# Intense solar radiation constrains plant species richness in global grasslands

Marie Spohn[a,1] (ID), Carlos Alberto Arnillas[b] (ID), Jonathan D. Bakker[c] (ID), Elizabeth T. Borer[d] (ID), Kari Anne Bråthen[e] (ID), Marc W. Cadotte[f] (ID), Clinton Carbutt[g,h] (ID), Jane A. Catford[i,j,k] (ID), Mary E. DuPre[l] (ID), Ciara Dwyer[m], Nico Eisenhauer[n,o] (ID), Catalina Estrada[p] (ID), Nicole Hagenah[q], Sylvia Haider[r], Kyle E. Harms[s] (ID), Yann Hautier[t] (ID), Erika I. Hersch-Green[u] (ID), Johannes M. H. Knops[v], Lauri Laanisto[w] (ID), Ramesh Laungani[x] (ID), Peter Macek[w,y], Holly Martinson[z] (ID), Jonathan Millett[aa] (ID), Meelis Pärtel[bb] (ID), Steven C. Pennings[cc] (ID), Pablo L. Peri[dd] (ID), Sally A. Power[ee], Anita C. Risch[ff], Christiane Roscher[n,gg], Eric W. Seabloom[d] (ID), Nicholas G. Smith[hh], Carly Stevens[ii], Risto Virtanen[jj], Glenda M. Wardle[kk] (ID), and Pengfei Zhang[d,ll] (ID)

Affiliations are included on p. 7.

The search for predictors of plant diversity has challenged scientists for decades. Here we identify intense photosynthetically active radiation (PAR) as a major factor constraining plant species richness in global grasslands. We show that the strength of the negative relationship between species richness and PAR increases with increasing elevation and that species richness is more strongly correlated with intense PAR than with UV-B radiation, climate variables, and atmospheric nitrogen deposition. In addition to species richness, plant biomass was also negatively correlated with PAR at higher elevations, indicating that intense PAR also constrains plant biomass in montane grasslands. Furthermore, we show that the decrease in plant species richness with increasing PAR is mainly caused by a decrease in species richness of forbs, sedges, and rushes. In contrast, species richness of grasses was only negatively correlated with PAR at high elevations, and species richness of legumes was not significantly correlated with PAR. Our results suggest that PAR constrains plant species richness in global grasslands and limits the extent to which plant species of specific functional groups can migrate uphill in response to climate warming.

plant species richness | solar radiation | plant diversity | environmental filters | grasslands

Despite the paramount role of biodiversity for ecosystem functioning, the factors that determine plant species richness in global grasslands are still not completely understood (1–3). Given the importance of photosynthetically active radiation (PAR) for plants, it could be that PAR affects species richness in global grasslands more strongly than atmospheric nitrogen deposition or climate. At low to moderate PAR, photosynthesis increases with increasing PAR, for example in the understory of forests with a very dense canopy (4). Yet, high PAR is a strong stressor for plants (4–7). At high PAR, the rate of photosynthesis is saturated, but light in excess of what is required for photosynthesis is still absorbed. This can lead to the production of chemical intermediates that cause photooxidative damage to plant cells, reducing photosynthesis (4–7). Therefore, PAR may act as an environmental filter (8–10) that constrains plant species richness in grasslands, preventing the establishment of species that cannot persist under intense PAR.

Photosynthesis is more efficient under diffuse sunlight than direct sunlight, particularly under intense solar radiation, because diffuse light provides more uniform irradiance of the canopy (11–17). Diffuse light is caused by light scattering through atmospheric aerosols and water vapor. Since atmospheric aerosols produce diffuse light, they positively affect photosynthesis in many ecosystems (18–22). At higher elevations, sunlight is less diffuse compared to lowlands, because the concentrations of atmospheric gases and aerosols decline with decreasing air pressure, and thus with increasing altitude above sea level (a.s.l.) (23–27). This can influence the establishment of plants. For instance, nondiffuse, intense sunlight negatively affects the establishment of tree seedlings in montane ecosystems (28–31). Accordingly, under conditions of intense solar radiation, shading (under the canopy of other plants) positively affects photosynthesis of many species, particularly at high elevations, because it reduces exposure to intense PAR (12, 14, 16, 28, 32, 33).

In contrast to PAR, which forms a major part of solar radiation on the Earth's surface, UV-B radiation typically contributes less than 10% of the energy of solar radiation at sea level (23, 24). Yet, the contribution of UV-B radiation to the total solar radiation increases with increasing altitude (23, 24, 26). Since UV-B radiation can destroy DNA and RNA, it is thought to affect the abundance of plants, particularly at high elevations (e.g., 34).

The purpose of this study is to understand the relationship between plant species richness and solar radiation in global grasslands. We hypothesize that (H1) plant species

## Significance

The question of what determines plant diversity is a key question in ecology. Here we identify intense photosynthetically active radiation (PAR) as a major factor constraining plant species richness in global grasslands. Furthermore, we show that the decrease in plant species richness with increasing PAR is mainly caused by a decrease in species richness of forbs and rushes. Our results suggest that PAR constrains plant species richness in global grasslands and limits the extent to which plant species of specific functional groups can migrate uphill in response to climate warming.

richness in global grasslands is negatively correlated with PAR, and especially with intense PAR, and that (H2) the strength of the negative correlation of species richness and PAR increases with increasing elevation (because of a decrease in diffusivity of PAR with increasing altitude a.s.l.). Furthermore, we hypothesize that (H3) plant biomass is negatively correlated with intense PAR due to the negative effect of intense PAR on photosynthesis. In addition, we hypothesize that (H4) plant species richness is more strongly correlated with PAR than with UV-B radiation. To test the four hypotheses, we collected standardized plant species richness and plant aboveground biomass data at 150 natural and seminatural grasslands on six continents (*SI Appendix*, Fig. S1) and analyzed them together with different measures of PAR and UV-B radiation derived from satellite data (with a temporal resolution of 3 h covering several decades) as well as other environmental variables.

