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Shedding light on the increased carbon uptake by a boreal forest under diffuse solar radiation across multiple scales

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Abstract

Solar radiation is scattered by cloud cover, aerosols and other particles in the atmosphere, all of which are affected by global changes. Furthermore, the diffuse fraction of solar radiation is increased by more frequent forest fires and likewise would be if climate interventions such as stratospheric aerosol injection were adopted. Forest ecosystem studies predict that an increase in diffuse radiation would result in higher productivity, but ecophysiological data are required to identify the processes responsible within the forest canopy. In our study, the response of a boreal forest to direct, diffuse and heterogeneous solar radiation conditions was examined during the daytime in the growing season to determine how carbon uptake is affected by radiation conditions at different scales. A 10-year data set of ecosystem, shoot and forest floor vegetation carbon and water-flux data was examined. Ecosystem-level carbon assimilation was higher under diffuse radiation conditions in comparison with direct radiation conditions at equivalent total photosynthetically active radiation (PAR). This was driven by both an increase in shoot and forest floor vegetation photosynthetic rate. Most notably, ecosystem-scale productivity was strongly related to the absolute amount of diffuse PAR, since it integrates both changes in total PAR and diffuse fraction. This finding provides a gateway to explore the processes by which absolute diffuse PAR enhances productivity, and the long-term persistence of this effect under scenarios of higher global diffuse radiation.

KEYWORDS

diffuse light, eddy covariance, light use efficiency, Scots pine, understorey

1 | INTRODUCTION

Boreal forests span across high latitudes of northern America, Europe and Asia, and capture roughly 20% of the carbon assimilated by forests globally (Pan et al., 2011). Global change will have a profound impact on boreal forests by changing biotic and abiotic conditions (Gauthier et al., 2015; Price et al., 2013; Venäläinen et al., 2020). Solar radiation is a key factor determining ecosystem

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carbon uptake. However, there is high uncertainty about how incident radiation is changing (IPCC, 2021), and how these changes will affect the terrestrial carbon budget (Lee et al., 2018).

Cloud cover in the boreal region is expected to increase (IPCC, 2021) due to global change because of rising temperature (Coumou et al., 2013; Hansen et al., 2006), changes in atmospheric circulation patterns (Horton et al., 2015; Screen et al., 2018), ground albedo (He et al., 2013; Manninen et al., 2019), elevated concentrations of greenhouse gases (Jones et al., 2023) and increased frequency and intensity of forest fires (de Groot et al., 2013). Clouds and atmospheric particles scatter and absorb the incoming radiation, thus changing not only the amount of incoming radiation transmitted to the biosphere (Ylivinkka et al., 2020; Zhang et al., 1996), but also its spectral composition and directionality (Bain & Preston, 2020; Bartlett et al., 1998; Durand et al., 2021). Additionally, climate warming lengthens the growing season (Pulliainen et al., 2017) and is expected to increase plant physiological activity in the boreal region (Lindner et al., 2010). This leads to higher emissions of plant volatile organic compounds (VOC) (Aalto et al., 2014). Higher VOC emissions contribute to the increased formation of atmospheric particles (Lihavainen et al., 2015; Petäjä et al., 2022) and thus cause increased scattering of solar radiation (Rap et al., 2018), both directly through increased concentration of aerosols in the air and indirectly through an enhanced formation of clouds (Zhao et al., 2017).

Ecosystem-level monitoring of carbon dioxide fluxes suggests that diffuse radiation can enhance gross primary productivity (GPP) compared with the equivalent amount of direct radiation (Dengel & Grace, 2010; Zhou et al., 2021). However, the enhancement effect of diffuse radiation is not universal (Alton, 2008; Letts et al., 2005). Zhou et al. (2021) found that the GPP of evergreen needleleaf forests seems to increase more than that of other ecosystems, like broadleaf forests, shrublands or croplands, in response to diffuse radiation. The degree to which diffuse radiation has a fertilizing effect has been linked to the surface area of plants' photosynthetically active organs (Wohlfahrt et al., 2008), their spatial distribution in the canopy (clumping) (Chen et al., 2012; Li et al., 2023), leaf transmittance and leaf angle (Knohl & Baldocchi, 2008).

Photosynthesis by canopy trees plays a crucial role in determining the carbon balance of forest ecosystems. In Scots pine-dominated boreal forests (*Pinus sylvestris*), photosynthesis by trees can account for ~90% of the annual GPP (Ilvesniemi et al., 2009). There are only a few in situ studies where leaf- or shoot-level gas exchange measurements of trees were conducted to investigate the impact of diffuse radiation (Berry & Goldsmith, 2020; Wang et al., 2018). Furthermore, to our knowledge, there is only one study site where leaf-level measurements have been directly compared to ecosystem-level data, allowing a comparison across these two scales (Urban et al., 2006, 2012). Carbon-flux response of forest floor vegetation to diffuse radiation has been investigated even less, although various monitoring studies from across the boreal region have reported that photosynthesis by forest floor vegetation in evergreen boreal forests can contribute from 3% to 18% of the GPP (Bergeron et al., 2009; Ilvesniemi et al., 2009; Kolari et al., 2006; Launiainen et al., 2005; Misson et al., 2007). A thorough comprehension of how CO_2 fluxes from the different components of a forest ecosystem are affected by diffuse radiation is crucial for predicting how climate change will affect carbon uptake in the boreal region. This knowledge becomes highly relevant when considering solar geoengineering methods such as the injection of sulphate aerosols into the stratosphere (Irvine et al., 2016) and the predicted increased frequency of forest fires (de Groot et al., 2013), both of which release particles in the atmosphere, enhancing the scattering of radiation.

This study investigates whether diffuse radiation promotes photosynthetic carbon assimilation in a Scots pine forest, and if photosynthesis is affected similarly at various scales—whole ecosystem, shoot and forest floor. Studies on shoots of conifer species other than Scots pine have found that both supplemental lamp treatment (Reinhardt & Smith, 2016) and solar diffuse radiation (Hughes et al., 2015; Urban et al., 2006) can enhance photosynthetic rates compared with direct or clear-sky radiation. It has been proposed that diffuse radiation enhances carbon uptake by improving light use efficiency (LUE), as solar radiation is distributed among shoots to reach the lower canopy without oversaturating the top canopy (Alton, 2008; Knohl & Baldocchi, 2008).

Forest floor CO_2 fluxes typically have high spatial variability due to the heterogeneous structure of the forest, where distributions of tree roots, fungal colonization and understorey plant respiration contribute to variation in heterotrophic respiration (Chi et al., 2021; Ryhti et al., 2021). During clear-sky conditions, the forest canopy creates an interplay of sunflecks, shade and partial shade, forming distinctive dynamic patterns of light on the forest floor (Durand et al., 2024). In a boreal Scots pine forest, up to 15% of the forest floor was found to receive direct radiation in clear-sky conditions at midday (Kolari et al., 2006), whereas under diffuse conditions, solar radiation has a more spatially uniform distribution (Lieffers et al., 1999). This could favour enhanced photosynthesis (Smith & Berry, 2013) for equivalent incident radiation, since generally it is considered that photosynthesis becomes saturated at low irradiances in understorey plants (Bergeron et al., 2009; Kolari et al., 2006), while sunflecks can result in sudden excess radiation and heat stress (Way & Pearcy, 2012). Given the findings of these studies, we hypothesize that diffuse radiation conditions in our Scots pine site in the boreal forest would increase both the ecosystem-level GPP and photosynthetic rates of Scots pine shoots and forest floor vegetation. Specifically, we anticipate that forest floor vegetation will benefit from increased radiation penetrating to the understorey under diffuse radiation conditions, while shoot photosynthesis will increase through improved light use efficiency.

2 | MATERIALS AND METHODS

2.1 | Study site

Data were collected at SMEAR (Station for Measuring Ecosystem-Atmosphere Relations) II in a boreal forest, in southern Finland (61°51′ N, 24°17′ E, 180 m a.s.l.). The forest was planted in 1962

(Hari et al., 2013), growing on Haplic podzol soil (average depths of 0.5–0.7 m) with small peat deposits in depressions (Aaltonen et al., 2011; Ilvesniemi et al., 2009). There is a consistent stand structure over the 150 m radius surrounding the eddy covariance flux tower (Alekseychik et al., 2013). The forest canopy is dominated by Scots pine (*Pinus sylvestris*). The midstorey is composed of sparse spruce (*Picea abies*), birch (*Betula pendula* and *Betula pubescens*), aspen (*Populus tremula*) and grey alder (*Alnus incana*) (Ilvesniemi et al., 2009). All-sided leaf area index of canopy and midstorey trees was 5.5 $m^2 m^{-2}$ in the 2007 growing season (Chen, Xavier, et al., 2021). The canopy clumping index, measured at the ground, was 0.52 after the 2011 growing season (Pisek & Oliphant, 2013). At the end of the study period (2019), the mean timber height was 18.6 m, the mean diameter at breast height was 17.4 cm and the stand basal area was 31 $m^2 ha^{-1}$ (Aalto et al., 2023).

Mosses, *Dicranum polysetum*, *Hylocomium splendens* and *Pleurozium schreberi*, cover 60% of the forest floor and account for 58% of green biomass, while the leaf mass of lingonberry (*Vaccinium vitis-idaea*) makes up 33% and bilberry (*Vaccinium myrtillus*) 9% of the total green biomass (Kolari et al., 2006). According to the Cajander site classification, the forest vegetation type is *Vaccinium* (Cajander, 1949). The stand is characteristic of a typical managed boreal pine forest and was thinned in 2002 (Vesala et al., 2005). The long-term mean air temperature is 3.5°C, and the annual mean precipitation at the site is 711 mm (Pirinen et al., 2012). A schematic map of the study site is shown in Appendix S1.

2.2 | Environmental monitoring

Total (diffuse and direct) photosynthetically active radiation (PARt, i.e. radiation in the wavelength range 400–700 nm) and diffuse photosynthetically active radiation (PARd) were measured every minute with a BF3/BF5 sunshine sensor (Delta-T Devices, Cambridge, UK) and averaged per half-hour. The sensor was located above the canopy (from the years 2010 to 2017 at 17 m in height, and from the years 2017 to 2019 at 35 m in height from the ground). The diffuse fraction was calculated as a ratio between measured PARd and PARt. Data were classified into predominantly *Direct*, *Diffuse* and *Heterogeneous* radiation conditions during each integrated half-hour period based on the diffuse fraction. Conditions were classified into discrete categories as *Direct* when the diffuse fraction was less than 0.2 (Emmel et al., 2020; Yue & Unger, 2018) and as *Diffuse* when the diffuse fraction was greater than 0.6, following Laffineur et al. (2013). Intermediate time points (>0.2 and <0.6) were classified as *Heterogeneous*. Data were collected only when a specific radiation condition lasted for at least an hour (i.e. two time points). Only mean primary productivity values from the second half-hour were used in the analysis to exclude transitional periods during which plants acclimated to new sunlight conditions. Data were restricted to the peak of the growing season (1 June to 31 August), and to periods within 3 h on either side of solar noon (i.e. 10:00–16:00). The density of data points across years, months and hours is presented in Appendix S2.

Restricting our analysis to the summer period excluded phenological variation between years as well as spring and autumn periods when temperature rather than sunlight is considered the primary determinant of photosynthesis (Lagergren et al., 2008; Williams et al., 2016). Morning and evening hours were omitted from analysis to prevent mislabelling time points with a naturally higher proportion of diffuse radiation and to control the effects of photosynthesis diurnal variability (Nichol et al., 2019). Ecosystem GPP, shoot and forest floor vegetation photosynthesis were collected for each corresponding *Direct*, *Diffuse* or *Heterogeneous* time points. Since shoot and forest floor vegetation flux data are instantaneous measurements, an additional criterion was applied when selecting data: radiation conditions at the minute of the measurement must align with the corresponding half-hour radiation conditions' category (i.e. *Direct*, *Diffuse* and *Heterogeneous*).

