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1 **Catchment properties and the photosynthetic trait composition of**  
2 **freshwater plant communities**

3 **Short title: Catchments rule aquatic plant traits**

4 **One sentence summary:** The geographical distribution of bicarbonate use in freshwater plants is  
5 controlled by catchment characteristics.

6  
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23 **ABSTRACT**

24 Unlike land plants, photosynthesis in many aquatic plants relies on bicarbonate in addition to  
25 CO<sub>2</sub> to compensate for the low diffusivity and potential depletion of CO<sub>2</sub> in water.  
26 Concentrations of bicarbonate and CO<sub>2</sub> vary greatly with catchment geology. Here we  
27 investigate whether there is a link between these concentrations and the frequency of freshwater  
28 plants possessing the bicarbonate use trait. We show, globally, that the frequency of plant species  
29 with this trait increases with bicarbonate concentration. Regionally however, the frequency of  
30 bicarbonate use is reduced at sites where the CO<sub>2</sub> concentration is substantially above air-  
31 equilibrium consistent with this trait being an adaptation to carbon limitation. Future  
32 anthropogenic changes of bicarbonate and CO<sub>2</sub> concentration may alter the species composition  
33 of freshwater plant communities.

34

35 **MAIN TEXT**

36 The biogeography of terrestrial plants is influenced by climatic factors; primarily air temperature  
37 and precipitation (1). Furthermore, the distribution of biochemical traits such as the two  
38 terrestrial CO<sub>2</sub> concentrating mechanisms, C<sub>4</sub> photosynthesis and Crassulacean Acid  
39 Metabolism, are linked to temperature and water availability (2). Although freshwater  
40 angiosperms evolved from terrestrial ancestors (3), their growth is controlled by light, nutrients  
41 and inorganic carbon (4) rather than water, and therefore the factors influencing their  
42 biogeography is likely to be different. Inorganic carbon potentially limits photosynthesis in  
43 aquatic systems, because the diffusion of CO<sub>2</sub> is 10<sup>4</sup>-fold lower in water than in air.  
44 Consequently, the CO<sub>2</sub> concentration needed to saturate photosynthesis is up to 12 times the air

45 equilibrium concentration (5). Moreover, rapid photosynthesis can reduce CO<sub>2</sub> in water  
46 substantially below air saturation (4).

47

48 In response to carbon limitation, a few aquatic angiosperms evolved the same CO<sub>2</sub> concentrating  
49 mechanisms found in their terrestrial ancestors, but the most frequent mechanism, found in about  
50 half of studied submerged freshwater plants, is the exploitation of bicarbonate (HCO<sub>3</sub><sup>-</sup>; (4,6)),  
51 derived from mineral weathering of soils and rocks in the catchment. Bicarbonate is the  
52 dominant form of inorganic carbon in fresh waters when pH is between ~6.3 and ~10.2, and its  
53 concentration often exceeds that of CO<sub>2</sub> by 10- to 100-fold (6). The ability to use bicarbonate is  
54 present in most taxonomic groups and appears to have evolved independently in cyanobacteria,  
55 eukaryotic algae and vascular aquatic plants (7). This shows the fundamental importance of  
56 bicarbonate use to plant fitness (6); increase of photosynthesis, growth and primary productivity  
57 at higher bicarbonate concentrations has been documented (8-10). However, bicarbonate use is  
58 not ubiquitous, because it involves costs as well as benefits. Costs include energy since it is an  
59 active process (11) and rates of photosynthesis at limiting concentrations of inorganic carbon are  
60 greater in CO<sub>2</sub> users than in bicarbonate users (5,12). Thus, where CO<sub>2</sub> concentrations are  
61 substantially above air saturation, as is often the case in streams, the benefit of bicarbonate use  
62 will be reduced (13). Furthermore, obligate CO<sub>2</sub> users can exploit alternative CO<sub>2</sub> sources in the  
63 air, lake sediment or in the water overlying the sediment (14), allowing continued photosynthesis  
64 without the need to invest in mechanisms required for bicarbonate use.

