1 Climate change impacts on the phylogenetic diversity of

2 the world's terrestrial birds: more than species numbers

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32	Keywords: species distribution models, mean pairwise distance, Faith phylogenetic diversity, species
33	range shifts; ecological forecasting; ISIMIP
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36	Type of paper: Primary research article
37	Running head: Phylogenetic diversity and climate change

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.

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

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.

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

leading to increasing diversification; or d) MPD could decrease whilst Faith PD increases leading to
increasing phylogenetic clustering of the species assemblage, i.e. increase in clusters of closely related
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 non147 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.

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

192 Materials and Methods

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

198 Species data

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

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 applied species-specific dispersal buffers. The size of the buffer was calculated as $\frac{d}{2}$, where d equals 230 231 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

To extract potential changes in species richness (SR), Faith PD as well as the mean pairwise distance (MPD), we derived current and future species assemblages for each grid cell globally based on the projected species distributions. 248 *Change in SR* was simply calculated as the proportional change between the number of species249 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).

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

(Fig. 1a). Finally, based on the 1000 repeats we calculated a two-sided p-value as the proportion of
random values that were smaller or larger than the observed value. This p-value indicates if there was
a significant difference between the projected change in the phylogenetic measures and the changes
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 Faith PD_(remaining + gain) minus Faith PD_{remaining} or 290 MPD_(remaining + gain) minus MPD_{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
- 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). 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).

Overall, when looking at projected changes in the two phylogenetic structure metrics (Fig. 2), we find that Faith PD and MPD are changing into opposite directions in approximately 60% of the global 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.

Focussing on the increases, we find that areas with significantly lower increases in Faith PD than would be expected through equivalent random species gains are most frequent at high northern 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

decreases through species projected to be gained under climate change, i.e. that assemblages gainspecies 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.

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

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

Focussing on the example of Europe (Figure 2), the increase in Faith PD in combination with the simultaneous decrease in MPD across the UK and Scandinavia indicates that, although these areas tend to gain species, the projected future assemblages might comprise more closely related species in the future than currently. The projected gains in species in these areas are in line with already observed northwards shifts of terrestrial bird species (Thomas & Lennon, 1999; Virkkala et al., 2014). The 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; Guiterrez, 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 phylogenetic restructuring (Winter et al., 2009). For example, it is well supported that anthropogenic 471 472 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 (Proches 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).

Second, we interpreted those assemblages with a projected loss of MPD and gain in Faith PD as experiencing increasing phylogenetic clustering, meaning that they are gaining species but these are mostly related to each other or to the species already occurring in the assemblage. Phylogenetic clustering has been observed in species assemblages that evolved under environmental filtering, which selected for species that are able to cope with the same conditions (Asefa et al., 2017; Emerson &

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

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

assumed, and our analyses highlight where projected richness changes might not fully reflect the risk

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

There are several data-related and methodological caveats that need to be considered when interpreting the results of this study. Firstly, we were gridding species distribution range maps at a 0.5° x 0.5° grid (circa 55x55 km) resolution. Aside from the debate around the utility of range maps for SDMs (Herkt et al., 2017), the coarse resolution of the resultant distribution data and the associated climate data used in the modelling may lead to potential misinterpretation of the finer-scale relationships between 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								
627	Acknowledgements							
628	We thank Dan Rosauer for valuable discussions on the study design and methodology.							
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							

636The authors declare no conflict of interest.

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1094

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 (vellow).

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

would be gained. A gain or loss in Faith PD signifies a significant increase or decrease in total evolutionary history represented, respectively; a gain or loss in MPD signifies a significant decrease or increase in average relatedness, respectively. White areas in each map have no significant changes compared to random species gain or loss. Results are shown for a medium emission scenario (RCP6.0) 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^2 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 species (as shown in Fig. 4). The area extent is given in km² as well as in terms of percentage of the 1169 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 2080. (RCP6.0) and a medium dispersal scenario by