## Results and Discussion

**Species Richness and PAR.** In agreement with H1, we found that plant species richness was negatively correlated with all measures of PAR (i.e., means and maximum values of total as well as intense PAR for different periods and different threshold values calculated across 22 y of continuous observation with a 3-h resolution; *SI Appendix*, Table S1) across 150 grassland sites. Specifically, plant species richness was negatively correlated with the mean PAR during the 140-day period of highest PAR ($PAR_{140 \text{ days}}$; $P < 0.001$; Fig. 1), which characterizes PAR during the main growing season. Plant species richness was most strongly negatively correlated with measures of intense PAR (*SI Appendix*, Table S1), such as $PAR300_{140 \text{ days}}$ ($P < 0.001$; Fig. 2), which is intense PAR during the 140-day period of highest PAR calculated with a threshold of 300 W m$^{-2}$ (for relationships between species richness and intense PAR with higher thresholds and for different periods, see *SI Appendix*, Table S1). The $R^2$ of the linear models of species richness as a function of PAR increases if we use intense PAR instead of PAR in the models, and it increases further if we increase the threshold of intense PAR (compare results of models with PAR250 to those with PAR300; *SI Appendix*, Table S1). This indicates that the negative relationship between PAR and species richness is due to the periods of intense PAR rather than total PAR.

$PAR_{140 \text{ days}}$ was significantly positively correlated with mean annual temperature (MAT; $R^2 = 0.27$, $P < 0.001$) and negatively with the absolute value of latitude ($R^2 = 0.17$; $P < 0.001$) and mean annual precipitation (MAP; $R^2 = 0.05$; $P = 0.008$), but not with elevation ($P = 0.812$) across all 150 sites. Furthermore, $PAR300_{140 \text{ days}}$ (i.e., intense PAR during the 140-day period of highest PAR) was significantly positively correlated with mean annual temperature (MAT; $R^2 = 0.33$, $P < 0.001$) and negatively with the absolute value of latitude ($R^2 = 0.26$; $P < 0.001$) and mean annual precipitation (MAP; $R^2 = 0.04$; $P = 0.014$), but not with elevation ($P = 0.059$) across all 150 sites.

This study reveals a negative relationship between plant species richness and PAR. The reason for the negative relationship is likely that intense PAR is a physiological stressor for plants (4–7) that is strong enough to act as an environmental filter. Intense PAR causes photooxidative damage to the two photosystems and other proteins and decreases the rate of photosynthesis (4–7). In addition, rapidly changing light conditions, i.e., changes between direct light and shade that can occur when light is not diffused, are a strong stressor for plants (4–6). Furthermore, PAR is also harmful for cell walls and contributes
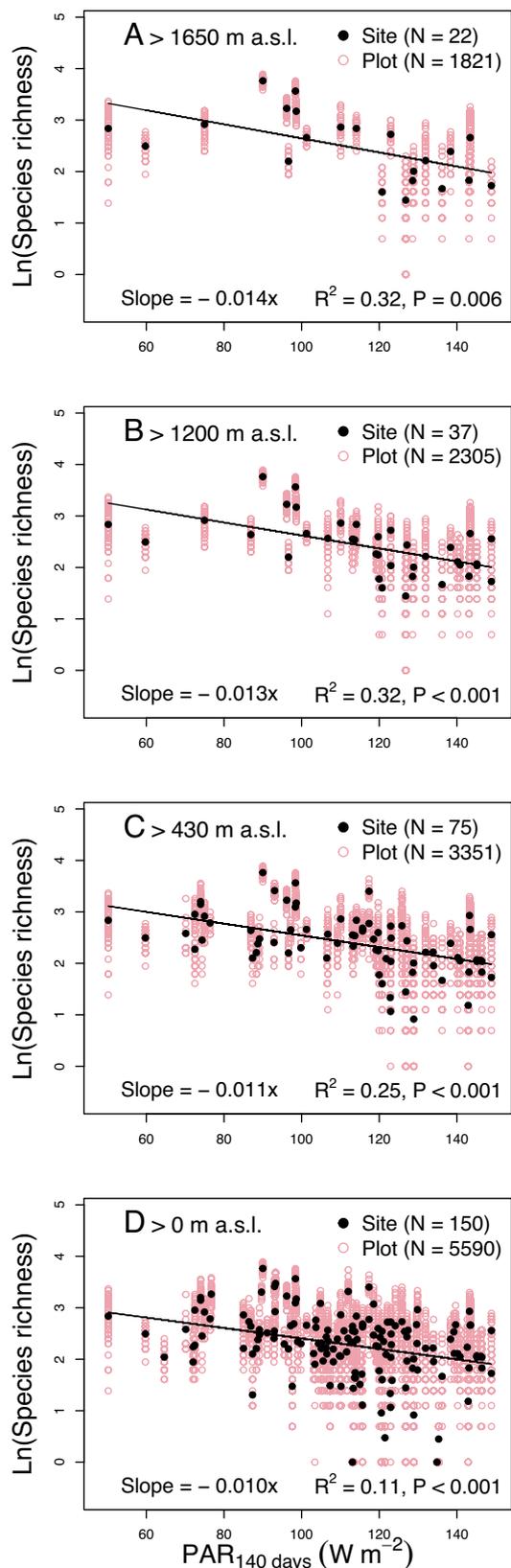


**Fig. 1.** Relationship between the log-transformed plant species richness and the mean PAR during the 140-day period of highest PAR ($PAR_{140 \text{ day}}$). The relationship is shown across sites at >1,650 m a.s.l. (*A*), at >1,200 m a.s.l. (*B*), at >430 m a.s.l. (*C*), and at >0 m a.s.l. (all sites; *D*). $PAR_{140 \text{ day}}$ was calculated based on 22 y of observation. The linear models were calculated based on the site-level data (and not based on the plot-level data, which are shown to give insight into the within-site variability). The sites were divided into different elevation categories by repeated binary splits. N indicates the number of observations.

to photodecomposition (35, 36). Our results suggest that intense PAR acts as an environmental filter, which is so strong that it constrains species richness in global grasslands, likely because species that cannot cope with this stressor do not establish in habitats that frequently experience intense PAR.