65

66 We hypothesized that since limitation of photosynthesis by inorganic carbon supply is  
67 widespread in freshwater plants, the relative concentration of bicarbonate and CO<sub>2</sub> at a particular

68 site should determine the proportion of plants that are obligate CO<sub>2</sub> users vs bicarbonate users.  
69 Since geochemical catchment characteristics determine bicarbonate concentration, there should  
70 be broad biogeographical patterns in the proportion of freshwater plants able to use bicarbonate  
71 while at a smaller scale, both the CO<sub>2</sub> and bicarbonate concentrations in lakes and streams might  
72 structure the functional group composition.

73

74 To test these hypotheses, we generated a database of freshwater angiosperms and their ability to  
75 use bicarbonate as an inorganic carbon source, based on data found in the literature. These were  
76 complemented with new data we gathered on 35 species from mainly tropical regions where few  
77 prior data existed (Table S1 and (15)). The resulting 131 species represent approximately 10%  
78 of known species with a submerged life stage (16) and of these, 58 (44%) could use bicarbonate.  
79 In order to quantify the distribution of bicarbonate users vs CO<sub>2</sub> users, we used: i) approximately  
80 1 million geo-referenced plant records; ii) global plant ecoregion species lists; and iii) 963 site  
81 specific plant compositions from northern hemisphere lakes and streams (Fig. S1). In each of the  
82 investigated 963 sites, plant composition was related to measured concentration of CO<sub>2</sub> and  
83 bicarbonate. The geo-referenced plant records and ecoregion species lists were linked to local  
84 bicarbonate concentrations derived from a constructed global map of bicarbonate concentration  
85 (Fig. S2 and (15)).

86

87 In the analyzed lake and stream sites, concentrations of both bicarbonate and CO<sub>2</sub> affected the  
88 occurrence of obligate CO<sub>2</sub> users vs bicarbonate users, but differently within and between lakes  
89 and streams (Fig. 1, and Fig. S3). The chance of observing a bicarbonate user in lakes and  
90 streams correlated directly with concentrations of bicarbonate and CO<sub>2</sub> ( $\Delta\text{Habitat} = -0.82 [-1.64;$

91 0.01] (mean [95% confidence intervals];  $\Delta$  represents the difference between streams and lakes  
92 in parameter estimates at the log(odds) scale, Fig S3)), Fig. 1A). However, with increasing  
93 bicarbonate concentrations, the likelihood of observing a bicarbonate user increased in lakes, but  
94 not in streams ( $\Delta\beta_{\text{Bicarbonate}} = -0.82 [-1.10; -0.54]$  Fig. 1B; see (15) for an explanation of  $\beta$ ).  
95 Moreover, with an increase in  $\text{CO}_2$ , the chance of observing a bicarbonate user decreased in both  
96 habitat types ( $\Delta\beta_{\text{CO}_2} = -0.04 [-0.22; 0.13]$ , Fig. 1C). The present study shows that the  
97 concentration of bicarbonate has a different effect on the proportion of bicarbonate users in lakes  
98 vs streams. Unlike in lakes, no relationship between bicarbonate availability and bicarbonate  
99 users was found in streams. This upholds our hypothesis that where concentrations of  $\text{CO}_2$  are  
100 high, the competitive advantage of using bicarbonate as a carbon source for photosynthesis will  
101 be reduced even if bicarbonate is available.

102

103 Across global plant regions (17), the shifting proportions of bicarbonate users vs obligate  $\text{CO}_2$   
104 users showed distinct spatial patterns (Fig. 2A). Compared to the overall mean, a higher  
105 proportion of bicarbonate users was observed in Africa, temperate Asia, and the northern part of  
106 North America (Fig. 2A). Globally, species utilizing bicarbonate were found in areas with higher  
107 bicarbonate concentrations (bicarbonate users -  $\text{CO}_2$  users =  $0.16 [0.02; 0.30]$  mM; Fig. 2C; see  
108 Fig. 3 for a local example). The proportion of bicarbonate using species increased with  
109 bicarbonate concentrations within ecoregions ( $\beta = 0.14 [0.05; 0.24]$ , (mean [95% confidence  
110 limits]), Fig. 2B). Because catchment geology and geological history shape the distribution of  
111 lakes and rivers, as well as the bicarbonate concentrations in freshwater ecosystems (18,19), they  
112 are the chief determinants of plant distribution in freshwaters.  $\text{CO}_2$  concentrations are largely  
113 regulated by local  $\text{CO}_2$  supersaturated inflow (20) and ecosystem metabolism, making modeling

114 difficult at large spatial scales (19,21). Thus, future models of freshwater CO<sub>2</sub> concentrations  
115 may improve the prediction of plant distributions even further. Although global lake and river  
116 data exist to some extent as annual means (22), given the temporal variability in CO<sub>2</sub>  
117 concentration, the appropriate concentration would be that during the growing season at the  
118 specific site (20).

