

# The increasing importance of atmospheric demand for ecosystem water and carbon fluxes

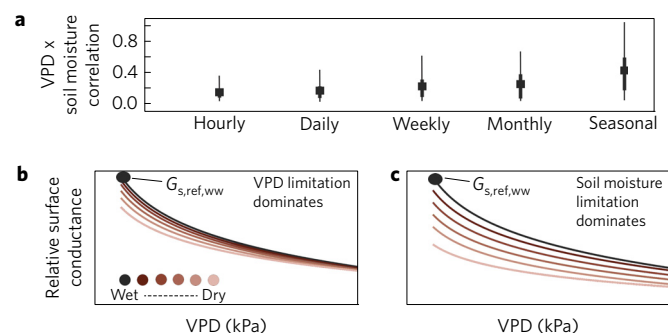
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**Soil moisture supply and atmospheric demand for water independently limit—and profoundly affect—vegetation productivity and water use during periods of hydrologic stress<sup>1–4</sup>. Disentangling the impact of these two drivers on ecosystem carbon and water cycling is difficult because they are often correlated, and experimental tools for manipulating atmospheric demand in the field are lacking. Consequently, the role of atmospheric demand is often not adequately factored into experiments or represented in models<sup>5–7</sup>. Here we show that atmospheric demand limits surface conductance and evapotranspiration to a greater extent than soil moisture in many biomes, including mesic forests that are of particular importance to the terrestrial carbon sink<sup>8,9</sup>. Further, using projections from ten general circulation models, we show that climate change will increase the importance of atmospheric constraints to carbon and water fluxes in all ecosystems. Consequently, atmospheric demand will become increasingly important for vegetation function, accounting for >70% of growing season limitation to surface conductance in mesic temperate forests. Our results suggest that failure to consider the limiting role of atmospheric demand in experimental designs, simulation models and land management strategies will lead to incorrect projections of ecosystem responses to future climate conditions.**

Ecosystem moisture stress is often characterized by changes in soil water availability<sup>10,11</sup>. Declining soil moisture impedes the movement of water to evaporating sites at the soil or leaf surface<sup>12</sup>, reducing the surface conductance to water vapour ( $G_s$ )—a key determinant of carbon and water cycling—and thereby evapotranspiration (ET). However, atmospheric demand for water, which is directly related to the atmospheric vapour pressure deficit (VPD), also affects  $G_s$  and ET. Plants close their stomata to prevent excessive water loss when VPD is high<sup>13–16</sup> and thus, increases in VPD during periods of hydrologic stress represent an independent constraint on plant carbon uptake and water use in ecosystems.

While the plant physiological community has long recognized the critical role of VPD in determining plant functioning, VPD

