











FACILITATIVE MECHANISMS UNDERLYING THE
EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING

Research Article

**Biodiversity facets affect community surface temperature via
3D canopy structure in grassland communities**

Claudia Guimarães-Steinicke¹  | Alexandra Weigelt^{1,2}  | Raphaël Proulx³  |
Thomas Lanners⁴ | Nico Eisenhauer^{2,5}  | Joaquín Duque-Lazo⁶  | Björn Reu⁷  |
Christiane Roscher^{2,8}  | Cameron Wagg^{9,10}  | Nina Buchmann¹¹  |
Christian Wirth^{1,2,12} 

¹Systematic Botany and Functional Biodiversity, Institute of Biology, Leipzig University, Leipzig, Germany; ²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; ³Canada Research Chair in Ecological Integrity, Centre de recherche sur les interactions bassins versants-écosystèmes aquatique (RIVE), Université du Québec à Trois-Rivières, Trois-Rivières, QC, Canada; ⁴Teyolia Botanicals, San Andres Cholula, Mexico; ⁵Experimental Interaction Ecology, Institute of Biology, Leipzig University, Leipzig, Germany; ⁶Agresta SCoop., Madrid, Spain; ⁷Escuela de Biología, Industrial University of Santander, Bucaramanga, Santander, Colombia; ⁸UFZ, Helmholtz Centre for Environmental Research, Physiological Diversity, Leipzig, Germany; ⁹Department of Evolutionary Biology and Environmental Studies, University of Zürich, Zürich, Switzerland; ¹⁰Fredericton Research and Development Center, Agriculture and Agri-Food Canada, Fredericton, NB, Canada; ¹¹ETH Zurich, Zurich, Switzerland and ¹²Max Planck Institute for Biogeochemistry, Jena, Germany

Correspondence

Claudia Guimarães-Steinicke
Email: claudia.steinicke@uni-leipzig.de

Funding information

Swiss National Science Foundation, Grant/
Award Number: 310030E-147487; Deutsche
Forschungsgemeinschaft, Grant/Award
Number: FOR 1451 and FZT 118

Handling Editor: Alexandra Wright

Abstract

1. Canopy structure is an important driver of the energy budget of grassland ecosystem and is, at the same time, altered by plant diversity. Diverse plant communities typically have taller and more densely packed canopies than less diverse communities. With this, they absorb more radiation, have a higher transpiring leaf surface and are better coupled to the atmosphere which leads to cooler canopy surfaces. However, whether plant diversity generally translates into a cooling potential remains unclear and lacks empirical evidence. Here, we assessed how functional identity, functional diversity and species richness of grassland communities in the Jena Experiment predict the mean and variation of plant surface temperature mediated via effects of canopy structure.
2. Using terrestrial laser scanning, we estimated canopy structure describing metrics of vertical structure (mean height, LAI), the distribution (evenness) and the highest allocation (centre of gravity) of biomass along height strata. As metrics of horizontal structure, we considered community stand gaps, canopy surface variation and emergent flowers. We measured surface temperature with a thermal camera. We used SEM models to predict biodiversity effects on the surface temperature during two seasonal peaks of biomass.
3. Before the first cut in May, herb-dominated communities directly promoted lower leaf surface temperatures. However, communities with lower centre of gravity (mostly herb dominated) also increased canopy surface temperatures compared

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with grass-dominated communities with higher biomass stored in the top canopy. Grass-dominated communities showed a smaller variation of surface temperatures, which was also positively affected by species richness via an increase in mean height. In August, mean surface temperature decreased with increasing community CC and LAI. The variation of surface temperature was greater in herb-dominated than in grass-dominated communities and increased with plant species richness (direct effects).

4. *Synthesis.* The mean and variation of canopy surface temperature were driven by differences in functional group composition (herbs- vs. grass dominance) and to a lesser extent by plant diversity. These effects were partly mediated the metrics of canopy structure but also by direct effects unrelated to the structural metrics considered.

KEYWORDS

community canopy structure, facilitation, grassland, sampling effects, surface temperature, terrestrial laser scanning, thermal regulation

1 | INTRODUCTION

The consequences of biodiversity loss for ecosystem functioning are still a preeminent concern in ecological research. So far, there is strong evidence that decreasing plant species richness reduces community productivity (Cardinale et al., 2012; Marquard, et al., 2009; Reich et al., 2012; Spehn et al., 2005; van Ruijven & Berendse, 2005) as well as many other ecosystem functions (Allan et al., 2013; Meyer et al., 2016). Here we focus on the role of grassland plant diversity in regulating the canopy surface temperature, which may mediate diversity effects on ecosystem functioning (Gottschall et al., 2019; Lange et al., 2014) and contribute to abiotic facilitation, especially during drought conditions (Bachmann et al., 2018; Wright et al., 2014, 2015, 2017). Such microclimatic effects of plant diversity can even cascade down to influencing soil microbial processes (Eisenhauer et al., 2010; Lange et al., 2014). Despite the strong empirical evidence, the microclimate aspects of abiotic facilitation effects have thus far been underrepresented in the biodiversity–ecosystem functioning literature (Bachmann et al., 2018; Barry, Mommer, et al., 2019; but see Wright et al., 2021). We lack analyses focusing on factors affecting the surface temperature in upper canopy layers, which reflects microclimatic cooling and may be relevant for processes like canopy leaf physiology, herbivory or flower visitation (Herrera & Medrano, 2017; Whitney et al., 2008). This paper presents a systematic assessment of plant role of plant diversity on surface temperature and its spatial variation.

Diverse plant communities typically have tall and dense canopies (Lorentzen et al., 2008; Spehn et al., 2000; Wacker et al., 2009). This is because they have a higher likelihood of containing tall species, which, if present, often dominate communities, resulting in a sampling or selection effect (Fox, 2005; Loreau, 1998; Tilman, 1997). At the same time, more diverse communities may be composed

of functionally dissimilar species that spatially complement each other, thus allowing for higher plant biomass packing through resource partitioning or facilitation (Barry, Mommer, et al., 2019; Isbell et al., 2009; Marquard, et al., 2009; van Ruijven & Berendse, 2005).

Changes in plant diversity thus span gradients in canopy height and biomass packing, two key elements of plant communities' functional structure promoting primary productivity (Williams et al., 2017). These gradients are associated with changes in canopy structure (e.g. canopy roughness and the distribution, orientation, and structure of leaves) and thus changes in physiological processes, especially transpiration. The differences in canopy modulate the energy exchange rates between the plant community and its environment, that is, its energy budget (Baldocchi et al., 2002; Jones et al., 2003; Niinemets, 2010; Vojtech et al., 2008), which drives the canopy surface temperature. The energy budget of a plant canopy includes how incoming short- and long-wave solar radiation is absorbed, reflected, transmitted or emitted and how energy is dissipated by the leaves (Figure 1). This dissipation happens via the turbulent (convective) transport of parcels of warm air (sensible heat flux) and via surface evaporation and transpiration (latent heat flux; Figure 1; Schulze et al., 2019). While leaf structure, leaf tilt angles and leaf distribution within the canopy affect the radiative energy components, canopy structure, that is, canopy openness, roughness, canopy height and leaf area index (LAI; leaf area per ground area), affects the wind speed within the canopy and therefore the turbulent sensible and latent heat fluxes. Furthermore, taller and more dense-packed canopies with a high leaf area index (LAI; leaf area per ground area) have more transpiring leaf area, increasing latent heat fluxes (Jones & Rotenberg, 2011; Verheyen et al., 2008), likely resulting in lower surface temperatures. In summary, plant diversity has the potential to affect canopy structure temperature and microclimatic conditions via its effect on canopy structure (Milcu et al., 2016).

