



# Responses of the structure and function of the understory plant communities to precipitation reduction across forest ecosystems in Germany

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## Abstract

• **Key message** Understory plant communities are essential for the recruitment of trees making up future forests. Independent of plant diversity, the understory across different forest ecosystems shows considerable physiological acclimation and structural stability towards drought events, which are expected to occur more frequently in future.

• **Context** Understory plant communities are essential for the recruitment of trees making up the future forest. It is so far poorly understood how climate change will affect understory in beech and conifer forests managed at different intensity levels.

• **Aims** We hypothesized that drought would affect transpiration and carbon isotope discrimination but not species richness and diversity. Moreover, we assumed that forest management intensity will modify the responses to drought of the understory community.

• **Methods** We set up roofs in forests with a gradient of management intensities (unmanaged beech—managed beech—intensively managed conifer forests) in three regions across Germany. A drought event close to the 2003 drought was imposed in two consecutive years.

• **Results** After 2 years, the realized precipitation reduction was between 27% and 34%. The averaged water content in the top 20 cm of the soil under the roof was reduced by 2% to 8% compared with the control. In the 1st year, leaf level transpiration was reduced for different functional groups, which scaled to community transpiration modified by additional effects of drought on functional group leaf area. Acclimation effects in most functional groups were observed in the 2nd year.

• **Conclusion** Forest understory shows high plasticity at the leaf and community level, and high structural stability to changing climate conditions with drought events.

**Keywords** Climate change · Herb layer · Stable carbon isotope · Functional traits · Diversity

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**Contribution of the co-authors** K.F. performed all experimental work and co-wrote the manuscript. M.B. measured photosynthetic active radiation (2012) and soil water content (2013). Z.E.K. supervised the work on isotope analysis and co-worked in paper writing. H. P. and A.U. participated in data analyzing and interpretation and provided editorial advice. A.G. participated in data interpretation, paper writing, and supervised and designed the experiment.

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## 1 Introduction

Variability in precipitation is expected to increase with climate change across Central Europe (IPCC 2012). Current climate projections predict strong reductions of summer precipitation all over Europe, and an increase in the occurrence of drought periods (IPCC 2012), with potentially severe consequences for forest ecosystems (Allen et al. 2010; Breda et al. 2006; McDowell et al. 2008). Even though projections on precipitation patterns include some uncertainty, especially drought periods with extreme reduction of precipitation, and thus water availability, will have the most pronounced effects on forest function and survival (Breda et al. 2006; McDowell et al. 2011). Only recently, Allen et al. (2015) pointed out that particularly hot droughts with a co-occurrence of high air temperatures, high atmospheric water vapour pressure deficit causing high evaporation, and soil water

deficit due to reduced precipitation, will have the most negative impact on forests. Since the forest understory is, however, thermally insulated by the overstory vegetation, extremely low air humidity and high temperatures are not likely to occur close to the ground in closed forests (Fotelli et al. 2003). Thus, soil water deficit at moderate temperatures will be the most important climate-related stress for the understory in future.

Research on physiological mechanisms behind drought-induced mortality of adult trees has grown significantly in recent years, and these observations and simulations have increasingly pointed to the negative impacts of climate change on forests (reviewed most recently in Allen et al. 2015). However, we lack information on drought impacts on the understory. It is important to shed more light on drought responses of the understory plant community, as these communities play a central role in ecosystem biogeochemistry, e.g., by influencing water availability, litter decomposition and nutrient cycling (Schulze 2000; von Rein et al. 2016), as well as tree recruitment of the future forest. The understory, as understood in the present study, comprises the stratum up to a height of 1 m above ground (Gilliam 2007), including herbaceous vascular plants and seedlings of trees and shrubs, and harbors a great portion of the plant diversity in forests (Gilliam 2007).

As a first short-term response of understory plants to soil water deficit, closure of the stomata and reduced transpiration rates are expected (Chaves et al. 2002; Tschaplinski et al. 1998; Wullschlegel et al. 1998), which, on the one hand reduces the risk of xylem cavitation, but in turn impairs carbon uptake. Drought and related soil water deficits thus forces plants, over the longer term, to narrow their carbon and hydraulic safety margins to points where they may be at risk of either hydraulic failure or carbon starvation (Martínez-Vilalta et al. 2002; McDowell et al. 2008, 2011).

The long term balance between stomatal conductance (determining  $\text{CO}_2$  supply) and  $\text{CO}_2$  assimilation is reflected in the carbon isotope ratio ( $\delta^{13}\text{C}$ ) of leaves, since photosynthetic carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) is proportional to the ratio of leaf internal ( $C_i$ ) to ambient  $\text{CO}_2$  concentration ( $C_a$ ) (Farquhar et al. 1982).  $\Delta^{13}\text{C}$  is reduced during water stress as a consequence of stomatal closure, which restricts  $\text{CO}_2$  supply and thus decreases  $C_i$  (Farquhar et al. 1989; Stewart et al. 1995). Therefore, changes in the carbon isotope composition of plant organic matter are indicative of drought exposure of a plant or plant community, and have been shown to be negatively correlated with precipitation and air humidity and positively to soil water deficit (Edwards et al. 2000; Lipp et al. 1996; Treydte et al. 2001; Treydte 2003). Alternatively, photosynthesis is reduced (and consequently  $C_i$  increased) under light-limiting (but not water-limiting) conditions, thus light availability can also affect  $\delta^{13}\text{C}$  (e.g., Gessler et al. 2001).  $\delta^{13}\text{C}$  and more directly  $\Delta^{13}\text{C}$  in organic matter of understory plants integrates information about stomatal conductance vs. assimilation over timescales (Fotelli et al. 2003), and can be scaled up as a stress

indicator from the plant/leaf level (e.g., Fotelli et al. 2001) to the stand or community level (Grossiord et al. 2013, 2014).

Chaves et al. (2002) reviewed the responses of herbs and annual plants, representing fast growing species, to soil water deficit, and found that these included stomata closure and a downregulation of photosynthetic activity. Depending on the duration and intensity, drought and related soil water deficit can decrease the leaf area index (LAI) (Muraoka et al. 1997; Sánchez-Gómez et al. 2013) and lead to reduced biomass and vegetation cover. Additionally, the understory community might react to drought with changes in biomass partitioning, resulting in an increased allocation to roots and increased root-to-shoot ratios, but also associated with reduced productivity (e.g., Breda et al. 2006; Fotelli et al. 2004; McDowell et al. 2008). Drought experiments have shown that the above-ground biomass of grasses and perennial herbs with extensive belowground storage organs partially dies off, but the fine root proportion increases (M. Baudis et al. unpublished data; Chaves et al. 2002; Fotelli et al. 2001; Rodrigues et al. 1995). This indicates markedly different strategies of drought response among functional groups, in particular between herbaceous and woody species.

Increasing drought duration might initiate a shift towards more drought tolerant species (e.g. Mueller et al. 2005), with unknown consequences for understory species composition and diversity. Ozolinčius et al. (2009) observed a strong reduction of ground vegetation coverage in a pine forest exposed to 3 years of drought, resulting in a 20% decrease in the Shannon diversity index. However, considerable stability of forest understory communities towards drought and other disturbances has also been observed (e.g., Archaux and Wolters 2006; De Grandpre and Bergeron 1997).

Besides soil and climatic conditions, understory species composition is affected by forest management and land-use history (Gilliam 2007). This is conveyed mainly by management-induced changes in overstory tree composition (e.g., Schmidt and Schmidt 2007) due to planting and selective felling (Foster et al. 2003; Gilliam et al. 1995), which can alter a variety of environmental conditions, including light, water and nutrient availability for the understory. Overstory stand density and LAI, as well as the dominance of evergreen vs. deciduous species determine the light climate and its seasonal variation on the forest floor. Consequently, management changes meso- and micro-climatic conditions in the stand (Bachmair et al. 2009; Kayler et al. 2005; Nicotra et al. 1999), as well as the carbon and nutrient input into the soil (Prescott 2002; Schmidt and Schmidt 2007) and soil fertility (Augusto et al. 2002), which significantly affects understory diversity and species composition (Battles et al. 2001; Gilliam 2007; Halpern and Spies 1995; Scheller and Mladenoff 2002). In grassland ecosystems, higher biodiversity can promote resistance to drought (Tilman and Downing 1994). Drought susceptibility of the understory community might thus be

modified by forest management via its effects on biodiversity. Accordingly, Grossiord et al. (2014) observed a positive correlation between forest tree diversity and drought resistance, but restricted this effect to environments characterized by the regular or occasional occurrence of drought periods. This definition included the area of distribution of Central European beech dominated forest stands. Experimental studies of the long-term impacts of land-use on understory functioning and survival during drought periods are, however, lacking. Fotelli et al. (2004) showed that nutrient uptake of plants in a beech forest understory was reduced under drought in thinned, compared to untreated, plots. In the latter study, however, only the short-term responses (one growing season after the management intervention) to selective felling were assessed, and, as a consequence, the species composition of the understory community did not change significantly between the treatments.

To shed more light on the effects of drought on the main plant functional groups [tree recruits, Graminoids (referred to hereafter as grasses), herbs, shrubs and ferns] of the understory as well as on the community as a whole, we designed a field experiment in the Biodiversity Exploratories (Fischer et al. 2010)—a research platform that provides a gradient in soil properties and climate. We investigated the response of the understory community to precipitation reduction as modified by forest management. We studied forest stands of different management intensity across three regions (Exploratories) in Germany. In this study, forest management treatments spanned a gradient from no/very low intervention intensity (unmanaged beech forests) to intensive felling and timber harvesting activities within the last 30–40 years, and replacement of the natural dominating tree species (beech) by conifers. This selection covered the whole gradient of management intensities in the three Biodiversity exploratories (see Fischer et al. 2010). Kahl and Bauhus (2014) developed a Forest Management Intensity index (ForMI) to characterize the intervention intensity for the last 30–40 years. They tested their index in the three Biodiversity Exploratories and could clearly group the unmanaged beech, managed beech, and managed conifer forest across all three exploratories. We constructed roofs to constrain total annual precipitation to an amount equivalent to the lower 2.5 percentile of the distribution of annual precipitations of the years 1950–2010, which was simulated for two growing seasons. During this period, we monitored different understory functional traits, as well as community structure and diversity. We characterized the functional traits after 1, 6, 15 and 18 months of precipitation reduction.