Table 1

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

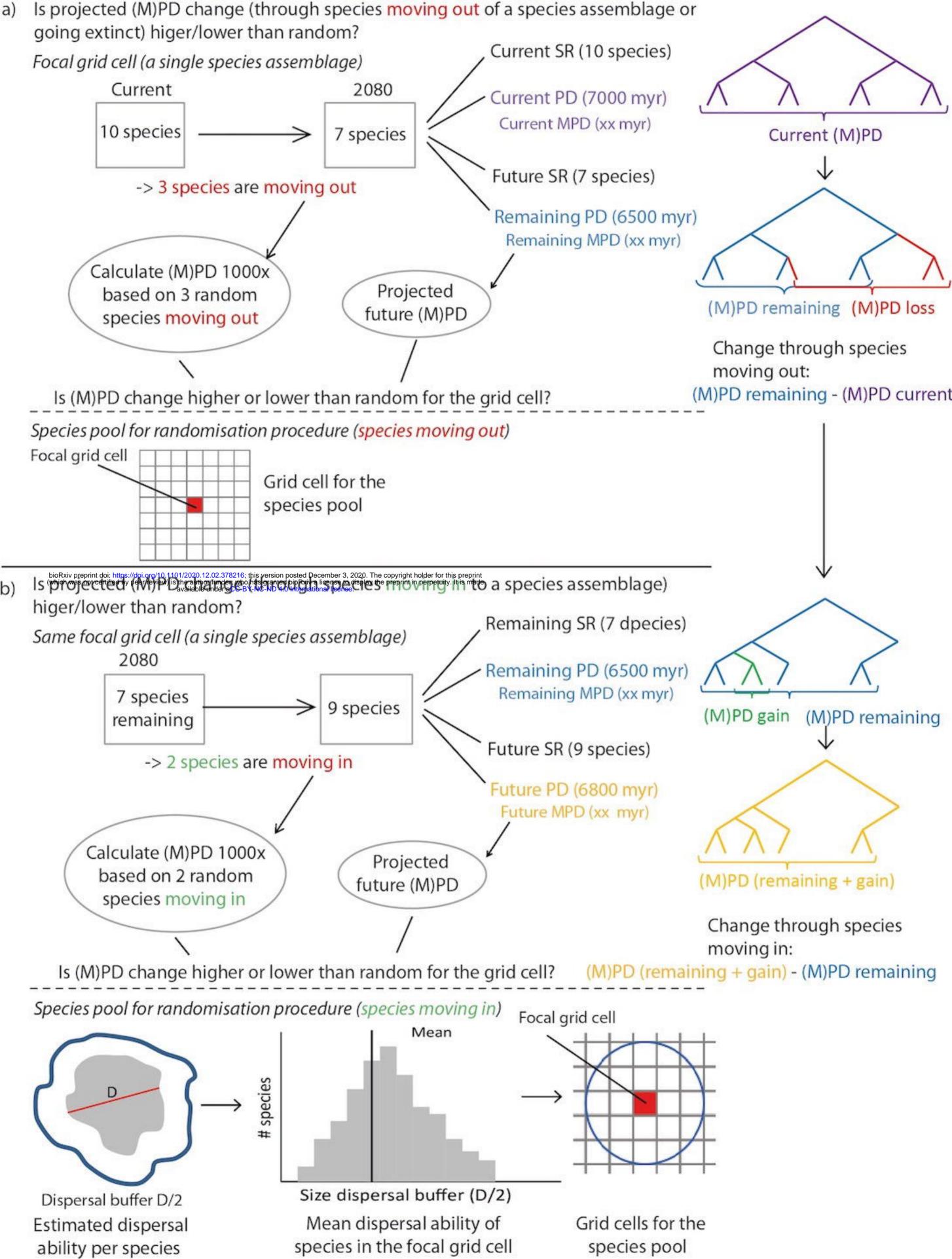
1174 Table 2

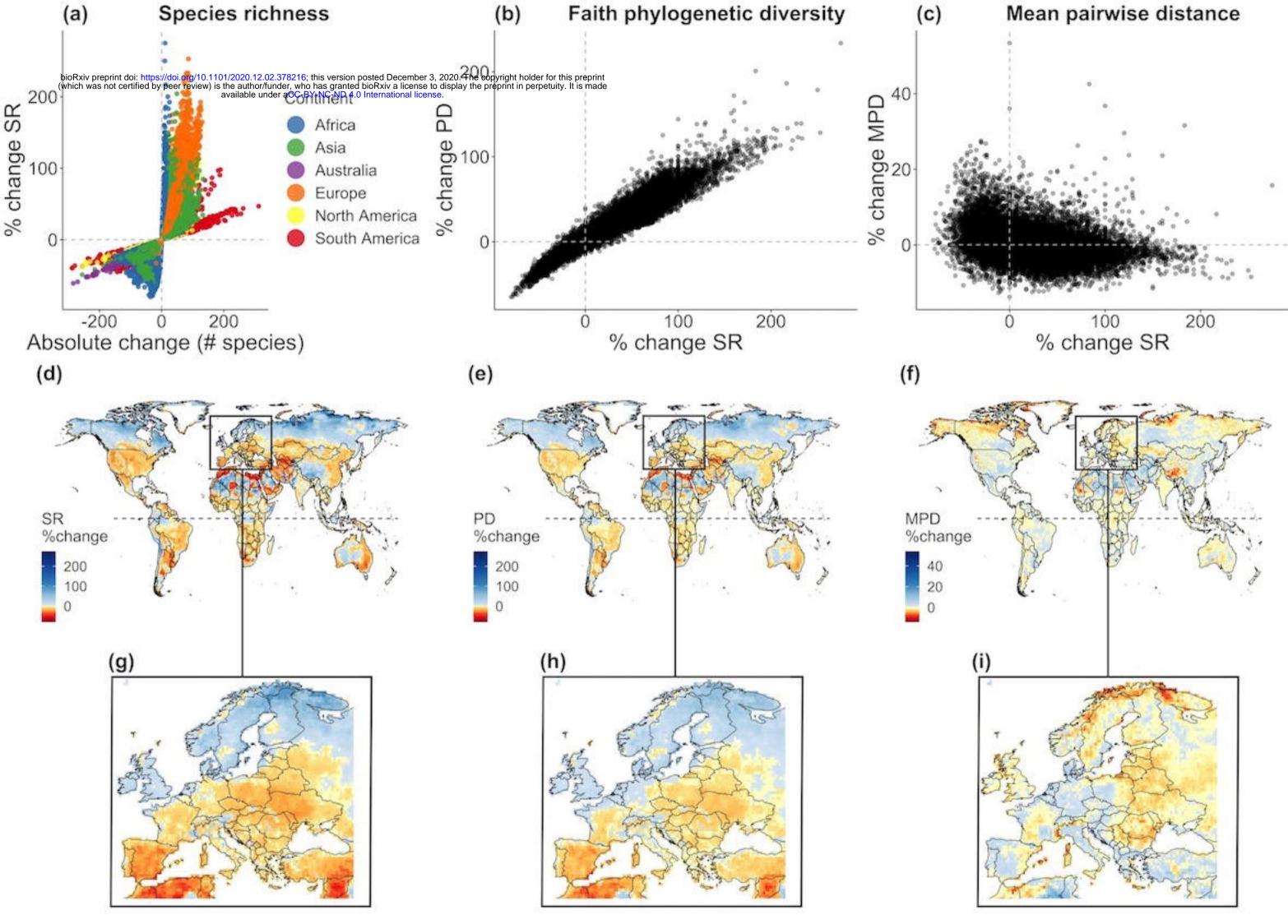
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Combinations of		Faith PD		MPD	
significantly non-random changes	Continent	Area in km ²	%	Area in km ²	%
	Africa	617,294	2.01	95,040	0.30
More decrease than under	Asia	1,018,127	3.54	95,338	0.28
random species loss	Australia	49,022	0.55	9,979	0.13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

