Impacts of forest management on stand and landscape-level microclimate heterogeneity of European beech forests

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Abstract

Context   Forest microclimate influences biodiversity and plays a crucial role in regulating forest ecosystem functions. It is modified by forest management as a result of changes in forest structure due to tree harvesting and thinning.

Objectives   Here, we investigate the impacts of even-aged and uneven-aged forest management on stand- and landscape-level heterogeneity of forest microclimates, in comparison with unmanaged, old-growth European beech forest.

Methods   We combined stand structural and topographical indices derived from airborne laser scanning with climate observations from 23 meteorological stations at permanent forest plots within the Hainich region, Germany. Based on a multiple linear regression model, we spatially interpolated the diurnal temperature range (DTR) as an indicator of forest microclimate across a 4338 ha section of the forest with 50 m spatial resolution. Microclimate heterogeneity was measured as α-, β-, and γ-diversity of thermal niches (i.e. DTR classes).

Results   Even-aged forests showed a higher γ-diversity of microclimates than uneven-aged and unmanaged forests. This was mainly due to a higher β-diversity resulting from the spatial coexistence of different forest developmental stages within the landscape. The greater structural complexity at the stand-level in uneven-aged stands did not increase α-diversity of microclimates. Predicted DTR was significantly lower and spatially more homogenous in unmanaged forest compared to both types of managed forest.

Conclusion   If forest management aims at creating a wide range of habitats with different microclimates within a landscape, spatially co-existing types of differently managed and unmanaged forests should be considered, instead of focusing on a specific type of management, or setting aside forest reserves only.

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Introduction

Forest microclimate plays an integral role for forest ecosystem processes (Aussenac 2000; De Frenne et al. 2021). It influences heat and energy exchanges and thereby affects basic physiological functions of individual organisms as well as ecosystem functions, such as soil respiration, evapotranspiration and nutrient cycling (Bonan 2015; Clarke 2017). Hence, the local microclimatic conditions within forest ecosystems, rather than macroclimatic means of a region, are relevant for the performance, diversity, composition, and spatio-temporal distribution of forest organisms, as well as their growth, reproduction, and mortality (Bramer et al. 2018; Zellweger et al. 2019). It is therefore important to better understand the drivers of forest understory microclimate and how it is impacted by forest management, particularly against the background of climate change and biodiversity decline.

Regional climate is modified by the topography and forest structure, which jointly constrain the microclimate of a site (De Frenne et al. 2021). Topographic variables that influence microclimate include elevation and exposition as well as the slope of the area and its relative position within the landscape matrix (e.g. valley bottom vs. hilltop, proximity to water bodies) (Jucker et al. 2018a; Macek et al. 2019). Effects of forest structure on forest microclimate are primarily determined by canopy height and canopy openness, the species composition, distance to forest edge as well as the horizontal and vertical complexity of a forest stand (Ehbrecht et al. 2017, 2019; Kovács et al. 2017).

It is well understood that forest management alters below-canopy microclimatic conditions by modifying the structural features of a stand (Blumröder et al. 2021; Ehbrecht et al. 2019). Disturbances through timber harvest change the local light conditions, temperature buffering capacity, rainfall interception, and stand-level transpiration, thereby impacting soil and air temperatures as well as water budgets (Chen et al. 1999).

Temperate broadleaved forests in Central Europe are usually managed under the principles of continuous cover forestry (Röhrig et al. 2020). Approaches of continuous cover forestry range from coarse-grained, even-aged (EA) management, focused on age class cohorts in larger patches (i.e. shelterwood system), to fine-grained, uneven-aged (UEA) management. In UEA management, single stems of mature trees with a certain target diameter are cut or desirable trees are promoted through liberation cuttings (Schall et al. 2018a, b). UEA-management promotes stand-level structural heterogeneity, which is reflected in multiple canopy layers resulting from an uneven age and size of trees, as well as a continuous canopy cover (Bauhus et al. 2009). In contrast, EA-management results in a mosaic of largely single- or two-layered stands of different developmental stages with trees of similar ages, thereby promoting a higher between-stand heterogeneity, but lower structural heterogeneity at stand level. The differences in stand structure resulting from the spatial grain of the two alternative management approaches likely translate into differences in below canopy microclimate variability.

While silvicultural guidelines in Europe and North America nowadays advocate UEA forest management over EA management, the impact of the two forest management regimes on biodiversity remains a matter of scientific debate (Giessen et al. 2013; Messier et al. 2015; Nolet et al. 2018). Consequently, a better understanding of the impacts of even-aged versus uneven-aged management on landscape-level microclimate heterogeneity at varying spatial scales is needed and can improve our understanding of forest management impacts on biodiversity.

Here, we investigate and model within- and between-stand as well as landscape-level microclimate heterogeneity—measured as α-, β-, and γ-diversity of thermal niches for a 4338 ha section of the Hainich European beech forest. The main objective of this study is to better understand the impacts of forest management on forest microclimate across spatial scales.

For this purpose, we combine airborne laser scanning (ALS) derived raster data of topographical and stand structural metrics with spatially-referenced information on forest stand features and *in-situ* climate observations. Based on statistical relationships between the DTR and forest structural as well as topographic variables, we model and predict DTR across

the study area for EA, UEA and UNM forests covered using the ALS data.

With our analyses, we aimed at testing the following hypotheses:

1. Even-aged forest management results in lower α-diversity, but higher β- and γ-gamma diversity of forest microclimates compared to uneven-aged or unmanaged forests.
2. Uneven-aged forest management results in higher α-diversity, but lower β- and γ-gamma diversity compared to even-aged and unmanaged forests.
3. Unmanaged old-growth forests show lower diurnal temperature ranges than managed forests.