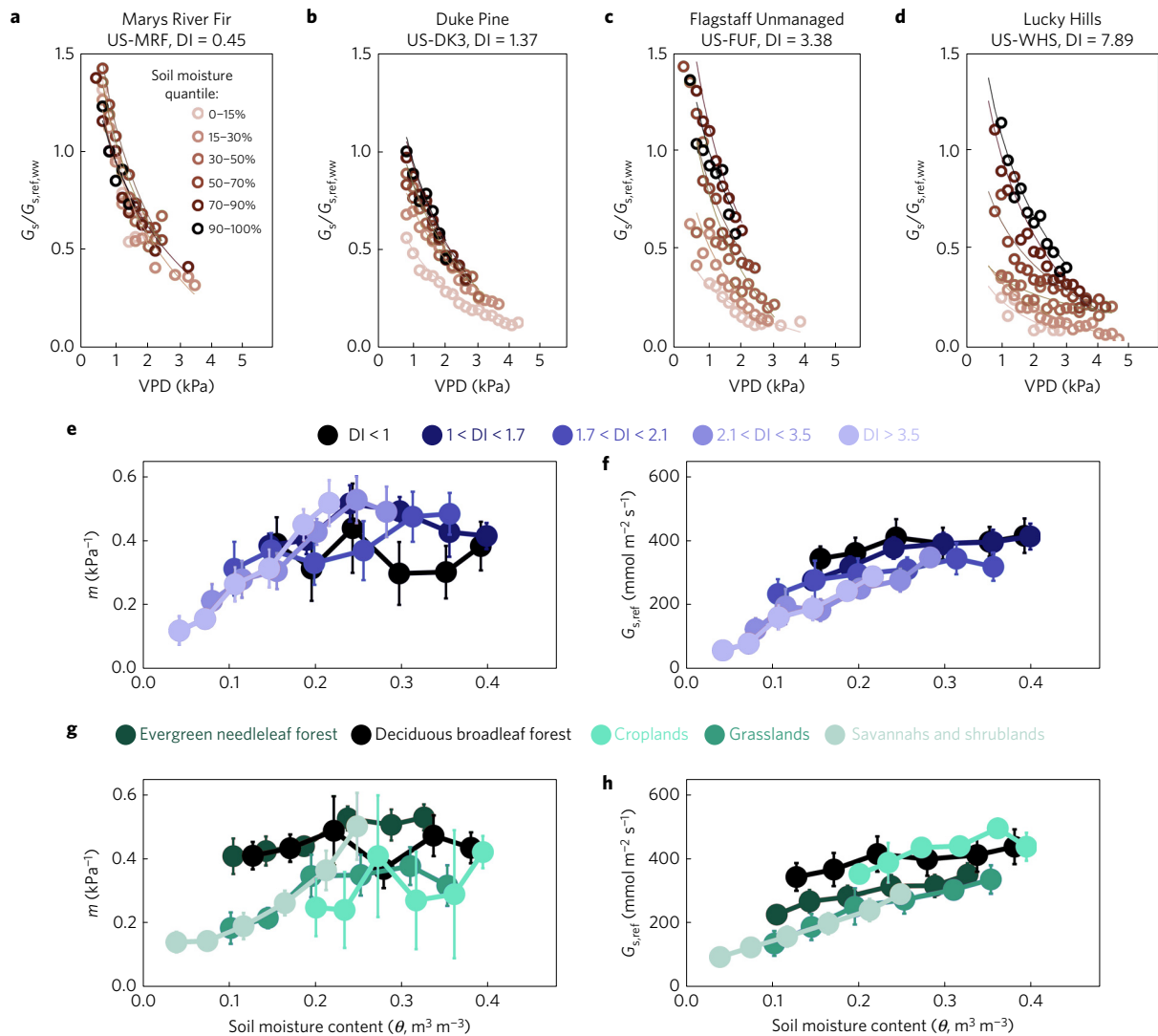
is often overlooked in many fields of hydrologic and climate science. For example, precipitation manipulation experiments are frequently used to draw conclusions about ecosystem response to drought stress, even though VPD is unaffected by precipitation manipulation<sup>10</sup>. Some terrestrial ecosystem and ecohydrological models do not permit stomatal conductance to vary with atmospheric demand<sup>5,11</sup>. Many models designed to capture these impacts rely on empirical parameterizations for soil moisture and VPD stress that promote compensating effects and model equifinality<sup>5</sup>, and/or use relative humidity instead of VPD as the primary driver, with significant consequences for projections of



**Figure 1 | Conceptual framework.** **a**, While soil moisture and vapour pressure deficit (VPD) are correlated at seasonal and monthly timescales, they are largely decoupled at daily and hourly timescales. Data points show the mean correlation coefficient across the 38 study sites. Thick bars show one standard deviation, and the thin bars show the entire range of correlations. This separation at different scales in time permits us to disentangle the role of VPD as compared with soil moisture in driving surface conductance ( $G_s$ ). **b,c**, Predicted changes in the relationship between  $G_s$  and VPD as soil dries at a site where VPD limitations dominate (**b**), and where soil moisture limitations dominate (**c**). The well-watered reference conductance rate ( $G_{s,ref,ww}$ ) is shown with black circles.