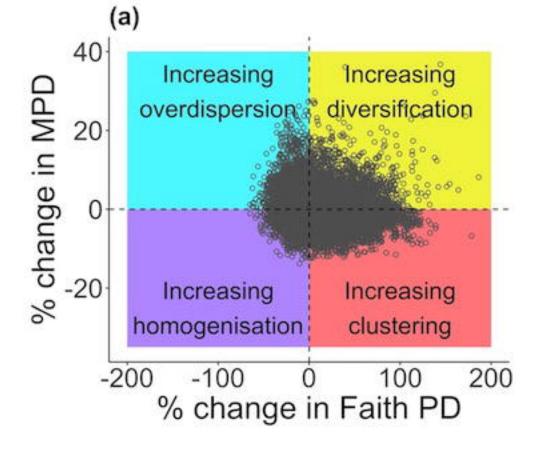
1176 Supplementary material

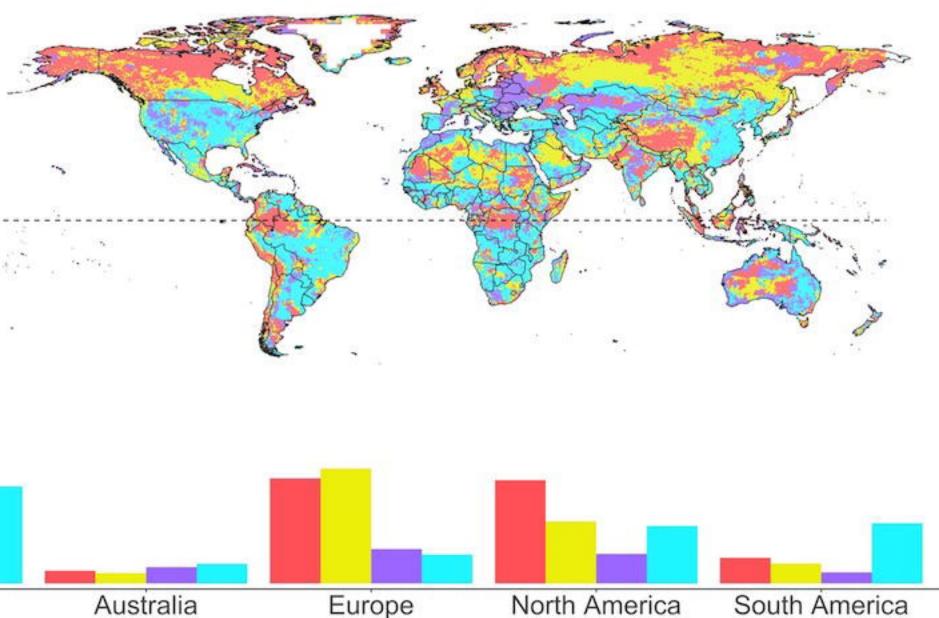
- 1177 **Figure S1:** Map of the distribution of the species that had to be excluded from the analysis due to
- 1178 limited range extent or low model performance
- 1179 Figure S2: Adapted figure 2: Projected changes in SR Faith PD and MPD for RCP 2.6 under a
- 1180 medium dispersal scenario
- 1181 Figure S3: Adapted figure 3: Comparison of phylogenetic assemblage structure for RCP 2.6 under a
- 1182 medium dispersal scenario
- **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
- **Figure S6:** Adapted figure 3: Comparison of phylogenetic assemblage structure for RCP 6.0 under a
- 1188 low dispersal scenario
- **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
- **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
- **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
- **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