Materials and methods

Study region

The study was conducted within the framework of the *Biodiversity Exploratories* (www.biodiversity-exploratories.de), a large-scale and long-term research initiative to investigate the impacts of land-use on biodiversity and associated ecosystem functions and services (Fischer et al. 2010). The study site *Hainich-Dün* is located in Thuringia, Central Germany (51º 16′ N, 10º 47′ E). With approximately 16,000 ha, the Hainich is one of the largest contiguous European beech dominated forests in Central Europe (Ehrbrecht et al. 2019; Fischer et al. 2010). Elevations range from 245 to 537 m above sea level. At the time of ALS data acquisition in summer 2015, mean annual precipitation in the region ranged from 500 to 800 mm, and mean annual temperatures ranged between 6.5 and 8 ºC (Nauss et al. 2015).

The Hainich presents a perfect study landscape to investigate structural and microclimatic differences resulting from the different spatial grain of forest management, as both even-aged and uneven-aged, as well as unmanaged old-growth European beech forests can be found under comparable site conditions. The forest plots of the *Biodiversity Exploratories* were selected along a gradient of management intensity, ranging from unmanaged stands in Hainich National Park (UNM), single tree selection systems (UEA management), to shelterwood systems, reflecting the different developmental stages under EA

forest management (Fischer et al. 2010; Schall et al. 2018a, b).

The unmanaged forests in the southern part of the Hainich region was declared a national park in 1997 as part of the UNESCO world heritage site *"Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany"* and are characterized by old-growth European beech stands. However, it needs to be taken into account that the stands of the Hainich National Park are not yet characterized by the structural features of primary forests, as they still show a footprint from former forest management. Stands are up to 250 years old, whereby management (coppice-with-standards and later on transformation to high forest systems) was ceased up to 70 years ago (Mund 2004; Schall et al. 2018a, b; Willim et al. 2022). Further details on forest management practices for EA and UEA and land-use history of UNM stands of the Hainich National Park are provided in Schall et al. (2018a, b) and Mund (2004).

Managed and unmanaged stands within the study landscape are strongly dominated by European beech (*Fagus sylvatica* L.), partially mixed with other broadleaved species, such as European ash (*Fraxinus excelsior* L.), Sycamore maple (*Acer pseudoplatanus* L.), Hornbeam (*Carpinus betulus* L.) and/or Small-leaved lime (*Tilia cordata* Mill.) (Mund 2004). Further information on stand age and stand structural characteristics for the study plots is provided in Table 6, Sect. 7.1 of the supporting information (SI). Differences in topography between the management systems are discussed in Sect. 7.2. of the SI).

Data acquisition and variable selection for landscape-level microclimate modelling

Microclimate data

We used the diurnal temperature range, maximum, minimum and mean temperature as indicators of forest microclimate. The temperature data was obtained in hourly intervals with sensors mounted 2 m above ground (MELA KPC 1/5-ME temperature sensor, *MELA Sensortechnik GmbH*, Germany) (Nauss et al. 2015). For statistical analysis and the development of microclimate models, the daily data from 23 meteorological stations was first aggregated to mean values for the summer months (June, July and August), and then averaged for the investigation period from

2014–2016 (Ehbrecht et al. 2016). DTR was calculated as the difference between daily maximum and minimum temperature. DTR, maximum and minimum temperature, as well as mean temperature were tested as dependent variables in a multiple linear regression (MLR) model explaining variability in microclimate (see supporting information, Sect. 7.4, Figs. 10–13). The ALS data was aquired in a flight campaign in summer 2015. By including the years before and after the ALS flight, a reasonable number of climate observations was included, while only minor changes in stand structural features, resulting from tree harvests, could be expected.

Airborne laser scanning data

All ALS data was provided through the remote sensing database (RSDB). For a detailed description of the functionality of RSDB see Wöllauer et al. (2020). The scanning flights of the Hainich took place in July 2015 with a Q780 Riegel Sensor, at an operating frequency of 400 kHz from approximately 950 m above ground, with an average point density of 36.24 pts. m^{-2} (Magdon and Kleinn 2016; Seidel et al. 2020). The flight covered a total area of 13,378 ha, 4,388 ha of which were European beech forest included in the analysis (see Fig. 4). All points were classified into ground and non-ground returns and a digital terrain model (DTM) was fit to the ground returns. This resulted in a raster file of 1 m^2 spatial resolution, where the pixel values represent height above sea level of the ground surface. Similarly, a digital surface model (DSM) was computed using the highest z-coordinates of each 1 m x 1 m grid cell, after removal of isolated returns. Subtracting DTM from DSM resulted in a canopy height model (CHM), a raster file with cells representing heights of vegetation and other non-ground returns measured from the ground level. Subtracting the DTM from each point value resulted in a normalized point cloud of the vegetation, where z-values of points correspond to their height above ground (Fig. 1).

DTM and CHM were subsequently used to calculate a set of stand structural and topographical metrics (see Table 1), assumed to modify forest microclimate. Details on metric computation are given in the reference list for each metric.

Understorey microclimate can be affected by clearings made tens of meters from forest gaps or edges (Chen et al. 1999; Ewers and Banks-Leite 2013). To capture the effect of canopy conditions in the vicinity of each meteorological station at an appropriate scale, all metrics were calculated for 50×50 m extents (pixel size) (sensu Jucker et al. 2018b).

Model selection

We tested the relationship between ALS metrics (as independent variables) and the microclimate indicators (as dependent variables) using linear regression models (see Fig. 2 for DTR and supplement Figs. 14–16 for the other temperature variables). All statistical analysis was done in R, version 3.5.2. (R Core Team, 2021).

We selected four topographic metrics that are known to impact air temperature and other climate variables due to changes in atmospheric pressure and site exposure (Bennie et al. 2008; Dobrowski 2011; Jucker et al. 2018a), and six canopy structural metrics, which have been shown to affect the microclimate below the canopy through shading, interception or modified air-flow (Bramer et al. 2018; Ehbrecht et al. 2019; Jucker et al. 2018b). Selected variables are summarized in Table 1 (see supplementary information Sect. 7.2 for further details).