To evaluate the radiation transmission through the canopy to the forest floor under different radiation conditions, we used below-canopy PAR. Below-canopy PAR was measured with four Li-Cor Li190SZ PAR sensors placed on a beam at 0.6 m height, spaced 1 m apart. Below-canopy PAR was calculated as the mean of the measurements in the four locations. These PAR sensors were cross-calibrated every year in June. In addition, other environmental variables relevant to primary productivity—air humidity and air temperature at 2 m height—were obtained from the Finnish Meteorological Institute (Open data interface at https://en.ilmatieteenlaitos.fi/open-data/) at the Hyytiälä weather station, approximately 440 m west of the study site, where measurements were taken every 10 min and averaged per half-hour.

2.3 | Measurements of primary productivity across different scales

2.3.1 | Ecosystem-scale measurements of gas exchange

Eddy covariance data measured at the SMEAR II flux tower (Ilvesniemi et al., 2010; Vesala et al., 1998) were used to calculate ecosystem-level GPP and evapotranspiration. GPP represents CO_2 assimilation and was calculated as the difference between measured net ecosystem exchange and the modelled ecosystem respiration. Total ecosystem respiration was modelled from night-time CO_2 flux based on soil temperature, as described in Kulmala et al. (2019). Only measured fluxes were included; gap-filled time points were excluded in both the GPP and evapotranspiration datasets.

2.3.2 | Scots pine shoot gas exchange in top canopy

Fluxes of CO_2 and H_2O were measured from Scots pine shoots enclosed in individual cylindrical (14.4 cm inner diameter, 3.5 dm^3 volume) or rectangular (2.1 dm^3 volume) chambers. The cylindrical chambers were made of 3 mm thick polymethyl methacrylate

(PMMA) with a fluorinated ethylene propylene inner coating to reduce particulate deposition on chamber walls. While the PMMA used in the chambers was transparent to PAR, the material does not transmit UV radiation (Raivonen et al., 2003). The sides of the rectangular chambers were made of the same material, while the top of the rectangular chambers was made of UV-transparent Röhm Sunactive 2458 PMMA (the manufacturer stated transmission was at 315 nm ≥ 80%, from 380 to 780 nm ≥ 90%). The lid of the cylindrical chamber was closed during measurements, whereas at other times the lid was open. Nevertheless, in cylindrical chambers, the shoot was not fully exposed to the surrounding environmental conditions, unlike in rectangular chambers. The rectangular chamber was closed for measurements, while at all other times it was open. The chambers closed automatically for 60 s prior to measurement, and sample airflow was drawn down into the infrared gas analyzer (Uras 4, Hartmann and Braun, Frankfurt am Main, Germany, until 2013, and afterwards LI-840A, LI-COR, Lincoln, NE, USA). A small fan ensured the homogeneous mixing of air when each chamber was closed. Measurements were taken 2–5 times every hour. At the end of the measuring period, the shoot area was measured, and gas exchange per area was calculated. A more detailed description of flux calculations can be found in Kolari et al. (2012).

Chambers were located on the topmost shoots of Scots pine trees, where they were not shaded by other trees. Only shoots at the top of the canopy were measured, to attribute observed changes more easily to changes in the atmospheric conditions and to standardize sampling across factors such as sun and shade acclimation and leaf age. The shoots were 1 or 2 years old, and each year 1–3 chambers were used (Appendix S3). Within the study period, the chambers were set up on three trees located close (<80 m) to the eddy covariance tower. Gross shoot photosynthesis was calculated as the difference between measured CO_2 flux (net assimilation) and modelled shoot respiration. Daytime shoot respiration was obtained, using temperature in the chamber at the time of measurement, and a linear model of the relationship between night-time CO_2 flux and air temperature calculated for each chamber and year combination (Appendix S4). The night-time was defined as hours between 10 p.m. and 4 a.m. when PARt (above the canopy) $<0\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$.

2.3.3 | Gas exchange from forest floor vegetation

Fluxes of CO_2 and H_2O were measured in three chambers on the forest floor (Appendix S3). The spacing between chambers ranged from 10 to 30 m, and the distance to the eddy flux tower was less than 70 m. Chambers were placed in different locations to represent the natural variation in the understorey. Chambers of 0.8 m length, 0.4 m width and 0.25 m height were mounted on collars of the same size that were previously installed in the soil, creating a seal. Chambers were made of an aluminium frame and fluorinated ethylene propylene film (0.05 mm) (Kolari et al., 2012), which has been shown to transmit more than 85% of 400–600 nm radiation (Jiang et al., 2019). The chambers closed automatically every 3 h for 15 min for measurements, during which time the sample airflow was drawn to an infrared gas analyzer. Fluxes were calibrated against the plant surface area that was measured at the time of chamber installation, as described in more detail by Aaltonen et al. (2013).

Gross forest floor photosynthesis was calculated as the difference between measured CO_2 flux and modelled respiration. The relationship between night-time respiration (identified as the night-time CO_2 flux) and temperature near the soil humus layer was modelled, similarly to shoot chambers, with a linear regression for each chamber and year combination (Appendix S5).

2.4 | Data availability and analysis

Solar radiation, GPP and evaporation data were collected from the Smart SMEAR open database (smear.avaa.csc.fi). Data from the period between 2010 and 2019 were utilized. Pine shoot flux data and forest floor flux data are openly available (Aalto, 2023). Data were analysed using R 4.2.3 (R Core Team, 2023). The source code is available at github.com/Santa-Neimane/GCB_carbon_uptake.

The photosynthetic rates of pine shoots and forest floor vegetation were scaled using the min-max scaling method for each chamber and year. This approach was chosen to account for differences in the absolute flux levels between different shoots, forest floor locations and chamber types. The minimum value was defined as the 0.05 quantile, while the maximum value was established as the 0.95 quantile for daytime photosynthetic rates (daytime defined as PARt (above canopy) $>0\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$).

For visualization, productivity PAR response curves were fitted with a rectangular hyperbola Michaelis–Menten-based model (Equation 1), according to De Lobo et al. (2013). Where P is productivity (GPP or photosynthetic rate), φ_{PAR0} is the quantum yield at 0 *PARt* and $P_{\max}$ is an estimate of maximum productivity. The rectangular hyperbola models were not used for further statistical analysis due to the absence of values where PARt was less than $500\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$, both under *Direct* and *Heterogenous* radiation conditions, which prevented the fitted model parameters from being biologically meaningful. The parameters of fitted models are shown in Appendix S6.

$$P = \frac{\varphi_{PAR_0} \times PARt \times P_{\max}}{\varphi_{PAR_0} \times PARt + P_{\max}}. \tag{1}$$

Statistical analysis of the response of gas exchange to PARt (Figure 1) was done with a mixed effect model, where radiation conditions and above-canopy PAR were fixed factors and the date was a random factor. In shoot and forest floor vegetation models, the chamber number was also set as a nested random factor with the date. Model residual normality and homoscedasticity were assessed visually. *Post-hoc* pairwise comparisons were performed using the Tukey–Kramer test. To account for multiple comparisons, the *p*-values were adjusted using the Bonferroni correction. In the results, *F*-value, numerator degrees of freedom, denominator degrees of freedom and post-hoc pairwise comparison *p*-values are given.

LUE was calculated by dividing GPP, shoot photosynthetic rate or forest floor vegetation photosynthetic rate by PARt. Water use efficiency (WUE) was calculated by dividing productivity with measured evapotranspiration. At the ecosystem scale, half-hour average values of both GPP and PARt, or evapotranspiration, were used. At the shoot and forest floor scales, instantaneous photosynthetic rate and PARt, or evapotranspiration at the minute of the measurement, were used.

The relationship between diffuse fraction and absolute diffuse PAR (Figure 3b) was described using a fourth-order dose response multistage model (Equation 2), where df is radiation diffuse fraction and $\gamma, \beta_1, \beta_2, \beta_3, \beta_4$ are modelled parameters. Both models were fitted with the R's minpack.lm package. For linear regressions, R^2 was calculated by subtracting the division of the sum of squares of residuals and the total sum of squares from one. While the calculation of pseudo-R^2 for non-linear regression was the same, the result cannot be identically interpreted since it may not fall within the range between zero and one.

$$PARd = \gamma + (1 - \gamma) \times \left(1 - e^{-\beta_1 df - \beta_2 df^2 - \beta_3 df^3 - \beta_4 df^4}\right). \qquad (2)$$

R's missMDA package was used to impute missing values using a regularized approach for principal component analysis (PCA). The data for PCA were scaled and centred. All variables describing the weather were set as active, while parameters describing productivity and resource use efficiency (LUE/WUE) were considered as quantitative supplementary variables for the PCA analysis.

The density graphs (Figure 5) for below-canopy PAR were made with the ggridges package, where the bandwidth was determined using the Sheather and Jones method.

3 | RESULTS

3.1 | Productivity under direct vs diffuse radiation at different scales

Productivity was significantly greater under *Diffuse* conditions than under *Direct* or *Heterogenous* radiation conditions at the ecosystem scale ($F_{(2,7738)} = 634$, comparisons $p < .001$, Figure 1a) and shoot scale ($F_{(2,8263)} = 2704$, comparisons *Diffuse:Direct* & *Diffuse:Heterogeneous*—$p < .001$, Figure 1b) when exposed to equal PARt. Under *Direct* radiation conditions, the mean (±1 SD) GPP was 16.4 ± 3.1 μmol m^{-2} s^{-1} and the mean PAR was 1351 ± 184 μmol m^{-2} s^{-1}, over the whole study period. Conversely, under *Diffuse* radiation conditions, the same GPP, was achieved with only 600 μmol m^{-2} s^{-1} PARt (Figure 1a), according to the productivity radiation response curve. There was no significant difference in shoot photosynthetic rate under *Direct* and *Heterogeneous* radiation conditions ($p = .08$).

The photosynthetic rate of forest floor vegetation (coefficient of variation (CV) = 0.41) was more variable than that of GPP ($CV = 0.32$) or shoot photosynthetic rate ($CV = 0.35$). Forest floor vegetation's photosynthetic rate was significantly greater under *Diffuse* radiation conditions compared to both *Direct* and *Heterogeneous* radiation conditions under equivalent PARt ($F_{(2,1084)} = 129$, $p < .001$, Figure 1c). As with shoot productivity, there was no significant difference in the photosynthetic rate between *Direct* and *Heterogeneous* radiation conditions ($p = .51$). Throughout the 10-year study period, productivity under *Diffuse* in comparison with *Direct* radiation conditions was consistently higher at ecosystem and shoot scales (Appendices S7 and S8). However, at the forest vegetation scale, this pattern was less evident due to the limited availability of photosynthetic rate measurements (Appendix S9).