We hypothesized that reduced precipitation would result in (1) changes in leaf traits (i.e., in a reduction in leaf transpiration and leaf area, and a decrease in  $\Delta^{13}\text{C}$ ) of the main functional groups as well as (2) comparable changes in whole understory community ecophysiological traits [community scale  $\Delta^{13}\text{C}$ , evapotranspiration (ET), community transpiration, soil evaporation (E)]. However, species richness and

diversity were not expected to change with precipitation reduction, indicating stability of the community during drought over two consecutive growing seasons. Moreover, we expected that (3) forest management intensity would modify the responses to drought of the understory community, resulting in stronger drought effects with more intensive management.

## 2 Materials and methods

### 2.1 Study site and experimental design

The study was carried out at the three regions of the Biodiversity Exploratories (<http://www.biodiversity-exploratories.de>; for details, see Fischer et al. 2010): Schorfheide-Chorin (S) in the north-east, Hainich Dün (H) in the middle, and Schwäbische Alb (A) in the south-west of Germany as described recently by Felsmann et al. (2015). In each of the Exploratories, we selected three forest stands, which represent different forest types, management intensities and comprise different vegetation communities (see table 1 in Gimbel et al. 2015), but are similar with respect to topography and soil type within each exploratory (Table 1). Schorfheide-Chorin is located in a young glacial landscape in the lowlands of north-eastern Germany. Forest soils have a texture from sandy loam to pure sand. At the Hainich site, the soils are generally loamy to clayey textured Luvisols and Stagnosols. At the Schwäbische Alb, the soils in the investigation regions are extremely rich in clay, and have a very high stone content (Fischer et al. 2010; Gimbel et al. 2015). At each exploratory, the three forest stands were selected according to a gradient in management intensity: (1) a stand that has been unmanaged for at least 60 years and is dominated by European beech (*Fagus sylvatica* L.) (bu), comprising understory representing the potential natural vegetation; (2) a managed stand, dominated by *F. sylvatica* (bm); and (3) an intensively managed stand dominated by conifers (cm), including Norway spruce (*Picea abies*) at Schwäbische Alb and Hainich, or Scots pine (*Pinus sylvestris* L.) at Schorfheide (see above, Table 1). At each of the nine stands (1000 m<sup>2</sup> each), we randomly established two central subplots, each with an area of 10 m × 10 m. We equipped one of the central subplots with a roof in January 2012 to apply the drought treatment; the other central subplot was kept as a control treatment. Additionally, we established four pairs of smaller satellite subplots comprising a roofed and an adjacent control subplot with a distance of at least 3 m, each with an area of 3 m × 3 m. In contrast to the main central subplot, which contained a central overstory tree, the satellite subplots were located in-between overstory trees (see online resource Fig. S1). These roof and control satellite subplots were used as replicates in order to cover the variation in understory vegetation and soil properties within a forest stand.

**Table 1** General stand information and characteristics. Stand properties were obtained from the control and roofed subplots for the different exploratories and management types. S Schorfheide-Chorin; H Hainich-Dün; A Schwäbische Alb; bu beech, unmanaged; bm beech, managed; cm conifer, intensively managed<sup>a</sup>

Stand ID	Exploratory	Altitude (m a.s.l.)	Mean annual temperature (°C) <sup>a</sup>	Mean annual precipitation (mm) <sup>a</sup>	Geology <sup>b</sup>	Main tree	Management type	Position		Soil type <sup>d</sup>	Texture <sup>d</sup>
								Longitude	Latitude		
Sbu	S	65–74	8–8.5	589	Young glacial landscape	Beech	Unmanaged	1.384.500	5.305.127	Cambisol	Loamy sand
Sbm						Beech	Managed	1.389.123	5.288.526	Cambisol	Loamy sand
Scm						Pine (conifer)	Intensively managed	1.386.399	5.307.658	Cambisol	Loamy sand
Hbu	H	330–410	7.2	533	Calcareous bedrock	Beech	Unmanaged	1.045.518	5.110.069	Luvisol	Loam
Hbm						Beech	Managed	1.037.834	5.117.893	Stagnosol	Loam
Hcm						Spruce (conifer)	Intensively managed	1.031.074	5.127.165	Luvisol	Loam
Abu	A	714–766	6.5	940	Calcareous bedrock with karst phenomena	Beech	Unmanaged	938.238	4.838.259	Cambisol	Silty clay
Abm						Beech	Managed	935.661	4.838.366	Leptosol	Silty clay
Acm						Spruce (conifer)	Intensively managed	939.868	4.837.891	Cambisol	Silty clay

<sup>a</sup> Data from German weather Service, years 1950–2010, Schorfheide: station-ID 00164, Hainich: station-ID 00487, Schwäbische Alb: station-ID 03402)

<sup>b</sup> Fischer et al. (2010)

<sup>c</sup> According to WRB (2006)

The roofs consisted of rain gutters, which alone caused a rainfall reduction of 11% for the main roofs. Acrylic transparent roofing elements could be easily mounted randomly between the rain gutters to increase the precipitation reduction up to 100%. The water retained by the roofing elements and the rain gutters was drained away from the subplot. Precipitation was reduced during the growing seasons 2012 and 2013, beginning 1 March 2012. The target precipitation reduction under the roofs corresponded to the lower 2.5 percentile of the annual precipitation from the last 50 years (1951–2011) for each exploratory. To calculate the reduction actually required, the reduced precipitation input under the roofs of the current month was compared with the target values. If the antecedent input fitted the target value, the reduction was set to the theoretical reduction obtained from the long-term series for the month to achieve the target value. If the antecedent input under the roof was above or below the target value, the reduction was set higher or lower according to the magnitude of deviation (Gimbel et al. 2015). Each month, not only was the coverage of the transparent roofing elements adjusted, but they were also moved randomly to avoid particular wet and dry spots. Though the reduction was calculated for the entire year, the roof remained uncovered from first snowfall until the end of the snow season, to avoid roof damage from heavy snowpack. During this period, precipitation was only reduced by 11 %. If this reduction was below the target values, the precipitation reduction was set higher after snowmelt (Gimbel et al. 2015). To assess possible roof effects on the microclimate, air temperature and humidity were measured continuously (sensors: HMP45C 21 with HUMICAP® 180 sensor, Campbell Scientific, Bremen, Germany) under the central roofs and at the corresponding control subplots (Gimbel et al. 2015). In addition, measurements of photosynthetic photon flux density (PPFD, DELTA OHM, HD 2102.2; Caselle di Selvazzano, Italy) were carried out in late summer 2012 (Baudis et al. 2014). Air temperature, humidity and soil temperature remained unaffected by the roof (Gimbel et al. 2015). PPFD mean values of the nine stands ranged from  $9.74 \pm 4.74$  to  $159.35 \pm 341.72 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $n = 10$ ; see Baudis, Table A6 in their publication) and there were no significant differences in PPFD between roofed and control subplots (Baudis et al. 2014). The target precipitation in the drought exposed subplots was close to the precipitation of the year 2003, which was an extreme drought year in large parts of Europe (Ciais et al. 2005), and 2 years of such conditions in sequence are assumed to impose a strong, though realistic, drought scenario under future climate conditions.

## 2.2 Soil water content

Soil water content (mm) in the upper 20 cm of soil of treatments and controls were calculated using the forest-hydrological model LWF-Brook90 (Hammel and Kennel



2001), which simulates the daily soil water budget as the result of infiltrating precipitation, water flow through the soil, and water loss by evapotranspiration. The necessary climate data were obtained for the period 2010–2013 from near-by stations of the German weather service (DWD). For further details, we refer to Felsmann et al. (2015). In addition to the simulated values, volumetric soil water contents (%) as an average of the upper 10 cm of the soil were determined in spring or early summer, and in late summer in 2012 and 2013. Samples from the main and satellite roofs (and controls) were obtained and averaged since no significant differences were observed. In 2012, soil samples were taken ( $n = 4$ ) with an auger, and field fresh and dried samples were weighed to obtain the volumetric soil water content. In 2013, volumetric soil water content was measured directly in the field (Theta Probe Type ML2x, DELTA-T Devices, Cambridge, UK) in the rooting zone of the understory ( $n > 10$ ).

### 2.3 Understory community structure

Species composition (Table S2), LAI, species richness and diversity (Shannon's diversity index) of the understory were determined according to Felsmann et al. (2015) during field campaigns in 2012 and 2013 (for dates, see Table S1). Species composition and richness were determined in field surveys. For the assessment of LAI for each species and subplot, we randomly collected field-fresh leaves from the main species (coverage  $> 0.5\%$ ) on all subplots (about 1 g fresh weight per leaf sample which equals 2–12 leaves/species). We took digital photos in the field of leaves sorted by species. From the photos, leaf area (spLA, defined as the area of an average leaf of a given species) was determined using the image analysis program ImageJ 1.45s (Schneider et al. 2012). We then took digital photos of four randomly chosen quadratic areas per subplot ( $n = 4$ ;  $A_{\text{total}} = 2.45 \text{ m}^2$ ) and counted the total number of leaves ( $N_{\text{leaves}}$ ) on these areas for each species separately. By multiplying the  $N_{\text{leaves}}$  with spLA within the known ground-surface area we calculated LAI ( $\text{m}^2/\text{m}^2$ ).

Additionally, we calculated the functional group LAI ( $\text{LAI}_{\text{fg}}$ , sum of the LAI of all species within a given functional group; separated into the groups grasses, herbs, ferns, shrubs, and tree seedlings) and the community LAI ( $\text{LAI}_{\text{s}}$ , total LAI of all species per subplot). We calculated the area covered by each species on the digital photos of the  $2.45 \text{ m}^2$  areas for each treatment to determine the Shannon diversity index ( $H'$ ) as described in Krebs (1999).

### 2.4 Understory functional traits

Measurements were conducted alternately in the roofed and the corresponding control subplots, within a timespan of at maximum 25 min to prevent any impact of diurnal courses of transpiration and evapotranspiration. We measured

between 10:00 and 15:00 h under comparable light conditions on cloudless sunny days.

