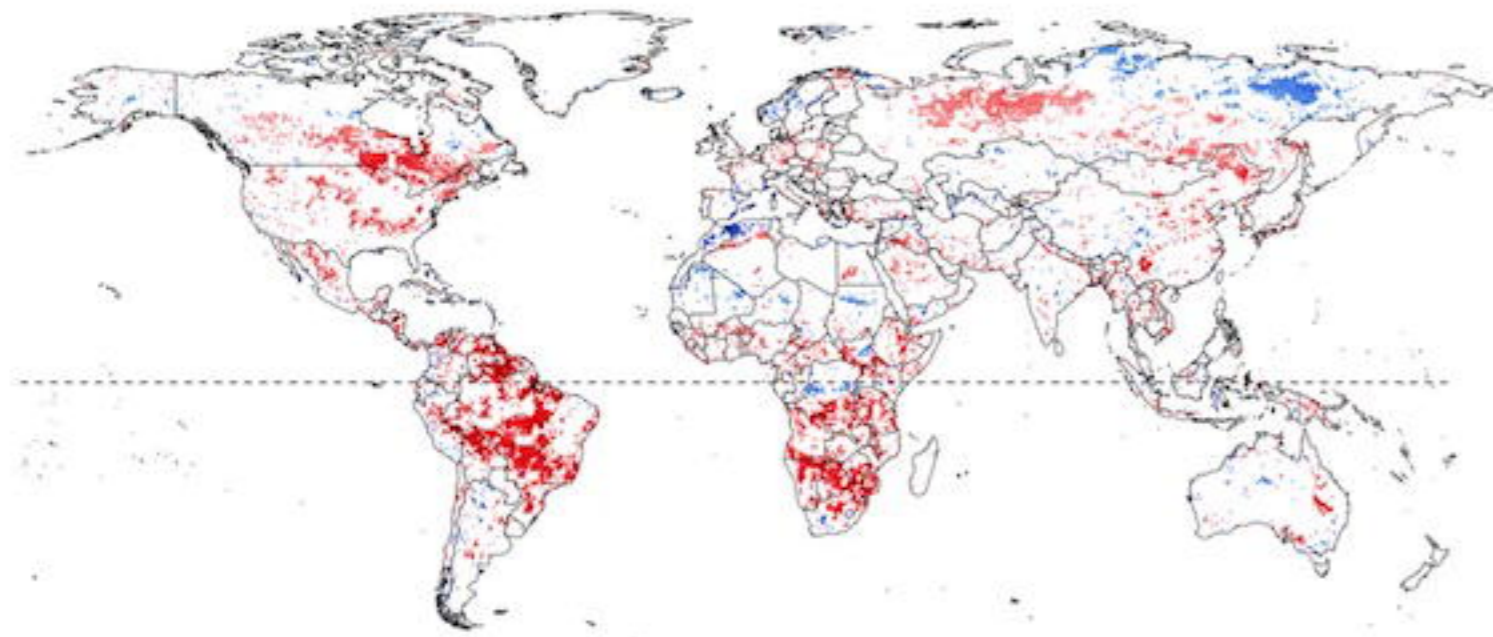


# of species  
assemblages



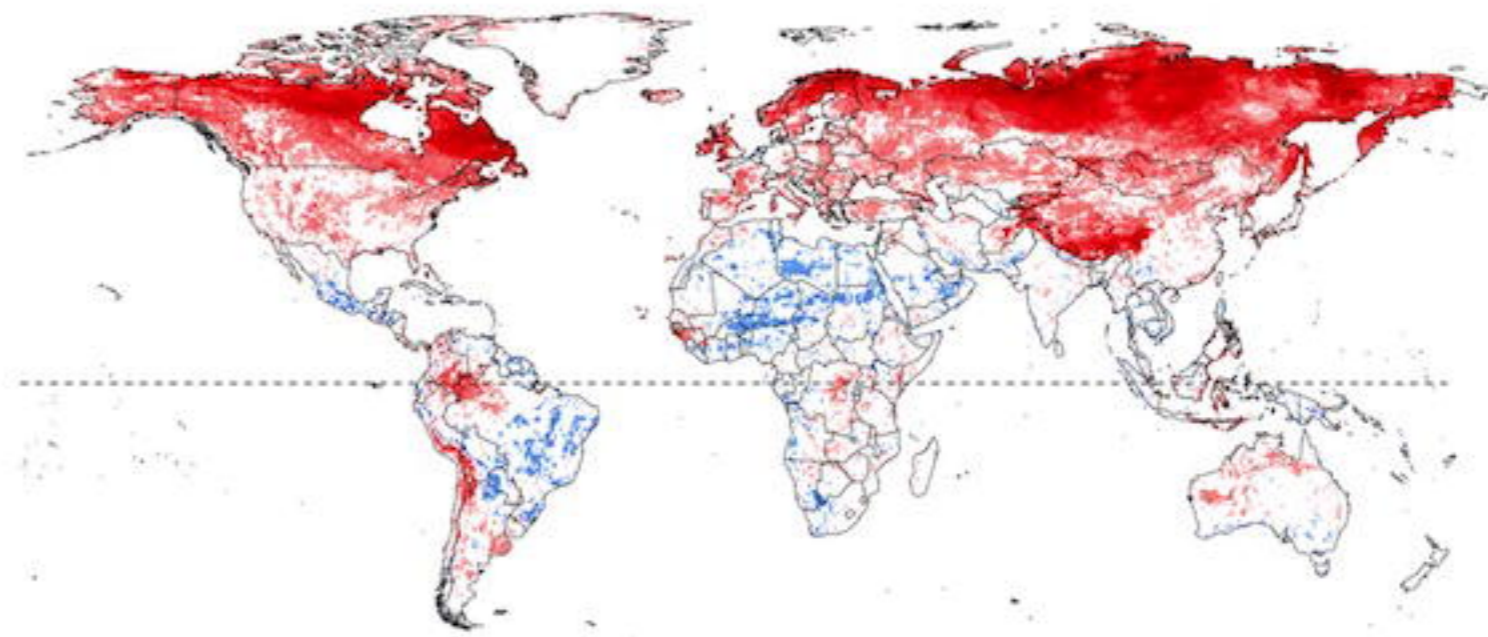
(a)

Change through species loss