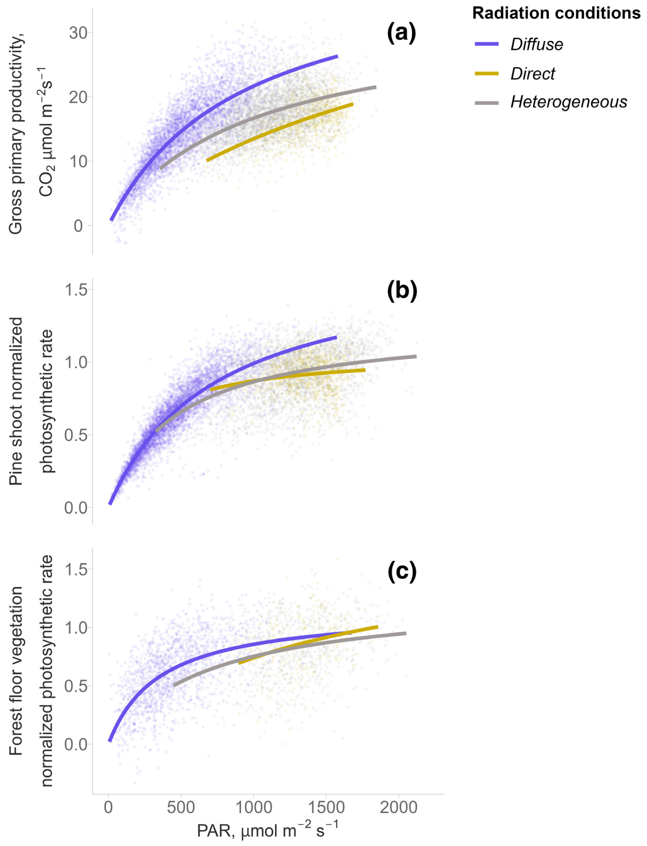

FIGURE 1 Productivity PAR response curve showing ecosystem (a), shoot (b) and forest floor vegetation (c) response to PARt. Colours denote different radiation conditions: Diffuse (violet), Direct (yellow) and Heterogeneous (grey). Lines show the fitted rectangular hyperbola Michaelis–Menten-based model (Equation 1). For ecosystem (a) GPP and PAR are means over 30 min, while shoot (b) and forest floor vegetation (c) photosynthesis and PAR show instantaneous measurements at the minute of measurement.

3.2 | Resource use efficiency

LUE, describing CO_2 assimilated per photon irradiance incident on the leaf, increased linearly with a higher diffuse radiation fraction across all scales (Figure 2). A higher LUE under diffuse radiation conditions implies that assimilation is higher relative to the available PARt.

Likewise, there was an increase in WUE, CO_2 assimilated per H_2O lost, at the ecosystem scale, implying less water loss per carbon

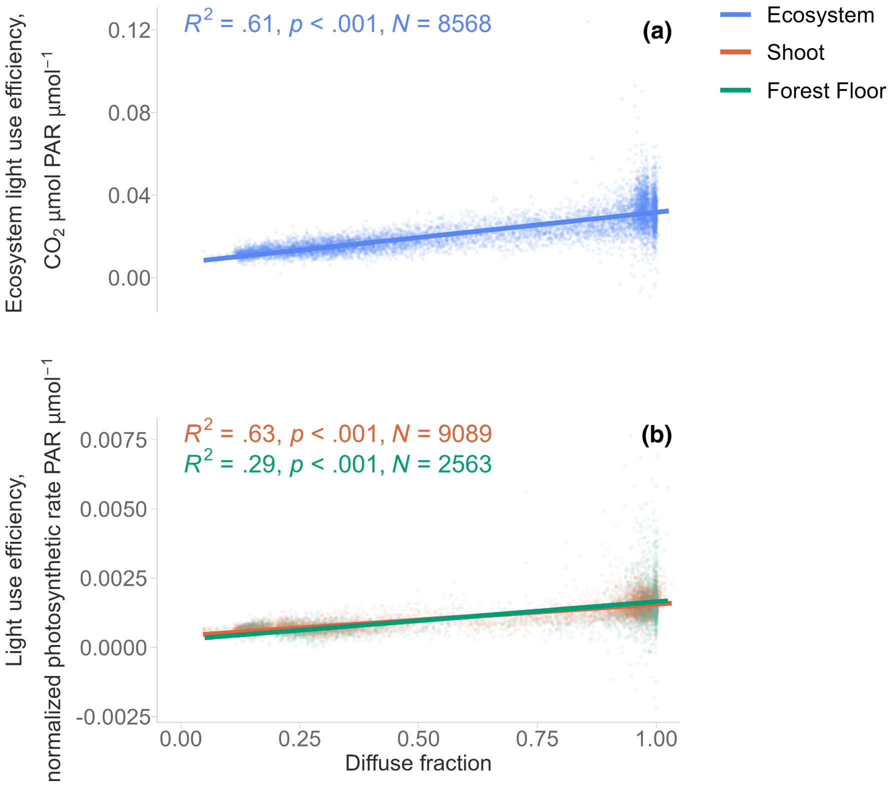

FIGURE 2 Linear relationships between diffuse fraction and light use efficiency at ecosystem (a, in blue), pine shoot (b, in orange) and forest floor (b, in green) scales. Points show observations, and lines show the linear regression (± SE ribbon too small to see). R^2, *p*-value and the total number of observations (*N*) are given.

gained (Appendix S10). WUE was also significantly positively correlated ($p<.001$) with the diffuse fraction at the shoot and vegetation scales; however, the coefficient of determination was very low (for shoots, $R^2=.05$ and for forest floor vegetation, $R^2<.01$). The model explains only a small proportion of the variance, as high WUE values were mainly associated with points where the diffuse fraction was above 0.95 under low PARt conditions.

3.3 | Environmental variables

As particles in the atmosphere diffuse radiation, they also provoke changes in other environmental factors. A higher diffuse fraction is also associated with linear decreases in PARt (Figure 3a), air temperature (Figure 3c), VPD (Figure 3e) and a linear increase in relative humidity (Figure 3d). Only the relationship between the diffuse fraction and the absolute amount of diffuse PAR did not follow a linear pattern (Figure 3b): based on the fitted model, the highest absolute PARd (603 $\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$) was recorded at a diffuse fraction of 0.79 (Figure 3b).

PCA provided insights about the variance in environmental conditions during the sampled time points. In Figure 4a, the results of the ecosystem-scale PCA analysis are presented, focusing on the first two principal components that collectively account for 82.9% of the variance. Only the first two principal components had eigenvalues higher than or equal to 1 (3.1 and 1.0). Among the variables, PARt (21.8%), temperature (21.7%), relative humidity (26.3%) and VPD (30.1%) contributed nearly equal loadings to the first principal component, which explains 62.3% of the variance. On the other hand, PARd (94.9%) loaded on the second PCA component. The first component can be interpreted as a measure of overall cloudiness, while the second component indicates the absolute amount of PARd. The PCA shows close positive correlations between PARt, temperature and VPD, which negatively correlate with RH. There is no indication of a significant relationship between PARd and PARt or other environmental variables, neither in the PCA (Figure 4) nor the correlation matrix (Appendix S11). Across all scales—ecosystem (Figure 4a), shoot (Figure 4b; Appendix S11) and forest floor vegetation (Figure 4c; Appendix S11)—environmental variable contribution to the axis and explained variance were very similar.

GPP, LUE and WUE were added as supplementary variables (e.g. not used in the PCA). LUE and WUE were associated with RH (Figure 4a). LUE was negatively correlated with PARt. Photosynthesis by both shoot and forest floor vegetation was more closely related to PARt on the primary axis than to PARd on the secondary axis (Figure 4b,c; Appendix S11). While ecosystem GPP was likewise associated with PARt, it aligned more closely than the other two measures of photosynthesis with the secondary axis (Comp.1: 0.42, Comp.2: 0.63), where PARd was the dominant contributor (94.9%) (Figure 4a; Appendix S11).

4 | DISCUSSION

The 10-year dataset revealed that productivity of the Scots pine forest was increased under diffuse radiation conditions (Figure 1). However, the underlying mechanisms responsible for this effect differed from our initial hypothesis. While LUE did increase with a

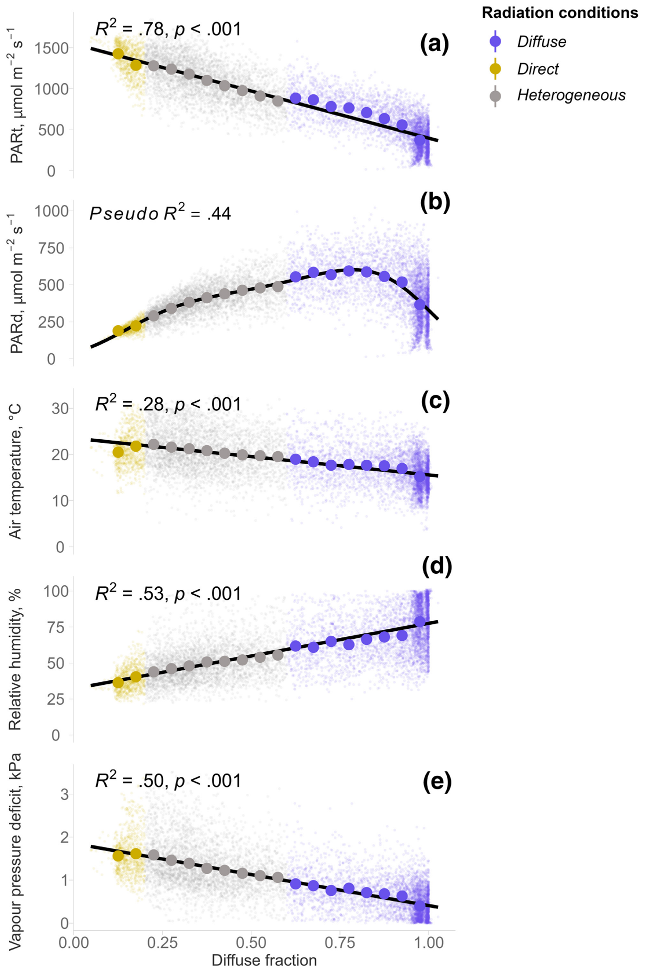

FIGURE 3 Relationship between observed diffuse fraction and environmental variables. Colours denote different radiation conditions: Diffuse (violet), Direct (yellow) and Heterogeneous (grey). Mean values are plotted at intervals of 0.05 in a diffuse fraction with large points. Error bars are shown, but they were smaller than the graph point size. Small points in the background show raw observations (30 min means). (a), (c), (d) and (e) fitted with linear regression, and (b) is fitted with a dose response multistage model (Equation 2).

higher diffuse fraction, GPP was most strongly associated with the absolute amount of PARd (Figures 1a and 4).

4.1 | Deconstructing gas exchange in the boreal forest

4.1.1 | Ecosystem flux

The GPP of the Scots pine forest increased significantly under diffuse radiation conditions (Figure 1), a result consistent with studies on spruce forests in central Europe (Urban et al., 2006) and Britain (Dengel & Grace, 2010), boreal and hemiboreal forests across Eurasia (Ezhova et al., 2018) and FLUXNET sites around the world (Zhou et al., 2021). It has been postulated that with an increase in the diffuse radiation fraction, the total canopy photosynthesis increases. This is because shaded leaves receive more incident irradiance, while the photosynthesis of sunlit leaves remains approximately constant, provided that irradiance remains above their light saturation point (Wohlfahrt et al., 2008). It has also been suggested that boreal forests may particularly benefit from increased diffuse radiation due to the long path length of sunlight through the canopy since the solar zenith angle is large at high latitudes (Zhou et al., 2021). Based on the findings presented in our study in southern Finland from 2010 to 2019, ecosystem productivity comparable to that found under clear skies was achieved at an irradiance of 600 μmol m^{-2} s^{-1} (PARt) above the canopy during diffuse radiation conditions (Figure 1). These conditions occurred in 35.2% of all half-hour periods over the study in summers from 10 a.m. to 4 p.m. However, while these favourable conditions exhibited an overall productivity boost, it is important to recognize that GPP measures the total amount of carbon that the ecosystem captures over its flux footprint area. Thus, it does not distinguish spatial and temporal patterns in assimilation partitioned between layers of the canopy and understorey vegetation.