119

120 Anthropogenic changes as a consequence of deforestation, cultivation of land, application of  
121 nitrate fertilizers and reduced atmospheric acid deposition (23) are causing large scale increases  
122 in bicarbonate concentrations (24,25). The observed increasing bicarbonate concentrations are  
123 expected to cause a severe impact on bicarbonate poor lakes, because higher bicarbonate  
124 concentrations will markedly change species composition (26) by allowing tall, fast growing  
125 bicarbonate users to colonize and suppress smaller species adapted to the use of CO<sub>2</sub> alone in or  
126 near the sediment (27). There is evidence for re-establishment of species that are able to use  
127 bicarbonate, after bicarbonate has increased because of liming (28) or as a result of reduction in  
128 acid deposition (29). Moreover, systematic changes in species composition caused by changes in  
129 CO<sub>2</sub> concentration has also been demonstrated in a river system where the proportion of CO<sub>2</sub>  
130 users declined as CO<sub>2</sub> decreased downstream (13). In contrast, increasing atmospheric CO<sub>2</sub>  
131 concentrations, even if they influence dissolved CO<sub>2</sub>, will have little effect on the abundance of  
132 bicarbonate users, since increases in CO<sub>2</sub> will be small relative to bicarbonate concentrations and  
133 will have little effect on plant photosynthesis rate (30).

134

135 Our study shows that bicarbonate use by aquatic angiosperms is widespread in fresh waters  
136 around the globe, and that the proportion of obligate CO<sub>2</sub> users to bicarbonate users is

137 significantly related to the bicarbonate concentration. Among terrestrial plants, the evolution of  
138 leaf traits and different photosynthetic pathways that enable rapid carbon assimilation and  
139 improved water economy (31) has resulted in global biogeographical patterns that are linked to  
140 variations in climate (32,33). In contrast, for freshwater plants, we show that biogeographical  
141 patterns of bicarbonate use exist and that these are caused by catchment properties that determine  
142 the concentration of bicarbonate and CO<sub>2</sub>. This insight will help evaluate the repercussions of  
143 future changes in concentration of bicarbonate and CO<sub>2</sub> on the biodiversity and ecosystem  
144 function for fresh waters.(34)

145

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220  
221

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234 framed the research questions, and wrote the manuscript, with input from the working group  
235 (A.B.H., J.A., A.B-P., P.B., P.A.C., F.E., T.F., J.H., T.S.J, S.J.M., T.R., L.S. and O.V.). L.L.I.  
236 analyzed the data and prepared the figures. A.B.H and O.P. performed the pH-drift experiments  
237 and together with A.W. searched the literature for bicarbonate uptake in aquatic plants. A.W.,  
238 L.L.I., and L.B-S. assembled the data for the global analysis. F.E., L.B-S, L.S., S.C.M., S.J.M,  
239 J.A., and T.F. assembled the site-specific lake data and the site-specific stream data was  
240 assembled by A. B.-P., P.B., P.A.C., D.G., K.S.-J., T.R, T.S.J., and O.V., A.W., L.L.I., and L. B-  
241 S. prepared the site-specific data for further analysis.

242

243 **Competing interests:** The authors declare no competing interests.

