



POTSDAM-INSTITUT FÜR  
KLIMAFOLGENFORSCHUNG

**Originally published as:**

**Shi, H., Tian, H., [Lange, S.](#), Yang, J., Pan, S., Fu, B., [Reyer, C. P. O.](#) (2021):**  
Terrestrial biodiversity threatened by increasing global aridity velocity under high-level  
warming. - Proceedings of the National Academy of Sciences of the United States of  
America (PNAS), 118, 36, e201552118.  
**DOI:** <https://doi.org/10.1073/pnas.201552118>

1 **Terrestrial biodiversity threatened by increasing global aridity velocity under high level**  
2 **warming**

3  
4 Hao Shi<sup>a,b</sup>, Hanqin Tian<sup>a,1</sup>, Stefan Lange<sup>c</sup>, Jia Yang<sup>a,d</sup>, Shufen Pan<sup>a</sup>, Bojie Fu<sup>b</sup>, Christopher P.O.  
5 Reyer<sup>c</sup>

6  
7  
8 <sup>a</sup>International Center for Climate and Global Change Research, School of Forestry and Wildlife  
9 Sciences, Auburn University, AL 36849, USA

10 <sup>b</sup>State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental  
11 Sciences, Chinese Academy of Sciences, Beijing 100085, China.

12 <sup>c</sup>Potsdam Institute for Climate Impact Research (PIK), Member of the Leibniz Association, P.O.  
13 Box 60 12 03, 14412 Potsdam, Germany

14 <sup>d</sup>Department of Forestry, Mississippi State University, Mississippi State, Mississippi, USA

15  
16  
17 <sup>1</sup>Corresponding author: Hanqin Tian ([tianhan@auburn.edu](mailto:tianhan@auburn.edu))

18  
19 **Keywords:** Terrestrial biodiversity, climate velocity, aridification, global warming  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42

## 43 **Abstract**

44 Global aridification is projected to intensify. Yet our knowledge of its potential impacts on species  
45 ranges remains limited. Here, we investigate global aridity velocity and its overlap with three  
46 sectors (natural protected areas, agricultural and urban areas) and terrestrial biodiversity in  
47 historical (1979-2016) and future periods (2050-2099), with and without considering vegetation  
48 physiological response to rising CO<sub>2</sub>. Both agricultural and urban areas showed a mean drying  
49 velocity in history, although the concurrent global aridity velocity was on average +0.05/+0.20 km  
50 yr<sup>-1</sup> (no CO<sub>2</sub> effects/with CO<sub>2</sub> effects; “+” denoting wetting). Moreover, in drylands the shifts of  
51 vegetation greenness isolines were found to be significantly coupled with the tracks of aridity  
52 velocity. In future, the aridity velocity in natural protected areas is projected to change from  
53 wetting to drying across RCP2.6, RCP6.0 and RCP8.5 scenarios. When accounting for spatial  
54 distribution of terrestrial taxa (including plants, mammals, birds and amphibians), the global  
55 aridity velocity would be -0.15/-0.02 km yr<sup>-1</sup> (“-” denoting drying; historical), -0.12/-0.15 km yr<sup>-1</sup>  
56 (RCP2.6), -0.36/-0.10 km yr<sup>-1</sup> (RCP6.0) and -0.75/-0.29 km yr<sup>-1</sup> (RCP8.5), with amphibians  
57 particularly negatively impacted. Under all scenarios, aridity velocity shows much higher multi-  
58 directionality than temperature velocity, which is mainly poleward. These results suggest that  
59 aridification risks may significantly influence the distribution of terrestrial species besides  
60 warming impacts and further impact the effectiveness of current protected areas in future,  
61 especially under RCP8.5, which best matches historical CO<sub>2</sub> emissions (1).

62

## 63 **Significance**

64 Under climate change, a point on a map needs to move in some speed and direction to maintain its  
65 current climate niche. We calculated the speeds and directions of aridity shifts across the globe to  
66 approximate species migration in natural-human systems driven by changes in water availability.  
67 We found historically the aridity shifts had driven migration of vegetation greenness isolines in  
68 multiple regions. Most importantly, global drying would be accelerated for terrestrial taxa without  
69 mitigation actions. This would leave some species unable to adapt quickly enough, especially  
70 amphibians, which will suffer the largest aridification speed against plants, birds and mammals.  
71 These findings suggest strong climate mitigation actions are required for the benefit of both  
72 terrestrial biodiversity and human well-being.

73

## 74 **Introduction**

75 There is general agreement that climate warming will be one of the greatest threats to ecosystem  
76 functioning in multiple ways and have substantial impacts on agriculture and human health (2, 3).  
77 As a response to warming, precipitation will also increase but with large spatial heterogeneity (4).  
78 The reshuffling of temperature and precipitation will lead to shift of current or emergence of new  
79 aridity regimes. These changes are predicted to result in complicated biological consequences as  
80 aridity plays an important role in controlling ecosystem dynamics and biogeochemical cycling (5-  
81 8). This is true even in humid regions as the temporal distribution of water availability is usually  
82 not uniform and species have adapted to high water availability. Take tropical ecosystems as an  
83 instance, even modest changes in dry-season length can increase tropical tree mortality (9) and  
84 longer dry seasons can change the population growth rates and structure of tropical bird

85 communities (10). Persistent drying would degrade tropical forest canopies (11) and further have  
86 detrimental effects on biodiversity (12), resulting in functional, taxonomic and phylogenetic  
87 homogenization (13).

88 Many studies have reported warming impacts on species ranges (14, 15), such as their poleward  
89 and uphill shifts. Yet, how aridity changes will drive species shifts has not been well addressed.  
90 Moreover, most previous studies ignored species like different varieties of crops and urban trees  
91 in human managed systems. To date, it is still a grand challenge to assess the shift rate of each of  
92 major species in response to climate forcing, as species-specific migration models are usually built  
93 upon very limited observations in the current climate conditions (16, 17) . Therefore, we use the  
94 generic but ecologically relevant local climate velocity to approximate species migration rates (15,  
95 18), which, through merging spatial and temporal gradients, describes the moving speed and  
96 direction required by a point to maintain its current climate domain. A number of studies have  
97 shown a remarkable correlation between observed terrestrial or marine species shifts and the  
98 velocity of climate warming (19-21). Since ecosystems are individually or jointly controlled by  
99 temperature and water availability, it is expected that ecosystems will also be impacted by the  
100 aridity velocity (derived from aridity index, the ratio of precipitation over potential  
101 evapotranspiration).