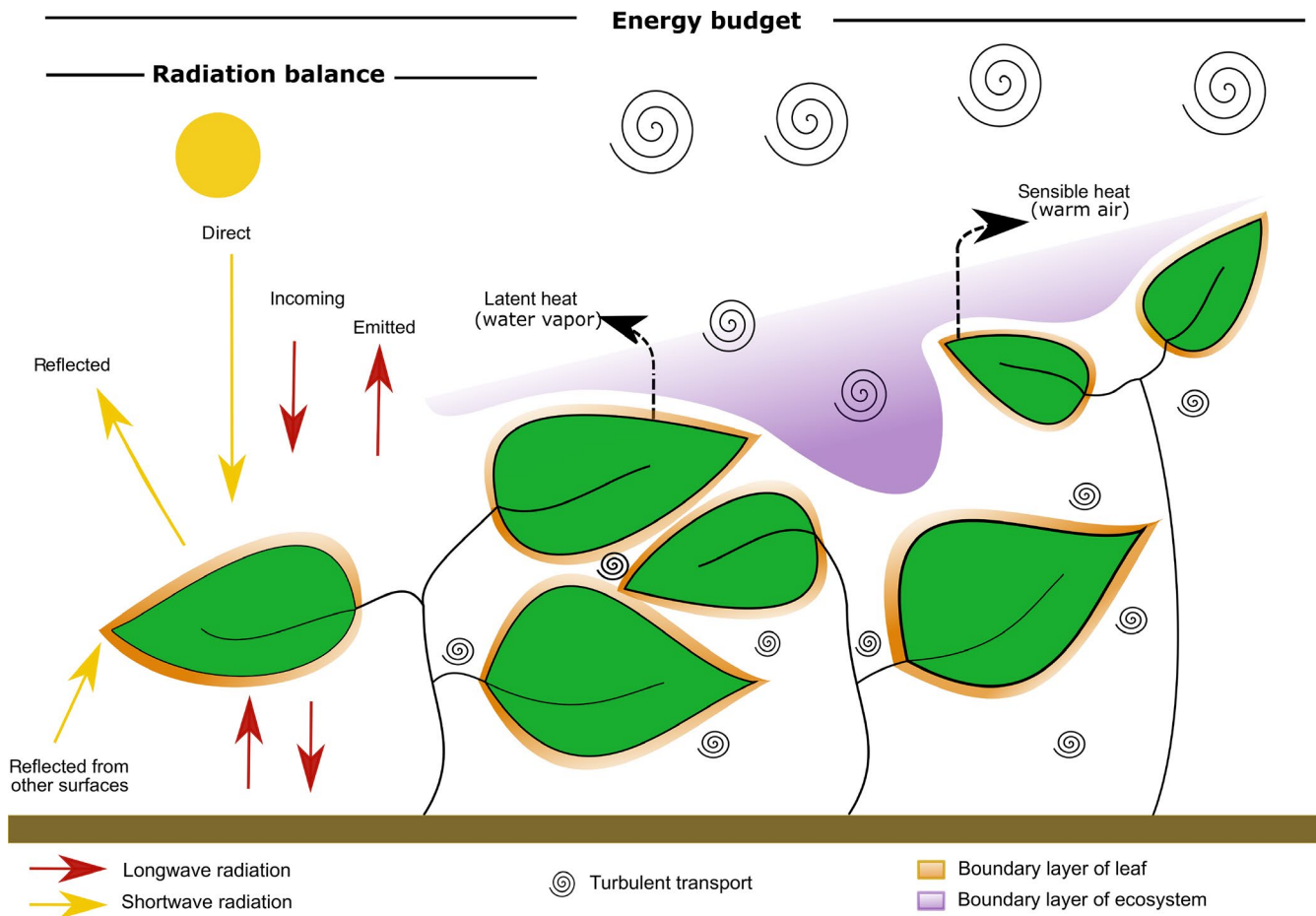


FIGURE 1 Schematic representation of the energy budget of a community canopy. On the left side, the radiation balance is represented by short-wave radiation from the sun, which becomes a net source of radiation of reflection and absorption to the ground and the community canopy. The long-wave radiation is also a source of incoming and outgoing emission to the surfaces (ground and community canopy) and the atmosphere. On the right side, the heat dissipation at the community canopy occurred via convective and turbulent mass transport of the latent heat (water vapour) and sensible heat flux (warm air)

However, whether plant species richness creates cooler vegetation surfaces remains unclear and lacks mechanistic evidence.

To understand how the canopy structure of grasslands differing in plant diversity controls community surface temperature, we need to quantify the structural characteristics of the communities involved in energy exchange processes (Jones, 2014). Here, in a first step, we considered how seven metrics of community canopy structure relate to plant diversity and, in a second step, how they predict the mean and variance of community surface temperature in temperate managed grasslands. The selected structural predictors fall into two groups describing either primarily the vertical structure (evenness, the centre of gravity, LAI and mean height) or the horizontal structure (canopy variation, species clumpiness and proportion of inflorescences) of plant canopies (Figure 2).

The vertical structure of a community canopy is primarily determined by plant height and the distribution and orientation of stems, leaves and flowers, and it varies with plant diversity (Liira et al., 2002). The tall and dense canopies of diverse plant communities (see above) are characterized by high LAI, high evenness of biomass distribution in the canopy, and vertical leaves, which increase

the scattering and reabsorption of radiation inside the canopy, thus increasing diffuse radiation as well as photosynthesis (Emmel et al., 2020). As a result, tall and dense canopies attenuate more radiation (Jones, 2014; Niinemets, 2010; Yang & van der Tol, 2018). Higher biomass transpires more than shorter canopies with lower LAI, thus reducing canopy surface temperature. Moreover, tall canopies (irrespective of density) are well coupled to the atmosphere (Schulze et al., 2019), which means that their boundary layers are thin. Simultaneously, surface conductance is high, promoting energy dissipation by increasing sensible and latent heat fluxes, thus creating cooler canopy surface temperatures. The microclimate of grassland mixture with low species richness and functional diversity will differ from this depending on the structural characteristics of the dominating plant species. For example, mixtures dominated by grasses and rosette forbs may have a low centre of gravity due to vertical, elongated leaves originating close to the ground may exhibit warmer canopy surfaces. While the LAI may still be high due to the vertical leaf orientation (Bonan, 2008; Hirose & Werger, 1995), due to the canopy's lower position, they are generally less well coupled to the atmosphere (thicker boundary layer). The low canopy may be