In order to develop a multiple linear regression (MLR) model explaining variability in below canopy temperature, we tested all possible combinations of explanatory variables, where collinearity did not exceed the threshold of r <|0.7|, as defined by Dormann et al. (2013). MLRs were rejected if one predictor variable was not significant (p > 0.05). The models with different variable combinations were then ranked according to their Akaike Information Criterion (AIC$_c$) and the MLR with lowest AIC$_c$ was used in the subsequent analysis (see Table 2). Additionally, an automated model selection using the "dredge" function, as implemented in the R package *MuMIn* (Bartoń, 2013), was used to confirm the manual model selection. Subsequently, we used hierarchical partitioning to assess the contributions of each predictor variable to the overall explained variance using the R package *hier.part* (Walsh and Nally 2020). We focused on DTR in subsequent analyses to model the stand- and landscape-level heterogeneity of forest microclimate, as DTR was shown to be a strong indicator of forest microclimate, accounting for both, maximum and minimum temperature (Ehbrecht et al.
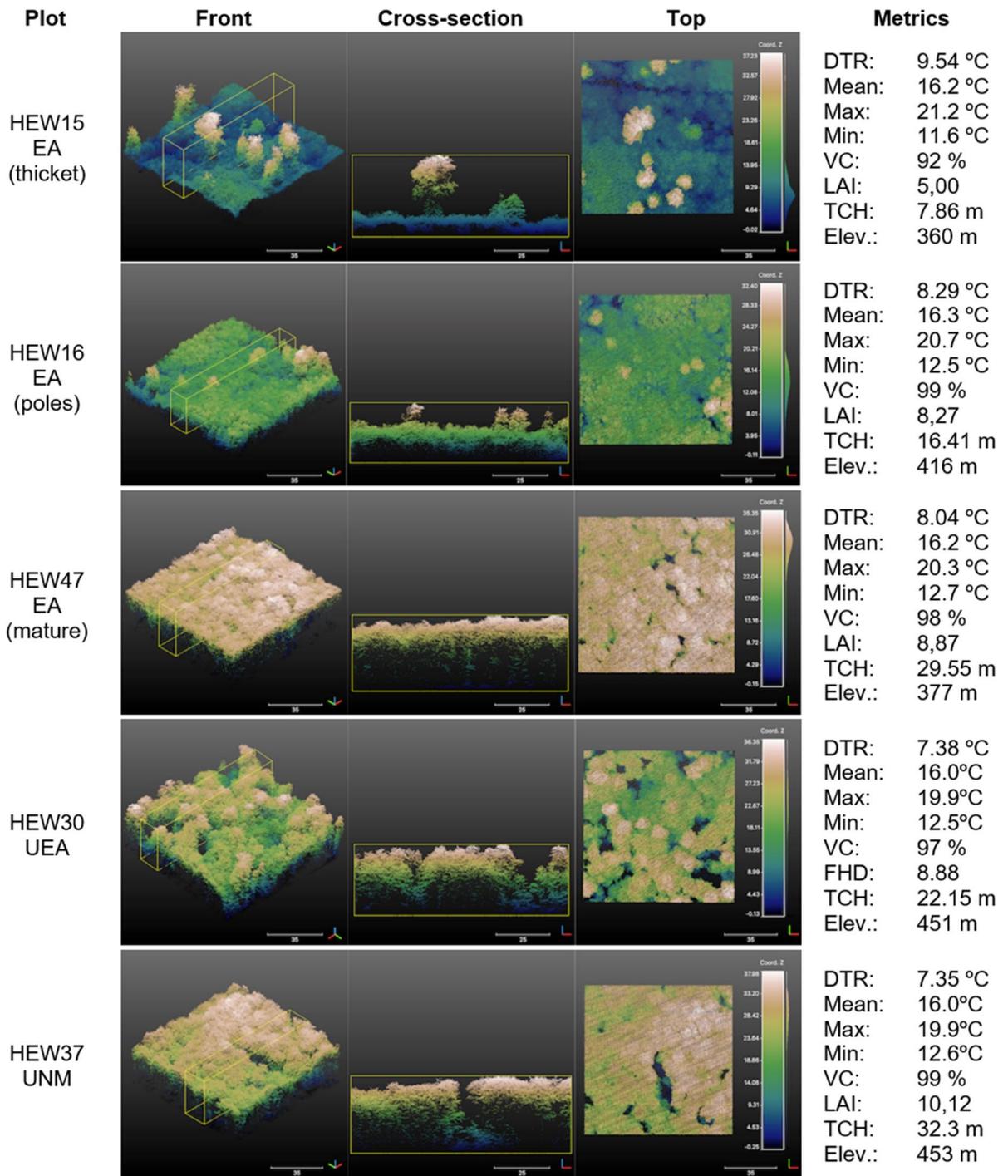
Fig. 1 Normalized point clouds and metrics values of selected exemplary forest plots of 100 m × 100 m (1 ha) size. The colour-scale is based on z-values of points above ground level. The scalar bar also depicts their distribution

Table 1 Description of stand structural and topographical metrics used in this study

ALS-based variable	Description
Elevation	Mean height of ground above ellipsoid, based on DTM raster pixels (Wöllauer et al. 2020)
Slope	Based on DTM raster pixels bilinear regression [%] (Wöllauer et al. 2020)
Sin(Aspect)	Based on DTM raster pixels bilinear regression [sin(rad)]: Positive numbers represent south and negative numbers north (Jucker et al. 2018a)
Topographic position Index (TPI)	The relative position of a pixel within the landscape based on DTM ranging from negative (concave terrain, e.g. gulleys) to positive (convex terrain, i.e. ridges) (Evans et al. 2021; Jucker et al. 2018a)
Vegetation cover (VC)	% of canopy returns higher than 5 m above ground level (based on CHM) (Wöllauer et al. 2020)
Mean top of canopy height (TCH)	Mean of the CHM for each pixel [m] (Wöllauer et al. 2020)
Vertical distribution ratio (VDR)	Normalized measure of vertical height distribution: TCH divided by maximum vegetation height (Müller et al. 2018)
Foliage height diversity	Derived from point cloud and penetration rates of canopy, understorey and regeneration strata (MacArthur and MacArthur 1961)
Leaf area index (LAI)	Calculated from normalized point cloud using (Detto et al. 2015; Getzin et al. 2017)

2019). In order to upscale DTR values over the entire landscape covered by the ALS flight, a raster map with 50 m spatial resolution was computed using ALS-derived raster files of the selected explanatory variables.