102 In this study we evaluate how aridity velocity changes from historical (1979-2016) to future  
103 periods, using the aridity index based on the FAO reference crop potential evapotranspiration  
104 model (AI\_RC) and one of its variants considering vegetation physiological responses to elevated  
105 CO<sub>2</sub> (AI\_CO<sub>2</sub>) developed by Yang *et al.* (22). Following Loarie *et al.* (15) and Diffenbaugh and  
106 Field (14), we focus on a future period (2050-2099) under three Representative Concentration  
107 Pathways (RCP2.6, RCP6.0 and RCP8.5) rather than the whole century as climate change is more  
108 linear within a limited time window, facilitating the assumption of linear trends in estimating  
109 climate velocity. Meanwhile, we also calculate the migration of isolines of vegetation greenness  
110 using satellite observations during 1982-2015 to compare with the concurrent aridity velocity.  
111 Furthermore, we stack the projected aridity velocity to the global distributions of terrestrial  
112 vertebrates and plants to identify areas and taxa of high aridification risks. Because aridity is a  
113 nonlinear function of multiple climatic variables that may have complex interactions, it is  
114 hypothesized that aridity velocity would show non-uniform change under different RCPs.

## 115 **Results**

116 Our results show that during 1979-2016 aridity velocities based on AI\_RC and AI\_CO<sub>2</sub> showed  
117 minor difference in either speed or direction (Figs. 1A and 1B). Aridity velocity exhibited wetting  
118 patterns in Sahel Africa, southwestern Africa, most parts of Asia, and Australia, but drying patterns  
119 in most of North and South America, Europe, Middle East, and west Russia (Figs. 1A and 1B). In  
120 contrast, the changes in the concurrent temperature velocity were more homogeneous (Fig. 1C).  
121 The directions of aridity and temperature velocities showed obvious differences that aridity  
122 velocity (for both AI\_RC and AI\_CO<sub>2</sub>) was more multi-directional at the global scale (*SI Appendix*,  
123 Figs. S1A and S1B) whereas temperature velocity was generally poleward (*SI Appendix*, Fig. S1C).  
124 But at the regional scale aridity velocity showed one uniform direction in some areas, such as in  
125 central U.S. (eastward), Sahel Africa (northward), and northwestern Australia (southward, *SI*  
126 *Appendix*, Figs. S1A and S1B). In future, the aridity velocity tends to be more southward and  
127 eastward (*SI Appendix*, Fig. S1). We also compared the aridity velocities (for AI\_RC) derived from  
128 two different historical climate datasets, i.e., EWEMBI and CRUNCEP, and found they were

129 generally consistent in the spatial patterns (*SI Appendix*, Fig. S2) and had comparable global mean  
130 aridity velocity ( $+0.05 \text{ km yr}^{-1}$  vs.  $+0.01 \text{ km yr}^{-1}$ ), with major differences located in east North  
131 America and east Australia (*SI Appendix*, Fig. S2).

132 <Figure 1 here>

133 Aridity velocities under RCP2.6 generally show a weaker magnitude than those in history, but  
134 there would be more areas with drying velocities in the Southern Hemisphere (Figs. 1D and 1E).  
135 Particularly in Australia, the historical wetting velocities would turn to drying velocities (Figs. 1D  
136 and 1E) directing to coastlines (*SI Appendix*, Figs. S1D and S1E). Higher warming under RCP6.0  
137 would greatly influence the spatial patterns of aridity velocities in the Northern Hemisphere (Figs.  
138 S1G and S1H). The most obvious changes occur in east North America, Europe west and east  
139 Siberia with the sign of aridity velocity reversed (Figs. 1G and 1H). Further warming under  
140 RCP8.5 results in similar spatial patterns of aridity velocities to those under RCP6.0 but with larger  
141 speeds, notably in North America, Europe, east Siberia, South America and southern Africa (Figs.  
142 1J and 1K). Across all the three RCP scenarios, the largest uncertainty (in standard deviation) of  
143 aridity velocity among different climate projections occurs in northern high latitudes, Amazon and  
144 Australia (*SI Appendix*, Fig. S4). The spatial patterns of uncertainty in future aridity velocity are  
145 similar to those of future temperature velocity (*SI Appendix*, Fig. S3) and both are related to  
146 topography (*SI Appendix*, Fig. S4 and Discussion S1).

147 To validate whether the estimated aridity velocities are indicative of vegetation shifts, we  
148 calculated isolines of multi-year mean annual vegetation greenness during 1982-1986 and 2011-  
149 2015, respectively, using the AVHRR NDVI3g v1 dataset. Northern Australia, Sahel and southern  
150 Africa (Fig. 2) were particularly taken as examples, because ecosystems in these regions are water-  
151 dominated and have relatively flat landscapes and low intensity of human activities, such as  
152 irrigation, grazing, wood harvest and deforestation (*SI Appendix*, Figs. S5-S8), which are  
153 particularly beneficial for detecting long-term expansion or contraction of vegetation ranges  
154 induced by aridity changes. The migration distances (*SI Appendix*, Method S1) of NDVI isolines  
155 in the three regions were all significantly correlated with the concurrent aridity velocities (Fig. 2).  
156 Moreover, we also used the AVHRR vegetation continuous fields (VCF) data to investigate  
157 whether the isolines of herbaceous fractions migrated following aridity velocity. The results show  
158 that herbaceous VCF was significantly coupled with aridity velocity in both Sahel ( $r = 0.35$  and  $p$   
159  $< 0.001$ ; *SI Appendix*, Fig. S9B) and southern Africa ( $r = 0.73$  and  $p < 0.001$ ; *SI Appendix*, Fig.  
160 S9C), except in northern Australia. The reason lies in that the responses of vegetation greenness  
161 and vegetation composition to drying or wetting are not always synchronous. In northern Australia,  
162 as wetting during 1982-2015, NDVI generally increased but herbaceous fraction decreased in a  
163 large extent (Fig. 2A and *SI Appendix*, Fig. S9A). Zhang *et al.* (23) also reported this phenomenon  
164 and found the altered rainfall climatology characterized by the increase of heavy rainfall favored  
165 woody vegetation in its competition with herbaceous vegetation.

166 <Figure 2 here>

167 Across the globe, aridity velocity basically obeys a Gaussian distribution, with the mean speed of  
168 AI\_RC based aridity velocity from  $+0.05 \text{ km yr}^{-1}$  in history changing to a drying speed of  $-0.06$   
169  $\text{km yr}^{-1}$  under RCP2.6,  $-0.19 \text{ km yr}^{-1}$  under RCP6.0 and  $-0.42 \text{ km yr}^{-1}$  under RCP8.5, respectively  
170 (Fig. 3A). The corresponding global mean speed of AI\_CO<sub>2</sub> based aridity velocity is  $+0.20 \text{ km yr}^{-1}$ ,  
171  $-0.11 \text{ km yr}^{-1}$ ,  $+0.13 \text{ km yr}^{-1}$ , and  $+0.15 \text{ km yr}^{-1}$ , respectively (Fig. 3E). Beyond the global  
172 average aridity velocities are their specific changes in protected areas, agricultural areas, and urban