4.1.2 | Pine shoots and needle acclimation

Particles in the atmosphere alter the distribution of sunlight reaching different forest canopy layers, affecting the dynamics of photosynthesis and transpiration within individual tree crowns (Hernandez-Moreno et al., 2017). In the long term, Scots pine trees may modify crown placement, structure and leaf mass to ensure light capture (Lintunen et al., 2011; Uria-Diez & Pommerening, 2017), whereas short-term responses to changes in light conditions can be assessed with shoot chambers (Ilvesniemi et al., 2009). In our study, the photosynthetic rate of shoots at the top of the canopy, that were acclimated to high irradiance, was highest under diffuse radiation conditions at equivalent PARt (Figure 1b). Although research on the effects of diffuse radiation at the shoot level on Scots pine is limited, an increase in the photosynthetic rate of shoots on branches harvested from young stands has also been reported under diffuse radiation compared with direct radiation treatments, though in controlled conditions with an artificial light source (Oker-Blom et al., 1992). Simulations of the interception of radiation by shoots suggested that diffuse radiation is beneficial even at a one-shoot scale because of reduced self-shading (under direct radiation, 54%–68% of the total needle surface area was shaded) (Oker-Blom et al., 1992). While we focused on leaves at the top of the canopy, the relative contribution of top and lower-canopy leaves to the overall ecosystem response to diffuse radiation is still unclear. This needs to be addressed with leaf-level data through the canopy vertical gradient before a comprehensive understanding of the canopy response to diffuse radiation can be achieved. At our study location, it is likely that enhancement of the photosynthetic rate of mid- and lower-canopy shoots under diffuse radiation conditions was greater than that found for canopy-top shoots. Such a pattern of photosynthetic enhancement in mid- and lower-canopy shoots in comparison with canopy-top shoots under

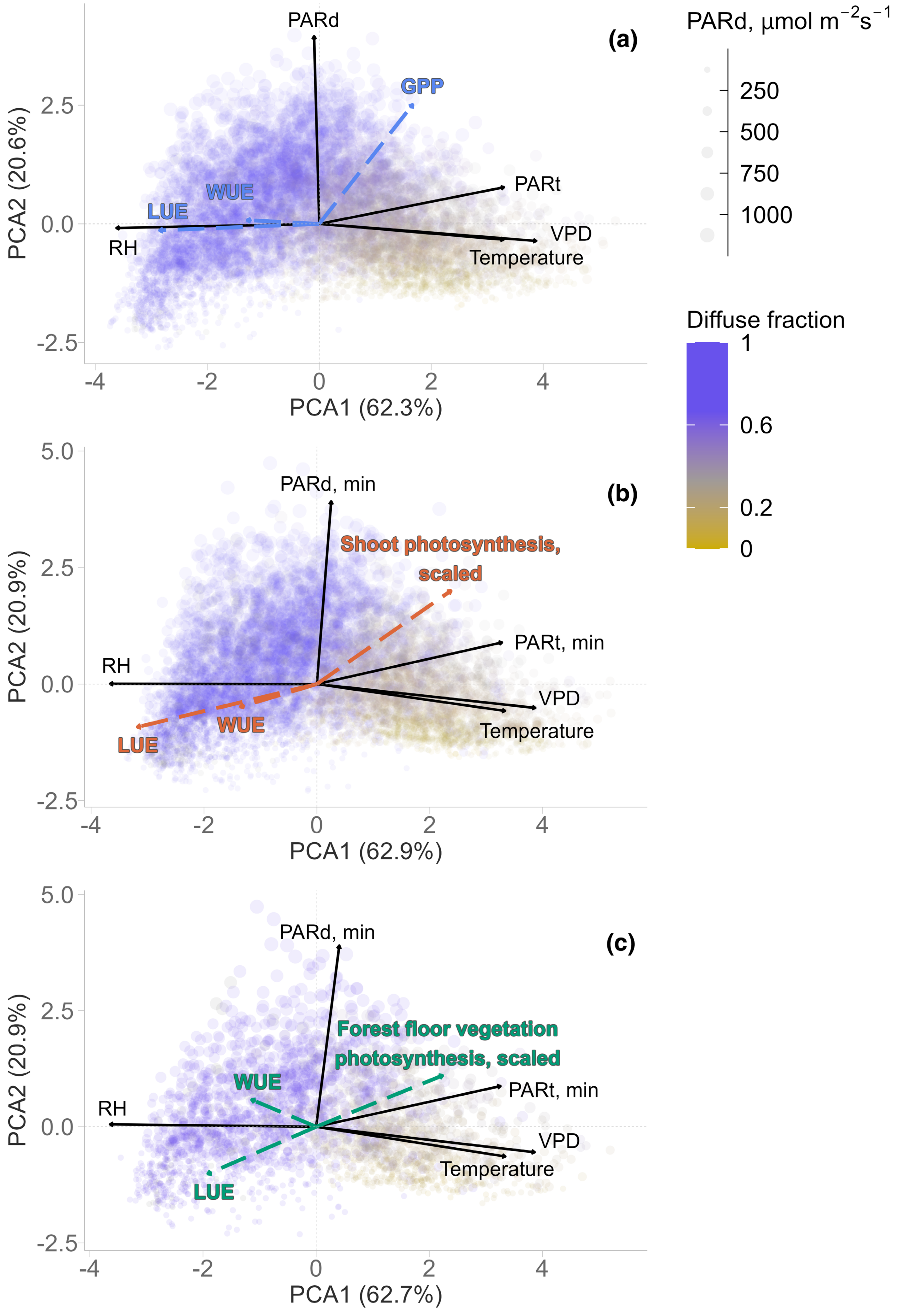

FIGURE 4 Principal component analysis of ecosystem (a), shoot (b) and forest floor vegetation (c) data. In the loading plot, active variables are depicted in black, while supplementary variables are denoted by other colours. Score plot points coloured according to radiation diffuse fraction; point size scaled in five bins according to the absolute amount of diffuse PAR above the canopy.

cloudy conditions has been recorded for Norway spruce trees over a week (Urban et al., 2012), one of the only studies examining leaf-level dynamics in situ.

The response of leaf-level photosynthetic rate to diffuse radiation depends on physiological and morphological acclimation of the leaf to light conditions (Brodersen et al., 2008). In sun- and shade-acclimated leaves, direct and diffuse radiation are differently transmitted and reflected (Gorton et al., 2010). Chlorophyll *b* in the light harvesting complex of chloroplasts ensures efficient utilization of diffuse radiation, whereas under direct radiation, chlorophyll *b* is excluded from the core antennae of photosystem II to avoid overheating. This suggests that shade leaves are adapted to use diffuse radiation more efficiently (Kume et al., 2019). Urban et al. (2012) further suggested that the whole forest canopy is likely to be acclimated to the most-prevalent radiation conditions. This suggestion is consistent with the findings of our study, whereby both shoot photosynthesis and GPP were highest under diffuse radiation conditions, which accounted for 61.0% of all the half-hour periods from 2010 to 2020, compared with 16.4% for direct radiation conditions.

4.1.3 | Vegetation on the forest floor

There are very few studies that examine the effects of diffuse on the photosynthesis of vegetation on the forest floor, and even fewer systematically compare direct to diffuse radiation conditions. Generally, these studies show that long-term diffuse irradiance increases growth (Feldmann et al., 2020; Fournier et al., 2004; Tinya

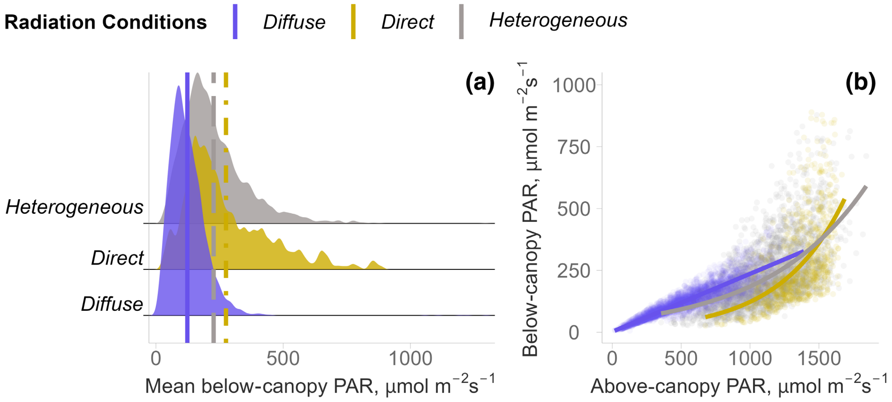

FIGURE 5 Radiation profile showing PAR below the canopy (averaged per 30 min) datapoint density under Diffuse (violet), Direct (yellow) and Heterogeneous (grey) radiation conditions (a). Vertical lines show the mean value under each radiation condition. Lines show relationship between above- and below-canopy PAR, linear relationship under Diffuse radiation conditions and exponential functions to represent the relationship under Direct and Heterogeneous conditions (b). Points are PAR measurements averaged per 30 min.

& Ódor, 2016). In North American broadleaf forests, a positive correlation was found between cumulative diffuse radiation, modelled from hemispherical pictures taken under an overcast sky, and the growth of understorey species American ginseng (*Panax quinquefolius*) (Fournier et al., 2004). In temperate forests of Central Europe, shoot growth of tree saplings in the understorey was found to be greater in locations receiving high diffuse radiation, as calculated based on canopy gap size (Feldmann et al., 2020). Similarly, in a deciduous-coniferous mixed forest in Central Europe, a positive correlation has been recorded between the amount of diffuse radiation at specific locations, estimated from canopy gap measurements at dusk, and total cover of understorey vascular plants (Tinya & Ódor, 2016). There are even fewer studies that focus on gradual responses of plant productivity to transient changes in diffuse radiation over a long period of time, as we have done. Our study presents evidence that in the boreal forest, where the understorey mostly consists of mosses and *Vaccinium* sp., diffuse radiation increases forest floor vegetation photosynthesis (Figure 1c). While it has been recorded that the photosynthetic rate of specific understorey species is higher under cloudy skies (Young & Smith, 1983), only lately has this response to diffuse radiation been reported to vary among species (Berry & Goldsmith, 2020).

The light saturation point of photosynthesis of forest floor vegetation differs between species, but generally occurs at relatively low irradiances compared with that of the canopy (Bergeron et al., 2009; Kolari et al., 2006). In our study, under diffused radiation conditions, photosynthesis of forest floor vegetation reached saturation at above-canopy PARt of ~600 m^{-2} s^{-1} (Figure 4c), where approximately one-third of PARt reached the understorey (Figure 5b). In comparison, the understorey received more light, on average, under direct radiation conditions than under diffuse radiation conditions (Figure 5a). This is likely to be due to the open canopy structure typical of Scots pine forests at high latitudes (Petersson et al., 2019). Nevertheless, the amplitude of variation in below-canopy PAR values was reduced under diffuse radiation, which presumably provided more stable conditions for photosynthesis (Figure 5a). This result is consistent with other research conducted in Scots pine forests, which also found that mean understorey irradiance did not significantly differ between clear and overcast sky conditions, but that there was less variation in understorey radiation under overcast conditions (Messier & Puttonen, 1995). The duration and intensity of fluctuating light have been found to control enzyme activities, stomatal conductance and non-photochemical quenching, all potentially reducing the efficiency of photosynthesis (Grieco et al., 2020; Han et al., 2022; Kaiser et al., 2018; Yamori et al., 2020).