Calculation of landscape level microclimate heterogeneity indices

In order to test our hypotheses that forest management affects microclimate heterogeneity, we calculated model predicted α-, β-, and γ- diversity of DTR classes from the computed DTR raster, following the framework of diversity partitioning based on effective numbers, as described in Hill (1973) and Jost (2006). Here, α-diversity (D_α) describes the average within-patch, β-diversity (D_β) the between-patch, and γ-diversity (D_γ) the overall-heterogeneity of microclimatic niches. We calculated diversity for each group (EA, UEA and UNM) as exponential Shannon index (^1D), following Jost (2007) (see also supplementary information Sect. 7.4).

To calculate α- and β-diversity for different scales, we assigned 4, 9, and 16 pixels to a patch (plot) respectively, by overlaying square grids with side length 100 m, 150 m, and 200 m over the extent of the DTR raster. Hereby, only those patches which were fully contained within a certain management system were included in the analysis of microclimate heterogeneity. In order to avoid edge-effects, we excluded all pixels within a 50 m buffer from the forest edge.

Predicted DTR values were aggregated to DTR-classes by rounding to the next 0.25 °C. In the context of this study, aggregated DTR classes can be interpreted as thermal niches. We calculated within-patch α-diversity of thermal niches ($^1D_\alpha$) for each patch size separately. Similarly, overall γ-diversity ($^1D_\gamma$) was calculated from abundance matrices of DTR classes per management system (i.e. the pooled sample) and for each neighbourhood size separately. All diversity calculations were carried out using the *vegan* package in R Studio (Oksanen, 2019). We then compared differences in means and distributions of DTR between management systems using one-way ANOVA and post-hoc Tukey test.

Furthermore, we applied non-metric multidimensional scaling (NMDS) to the dataset using the *vegan* package in R-Studio (Dixon, 2003; Oksanen, 2019). NMDS is used in multivariate statistics to ordinate (dis-)similarities between site observations and was used here as a tool to assess the β-diversity of thermal niches between the three management systems.

Results

ALS-based metrics of forest structure and topography explained the variability of forest microclimate within the studied plots. While the canopy structural indices explained between 36% (VC) and 70% (FHD) of the variance in DTR, topographic variables were less important for the variability in microclimate in
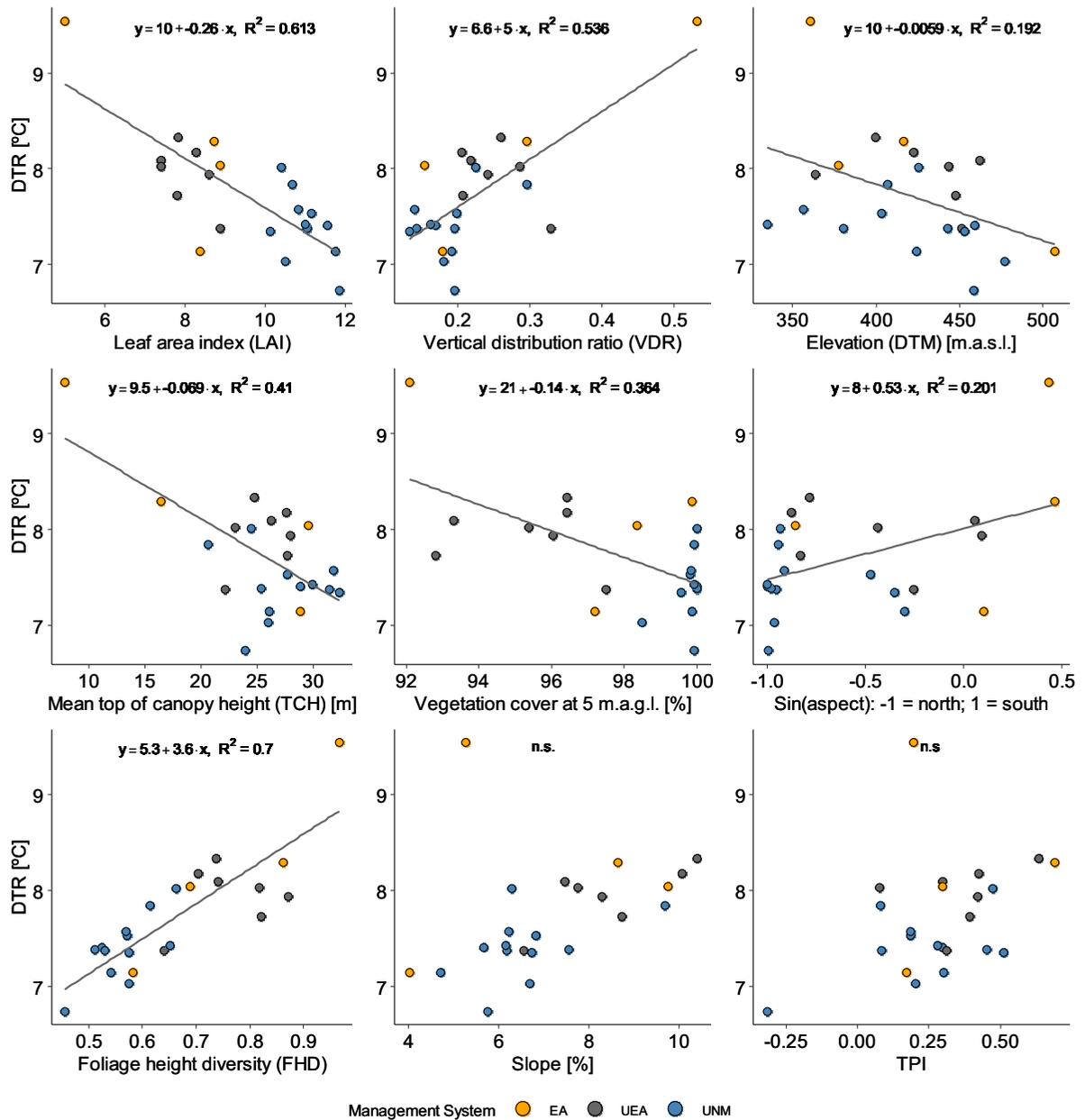
Fig. 2 Linear regression models of ALS-derived topographical and canopy structural metrics and mean diurnal temperature range (DTR), measured at 23 plots in even-aged (EA) uneven-aged (UEA) and unmanaged forests (UNM), during the vegetation periods of 2014–2016. The coefficient of determination (R^2) and the equation of the linear regression model are shown for each variable but slope and TPI, which were not significantly correlated ($p < 0.01$) with DTR in the Hainich