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**Figure 2 | How the relationship between surface conductance and vapour pressure deficit varies with soil moisture.** **a–d**, Illustrations of how the relationship between surface conductance ( $G_s$ ), normalized by its well-watered reference rate ( $G_{s,ref,ww}$ ), and vapour pressure deficit (VPD) changes as soil moisture declines in four (of 38) AmeriFlux sites that span a range of dryness index (see Supplementary Information for more details on study sites). Circles show the average  $G_s/G_{s,ref,ww}$  within unique VPD and soil moisture bins. **e–h**, The slope and intercept of equation (1) ( $m$  and  $G_{s,ref}$ ) as a function of soil moisture content when data are pooled by dryness index ( $DI = PET_{PM}/P$ ; **e,f**) or plant functional type (**g,h**). Error bars show the standard error of the mean.

carbon uptake<sup>7</sup>. Furthermore, while much attention has been focused on hydrologic cycle feedbacks driven by stomatal closure under elevated  $CO_2$  (refs 17–19), scarce attention has been paid to the potential for hydrologic cycle feedbacks driven by stomatal closure under increasing VPD.

Looking to the future, it will become even more important to separately resolve VPD and soil moisture effects on ecosystem functioning. VPD is highly sensitive to changes in air temperature and is thus expected to rise globally in the future<sup>1,20</sup>. On the other hand, projected changes in precipitation and soil moisture are less certain, more spatially variable, and smaller in relative magnitude<sup>21</sup>. As a result, soil moisture and VPD will probably become more decoupled, which could cause the ecological impacts of droughts to diverge even further from our present understanding. As a consequence, models may over-predict the magnitude of carbon and water fluxes during periods of intermediate to high VPD, and management approaches that improve soil moisture balance, including irrigation and forest thinning, may become less effective at mitigating hydrologic stress.

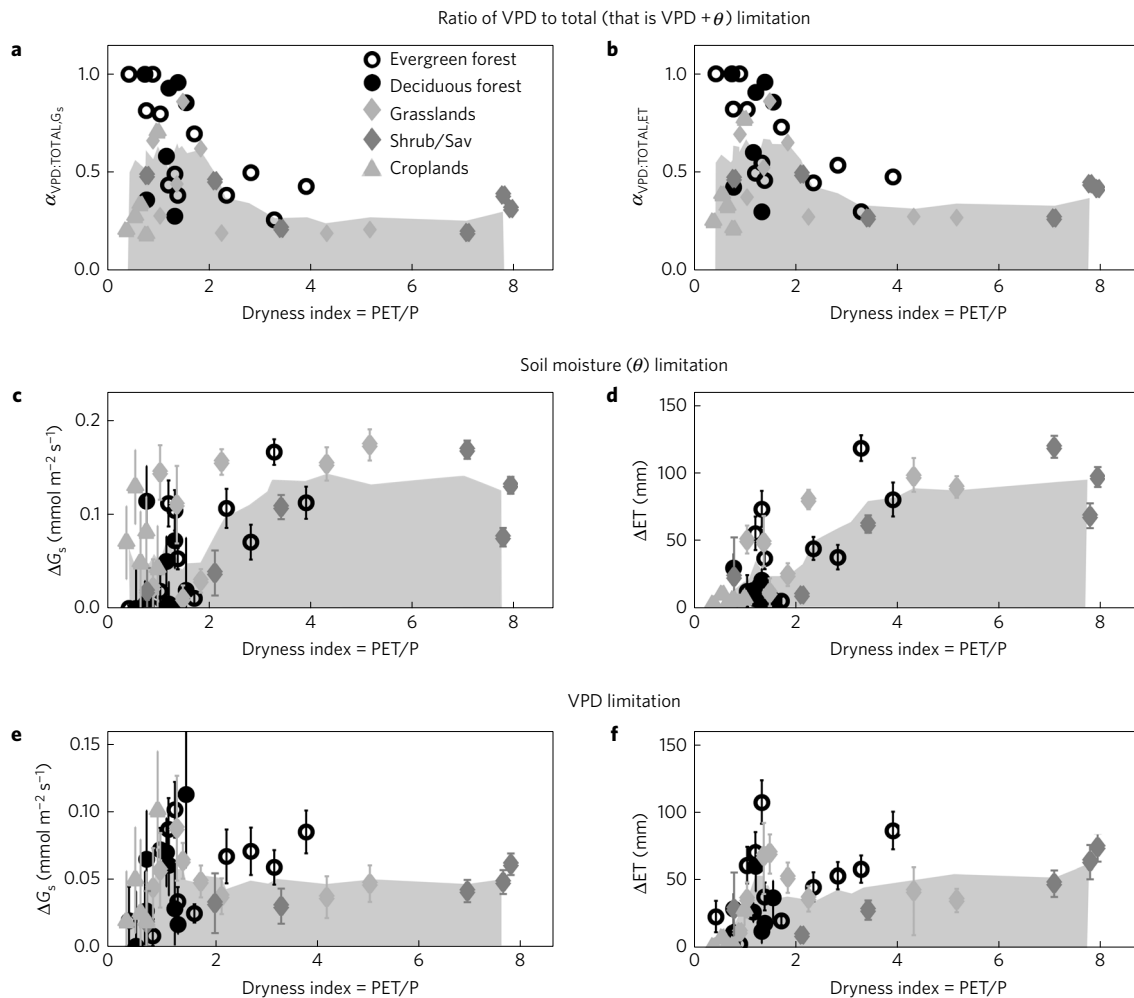
In this study, we use surface flux observations and multiple climate models to quantify the extent to which soil moisture and VPD independently limit growing season  $G_s$  and ET during periods