4.2 | Microclimate and resource use efficiency

Changes in sky conditions not only affect radiation transmission, but also other microclimatic factors that can impact photosynthesis (Gu et al., 2002; Urban et al., 2012; Wohlfahrt et al., 2008). In our study, as the diffuse fraction increased, air temperature decreased and air humidity increased, and thus VPD was reduced (Figure 3). These abiotic factors were not strongly linked with productivity at any scale (Figure 4) during the daytime through the growing season. However, Cheng et al. (2015) found that up to 32% of the variation in GPP in conifer forests, beyond that explained by PARt and PARd, could be explained by temperature and VPD (taking into account diurnal variation). Similarly, Wang et al. (2018) found that lower VPD under diffuse radiation conditions results in an increased photosynthetic rate in the sun leaves of young poplar trees growing in a temperate continental monsoon climate. Ecosystem-specific thresholds for temperature and VPD have also been reported, beyond which the role of these abiotic factors becomes important in determining ecosystem productivity (Gui et al., 2021; Zhang et al., 2020). In our study, under diffuse radiation conditions, mean air temperature was 16.3°C with a relative humidity of 73.2% and a VPD of 0.5 kPa, while under direct radiation conditions, mean temperature was higher by 4.9°C, humidity dropped by 34.6%, and VPD increased by 1.0 kPa. The lack of a significant relationship between productivity and these changes in the abiotic conditions, even under direct radiation conditions, might suggest that they did not exceed the thresholds that define their optimum range for this Scots pine forest. Our study is confined to the boreal forest, and whether the conclusions extrapolate to other biomes remains to be determined. Cheng et al. (2015) report that the GPP of deciduous forests in the northern United States was not affected by variation in temperature and VPD across different radiation conditions. We anticipate that young forests, and forests situated in regions characterized by high temperatures and low soil moisture, would additionally benefit from diffuse radiation conditions through the concurrent reduction in temperature and VPD (Mirabel et al., 2023).

Experiments employing diffusive films over crops to create diffuse solar radiation treatments have found that diffuse radiation increases productivity by improving light use efficiency (Shao et al., 2020). Under direct radiation conditions, only a fraction of canopy leaves are illuminated, and PAR can reach the light saturation point (Berry & Goldsmith, 2020; Gu et al., 2002). Furthermore, land-surface model simulations suggest that more equitable sharing of PAR among leaves is the main driver behind increased LUE in forests, as opposed to environmental factors (temperature, VPD) or differences in the mean vertical profile of solar radiation (Alton et al., 2007). Under controlled conditions, increasing the diffuse fraction of light has been found to increase stomatal opening and photosynthesis in comparison with direct-beam light (Reinhardt & Smith, 2016). Both our study (Figure 2) and others (Alton et al., 2007; Ezhova et al., 2018) report increases in LUE with a greater diffuse fraction in boreal forests. In our study, ecosystem LUE was 140% higher under diffuse than direct radiation conditions (Figure 2), whereas Alton et al. (2007) reported only a 6%–33% increase when studying boreal needleleaf, temperate broadleaf and tropical broadleaf forests. This difference in the scale of effect may be attributed to differences in the study design. In Alton et al. (2007), diffuse fraction was not directly measured, and the criteria set for timepoint classification differed, whereby conditions with a diffuse fraction greater than 0.5 were categorized as diffuse radiation conditions, while those with a diffuse fraction less than 0.5 were categorized as direct radiation conditions. In contrast, our study introduced a third heterogeneous radiation category, which resulted in narrower ranges of diffuse fraction values within each category. Similarly, Ezhova et al. (2018) reported a *c* 300% increase in LUE under diffuse radiation conditions in a mixed forest in the hemiboreal zone, compared with only a *c* 90% increase in LUE in the same Scots pine forest as studied here. The time period studied by Ezhova et al. (2018) was 2 years (2008–2009) compared to our 10-year study, and their methodology differed—as PAR was estimated from solar broadband radiation for part of the period and all points with PAR $<200\,\mu\text{mol}\,\text{s}^{-1}\,\text{m}^{-2}$ were filtered out. The larger increase in LUE that we report could be partly attributed to our unique methodological approach, which accounted for the time needed for plants to acclimate to radiation conditions. Regarding WUE, with increasing diffuse fraction, WUE increased in our study (Appendix S10) and others (Liu et al., 2022; Rocha et al., 2004; Wang et al., 2023). Overall, WUE was weakly associated with a suite of environmental factors (Figure 4), but had we assessed this relationship independently for each radiation condition, we might have found a strong relationship. Accordingly, a global assessment of FLUXNET data found direct radiation, diffuse radiation, air temperature, VPD, and CO_2 concentration to colimit WUE, but with a differing hierarchy of importance according to the prevailing radiation conditions (Wang et al., 2023).

PARd had the strongest link with GPP in our study and was likewise the most important determinant of GPP in a subtropical coniferous forest at daily and monthly scales (Han et al., 2020), and across a wide range of other biomes (Wang et al., 2023). In structurally complex canopies, such as forests, PARd may serve as a more accurate indicator of available light for photosynthesis than PARt. Thus, partitioning out PARd from PARt when looking at causal relationships may improve the predictive power of models of productivity (Chen, Sui, et al., 2021). The weak association between PARd and photosynthetic rate at both shoot and forest floor scales may be due to the lack of irradiance measurements at the specific location of each chamber. Nevertheless, the photosynthetic rate is still highest under diffuse radiation conditions at both scales (Figure 1b,c).

5 | FUTURE IMPLICATIONS

This study illustrates how transient diffuse radiation conditions have a consistent fertilizing effect on the productivity of a Scots pine forest compared to direct radiation conditions. Nevertheless, we cannot reliably infer that a change in climate affecting cloudiness or atmospheric composition and leading to longer periods of prevailing diffuse radiation conditions would necessarily boost forest productivity. This is because plants may acclimate to the new prevailing diffuse radiation conditions by forming denser canopies or altering other structural or morphological traits, which could modulate the fertilization effect (Li & Yang, 2015; Shao et al., 2020). For example, a reduction in height with increased diffuse radiation was recorded in silver fir saplings growing in forest gaps naturally exposed to varying amounts of diffuse radiation (Orman et al., 2021). Thus, the fertilization effect of diffuse radiation may resemble the widely studied CO_2 fertilization effect, wherein productivity gains have been found to diminish over long time scales (Girardin et al., 2011; Wang et al., 2020). Furthermore, at a global scale, a strong positive ecosystem-level feedback loop between biogenic volatile organic compound (BVOC) emissions and plant productivity has been reported (Rap et al., 2018), whereby climate change has led to increased BVOC emission, resulting in an increased diffuse fraction and thus higher GPP, which in turn results in increased BVOC. This feedback loop highlights the interconnectedness of various ecological and atmospheric processes, and underscores the complexity of interactions between the biosphere and atmosphere. When modelling the potential impacts of increased global diffuse radiation resulting from solar radiation modification (Xia et al., 2016; Yang et al., 2020), climate change, or the regional effects of frequent forest fires (Rap et al., 2015), it is crucial to consider these potential long-term feedbacks. Until these data are acquired, scientists are unable to make confident predictions regarding the long-term implications for productivity stemming from changes in diffuse radiation.

6 | CONCLUSION

Ecosystem productivity was higher under diffuse than direct radiation conditions at equivalent PAR in our boreal Scots pine forest. This increase in productivity reflected an increased photosynthetic rate of both pine shoots and forest floor vegetation. To our knowledge, this is the first study to integrate the effects of diffuse and direct radiation on carbon fluxes across scales. The in situ shoot-level measurements we report are crucial for unravelling the mechanisms underlying ecosystem trends. The absolute amount of diffuse PAR was the best predictor of ecosystem carbon uptake, independent of all other environmental drivers. Both follow a Gaussian curve, whereby maxima are reached when the increase in diffuse fraction leads to a decline in the total amount of solar radiation. If this finding is consistent across environments, this would give us a metric by which canopy traits could be evaluated according to their ability to enhance photosynthesis within the canopy via diffuse radiation. Only by thoroughly examining the dynamic functioning of each canopy element in interaction with the rest of the ecosystem through in situ measurements, can we understand the effect of cloudiness and aerosols on plant canopies, upon which environmental policies are based.

AUTHOR CONTRIBUTIONS

Santa Neimane-Šroma: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Maxime Durand:** Formal analysis; methodology; supervision; writing – review and editing. **Anna Lintunen:** Methodology; supervision; writing – review and editing. **Juho Aalto:** Data curation; writing – review and editing. **T. Matthew Robson:** Methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data (solar radiation, gross primary productivity and evaporation data) that support the findings of this study are openly available in Smart SMEAR open database at https://smear.avaa.csc.fi. Pine shoot flux data and forest floors flux data is openly available in Zenodo at https://doi.org/10.5281/zenodo.10360968. Environmental data (air humidity, temperature, precipitation) are openly available from the Finnish Meteorological Institute, Open data interface at https://en.ilmatieteenlaitos.fi/open-data/ (Hyytiälä weather station).

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REFERENCES

Aalto, J. (2023). Hyytiälä SMEAR II Scots pine shoot and forest floor CO_2 and water vapour exchange rates 2009–2019 [dataset]. *Zenodo*, https://doi.org/10.5281/zenodo.10360968

Aalto, J., Kolari, P., Hari, P., Kerminen, V.-M., Schiestl-Aalto, P., Aaltonen, H., Levula, J., Siivola, E., Kulmala, M., & Bäck, J. (2014). New foliage growth is a significant, unaccounted source for volatiles in boreal evergreen forests. *Biogeosciences*, *11*(5), 1331–1344. https://doi.org/10.5194/bg-11-1331-2014

Aalto, J., Kolari, P., Korpela, I., Schiestl-Aalto, P., & Bäck, J. (2023). SMEAR II forest thinning: Description of the methods and background information for carbon storage estimation [dataset]. *Zenodo*, https://doi.org/10.5281/zenodo.8138946

Aaltonen, H., Aalto, J., Kolari, P., Pihlatie, M., Pumpanen, J., Kulmala, M., Nikinmaa, E., Vesala, T., & Bäck, J. (2013). Continuous VOC flux measurements on boreal forest floor. *Plant and Soil*, *369*(1–2), 241–256. https://doi.org/10.1007/s11104-012-1553-4

Aaltonen, H., Pumpanen, J., Pihlatie, M., Hakola, H., Hellén, H., Kulmala, L., Vesala, T., & Bäck, J. (2011). Boreal pine forest floor biogenic volatile organic compound emissions peak in early summer and autumn. *Agricultural and Forest Meteorology*, *151*(6), 682–691. https://doi.org/10.1016/j.agrformet.2010.12.010

Alekseychik, P., Mammarella, I., Launiainen, S., Rannik, Ü., & Vesala, T. (2013). Evolution of the nocturnal decoupled layer in a pine forest canopy. *Agricultural and Forest Meteorology*, *174–175*, 15–27. https://doi.org/10.1016/j.agrformet.2013.01.011

Alton, P. B. (2008). Reduced carbon sequestration in terrestrial ecosystems under overcast skies compared to clear skies. *Agricultural and Forest Meteorology*, *148*(10), 1641–1653. https://doi.org/10.1016/j.agrformet.2008.05.014

Alton, P. B., North, P. R., & Los, S. O. (2007). The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes: Impact of diffuse sunlight on canopy LUE, GPP and NEE. *Global Change Biology*, *13*(4), 776–787. https://doi.org/10.1111/j.1365-2486.2007.01316.x

Bain, A., & Preston, T. C. (2020). The wavelength-dependent optical properties of weakly absorbing aqueous aerosol particles. *Chemical Communications*, *56*(63), 8928–8931. https://doi.org/10.1039/D0CC02737E