the Hainich and only elevation ($R^2 = 0.19$) and the sinus of aspect ($R^2 = 0.20$) were significantly correlated with DTR (Fig. 2, supplementary information Figs. 14–16 for other temperature variables).

The best performing multivariate model explained 82% of variance in DTR, leveraging LAI, TCH and elevation as explanatory variables. Elevation contributed 20% to the overall explanatory power of the
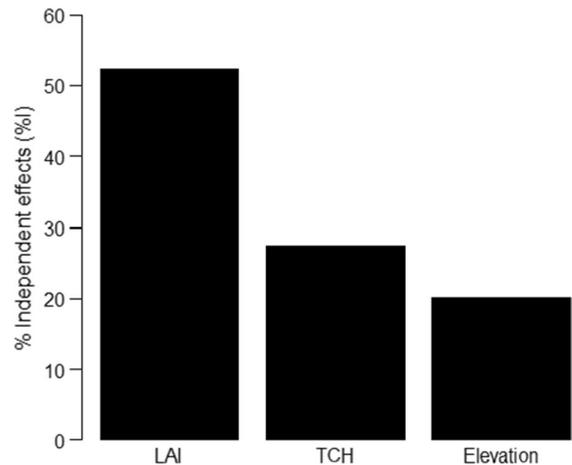
Table 2 Coefficient of determination (Adj. R^2), Akaike information criterion (AIC_c), difference in AIC_c between the respective model and the "best" model (ΔAIC_c), and root mean squared error (RMSE) of each MLR model predicting DTR at 23 meteorological stations within the Hainich

Model (lm(DTR ~ x)	Adj. R^2	AIC_c	ΔAIC_c	RMSE	Rank
Elevation + LAI + TCH	0.82	9.96	0.00	0.22	1
Elevation + LAI + VDR	0.80	12.72	2.76	0.24	2
Elevation + LAI	0.76	14.64	4.68	0.27	3
Elevation + FHD + VDR	0.76	16.73	6.77	0.26	4
Elevation + FHD + TCH	0.76	17.16	7.20	0.26	5
FHD + VDR	0.73	17.63	7.66	0.28	6
FHD + TCH	0.72	18.54	8.58	0.29	7
FHD	0.69	19.19	9.23	0.31	8
Elevation + TCH + VC	0.71	21.07	11.11	0.29	9
Elevation + VDR + VC	0.69	22.59	12.63	0.29	10
LAI + VDR	0.66	22.62	12.66	0.32	11
LAI + TCH	0.66	22.94	12.97	0.32	12
LAI	0.59	25.04	15.08	0.36	13
Elevation + VDR	0.60	26.31	16.35	0.34	14
VDR + VC	0.56	28.94	18.98	0.36	15
VDR	0.51	29.21	19.25	0.39	16
Elevation + VC	0.55	29.45	19.49	0.37	17
Elevation + TCH	0.52	30.60	20.64	0.38	18
TCH + VC	0.52	30.65	20.69	0.38	19
TCH	0.38	34.71	24.75	0.44	20
VC	0.33	36.46	26.50	0.46	21
Elevation + Sin(aspect)	0.35	37.54	27.58	0.44	22
Sin(aspect)	0.16	41.68	31.72	0.51	23
Elevation	0.15	41.97	32.00	0.51	24



Fig. 3 Hierarchically partitioned contributions of predictor variables to the overall explanatory power of the selected model

model, compared to 52% by LAI and 28% by TCH (Table 2, Fig. 3).

Figure 4a depicts a map of model predicted DTR across the study area. On average, predicted DTR was highest in EA forests (8.16 °C), followed by UEA forests (8.12 °C), and lowest in UNM forest in the National Park (7.46 °C) (p < 0.01, Fig. 4c).

Table 3 summarizes α- β- and γ-diversity of thermal niches between EA, UEA and UNM forest for three different patch sizes (1 ha, 2.25 ha, and 4 ha).

Distributions of α-diversity of thermal niches are shown in Fig. 5.

Overall γ-diversity of thermal niches was highest in EA on all scales, but only marginally higher than UEA at the 4 ha scale. $^1D_\alpha$ was highest in UEA at the 1 ha scale, but not significantly different from EA on all three scales, while $^1D_\alpha$ was higher in EA at the 2.25 ha and 4 ha scale. However, microclimatic α-diversity of both EA and UEA was significantly higher than in UNM for all three scales, indicating a generally positive effect of management on microclimate heterogeneity on plot-level. While significant differences of microclimatic α-diversity between managed and unmanaged are only marginal at a 1 ha scale, they become more pronounced on greater spatial scales. D_β was highest in EA forest at 1 ha and 2.25 ha scales, but similar to UEA at the 4 ha scale.