173 areas. Protection areas have covered 4~25% of 14 major terrestrial biomes since 2009 (24) and  
174 contain high levels of endemism and small-ranged species. Thus, the changes of aridity velocity  
175 therein are more meaningful than the global average. Our analysis shows the aridity velocity in  
176 protected areas would change from historical  $+0.22 \text{ km yr}^{-1}/+0.36 \text{ km yr}^{-1}$  (no  $\text{CO}_2$  effects/with  
177  $\text{CO}_2$  effects) to  $-0.72 \text{ km yr}^{-1}/-0.24 \text{ km yr}^{-1}$  under RCP8.5 (Fig. 3). The aridity velocity also  
178 manifests a significant change from historical  $-0.56 \text{ km yr}^{-1}/-0.41 \text{ km yr}^{-1}$  to  $-0.65 \text{ km yr}^{-1}/-0.13$   
179  $\text{km yr}^{-1}$  under RCP8.5 in agricultural areas (Fig. 3). In urban areas, the corresponding values are  
180 changing from  $-0.66 \text{ km yr}^{-1}/-0.52 \text{ km yr}^{-1}$  to  $-0.77 \text{ km yr}^{-1}/-0.24 \text{ km yr}^{-1}$  (Fig. 3). Of 18 socio-  
181 economic regions (*SI Appendix*, Fig. S10), protected areas in Brazil, Southern Africa, Central  
182 America and Oceania, agricultural areas in Brazil, Europe, Southern Africa and Central America,  
183 and urban areas in Southern Africa, Europe, and Brazil would experience the largest drying  
184 velocity under RCP8.5 (*SI Appendix*, Fig. S11 and Discussion S2).

185 <Figure 3 here>

186 Since most wetting velocities occur in high latitudes under RCP6.0 and RCP8.5 (Fig. 1) while  
187 most terrestrial species live in low- and high-latitudes, it is necessary to consider the spatial pattern  
188 of terrestrial biodiversity to evaluate potential impacts of changing aridity velocity. When  
189 accounting for richness distribution of terrestrial taxa (including amphibians, birds, mammals and  
190 plants), the global mean aridity velocity changes from historical  $-0.15 \text{ km yr}^{-1}$  to  $-0.12 \text{ km yr}^{-1}$ ,  $-$   
191  $0.36 \text{ km yr}^{-1}$  and  $-0.75 \text{ km yr}^{-1}$  based on AI\_RC or from historical  $-0.02 \text{ km yr}^{-1}$  to  $-0.15 \text{ km yr}^{-1}$ ,  $-$   
192  $0.10 \text{ km yr}^{-1}$  and  $-0.29 \text{ km yr}^{-1}$  based on AI\_CO<sub>2</sub>, respectively, under the three RCPs. Across all  
193 scenarios, taxa in arid regions would experience the largest change in aridity velocity from  
194 historical wetting to future drying (Fig. 4). Taxa in humid regions, which have the highest species  
195 richness, would experience the largest drying velocities under RCP8.5 (Fig. 4). Of all taxa,  
196 amphibians are projected to be most negatively impacted, particularly those in semi-arid, semi-  
197 humid and humid regions under RCP8.5, which tracks closely cumulative CO<sub>2</sub> emissions until  
198 now (1).

199 <Figure 4 here>

200

## 201 Discussion

202 The selected dryness metric is of central importance for aridity projection. AI\_RC is questioned  
203 about overestimation of future dryness as it lacks description of vegetation physiological response  
204 to increasing CO<sub>2</sub> (24, 25). AI\_CO<sub>2</sub> could reproduce CMIP5 projected runoff using the offline  
205 Budyko model over most of the globe through water saving effects of elevated CO<sub>2</sub> (22). But it  
206 must be noted that such water-saving effects are not always persistent. For example, Ukkola *et al.*  
207 (26) reported that elevated CO<sub>2</sub> lead to vegetation greening (through CO<sub>2</sub> fertilization effects) and  
208 more water consumption in sub-humid and semi-arid basins but nonsignificant changes in NDVI  
209 and reductions in evapotranspiration in wet and arid basins across Australia during 1982-2010.  
210 Shimono *et al.* (27) also found that canopy evapotranspiration rate showed much lower  
211 responsiveness than stomatal conductance to open-air CO<sub>2</sub> elevation in rice. These observations  
212 mean that our original AI\_RC formulation is still a reasonable approach in reflecting aridity  
213 changes even in a world of increasing CO<sub>2</sub> concentration. Therefore, AI\_RC and AI\_CO<sub>2</sub> are  
214 simultaneously used in this study to represent a spectrum of possible dryness change in future.

215 Before this effort, little research has focused on the impacts of water availability on species shifts  
216 except few examples (3, 28). However, these exceptional studies still used precipitation to indicate  
217 water availability, which is projected to have an increasing trend opposite to aridity (*SI Appendix*,  
218 Fig. S12). Therefore, previous estimates, based on temperature only or even taking precipitation  
219 into account, when assessing threats of climate change to species shifts and the associated  
220 complexity could be underestimated. From this perspective, our results can provide complementary  
221 references for guiding allocation of limited conservation and adaptation resources.

222 For nature conservation, our estimated aridity velocity can help identify priority regions where  
223 species shifts are influenced by water availability, particularly at the leading edges of species range  
224 and for narrow-ranged species (16). In the identified hotspot areas, conservation actions may focus  
225 on monitoring of immigration or emigration of species and devote to mitigating other disturbances  
226 to aid indigenous species to adapt (16). A more specific example is that Malhi *et al.* (29)  
227 recommended to keep the core northwest Amazon intact as a biological refuge as it hosts the  
228 highest biodiversity and was expected to be the most resistant to climate drying in Amazon based  
229 on previous mid-range (A1B) emission scenarios. Our analysis, however, shows the northwest  
230 Amazon is also projected to experience considerable drying under high emission scenarios (Fig.  
231 1), implying the imperative requirement for conservation actions to mitigate negative impacts of  
232 other factors in this area, such as reducing deforestation and controlling fires. Moreover, our results  
233 show that along coastal areas aridity velocities may point to coastlines (e.g., Australia; *SI Appendix*,  
234 Fig. S1), which means many coastal niches could not find their climate analogs due to the ocean  
235 barrier. In addition, our methodology and results can help the design of protected area networks  
236 and ecological corridors to connect large nature reserves across a continent. An excellent effort  
237 has been conducted in informing the design of the North American protected area network (28).  
238 Batllori *et al.* (28) found the majority of protected areas in North America might be exposed to  
239 high climate velocity and the nearest climatic analogs are outside the current network of protected  
240 areas. Thus, they suggest that conservation plan needs to take advantage of these unprotected  
241 climate refuges and avoid additional threats there beyond climate change.