#### 2.4.1 Evapotranspiration

In the field, large gas-exchange chambers (height  $\times$  width  $\times$  length =  $52 \times 77.5 \times 78.5 \text{ cm}$ ; area =  $0.61 \text{ m}^2$ ) as described in Yezpe et al. (2005) were used for measuring evapotranspiration (ET) rates. Measurements were carried out during two campaigns in each of the years 2012 (spring, late summer) and 2013 (early summer, late summer) (see online resource Table S1) in all three exploratories with the three management intensities. Chambers were sealed on the soil and build-up of the vapor concentration was determined with a laser spectrometer (PICARRO L1102-i; Picarro, Santa Clara, CA). We measured two chambers under the main roof, two chambers under two satellite roofs and at the corresponding control subplots. The setup of the system with the connection between spectrometer and chamber is described in detail by Volkmann et al. (2016). ET rates were calculated from the linear increase in water vapor concentration over time, and based on the ground area ( $\text{mmol cm}^{-2} \text{ s}^{-1}$ ).

#### 2.4.2 Transpiration rates

We determined leaf transpiration rates ( $\text{mmol H}_2\text{O m}^{-2} \text{ leaf area s}^{-1}$ ) for the most abundant species of each management treatment in all three exploratories (Species list see Table S2). Transpiration rates were measured on all four campaigns in 2012 and 2013 with a LI-6400 (Licor Portable Photosynthesis System, Lincoln, NE).  $\text{CO}_2$  concentration was adjusted to 380 ppm and the cuvette was configured to track ambient temperature and light conditions. Measurements were conducted on three (control subplots) or six (three main and three satellite roof subplots) fully expanded leaves per species. From the leaf transpiration, we determined LAI-weighted average functional group transpiration ( $T_{\text{fg}}$ ) for tree seedlings, shrubs, herbs, grasses and ferns.

In addition to the leaf level rates, we calculated community transpiration ( $\text{mmol H}_2\text{O m}^{-2} \text{ ground area s}^{-1}$ ) ( $T_{\text{s}}$ ) for each subplot by multiplying leaf level transpiration rates with the respective LAI, and summing up these values for all species present on a particular subplot.

To obtain subplot evaporation rates, we calculated the differences between subplot ET rates and the corresponding subplot community transpiration rates, both based on the same ground area.

#### 2.4.3 Carbon isotope analysis

For carbon isotope analyses we harvested leaves of the most abundant species as shown in Table S2. We sampled three leaves per species and subplot (main roof and corresponding control), which were immediately frozen and stored at  $-20^\circ \text{C}$ .  $\delta^{13}\text{C}$  was determined in the total (bulk) organic matter fraction

of leaves as described by Nitzsche et al. (2016) and expressed relative to the Vienna Pee Dee Belemnite (VPDB). From the  $\delta$  values, we calculated the photosynthetic carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) according to Farquhar et al. (1982) assuming  $\delta^{13}\text{C}$  of  $\text{CO}_2$  to be  $-8\text{‰}$ . We acknowledge that understory species might be affected by soil respired  $\text{CO}_2$  that is isotopically lighter than average atmospheric  $\text{CO}_2$ . Fotelli et al. (2003), however, suggested such influence to be small. Gimbel et al. (2015) showed a comparable coupling of the airspace close to the ground to the atmosphere on roof covered and control subplots. Thus it is unlikely that the drought treatment affected the isotope signature of the plants via increased contribution of respired  $\text{CO}_2$ .

We calculated the mean  $\Delta^{13}\text{C}$  of the different functional groups ( $\Delta^{13}\text{C}_{\text{fg}}$ ) by averaging  $\Delta^{13}\text{C}$  of the species belonging to a given functional group, with the LAI as weighting factor. Community  $\Delta^{13}\text{C}$  ( $\Delta^{13}\text{C}_{\text{s}}$ ) was calculated according to Grossiord et al. (2013), (2014) taking into account  $\Delta^{13}\text{C}$  of all species on a subplot with LAI as the weighting factor for the contribution of each species.

## 2.5 Data processing and statistical analysis

Transpiration and  $\Delta^{13}\text{C}$  of the functional groups as well as transpiration,  $\Delta^{13}\text{C}$ , ET, evaporation, diversity, richness and LAI parameters of the whole understory community were compared using a nested design. To exclude differences between the main and satellite roofs, we tested with linear mixed effects models for the differences of leaf transpiration, LAI, community transpiration and LAI, ET, evaporation, species richness and diversity as a function of exploratory, management intensity and roof (main roof vs. satellite roof) and the interaction of management and roof. The differences between the three exploratories, the three management intensities, functional groups and the reduced precipitation treatment vs. control were tested with a linear mixed effects model with exploratory, management, functional groups and reduced precipitation treatment as fixed factors and subplot nested in forest stand as random factors. We consider the different management types as true replicates at the region level. Thus, each exploratory had experiments set up in different types of forest. As there were no replicates for the combination of exploratory and management type, we could not test for the interactions of both these factors. For the multiple comparisons of means we used the Tukey contrasts and corrected the  $P$  values with the Bonferroni method. The statistical analysis was carried out with the R software (R-3.2.1, The R Foundation for Statistical Computing 2013; packages: lme4; nlme) (Bates et al. 2014; Pinheiro et al. 2014). We calculated the difference in community  $\Delta^{13}\text{C}$  and community transpiration between the drought treatments (roof subplots) and controls (as measure of drought induced changes). We used Kendall's rank-based measure of association (R-3.2.1) to test the relationship between the Shannon diversity index of spring 2012 (baseline subplot diversity) and

these differences. We also tested for significant correlations between understory diversity, community transpiration and community  $\Delta^{13}\text{C}$  signatures at each campaign by Kendall's rank-based measure of association (R-3.2.1).

## 2.6 Data availability

The key data of this publication are available in the Zenodo data repository under: <https://doi.org/10.5281/zenodo.1050301>.

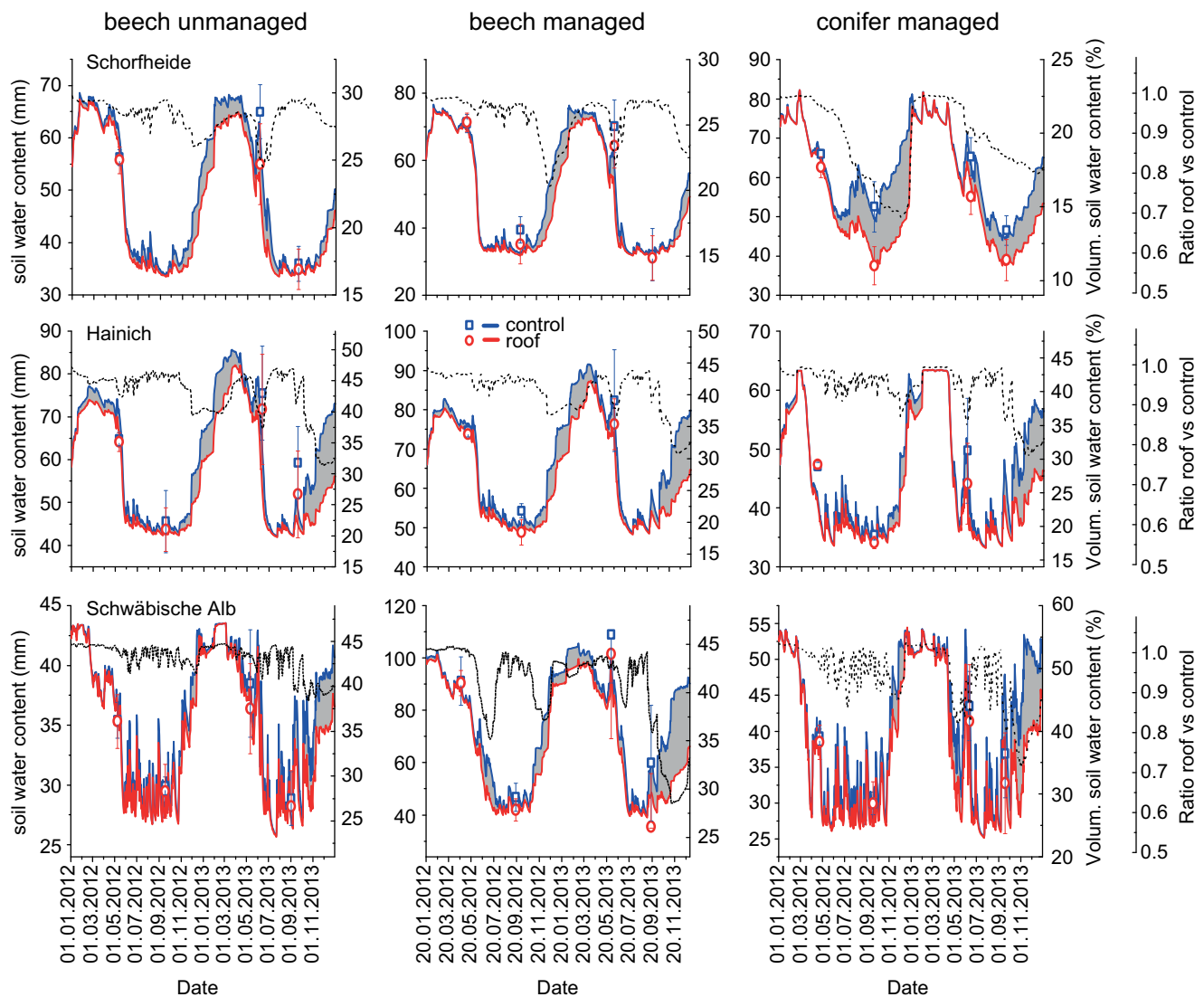
## 3 Results

We could not detect any differences between main and satellite roofs for our measurements (Tables S15–S22).