We assessed relative dissimilarities of microclimates between the three management approaches by plotting a subsample of the DTR-map in multidimensional space and then re-projecting it into two dimensions by means of NMDS (Fig. 6). The subsample shown here is based on the abundance matrix used to calculate D_α. Each point represents a plot for each scale, respectively. The ordination shows that UNM forests in the NP feature a different microclimate than both types of production forests EA und UEA. The latter two largely overlap (are similar). EA forests have a larger standard deviation of the projected

(a)

(b)

(c)

(d)
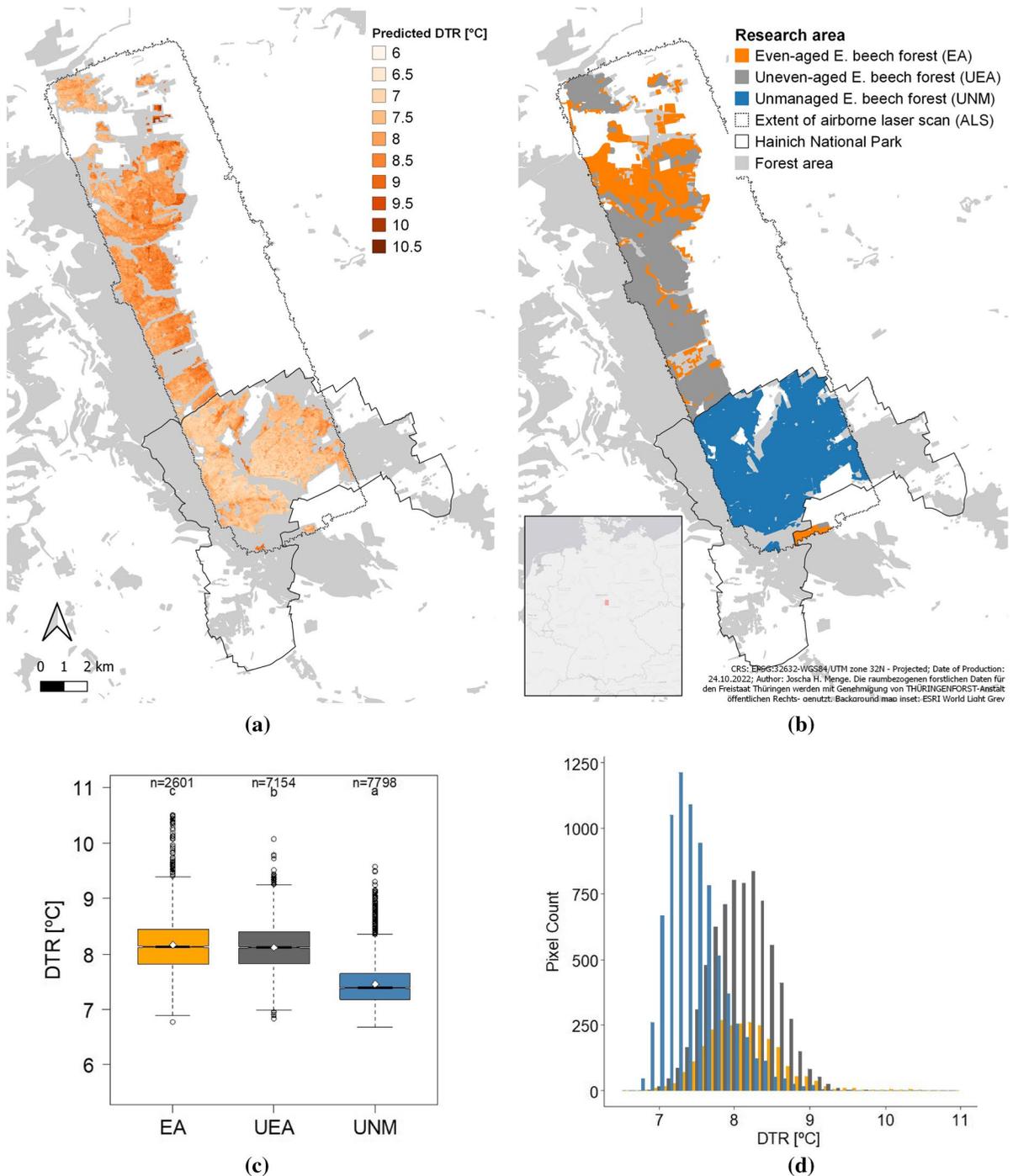
Fig. 4 a Map of model-predicted DTR for a 4388 ha section of the Hainich covered by an airborne laser scan (ALS) in 2015. One pixel corresponds to 50×50 m (0.25 ha). Pixels within a 50 m buffer from the forest edge and outside of the latitudinal range of the plots were excluded from the analysis. **b** Overview of management systems of the study area (coniferous plantations and young secondary forest in the national park were excluded). **c** Distributions of predicted DTR values as boxplots by management system. The number of pixels in each management system are shown (n). Average DTR values are indicated by a white dot and medians by a black line within the box (interquartile range. All three means were significantly different from each other ($p < 0.001$), as indicated by different letters. **d** Histogram of DTR-classes (thermal-niches) by management system (bin-width $= 0.125$ °C)

Table 3 α-, β-, and γ-diversity of thermal niches (^{1}D). DTR-classes were aggregated by rounding to the next 0.25 °C

Plotsize	Type of management	Number of plots (n)	Mean $^1D_\alpha$	± SD	cld	$^1D_\beta$	$^1D_\gamma$
1 ha = 2×2 pixel	EA	441	2.30	0.69	b	3.19	7.35
	UEA	1457	2.37	0.72	b	2.87	6.81
	UNM	1708	2.16	0.71	a	2.63	5.67
2.25 ha = 3×3 pixel	EA	142	3.15	0.87	b	2.32	7.33
	UEA	528	3.10	0.81	b	2.16	6.71
	UNM	665	2.81	0.87	a	1.91	5.38
4 ha = 4×4 pixel	EA	55	3.50	0.97	b	1.93	6.76
	UEA	240	3.51	0.84	b	1.91	6.70
	UNM	322	3.12	0.91	a	1.70	5.31