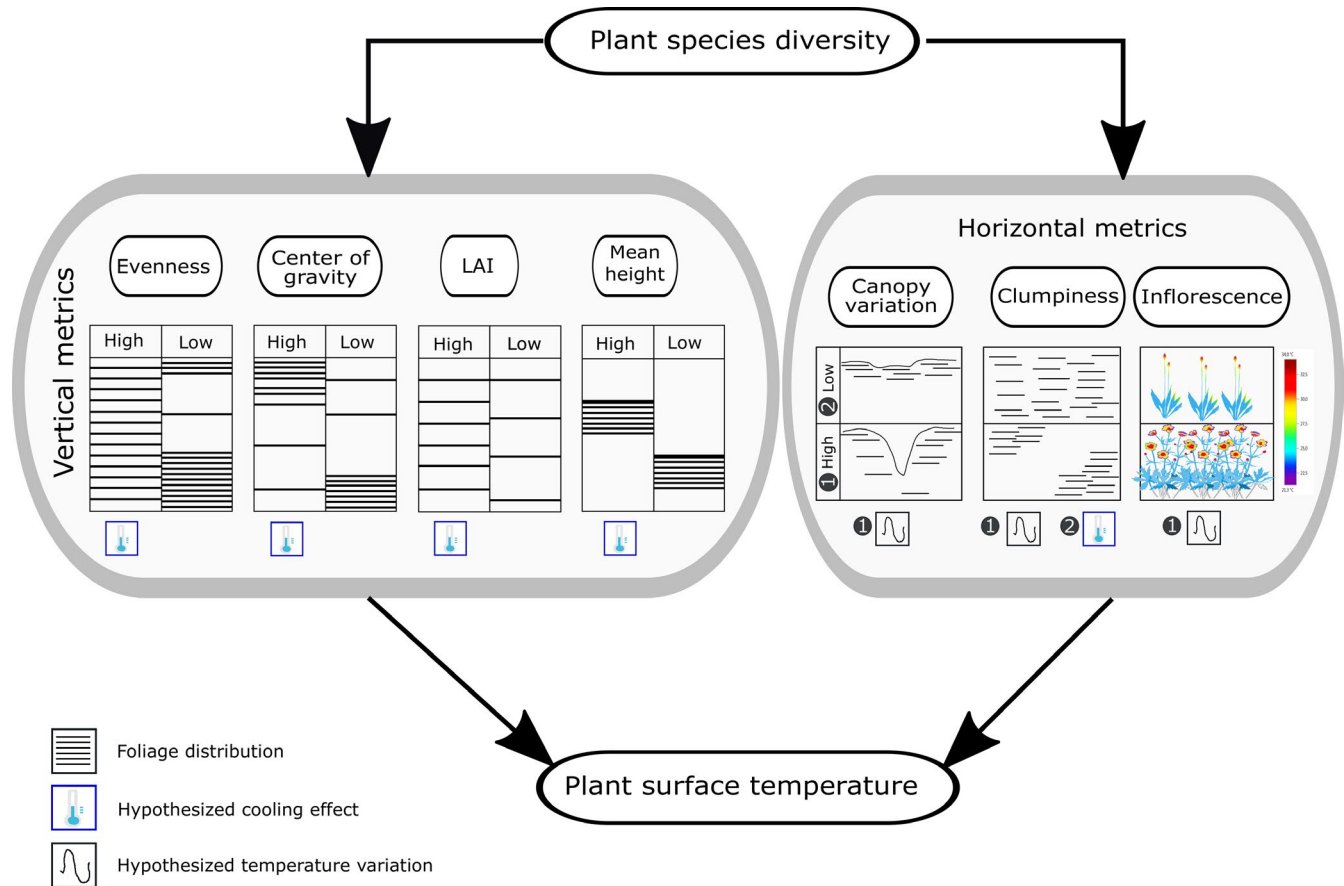


FIGURE 2 The conceptual understanding of how plant diversity may affect plant surface temperature via plant structure used in the pSEM model. Plant diversity represents the three different biodiversity facets: functional identity, functional diversity and species richness. Terrestrial laser scanning-derived metrics of the canopy structure, LAI, and Normalized Green–Blue Difference Index (NGBDI) representing the difference between the green and the blue bands divided by their sum. All variables are defined along the vertical (left) and horizontal (right) dimensions, and depending on their variation (High or Low), there will be a cooling effect or variation on the plant community surface temperature. Main expectations regarding temperature are shown below the canopy metrics. For further information, see the text

overtopped by individual plants or scattered inflorescences (creating a low 'evenness') that may act as a windbreak, further slowing down convective transport and energy dissipation via sensible and latent heat fluxes. In turn, tall-statured forbs concentrate large horizontally oriented leaves in the upper canopy layers (high 'centre of gravity', low 'evenness'; Bonan, 2008). While being taller and more exposed to the wind, the smooth umbrella formed by the upper leaf layers comes with a lower LAI and may reduce turbulent transport and reduce attenuation of radiation. In combination, this may result in intermediate surface temperatures. However, evidence of how plant diversity affects these biophysical processes remains scarce (Lundholm, 2015).

Spatial variation of plant species with their unique physiologies and leaf properties may also affect the community surface temperature and, in particular, its spatial variation (Breshears et al., 2009; Castro & Fetcher, 1999; Norman & Campbell, 1989). Here, we focus on three horizontal metrics describing the canopy surface (a) the variation of the community canopy surface, (b) community stand gaps (clumpiness) and (c) the proportion of inflorescences. Variation

in the community canopy surface considers the topography, that is, horizontal distribution of peaks, valleys and gaps created by plant modules. Such canopy surface variation is closely related to the canopy coupling discussed above. Higher variation entails higher coupling to the atmosphere and may result in higher turbulence deeper down in the canopy. However, very deep valleys, that is, canopy gaps, may be sheltered from turbulence and even expose soil that lacks transpiration and only evaporates it, rendering it warmer than the surrounding plant canopies and increasing spatial temperature variation. At the same time, inflorescence peaks protrude out of the canopy into regions of higher wind velocity and air turbulence. This may increase spatial variation in canopy surface temperatures creating cool or hot spots depending on the inflorescences' morphology (Dietrich & Körner, 2014; Jones, 2014; Figure 2—horizontal metrics). Large-statured or clonal species tend to form clumps of local dominance, particularly on a small spatial scale (Weigelt et al., 2008), contributing to spatial variation in surface temperature if the species differ in architectural and physiological traits. Grassland species differ in plant stature, branching patterns and leaf angularity

(Lorentzen et al., 2008; Migliavacca et al., 2017; Wacker et al., 2009), in their leaf reflectance due to hairiness, thickness, cuticle and pigmentation (Feller & Vaseva, 2014; Grant et al., 1995; Lambers et al., 2008; Sánchez et al., 2001), and in the characteristics of their inflorescences (Dietrich & Körner, 2014). They also differ greatly in their ability to transport and transpire water. For example, stomatal conductance measured in our experimental species varied by a factor of 7.4 (data used in Bachmann et al., 2015; Schroeder-Georgi et al., 2016; van der Plas et al., 2020). Such species differences may translate into a patchy distribution of canopy surfaces. For instance, shallow-rooted Mediterranean shrubs with limited water access and conservative water use have been shown to create hot spots of surface temperature (Fort et al., 2013; Hernández et al., 2010). Hence, increasing the canopy variation and clumpiness of grassland communities and species richness and the presence of different plant functional types are predicted to increase the spatial variation of canopy surface temperatures, thus creating a heterogeneous 'heat-scape' pattern within the sward.

Here, we take advantage of a long-term biodiversity experiment in a grassland ecosystem (Trait-Based Biodiversity Experiment; Ebeling et al., 2014) with high-resolution data of the community canopy structure obtained by terrestrial laser scanning (TLS) for two periods during the growing season. We use thermal imaging from an infrared camera (IR) to calculate the mean and variation of the grassland communities' canopy surface temperature. The 'Trait-Based Biodiversity Experiment' manipulates species richness as well as plant trait and species composition. We calculate community-weighted means of species traits (CWM) as a measure of functional identity and functional dispersion (FDIs) as a measure of functional diversity based on species proportions in the above-ground biomass. Using these indices, we aim to reveal the potential effect of different biodiversity facets on canopy surface temperature. We use structural equation modelling (SEM) to analyse the relative contribution of direct and indirect effects of biodiversity facets (functional identity, functional diversity and species richness) mediated by horizontal and vertical metrics of canopy structure on the mean and the variation of surface temperature. We predict that the mean canopy temperature is mediated by the vertical structure and is jointly controlled by the functional diversity and species' identity. In addition, we expect that functional identity and species richness control the spatial variation of canopy temperatures mediated by the horizontal structure of plant communities (Figure 2).

2 | MATERIALS AND METHODS

2.1 | Study site and Trait-Based Experiment

Field data were collected within the Trait-Based Biodiversity Experiment in 2014 (TBE; Ebeling et al., 2014) at the Jena Experiment site (Thuringia, Germany; 50°55'N, 11°35'E, 130 m a.s.l., Roscher et al., 2004; Weisser et al., 2017) with a mean annual air temperature of 9.3°C and annual precipitation of 534.42 mm (average from 2002,

i.e. start of the Jena Experiment, to 2015; Deutscher Wetterdienst et al., 2014). The TBE, established in 2010, manipulated trait diversity of plant communities based on their variation in phenology and above- and below-ground resource acquisition. In brief, the traits, that is, plant height, leaf size, rooting depth, root length density, were associated with spatial resource acquisition and the growth starting date and the flowering starting date being related to phenological traits (see Ebeling et al., 2014).

Based on these functional traits, Ebeling et al. (2014) performed a principal component analysis (PCA) in which plant species were grouped into two pools, representing a subset of the 48 non-legume species of the Jena Experiment species pool (Roscher et al., 2004). Axis 1 (pool 1) discriminates species according to their spatial resource use (above- and below-ground) (explaining 35% of the variance) and axis 2 (pool 2) according to their temporal variation in resource acquisition (with 31% of the variance explained). We conducted this study in 92 plots of the TBE experiment (3.5 m × 3.5 m size), comprehending the two species pools, with a gradient of plant species richness of one to eight species (Table S5). The grasslands were managed with two cuts per year (June and September) and no fertilization. This is the most common practice of extensively managed grasslands in Thuringia, Germany, where the TBE is located (Roscher et al., 2004). Plots were weeded three times per year (April, July and October) to maintain the sown species richness gradient (Weisser et al., 2017). We conducted our community scanning and temperature measurements in 16 monocultures, 32 two-species mixtures, 24 three-species mixtures, 18 four-species mixtures and 2 eight-species mixtures.