### 3.1 Precipitation reduction and the effect on soil water content

Our calculated precipitation reduction target level of the lower 2.5% percentile of cumulative annual precipitation corresponds to a reduction by 27% at Schorfeide, 33% at Hainich and 26% at the Schwäbische Alb. Until September 2013, the realized precipitation reduction was 32% at the Schorfeide exploratory, 34% at Hainich and 27% at the Schwäbische Alb. Details on the seasonality of precipitation in 2012 and 2013 and the required precipitation reduction are given in Table S23 and by Gimbel et al. (2015, Fig. 4 in their publication). During the two growing seasons (1 March 2012–31 August 2013), the averaged water content in the top 20 cm of the soil in the roofed subplots was reduced by 2% to 8% compared with the control subplots, as indicated by the forest-hydrological model LWF-Brook90 (Fig. 1). The seasonal variation in the soil water content in the uppermost 20 cm for the control subplots was comparable between the two years for a given region. Total water contents were, however, slightly different among exploratories and silvicultural treatments. The roof treatments resulted in a comparable reduction of the soil water contents in the two years at the three stands in the Schorfeide Exploratory, and to rather stronger reductions in the second year at Hainich and Schwäbische Alb. During the 18 months of drought treatment, the strongest reduction of soil water content occurred on the intensively managed pine stand at Schorfeide in both years, which is due to the sandy soil profile of this stand. Most of the other stands showed comparable patterns of precipitation reduction with lowest reduction in the unmanaged stands at Schorfeide and Hainich.

Seasonal patterns of the modelled water content were similar to the seasonal variations of measured volumetric water content (Fig. 1). The reductions calculated by LWF-Brook90 were comparable in direction and extent with the measured values.



**Fig. 1.** Soil water contents of the upper 20 cm (mm) of the soil of forest stands with different management intensity (unmanaged beech, managed beech and managed conifer forest) in the three different biodiversity exploratories (Schorfheide, Hainich, Schwäbische Alb) as calculated by the forest-hydrological model LWF- Brook90 (solid lines) and measured volumetric soil water contents (%) averaged over the upper 10 cm (symbols). Solid blue lines Computed soil water content for the control subplots without roofs, solid red lines soil water content in the precipitation reduction treatment, grey areas between the lines

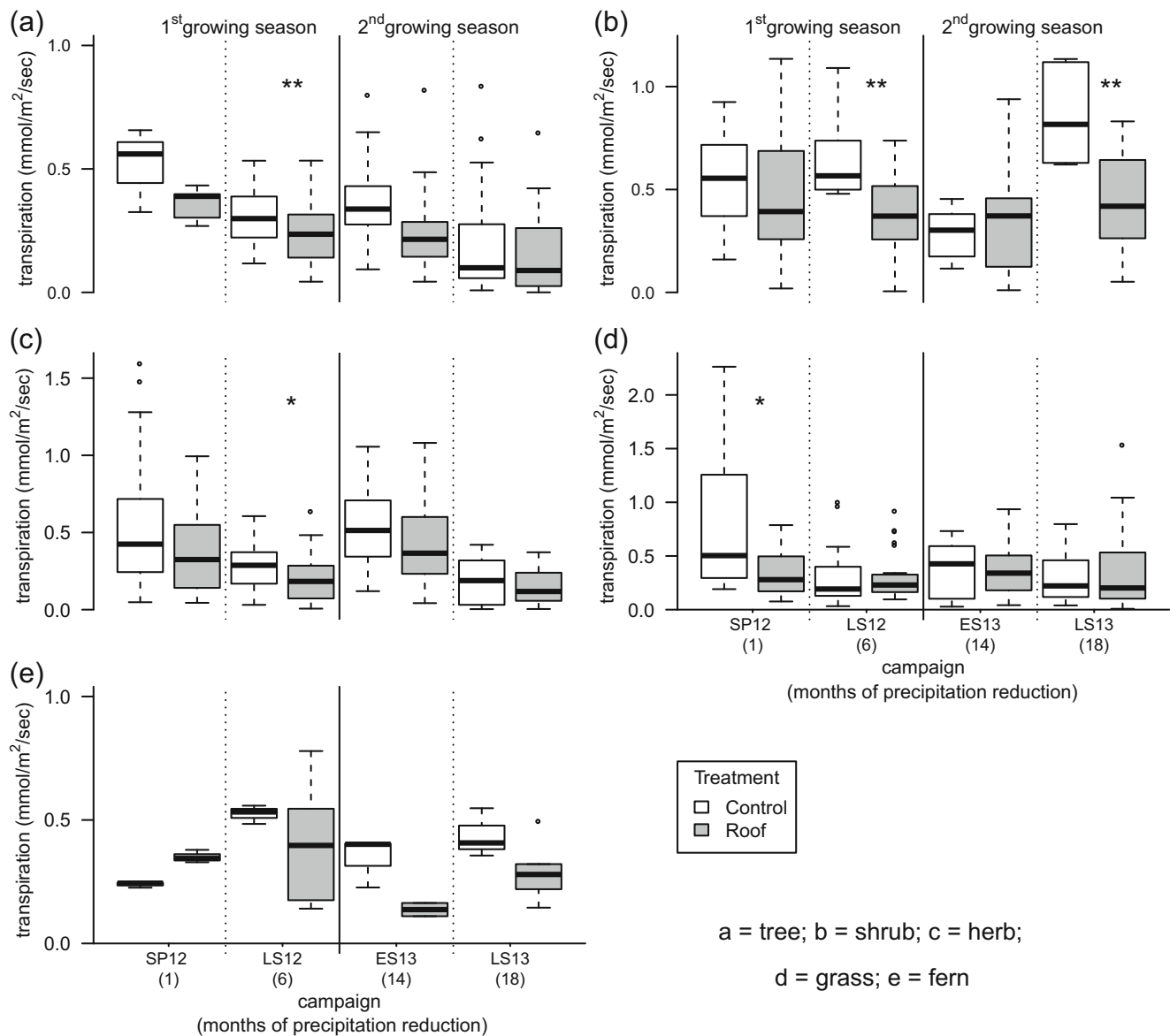
reduction in soil water content by the precipitation reduction treatment, dashed lines ratio of the soil water content between reduced precipitation and control subplots, blue squares measured volumetric water contents as determined in spring/early summer and late summer in 2012 and 2013 on the control subplots ( $\pm$  SD), red circles measured values of the roofed subplots. Note that the y-axes for computed soil water content and for measured volumetric soil water content differ among exploratories and silvicultural treatments. Measured values were not obtained for all management treatments in all exploratories at all four time points

### 3.2 Effects of precipitation reduction on functional group leaf level traits

Transpiration rates for all functional groups ( $T_{fg}$ ) and campaigns are shown in Fig. 2. Reduced precipitation affected the leaf-level transpiration over the whole experiment (Table S3) and differed among functional groups. In the spring of the first growing season, grasses decreased transpiration by 58.0 % compared to the control subplots (spring:  $P=0.02$ , Fig. 2, see Table S3), thus showing the fastest response. The functional groups herbs, shrubs and trees significantly decreased transpiration rates by 29.4%, 44.9% and

24.2% under the roof at the end of the first growing season (herb:  $P=0.02$ , shrub:  $P=0.001$ , tree:  $P=0.006$ ). In the second growing season transpiration rates were significantly lower under the roof only for the functional group shrubs (decreased by: 47.1 % compared to the control;  $P=0.005$ ; Fig. 2, see Table S3).

Functional group  $\Delta^{13}C_{fg}$  was unaffected by the drought treatment for all functional groups except for grass, where we found a significantly higher  $\Delta^{13}C$  under the roof in comparison to the control after 18 months of precipitation reduction ( $P=0.03$ ; Fig. 3, Table S4). We detected a significant reduction in LAI<sub>fg</sub> by 64.4% only for the group shrubs in late summer 2013 (see Table S5).



**Fig. 2.** Leaf transpiration rates (control  $n = 3$ , roof  $n = 6$  per stand and species) of the five functional groups ( $T_{fg}$ ) at different campaigns during two growing seasons. The boxes show medians and quartiles, the whiskers show 1.5 times the interquartile range of the data. The asterisks mark significant differences ( $P < 0.05^*$ ;  $P < 0.001^{**}$ ) tested with a linear model on the basis of the mean values. SP12 Spring 2012,

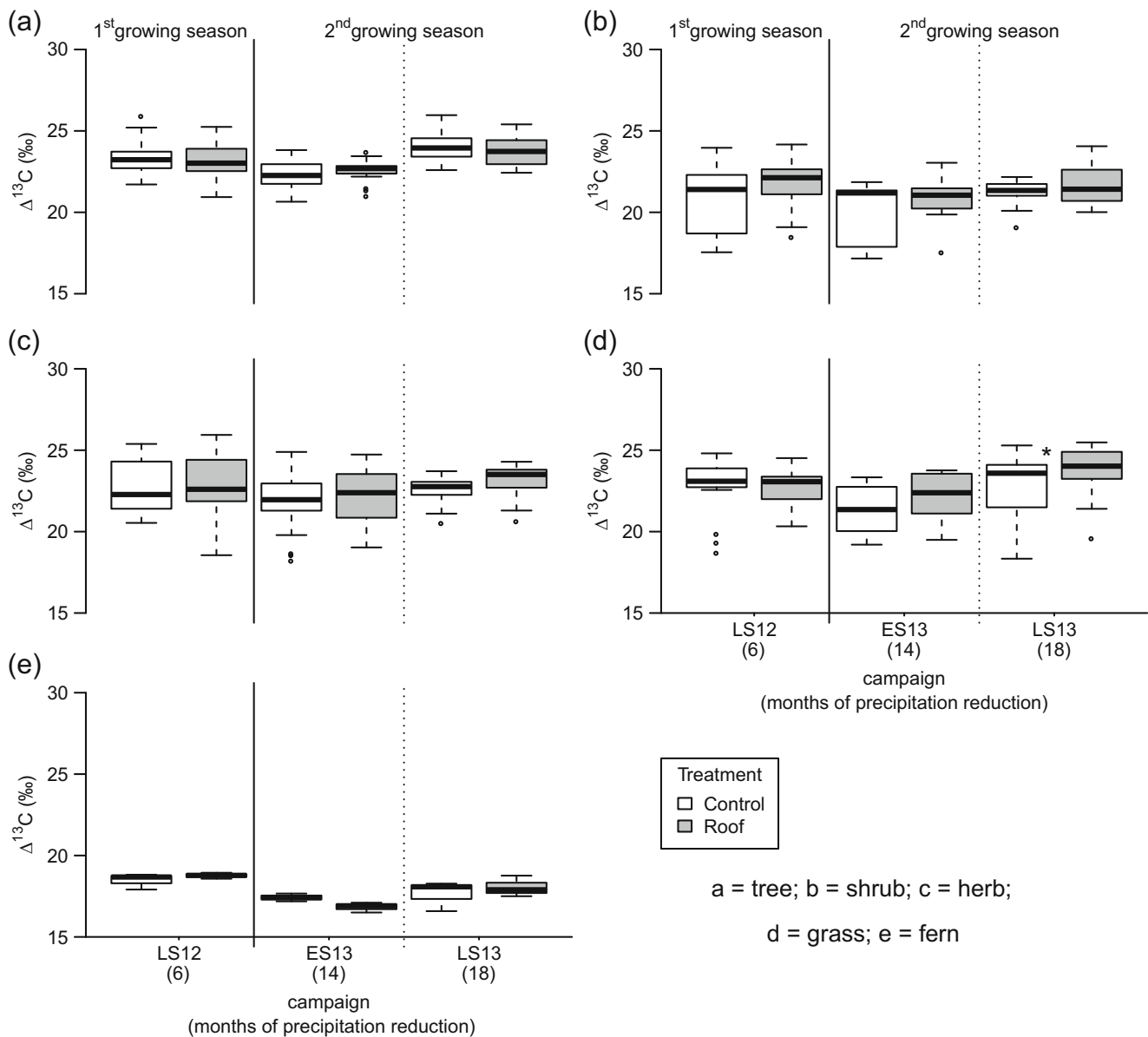
LS12 late summer 2012, ES13 early summer 2013, LS13 late summer 2013. The results of the linear mixed effects model for the transpiration of the different functional groups as a function of exploratory, management intensity, treatment (precipitation reduction), group and the interaction of group and treatment are given in Table S3. Note that the y-axes for leaf transpiration rates differ among the functional groups

