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ABSTRACT

Unlike land plants, photosynthesis in many aquatic plants relies on bicarbonate in addition to CO_2 to compensate for the low diffusivity and potential depletion of CO_2 in water. Concentrations of bicarbonate and CO_2 vary greatly with catchment geology. Here we investigate whether there is a link between these concentrations and the frequency of freshwater plants possessing the bicarbonate use trait. We show, globally, that the frequency of plant species with this trait increases with bicarbonate concentration. Regionally however, the frequency of bicarbonate use is reduced at sites where the CO_2 concentration is substantially above air-equilibrium consistent with this trait being an adaptation to carbon limitation. Future anthropogenic changes of bicarbonate and CO_2 concentration may alter the species composition of freshwater plant communities.

MAIN TEXT

The biogeography of terrestrial plants is influenced by climatic factors; primarily air temperature and precipitation (*1*). Furthermore, the distribution of biochemical traits such as the two terrestrial CO_2 concentrating mechanisms, C_4 photosynthesis and Crassulacean Acid Metabolism, are linked to temperature and water availability (*2*). Although freshwater angiosperms evolved from terrestrial ancestors (*3*), their growth is controlled by light, nutrients and inorganic carbon (*4*) rather than water, and therefore the factors influencing their biogeography is likely to be different. Inorganic carbon potentially limits photosynthesis in aquatic systems, because the diffusion of CO_2 is 10^4-fold lower in water than in air. Consequently, the CO_2 concentration needed to saturate photosynthesis is up to 12 times the air equilibrium concentration (*5*). Moreover, rapid photosynthesis can reduce CO_2 in water substantially below air saturation (*4*).

In response to carbon limitation, a few aquatic angiosperms evolved the same CO_2 concentrating mechanisms found in their terrestrial ancestors, but the most frequent mechanism, found in about half of studied submerged freshwater plants, is the exploitation of bicarbonate (HCO_3^-; (*4,6*)), derived from mineral weathering of soils and rocks in the catchment. Bicarbonate is the dominant form of inorganic carbon in fresh waters when pH is between ~6.3 and ~10.2, and its concentration often exceeds that of CO_2 by 10- to 100-fold (*6*). The ability to use bicarbonate is present in most taxonomic groups and appears to have evolved independently in cyanobacteria, eukaryotic algae and vascular aquatic plants (*7*). This shows the fundamental importance of bicarbonate use to plant fitness (*6*); increase of photosynthesis, growth and primary productivity at higher bicarbonate concentrations has been documented (*8-10*). However, bicarbonate use is not ubiquitous, because it involves costs as well as benefits. Costs include energy since it is an active process (*11*) and rates of photosynthesis at limiting concentrations of inorganic carbon are greater in CO_2 users than in bicarbonate users (*5,12*). Thus, where CO_2 concentrations are substantially above air saturation, as is often the case in streams, the benefit of bicarbonate use will be reduced (*13*). Furthermore, obligate CO_2 users can exploit alternative CO_2 sources in the air, lake sediment or in the water overlying the sediment (*14*), allowing continued photosynthesis without the need to invest in mechanisms required for bicarbonate use.

We hypothesized that since limitation of photosynthesis by inorganic carbon supply is widespread in freshwater plants, the relative concentration of bicarbonate and CO_2 at a particular site should determine the proportion of plants that are obligate CO_2 users *vs* bicarbonate users. Since geochemical catchment characteristics determine bicarbonate concentration, there should be broad biogeographical patterns in the proportion of freshwater plants able to use bicarbonate while at a smaller scale, both the CO_2 and bicarbonate concentrations in lakes and streams might structure the functional group composition.