2.2 | Diversity facets: Species richness, functional dispersion and identity

To test how different biodiversity facets are associated with canopy surface temperature and its variation through plant community canopy structure, we used a plot-level assessment of three different facets of plant diversity: functional identity, functional diversity and species richness. The two functional diversity indices, identity and diversity describe variation in the distribution of the functional traits within a community. To quantify functional diversity, we calculated the functional dispersion index (FDIs), representing the sum of abundance-weighted distances from the centre of all species in the multidimensional trait space (Laliberté & Legendre, 2010). As such, the functional dispersion shifts the position of the centre towards more abundant species (Cadotte, 2017). Second, we computed community-weighted means of species traits (CWM), which describe the mean trait values of all species weighted by their abundances in a community (Lavorel et al., 2008). For both functional indices, we used a total of 11 functional traits measured for our species in three experiments. From a mesocosm experiment, we used leaf thickness and root diameter (see details Schroeder-Georgi et al., 2016). We further included leaf area, leaf dry matter content, specific leaf area, leaf nitrogen concentration and stomatal conductance, directly

measured at the Jena Experiment in 2011 and 2012 (for leaf nitrogen concentrations) in May and August (see details Bachmann et al., 2018). Finally, the specific root length, rooting depth, root length density and maximum plant height were obtained from the Trait-Based Experiment design database and measured in monocultures of the Jena Experiment (see Ebeling et al., 2014). These functional traits correspond to different aspects of plant morphology and their ecophysiological performance in regulating plant surface temperature. Lastly, sown species richness was included as the third facet of biodiversity. Abundance data for the calculation of the functional diversity indices were derived from harvested biomass in May and August of 2014 (two peaks of biomass during the season). To obtain an aggregate index representing the functional identity of plant species at the community level, we ran a PCA on the CWM for all 11 traits for all plots. As the scores of PCA axis 1 explained around 49% of variance (Figure S1 for May and S2 for August), we used this axis to characterize the functional identity of the plant communities. Functional diversity indices were calculated for May and August using the function `dbFD` from the R package `FD`.

2.3 | Terrestrial laser scanning: Data acquisition and processing

To perform a non-destructive measurement of plant community canopy structure at high resolution, we used a terrestrial laser scanner (TLS) Faro Focus 3D X330 (FARO Technologies Inc., 2019). We scanned 92 plots on 31 April (the first peak of biomass) and 20 August 2014 (the second biomass peak). The TLS was mounted upside-down on a tripod that was elevated 3.35 m above-ground level. The legs of the tripod were centred on permanent survey markers to guarantee identical scanning areas on both dates. We extracted an area of 3.75 m² (1.5 m × 2.5 m) in each plot below the scanner to reduce the effect of shadows within scans. The discrete returns of the laser beams produced a point cloud image of the surface of the grassland vegetation with a scan size of the scan 10,154 × 1,138 points horizontally × vertically. The laser beams emit an infrared pulse of 1,550 nm with a beam divergence of 0.011° (0.19 mrad) at a range of 0.6 to 130 m. The scanning parameters used for defining the resolution were (i) 44.4 million points (full scan) and (ii) the first level of quality (1x) to maximize the efficiency of the scanning processes (FARO Technologies Inc., 2019). Point clouds of all scan plots were transformed into XYZ coordinates using the proprietary software 'Scene' (version 5.2.0, Faro Technologies, Inc.).

We used two filtering processes of the point cloud to aid higher accuracy and reduction of errors. First, we applied a statistical outlier removal (SOR), a distance-based approach (points coordinates) assigning an outlier probability for each point based on its distance to neighbouring points. The SOR algorithm assumes that the distance between a given point to its neighbours is normally distributed. In the next step, for each point in the point cloud, the mean and the standard deviation of Euclidean distance considering N-nearest neighbours were computed (Carrilho et al., 2018). As a result, every point that falls

outside the mean ± 1 standard deviation is viewed as an outlier. SOR computes the average distance of every sixth point ($K = 6$ and $N = 1$) to its neighbours and rejects points farther away than the average distance ($\alpha = 1.5$). Second, we used a noise filter that removed the points far away from the fitted plane in a 2 mm circumference plane. The software 'CloudCompare 2.8.1' performed both filtering processes using the function `S.O.R` (<http://www.cloudcompare.org>). To obtain canopy structure metrics derived from the point cloud, we used the `LAStools` software (<http://www.lastools.org>, (Ilsenburg, 2014)). `LAS` format files were derived from the XYZ coordinates of the point clouds. Furthermore, points were classified as 'ground points'—from the ground surface to 5 cm height and the remaining points as 'non-ground points' up to the upper canopy layers. To obtain height above-ground level, we normalized the height of the community canopy returns and applied a digital terrain model based on a triangular irregular network (TIN) approach. It is important to note that although Faro Scanner produces discrete-return laser beams that can reduce the information below the canopy, we still believe it provides a fair proxy for the height distribution due to the density of points obtained in all plots.

2.4 | Canopy structure metrics

2.4.1 | Vertical structure

We used the 3D point clouds obtained from terrestrial laser scanning to calculate metrics characterizing vertical and horizontal dimensions of the community canopy structure. First, we produced height-based metrics from the point cloud of each community. We used mean height as the first vertical dimension metric. Furthermore, the LAI was also measured at the same time in all 92 plots using the LAI-2000 plant canopy analyser (LI-Cor Inc, 2013). Ten random measurements were averaged to a mean of LAI value per plot. Hence, we used LAI as an additional vertical dimensional metric to characterize plant ground area covered by the plant community.

To characterize vertical space-filling properties, we calculated the evenness and the centre of gravity of the point cloud. Evenness reports the homogeneity of the point cloud density in their vertical distribution, while the centre of gravity identifies the height stratum (definition see below) with the highest density of points (Barry et al., 2020; Spehn et al., 2000). As a baseline for only these two vertical metrics (evenness and centre of gravity), we calculated voxel grids from the 3D point cloud for each plot. A 'voxel grid' is a digital description of a volumetric object that subdivides the point clouds into a regular grid in three-dimensional space with a defined size (Schulze-Brüninghoff et al., 2019). We then only used voxels that contained at least one 3D point. For each scan, a voxel grid of 5 cm was created containing at least one laser return, and the volume was then calculated as the product of the cell area and the attributed height. We used the function 'vox' from the R package `VoxR` (Lecigne et al., 2014).

We used the voxel grids to define five different strata of height (0.3–20, 20–40, 40–60, 60–80 and 80–100 cm). For every stratum, we applied the method 'Sum of Voxel', which calculated the sum of

all voxels separately for each of the five strata. As a result, we obtained volumetric data based on 3D point clouds for five different strata and the community canopy height. Based on this information, the evenness metric represents the mean proportion of filled voxels across strata of vegetation height, calculated as the sum of all five voxel strata volumes divided by 5. The centre of gravity, in turn, used the volume of voxel grids per height strata to identify the location with the highest density of points. This location was measured in terms of the height-weighted average volume allocation of the community. We then calculated the centre of gravity by multiplying each stratum's volume with the mean height of the strata and dividing by the total community volume. Centre of gravity range from 1 to 5, in which 1 is the bottom layer (0–20 cm) and 5 the top canopy (80–100 cm).

2.4.2 | Horizontal structure

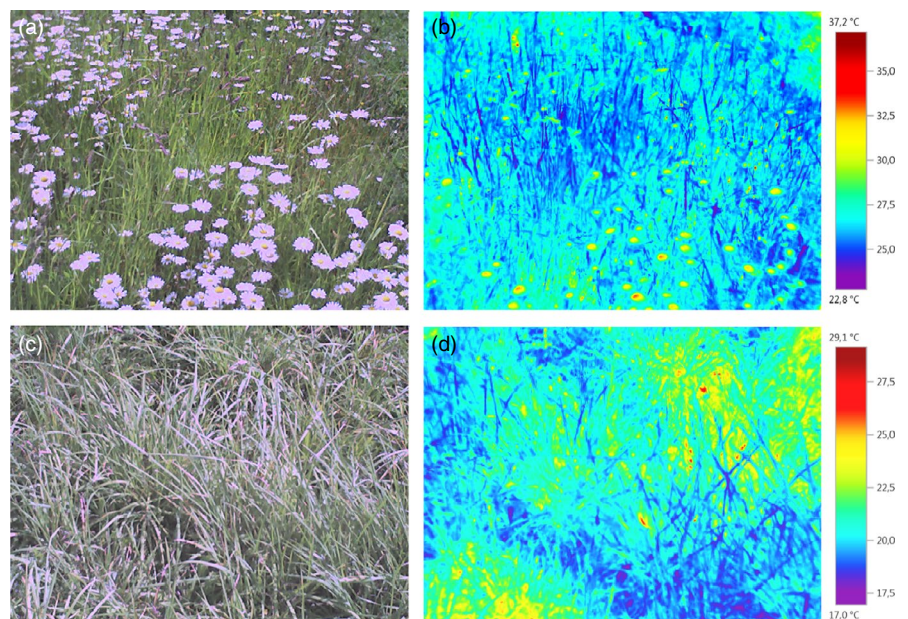
To assess the horizontal heterogeneity of the plant community for each plot, we also calculated two horizontal metrics describing the canopy surface variation and clumpiness. We used the surface reconstruction method, which fits a mesh on the 3D point cloud density of each plot (the filtered point clouds and not voxel grids) (Attene & Spagnuolo, 2000). We applied the Poisson surface reconstruction method, which fits a mesh on all oriented points (perpendicular vectors to the tangential plane to the surface at that point) (Kazhdan & Hoppe, 2019). Poisson surface reconstruction is the preferred method for TLS data due to its stability and reliability (Berger et al., 2014; Gupta & Shukla, 2018). The Poisson surface reconstruction was generated using the open-source software CloudCompare (CloudCompare Omnia, 2019). After producing the surface mesh for all plots, a surface area of the mesh in square metres was calculated and divided by the area of the plot (3.75 m²). The variation metric is a dimensionless ratio between the mesh surface area and the ground

area. For clumpiness, we evaluated the size and distribution of clusters in the spatial arrangement of the point cloud into two dimensions based on the rasterized 3D point clouds. For this, we computed Geary's index, an identifier of cluster points with similar attributes, assessed by the pixel spatial autocorrelation. We used the function Geary from the R package RASTER.