### 3.3 Effects of precipitation reduction on understory community traits

In late summer of both growing seasons, ET rates were reduced by the treatment. The reduction was 21.1% in 2012 and 38.5% in 2013 (2012:  $P = 0.03$ ; 2013:  $P = 0.006$ ). Since we found significant treatment effects for soil evaporation only in spring 2012 ( $P = 0.007$ ) and in early summer 2013 at the conifer stands ( $P = 0.01$ ) but not in late summer, these significant treatment effects on ET are attributed mainly to community transpiration ( $T_s$ ), and we could in fact detect a significant treatment effect for  $T_s$  for all campaigns (Tables S6–S9).  $T_s$  under the roofs were 47.9 %, 45.9%, 11.1 % and 60.8% lower than in the control subplots in spring and late summer 2012, and in early summer and late summer 2013, respectively. In general, we found a tendency for lower or equal  $T_s$  under the roof subplots in comparison to the controls for all nine stands and campaigns, with the exception of the conifer stand at the Alb in early summer 2013 (Fig. 4). Furthermore, community  $\Delta^{13}C_s$  values were higher in the precipitation reduction treatment in early summer of the second growing season ( $P = < 0.001$ , Fig. 5, see Table S10). Reduced precipitation also affected the community LAI ( $LAI_s$ ) in late summer 2012 (decreased by 23.1% in comparison to the control;  $P = 0.018$ ) and during the second growing season (early summer: decreased by

45.9%, 11.1 % and 60.8% lower than in the control subplots in spring and late summer 2012, and in early summer and late summer 2013, respectively. In general, we found a tendency for lower or equal  $T_s$  under the roof subplots in comparison to the controls for all nine stands and campaigns, with the exception of the conifer stand at the Alb in early summer 2013 (Fig. 4). Furthermore, community  $\Delta^{13}C_s$  values were higher in the precipitation reduction treatment in early summer of the second growing season ( $P = < 0.001$ , Fig. 5, see Table S10). Reduced precipitation also affected the community LAI ( $LAI_s$ ) in late summer 2012 (decreased by 23.1% in comparison to the control;  $P = 0.018$ ) and during the second growing season (early summer: decreased by





**Fig. 3.** Leaf  $\Delta^{13}\text{C}$  discrimination (control  $n = 3$ , roof  $n = 3$  per stand and species) of the five functional groups ( $\Delta^{13}\text{C}_{\text{eg}}$ ) at different campaigns during two growing seasons. The boxes show medians and quartiles, the whiskers show 1.5 times the interquartile range of the data. The asterisks marks significant differences ( $P < 0.05^*$ ) tested with a linear model on the basis of the mean values. *LS12* Late summer 2012, *ES13*

early summer 2013, *LS13* late summer 2013. The results of the linear mixed effects model for the  $\Delta^{13}\text{C}$  of the different functional groups as a function of exploratory, management intensity, treatment (precipitation reduction), group and the interaction of group and treatment are given in Table S4

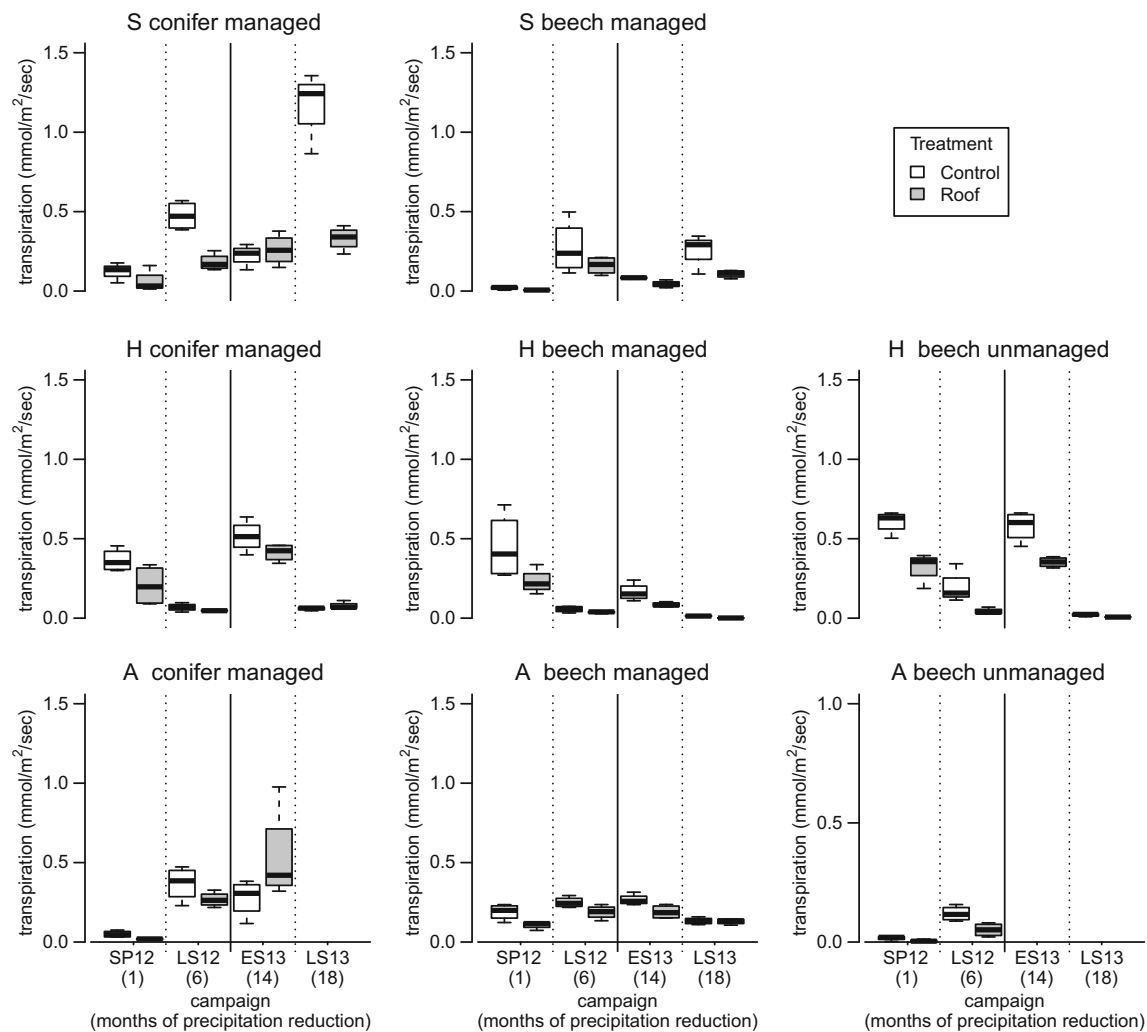
11.4% in comparison to the control;  $P = 0.004$ ; late summer: decreased by 21.1% in comparison to the control;  $P = 0.034$ ) (Fig. 6, see Tables S11–S14).

After 1 month of precipitation reduction, we found a tendency for higher species richness in most of the roofed subplots (Table 2), but this might need to be attributed to the general heterogeneity of the stands as drought effects are not to be expected after such a short treatment period. After 18 months, however, this pattern was inverted, now indicating lower understory species richness on the drought exposed subplots (decreased by 9.9 % in comparison to control;  $P = 0.035$ ; Table S14). In spring 2012, Shannon's diversity

index of the understory community was significantly affected by the treatment ( $P = 0.018$ ), but this effect was absent in late summer 2012 and during both measurement campaigns in 2013 (see Tables S11–S14).