To test these hypotheses, we generated a database of freshwater angiosperms and their ability to use bicarbonate as an inorganic carbon source, based on data found in the literature. These were complemented with new data we gathered on 35 species from mainly tropical regions where few prior data existed (Table S1 and (*15*)). The resulting 131 species represent approximately 10% of known species with a submerged life stage (*16*) and of these, 58 (44%) could use bicarbonate. In order to quantify the distribution of bicarbonate users *vs* CO_2 users, we used: i) approximately 1 million geo-referenced plant records; ii) global plant ecoregion species lists; and iii) 963 site specific plant compositions from northern hemisphere lakes and streams (Fig. S1). In each of the investigated 963 sites, plant composition was related to measured concentration of CO_2 and bicarbonate. The geo-referenced plant records and ecoregion species lists were linked to local bicarbonate concentrations derived from a constructed global map of bicarbonate concentration (Fig. S2 and (*15*)).

In the analyzed lake and stream sites, concentrations of both bicarbonate and CO_2 affected the occurrence of obligate CO_2 users *vs* bicarbonate users, but differently within and between lakes and streams (Fig. 1, and Fig. S3). The chance of observing a bicarbonate user in lakes and streams correlated directly with concentrations of bicarbonate and CO_2 (ΔHabitat = -0.82 [-1.64;

0.01] (mean [95% confidence intervals]; Δ represents the difference between streams and lakes in parameter estimates at the log(odds) scale, Fig S3)), Fig. 1A). However, with increasing bicarbonate concentrations, the likelihood of observing a bicarbonate user increased in lakes, but not in streams ($\Delta\beta_{Bicarbonate}$ = -0.82 [-1.10; -0.54] Fig. 1B; see (*15*) for an explanation of β). Moreover, with an increase in CO_2, the chance of observing a bicarbonate user decreased in both habitat types ($\Delta\beta_{CO2}$= -0.04 [-0.22; 0.13], Fig. 1C). The present study shows that the concentration of bicarbonate has a different effect on the proportion of bicarbonate users in lakes *vs* streams. Unlike in lakes, no relationship between bicarbonate availability and bicarbonate users was found in streams. This upholds our hypothesis that where concentrations of CO_2 are high, the competitive advantage of using bicarbonate as a carbon source for photosynthesis will be reduced even if bicarbonate is available.

Across global plant regions (*17*), the shifting proportions of bicarbonate users *vs* obligate CO_2 users showed distinct spatial patterns (Fig. 2A). Compared to the overall mean, a higher proportion of bicarbonate users was observed in Africa, temperate Asia, and the northern part of North America (Fig. 2A). Globally, species utilizing bicarbonate were found in areas with higher bicarbonate concentrations (bicarbonate users - CO_2 users = 0.16 [0.02; 0.30] mM; Fig. 2C; see Fig. 3 for a local example). The proportion of bicarbonate using species increased with bicarbonate concentrations within ecoregions (β = 0.14 [0.05; 0.24], (mean [95% confidence limits]), Fig. 2B). Because catchment geology and geological history shape the distribution of lakes and rivers, as well as the bicarbonate concentrations in freshwater ecosystems (*18,19*), they are the chief determinants of plant distribution in freshwaters. CO_2 concentrations are largely regulated by local CO_2 supersaturated inflow (*20*) and ecosystem metabolism, making modeling difficult at large spatial scales (*19,21*). Thus, future models of freshwater CO_2 concentrations may improve the prediction of plant distributions even further. Although global lake and river data exist to some extent as annual means (*22*), given the temporal variability in CO_2 concentration, the appropriate concentration would be that during the growing season at the specific site (*20*).

Anthropogenic changes as a consequence of deforestation, cultivation of land, application of nitrate fertilizers and reduced atmospheric acid deposition (*23*) are causing large scale increases in bicarbonate concentrations (*24,25*). The observed increasing bicarbonate concentrations are expected to cause a severe impact on bicarbonate poor lakes, because higher bicarbonate concentrations will markedly change species composition (*26*) by allowing tall, fast growing bicarbonate users to colonize and suppress smaller species adapted to the use of CO_2 alone in or near the sediment (*27*). There is evidence for re-establishment of species that are able to use bicarbonate, after bicarbonate has increased because of liming (*28*) or as a result of reduction in acid deposition (*29*). Moreover, systematic changes in species composition caused by changes in CO_2 concentration has also been demonstrated in a river system where the proportion of CO_2 users declined as CO_2 decreased downstream (*13*). In contrast, increasing atmospheric CO_2 concentrations, even if they influence dissolved CO_2, will have little effect on the abundance of bicarbonate users, since increases in CO_2 will be small relative to bicarbonate concentrations and will have little effect on plant photosynthesis rate (*30*).