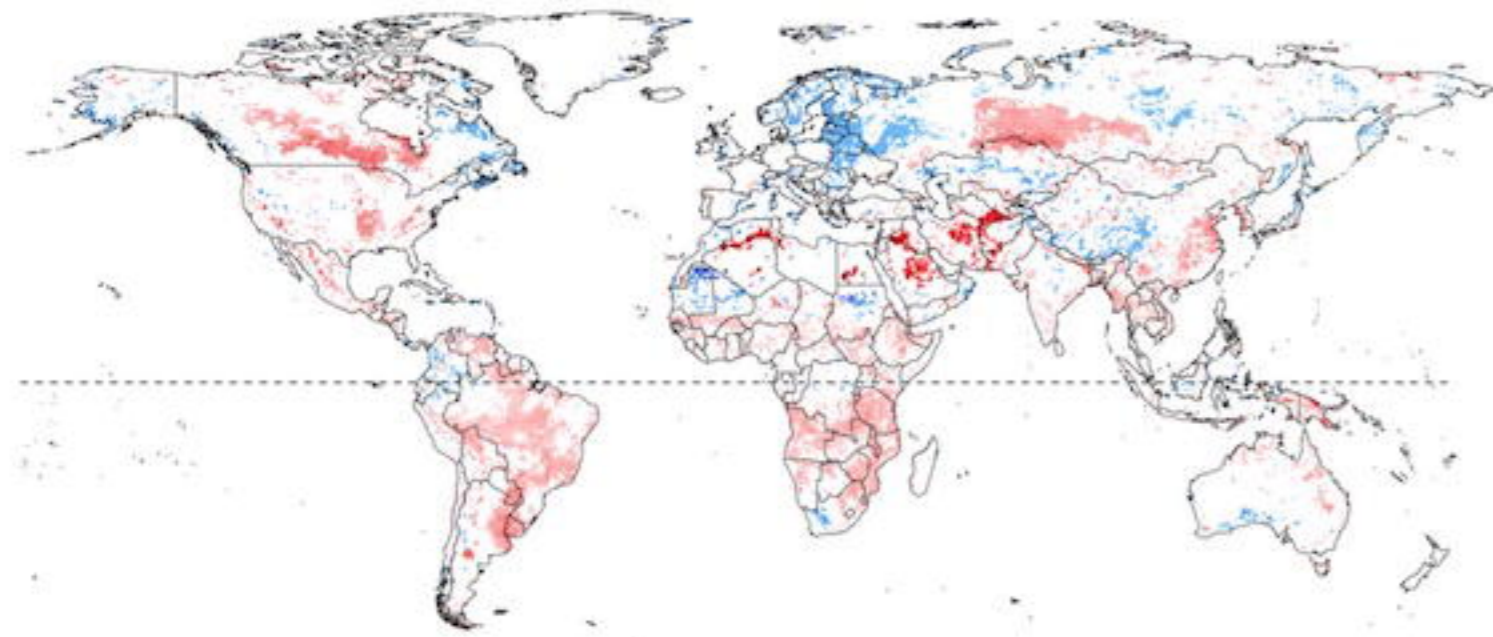
Projected PD change  
- random PD changeStronger decrease  
than randomWeaker decrease  
than random