Bartlett, J. S., Ciotti, Á. M., Davis, R. F., & Cullen, J. J. (1998). The spectral effects of clouds on solar irradiance. *Journal of Geophysical Research: Oceans*, *103*(C13), 31017–31031. https://doi.org/10.1029/1998JC900002

Bergeron, O., Margolis, H. A., & Coursolle, C. (2009). Forest floor carbon exchange of a boreal black spruce forest in eastern North America. *Biogeosciences*, *6*(9), 1849–1864. https://doi.org/10.5194/bg-6-1849-2009

Berry, Z. C., & Goldsmith, G. R. (2020). Diffuse light and wetting differentially affect tropical tree leaf photosynthesis. *New Phytologist*, *225*(1), 143–153. https://doi.org/10.1111/nph.16121

Brodersen, C. R., Vogelmann, T. C., Williams, W. E., & Gorton, H. L. (2008). A new paradigm in leaf-level photosynthesis: Direct and diffuse lights are not equal. *Plant, Cell & Environment*, *31*(1), 159–164. https://doi.org/10.1111/j.1365-3040.2007.01751.x

Cajander, A. (1949). Forest types and their significance. *Acta Forestalia Fennica*, *56*(5), 7396. https://doi.org/10.14214/aff.7396

Chen, D., Xavier, C., Clusius, P., Nieminen, T., Roldin, P., Qi, X., Pichelstorfer, L., Kulmala, M., Rantala, P., Aalto, J., Sarnela, N., Kolari, P., Keronen, P., Rissanen, M. P., Taipale, D., Foreback, B., Baykara, M., Zhou, P., & Boy, M. (2021). A modelling study of OH, NO_3 and H_2SO_4 in 2007–2018 at SMEAR II, Finland: Analysis of long-term trends. *Environmental Science: Atmospheres*, *1*(6), 449–472. https://doi.org/10.1039/D1EA00020A

Chen, J. M., Mo, G., Pisek, J., Liu, J., Deng, F., Ishizawa, M., & Chan, D. (2012). Effects of foliage clumping on the estimation of global terrestrial gross primary productivity. *Global Biogeochemical Cycles*, *26*(1), 2010GB003996. https://doi.org/10.1029/2010GB003996

Chen, S., Sui, L., Liu, L., & Liu, X. (2021). Effect of the partitioning of diffuse and direct APAR on GPP estimation. *Remote Sensing*, *14*(1), 57. https://doi.org/10.3390/rs14010057

Cheng, S. J., Bohrer, G., Steiner, A. L., Hollinger, D. Y., Suyker, A., Phillips, R. P., & Nadelhoffer, K. J. (2015). Variations in the influence of diffuse light on gross primary productivity in temperate ecosystems. *Agricultural and Forest Meteorology*, *201*, 98–110. https://doi.org/10.1016/j.agrformet.2014.11.002

Chi, J., Zhao, P., Klosterhalfen, A., Jocher, G., Kljun, N., Nilsson, M. B., & Peichl, M. (2021). Forest floor fluxes drive differences in the carbon balance of contrasting boreal forest stands. *Agricultural and Forest Meteorology*, *306*, 108454. https://doi.org/10.1016/j.agrformet.2021.108454

Coumou, D., Robinson, A., & Rahmstorf, S. (2013). Global increase in record-breaking monthly-mean temperatures. *Climatic Change*, *118*(3–4), 771–782. https://doi.org/10.1007/s10584-012-0668-1

de Groot, W. J., Flannigan, M. D., & Cantin, A. S. (2013). Climate change impacts on future boreal fire regimes. *Forest Ecology and Management*, *294*, 35–44. https://doi.org/10.1016/j.foreco.2012.09.027

De Lobo, F. A., De Barros, M. P., Dalmagro, H. J., Dalmolin, Â. C., Pereira, W. E., De Souza, É. C., Vourlitis, G. L., & Rodríguez Ortíz, C. E. (2013). Fitting net photosynthetic light-response curves with Microsoft Excel—A critical look at the models. *Photosynthetica*, *51*(3), 445–456. https://doi.org/10.1007/s11099-013-0045-y

Dengel, S., & Grace, J. (2010). Carbon dioxide exchange and canopy conductance of two coniferous forests under various sky conditions. *Oecologia*, *164*(3), 797–808. https://doi.org/10.1007/s00442-010-1687-0

Durand, M., Daviaud, A., & Robson, T. M. (2024). How tree stand phenology determines understorey senescence—A case study from boreal forests. *Agricultural and Forest Meteorology*, *344*, 109807. https://doi.org/10.1016/j.agrformet.2023.109807

Durand, M., Murchie, E. H., Lindfors, A. V., Urban, O., Aphalo, P. J., & Robson, T. M. (2021). Diffuse solar radiation and canopy photosynthesis in a changing environment. *Agricultural and Forest Meteorology*, *311*, 108684. https://doi.org/10.1016/j.agrformet.2021.108684

Emmel, C., D'Odorico, P., Revill, A., Hörtnagl, L., Ammann, C., Buchmann, N., & Eugster, W. (2020). Canopy photosynthesis of six major arable crops is enhanced under diffuse light due to canopy architecture. *Global Change Biology*, *26*(9), 5164–5177. https://doi.org/10.1111/gcb.15226

Ezhova, E., Ylivinkka, I., Kuusk, J., Komsaare, K., Vana, M., Krasnova, A., Noe, S., Arshinov, M., Belan, B., Park, S.-B., Lavrič, J. V., Heimann, M., Petäjä, T., Vesala, T., Mammarella, I., Kolari, P., Bäck, J., Rannik, Ü., Kerminen, V.-M., & Kulmala, M. (2018). Direct effect of aerosols on solar radiation and gross primary production in boreal and hemiboreal forests. *Atmospheric Chemistry and Physics*, *18*(24), 17863–17881. https://doi.org/10.5194/acp-18-17863-2018

Feldmann, E., Glatthorn, J., Ammer, C., & Leuschner, C. (2020). Regeneration dynamics following the formation of understory gaps in a Slovakian beech virgin forest. *Forests*, *11*(5), 585. https://doi.org/10.3390/f11050585

Fournier, A. R., Gosselin, A., Proctor, J. T. A., Gauthier, L., Khanizadeh, S., & Dorais, M. (2004). Relationship between understory light and growth of Forest-grown American ginseng (*Panax quinquefolius* L.). *Journal of the American Society for Horticultural Science*, *129*(3), 425–432. https://doi.org/10.21273/JASHS.129.3.0425

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, *349*(6250), 819–822. https://doi.org/10.1126/science.aaa9092

Girardin, M. P., Bernier, P. Y., Raulier, F., Tardif, J. C., Conciatori, F., & Guo, X. J. (2011). Testing for a CO_2 fertilization effect on growth of Canadian boreal forests. *Journal of Geophysical Research*, *116*(G1), G01012. https://doi.org/10.1029/2010JG001287

Gorton, H. L., Brodersen, C. R., Williams, W. E., & Vogelmann, T. C. (2010). Measurement of the optical properties of leaves under diffuse light. *Photochemistry and Photobiology*, *86*(5), 1076–1083. https://doi.org/10.1111/j.1751-1097.2010.00761.x

Grieco, M., Roustan, V., Dermendjiev, G., Rantala, S., Jain, A., Leonardelli, M., Neumann, K., Berger, V., Engelmeier, D., Bachmann, G., Ebersberger, I., Aro, E., Weckwerth, W., & Teige, M. (2020). Adjustment of photosynthetic activity to drought and fluctuating light in wheat. *Plant, Cell & Environment*, *43*(6), 1484–1500. https://doi.org/10.1111/pce.13756

Gu, L., Baldocchi, D., Verma, S. B., Black, T. A., Vesala, T., Falge, E. M., & Dowty, P. R. (2002). Advantages of diffuse radiation for terrestrial ecosystem productivity. *Journal of Geophysical Research: Atmospheres*, *107*(D6), ACL 2-1–ACL 2-23. https://doi.org/10.1029/2001JD001242

Gui, X., Wang, L., Su, X., Yi, X., Chen, X., Yao, R., & Wang, S. (2021). Environmental factors modulate the diffuse fertilization effect on gross primary productivity across Chinese ecosystems. *Science of the Total Environment*, *793*, 148443. https://doi.org/10.1016/j.scitotenv.2021.148443

Han, J., Gu, L., Warren, J. M., Guha, A., Mclennan, D. A., Zhang, W., & Zhang, Y. (2022). The roles of photochemical and non-photochemical quenching in regulating photosynthesis depend on the phases of fluctuating light conditions. *Tree Physiology*, *42*(4), 848–861. https://doi.org/10.1093/treephys/tpab133

Han, J., Guo, C., Ye, S., Zhang, L., Li, S., Wang, H., & Yu, G. (2020). Effects of diffuse photosynthetically active radiation on gross primary productivity in a subtropical coniferous plantation vary in different timescales. *Ecological Indicators*, *115*, 106403. https://doi.org/10.1016/j.ecolind.2020.106403

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W., & Medina-Elizade, M. (2006). Global temperature change. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(39), 14288–14293. https://doi.org/10.1073/pnas.0606291103

Hari, P., Nikinmaa, E., Pohja, T., Siivola, E., Bäck, J., Vesala, T., & Kulmala, M. (2013). Station for measuring ecosystem-atmosphere relations: SMEAR. In P. Hari, K. Heliövaara, & L. Kulmala (Eds.), *Physical and physiological forest ecology* (pp. 471–487). Springer Netherlands. https://doi.org/10.1007/978-94-027-5603-8_9

He, T., Liang, S., Yu, Y., Wang, D., Gao, F., & Liu, Q. (2013). Greenland surface albedo changes in July 1981–2012 from satellite observations. *Environmental Research Letters*, *8*(4), 044043. https://doi.org/10.1088/1748-9326/8/4/044043

Hernandez-Moreno, J. M., Bayeur, N. M., Coley, H. D., & Hughes, N. M. (2017). Clouds homogenize shoot temperatures, transpiration, and photosynthesis within crowns of *Abies fraseri* (Pursh.)

Poiret. *Oecologia*, *183*(3), 667–676. https://doi.org/10.1007/s00442-016-3799-7

Horton, D. E., Johnson, N. C., Singh, D., Swain, D. L., Rajaratnam, B., & Diffenbaugh, N. S. (2015). Contribution of changes in atmospheric circulation patterns to extreme temperature trends. *Nature*, *522*(7557), 465–469. https://doi.org/10.1038/nature14550

Hughes, N. M., Carpenter, K. L., Cook, D. K., Keidel, T. S., Miller, C. N., Neal, J. L., Sanchez, A., & Smith, W. K. (2015). Effects of cumulus clouds on microclimate and shoot-level photosynthetic gas exchange in *Picea engelmannii* and *Abies lasiocarpa* at treeline, Medicine Bow Mountains, Wyoming, USA. *Agricultural and Forest Meteorology*, *201*, 26–37. https://doi.org/10.1016/j.agrformet.2014.10.012

Ilvesniemi, H., Levula, J., Ojansuu, R., Kolari, P., Kulmala, L., Pumpanen, J., Launiainen, S., Vesala, T., & Nikinmaa, E. (2009). Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem. *Boreal Environment Research*, *14*, 731–753.

Ilvesniemi, H., Pumpanen, J., Duursma, R., Hari, P., Keronen, P., Kolari, P., Kulmala, M., Mammarella, I., Nikinmaa, E., Rannik, Ü., Pohja, T., Siivola, E., & Vesala, T. (2010). Water balance of a boreal Scots pine forest. *Boreal Environment Research*, *15*(4), 375–396.