Our study shows that bicarbonate use by aquatic angiosperms is widespread in fresh waters around the globe, and that the proportion of obligate CO_2 users to bicarbonate users is significantly related to the bicarbonate concentration. Among terrestrial plants, the evolution of leaf traits and different photosynthetic pathways that enable rapid carbon assimilation and improved water economy (*31*) has resulted in global biogeographical patterns that are linked to variations in climate (*32*,*33*). In contrast, for freshwater plants, we show that biogeographical patterns of bicarbonate use exist and that these are caused by catchment properties that determine the concentration of bicarbonate and CO_2. This insight will help evaluate the repercussions of future changes in concentration of bicarbonate and CO_2 on the biodiversity and ecosystem function for fresh waters.(*34*)

REFERENCES AND NOTES

1. M. C. Peel, B. L. Finlayson, T. A. McMahon, Updated world map of the Köppen-Geiger climate classification. *Hydro. Earth Syst. Sci. Discus.* **4**, 439-473 (2007).
2. C. J. Still, J. A. Berry, G. J. Collatz, R. S. DeFries, Global distribution of C_3 and C_4 vegetation: carbon cycle implications. *Global Biogeochem. Cycles* **17**, 6-1 (2003).
3. D. H. Les, N. P. Tippery, In time and with water ... the systematics of alismatid monocotyledons. *Early Events Monocot Evol.* **83**, 118-164 (2013).
4. T. V. Madsen, S. C. Maberly, Diurnal variation in light and carbon limitation of photosynthesis by two species of submerged freshwater macrophyte with a differential ability to use bicarbonate. *Freshw. Biol.* **26**, 175-187 (1991).
5. S. C. Maberly, T. V. Madsen, Affinity for CO_2 in relation to the ability of freshwater macrophytes to use HCO_3^-. *Func. Ecol.* **12**, 99-106 (1998).
6. S. C. Maberly, B. Gontero, Ecological imperatives for aquatic CO_2-concentrating mechanisms. *J. Exp. Bot.* **68**, 3797-3814 (2017).
7. M. Giordano, J. Beardall, J. A. Raven, CO_2 concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution. *Annu. Rev. Plant Biol.* **56**, 99-131 (2005).
8. K. Sand-Jensen, H. Frost-Christensen, Photosynthesis of amphibious and obligately submerged plants in CO_2-rich lowland streams. *Oecologia* **117**, 31-39 (1998).
9. M. R. Andersen, T. Kragh, K. Sand-Jensen, Extreme diel oxygen and carbon cycles in shallow vegetated lakes. *Proc. R. Soc. B Biol. Sci.* **284**, 20171427 (2017).
10. T. V. Madsen, K. Sand-Jensen, Photosynthetic capacity, bicarbonate affinity and growth of *Elodea canadensis* exposed to different concentrations of inorganic carbon. *Oikos* **50**, 176-182 (1987).
11. J. A. Raven, J. Beardall, M. Giordano, Energy costs of carbon dioxide concentrating mechanisms in aquatic organisms. *Photosynth. Res.* **121**, 111-124 (2014).