**Species Richness and PAR at Different Elevations.** In accordance with H2, we found that the coefficient of determination ($R^2$) of the negative relationship between species richness and PAR increased with increasing elevation (Figs. 1 and 2 and *SI Appendix, Table S1*). The $R^2$ of the models of species richness as a function of $PAR_{140 \, days}$ was 0.11 across all sites, 0.25 across sites located above 430 m a.s.l., and 0.32 across sites located above 1,200 m a.s.l. (all $P < 0.01$, Fig. 1). The $R^2$ of the models of species richness as a function of $PAR300_{140 \, days}$ also increased with elevation, and it was 0.14 across all sites, 0.27 across sites located above 430 m a.s.l., 0.42 across sites located above 1,200 m a.s.l., and 0.48 across sites located above 1,650 m a.s.l. (all $P < 0.001$, Fig. 2). Species richness and PAR were also significantly negatively correlated across sites located below 430 m a.s.l., albeit less strongly than at higher elevations (*SI Appendix, Table S1*). The sites were divided into different elevation categories by repeated binary splits (Figs. 1–3). The $R^2$ also increased with increasing elevation when the sites were divided along different elevation thresholds (*SI Appendix, Table S2*), confirming that the results do not depend on the specific elevation categories chosen in this study.

Species richness was not significantly correlated with the absolute value of latitude ($P = 0.233$) but was weakly positively correlated with elevation across all sites ($R^2 = 0.02$, $P = 0.037$). PAR and elevation did not significantly interact in their relationships with species richness (i.e., the interaction term in Eq. **1** has a $P = 0.52$) since species richness was negatively correlated with PAR at all elevations. However, with increasing elevation, fewer sites diverged strongly from the linear relationship between species richness and PAR, leading to an increase in the $R^2$ with increasing elevation (Figs. 1 and 2). Furthermore, the slope of the linear models describing species richness as a function of PAR tended to increase in steepness with increasing elevation (Figs. 1 and 2). These results suggest that PAR acts more strongly as an environmental filter at higher elevations, likely because PAR is less diffuse at higher altitudes a.s.l. (24–26). It has been shown that intense, nondiffuse sunlight negatively affects tree seedlings in montane ecosystems (28–31). Our results are in accordance with these findings and extend knowledge about solar radiation and plant species further, by showing that species richness in grasslands is related to PAR. The results are also consistent with studies reporting that photosynthesis is more efficient under diffuse and less intense light (11–16), as caused by atmospheric aerosols (18–22), particularly at low elevations (18–24, 26). Furthermore, the positive correlation between species richness and elevation is in agreement with a recent study based on a subset of sites explored here, which reported that plant diversity was positively correlated with elevation but not significantly with soil texture, soil nutrient contents, pH, or other environmental variables (37).

**Plant Biomass, Species Richness, and PAR at Different Elevations.** In agreement with H3, we found that plant aboveground biomass was negatively correlated with PAR across all sites (Fig. 3 and *SI Appendix, Table S3*). The $R^2$ of the relationship between plant biomass and PAR increased with increasing elevation (up to $R^2 = 0.54$, $P < 0.001$ at >1,650 m a.s.l.; Fig. 3), and the absolute value of the slope of the linear models also increased with increasing elevation (Fig. 3). The absolute value of the slope was significantly higher for models calculated across sites located at
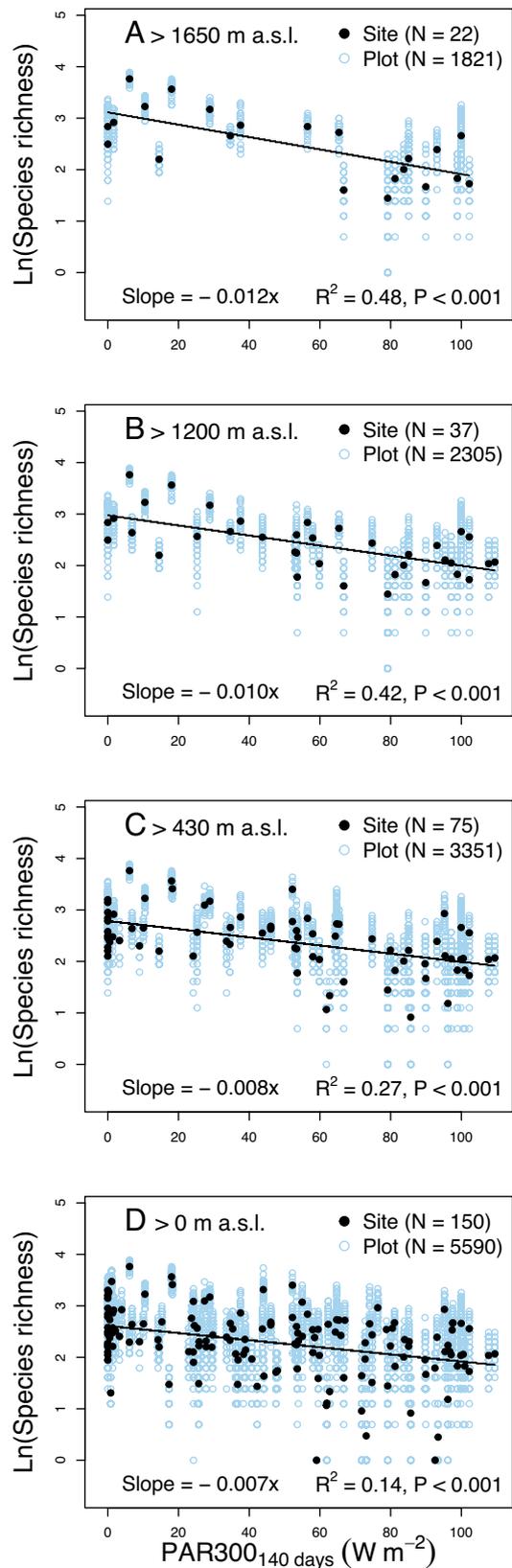