Compact letter display (cld) indicates significant differences in means

a) Plot-size 1 ha (2x2 pixel) b) Plot-size 2.25 ha (3x3 pixel) c) Plot-size 4 ha (4x4 pixel)
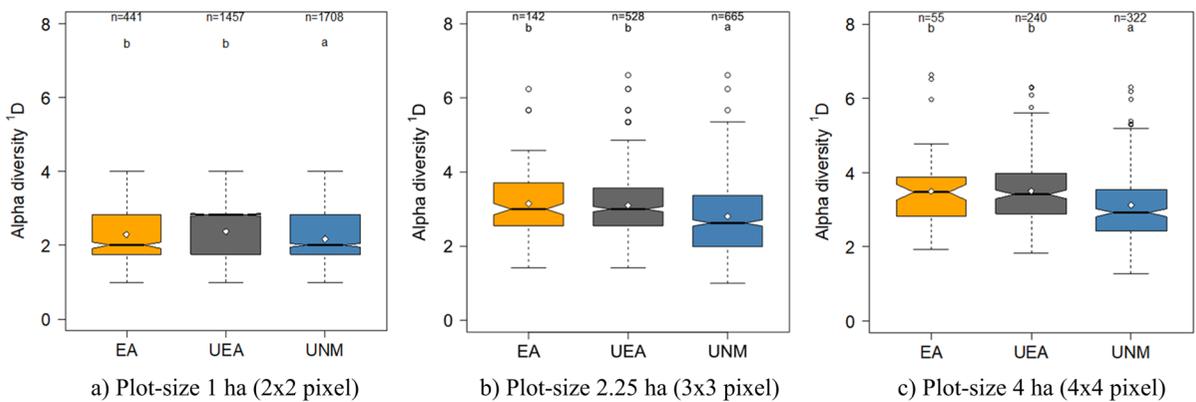
Fig. 5 Comparison of α-diversity of thermal niches ($^1D_\alpha$), between EA, UEA, and UNM forest for three different plot sizes. Plots (n) were only included in the analysis if all pixel of a plot lay within a respective management system. White points indicate the mean, black lines the median of distributions. Outliers outside of the whiskers are indicated by a white dot. Significant differences (ANOVA; $p < 0.05$) are indicated by different letters

a) Plot-size 1 ha (2x2 pixel) b) Plot-size 2.25 ha (3x3 pixel) c) Plot-size 4 ha (4x4 pixel)
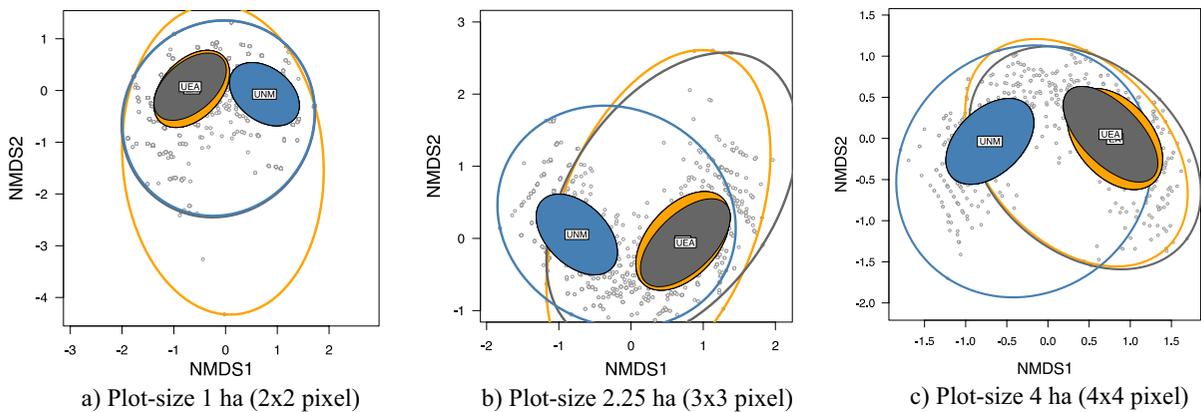
Fig. 6 NMDS ordination for three different plot-sizes: The outer ellipsoids depict the minimal volume of each forest management system in multi-dimensional space (i.e. the projected "area" in 2D), such that all points (i.e. plots) lie just inside or on the boundary of the ellipsoid

distance of points as well as a larger minimal volume in multidimensional space.

Discussion

Our results show that microclimate-heterogeneity in European beech forests is largely determined by the type of forest management and the resulting differences in forest structure. Silvicultural treatments such as thinning and tree harvest shape stand structures, which was more important for explaining the variability of microclimates in the study area than topography (Fig. 3) (Ehbrecht et al. 2016, 2017; Juchheim et al. 2017). We found that forest management results in significant differences of α-, β-, and γ-diversity of microclimates in comparison with unmanaged forests. Landscape-level microclimate heterogeneity was highest in EA forests, because stands of different developmental stages and forest structures -ranging from thickets and pole woods, to immature and mature stands- featured a large variability of DTR across the different stands, leading to a higher β-diversity, and thereby γ-diversity of microclimates (Table 3).

Since the plots of the *Biodiversity Exploratories* did not cover sites with steep slopes or strongly undulating terrain, the observed impact of slope and aspect and topographic position on forest understorey microclimate was limited (Fischer et al. 2010). This limitation must be kept in mind when interpreting predicted DTR for raster pixel in areas of topographically more extreme terrain, such as hilltops, steep slopes or valley bottoms (see also Sect. 7.2 in the Supplementary Information for parts of the prediction area that were outside the topographical range covered by our plots). However, the well-understood relationship between altitude, air-pressure, and temperature, was accounted for in the model due to the inclusion of elevation as explanatory variable (Körner 2007). Since the effects of forest structure on microclimate can be expected to be even more pronounced in topographically less heterogeneous landscapes (e.g. lowland E. beech forest), we deem our results to be transferable to other managed beech forest in central Europe.