242 Under all the three RCPs, some regions are projected to experience large aridification risks for  
243 crop species and food production, particularly in rain-fed areas like Southern Africa and Brazil (*SI*  
244 *Appendix*, Fig. S13). Unfortunately, there has been much less research on migration of crop species,  
245 pasture, weeds and insects, etc. in responding to climate velocity. But limited evidence shows that  
246 crop wild relatives could lose up to 91% of their distribution range in protected areas even with  
247 full dispersal under RCP8.5, which is 50% higher than that under RCP2.6 (30). Yield loss risk for  
248 four major crops (wheat, maize, rice and soybeans) has also been reported across moderate to  
249 exceptional drought conditions, particularly in the US, and it could be amplified by high  
250 temperature (31). A very recent study (32) also shows that changes in growing season temperature  
251 had driven migration of the harvested areas of rainfed maize, wheat, rice and soybean during 1973-  
252 2012. For species that are highly sensitive to climate change, the situation could be more severe.  
253 Take coffee for instance, its distribution area is predicted to decrease by about 50% across RCPs,  
254 and the new suitable habitats are far from the current plantation locations and currently occupied  
255 by forests (33). In addition, insects like locusts generally thrive in warm and dry conditions (34),  
256 and their dispersal tracking aridity velocity will no doubt deteriorate food production. Therefore,  
257 as population increases, this might drive agricultural area, irrigated fraction or fertilizer application  
258 to increase to compensate for yield loss, in which case securing food supply would inevitably  
259 conflict with the exacerbated aridity velocity predicted here and environmental externalities of

260 crop production increase. To cope with this situation, crop drought traits and planting structure  
261 should be improved.

262 The drying velocities in urban areas (e.g., in Central America and Europe; *SI Appendix*, Fig. S11)  
263 could greatly influence plants, animals and human health there. Since urban landscapes are usually  
264 highly fragmented, urban trees or forests are unlikely to escape from increased aridity through  
265 spatial shifts. Those tree species that are not suited to low water availability would have to be  
266 substituted by drought-tolerant species or irrigated more often, which will increase maintenance  
267 cost. Animals that depend on original trees or forests may suffer from water scarcity and loss of  
268 feeding source or shelters, and it is difficult for them to cross the urban barrier to migrate elsewhere.  
269 The possible decreased benefits provided by urban trees or forests, such as aesthetic value, tree  
270 shade, and air and water quality, are associated with health problems (35-37). The efforts for  
271 enabling urban areas to adapt to the drying aridity velocity may involve high cost, for example,  
272 infrastructure upgrade fee.

273 It is important to note that climate velocity has its own caveats. Brito-Morales *et al.* (16)  
274 summarized that climate velocity does not include biological information and may be misleading  
275 due to its fractional nature (i.e., ratio of a temporal trend over a spatial gradient). In our analysis,  
276 we also noticed that there existed some aridity velocities of abnormally large magnitudes compared  
277 to their neighboring counterparts (Fig. 2) and the migration of vegetation herbaceous fraction does  
278 not always track climate velocity (*SI Appendix*, Fig. S9A). Therefore, interpretation of changes in  
279 climate velocity and their impacts on biodiversity needs carefulness and fully considering the  
280 exposure, sensitivity, and vulnerability of individual species to climate change, together with their  
281 adaptive capacities (38). However, the magnitude and direction of climate velocity are still  
282 indicative in reflecting expected shifts of species ranges.

283 The spatial and temporal resolutions used in this analysis are also a potential source of uncertainty  
284 in estimating aridity velocity and its impacts on biodiversity. The half-degree climate data doesn't  
285 capture fine-scale topographic differences in climate and may underestimate climate  
286 heterogeneity, especially for urban or mountain areas. Therefore, our results may underestimate  
287 drying velocity in urban areas, as cities usually have higher temperature than neighboring areas  
288 due to the heat island effect. Meanwhile, the annual time step can obscure the signal of intra-annual  
289 variations in water availability, which may have considerable impacts on changes in ecosystem  
290 production and composition (9, 10). However, urban extent data and parameters and climate data  
291 at the half-degree or similar resolutions have been employed to examine interaction between urban  
292 expansion and climate warming (39-41), providing a certain confidence for employing climate  
293 data of the half-degree resolution. Moreover, consideration of long-term changes in aridity velocity  
294 of different seasons would be much more complex as different species or biological processes have  
295 different matching temporal windows (16). Therefore, for this study we still focus on the annual  
296 changes in aridity velocity to keep it simple and leave seasonal climate velocity in future research,  
297 which could be another great story to explore.

298

299

300

301

302



## 303 Materials and Methods

304 **Aridity index.** We used the aridity index, the ratio of precipitation to potential evapotranspiration  
305 (PET), to indicate aridity. PET is estimated through the FAO reference method (42; PET\_RC) and  
306 one of its variants considering surface response to elevated CO<sub>2</sub> (22; PET\_CO<sub>2</sub>), which are  
307 parameterized, respectively, as:

$$308 \quad PET\_RC = \frac{0.408\Delta R_n^* + \gamma \frac{900}{T+273} uD}{\Delta + \gamma(1+0.34u)} \quad (1)$$

$$309 \quad PET\_CO_2 = \frac{0.408\Delta R_n^* + \gamma \frac{900}{T+273} uD}{\Delta + \gamma(1+u(0.34+2.4 \times 10^{-4}([CO_2]-300)))} \quad (2)$$

310 where  $\Delta$  (Pa K<sup>-1</sup>) is the gradient of saturation vapor pressure against temperature,  $R_n^*$  (MJ m<sup>-2</sup> d<sup>-1</sup>)  
311 is the surface available net radiation,  $\gamma$  (Pa K<sup>-1</sup>) is the psychrometric constant,  $T$  (°C) is the air  
312 temperature at 2 m height,  $D$  (Pa) is air vapor pressure deficit,  $u$  (m s<sup>-1</sup>) is the wind speed at 2 m  
313 height, and [CO<sub>2</sub>] is the atmospheric CO<sub>2</sub> concentration. These PET models take into account  
314 changes in available energy, atmospheric humidity and wind speed, and thus can give more  
315 realistic estimation of PET than those methods only considering changes in temperature. During  
316 1979-2016, the daily EWEMBI (40) (E2OBS, WFDEI and ERAI data Merged and Bias-corrected  
317 for ISIMIP) and CRU-NCEP v8.0 dataset (both at a 0.5° resolution), including surface air  
318 temperature, precipitation, surface wind speed, atmospheric pressure, specific humidity and  
319 downward shortwave radiation, were used to estimate daily PET, which then was aggregated to  
320 the annual time-scale to derive annual aridity index. For the future period, according to the RCP  
321 and daily data availability, we used outputs of nine global climate models (including CSIRO-  
322 Mk3.6.0, GFDL-CM3, GFDL-ESM2M, HadGEM2-ES, IPSL-CM5A-LR, MIROC5, MIROC-  
323 ESM-CHEM, MRI-CGCM3, and NorESM1-M) to derive aridity index under RCP2.6, RCP6.0  
324 and RCP8.5. These models can well represent the CMIP5 ensemble in terms of equilibrium climate  
325 sensitivity (3.55 °C vs. 3.22 °C) and transient climate response (1.81 °C vs. 1.84 °C; *SI Appendix*,  
326 Fig. S14). The climate projections have been bias-corrected at a daily timestep and downscaled  
327 referring to EWEMBI. The annual aridity velocities of each of the nine models and the ensemble  
328 mean were adopted to represent the future aridity velocity under the three RCP scenarios and the  
329 corresponding standard deviation.