**Fig. 2.** Relationship between the log-transformed plant species richness and intense PAR during the 140-day period of highest PAR ($PAR300_{140 \, days}$). $PAR300_{140 \, days}$ is calculated as the mean PAR during the 140-day period of highest PAR after setting all 3-h periods with PAR <300 to 0 W m$^{-2}$ based on 22 y of observation. The relationship is shown across sites at >1,650 m a.s.l. (*A*), at >1,200 m a.s.l. (*B*), at >430 m a.s.l. (*C*), and at >0 m a.s.l. (all sites; *D*). The sites were divided into different elevation categories by repeated binary splits. The linear models were calculated based on the site-level data (and not based on the plot-level data, which are shown to give insight into the within-site variability).
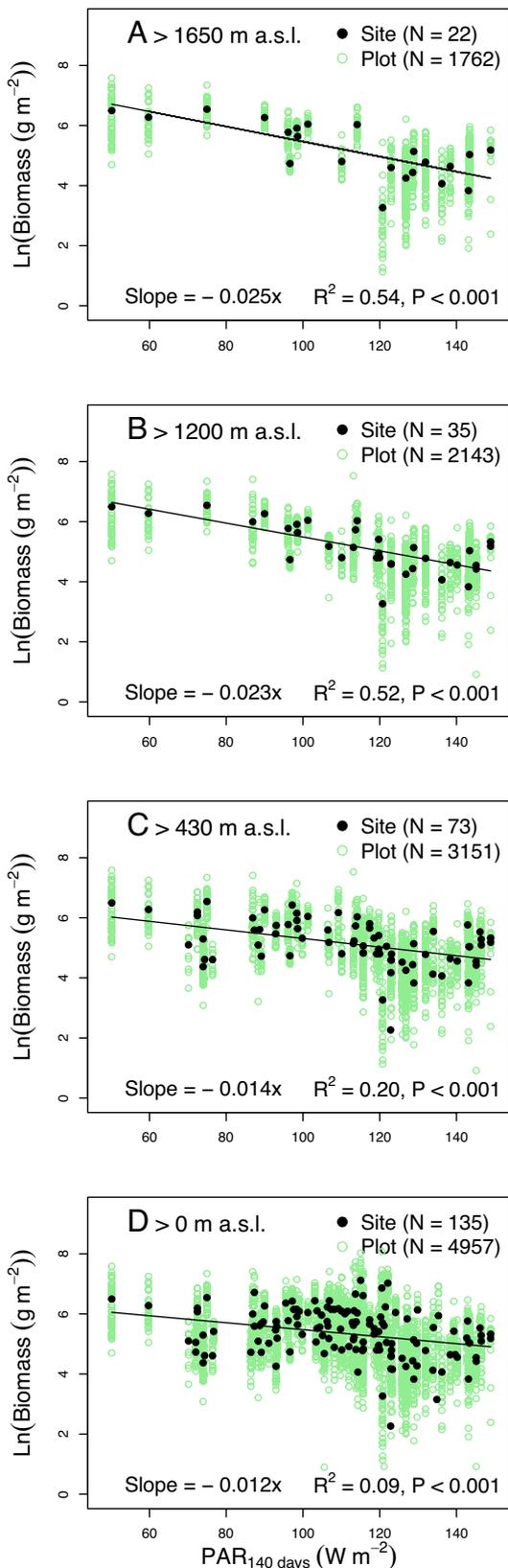
**Fig. 3.** Relationship between the log-transformed plant aboveground biomass and the mean PAR during the 140-day period of highest PAR (PAR$_{140 \text{ days}}$). The relationship is shown across sites at >1,650 m a.s.l. (*A*), at >1,200 m a.s.l. (*B*), at >430 m a.s.l. (*C*), and at >0 m a.s.l. (all sites; *D*). PAR$_{140 \text{ days}}$ was calculated based on 22 y of observation. The sites were divided into different elevation categories by repeated binary splits. The linear models were calculated based on the site-level data (and not based on the plot-level data, which are shown to give insight into the within-site variability).

>1,650 m a.s.l. and at >1,200 m a.s.l. than across all sites (the *P* values of comparison of the slopes by Welch's *T* test are 0.034 and 0.031, respectively). Furthermore, PAR$_{140 \text{ days}}$ and elevation significantly interacted in their relationships with plant biomass across all sites (i.e., the interaction term in Eq. **1** has a *P* < 0.001) since the relationship between biomass and PAR depended on elevation and was not significant across sites located below 430 m a.s.l. (*SI Appendix*, Table S3). The negative relationship between plant biomass and PAR is likely due to the inhibitory effect of intense, direct PAR on photosynthesis (17–22), which occurs more frequently at higher elevations due to less strong scattering of PAR at high altitudes a.s.l. (23, 24, 26).

Species richness and biomass were positively correlated across sites located above 430 m a.s.l. (P < 0.001; *SI Appendix*, Fig. S2 and Table S4), but not across all sites (*P* = 0.717; *SI Appendix*, Fig. S2 and Table S4). At elevations higher than 1,200 m a.s.l., biomass explained 45% of the variability of species richness (*SI Appendix*, Fig. S2, *P* < 0.001, R$^2$ = 0.45). PAR and biomass together explained a larger share of the variability of plant species richness than PAR alone at most elevations (*SI Appendix*, Table S5). Our results reveal that species richness and biomass are only significantly correlated at higher elevations (*SI Appendix*, Fig. S2 and Table S4). Thus, it can be speculated that the strength of the relationship between species richness and PAR increases with increasing elevation because plant species benefit from shading by the biomass of other species mostly at high elevations, where PAR is only marginally diffused (12, 16, 28, 32, 33, 38). Our study provides insights regarding the long-standing question about the relationship between plant species richness and biomass in grasslands (1, 39, 40). The dependence of the relationship between plant species richness and biomass in grasslands on elevation might explain why there are apparently contradicting results about this relationship in the literature (e.g., 40).