(b)

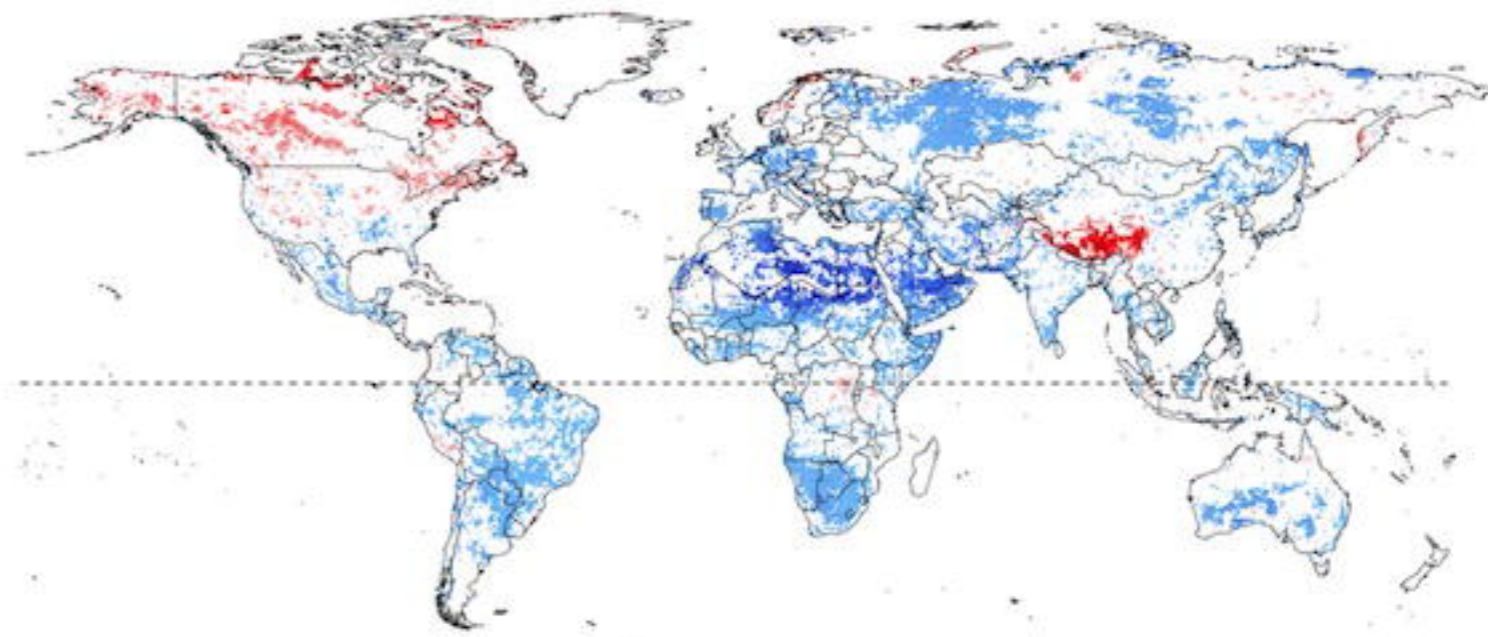
Change through species gain

Projected PD change  
- random PD changeStronger increase  
than randomWeaker increase  
than random

(c)

Projected MPD change  
- random MPD changeStronger decrease  
than randomWeaker decrease  
than random

(d)

Projected MPD change  
- random MPD changeStronger increase  
than randomWeaker increase  
than random