2.5 | Thermal images

The two response variables, the mean and the coefficient of variation (hereafter CV) of community surface temperature were obtained using the Testo 882 Thermal Imaging Camera, which also recorded RGB images of all 92 plots (e.g. Figure 3). We obtained the thermal data and terrestrial laser scans within 2 days. All thermal measurements were carried out around noon (12:30–13:30), at 150 cm height, and facing north. The thermal camera settings controlled the canopy's emissivity as 0.95 with reflectance temperature at 20°C. The sensor detects long-wave infrared radiation in the spectral range from 7.5 to 14 μm and has a thermal sensitivity of 50 mK at +30°C and accuracy of ±2.0°C. The optical resolution is 640 × 480 pixels with a field of view of 32°×23° and a minimum focus distance of 0.2 m. The IRTSoft software processed both thermal images and RGB converting the radiation into the surface temperature among image pixels. With the thermal matrix (registered pixel temperature with an original resolution of 640 × 480), we computed the mean and the coefficient of variation of surface temperature for each plot. As flower heads are often 10 K warmer than the surrounding leaves of herbs and grasses, we calculated the Normalized Green–Red Difference Index (NGRDI, the difference between the green and red bands divided by their sum (Pérez et al., 2000). Further, we also calculated the Normalized Green–Blue Difference Index (NGBDI, the difference between the green and the blue bands divided by their sum (Wang Xiaoqin et al., 2015) better to distinguish the hot spots of

FIGURE 3 RGB image (a) of the plot OBA003 of the Trait-Based Experiment containing *Leucanthemum vulgare*, *Anthoxanthum odoratum*, *Dactylis glomerata* and *Ranunculus acris*. The image was taken with the thermal infrared camera in May, which measures the emitted thermal radiation with a thermal emissivity factor of 0.95. (b) is an infrared image of the same plot in May with the conversion from the long-wave radiation to surface temperature (Temperature scale bar on the right side in degrees Celsius). (c and d) RGB and infrared image of the same plot taken in August



inflorescences and green vegetation. Preliminary tests showed that the blue band discriminates better than the red band between the green vegetation and colourful flowers retaining high temperatures. We, therefore, used the blue band to correct the inflorescence surface temperature in the final analysis.

2.6 | Data analyses

2.6.1 | Bivariate relationship between biodiversity facets and surface temperature

We applied linear mixed-effects models to test the direct effects of functional identity (PCA 1), functional dispersion and plant species richness on both mean and variation of community surface temperature in separate models for May and August. The block treatment of the TBE experiment was considered as a random factor allowing responses to vary randomly between blocks and plots (Pinheiro & Bates, 2000), and the fixed effects were the biodiversity facets (FI, FDis and SR). We fitted models using the *NLME* package and inspected residuals for homogeneity and quantile–quantile normality. Plant species richness was log-transformed to meet normality assumptions.

2.6.2 | PiecewiseSEM

We expected that biodiversity effects on mean canopy surface temperature are indirectly mediated by predictors related to vertical structure metrics, while biodiversity effects on temperature CV are mediated by the horizontal structure. To test these assumptions further, we constructed a more detailed formal hypothesis using linear mixed-effects models within a PiecewiseSEM (Lefcheck, 2016). We controlled for multicollinearity among canopy structure metrics by ensuring that the variation inflation factor was below <3 (O'Brien, 2007). First, we ran the initial SEM model as a list of causal relationships between canopy structure and biodiversity facets. The last linear model inside the SEM was between the mean and CV of surface temperature and biodiversity facets (functional identity, dispersion and species richness) and all canopy structure metrics to test the fit of the model to the data. Second, we inspected this initial SEM model results for goodness-of-fit tests for both the full and causal relationships, we then added the predictors that significantly improved the model fit with *P* values higher than 0.05.

We treated blocks as random factors within the SEM by using the *lme* function in the *NLME* package of the statistical software R (Pinheiro & Bates, 2000; R Core Team, 2017; Zuur et al., 2009). We fitted four separate SEM, that is, modelling mean and CV of surface temperature for May and August harvests. We assessed each SEM model fit using the Fisher's *C* statistic ($p > 0.10$). The variables 'mean plant height' and 'species richness' were log-transformed. FDis, FI (PCA axis 1 of the CWM) and all seven canopy structure metrics (Figure 2) were z-transformed to stabilize the variance. We

inspected the assumptions of normality visually. PiecewiseSEM was performed using the R package *PIECEWISESEM* (Lefcheck, 2016).

3 | RESULTS

3.1 | Mean surface temperature of grassland communities

Surface temperature measured by the thermal camera ranged from 22.8°C to 29.8°C across 92 plots in May and from 18.4°C to 25.2°C in August. In the thermal images taken at the beginning of August, the mean community surface temperature presented a left-skewed distribution with a mode around 20°C, while in May, more plots had around 25°C (Figure S3).

3.2 | Bivariate relationships between biodiversity facets and the mean and the variation of canopy surface temperature

There was no significant direct bivariate relationship between the biodiversity facets investigated (functional identity, functional dispersion and plant species richness) and mean canopy surface temperature in May (Figure S6) and in August (Figure S8). However, functional identity and species richness were directly positively related to temperature CV in both months (Figures S7 and S9). Yet, the above predictors explained a low fraction of the variation in the temperature mean (marginal R^2 varying from 0.003 to 0.006) and the CV (marginal R^2 ranging from 0.001 to 0.18) (Figures S6–S9, Marginal R^2). These weak univariate relationships illustrated the need to consider the indirect effect of biodiversity predictors mediated by structural vertical and horizontal metrics of community canopy structure.

3.3 | The relationship of biodiversity facets effects on the mean and the variation of canopy surface temperature in May

Using piecewiseSEM, we tested the direct and indirect effects (via canopy structure) of biodiversity descriptors on community surface temperature in May. Overall, SEM fitted mean surface temperature (Fisher's $C = 8.048$, $df = 14$, $p = 0.887$ and mean temperature $R^2 = 0.35$) and temperature CV (Fisher's $C = 12.29$, $df = 16$, $p = 0.724$ and CV $R^2 = 0.69$) well (Figure 4a,b). Functional identity was associated directly and indirectly (i.e. via the centre of gravity) to the mean and CV of surface temperature (Figure 4a; Figure S1). It is important to note that the effects originating from functional identity (hereafter FI) are based on the PCA analysis in which high scores indicate communities dominated by herb species and low scores those dominated by grass species (Figure S1). Independent of canopy structure (direct effects), communities dominated by grass species had, on average, 0.28°C higher mean