### 3.4 Interaction between reduced precipitation and forest management

We first tested if the initial diversity at the beginning of the experiment affected the intensity of the drought reaction of the understory communities at the different time points during the

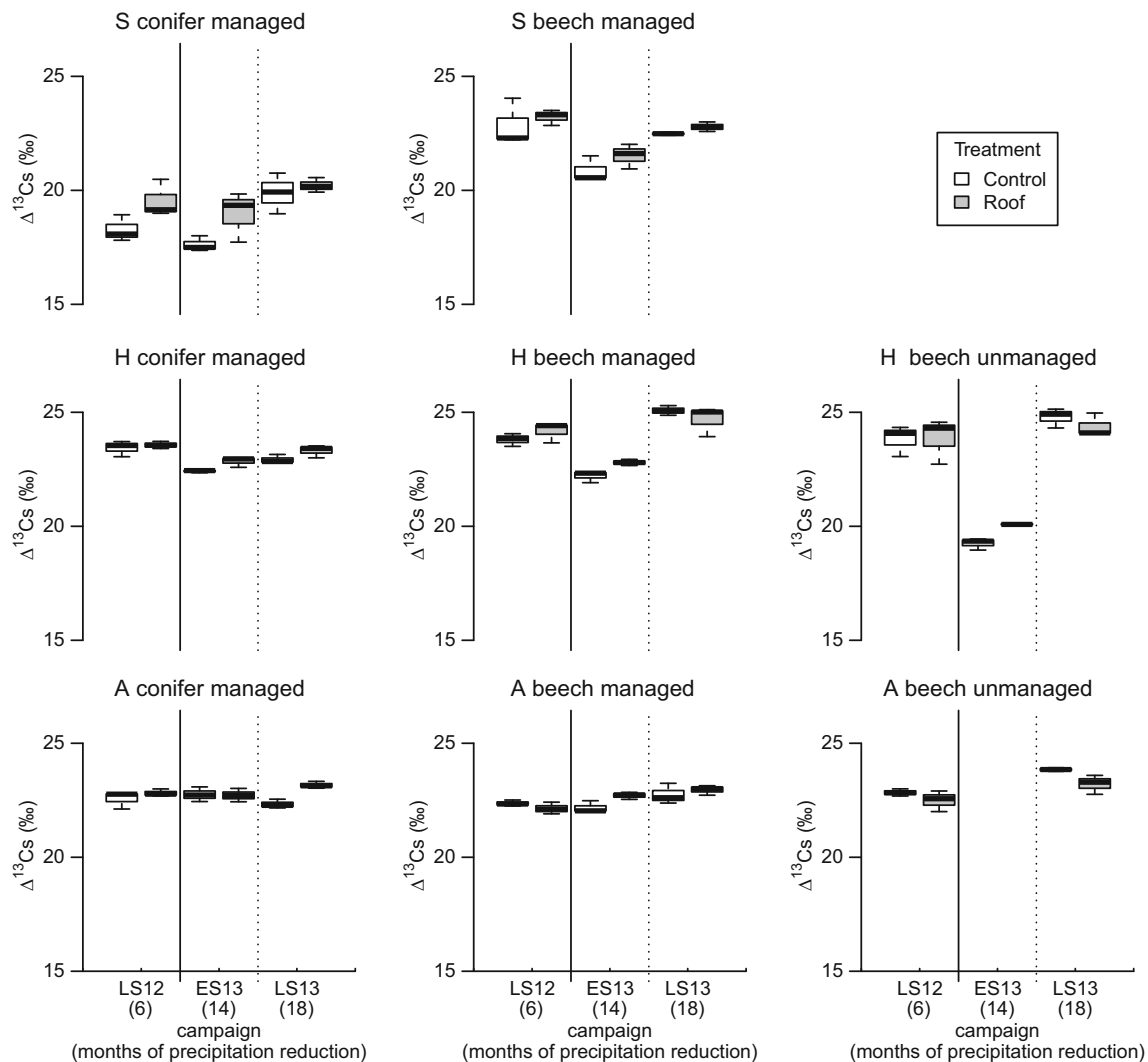


**Fig. 4.** Community transpiration rates ( $T_s$ ) of the treatments and eight different stands at different campaigns during two growing seasons. The *boxes* show medians and quartiles, the *whiskers* show 1.5 times the interquartile range of the data. For statistical analyses see Tables S6–S9. S Schorfheide, H Hainich, A Schwäbische Alb, SP12 spring 2012, LS12 late summer 2012, ES13 early summer 2013, LS13 late summer 2013. At

the Schwäbische Alb in early summer 2013, we could not measure the transpiration rates at the beech unmanaged stand because of rain. In late summer 2013, we could not measure the transpiration rates at beech unmanaged and at the beech managed stand because the device was broken. We did not measure stand Schorfheide beech unmanaged, because the understory coverage was <0.5%

two growing seasons. We did not observe any correlation between this initial diversity at the beginning of the experiment in spring 2012 and drought-induced changes in community transpiration ( $T_s$ ;  $P = 0.83$ ,  $\tau = 0.03$ ; see Fig. S2) or community weighted  $\Delta^{13}C$  ( $\Delta^{13}C_s$ ;  $P = 0.81$ ,  $\tau = -0.04$ ; Fig. S2) during the whole drought treatment. In a second approach, we tested if the actual diversity assessed at the different time points during the two growing seasons affected the actual drought response. Actual diversity values and drought induced changes in transpiration ( $T_s$ ;  $P = 0.80$ ,  $\tau = 0.03$ ) or  $\Delta^{13}C$  ( $\Delta^{13}C_s$ ;  $P = 0.66$ ,  $\tau = 0.07$ ) of each campaign at the different time points also showed no significant correlation. We observed, however, significant interactions of precipitation reduction and management on community transpiration in the 2nd year of the experiment. In late summer, a significant transpiration reduction was observed in the conifer stands

(Table S9), mainly caused by the strong drought effect in the Schorfheide exploratory (Scm): decreased by 71.8 % in comparison to the control; Fig 4). The particular drought effect on transpiration in the conifer stands coincided with a significant reduction of LAI under the roof in only these stands at the end of the second growing season (Scm: decreased by 54.2 % in comparison to the control; see Table S14). Significant interactions between the drought treatment and management on community LAI ( $LAI_s$ ) were observed in late summer 2012 ( $P = 0.020$ ) and late summer 2013 ( $P = 0.028$ ). There were significant decreases in  $LAI_s$  in the conifer stands upon drought in 2012 (Scm) decreased by 24.8 %; Hcm (Hainich) decreased by 43.9 %; Acm (Alb) decreased by 12.4 % in comparison to the controls;  $P = 0.001$ ), for late summer 2013 (Scm decreased by 54.3 %; Hcm decreased by 26.4 %; Acm decreased by 35.06 % in comparison to the controls;



**Fig. 5.** Understory community  $^{13}\text{C}$  discrimination ( $C_s$ ) of the eight different managed stands at three different campaigns. The boxes show medians and quartiles, the whiskers show 1.5 times the interquartile range of the data. For statistical analyses see Table S10. *S* Schorfheide, *H* Hainich, *A* Schwäbische Alb, *LS12* late summer 2012, *ES13* early summer 2013, *LS13* late summer 2013. Note: In the leaf bulk material is a mixture of structural carbon as well as of storage compounds and

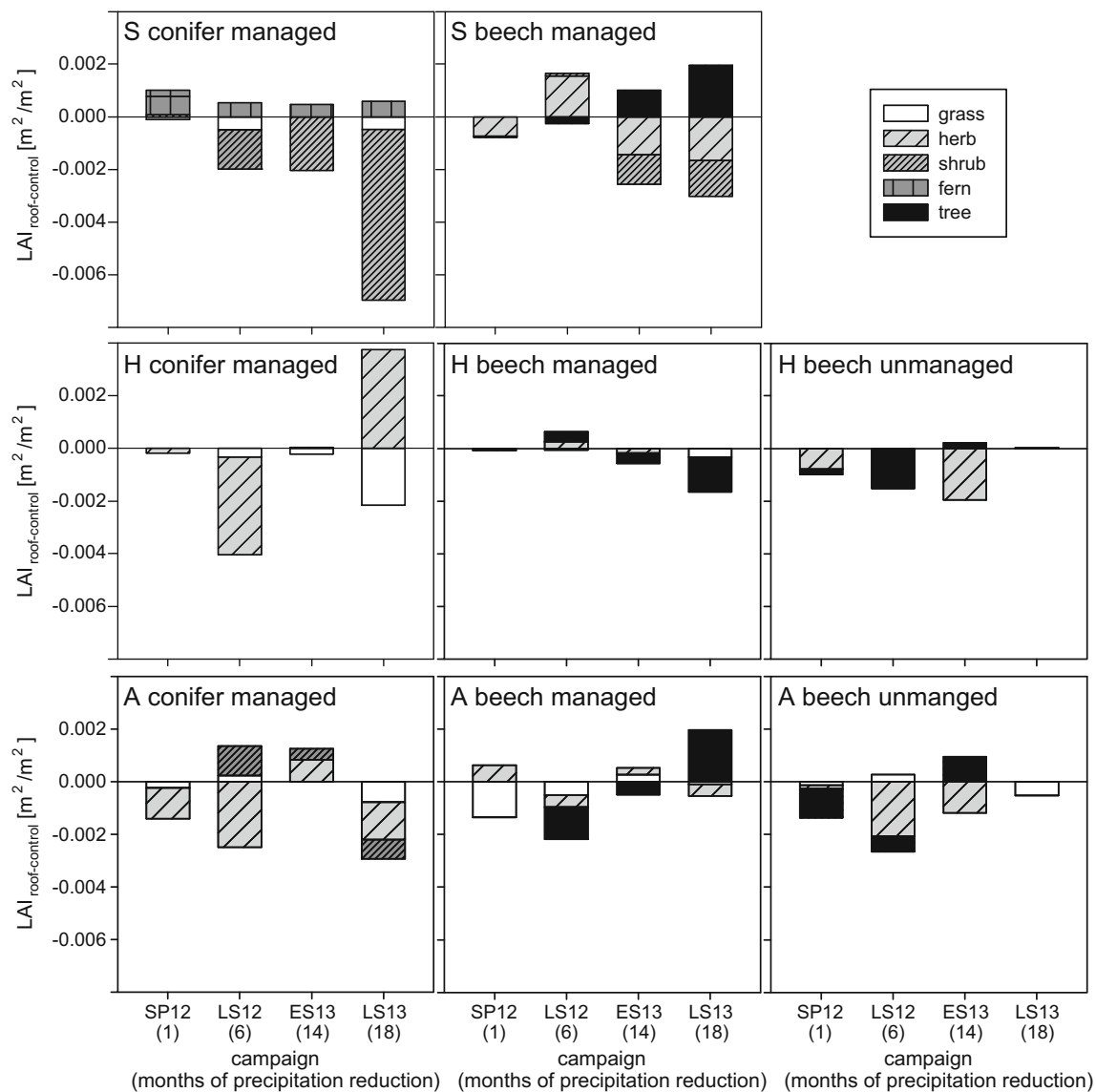
freshly assimilated carbon (Adams and Grierson 2001; Werner et al. 2012). Stored carbon is used for early leaf growth in plants (Gaudinski et al. 2009; Muhr et al. 2016). Thus, we did not analyze the leaf samples for  $\Delta^{13}\text{C}$  in spring 2012. At the Schwäbische Alb in early summer 2013 we could not take  $\Delta^{13}\text{C}$  samples at the beech unmanaged stand because of rain. We did not measure stand Schorfheide beech unmanaged, because the understory coverage was  $<0.5\%$