of hydrologic stress for present and future climate conditions. Consistent with classical approaches to exploring ET limitations<sup>22,23</sup>, we conducted the study across sites that span a range of dryness indices (DI), defined as the ratio of annual potential ET to annual precipitation ( $DI = PET/P$ ). We explore multi-year measurements of half-hourly ET and relevant meteorological drivers from 38 AmeriFlux sites spanning a range of xeric to mesic biomes. From these observations, we obtained estimates of hourly  $G_s$  by inverting the Penman–Monteith equation<sup>24</sup>, noting that  $G_s$  derived in this way reflects contributions from both stomatal and soil conductances. Our approach exploits the fact that while VPD and soil moisture are coupled at scales of weeks to years, they are significantly decoupled ( $r^2 < 0.2$ ) at the hourly timescales at which the AmeriFlux data are collected (Fig. 1a).

We quantify how variation in the relationship between  $G_s$  and VPD changes with soil moisture using<sup>13</sup>:

$$G_s = G_{s,ref} [1 - m \times \ln(\text{VPD})] \quad (1)$$

where the intercept parameter  $G_{s,ref}$  is a reference surface conductance rate ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) at  $\text{VPD} = 1$  (kPa). The parameter  $G_{s,ref}$



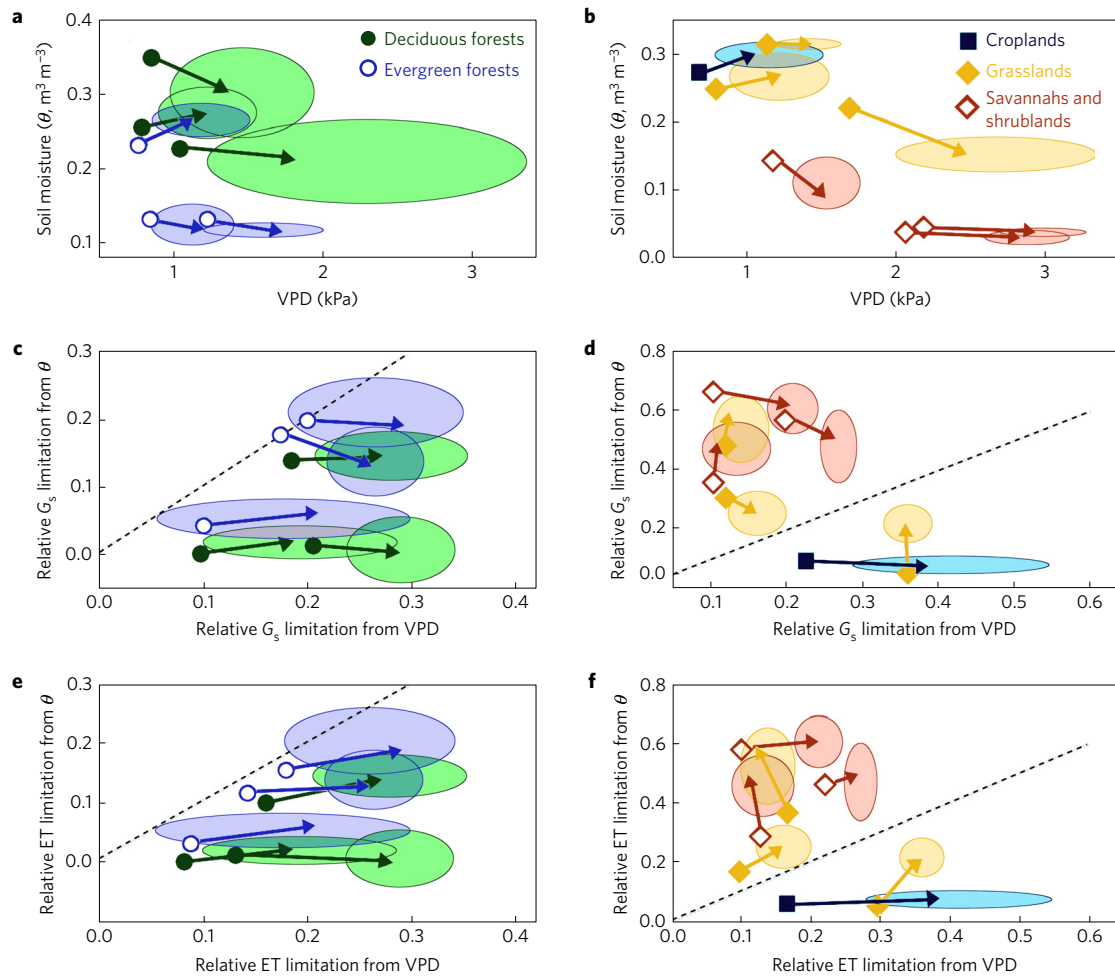