IPCC. (2021). *Climate change 2021: The physical science basis*. IPCC. https://doi.org/10.1017/9781009157896

Irvine, P. J., Kravitz, B., Lawrence, M. G., & Muri, H. (2016). An overview of the Earth system science of solar geoengineering. *WIREs Climate Change*, *7*(6), 815–833. https://doi.org/10.1002/wcc.423

Jiang, Y., Wu, G., Li, Y., & Wu, W. (2019). Diameter-definable tubing-microchips for applications in both continuous-flow and TEC-modulated on-chip qPCRs with reaction signal analyzed between different types of Teflon-polymers: PTFE and FEP. *RSC Advances*, *9*(5), 2650–2656. https://doi.org/10.1039/C8RA09773A

Jones, M. W., Peters, G. P., Gasser, T., Andrew, R. M., Schwingshackl, C., Gütschow, J., Houghton, R. A., Friedlingstein, P., Pongratz, J., & Le Quéré, C. (2023). National contributions to climate change due to historical emissions of carbon dioxide, methane, and nitrous oxide since 1850. *Scientific Data*, *10*(1), 155. https://doi.org/10.1038/s41597-023-02041-1

Kaiser, E., Morales, A., & Harbinson, J. (2018). Fluctuating light takes crop photosynthesis on a rollercoaster ride. *Plant Physiology*, *176*(2), 977–989. https://doi.org/10.1104/pp.17.01250

Knohl, A., & Baldocchi, D. D. (2008). Effects of diffuse radiation on canopy gas exchange processes in a forest ecosystem: Diffuse radiation effects in forest. *Journal of Geophysical Research: Biogeosciences*, *113*(G2). https://doi.org/10.1029/2007JG000663

Kolari, P., Bäck, J., Taipale, R., Ruuskanen, T. M., Kajos, M. K., Rinne, J., Kulmala, M., & Hari, P. (2012). Evaluation of accuracy in measurements of VOC emissions with dynamic chamber system. *Atmospheric Environment*, *62*, 344–351. https://doi.org/10.1016/j.atmosenv.2012.08.054

Kolari, P., Pumpanen, J., Kulmala, L., Ilvesniemi, H., Nikinmaa, E., Grönholm, T., & Hari, P. (2006). Forest floor vegetation plays an important role in photosynthetic production of boreal forests. *Forest Ecology and Management*, *221*(1), 241–248. https://doi.org/10.1016/j.foreco.2005.10.021

Kulmala, L., Pumpanen, J., Kolari, P., Dengel, S., Berninger, F., Köster, K., Matkala, L., Vanhatalo, A., Vesala, T., & Bäck, J. (2019). Inter- and intra-annual dynamics of photosynthesis differ between forest floor vegetation and tree canopy in a subarctic Scots pine stand. *Agricultural and Forest Meteorology*, *271*, 1–11. https://doi.org/10.1016/j.agrformet.2019.02.029

Kume, A., Akitsu, T., & Nasahara, K. N. (2019). Correction to: Why is chlorophyll *b* only used in light-harvesting systems? *Journal of Plant Research*, *132*(3), 457. https://doi.org/10.1007/s10265-019-01104-y

Laffineur, Q., Aubinet, M., Schoon, N., Amelynck, C., Müller, J.-F., Dewulf, J., Steppe, K., & Heinesch, B. (2013). Impact of diffuse light on isoprene and monoterpene emissions from a mixed temperate forest. *Atmospheric Environment*, *74*, 385–392. https://doi.org/10.1016/j.atmosenv.2013.04.025

Lagergren, F., Lindroth, A., Dellwik, E., Ibrom, A., Lankreijer, H., Launiainen, S., Mölder, M., Kolari, P., Pilegaard, K., & Vesala, T. (2008). Biophysical controls on CO_2 fluxes of three northern forests based on long-term eddy covariance data. *Tellus B*, *60*(2), 143–152. https://doi.org/10.1111/j.1600-0889.2006.00324.x

Launiainen, S., Rinne, J., Pumpanen, J., Kulmala, L., Kolari, P., Keronen, P., Siivola, E., Pohja, T., Hari, P., & Vesala, T. (2005). Eddy covariance measurements of CO_2 and sensible and latent heat fluxes during a full year in a boreal pine forest trunk-space. *Boreal Environment Research*, *10*, 569–588.

Lee, M. S., Hollinger, D. Y., Keenan, T. F., Ouimette, A. P., Ollinger, S. V., & Richardson, A. D. (2018). Model-based analysis of the impact of diffuse radiation on CO_2 exchange in a temperate deciduous forest. *Agricultural and Forest Meteorology*, *249*, 377–389. https://doi.org/10.1016/j.agrformet.2017.11.016

Letts, M. G., Lafleur, P. M., & Roulet, N. T. (2005). On the relationship between cloudiness and net ecosystem carbon dioxide exchange in a peatland ecosystem. *Écoscience*, *12*(1), 53–69. https://doi.org/10.2980/i1195-6860-12-1-53.1

Li, F., Hao, D., Zhu, Q., Yuan, K., Braghiere, R. K., He, L., Luo, X., Wei, S., Riley, W. J., Zeng, Y., & Chen, M. (2023). Vegetation clumping modulates global photosynthesis through adjusting canopy light environment. *Global Change Biology*, *29*(3), 731–746. https://doi.org/10.1111/gcb.16503

Li, T., & Yang, Q. (2015). Advantages of diffuse light for horticultural production and perspectives for further research. *Frontiers in Plant Science*, *6*, 704. https://doi.org/10.3389/fpls.2015.00704

Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., & Comeau, P. G. (1999). Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research*, *29*(6), 796–811. https://doi.org/10.1139/x98-165

Lihavainen, H., Asmi, E., Aaltonen, V., Makkonen, U., & Kerminen, V.-M. (2015). Direct radiative feedback due to biogenic secondary organic aerosol estimated from boreal forest site observations. *Environmental Research Letters*, *10*(10), 104005. https://doi.org/10.1088/1748-9326/10/10/104005

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M. J., & Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, *259*(4), 698–709. https://doi.org/10.1016/j.foreco.2009.09.023

Lintunen, A., Sievänen, R., Kaitaniemi, P., & Perttunen, J. (2011). Models of 3D crown structure for Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) grown in mixed forest. *Canadian Journal of Forest Research*, *41*(9), 1779–1794. https://doi.org/10.1139/x11-092

Liu, P., Tong, X., Meng, P., Zhang, J., Li, J., Zhang, J., & Zhou, Y. (2022). Biophysical controls on water use efficiency of six plantations under different sky conditions. *Agricultural and Forest Meteorology*, *320*, 108938. https://doi.org/10.1016/j.agrformet.2022.108938

Manninen, T., Aalto, T., Markkanen, T., Peltoniemi, M., Böttcher, K., Metsämäki, S., Anttila, K., Pirinen, P., Leppänen, A., & Arslan, A. N. (2019). Monitoring changes in forestry and seasonal snow using surface albedo during 1982–2016 as an indicator. *Biogeosciences*, *16*(2), 223–240. https://doi.org/10.5194/bg-16-223-2019

Messier, C., & Puttonen, P. (1995). Spatial and temporal variation in the Bight environment of developing Scots pine stands: The basis for a quick and efficient method of characterizing Bight. *Canadian Journal of Forest Research*, *25*(2), 343–354. https://doi.org/10.1139/x95-038

Mirabel, A., Girardin, M. P., Metsaranta, J., Way, D., & Reich, P. B. (2023). Increasing atmospheric dryness reduces boreal forest tree growth. *Nature Communications*, *14*(1), 6901. https://doi.org/10.1038/s41467-023-42466-1

Misson, L., Baldocchi, D. D., Black, T. A., Blanken, P. D., Brunet, Y., Curiel Yuste, J., Dorsey, J. R., Falk, M., Granier, A., Irvine, M. R., Jarosz, N., Lamaud, E., Launiainen, S., Law, B. E., Longdoz, B., Loustau, D., McKay, M., Paw U, K. T., Vesala, T., … Goldstein, A. H. (2007). Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: A synthesis based on FLUXNET data. *Agricultural and Forest Meteorology*, *144*(1–2), 14–31. https://doi.org/10.1016/j.agrformet.2007.01.006

Nichol, C., Drolet, G., Porcar-Castell, A., Wade, T., Sabater, N., Middleton, E., MacLellan, C., Levula, J., Mammarella, I., Vesala, T., & Atherton, J. (2019). Diurnal and seasonal solar induced chlorophyll fluorescence and photosynthesis in a boreal Scots pine canopy. *Remote Sensing*, *11*(3), 273. https://doi.org/10.3390/rs11030273

Oker-Blom, P., Lahti, T., & Smolander, H. (1992). Photosynthesis of a Scots pine shoot: A comparison of two models of shoot photosynthesis in direct and diffuse radiation fields. *Tree Physiology*, *10*(2), 111–125. https://doi.org/10.1093/treephys/10.2.111

Orman, O., Wrzesiński, P., Dobrowolska, D., & Szewczyk, J. (2021). Regeneration growth and crown architecture of European beech and silver fir depend on gap characteristics and light gradient in the mixed montane old-growth stands. *Forest Ecology and Management*, *482*, 118866. https://doi.org/10.1016/j.foreco.2020.118866

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(6045), 988–993. https://doi.org/10.1126/science.1201609

Petäjä, T., Tabakova, K., Manninen, A., Ezhova, E., O'Connor, E., Moisseev, D., Sinclair, V. A., Backman, J., Levula, J., Luoma, K., Virkkula, A., Paramonov, M., Räty, M., Äijälä, M., Heikkinen, L., Ehn, M., Sipilä, M., Yli-Juuti, T., Virtanen, A., … Kerminen, V. M. (2022). Influence of biogenic emissions from boreal forests on aerosol–cloud interactions. *Nature Geoscience*, *15*(1), 42–47. https://doi.org/10.1038/s41561-021-00876-0

Petersson, L., Holmström, E., Lindbladh, M., & Felton, A. (2019). Tree species impact on understory vegetation: Vascular plant communities of Scots pine and Norway spruce managed stands in northern Europe. *Forest Ecology and Management*, *448*, 330–345. https://doi.org/10.1016/j.foreco.2019.06.011

Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J., Karlsson, P., & Ruuhela, R. (2012). *Tilastoja Suomen Ilmastosta 1981–2010 (climatological statistics of Finland 1981–2010)*. (Meteorological Institute Reports 2012/1). Finnish Meteorological Institute.

Pisek, J., & Oliphant, A. J. (2013). A note on the height variation of foliage clumping: Comparison with remote sensing retrievals. *Remote Sensing Letters*, *4*(4), 400–408. https://doi.org/10.1080/2150704X.2012.742212

Price, D. T., Alfaro, R. I., Brown, K. J., Flannigan, M. D., Fleming, R. A., Hogg, E. H., Girardin, M. P., Lakusta, T., Johnston, M., McKenney, D. W., Pedlar, J. H., Stratton, T., Sturrock, R. N., Thompson, I. D., Trofymow, J. A., & Venier, L. A. (2013). Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews*, *21*(4), 322–365. https://doi.org/10.1139/er-2013-0042

Pulliainen, J., Aurela, M., Laurila, T., Aalto, T., Takala, M., Salminen, M., Kulmala, M., Barr, A., Heimann, M., Lindroth, A., Laaksonen, A., Derksen, C., Mäkelä, A., Markkanen, T., Lemmetyinen, J., Susiluoto, J., Dengel, S., Mammarella, I., Tuovinen, J. P., & Vesala, T. (2017). Early snowmelt significantly enhances boreal springtime carbon uptake. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(42), 11081–11086. https://doi.org/10.1073/pnas.1707889114

R Core Team. (2023). *R: A language and environment for statistical computing* [computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Raivonen, M., Keronen, P., Vesala, T., Kulmala, M., & Hari, P. (2003). Measuring shoot-level NO_x flux in field conditions: The role of blank chambers. *Boreal Environment Research*, *8*(4), 445–455.