$P = 0.004$ ) as well as in the unmanaged beech stands in 2012 [Sbu (Schorfheide beech unmanaged): community  $\text{LAI} < 0.005\text{m}^2/\text{m}^2$ ; Hbu (Hainich): decreased by 39.9 %; Abu (Alb) decreased by 39.3 % in comparison to control;  $P = 0.020$ ). This was not the case in the unmanaged beech forests in 2013 and in the managed beech forests in 2012 and 2013 (Table S12 and S14). The lower  $\text{LAI}_s$  values in the drought treatments of the unmanaged beech stands compared to the controls in 2012 can be explained mainly by the lower  $\text{LAI}$  of the functional groups trees and herbs (Fig. 6). In 2012, the decrease in  $\text{LAI}_s$  in the conifer stands correlated with a decrease in  $\text{LAI}$  of the functional groups of grasses and shrubs at the Schorfheide, of grasses and herbs at the Hainich and of herbs at the Schwäbische Alb (Fig. 6). In 2013, the decrease in

$\text{LAI}_s$  in the conifer stands correlated with a  $\text{LAI}$  decrease for the functional groups of grasses and shrubs at the Schorfheide, of grasses at the Hainich and of grasses, herbs and shrubs at the Schwäbische Alb (Fig. 6).

## 4 Discussion

The imposed reduction of precipitation over 2 years, resembling the precipitation regime (seasonally as well as in the total yearly sum) of the driest year of the period between 1950 and 2011 (cf. Gimbel et al. 2015), resulted in moderate but clear reduction of soil water content. The target precipitation in the drought exposed subplots was close to the precipitation of the



**Fig. 6.** Mean changes of specific functional group LAI ( $LAI_{fg}$ ) between roof ( $n = 4$ ) and control ( $n = 4$ ) subplots of the eight different managed stands at different times during two growing seasons. For statistical analyses see Tables S11–S14. S Schorheide, H Hainich, A

Schwäbische Alb, SP12 spring 2012, LS12 late summer 2012, ES13 early summer 2013, LS13 late summer 2013. We did not measure stand Schorheide beech unmanaged, because the understory coverage was <0.5%

year 2003, which was an extreme drought year in large parts of Europe (Ciais et al. 2005), and 2 years of such conditions in succession are assumed to impose a strong, though realistic, drought scenario under future climate conditions.

#### 4.1 Effect of precipitation reduction on functional group specific transpiration rates and $\Delta^{13}C$

Leaf level transpiration rates were reduced upon drought in almost all functional groups and at various time points during the first growing season. This is clearly a result of the reduced soil water content as the roofs were not affecting air humidity or air temperature (Gimbel et al. 2015). Grasses rapidly responded to the soil moisture reduction with stomatal closure already in

spring, followed by the functional groups herbs, shrubs and trees in late summer of the first growing season. Closure of stomata is a well-known mechanism for short-term regulation of water use under drought conditions (Chaves et al. 2002; Flexas et al. 2002, 2004, 2008; Galmés et al. 2007). Beech (Baudis et al. 2014; Fotelli et al. 2001) and other understory tree seedlings and herbaceous plants (Hommel et al. 2014) reduce their stomatal conductance as a first response to drought. Chaves et al. (2002) reviewed the stress responses of herbs and annual plants, representing fast growing species, and found that these included stomata closure and a down regulation of photosynthetic activity, and were higher in late summer than in spring and early summer. In agreement with this finding, the



**Table 2** Mean Shannon's diversity index ( $H' \pm SD$ ,  $n = 4$ ) and mean species richness (richness  $\pm SD$ ,  $n = 4$ ) of the control and roofed (reduced precipitation) subplot of the eight different managed stands during two growing seasons. For statistical analysis see Table S10–S14. We did not measure stand Schorfheide beech unmanged, because the understory coverage was  $<0.5\%$

Stand ID	Treatment	Spring 2012		Late summer 2012		Early summer 2013		Late summer 2013	
		$H'$	Richness	$H'$	Richness	$H'$	Richness	$H'$	Richness
Sbm	Control	0.12 $\pm$ 0.18	1.5 $\pm$ 0.5	1.01 $\pm$ 0.34	4.5 $\pm$ 1.1	1.48 $\pm$ 0.10	4.3 $\pm$ 0.4	1.14 $\pm$ 0.03	4.0 $\pm$ 0
	Roof	0.64 $\pm$ 0.20	2.5 $\pm$ 0.5	0.85 $\pm$ 0.43	4.0 $\pm$ 1.2	1.21 $\pm$ 0.05	5.5 $\pm$ 0.9	1.30 $\pm$ 0.26	5.0 $\pm$ 0.7
Scm	Control	0.39 $\pm$ 0.15	2.0 $\pm$ 0	0.87 $\pm$ 0.23	3.5 $\pm$ 0.9	0.55 $\pm$ 0.23	2.8 $\pm$ 0.8	0.70 $\pm$ 0.23	3.3 $\pm$ 1.1
	Roof	0.52 $\pm$ 0.10	2.25 $\pm$ 0.4	0.76 $\pm$ 0.24	2.8 $\pm$ 0.4	0.72 $\pm$ 0.20	3.0 $\pm$ 0	0.70 $\pm$ 0.31	2.3 $\pm$ 0.5
Hbu	Control	0.19 $\pm$ 0.10	2.0 $\pm$ 0	0.63 $\pm$ 0.24	2.5 $\pm$ 0.5	0.62 $\pm$ 0.25	3.3 $\pm$ 0.4	0.56 $\pm$ 0.33	2.3 $\pm$ 0.8
	Roof	0.13 $\pm$ 0.06	2.0 $\pm$ 0	0.67 $\pm$ 0.12	2.5 $\pm$ 0.5	0.70 $\pm$ 0.21	2.5 $\pm$ 0.9	0.52 $\pm$ 0.40	2.3 $\pm$ 0.8
Hbm	Control	0.27 $\pm$ 0.20	3.0 $\pm$ 0	1.04 $\pm$ 0.33	4.75 $\pm$ 0.4	1.32 $\pm$ 0.15	4.8 $\pm$ 0.8	0.88 $\pm$ 0.14	4.0 $\pm$ 0.7
	Roof	0.44 $\pm$ 0.11	2.75 $\pm$ 0.7	1.49 $\pm$ 0.19	6.75 $\pm$ 0.4	1.41 $\pm$ 0.20	5.5 $\pm$ 0.5	0.91 $\pm$ 0.40	3.8 $\pm$ 0.8
Hcm	Control	1.03 $\pm$ 0.17	4.0 $\pm$ 0	0.96 $\pm$ 0.16	4.3 $\pm$ 0.8	1.02 $\pm$ 0.14	3.3 $\pm$ 0.4	1.35 $\pm$ 0.16	5.0 $\pm$ 0.7
	Roof	1.14 $\pm$ 0.19	4.25 $\pm$ 0.4	0.96 $\pm$ 0.14	4.3 $\pm$ 0.4	0.97 $\pm$ 0.12	3.3 $\pm$ 0.4	1.19 $\pm$ 0.10	5.0 $\pm$ 0.7
Abu	Control	0.43 $\pm$ 0.27	2.0 $\pm$ 0.7	1.29 $\pm$ 0.12	5.5 $\pm$ 0.5	1.13 $\pm$ 0.34	4.0 $\pm$ 1.2	1.08 $\pm$ 0.29	4.5 $\pm$ 1.5
	Roof	0.51 $\pm$ 0.30	2.0 $\pm$ 0.7	0.90 $\pm$ 0.34	3.5 $\pm$ 0.5	1.10 $\pm$ 0.43	4.0 $\pm$ 1.6	0.66 $\pm$ 0.66	2.8 $\pm$ 1.8
Abm	Control	0.62 $\pm$ 0.16	2.5 $\pm$ 0.5	1.53 $\pm$ 0.22	6.5 $\pm$ 1.1	1.58 $\pm$ 0.19	5.8 $\pm$ 1.5	1.47 $\pm$ 0.21	6.5 $\pm$ 0.5
	Roof	0.70 $\pm$ 0.09	2.5 $\pm$ 0.5	1.47 $\pm$ 0.19	6.0 $\pm$ 1	1.70 $\pm$ 0.16	7.3 $\pm$ 0.8	1.29 $\pm$ 0.30	6.0 $\pm$ 0.8
Acm	Control	0.72 $\pm$ 0.05	4.0 $\pm$ 0	1.19 $\pm$ 0.20	6.5 $\pm$ 1.1	1.20 $\pm$ 0.22	5.0 $\pm$ 1.0	1.41 $\pm$ 0.12	7.3 $\pm$ 1.1
	Roof	0.63 $\pm$ 0.16	5.0 $\pm$ 0.7	1.42 $\pm$ 0.05	7.0 $\pm$ 0.7	1.34 $\pm$ 0.07	6.3 $\pm$ 0.8	1.37 $\pm$ 0.13	6.5 $\pm$ 0.9

reduction in transpiration was most pronounced in late summer of the first growing season in our study.