330 **Aridity velocity.** The local climate velocity approach (15) was used to calculate the moving speed  
331 and direction of aridity. Originally, the approach was introduced to estimate the local migration  
332 velocity of species to maintain their favorable temperatures as global warming shifts temperature  
333 isolines in space. Here we apply the approach to both AI\_RC and AI\_CO<sub>2</sub> instead of to  
334 temperature. Specifically, climate velocity is calculated as  $\frac{Temporal\ slope}{Spatial\ gradient}$ . The temporal slope is

335 derived by linearly regressing the annual time series in a grid cell. The spatial gradient is  
336 determined from a 3×3 window of mean climate during 1979-2016 using the cell-neighborhood  
337 method. The direction of climate velocity depends on both the sign of the temporal slope and the  
338 direction of the spatial gradient. The value of a velocity direction ranges from 0° to 360°, with 180°  
339 towards the straight south. Assuming the aridity velocity has a positive value of 1 km yr<sup>-1</sup> and a  
340 spatial gradient direction of 90° during 2017-2050 and the reference mean climate is calculated  
341 from 1979-2016, the mean aridity in a specific grid cell during 1979-2016 could be found 33 km  
342 to the east by the year 2050, where it has a drier climate than the grid during 1979-2016. In our  
343 analysis, the reference period was set to 1979-2016 to calculate the climatology of aridity index to  
344 derive the spatial gradient.

345 **Land use, region classification, vegetation greenness, herbaceous cover fraction and**  
346 **biodiversity richness.** The protected areas (*SI Appendix*, Fig. S8) were compiled from the World  
347 Database on Protected Areas (WDPA, <https://protectedplanet.net/>), April 2019. The WDPA is the  
348 most comprehensive database of terrestrial and marine protected areas, jointly developed by UN  
349 Environment and the International Union for Conservation of Nature. There are now over 220,000  
350 protected areas and only terrestrial ones are used here. The agricultural areas (including crops and  
351 pastures), urban areas and irrigation fractions in 2018 (*SI Appendix*, Fig. S13) were from the LUH2  
352 v2h (land use harmonization, <http://luh.umd.edu>) data, which has a spatial resolution of  
353  $0.25^{\circ} \times 0.25^{\circ}$  and an annual time-step. The region classification is shown in supplemental material  
354 (*SI Appendix*, Fig. S10). The AVHRR (Advanced Very High Resolution Radiometer) GIMMS  
355 (Global Inventory Monitoring and Modeling System) Normalized Difference Vegetation Index  
356 (NDVI) data (NDVI3g.v1) in 1982-1986 and 2011-2015 was resampled from 1 km to  $0.5^{\circ}$  to show  
357 the spatial shifts of vegetation greenness isolines. The AVHRR vegetation continuous fields (VCF)  
358 data (<https://lpdaac.usgs.gov/products/vcf5kyrv001/>) was also resampled from  $0.05^{\circ}$  to  $0.5^{\circ}$  to  
359 identify the spatial shifts of herbaceous fraction isolines. The plant biodiversity data was developed  
360 by combining spatially explicit models and estimates for native species loss and gains (43) and  
361 was achieved at <http://ecotope.org/anthromes/biodiversity/plants/data/>. The richness data for  
362 amphibians, birds, and mammals were mapped based on >21,000 species and at a spatial grain of  
363  $10 \times 10$  km (44) and available at <https://biodiversitymapping.org/wordpress/index.php/home/>.

364

### 365 **Acknowledgments and Data**

366 This study has been supported by National Science Foundation (grant no. 1903722, 243232 and  
367 1922687) and National Key R&D Program of China (No. 2017YFA0604700), SKLURE Grant  
368 (SKLURE2017-1-6). The ISIMIP research was supported in part by the German Federal Ministry  
369 of Education and Research (BMBF, grant no. 01LS1201A2 and 01LS1711A). This work also has  
370 received funding from the European Union's Horizon 2020 research and innovation programme  
371 under grant agreement no. 641816 "Coordinated Research in Earth Systems and Climate:  
372 Experiments, kNowledge, Dissemination and Outreach" (CRESCENDO) and under grant  
373 agreement 821010 "Cascading climate risks: towards adaptive and resilient European societies"  
374 (CASCADES); The CRU-NCEP data are freely available at  
375 [https://vesg.ipsl.upmc.fr/thredds/catalog/work/p529vio/cruncep/V8\\_1901\\_2016/catalog.html](https://vesg.ipsl.upmc.fr/thredds/catalog/work/p529vio/cruncep/V8_1901_2016/catalog.html).  
376 The bias-corrected GCMs outputs can be accessed from ISIMIP data portal  
377 (<https://www.isimip.org/>) upon request.