12. T. V. Madsen, S. C. Maberly, High internal resistance to CO_2 uptake by submerged macrophytes that use HCO_3^-: measurements in air, nitrogen and helium. *Photosynth. Res.* **77**, 183-190 (2003).
13. S. C. Maberly, S. A. Berthelot, A. W. Stott, B. Gontero, Adaptation by macrophytes to inorganic carbon down a river with naturally variable concentrations of CO_2. *J. Plant. Physiol.* **172**, 120-127 (2015).
14. T. V. Madsen, K. Sand-Jensen, Photosynthetic carbon assimilation in aquatic macrophytes. *Aquat. Bot.* **41**, 5-40 (1991).
15. See supplementary materials.
16. K. Murphy *et al.*, World distribution, diversity and endemism of aquatic macrophytes. *Aquat. Bot.* **158**, 103127 (2019).
17. R. K. Brummitt, F. Pando, S. Hollis, N. A. Brummitt, *World geographical scheme for recording plant distributions*. (International Working Group on Taxonomic Databases for Plant Sciences (TDWG …, 2001).
18. R. Lauerwald, J. Hartmann, N. Moosdorf, S. Kempe, P. A. Raymond, What controls the spatial patterns of the riverine carbonate system?—A case study for North America. *Chem. Geol.* **337**, 114-127 (2013).
19. R. Marcé *et al.*, Carbonate weathering as a driver of CO_2 supersaturation in lakes. *Nat. Geosci.* **8**, 107-111 (2015).
20. S. C. Maberly, P. A. Barker, A. W. Stott, M. M. De Ville, Catchment productivity controls CO_2 emissions from lakes. *Nat. Clim. Change* **3**, 391 (2013).
21. L. J. Tranvik *et al.*, Lakes and reservoirs as regulators of carbon cycling and climate. *Limnol. Oceanogr.* **54**, 2298-2314 (2009).
22. P. A. Raymond *et al.*, Global carbon dioxide emissions from inland waters. *Nature* **503**, 355 (2013).
23. P. A. Raymond, S. K. Hamilton, Anthropogenic influences on riverine fluxes of dissolved inorganic carbon to the oceans. *Limnol. Oceanogr. Let.* **3**, 143-155 (2018).
24. P. A. Raymond, N.-H. Oh, R. E. Turner, W. Broussard, Anthropogenically enhanced fluxes of water and carbon from the Mississippi River. *Nature* **451**, 449 (2008).
25. J. L. Stoddard *et al.*, Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **401**, 575 (1999).
26. O. Vestergaard, K. Sand-Jensen, Alkalinity and trophic state regulate aquatic plant distribution in Danish lakes. *Aquat. Bot.* **67**, 85-107 (2000).
27. K. Sand-Jensen, M. Sondergaard, Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Internationale Revue Der Gesamten Hydrobiologie* **66**, 529-552 (1981).
28. T. E. Brandrud, Effects of liming on aquatic macrophytes, with emphasis on Scandinavia. *Aquat. Bot.* **73**, 395-404 (2002).
29. D. T. Monteith *et al.*, Biological responses to the chemical recovery of acidified fresh waters in the UK. *Environ. Pollut.* **137**, 83-101 (2005).
30. G. Bowes, Facing the inevitable: plants and increasing atmospheric CO_2. *Annu. Rev. Plant Biol.* **44**, 309-332 (1993).
31. I. J. Wright *et al.*, The worldwide leaf economics spectrum. *Nature* **428**, 821-827 (2004).

32. H. Lambers, F. S. Chapin Iii, T. L. Pons, *Plant physiological ecology*. (Springer Science & Business Media, 2008).
33. I. J. Wright *et al.*, Global climatic drivers of leaf size. *Science* **357**, 917-921 (2017).
34. L. L. Iversen. (2019).

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Competing interests: The authors declare no competing interests.

Data availability: All R scripts and cleaned datasets used for this analysis are available at the Dryad Digital Repository.