**Figure 3 | Growing season limitations to  $G_s$  and ET.** **a,b**, The ratio of VPD to total limitations to growing season  $G_s$  ( $\alpha_{\text{VPD:TOTAL},G_s}$ ; **a**) and ET ( $\alpha_{\text{VPD:TOTAL},ET}$ ; **b**). A value of 1.0 indicates that soil moisture limitations are negligible. **c-f**, The magnitude of reductions in growing season surface conductance ( $G_s$ , left column) and evapotranspiration (ET, right column) imposed by soil moisture ( $\theta$ ; **c,d**) and vapour pressure deficit (VPD; **e,f**) across the range of dryness indices observed at 38 Ameriflux sites. Error bars show the 50th percentile range in hourly  $G_{s,\text{ref},\text{ww}} - G_s$  (for **c,e**) and  $\text{PET} - \text{ET}$  (for **d,f**). Shaded areas show the moving average across the range of dryness index.

is also sensitive to variations in radiation and temperature<sup>25,26</sup>, but neglecting those dependencies does not bias the present analysis, as discussed in the Supplementary Information. The parameter  $m$  describes the sensitivity of surface conductance to VPD. If  $G_s$  is dominated by stomatal conductance, then  $m$  is expected to be about  $0.6 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ kPa}^{-1}$  (ref. 13). The parameter  $m$  will decrease as the contribution of soil conductance to  $G_s$  increases, or in response to plant regulation of leaf water potential during periods of hydrologic stress<sup>27</sup>. For sites in which limitations from VPD dominate  $G_s$ , there will be little change in  $G_{s,\text{ref}}$  as soil moisture declines (Fig. 1b). In sites where soil moisture limitations are important,  $G_{s,\text{ref}}$  will decline as soil dries, and  $m$  may concurrently decrease (Fig. 1c).