378

379

380

381

382

383

384

385

386 **References**

- 387 1. C. R. Schwalm, S. Glendon, P. B. Duffy, RCP8.5 tracks cumulative CO<sub>2</sub> emissions.  
388 *Proceedings of the National Academy of Sciences* **117**, 19656-19657 (2020).
- 389 2. N. S. Diffenbaugh, D. L. Swain, D. Touma, Anthropogenic warming has increased drought  
390 risk in California. *Proceedings of the National Academy of Sciences* **112**, 3931-3936 (2015).
- 391 3. J. VanDerWal *et al.*, Focus on poleward shifts in species distribution underestimates the  
392 fingerprint of climate change. *Nature Climate Change* **3**, 239 (2012).
- 393 4. A. G. Pendergrass, D. L. Hartmann, The atmospheric energy constraint on global-mean  
394 precipitation change. *Journal of Climate* **27**, 757-768 (2014).
- 395 5. J. Bai *et al.*, Satellite-observed vegetation stability in response to changes in climate and  
396 total water storage in Central Asia. *Science of The Total Environment* **659**, 862-871 (2019).
- 397 6. M. Delgado-Baquerizo *et al.*, Decoupling of soil nutrient cycles as a function of aridity in  
398 global drylands. *Nature* **502**, 672 (2013).
- 399 7. C. Wang *et al.*, Aridity threshold in controlling ecosystem nitrogen cycling in arid and  
400 semi-arid grasslands. *Nature Communications* **5**, 4799 (2014).
- 401 8. J. Yang *et al.*, Amazon drought and forest response: Largely reduced forest photosynthesis  
402 but slightly increased canopy greenness during the extreme drought of 2015/2016. *Global*  
403 *change biology* **24**, 1919-1934 (2018).
- 404 9. N. McDowell *et al.*, Drivers and mechanisms of tree mortality in moist tropical forests.  
405 *New Phytologist* **219**, 851-869 (2018).
- 406 10. J. D. Brawn, T. J. Benson, M. Stager, N. D. Sly, C. E. Tarwater, Impacts of changing  
407 rainfall regime on the demography of tropical birds. *Nature Climate Change* **7**, 133-136  
408 (2017).
- 409 11. T. Hilker *et al.*, Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings*  
410 *of the National Academy of Sciences* **111**, 16041-16046 (2014).
- 411 12. L. Gibson *et al.*, Primary forests are irreplaceable for sustaining tropical biodiversity.  
412 *Nature* **478**, 378-381 (2011).
- 413 13. J. Aguirre-Gutiérrez *et al.*, Long-term droughts may drive drier tropical forests towards  
414 increased functional, taxonomic and phylogenetic homogeneity. *Nature communications*  
415 **11**, 1-10 (2020).
- 416 14. N. S. Diffenbaugh, C. B. Field, Changes in Ecologically Critical Terrestrial Climate  
417 Conditions. *Science* **341**, 486-492 (2013).
- 418 15. S. R. Loarie *et al.*, The velocity of climate change. *Nature* **462**, 1052 (2009).
- 419 16. I. Brito-Morales *et al.*, Climate velocity can inform conservation in a warming world.  
420 *Trends in ecology & evolution* **33**, 441-457 (2018).
- 421 17. A. Ordóñez, J. W. Williams, Projected climate reshuffling based on multivariate climate-  
422 availability, climate-analog, and climate-velocity analyses: implications for community  
423 disaggregation. *Climatic Change* **119**, 659-675 (2013).
- 424 18. M. T. Burrows *et al.*, Geographical limits to species-range shifts are suggested by climate  
425 velocity. *Nature* **507**, 492 (2014).
- 426 19. I.-C. Chen, J. K. Hill, R. Ohlemüller, D. B. Roy, C. D. Thomas, Rapid range shifts of  
427 species associated with high levels of climate warming. *Science* **333**, 1024-1026 (2011).
- 428 20. M. L. Pinsky, B. Worm, M. J. Fogarty, J. L. Sarmiento, S. A. Levin, Marine taxa track  
429 local climate velocities. *Science* **341**, 1239-1242 (2013).
- 430 21. J. M. Sunday *et al.*, Species traits and climate velocity explain geographic range shifts in  
431 an ocean-warming hotspot. *Ecology letters* **18**, 944-953 (2015).

- 432 22. Y. Yang, M. L. Roderick, S. Zhang, T. R. McVicar, R. J. Donohue, Hydrologic  
433 implications of vegetation response to elevated CO<sub>2</sub> in climate projections. *Nature Climate*  
434 *Change* **9**, 44-48 (2019).
- 435 23. W. Zhang *et al.*, Ecosystem structural changes controlled by altered rainfall climatology in  
436 tropical savannas. *Nature communications* **10**, 1-7 (2019).
- 437 24. A. Berg, K. A. McColl, No projected global drylands expansion under greenhouse warming.  
438 *Nature Climate Change* **11**, 331-337 (2021).
- 439 25. T. F. Keenan, X. Luo, Y. Zhang, S. Zhou, Ecosystem aridity and atmospheric CO<sub>2</sub>. *Science*  
440 **368**, 251-252 (2020).
- 441 26. A. M. Ukkola *et al.*, Reduced streamflow in water-stressed climates consistent with CO<sub>2</sub>  
442 effects on vegetation. *Nature Climate Change* **6**, 75-78 (2016).
- 443 27. H. Shimono, H. Nakamura, T. Hasegawa, M. Okada, Lower responsiveness of canopy  
444 evapotranspiration rate than of leaf stomatal conductance to open-air CO<sub>2</sub> elevation in rice.  
445 *Global change biology* **19**, 2444-2453 (2013).
- 446 28. E. Batllori, M.-A. Parisien, S. A. Parks, M. A. Moritz, C. Miller, Potential relocation of  
447 climatic environments suggests high rates of climate displacement within the North  
448 American protection network. *Global Change Biology* **23**, 3219-3230 (2017).
- 449 29. Y. Malhi *et al.*, Climate change, deforestation, and the fate of the Amazon. *science* **319**,  
450 169-172 (2008).
- 451 30. J. Aguirre-Gutiérrez, R. van Treuren, R. Hoekstra, T. J. L. van Hintum, Crop wild relatives  
452 range shifts and conservation in Europe under climate change. *Diversity and Distributions*  
453 **23**, 739-750 (2017).
- 454 31. G. Leng, J. Hall, Crop yield sensitivity of global major agricultural countries to droughts  
455 and the projected changes in the future. *Science of The Total Environment* **654**, 811-821  
456 (2019).
- 457 32. L. L. Sloat *et al.*, Climate adaptation by crop migration. *Nature communications* **11**, 1-9  
458 (2020).
- 459 33. C. Bunn, P. Läderach, O. Ovalle Rivera, D. Kirschke, A bitter cup: climate change profile  
460 of global production of Arabica and Robusta coffee. *Climatic Change* **129**, 89-101 (2015).
- 461 34. A. Maxmen, Crop pests: Under attack. *Nature* **501**, S15 (2013).
- 462 35. A. F. Taylor, F. E. Kuo, W. C. Sullivan, Views of Nature and self-discipline: evidence  
463 from inner city children. *Journal of Environmental Psychology* **22**, 49-63 (2002).
- 464 36. R. Ulrich, View through a window may influence recovery from surgery. *Science* **224**, 420-  
465 421 (1984).
- 466 37. Y. You, S. Pan, Urban Vegetation Slows Down the Spread of Coronavirus Disease  
467 (COVID-19) in the United States. *Geophysical Research Letters* **47**, e2020GL089286  
468 (2020).
- 469 38. T. P. Dawson, S. T. Jackson, J. I. House, I. C. Prentice, G. M. Mace, Beyond predictions:  
470 biodiversity conservation in a changing climate. *science* **332**, 53-58 (2011).
- 471 39. K. Huang, X. Li, X. Liu, K. C. Seto, Projecting global urban land expansion and heat island  
472 intensification through 2050. *Environmental Research Letters* **14**, 114037 (2019).
- 473 40. E. S. Krayenhoff, M. Moustauoui, A. M. Broadbent, V. Gupta, M. Georgescu, Diurnal  
474 interaction between urban expansion, climate change and adaptation in US cities. *Nature*  
475 *Climate Change* **8**, 1097-1103 (2018).

476 41. K. W. Oleson, G. B. Bonan, J. Feddema, T. Jackson, An examination of urban heat island  
477 characteristics in a global climate model. *International Journal of Climatology* **31**, 1848-  
478 1865 (2011).