Due to a higher variability and intermingling of different tree sizes, multiple-layered stands under UEA management are characterized by a higher structural complexity on plot or stand level than most developmental stages under EA management (Ehbrecht et al. 2016). However, a higher structural complexity on stand level did not translate into a significantly higher α-diversity of microclimates in comparison with EA management. Being considered the "archetype" of continuous cover forestry (sensu Pretzsch, 2009), UEA management is characterized by a continuous maintenance of canopy cover. A reduction in canopy cover in upper canopy layers due to harvesting of mature trees may be compensated for by trees crowns occupying mid- to lower canopy layers and vice versa. i.e., a higher structural complexity on stand level may result in a significantly, though marginally lower mean DTR, but not necessarily in a higher α-diversity of microclimates in comparison with EA management. These findings are in line with Ehbrecht et al. (2019), who pointed out that structural characteristics other than canopy openness contribute marginally to variations in DTR.

NMDS ordination (Fig. 6) clearly showed that both types of managed forests differed distinctly from unmanaged forest with regards to their microclimate heterogeneity, while both EA and UEA forests were relatively similar to each other. The unmanaged European beech stands (UNM) in the Hainich National Park have developed from formerly managed stands into coherent closed-canopy, old-growth forest (Mund 2004). These old-growth stands show a high structural complexity and significantly lower canopy openness on stand level (Ehbrecht et al. 2017), but little variability of forest structure at larger scales. While the very low canopy openness (and thus high LAI) and high canopy height may explain the overall significantly lower mean DTR, the low variability of forest structures at larger spatial scales may explain the lower γ-diversity of microclimates. The relatively low variability of forest structures most likely explains the dissimilarity in microclimates in comparison with stands under EA and UEA management. However, it should be noted that the structure of European beech stands within the forest reserve is still influenced by former management and not yet characterized by more pronounced structural heterogeneity due to natural disturbance and/or tree mortality. Natural disturbances and individual tree mortality may lead to the formation of canopy gaps of different sizes in the future, thereby creating more variable microclimatic conditions. Already existing smaller canopy gaps may have not been detected by the ALS data due to the

spatial resolution of 50×50 m. Still, a more fine-scale assessment of 3D forest structure based on terrestrial laser scanning did not reveal a pronounced spatial heterogeneity of canopy openness (Willim et al. 2022).

Heterogeneity of microclimates within a landscape is known to be an important driver of local biodiversity (Stein et al. 2014). Enhancing landscape-level heterogeneity of microclimates can therefore be seen as strategy in forest management to promote overall species diversity (Schall et al. 2020; Schütz 2002). In this regard, our results suggest a positive effect of management on landscape-level microclimate heterogeneity, with the highest γ-diversity of microclimates in EA forests. Thereby, our results may help to explain the findings of the multi-taxa species inventory conducted in the *Hainich-Dün* region (Schall, et al. 2018a, b). The inventory showed that EA forests in fact featured the highest multi-taxa γ-biodiversity, which was likely driven by differences in stand structure, and in turn, light availability and below canopy microclimatic conditions between stands of different developmental stages or age classes (β-diversity).

On the contrary, our analysis showed that mean DTR was significantly lower in unmanaged, old-growth forest compared to managed forests, which might be especially relevant for the conservation of taxa that depend on stable and less variable microclimatic conditions. DTR in the Hainich National Park was on average 0.70 °C lower than in EA forest and 0.66 °C lower than in UEA forest, suggesting a higher thermal buffering capacity in closed canopy old-growth forests than in managed forests. In this regard, forest nature reserves such as the Hainich National Park, where European beech forests can develop into old-growth-stages, play an important role in alleviating pressure on species threatened by climate change (Frey et al. 2016). Against the background of climate change, understorey microclimate is considered more important for performance and survival of forest dwelling species than macroclimate (De Frenne et al. 2021). The temperature buffering effect of forest canopies may partially decouple change rates in macroclimate from change rates in understorey microclimate (Bertrand et al., 2016).

In the light of the recent calamities in European beech forest following drought throughout Germany and Central Europe, drastic changes in forest structure can be expected in some areas in the future (BMEL 2020; Leuschner 2020), which will also impact the microclimate heterogeneity of affected stands. The methodology of predicting microclimate variables by combining vegetation structure and topography indices derived from ALS observations with in-situ meteorological data, allows a direct comparison of the results from 2015 presented here with updated information on stand structure and below canopy weather records. Future research should therefore focus on investigating how management- and mortality-induced changes of three-dimensional forest structure affect microclimate in the Hainich and other European beech forests. Furthermore, the role of microclimate as a predisposing factor for beech calamities could be investigated by overlaying fine-scale maps of microclimate parameters with the spatial distribution patterns of vitality loss and mortality in European beech forests. Thus, the methodology presented offers new ways of monitoring the effects of both silvicultural interventions and natural disturbances on forest structure, and how they interact with regional climate changes in shaping understorey microclimate at different points in time. In future studies, our model may be refined by taking topographically more heterogeneous sites and edge effects into account as well as considering smaller spatial resolutions of ALS data to account for smaller canopy gaps.

Conclusion

If a goal of forest management is to create a broader range of habitat types and microclimates aiming at biodiversity conservation, a spatial coexistence of differently managed and unmanaged stands within a landscape should be considered, instead of focusing on a specific type of forest management or setting aside forest reserves, only. EA management resulted in overall higher γ-diversity of microclimates due to higher between-patch β-diversity, most probably resulting from the spatial coexistence of different developmental stages within the landscape. Compared to both types of managed forests, unmanaged forest showed the lowest diurnal variations in forest microclimate on plot level. Thus, unmanaged forest reserves may act as refugia for species that require a microclimate with lower fluctuations in below-canopy air temperatures and thereby play an important role in landscape-level biodiversity conservation.

Declarations

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