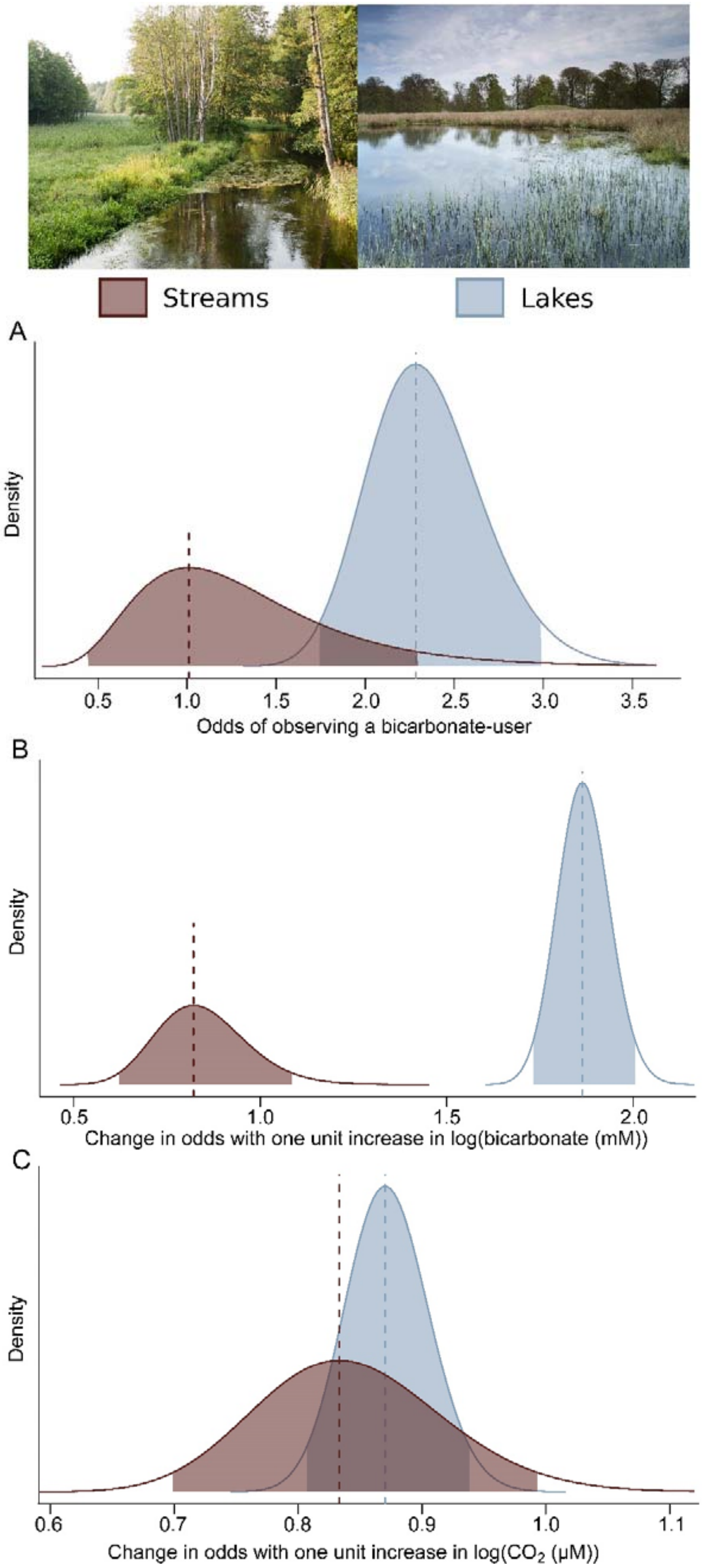

Fig. 1

Bicarbonate use in submerged freshwater plant communities. (**A**) likelihood of observing a bicarbonate user *vs* a CO_2 user in streams (n=172, red) and lakes (n=791, blue); (**B** and **C**)**,** modeled odds of observing a bicarbonate user *vs* a CO_2 user as a function of bicarbonate (**B**) and CO_2 (**C**) concentrations. Values > 1 indicate a higher likelihood (**A**) or increase in likelihood (**B** and **C**) of observing a bicarbonate user *vs* a CO_2 user with a one unit increase in bicarbonate (**B**) and CO_2 concentrations (**C**). The dotted vertical lines show mean estimates and shaded areas the 95% confidence limits around the mean.