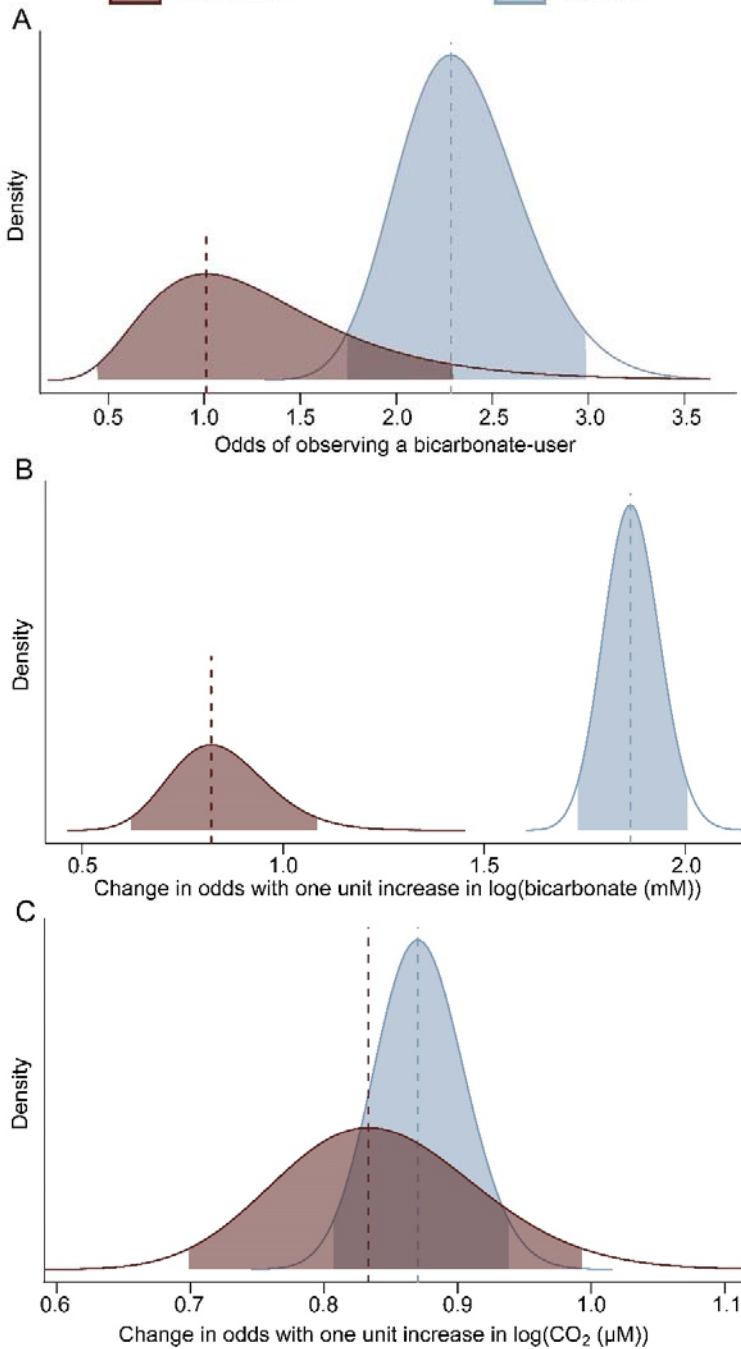
244

245 **Data availability:** All R scripts and cleaned datasets used for this analysis are available at the