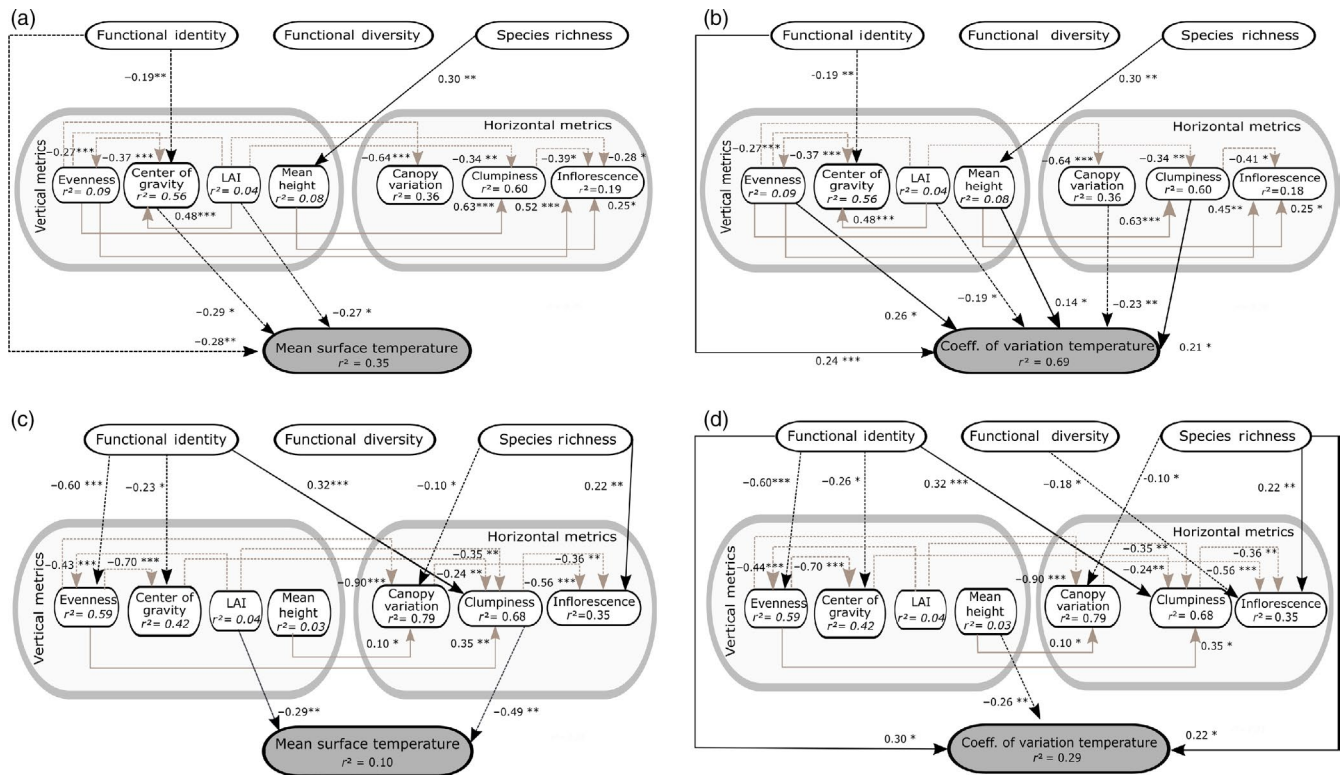


FIGURE 4 Structural equation models for different facets of diversity testing the effects via plant canopy architecture on plant surface temperature. a and b are SEM models for May, while c and d are for August 2014. (a) is a SEM model using mean surface temperature as the response variable, Fisher's C = 11.853, $p = 0.618$; (b) Response variable is coefficient of variation on plant surface temperature, Fischer's C = 12.322, $p = 0.724$. (c) SEM model using mean surface temperature as response variable, Fisher's C = 10.692, $p = 0.828$; (d) Response variable is coefficient of variation on plant surface temperature, Fischer's C = 7.197, $p = 0.927$. Solid lines represent positive relationships, dotted lines negative relationships and light brown lines indicate the relationship between vertical and horizontal dimensions of plant canopy architecture metrics. Each arrow connection among variables indicates standardized path coefficients and significant levels (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). Detailed model summaries with unstandardized path coefficients are shown in the Supporting Information (Table S1 and S2)

surface temperature (Table S1) and, on average, 0.24°C lower temperature CV compared to communities dominated by herbs (Table S2). Plant species richness was not associated with the mean surface temperature but increased temperature CV indirectly via plant canopy height (Figure 4b). Functional diversity did not influence any of the response or canopy structure variables. The centre of gravity and the clumpiness explained the highest proportion of the variance in both SEMs ($R^2 = 0.56$ and $R^2 = 0.60$ respectively) (Figure 4a,b; Table S1). However, clumpiness did not appear as a significant driver of biodiversity effects on the mean community surface temperature (Figure 4a). Together, biodiversity facets explained 35% (marginal R^2) of the variance in mean surface temperature (Table S1). For the SEM model testing, the causal associations between biodiversity facets and the coefficient of variation via community structure explained 69% of the variance (marginal R^2), and the joint fixed and random effects explained 69% (Figure 4b; Table S2).

We found that herb-dominated communities (FI with high scores) displayed a lower mean surface temperature (Figure 4a; direct path coeff. = -0.28). However, communities with a lower centre of gravity (-0.19) (which were often herb-dominated communities) tended to

have a higher mean surface temperature (-0.29) (Figures 4a and 5a). We found no evidence for direct or indirect causal relations between functional dispersion or species richness and the mean surface temperature in May. Instead, species richness was solely and strongly associated with mean height (0.30) (Figure 4a), which did not influence mean surface temperature. As hypothesized in Figure 2, we further observed a negative relationship between LAI and the mean surface temperature (-0.27), which was not related to any diversity facets. None of the horizontal metrics had a direct and significant path to mean surface temperature.

For the SEM model considering the CV in surface temperature in May, we found that herb-dominated communities directly (0.24) and species richness indirectly (via mean height 0.14) promoted the variation of community surface temperature (Figure 4b). Although herb-dominated communities presented a lower foliage distribution (-0.19), there was no influence of the centre of gravity on the CV of surface temperature. As hypothesized in our conceptual model (Figure 2), clumpiness increased the CV (0.21) as well as evenness and mean height (0.26 and 0.21 respectively). Following our expectations, LAI presented a negative effect on the CV of surface temperature and canopy variation (-0.19 and -0.23 respectively). None

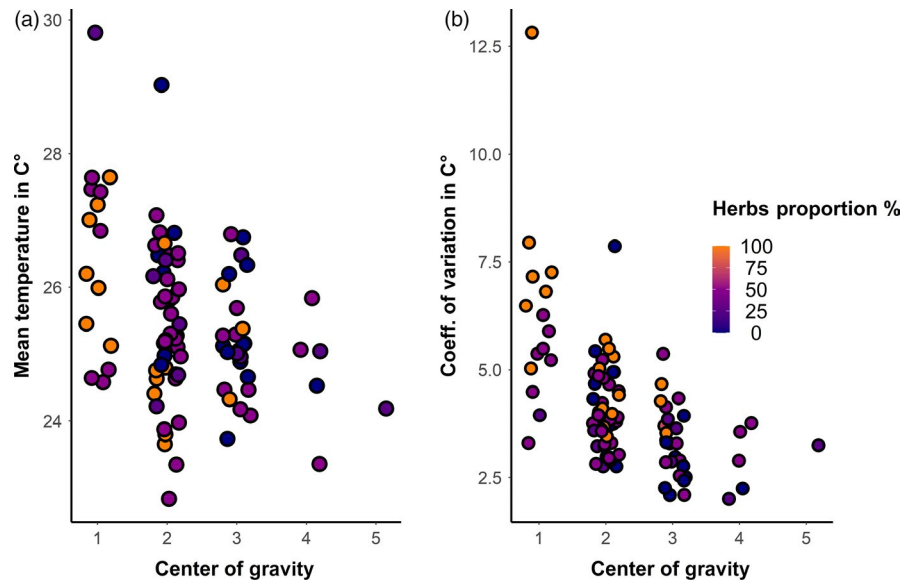


FIGURE 5 Correlation between the centre of gravity and (a) mean and (b) coefficient of variation of the surface temperature of grassland communities in May. The centre of gravity represents the height stratum with the highest density of points. The location was measured in terms of the height-weighted average volume allocation of the community. The five different strata of height considered in the calculation of the centre of gravity relates to figure x-axis as (1) 0.3–20 cm, (2) 20–40 cm, (3) 40–60 cm, (4) 60–80 cm and (5) 80–100 cm. A gradient of colours indicates the herb's proportions. (a) Herb-dominated communities (orange colour) with a low centre of gravity promote warming, and (b) have higher surface temperature variation than grass-dominated communities

of these structural metrics, except mean height, was affected by biodiversity facets (Figure 4b; Table S2).

3.4 | The relationship of biodiversity facets effects on the mean and variation of canopy surface temperature in August

Late in the growing season, both, the SEM of mean surface temperature (Fisher's $C = 10.692$, $df = 16$, $p = 0.828$) and the SEM model of temperature CV (Fisher's $C = 7.197$, $df = 14$, $p = 0.927$) fitted the data well. We found that the functional identity directly and indirectly (via canopy structure) influenced the surface temperature mean and CV (Figure 4c,d). Communities dominated by herbs (high FI) exhibited a more clumpy distribution (horizontal metric), with LAI (vertical metric) jointly controlling the mean surface temperature. Plant species richness only directly affected surface temperature CV (Figure 4d). Horizontal metrics such as canopy variation and clumpiness, but also evenness (vertical metric), explained the highest proportion of the variance in both SEM ($R^2 = 0.79$, $R^2 = 0.68$ and $R^2 = 0.59$ respectively). As in May, the SEM predicting surface temperature CV explained a higher proportion of the variance in the SEM (marginal $R^2 = 0.29$, Figure 4d) compared to the mean surface temperature explaining only 10% of the variance (marginal R^2 , Figure 4c).