**Species Richness of Specific Functional Groups and PAR.** Species richness of forbs was negatively correlated with PAR300$_{140 \text{ days}}$ across all sites (*P* < 0.001), and the R$^2$ and the absolute value of the slope of this relationship increased with increasing elevation (*SI Appendix*, Fig. S3). Furthermore, species richness of graminoids (i.e., sedges and rushes) was negatively correlated with PAR300$_{140 \text{ days}}$ across all sites (*P* < 0.001), and the R$^2$ of these relationships increased with increasing elevation up to R$^2$ = 0.46 across sites located above 1,200 m a.s.l. (*SI Appendix*, Fig. S4). In addition, the sum of graminoids (i.e., sedges and rushes) and forbs was significantly correlated with PAR300$_{140 \text{ days}}$ across all sites (*P* < 0.001), and the R$^2$ of these relationships increased with increasing elevation up to R$^2$ = 0.39 across sites located above 1,200 m a.s.l. (*SI Appendix*, Fig. S5). In contrast, species richness of grasses was only significantly negatively correlated with PAR across sites located above 1,650 m a.s.l., but not at lower elevations (*SI Appendix*, Fig. S6). The reason why species richness of grasses was not significantly correlated with PAR across all sites or across sites located below 1,650 m a.s.l. is likely that grasses are better adapted to intense PAR than forbs and graminoids. The leaf area of grasses is negatively correlated with PAR globally, which seems to be an adaptation to intense PAR (41). In addition, grasses accumulate larger amounts of silicon than forbs, legumes, and rushes (42–45). Silicon forms silicate minerals, so-called phytoliths, in grass leaves, which play an important role in diffusing solar radiation before solar radiation hits the photosystems (44–46). The light diffusion by silicate minerals in the leaves makes grasses more tolerant to intense solar radiation than other plant functional groups (44, 45, 47). The high leaf silicon content of

grasses compared to forbs, legumes, and rushes was confirmed by an analysis of leaf silicon content in different plant functional groups (*SI Appendix*, Fig. S7). Furthermore, we did not find a significant relationship between species richness of legumes and PAR300$_{140\ days}$, neither across all sites nor across sites located at specific elevations (all $P > 0.15$). The reason for this could be that many legumes can move their leaves through phototropism (48, 49), changing the leaf angle relative to the sun, which might make them less susceptible to strong solar radiation (48, 50).

The combined species richness of forbs and graminoids was positively correlated with the combined cover of the four main plant functional groups (grass, forb, legume, graminoid; *SI Appendix*, Fig. S8), and the $R^2$ of this relationship increased with increasing elevation up to $R^2 = 0.55$ across sites located above 1,650 m a.s.l. (*SI Appendix*, Fig. S8). This positive relationship might be caused by forbs and graminoids benefiting from shading, particularly at high elevations where solar radiation is only marginally diffused through aerosols. This is in accordance with studies reporting that under conditions of intense solar radiation, shading positively affects photosynthesis of many species, particularly at high elevations, because it reduces exposure to intense PAR (12, 14, 16, 28, 32, 33, 51).

**Species Richness, UV-B, and PAR.** In agreement with H4, we found that plant species richness was not significantly correlated with measures of UV-B radiation across all sites or at sites located above 430 m a.s.l., and the $P$ values of the regressions increased with increasing elevation for most measures of UV-B radiation (*SI Appendix*, Table S6). Species richness and different measures of UV-B radiation were only significantly negatively correlated across sites located below 430 m a.s.l. ($P < 0.001$; *SI Appendix*, Table S7) in contrast to PAR, despite UV-B being higher at higher elevations (*SI Appendix*, Table S6) in accordance with global patterns (23, 27, 52, 53). This shows that the effects of UV-B and PAR on plant species richness are independent of each other and not interactive as also indicated by multiple regression models with mean annual UV-B and PAR as interacting explanatory variables ($P$ value of the interaction term $> 0.05$; $P = 0.458$ for PAR$_{140\ days}$ and $P = 0.105$ for PAR300$_{140\ days}$). Mean annual UV-B radiation was strongly negatively correlated with the absolute value of latitude ($R^2 = 0.84$; $P < 0.001$). Furthermore, it was significantly positively correlated with mean annual PAR ($R^2 = 0.46$; $P < 0.001$), elevation ($R^2 = 0.30$; $P < 0.001$), MAT ($R^2 = 0.27$; $P < 0.001$), and the aridity index ($R^2 = 0.15$; $P < 0.001$), but not significantly with MAP ($P = 0.284$). Plant biomass was not significantly correlated with any measure of UV-B across all 150 sites or across sites located below 430 m a.s.l. ($P > 0.05$).

Our findings suggest that the negative effect of PAR on plant species richness supersedes the effect of UV-B at elevations above 430 m a.s.l. Thus, the results are in accordance with the current view that plants in montane and alpine ecosystems are more strongly influenced by intense solar radiation than by UV-B radiation (54, 55). The reason for this seems to be that plants can adapt to high UV-B radiation by producing (phenolic) compounds that screen UV-B radiation (54–56). In contrast, plants of several functional groups seem not to be able to protect themselves very effectively from PAR (see above). The lack of a relationship between species richness and UV-B across sites located above 430 m a.s.l. is important because it strongly suggests that the relationships between PAR and both plant species richness and biomass are most likely driven by PAR as opposed to associated UV-B radiation.

**Species Richness, Climate, and Nitrogen Deposition.** We found that plant species richness was more strongly correlated with intense PAR (PAR300$_{140\ days}$) than with UV-B radiation, MAT, MAP, the aridity index, atmospheric nitrogen deposition, and plant biomass (compare *SI Appendix*, Tables S1 and S4). Notably, species richness was not significantly correlated with atmospheric nitrogen deposition (*SI Appendix*, Table S4). Furthermore, species richness was not significantly correlated with MAT at sites located above 430 m a.s.l. (*SI Appendix*, Table S4). Yet, species richness was significantly correlated with MAP across sites located above 430 m a.s.l. but not as strongly as with PAR$_{140\ days}$ and PAR300$_{140\ days}$ (compare *SI Appendix*, Tables S1 and S4).