We further hypothesized that leaf  $\Delta^{13}\text{C}$  would decrease in the main functional groups due to stomatal closure as a consequence of reduced water content. Even though the reduced transpiration rates observed during the first growing season indicate closure of stomata, no significant decrease in  $\Delta^{13}\text{C}$  could be detected in both growing seasons.  $\Delta^{13}\text{C}$  in the leaf organic matter is a signal integrating  $C_i/C_a$  over the leaf life time, and the leaf bulk material is a mixture of structural carbon as well as of storage compounds and freshly assimilated carbon (Adams and Grierson 2001; Werner et al. 2012). Stored carbon is used for early leaf growth in plants with significant carbon storage capacities such as trees, shrubs and perennial herbs (Gaudinski et al. 2009; Muhr et al. 2016), which could explain the missing environmental signal in early summer also in the 2nd year, as it is assumed that remobilized storage reserves can be older than 1 year at least in woody species (Gessler and Treydte 2016). However, the response to reduced precipitation in total leaf organic matter should become visible later in the growing season, when new assimilates and their integration in fresh structural organic matter contribute significantly to the leaf carbon pool. In fact, Fotelli et al. (2003) showed that the carbon isotope composition in leaves of different functional groups of the forest understory was indicative for recent environmental conditions (including changes in soil water content) in summer. The missing effect of the drought treatment despite a reduction in

soil water content and in transpiration might be explained by the fact that not only stomatal conductance but also RubisCO activity were reduced, leading to a constant ratio of assimilation rate ( $A$ ) to stomatal conductance ( $g_s$ ) and thus constant  $\Delta^{13}\text{C}$ . This is in agreement with previous observations in various understory species (Hommel et al. 2014; Yan et al. 2016). Moreover, Hommel et al. (2014) also observed that drought could have stronger effects on assimilation rate than on stomatal conductance, thus potentially explaining the increase in  $\Delta^{13}\text{C}$  upon drought in grasses in late summer 2013 (Fig. 3). In addition, we need to acknowledge that grouping plants to functional groups composed of different species on different subplots might have resulted in some variation of  $\Delta^{13}\text{C}$  due to species-specific factors that affect photosynthetic and post-photosynthetic carbon isotope fractionation.

In the second growing season, only shrubs decreased their transpiration rates in response to reduced soil water. The soil water reduction was as least as strong in the 2nd as in the 1st year, and, in the Hainich and Schwäbische Alb exploratories, even slightly more pronounced in 2013 (Fig. 1). Our finding might indicate that some acclimation occurred to all functional groups except shrubs. Plants may acclimated by allocating more biomass to roots (Eghball et al. 1993; Hommel et al. 2016), thus improving the exploitation of soil water resources. We might thus speculate that, in the 2nd year, the reduced soil water content might have been compensated for by deeper and more extensive roots in most functional groups. Under drought conditions, the above ground biomass of perennial grasses might partially die

off, but the fine root proportion has been shown to increase (Couso and Fernández 2012; Fernandez and Reynolds 2000; M. Baudis et al., unpublished data). Indeed, in some stands we found reduced grass leaf area in the treatment compared to the control subplots, accompanied by a significant higher leaf  $\Delta^{13}\text{C}$  in grasses under the roof in late summer 2013. Enhanced allocation to roots may enable plants to extract more water from deeper soil layers thus contributing to the observed  $\Delta^{13}\text{C}$  patterns. However, the higher discrimination might also be attributable to lower photosynthesis rates (see above), which could indicate that the remaining aboveground biomass of grasses was physiologically impaired by drought. Ferns neither showed any significant change in transpiration nor in leaf  $\Delta^{13}\text{C}$  upon drought during both growing seasons. A comparison of drought responses between ferns and angiosperms showed faster closure of stomata in ferns as protection against hydraulic failure (Brodribb and Holbrook 2004). Ferns (i.e., the species *Dryopteris dilatata*) were assessed only in the intensively managed conifer stand in the Exploratory Schorfheide (see Table S2), where the strongest reduction in soil water content occurred and only ferns increased leaf area upon drought while the other groups showed reduced LAI (Fig. 6). Even though ferns are often assumed to be highly drought sensitive and not to have access to deeper soil water resources, there are indications that particular fern species (including those of the genus *Dryopteris*) also tolerate dry conditions (Baer et al. 2016). Furthermore, ferns possibly grew in particular microhabitats at our stand (e.g., under the shelter of the closed canopy rather than in canopy gaps), which might have been less drought exposed than the rest of the understory. However, our results call for further assessment of the drought response of *D. dilatata*.

All other functional groups comprised various species (Table S2) differing in physiology and phenology, and thus in traits related to the complexity of growth conditions occurring close to the forest ground. Such higher trait variability might conceal and reduce functional groups' reactions towards environmental drivers (Fotelli et al. 2003).

Our results partially support our first hypothesis, as we observed reduced transpiration rates across most functional groups as fast response to drought in the first growing season. The less pronounced transpiration reaction in trees, herbs and grasses in the second growing season might point to acclimation of these functional groups to the reduced water content.

## 4.2 Effects of precipitation reduction on the understory community

In late summer of both growing seasons, ET rates were affected by the precipitation reduction. Since we found significant treatment effects for soil evaporation only in spring 2012 and in early summer 2013 at the conifer stands but not in late summer, we attribute these effects primarily to community transpiration. Though differences in soil water content of the

upper soil layer between the roof and control in late summer might be less pronounced due to the normal summer reduction of soil water content occurring also on the control subplots (Fig. 1), the treatment decreased in general community transpiration rates of the understory in the different forest stands with the exception of the conifer stand at the Alb in early summer 2013 (Fig. 4). This might indicate that the understory of the control subplots, contrary to the plants under the roof, still have the possibility of tapping into existing water reserves through their roots. During the first growing season, this reduction pattern is mainly explained by the drought reaction of the particular functional groups. The decrease in community transpiration in spring is strongly driven by grasses, which responded rapidly to drought. At five of our eight forest stands grass species were present with LAI<sub>s</sub> from 0.008 up to 0.23 m<sup>2</sup>/m<sup>2</sup> (Table S2), thus being among the functional groups with the highest LAI. In late summer of the first growing season, the drought induced reduction of transpiration in the functional groups herbs, shrubs and trees governed the whole community response. In addition, first reductions in LAI were observed upon the treatment (Fig. 6, Table S12), which enhanced the reduction of leaf level changes when scaled to the whole community. For the second growing season, the reduction of community transpiration in the drought treatment could not be attributed directly to the patterns of leaf level transpiration of the functional groups as they were mostly not affected. However, plant leaf area was reduced in the treatments (Fig. 6, Tables S13–S14), resulting in a reduction of the transpiring area, and there was a displacement of functional groups within particular stands. As an example, tree LAI increased at the expense of herbs and shrubs at the managed beech stand in the Schorfheide exploratory (Fig. 6). Since functional groups differ in their leaf level transpiration rates (Table S3) with shrubs and herbs showing generally higher rates than trees, a substantial shift in functional group LAI will have a corresponding shift in the community transpiration rates, partly explaining the patterns we observed.

$\Delta^{13}\text{C}$  of community and functional group level was weakly affected by drought: Only in early summer 2013 did we observe a significant treatment effect resulting in increased  $\Delta^{13}\text{C}$ . This could not be explained by functional group level response in  $\Delta^{13}\text{C}$  to drought (cf. Fig. 3). However, since functional groups differed significantly in their  $\Delta^{13}\text{C}$  (Table S4), subtle changes in the LAI relationships might have been responsible for this observation.

We also expected no changes in species richness and Shannon diversity, indicating stability of the community during drought. After 18 months there was a significant tendency for lower understory species richness, but diversity was unaffected on the drought-exposed subplots. This points to the high plasticity of the understory vegetation to moderate soil water content reduction. We however, also need to acknowledge that shifts in phenology due to drought effects as

observed recently in grassland and heath species (Jentsch et al. 2009) might affect the results of our assessment, that have been performed at defined time points. Any retardation or advancement of vegetative growth due to drought might have thus caused us to find plant species already developed in the treatment but not in the control or vice versa.

Our results indicate that effects of drought on the understory water use on the community level can be enhanced compared to leaf level reactions. This is due to changes in total leaf area and relative contribution of different functional groups to total leaf area. The fact that drought effects were observed on the community level supports our second hypothesis. Our results also indicate that single functional groups can drive the average community responses to drought. This is in agreement with the findings of Forrester et al. (2016) and Grossiord et al. (2014) for overstory forest communities, where community-level responses to drought were shown to be often caused by only one species within each given community. In our case, however, additional seasonal differences in the contribution of different species/functional groups to the community response were observed. At the end of our experiment we could also detect a tendency towards species loss, which was not reflected in understory diversity. Therefore, we must reject this part of our second hypothesis.

### 4.3 The interaction between reduced precipitation and forest management

Kahl and Bauhus (2014) developed a Forest Management Intensity index (ForMI) and could clearly group unmanaged beech, managed beech, managed conifer forest across all three exploratories. This result indicates that our selection is well suited to compare management activities across the exploratories with a gradient from no or very low intervention (unmanaged beech) to high timber harvest and tree felling activities in the past together with the change of the natural vegetation (intensively managed stands with conifers).

We observed interactions between forest management and drought treatment primarily through changes in LAI and community transpiration, but these effects were not consistent over the whole experimental period. Grossiord et al. (2014) observed that forests with high tree species diversity can be more resistant to drought. We aimed to test if such a relationship could also be observed for the understory of beech dominated forests and conifer replacement stands. We found that understory Shannon diversity was, in fact, lower in the unmanaged beech stands compared to the other two management intensities and significantly higher at the Schwäbische Alb exploratory compared to the other two exploratories (Felsmann et al. 2015). Plotting

Shannon diversity against the impact of the drought treatment on community transpiration or community  $\Delta^{13}\text{C}$ , however, showed that understory diversity had no influence on the strength of the responses to drought (see Fig. S2). Our findings are in line with the main conclusion of Grossiord et al. (2014) that species diversity in forest ecosystems does not necessarily assure improved stability to the more severe and frequent drought events predicted for the future, and extends this assumption to the forest understory. Forest understory communities are thus comparable to the forest overstory (Grossiord et al. 2014). In grasslands in contrast, higher resistance to drought with increasing biodiversity has been observed (cf. Tilman and Downing 1994) but there are also reports that management is far more important for drought resistance than species diversity (Vogel et al. 2012), and Van Ruijven and Berendse (2010) found no relationship between drought resistance and diversity at all.

Still, our results show that the forest understory shows considerable drought responses and high plasticity on the leaf and community level. This is indicated by the regulation of water use on the leaf level in the 1st year and potential acclimation effects in most functional groups in the 2nd year of drought. Moreover, plant diversity was not negatively affected upon drought indicating not only functional but also structural stability of the community. We did not observe a consistent influence of management intensity or understory diversity on the responses to drought of the understory community.

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### Compliance with ethical standards

**Conflict Of Interest** The authors declare that they have no conflict of interest.

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