In each site, we sorted the surface conductance data into six bins delineated on the basis of volumetric soil moisture ( $\theta$ ). Then, we determined the parameters of equation (1) within each soil moisture bin by linear regression of the tower-derived  $G_s$  with the observed  $\ln(\text{VPD})$ . We limited the analysis to periods of relatively stationary leaf area and near-neutral or unstable atmospheric conditions, as discussed in more detail in the Supplementary Information. The data-driven, soil moisture-specific parameterizations of equation (1) were then used to quantify the total and relative growing season limitation to  $G_s$  and ET imposed by  $\theta$  and VPD.

Across all sites and soil moisture conditions, the parameter  $m$  was almost always greater than zero, indicating stomatal limitation to  $G_s$  (Fig. 2a–e,g). The sensitivity parameter  $m$  was reduced at low  $\theta$  in sites with intermediate and high DI (Fig. 2e), and in ecosystems with sparser and shorter vegetation (Fig. 2g). In all but the very wettest sites with  $\text{DI} < 1$ , the intercept parameter  $G_{s,\text{ref}}$  declined with declining  $\theta$ , indicating soil moisture limitation to  $G_s$ . These declines were most pronounced in sparsely vegetated ecosystems with  $\text{DI} > 4$  (Fig. 2f,h).

Over the course of the growing season, the ratio of VPD to total (VPD +  $\theta$ ) limitation for  $G_s$  (hereafter  $\alpha_{\text{VPD:TOTAL},G_s}$ ) was  $>0.5$ , on average, in wet and mesic sites ( $\text{DI} < 2.5$ ), indicating that VPD was the dominant limiting driver to  $G_s$  (Fig. 3a). Many of these mesic sites are forested ecosystems, where the mean  $\alpha_{\text{VPD:TOTAL},G_s} = 0.61$  (range of 0.06 to 1.0). In contrast,  $\alpha_{\text{VPD:TOTAL},G_s}$  was  $<0.5$  in drier, typically non-forested sites where  $\theta$  was more important to  $G_s$  variability (Fig. 3a). These trends were driven by the fact that VPD limitations to  $G_s$  peaked in intermediately wet sites (Fig. 3e) while soil moisture limitations to  $G_s$  tended to increase monotonically across the gradient of dryness index (Fig. 3c). The ratio of VPD to total limitation for ET ( $\alpha_{\text{VPD:TOTAL},ET}$ ) was also  $>0.5$  in relatively wet sites ( $\text{DI} < 2.5$ ), and  $>0.70$  in forests, but decreased in drier sites (Fig. 3b,d,f).



**Figure 4 | The projected shifts in key study variables from present to future climate conditions. a,b,** The models predict global increases in VPD, but projected shifts in soil moisture content are smaller and less uniform. Arrows show the magnitude and direction of projected shifts in growing season averages of study variables. Ovals show the range in growing season averages emerging from the 10 general circulation models. Each arrow represents one of a subset of thirteen Ameriflux sites used in this analysis of future climate impacts. **c,d,** illustrate how the predicted changes in soil moisture and VPD translate into predicted shifts in limitations to  $G_s$ . **e,f,** illustrate how the predicted changes in soil moisture and VPD translate into predicted shifts in limitations to ET. Limitations to  $G_s$  and ET are shown as relative quantities, normalized by the growing season  $G_{s,ref,ww}$  and PET, respectively. Sites located to the right of the 1:1 line in **c-f** experience relatively greater limitation from VPD than soil moisture. Note that the axis shifts from one panel to the next.