246 Dryad Digital Repository.



Streams Lakes

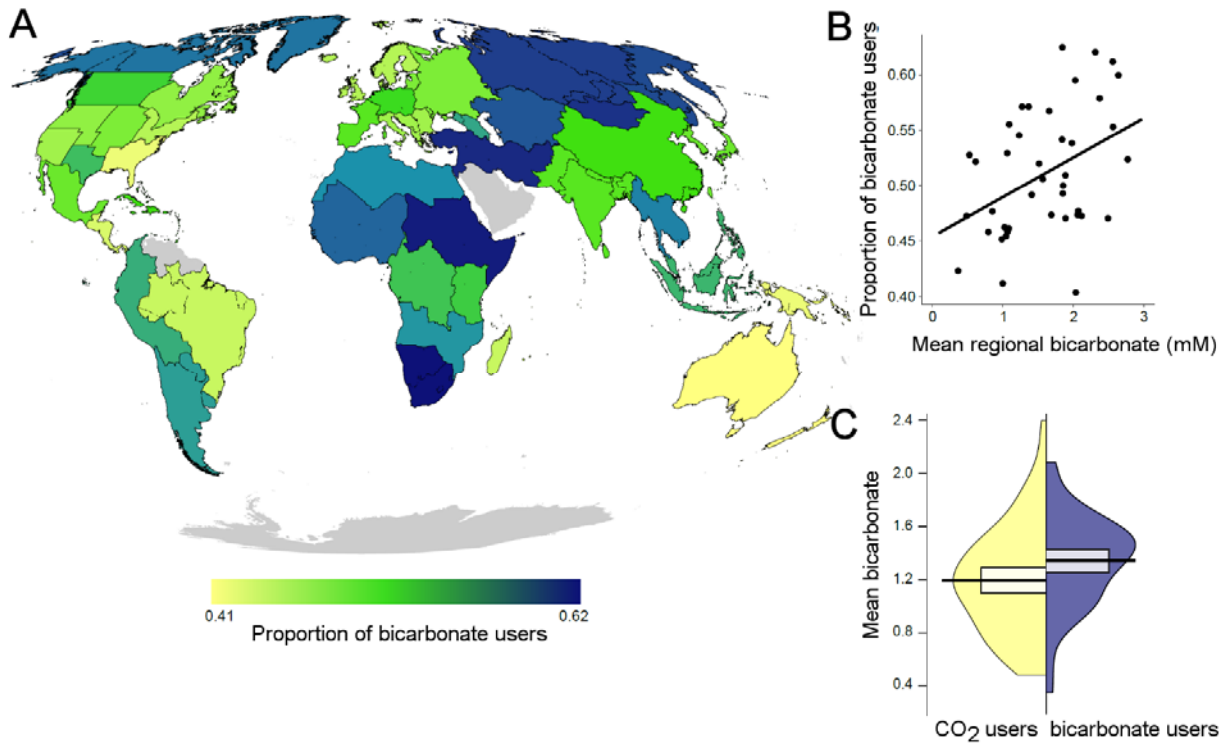


**Fig. 1**

**Bicarbonate use in submerged freshwater plant communities.**

(A) likelihood of observing a bicarbonate user vs a CO<sub>2</sub> user in streams (n=172, red) and lakes (n=791, blue); (B and C), modeled odds of observing a bicarbonate user vs a CO<sub>2</sub> user as a function of bicarbonate (B) and CO<sub>2</sub> (C) concentrations. Values > 1 indicate a higher likelihood (A) or increase in likelihood (B and C) of observing a bicarbonate user vs a CO<sub>2</sub> user with a one unit increase in bicarbonate (B) and CO<sub>2</sub> concentrations (C). The dotted vertical lines show mean estimates and shaded areas the 95% confidence limits around the mean.

283



284

285

286

**Fig. 2**

287 **Global relationship between bicarbonate and the proportion of bicarbonate users in**

288 **freshwater plants.** (A) Proportion of bicarbonate using species across 52 plant ecoregions. Grey

289 areas indicate regions where information on bicarbonate use in local plants is not available. (B)

290 Relationship between mean bicarbonate concentration in plant regions and frequency of

291 bicarbonate users. The line represents the mean proportion of bicarbonate users. (C) Density