479 42. R. G. Allen, L. S. Pereira, D. Raes, M. Smith, Crop evapotranspiration-Guidelines for  
480 computing crop water requirements-FAO Irrigation and drainage paper 56. *FAO, Rome*  
481 **300**, D05109 (1998).

482 43. E. C. Ellis, E. C. Antill, H. Kreft, All Is not loss: Plant biodiversity in the Anthropocene.  
483 *PLOS ONE* **7**, e30535 (2012).

484 44. C. N. Jenkins, S. L. Pimm, L. N. Joppa, Global patterns of terrestrial vertebrate diversity  
485 and conservation. *Proceedings of the National Academy of Sciences* **110**, E2602-E2610  
486 (2013).

487

488

489

490

491

492

493

494

495

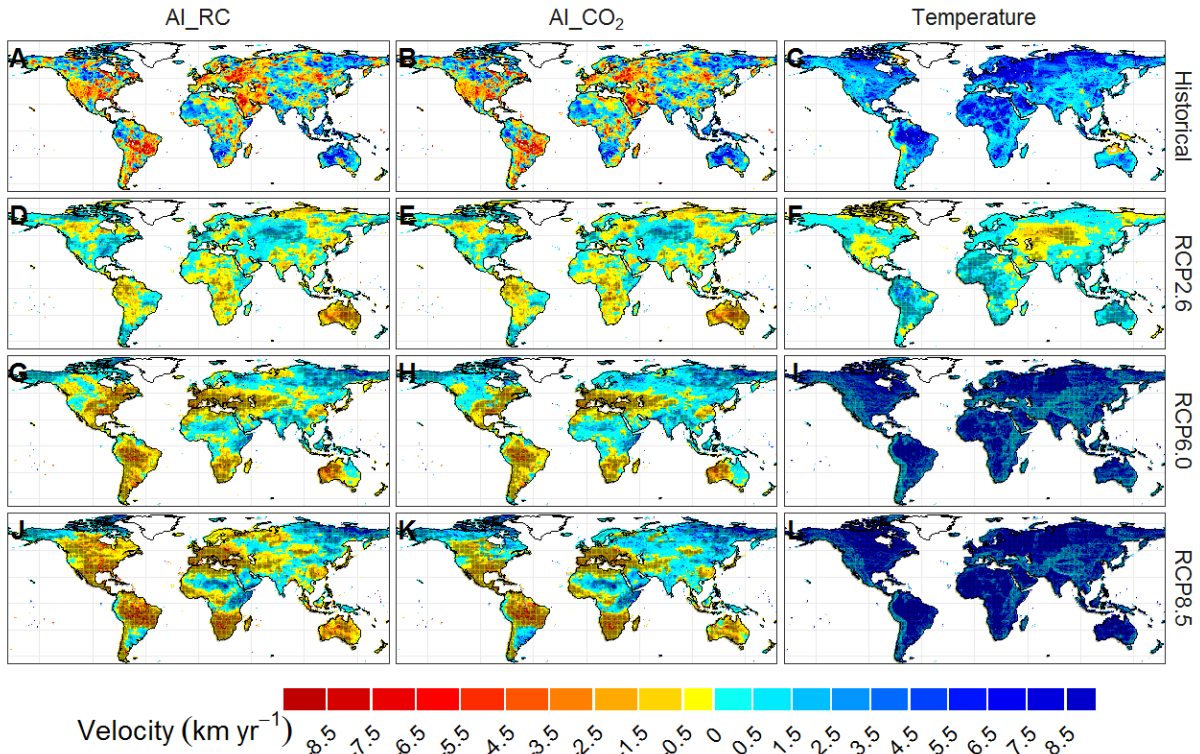
496

497

498

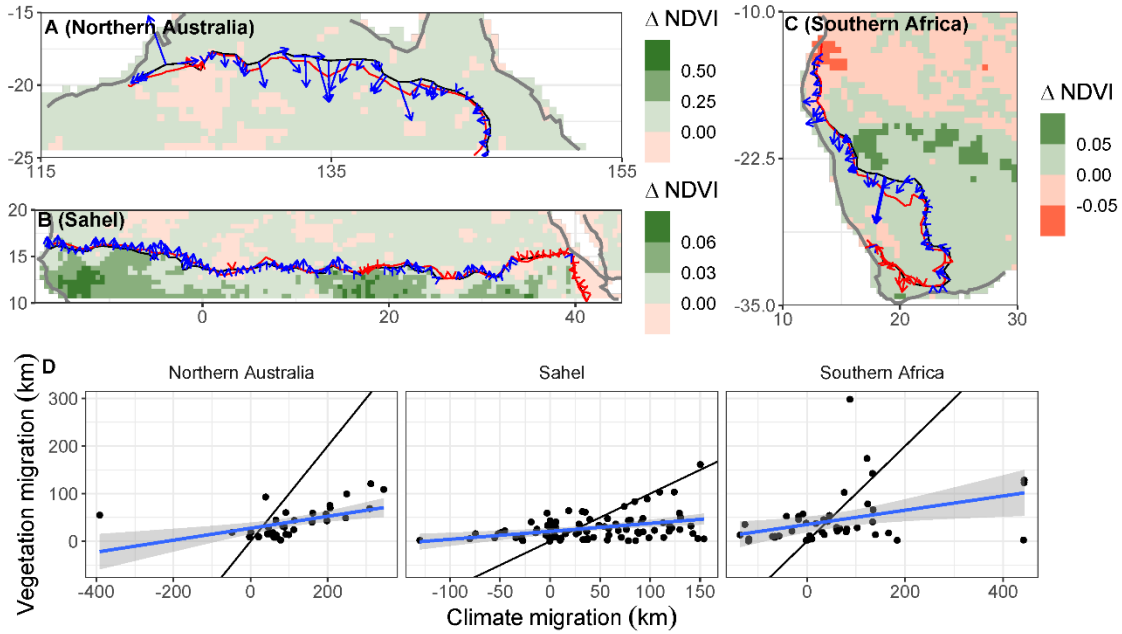
499

500



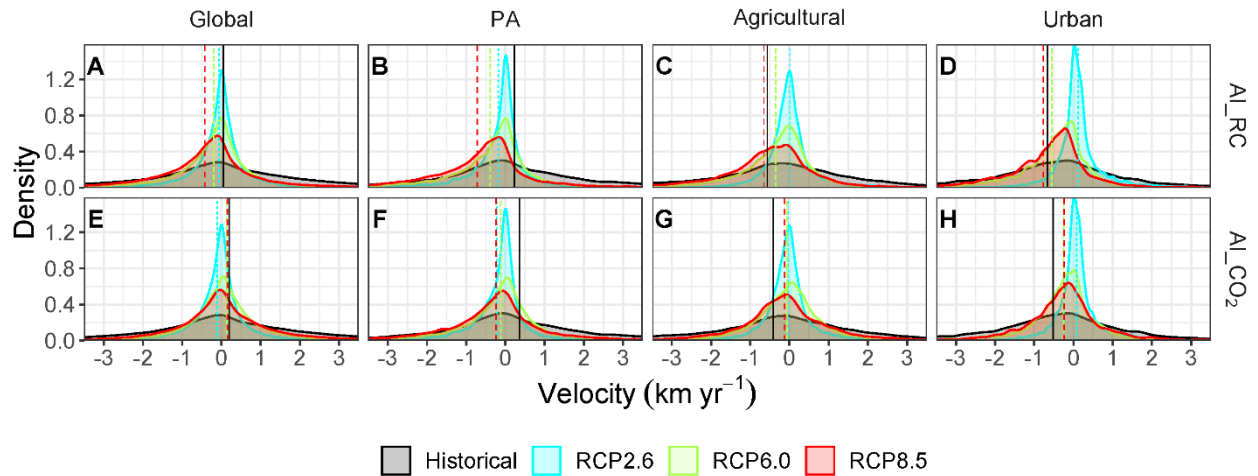
501  
502  
503  
504  
505  
506  
507  
508  
509  
510  
511  
512  
513  
514  
515  
516  
517  
518  
519  
520

**Fig. 1. Speed maps of historical and future aridity and temperature velocities.** The negative sign of speed indicates drying/cooling and the positive sign indicating wetting/warming. The future speed values are the ensemble mean of multiple models. Pixels in each speed map with values outside the 0.5-99.5% quantiles are removed. All velocities are calculated by using the spatial gradient during 1979-2016. Stippling indicates the agreement in the sign of estimated velocities under RCPs across at least seven of nine models (75% of models). AI\_RC refers to the aridity index based on the FAO reference crop potential evapotranspiration model and AI\_CO<sub>2</sub> to one of its variants considering vegetation physiological responses to elevated CO<sub>2</sub>.



521  
 522 **Fig. 2. Coupling between aridity velocity (without considering CO<sub>2</sub> effects) and migration of**  
 523 **NDVI isolines at multiple regions during 1982-2015. (A)** The migration of NDVI isolines  
 524 (NDVI=0.30) in northern Australia during 1982-2015. **(B)** The migration of NDVI isolines  
 525 (NDVI=0.20) in Sahel during 1982-2015. **(C)** The migration of NDVI isolines (NDVI=0.20) in  
 526 southern Africa during 1982-2015. **(A-C)** The black and red lines denote NDVI isolines during  
 527 1982-1986 and during 2011-2015, respectively. The blue arrows indicate the directions of wetting  