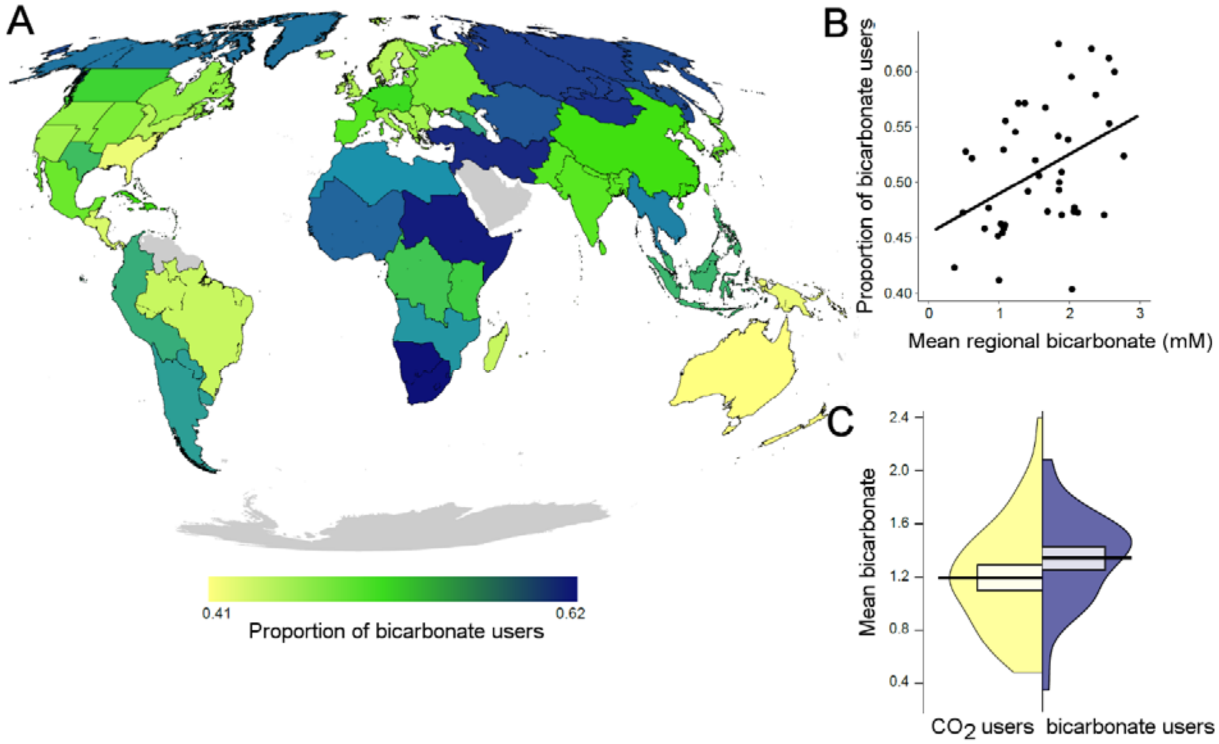

Fig. 2

Global relationship between bicarbonate and the proportion of bicarbonate users in freshwater plants. (**A**) Proportion of bicarbonate using species across 52 plant ecoregions. Grey areas indicate regions where information on bicarbonate use in local plants is not available. (**B**) Relationship between mean bicarbonate concentration in plant regions and frequency of bicarbonate users. The line represents the mean proportion of bicarbonate users. (**C**) Density plots of bicarbonate preferences for bicarbonate users (n = 57) and obligate CO_2 users (n = 72). The central horizontal black line represents the mean and the boxes indicate the 95% confidence intervals around the mean.