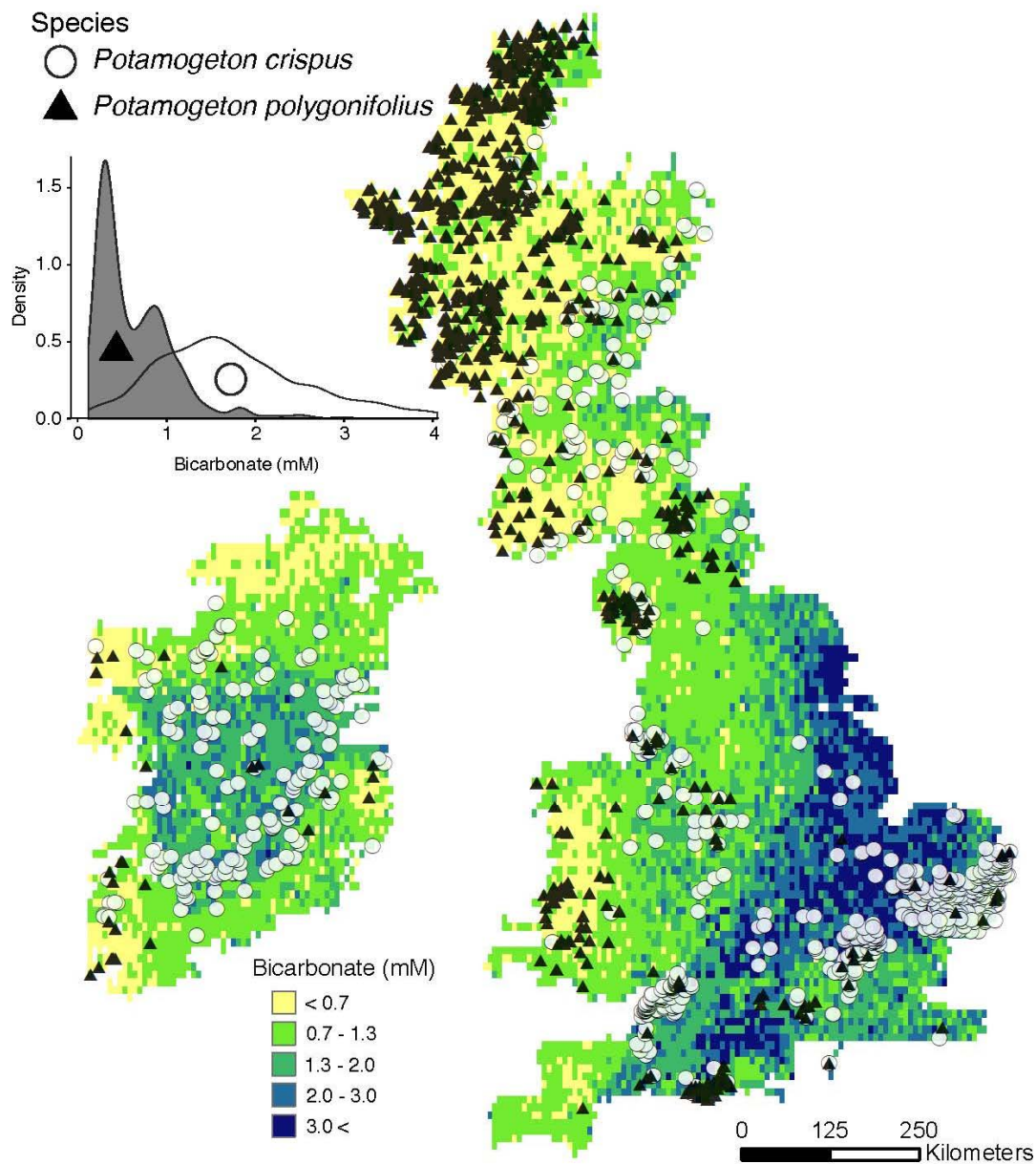
292 plots of bicarbonate preferences for bicarbonate users (n = 57) and obligate CO<sub>2</sub> users (n = 72).

293 The central horizontal black line represents the mean and the boxes indicate the 95% confidence

294 intervals around the mean.

295

296



297  
298  
299

**Fig. 3**

300 **Steep gradients in bicarbonate concentrations and spatial separation in species distribution**  
 301 **in the British Isles.** Distribution of two pondweed species with contrasting bicarbonate use in  
 302 the British Isles. *Potamogeton polygonifolius* (obligate CO<sub>2</sub> user, black triangles) is found in  
 303 areas with lower bicarbonate concentrations compared to *Potamogeton crispus* (bicarbonate user,  
 304 white circles). The top left insert shows the density distribution of the two species across

305 bicarbonate concentrations. Bicarbonate concentrations are from the global bicarbonate map  
306 (Fig. S2) and species data were extracted from the geo-referenced plant occurrences (15).

307

### 308 **Supplementary Materials**

309 Materials and Methods (15).

310 References (34-90).

311 Fig. S1 - Site-specific observations of bicarbonate use.

312 Fig. S2 - Global bicarbonate map.

313 Fig. S3 - The probability of observing bicarbonate use in a species at 963 study sites.

314 Fig. S4 - Overview of *in situ* lake bicarbonate measurements.

315 Fig. S5 - Variable importance plot of the Random Forest modelling global bicarbonate  
316 concentrations.

317 Fig. S6 - Partial dependence plots of the eight variables used to model global bicarbonate  
318 concentrations.

319 Fig. S7 - Histogram of taxonomic distinctness for 1000 random subsamples of a fixed number of  
320 131 species drawn from a common species pool.

321 Table S1 - List of freshwater angiosperms and their trait of inorganic carbon use.