We found that clumpiness was the sole metric with a significant effect on mean surface temperature with an indirect effect of one of the biodiversity facets, here of FI ($R^2 = 0.68$; Figure 4c), while LAI also significantly decreased mean temperature independent of biodiversity effects. Herb-dominated communities (high FI scores)

were clumpier (0.32), and clumpier canopies induced lower surface temperatures (-0.49) (Figure 4c,d). Herb-dominated communities also expressed a less even distribution of foliage (-0.60), which, in turn, led to a higher clumpiness (0.35). They also had a lower centre of gravity (-0.23), which also tended to increase clumpiness (-0.24)—all of it eventually translating into lower surface temperatures (path coeff. -0.49). Finally, herb-dominated communities with a lower centre of gravity and less foliage distribution exerted a stronger negative effect on canopy surface variation (-0.90) (Figure 4c,d). Species richness had a weak effect by decreasing canopy surface variation (-0.10). To summarize, herb dominance and functional diversity jointly induced lower canopy surface temperatures via a network of indirect causal pathways regulating clumpiness.

In contrast to May, we found no evidence of the indirect effects of different biodiversity facets via canopy structure on the CV of temperature in August (Figure 4d). Herb-dominated (0.30) and richer communities (0.22) promoted a higher temperature CV (Figure 4d), but this could not be traced back to structural features. FDis showed a negative effect on the presence of inflorescences (-0.18). Yet, late in the season, the contribution of canopy structure as a mediator of biodiversity effects on temperature seemed to solely influence the mean rather than the variation of community surface temperature (Figure 4c,d).

4 | DISCUSSION

We expected that functional identity (FI) and functional diversity (FDis) exert control on community surface temperature and

that this control would be mostly mediated via metrics of vertical canopy structure. During peak biomass in spring, we found opposing effects of FI on mean surface temperature: herb-dominated communities directly promoted lower mean surface temperatures. However, communities with lower centre of gravity (mostly herb-dominated communities) also increased canopy mean surface temperatures compared to grass-dominated communities with more biomass at the top of the canopy. Against our expectation, clumpiness, a horizontal metric, took over the mediating role of cooling the surface temperature in the late season. In both seasons, LAI, a vertical metric, decreased surface temperature but was not related to biodiversity. We further expected that the spatial variation of community surface temperature would be controlled by biodiversity via metrics of horizontal community structure. Instead, we found that in spring, the biodiversity control was mediated by a vertical metric (mean height) and that, apart from this, direct pathways of temperature control were more important. This tendency was even more pronounced in the late season, where both FI and species richness exerted direct control on the spatial variation of temperature. Across both seasons, functional diversity was neither significant for mean surface temperature nor temperature CV. These findings are relevant for a deeper mechanistic understanding of how biodiversity controls the surface temperature of plant communities via canopy structure and, consequently, ecophysiological activities in the current scenarios of biodiversity loss and climate change. These findings call for further research exploring the relative contribution of biotic and abiotic facilitation effects on ecosystem functioning.

4.1 | Biodiversity effects on mean and variation of community surface temperature via vertical metrics and their seasonal variation

Vertical metrics of canopy structure served as mediators of FI and species richness effects on the mean and variation of community surface temperature, particularly in spring. Communities with lower centre of gravity (mostly herb-dominated communities with higher PCA scores) promoted an increase in community mean surface temperature (Figure 4a). Some of our dominant herb species concentrate leaves closer to the ground (e.g. *Knautia arvensis*, *Centaurea jacea*, *Plantago lanceolata*), which likely contributed to higher mean surface temperature. As the increase in temperature was not mediated by mean height, we speculate that an upper layer of scattered plant organs (stems, single leaves, flowers) overtopping a dense layer of leaves from smaller herbs and ground rosette leaves from larger herbs may have served as windbreak creating turbulence far above the zone where incident radiation warms the majority of leaves. As a net result, this may have increased the boundary layer directly above the low leaf layer. This decreases the coupling to the atmosphere and lowers transpiration and convective cooling. Besides, the higher mean temperature in May compared to August (despite lower ambient temperatures in

May) could be caused by flowering species such as *Leucanthemum vulgare*, which create hot spots without casting too much shade (Figure 3).

At the same time, communities with higher centre of gravity (mostly grass dominated—low FI) exhibited lower mean surface canopy temperatures characterized by more vertical leaves. Against our expectation, grass dominance did not have a direct effect on the LAI in our SEM, although vertical leaf orientation is known to increase LAI (Bonan, 2008; Hirose & Werger, 1995). Given that centre of gravity and LAI were positively correlated (Figure 4a,b, positive correlation between the centre of gravity and LAI, Figure S4), it is possible that grass-dominated swards resembled the situation we had originally ascribed to diverse communities, where a denser canopy further away from the ground attenuate more radiation (Hirose & Werger, 1995; Jones, 2014; Niinemets, 2010; Yang & van der Tol, 2018) and transpires more in higher canopy layers which are better coupled to the atmosphere with smaller boundary layers and high surface conductance. Thus, energy dissipation via sensible and latent heat fluxes is promoted higher up in the canopy leading to lower canopy surface temperatures. This scenario is further supported by higher canopy roughness given the strong positive relationship between canopy roughness and centre of gravity (Figure S4) in our swards. Thus, a higher centre of gravity might indicate that more biomass is protruding into upper layers with higher wind speed, which may have contributed to the reduction of canopy surface temperature (Bonan, 2015).

The spatial variation of surface temperature was influenced by three of four vertical metrics in spring. This is surprising given that we expected a dominating control by horizontal metrics. Surface temperature variation was high in tall communities with an even foliage distribution and lower LAI (Figure 4b). The differences in species characteristics forming hot and cold spots may become more prominent in taller herbaceous canopies. Taller plants often also occupy a larger area and thus create more patchiness. Because the calculation of evenness averages across space, high values are not incompatible with a situation where leaves of different plant species positioned in low and upper layers of the canopy occur side by side rather than on top of each other. This is supported by the fact that evenness appeared to increase clumpiness early and late in the season. In other words, the vertical metrics may carry a signature of horizontal variation of structural elements, which is why they may also have explanatory power for the spatial variation in temperature.

4.2 | Biodiversity effects on mean and variation of community surface temperature via horizontal metrics and their seasonal variation

In spring, there was no effect of diversity on spatial metrics of community structure reflected by the canopy variation and clumpiness. While these spatial metrics did not affect the mean

temperature, they influenced the variation of community surface temperature (Figure 4a,c). Later in the season, we found that FI (i.e. herb dominance) increased clumpiness, which, in turn, decreased the mean surface temperature (Figure 4c). We had expected that spatial variation in canopy height would be one important variable to reduce the mean surface temperature by increasing the average boundary layer conductance for convective heat and water vapour fluxes (Jones, 2014; Schulze et al., 2019). We assumed that diversity might create a surplus of canopy variation beyond the simple approximation that roughness length increases linearly with canopy height (~0.1 per unit of the canopy height) (Bonan, 2008; Grace, 1983). However, our results do not support the importance of canopy variation on mean surface temperature as hypothesized. Instead, we found that the clumpiness of herb-dominated communities reduced mean surface temperature but only after regrowth from a first cut (Figure 4c). As discussed above, this might be related to the pronounced spatial clusters of some tall herbs, especially *Geranium pratense*, which is more dominant later in the season. More clumpy vegetation might again increase the average boundary layer conductance.

We had also predicted that the effect of diversity on the spatial variation of canopy surface temperatures is primarily mediated by the horizontal structure of plant communities (Figure 2). During peak biomass in spring, we did find that clumpiness promotes variation of surface temperature according to our original expectation. At the same time, surface variation had a spatially equalizing effect reducing temperature variation (Figure 4b), which could be induced by the mixing effect of increased turbulence over a rougher canopy. However, earlier, we argued that high canopy variation in the community is predicted to form a mosaic of cold- and hot spots leading to increased variation in surface temperatures. Our data do not support this in a particular scenario. Yet, all diversity facets significantly affected at least one horizontal metric in autumn. However, there was no indirect pathway between diversity and variation of community surface temperature mediated via the horizontal structure of plant communities (Figure 4d). We had expected that the patchier structures of herbs and grasses might have reflected general differences in functional traits, potentially inducing temperature variation. Above-ground differences in stomatal conductance or hairiness could increase variation in surface temperature. Below-ground, herbs tend to have deeper roots (Fischer et al., 2019; Leimer et al., 2014) but lower specific root length and lower root length density per volume of soil (Schroeder-Georgi et al., 2016), Figures S1 and S2). Even though there is no evidence that differences in rooting patterns lead to complementarity in soil water use with increasing diversity from this experiment (Bachmann et al., 2018; Barry et al., 2020; Jesch et al., 2018) or grassland experiments in general (Barry, Weigelt, et al., 2019), grasses still transpire more water per ground area because they have a much higher overall root surface area per volume of soil (Oram et al., 2018; Ravenek et al., 2014). Thus, patchy horizontal distribution of functional groups could have led to differences

in transpiration due to combined effects of hydrological traits (Asbjornsen et al., 2011), but we found no evidence for this.