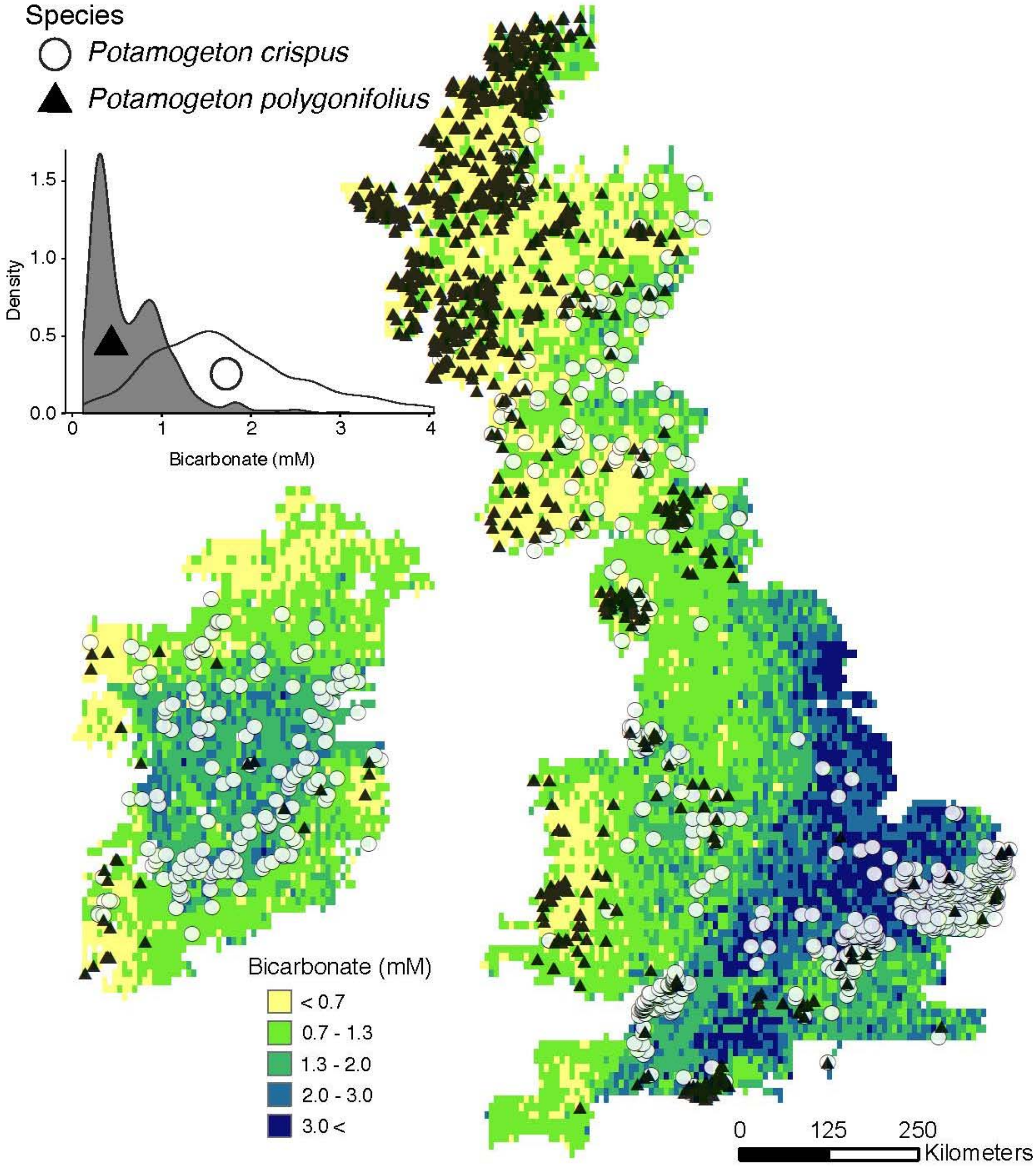

Fig. 3

Steep gradients in bicarbonate concentrations and spatial separation in species distribution in the British Isles. Distribution of two pondweed species with contrasting bicarbonate use in the British Isles. *Potamogeton polygonifolius* (obligate CO_2 user, black triangles) is found in areas with lower bicarbonate concentrations compared to *Potamogeton crispus* (bicarbonate user, white circles). The top left insert shows the density distribution of the two species across bicarbonate concentrations. Bicarbonate concentrations are from the global bicarbonate map (Fig. S2) and species data were extracted from the geo-referenced plant occurrences (*15*).

Supplementary Materials

Materials and Methods (*15*).

References (*34*-*90*).

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

Fig. S2 - Global bicarbonate map.

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

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

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

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

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

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