Species richness was also significantly positively correlated with the aridity index (*SI Appendix*, Table S4 and Fig. S9, note that the aridity index by definition decreases with increasing aridity), but not as strongly as with PAR300$_{140\ days}$ (compare *SI Appendix*, Tables S1 and S4). If we include the aridity index in the model of species richness alongside PAR$_{140\ days}$ or PAR300$_{140\ days}$, the adjusted $R^2$ increases only across sites located at $>1,650$ m a.s.l. but not at lower elevations, and the AIC of most models increases (*SI Appendix*, Table S8), suggesting a less good model fit. This indicates that PAR explains more of the variability of species richness than the aridity index. PAR and the aridity index are correlated, particularly at high elevations (*SI Appendix*, Fig. S10). However, in a linear regression analysis with stepwise forward selection, measures of PAR and biomass, but not the aridity index, were selected as predictors of species richness (*SI Appendix*, Table S9), showing that PAR can better predict species richness in global grasslands than the aridity index. Furthermore, in Random Forest models, the best predictors of plant species richness were PAR and biomass, but not the aridity index, at all elevations (*SI Appendix*, Fig. S11). Future studies should further test these relationships experimentally by manipulating aridity in grasslands at different elevations.

The relationship between plant biomass and PAR was similarly strong as the one between biomass and the aridity index (*SI Appendix*, Table S3). This is in agreement with a recent study that explored the relationship between plant biomass and different abiotic and biotic variables (including soil properties but not PAR) in a subset of the sites studied here and found that MAP was the best predictor of plant biomass followed by the aridity index (37). PAR, MAP, and the aridity index are intrinsically connected since all three are related to cloud cover. In addition, both the aridity index and solar radiation are related to temperature. Hence, high PAR, especially when occurring over long periods, is usually associated with aridity, which makes it impossible to completely disentangle the effects of PAR and aridity. Yet, the increase in the $R^2$ and the slope of the regression between plant biomass and either PAR or the aridity index with elevation suggests that these relationships are mostly driven by PAR because the diffusivity of PAR declines with increasing elevation, whereas the quality of aridity does not change with elevation.

While our dataset includes tropical sites from various continents, there is an underrepresentation of tropical sites relative to temperate sites in the dataset. Therefore, future studies should investigate the relationship between plant species richness and PAR specifically in tropical grasslands. To explore whether the underrepresentation of tropical sites in our dataset affected our results, we conducted multiple regression analyses with interactions between PAR and latitude or PAR and climate variables to check whether climate modulates the relationship between PAR and plants. PAR did not interact significantly with latitude, MAT, or MAP in its relationship with plant species richness and biomass (*SI Appendix*, Table S10). Thus, the underrepresentation of tropical sites has very likely no substantial

effect on the conclusions of this study. Furthermore, PAR did not interact significantly with the aridity index in its relationship with species richness, but it interacted with the aridity index in its relationship with biomass (*SI Appendix,* Table S10). To further test if the relationships between PAR and species richness as well as PAR and biomass depend on the arid sites, we calculated the regressions shown in Figs. 1–3 after removing the very arid sites (i.e., the 21 sites with an aridity index < 0.2). The results of this analysis show that the relationships between PAR and species richness as well as PAR and biomass also hold if we remove the arid sites (*SI Appendix,* Table S11). These results confirm that the relationships found here between PAR and species richness as well as PAR and biomass (Figs. 1–3) are not driven by aridity.

The present study is based on observational data and not on experiments. Future studies should explore the relationship between PAR and plant species richness as well as PAR and plant biomass experimentally at different elevations. This could be done by experimental shading. To understand the relationship between PAR and aridity, the shading treatments should be combined with irrigation treatments in arid ecosystems.

**Conclusions.** This study provides empirical support for the hypothesis that intense PAR constrains plant species richness, particularly at high elevations. We show that the decrease in plant species richness with increasing PAR is mainly caused by a decrease in species richness of forbs, sedges, and rushes, while species richness of grasses was only negatively correlated with PAR at high elevations, and species richness of legumes was not significantly correlated with PAR. Given that grasslands cover approximately a third of the Earth's land surface (57), the results of this study apply to a large proportion of earth's terrestrial biomes.

The study has important implications as it suggests that PAR might limit the extent to which plant species, and specifically forb and rush species, can migrate uphill in response to climate warming. This supports the concern that these species are currently "riding the elevator to extinction" (58). Contrary to earlier estimates (34), our results suggest that PAR rather than UV-B radiation limits plant migration uphill. Future studies should further test these relationships experimentally, for example by manipulating PAR through experimental shading.

## Materials and Methods

**Study Sites.** All 150 grassland sites studied here are natural or seminatural grasslands. They are located on six continents (for a map, see *SI Appendix,* Fig. S1) and their elevation ranges between 0 and 4,400 m a.s.l. (median = 430 m a.s.l.). The sites are part of the Nutrient Network Global Research Cooperative (59). They did not receive any fertilizer and were not experimentally manipulated at the time of study. All 150 sites had at least one grass species, 147 sites had at least one forb species, 122 sites had at least one legume species, and 95 sites had at least one graminoid species (graminoids being sedges and rushes).

**Plant Data Collection.** Plant species richness, plant aboveground biomass, and plant cover were measured at peak biomass, i.e., at the specific time of the year when aboveground plant biomass is highest. Data were collected between 2007 and 2022, and the same sampling protocol was applied at all sites (59). At each site, on average about 30 plots were established (range from 10 to 60 plots per site) each with a size of 5 m × 5 m. In total, there were 5,590 plots distributed across 150 sites. Plant species richness (i.e., number of plant species per m$^2$) was determined in a randomly designated 1 m × 1 m subplot within each 5 × 5 m plot at peak biomass. In the same 1 × 1 m subplot, cover was estimated visually to the nearest 1% for every species overhanging the subplot. All plant species were assigned to one of the following plant functional groups; grass, forb, legume, graminoid (sedge or rush), bryophyte, fern, cactus, woody, or liverwort. We analyzed the relationship between environmental factors and plant species richness

at the plot-scale and not at the site-scale because the plots have the same size at all sites, while the sites differ in size due to the differing number of plots per site.