Rap, A., Scott, C. E., Reddington, C. L., Mercado, L., Ellis, R. J., Garraway, S., Evans, M. J., Beerling, D. J., MacKenzie, A. R., Hewitt, C. N., & Spracklen, D. V. (2018). Enhanced global primary production by biogenic aerosol via diffuse radiation fertilization. *Nature Geoscience*, *11*(9), 640–644. https://doi.org/10.1038/s41561-018-0208-3

Rap, A., Spracklen, D. V., Mercado, L., Reddington, C. L., Haywood, J. M., Ellis, R. J., Phillips, O. L., Artaxo, P., Bonal, D., Restrepo Coupe, N., & Butt, N. (2015). Fires increase Amazon forest productivity through increases in diffuse radiation. *Geophysical Research Letters*, *42*(11), 4654–4662. https://doi.org/10.1002/2015GL063719

Reinhardt, K., & Smith, W. K. (2016). Chlorophyll fluorescence and photosynthetic gas exchange under direct versus diffuse light in evergreen conifer (*Picea pungens*) shoots and broadleaf shrub (*Rhododendron ponticum*) leaves. *Plant Ecology*, *217*(4), 443–450. https://doi.org/10.1007/s11258-016-0586-9

Rocha, A. V., Su, H.-B., Vogel, C. S., Schmid, H. P., & Curtis, P. S. (2004). Photosynthetic and water use efficiency responses to diffuse radiation by an aspen-dominated northern hardwood forest. *Forest Science*, *50*(6), 793–801. https://doi.org/10.1093/forestscience/50.6.793

Ryhti, K., Kulmala, L., Pumpanen, J., Isotalo, J., Pihlatie, M., Helmisaari, H. S., Leppälammi-Kujansuu, J., Kieloaho, A. J., Bäck, J., & Heinonsalo, J. (2021). Partitioning of forest floor CO_2 emissions reveals the belowground interactions between different plant groups in a Scots pine stand in southern Finland. *Agricultural and Forest Meteorology*, *297*, 108266. https://doi.org/10.1016/j.agrformet.2020.108266

Screen, J. A., Bracegirdle, T. J., & Simmonds, I. (2018). Polar climate change as manifest in atmospheric circulation. *Current Climate Change Reports*, *4*(4), 383–395. https://doi.org/10.1007/s40641-018-0111-4

Shao, L., Li, G., Zhao, Q., Li, Y., Sun, Y., Wang, W., Cai, C., Chen, W., Liu, R., Luo, W., Yin, X., & Lee, X. (2020). The fertilization effect of global dimming on crop yields is not attributed to an improved light interception. *Global Change Biology*, *26*(3), 1697–1713. https://doi.org/10.1111/gcb.14822

Smith, W. K., & Berry, Z. C. (2013). Sunflecks? *Tree Physiology*, *33*(3), 233–237. https://doi.org/10.1093/treephys/tpt005

Tinya, F., & Ódor, P. (2016). Congruence of the spatial pattern of light and understory vegetation in an old-growth, temperate mixed forest. *Forest Ecology and Management*, *381*, 84–92. https://doi.org/10.1016/j.foreco.2016.09.027

Urban, O., Janouš, D., Acosta, M., Czerný, R., Marková, I., Navrátil, M., Pavelka, M., Pokorný, R., Šprtová, M., Zhang, R., Špunda, V., Grace, J., & Marek, M. V. (2006). Ecophysiological controls over the net ecosystem exchange of mountain spruce stand. Comparison of the response in direct vs. diffuse solar radiation. *Global Change Biology*, *13*(1), 157–168. https://doi.org/10.1111/j.1365-2486.2006.01265.x

Urban, O., Klem, K., Ač, A., Havránková, K., Holišová, P., Navrátil, M., Zitová, M., Kozlová, K., Pokorný, R., Šprtová, M., Tomášková, I., Špunda, V., & Grace, J. (2012). Impact of clear and cloudy sky conditions on the vertical distribution of photosynthetic CO_2 uptake within a spruce canopy: Vertical distribution of photosynthesis. *Functional Ecology*, *26*(1), 46–55. https://doi.org/10.1111/j.1365-2435.2011.01934.x

Uria-Diez, J., & Pommerening, A. (2017). Crown plasticity in Scots pine (*Pinus sylvestris* L.) as a strategy of adaptation to competition and environmental factors. *Ecological Modelling*, *356*, 117–126. https://doi.org/10.1016/j.ecolmodel.2017.03.018

Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O., Viiri, H., Ikonen, V., & Peltola, H. (2020). Climate change induces multiple risks to boreal forests and forestry in Finland: A literature review. *Global Change Biology*, *26*(8), 4178–4196. https://doi.org/10.1111/gcb.15183

Vesala, T., Haataja, J., Aalto, P., Altimir, N., Buzorius, G., Garam, E., Hämeri, K., Ilvesniemi, H., Jokinen, V., Keronen, P., Lahti, T., Markkanen, T., Mäkelä, J. M., Nikinmaa, E., Palmroth, S., Palva, L., Pohja, T., Pumpanen, J., Rannik, Ü., … Kulmala, M. (1998). Long-term field measurements of atmosphere-surface interactions in boreal forest combining forest ecology, micrometeorology, aerosol physics and atmospheric chemistry. *Trends in Heat & Mass Transfer*, *4*, 17–35.

Vesala, T., Suni, T., Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ilvesniemi, H., Ojansuu, R., Uotila, A., Levula, J., Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., … Hari, P. (2005). Effect of thinning on surface fluxes in a boreal forest: Thinning and surface fluxes in boreal forest. *Global Biogeochemical Cycles*, *19*(2). https://doi.org/10.1029/2004GB002316

Wang, B., Yue, X., Zhou, H., Lu, X., & Zhu, J. (2023). Enhanced ecosystem water-use efficiency under the more diffuse radiation conditions. *Global Biogeochemical Cycles*, *37*(3), e2022GB007606. https://doi.org/10.1029/2022GB007606

Wang, S., Zhang, Y., Ju, W., Chen, J. M., Ciais, P., Cescatti, A., Sardans, J., Janssens, I. A., Wu, M., Berry, J. A., Campbell, E., Fernández-Martínez, M., Alkama, R., Sitch, S., Friedlingstein, P., Smith, W. K., Yuan, W., He, W., Lombardozzi, D., … Peñuelas, J. (2020). Recent global decline of CO_2 fertilization effects on vegetation photosynthesis. *Science*, *370*(6522), 1295–1300. https://doi.org/10.1126/science.abb7772

Wang, X., Wu, J., Chen, M., Xu, X., Wang, Z., Wang, B., Wang, C., Piao, S., Lin, W., Miao, G., Deng, M., Qiao, C., Wang, J., Xu, S., & Liu, L. (2018). Field evidences for the positive effects of aerosols on tree growth. *Global Change Biology*, *24*(10), 4983–4992. https://doi.org/10.1111/gcb.14339

Way, D. A., & Pearcy, R. W. (2012). Sunflecks in trees and forests: From photosynthetic physiology to global change biology. *Tree Physiology*, *32*(9), 1066–1081. https://doi.org/10.1093/treephys/tps064

Williams, I. N., Riley, W. J., Kueppers, L. M., Biraud, S. C., & Torn, M. S. (2016). Separating the effects of phenology and diffuse radiation on gross primary productivity in winter wheat. *Journal of Geophysical Research: Biogeosciences*, *121*(7), 1903–1915. https://doi.org/10.1002/2015JG003317

Wohlfahrt, G., Hammerle, A., Haslwanter, A., Bahn, M., Tappeiner, U., & Cernusca, A. (2008). Disentangling leaf area and environmental effects on the response of the net ecosystem CO_2 exchange to diffuse radiation. *Geophysical Research Letters*, *35*(16). https://doi.org/10.1029/2008GL035090

Xia, L., Robock, A., Tilmes, S., & Neely, R. R., III. (2016). Stratospheric sulfate geoengineering could enhance the terrestrial photosynthesis rate. *Atmospheric Chemistry and Physics*, *16*(3), 1479–1489. https://doi.org/10.5194/acp-16-1479-2016

Yamori, W., Kusumi, K., Iba, K., & Terashima, I. (2020). Increased stomatal conductance induces rapid changes to photosynthetic rate in response to naturally fluctuating light conditions in rice. *Plant, Cell & Environment*, *43*(5), 1230–1240. https://doi.org/10.1111/pce.13725

Yang, C. E., Hoffman, F. M., Ricciuto, D. M., Tilmes, S., Xia, L., MacMartin, D. G., Kravitz, B., Richter, J. H., Mills, M., & Fu, J. S. (2020). Assessing terrestrial biogeochemical feedbacks in a strategically geoengineered climate. *Environmental Research Letters*, *15*(10), 104043. https://doi.org/10.1088/1748-9326/abacf7

Ylivinkka, I., Kaupinmäki, S., Virman, M., Peltola, M., Taipale, D., Petäjä, T., Kerminen, V. M., Kulmala, M., & Ezhova, E. (2020). Clouds over Hyytiälä, Finland: An algorithm to classify clouds based on solar radiation and cloud base height measurements. *Atmospheric Measurement Techniques*, *13*(10), 5595–5619. https://doi.org/10.5194/amt-13-5595-2020

Young, D. R., & Smith, W. K. (1983). Effect of cloud cover on photosynthesis and transpiration in the subalpine understory species *Arnica latifolia*. *Ecology*, *64*(4), 681–687. https://doi.org/10.2307/1937189

Yue, X., & Unger, N. (2018). Fire air pollution reduces global terrestrial productivity. *Nature Communications*, *9*(1), 5413. https://doi.org/10.1038/s41467-018-07921-4

Zhang, T., Stamnes, K., & Bowling, S. A. (1996). Impact of clouds on surface radiative fluxes and snowmelt in the Arctic and subarctic. *Journal of Climate*, *9*(9), 2110–2123. https://doi.org/10.1175/1520-0442(1996)009<2110:IOCOSR>2.0.CO;2

Zhang, Y., Bastos, A., Maignan, F., Goll, D., Boucher, O., Li, L., Cescatti, A., Vuichard, N., Chen, X., Ammann, C., Arain, M. A., Black, T. A., Chojnicki, B., Kato, T., Mammarella, I., Montagnani, L., Roupsard, O., Sanz, M. J., Siebicke, L., … Ciais, P. (2020). Modeling the impacts of diffuse light fraction on photosynthesis in ORCHIDEE (v5453) land surface model. *Geoscientific Model Development*, *13*(11), 5401–5423. https://doi.org/10.5194/gmd-13-5401-2020

Zhao, D. F., Buchholz, A., Tillmann, R., Kleist, E., Wu, C., Rubach, F., Kiendler-Scharr, A., Rudich, Y., Wildt, J., & Mentel, T. F. (2017). Environmental conditions regulate the impact of plants on cloud formation. *Nature Communications*, *8*(1), 14067. https://doi.org/10.1038/ncomms14067

Zhou, H., Yue, X., Lei, Y., Zhang, T., Tian, C., Ma, Y., & Cao, Y. (2021). Responses of gross primary productivity to diffuse radiation at global FLUXNET sites. *Atmospheric Environment*, *244*, 117905. https://doi.org/10.1016/j.atmosenv.2020.117905

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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