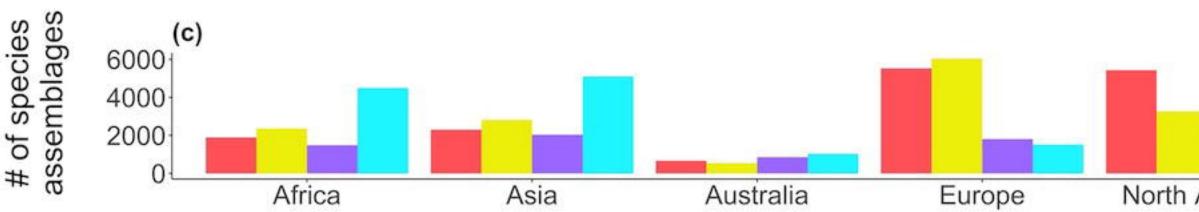








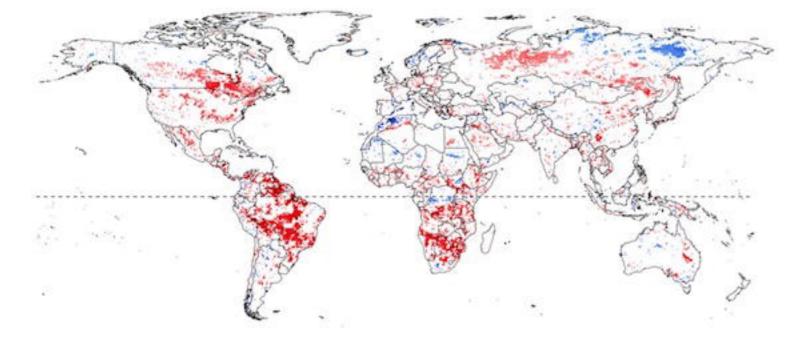




(b)



Change through species loss

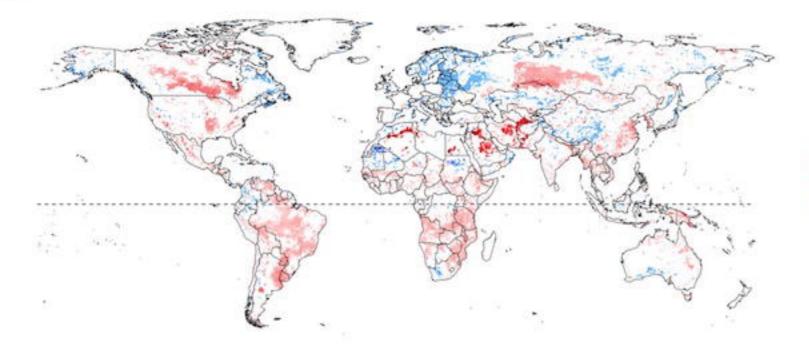


Projected PD change - random PD change

Stronger decrease than random

Weaker decrease than random

(c)



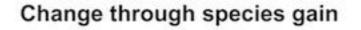
Projected MPD change - random MPD change

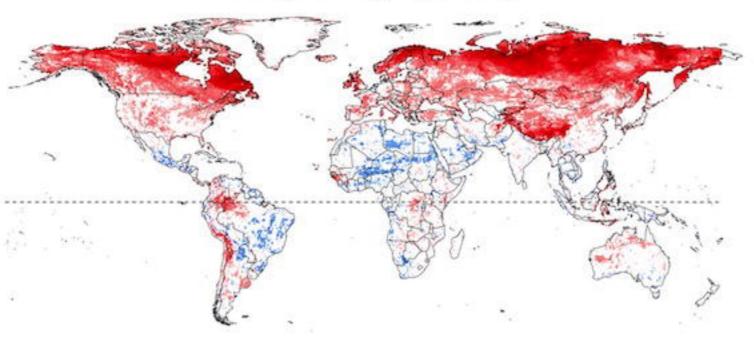
Stronger decrease than random

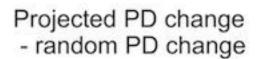
Weaker decrease than random

(b)

(d)

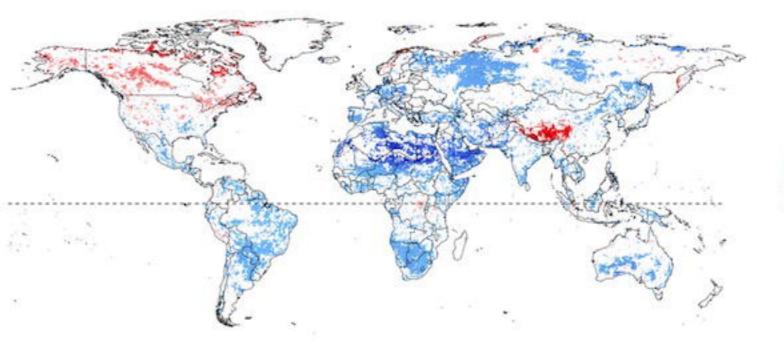






Stronger increase than random

Weaker increase than random



Projected MPD change - random MPD change

Stronger increase than random

Weaker increase than random