We observed considerable variability in the relative importance of VPD limitations among more mesic sites growing at similar DI. For example, soil moisture limitations tended to be higher in short-statured ecosystems than in forests (Fig. 3a), which may highlight the importance of plant reliance on stored water or deep rooting systems in taller ecosystems<sup>6</sup>. Plant water use strategy (for example, isohydric or anisohydric) has also been identified as a factor determining the sensitivity of stomatal conductance to VPD<sup>1,27,28</sup>. Accounting for all these sources of variability was outside the scope of this particular study, but should motivate future research.

To understand whether predicted changes in climate have the potential to alter the relative importance of VPD versus soil moisture limitations to  $G_s$ , we obtained projected future meteorological time series from ten downscaled general circulation models (see Supplementary Information) for a subset of 13 of the longer-running Ameriflux sites that are representative of a broad range of ecosystem types. Increases in mean growing season VPD were projected for every site (Fig. 4a,b). In contrast, and consistent with other studies<sup>21</sup>, soil moisture was projected to increase at some sites but remained unchanged at others, with small overall changes relative to inter-model variability (Fig. 4a,b). As a result, we predict that VPD limitation to  $G_s$  will increase under future climate scenarios in most

ecosystems, whereas the trends for future soil moisture limitation to  $G_s$  are mixed (Fig. 4c,d). Future VPD limitations are particularly important in forest ecosystems, where we project that the future  $\alpha_{VPD:TOTAL,G_s}$  will exceed 0.7 on average. Interestingly, soil moisture limitations to ET will also increase in nearly all sites (Fig. 4e,f), even though soil moisture limitations to  $G_s$  are less consistent. This apparent paradox, which has been reported elsewhere<sup>3</sup>, reflects the fact that the relationship between ET and  $G_s$  is hyperbolic (see Supplementary Equation 2), and future ET is thus sensitive to changes in the variance or skewness of the  $\theta$  distribution, even if changes in the mean  $\theta$  are small.

The climate projections are designed to isolate the impact of future changes in VPD and soil moisture on  $G_s$  and ET. Stomatal conductance may be independently reduced in the future by higher water use efficiency under elevated  $CO_2$ , with relative reductions on the order of about ~20% predicted by both modelling and experimental work<sup>17-19</sup>. Here, we report relative reductions in  $G_s$  driven by rising VPD on the order of 10% in most forest ecosystems, which would imply even greater relative reductions in canopy stomatal conductance since  $G_s$  is influenced by soil conductance, which is not sensitive to VPD. While VPD and  $CO_2$  concentrations are assumed to be independent drivers of stomatal conductance

in theoretical formulations<sup>17,19</sup>, the extent to which their effects on stomatal conductance are additive remains an important topic for future work, which must also consider the confounding effects of increasing leaf area index<sup>29</sup>.

In summary, our results indicate that atmospheric constraints play a critical and increasingly important role in controlling ecosystem fluxes of carbon and water. In the future, warmer temperatures will increase the relative importance of VPD in limiting  $G_s$  and ET across the biomes studied here, especially in mesic forest ecosystems that drive the terrestrial carbon sink<sup>9</sup>. Consequently, conceptual and mathematical models that do not independently resolve VPD and soil moisture limitations will not adequately capture the magnitude of ecosystem response to future hydrologic stress. Our results also have important implications for the effective application of management approaches such as irrigation and thinning for alleviating future drought stress. While these approaches improve the soil moisture balance<sup>30</sup>, unless applied over large land areas, they probably have little effect on local VPD, which we project will become the dominant limiting driver in many biomes.

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## Author contributions

K.A.N. designed the study and methodology, with substantial input from all co-authors, especially D.L.F., C.A.W. and R.P.P. D.L.F. obtained and processed the future climate projections. K.A.N., G.B., S.A.P., P.D.B., A.N., B.N.S., R.L.S., R.P.P. and P.C.S. contributed ecosystem flux data. All authors contributed to data analysis and interpretation. K.A.N. and D.L.F. drafted the manuscript. All authors commented on and approved the final manuscript.

## Additional information

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## Competing financial interests

The authors declare no competing financial interests.