Live vascular plant aboveground biomass (hereafter plant biomass or biomass) was measured at peak biomass (i.e., at the specific time of the year when aboveground plant biomass is highest). This was done destructively by clipping all aboveground biomass at ground level of plants rooted within two 1 m × 0.1 m strips (for a total of 0.2 m$^2$) adjacent to the 1 m × 1 m subplot where plant species richness was determined. All biomass was dried at 60 °C to constant mass before weighing to the nearest 0.01 g. Aboveground plant biomass was determined at 135 sites.

**PAR, UV-B, Climate, and Atmospheric Nitrogen Deposition Data.** We obtained data on PAR (MCD18C2 Version 6.1) for the period 2002-03-01 to 2024-05-31 from NASA. PAR is incident solar radiation in the visible spectrum (400 to 700 nm). The PAR data product (MCD18C2 Version 6.1) is derived from Moderate Resolution Imaging Spectroradiometer (MODIS) data from NASA's satellite Terra and has a temporal resolution of 3 h and a spatial resolution of 0.05°. The MCD18 products are based on an algorithm that uses multitemporal signatures of MODIS data to derive surface reflectance and then calculate PAR using the look-up table (LUT) approach. The LUTs consider different types of loadings of aerosols and clouds at a variety of illumination/viewing geometries. The accuracy of the PAR data product was confirmed with ground reference data by NASA (60, 61).

We obtained data on UV-B radiation from glUV, a global UV-B radiation dataset. Specifically, we used the variables mean annual UV-B, mean UV-B of the month with the highest UV-B, and mean UV-B of the quarter of the year with highest UV-B (62).

We obtained data on mean annual precipitation (MAP) and mean annual temperature (MAT) from Worldclim 2.0 (63) and data on atmospheric nitrogen deposition from Ackerman et al. (64).

We obtained data on potential evapotranspiration (PET) from the Consultative Group for International Agricultural Research (CGIAR), and we calculated the aridity index (AI) by dividing MAP by PET. Thus, AI decreases with increasing aridity (65).

**Calculations of PAR.** We calculated means of PAR for all 3-h periods and for all sites across all 22 y (to level out interannual variability). This resulted in a dataset with eight observations for all days of the year for each site. Based on this dataset, we calculated different measures of PAR (*SI Appendix,* Table S1). First, we calculated the Daily mean PAR and the daily maximum PAR (called Daily max PAR) for each day of the year and each site. Next, we calculated the Annual mean PAR and the annual maximum (called Annual max PAR) for each site.

We also calculated measures of PAR that represent the mean PAR during the time of highest PAR for each site. More specifically, we calculated PAR$_{x\,days}$ as the average daily mean PAR for periods of X consecutive days of highest daily mean PAR for each site. For example, PAR$_{140\,days}$ is the mean PAR during the 140-day period of highest PAR. This was done by computing moving averages (i.e., running means) of the daily mean PAR across X consecutive days, and selecting the highest of these averages. This was done separately for X equaling 42, 140, 175, or 240 days. Similarly, we calculated maxPAR$_{x\,days}$ (the mean of Daily max) based on Daily max PAR during X consecutive days of the highest Daily max PAR, with X equaling 42, 140, 175, or 240 days (using the approach of computing moving averages and selecting the largest one, see above).

We also calculated measures of PAR that capture intense PAR over different periods of time (PARY$_{x\,days}$) for each site. These measures of PAR represent the mean PAR that a plant, which is only sensitive to PAR above a specific threshold (Y), would perceive during a period of X days. These thresholds were 250, 300, and 350 W m$^{-2}$. We choose 300 W m$^{-2}$ as the threshold for intense PAR (i.e., PAR300) in most analyses because if we use higher thresholds, we miss out periods of intense PAR (for relationships between species richness and intense PAR with a threshold of 350 W m$^{-2}$ see *SI Appendix,* Table S1). This can be seen from the fact that the mean PAR350 is lower than the mean PAR300. Specifically, we first calculated PARY after setting all 3-h periods with PAR < Y to 0 W m$^{-2}$, which is the nighttime value of PAR, for Y equaling 250, 300, or 350 W m$^{-2}$ (22). Next, we calculated the daily mean of PARY for all days. Like PAR$_{x\,days}$, we then calculated PARY$_{x\,days}$. For example, PAR300$_{140\,days}$ would be the mean PAR300 during the 140-day period of highest PAR. For this purpose, we computed moving averages of the daily mean PARY across X consecutive days and selected the highest of these averages. This was done separately for X equaling 42, 140, 175, or 240 days. In addition, we calculated annual mean PARY across all days of the year

after setting all 3-h periods with PAR < Y to 0 W m$^{-2}$ (i.e., night); with Y equaling 250, 300, or 350 W m$^{-2}$.

**Calculations and Statistical analyses.** We computed arithmetic means of plant species richness and plant biomass across all plots of each site (called site-level data in the following). We aggregated the data at the site-level because PAR and climate variables do not vary among the plots of one site. In addition, different plots within one site are not independent of each other (which is a prerequisite for regression analysis). Aggregating plot-level data by computing means is common practice in global studies in ecology (1). We include the data from all plots in the figures to give insight into the within-site variability.

We divided the sites according to their elevation based on repeated binary splits of the whole dataset. This approach allows us to test the hypotheses that plant species richness and PAR are negatively correlated across all sites, and that the strength of the correlation between PAR and species richness increases with increasing elevation. Specifically, we first divided all 150 sites into two halves (each containing 75 sites) according to their elevation (below and above 430 m a.s.l.). Next, we divided the group of sites with an elevation >430 m a.s.l. into two halves (below and above 1,200 m a.s.l.). Subsequently, we divided the group of sites with an elevation >1,200 m a.s.l. into two groups (below and above 1,650 m a.s.l.). We chose the last group to contain 22 sites to have a reasonably high number of sites for the regression analysis. The 22 sites located above 1,650 m a.s.l. are in Australia, China, Ecuador, India, Iran, South Africa, Switzerland, and USA, spanning six continents. They represent many major mountain massifs, including the Alborz, the Alps, the Andes, the Australian Alps, the Drakensberg, the Rocky Mountains, and the Tibetan Plateau.