 528 velocity and the red arrows indicating directions of drying velocity. The length of arrows  
 529 represents the migration distances of aridity velocity. The aridity velocities are calculated based  
 530 on the spatial gradient during 1982-2015. The pixel values indicate the differences between NDVI  
 531 during 1982-1986 and that during 2011-2015. **(D)** Correlations between migration distances of  
 532 points along the NDVI isolines and the climate migration distances derived using the aridity  
 533 velocity of these points. The black line is 1:1 line. All correlations are statistically significant with  
 534  $r = 0.52$  &  $p < 0.002$ ,  $r = 0.37$  &  $p < 0.001$ , and  $r = 0.36$  &  $p < 0.015$ , respectively.

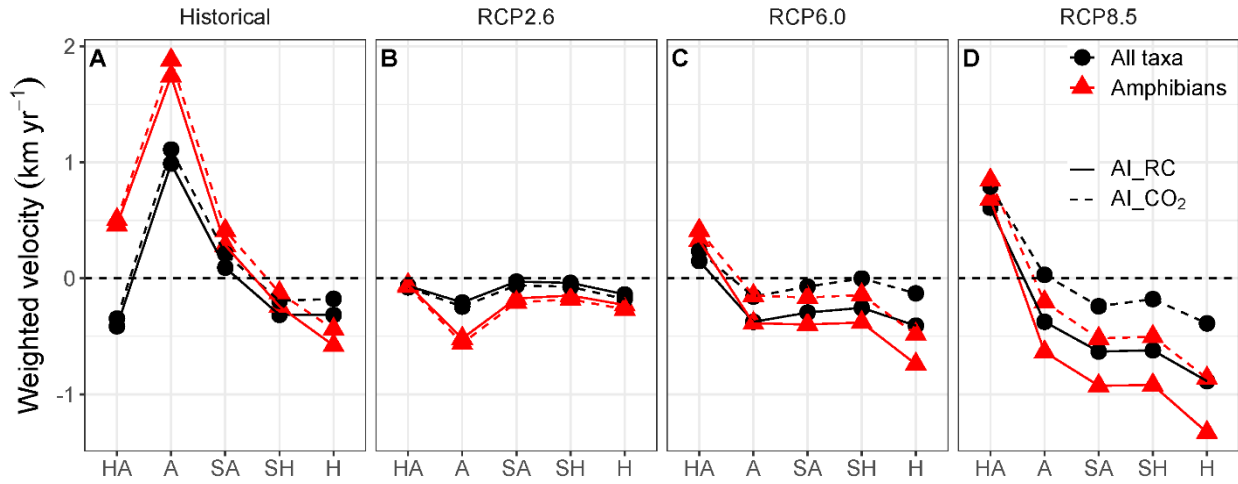
535  
 536  
 537



538  
 539 **Fig. 3. Probability density distribution of aridity velocity based on AI\_RC or AI\_CO<sub>2</sub> across**  
 540 **different land use types. (A-D)** Probability density distribution of speeds of aridity velocity for  
 541 the globe, protected areas (PA), agricultural areas, and urban areas. Negative values indicate drying  
 542 while the positive values indicating wetting. In each land use type, the two sample *t*-test is  
 543 conducted for aridity velocities under different scenarios and the results show they are all  
 544 significantly different ( $p < 0.001$ ). AI\_RC refers to the aridity index based on the FAO reference  
 545 crop potential evapotranspiration model and AI\_CO<sub>2</sub> to one of its variants considering vegetation  
 546 physiological responses to elevated CO<sub>2</sub>.

547  
 548  
 549  
 550  
 551  
 552  
 553  
 554  
 555  
 556  
 557





558  
559

560 **Fig. 4. Aridity velocities for all taxa (amphibians, birds, mammals and plants) and**  
 561 **amphibians under different scenarios.** The mean speed of aridity velocity for each taxon is  
 562 weighted by grid area and species richness, in hyper-arid (HA), arid (A), semi-arid (SA), sub-  
 563 humid (SH), and humid (H) regions. AI\_RC refers to the aridity index based on the FAO reference  
 564 crop potential evapotranspiration model and AI\_CO<sub>2</sub> to one of its variants considering vegetation  
 565 physiological responses to elevated CO<sub>2</sub>.