4.3 | Direct biodiversity effects on mean and variation of community surface temperature and their seasonal variation

In our SEMs, we also allowed direct paths to capture the influence of diversity facets on mean and CV or surface temperatures irrespective of the vertical and horizontal metric of canopy structure. There was a direct lower temperature effect of herb-dominated communities at the biomass peak in May (Figure 4a—direct effects). Lundholm et al. (2010) found that tall herbs growing in mixtures with grasses and succulents also showed a high-temperature reduction performance. They related these effects of tall herbs to their high capacity for soil water extraction, evapotranspiration and albedo. Although Bachmann and colleagues (2018) found that some herbs indeed exhibited a higher stomatal conductance compared to grass species in the Jena Experiment, the selection of species in the Trait-Based Experiment in our study (seven grasses and six herbs species of the pool of 60 species in the Jena Experiment) did not reflect this pattern. For our species, stomata conductance rates loaded negatively on the first PCA axis with lower scores for grasses (see Figures S1 and S2). More work is needed to elucidate the mechanism why grasses are warmer independently of canopy structure in this experimental design.

In May and August, herb dominance directly affected spatial variation of community surface temperature. This is understandable from the fact that herb species tend to form pronounced spatial clusters (e.g. *Geranium pratense*). Furthermore, we showed evidence that species richness per se directly increased the surface temperature CV of grassland communities later in the summer (Figure 4d). This result points out that grassland species mixtures likely result in greater variation of microclimate because they provide greater canopy variation driven by functional trait variation (Opedal et al., 2015; Wright et al., 2015, 2017), even though this is not reflected by an increased clumpiness (see above). Moreover, by increasing species richness, grassland communities provide more thermal niches adjacent to one another (Potter et al., 2013; Zellweger et al., 2020).

4.4 | Mechanisms behind biodiversity effects on community surface temperature with special reference to abiotic facilitation

The previous three paragraphs have tracked diversity effects of surface temperature via three different pathways, that is, via vertical and horizontal metrics and direct effects. Across all of these pathways, we found functional composition to be the dominating biotic driver. The strong influence of FI (PCA scores) on both the community surface mean and variation of surface temperature

lends support to the notion that canopy microclimate might be one of the ecosystem functions that are predominantly controlled by species identity (herb- vs. grass dominance) and not by measures of species diversity (here FDis or species richness) (Fry et al., 2013; Mokany et al., 2008; Tilman et al., 2001). We acknowledge that there may be diversity-mediated sampling effects for functional characteristics that we do not capture with our structural measurements. These could translate into identity effects related to physiological performance, for example, water uptake or transpiration. However, abiotic facilitation, as a mechanism linking biodiversity and ecosystem functions and the focus of the special issue, would require diversity control, which leaves us with the question of whether in our data there is any indication of abiotic facilitation to operate. We note that in the late season, there was a significant direct path from species richness to variation of surface temperature (see Section 4.3—direct effects). This indicates that species-rich communities are more likely to host species with controls of surface temperature (Cowles et al., 2016), such as higher transpiration rates (Wright et al., 2015), higher leaf reflectance (Lundholm, 2015) and water retention in the soil (via root surface area per volume of soil) (Caldeira et al., 2001) causing higher variation of the community surface temperature. Cool spots created by some species are most likely associated with higher latent heat fluxes, that is, with the generation of moist air parcels. We may speculate that these may after turbulent mixing alleviate vapour pressure deficits in the canopy as a whole. Under hot and dry conditions, this could potentially translate into a facilitative mechanism (*sensu* Wright et al., 2017) in which one plant species benefits from another via amelioration of the microclimate (Barry, Mommer, et al., 2019). However, we shall note that weather conditions in the late seasons were even slightly cooler than in May (Table S5).

5 | CONCLUSIONS

In the micrometeorological theory, metrics of canopy structure such as height, roughness and LAI are considered key drivers of ecosystems' energy budget and occur as predictor variables in well-tested models. We further know from almost three decades of biodiversity-ecosystem functioning research that grassland diversity has a strong influence on canopy structure. Combining two proximal sensing methods (thermal imaging and laser scanning), we were able to create a dataset that allowed us to trace diversity effects mediated via structure. In the introduction, we developed likely scenarios according to which species-rich or functionally diverse mixtures are expected to create dense and tall canopies with high LAI and a high centre of gravity that should generally be cooler and—due to the higher diversity—also be patchier in terms of hot and cool spots. Instead, we found that the functional group composition (herb- vs. grass dominance) was a major driver of both mean and CV of surface temperature. In general, herb dominance could translate into a cooling or warming effect depending on the pathway. The direct effect

was one of cooling that we were unable to explain. Our herb species did not exhibit higher transpiration rates than grasses (see PCA analysis in the Suppl. material). As a direct effect, it was by definition not related to the herb's influence on canopy structures promoting a cooling such as LAI or height. Instead, the structural influence of herbs was one of warming via their low centre of gravity. Importantly, we found little direct evidence for plant diversity effects, although we cannot exclude diversity-driven sampling mechanisms translating into identity effects for functional characteristics we have not quantified. Functional diversity was only associated with structural metrics that did not translate into temperature effects, and species richness only influenced the CV of temperature late in the growing season. Evidence for abiotic facilitation was only indirect. Herb-dominated species-rich communities exhibited a higher variation of surface temperature, thus creating more thermal niches for dependent organisms. Future studies should expand our work and test our predictions with synchronous field measurements of transpiration rates under variable environmental conditions (indirect and direct radiation, wind speed). They also should proceed to investigate how surface temperature, here quantified by infra-red emission, relates to the distribution of actual canopy and soil temperature, ultimately driving ecosystem processes, such as photosynthesis, growth and soil activity.

ACKNOWLEDGEMENTS

We gratefully acknowledge Prof. Dr Raphaël Proulx for the support during the stay in Canada for further development of this study and Dr Anne Ebeling and Dr Dörte Bachmann for data contribution. We thank all the coordinators, the gardener team of the Jena Experiment, and many field assistants and student helpers for maintaining the field. The Jena Experiment is funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; FOR 1451) and the Swiss National Science Foundation (project 310030E-147487). Further support came from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118). Open Access funding enabled and organized by Projekt DEAL.

AUTHORS' CONTRIBUTIONS

C.G.-S., C.Wi., A.W., R.P., N.B., T.L. and B.R., conceived the ideas and designed the methodology; C.G.-S., J.D.-L., T.L., C.Wa., N.E. and C.R. collected and contributed data; C.G.-S. conducted the statistical analyses and wrote the manuscript with a critical contribution to the drafts from all co-authors.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13631>.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.866t1g1q1> (Guimarães-Steinicke et al., 2021).

ORCID

Claudia Guimarães-Steinicke  <https://orcid.org/0000-0001-7829-641X>
 Alexandra Weigelt  <https://orcid.org/0000-0001-6242-603X>
 Raphaël Proulx  <https://orcid.org/0000-0002-9188-9225>
 Nico Eisenhauer  <https://orcid.org/0000-0002-0371-6720>
 Joaquín Duque-Lazo  <https://orcid.org/0000-0003-4223-5070>
 Björn Reu  <https://orcid.org/0000-0001-5271-6420>
 Christiane Roscher  <https://orcid.org/0000-0001-9301-7909>
 Cameron Wagg  <https://orcid.org/0000-0002-9738-6901>
 Nina Buchmann  <https://orcid.org/0000-0003-0826-2980>
 Christian Wirth  <https://orcid.org/0000-0003-2604-8056>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Guimarães-Steinicke C, Weigelt A, Proulx R, et al. Biodiversity facets affect community surface temperature via 3D canopy structure in grassland communities. *J Ecol.* 2021;109:1969–1985. <https://doi.org/10.1111/1365-2745.13631>