We calculated linear models based on site-level data with one or more independent variable(s). We calculated linear models of plant biomass or species richness as a function of PAR and another variable with an interaction between them (Eq. **1**).

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon. \qquad \textbf{[1]}$$

We also computed logistic models of plant species richness as a function of biomass to estimate the asymptote. Furthermore, we calculated quadratic models for plant species richness as a function of the aridity index. We compared models based on the Akaike Information Criterion (AIC) and considered models with a smaller AIC ($\Delta$AIC < 2) to fit the data better (66). We conducted a multiple linear regression analysis with stepwise forward selection of predictor variables to identify the best-fitting predictors of species richness. Furthermore, we calculated Random Forest models of plant species richness using the R package randomForest, and we plotted the relative importance of different predictors in the Random Forest models using the VarImpPlot function.

Species richness was transformed by calculating its natural logarithm in regressions in which it was the dependent variable because the residuals of the regression models were not normally distributed prior to the log-transformation or because we observed heteroscedasticity when plotting the nontransformed data. Data on species richness of specific functional groups were transformed using inverse hyperbolic sine (IHS) transformation, which was chosen because it allows transformation of zero values in contrast to a log-transformation. We compared the slopes of regressions using Welch's T test. We used the R package tidyverse (version 2.0.0) for merging different data frames, the R package AICcmodavg (version 2.3.3) for calculating the AIC, the R package randomForest (version 4.7-1.2) for calculating Random Forest models, and the R package maps (version 3.4.2.1) for producing a map. All calculations were done in R (version 4.2.1) (67).

We analyzed data compiled for a recent review paper about silicon in plants (68). This dataset contains data from the TRY Plant Trait Database and the AusTraits database. We calculated the leaf silicon content of five functional plant groups that occur in grasslands. We tested significant differences among the plant functional groups by the Kruskal–Wallis test followed by the Dunn post hoc test (using the R package FSA, version 0.9.4), whereby $P < 0.050$ was considered to indicate statistically significant differences. Data and R code to reproduce the results are available in refs. 69, 70.

**Data, Materials, and Software Availability.** All R code and data necessary to reproduce the results are available at Zenodo (https://doi.org/10.5281/zenodo.18146296 and https://zenodo.org/records/18068106) (69, 70).

Author affiliations: ªDepartment of Soil and Environment, Swedish University of Agricultural Sciences, Uppsala 75007, Sweden; ᵇDepartment of Physical and Environmental Sciences, University of Toronto Scarborough, Scarborough, ON M1C 1A4, Canada; ᶜSchool of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195; ᵈDepartment of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108; ᵉDepartment of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø 9019, Norway; ᶠDepartment of Biological Sciences, University of Toronto, Scarborough, ON M1C 1A4, Canada; ᵍSchool of Agriculture and Science, University of KwaZulu-Natal, Scottsville 3209, South Africa; ʰScientific Services, Ezemvelo KwaZulu-Natal Wildlife, Cascades 3202, South Africa; ⁱDepartment of Geography, King's College London, London WC2B 4BG, United Kingdom; ʲSchool of Agriculture, Food & Ecosystem Sciences, University of Melbourne, Parkville, VIC 3010, Australia; ᵏFenner School of Environment & Society, The Australian National University, Canberra, ACT 2601, Australia; ˡMPG Ranch, Missoula, MT 59801; ᵐCentre for Environmental and Climate Science, Lund University, Lund 22362, Sweden; ⁿGerman Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, Leipzig 04103, Germany; ᵒInstitute of Biology, Leipzig University, Leipzig 04103, Germany; ᵖDepartment of Life Sciences, Imperial College London, Ascot SL57PY, United Kingdom; �q Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa; ʳVegetation Ecology and Biodiversity Conservation Group, Institute of Ecology, Leuphana University of Lüneburg, Lüneburg 21335, Germany; ˢDepartment of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803; ᵗEcology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht 3584 CH, The Netherlands; ᵘDepartment of Biological Sciences, Michigan Technological University, Houghton, MI 49931; ᵛDepartment of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou 215123, China; ʷChair of Biodiversity and Nature Tourism, Estonian University of Life Sciences, Tartu 51006, Estonia; ˣDepartment of Environmental Science and Policy, Marist University, Poughkeepsie, NY 12601; ʸDepartment of Aquatic Microbial Ecology, Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, Ceske Budejovice 370 05, Czech Republic; ᶻDepartment of Biology, McDaniel College, Westminster, MD 21157; ªªDepartment of Geography & Environment, Loughborough University, Loughborough LE11 3TU, United Kingdom; ᵇᵇDepartment of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu 50409, Estonia; ᶜᶜDepartment of Biology and Biochemistry, University of Houston, Houston, TX 77204; ᵈᵈEstación Experimental Santa Cruz, Instituto Nacional de Tecnología Agropecuaria, Rio Gallegos, Santa Cruz 9400, Argentina; ᵉᵉHawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2751, Australia; ᶠᶠResearch Unit Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf 8903, Switzerland; ᵍᵍDepartment of Physiological Diversity, Helmholtz Centre for Environmental Research, Physiological Diversity, Leipzig 04318, Germany; ʰʰDepartment of Biological Sciences, Texas Tech University, Lubbock, TX 79409; ⁱⁱLancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, United Kingdom; ʲʲEcology & Genetics, University of Oulu, Oulu 90014, Finland; ᵏᵏSchool of Environmental and Life Sciences, The University of Sydney, Sydney, NSW 2006, Australia; and ˡˡState Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, College of Ecology, Lanzhou University, Lanzhou Gansu 730000, People's Republic of China

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