Plant functional diversity increases grassland productivity-related water vapor fluxes: an Ecotron and modeling approach

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Abstract. The impact of species richness and functional diversity of plants on ecosystem water vapor fluxes has been little investigated. To address this knowledge gap, we combined a lysimeter setup in a controlled environment facility (Ecotron) with large ecosystem samples/monoliths originating from a long-term biodiversity experiment (The Jena Experiment) and a modeling approach. Our goals were (1) quantifying the impact of plant species richness (four vs. 16 species) on day- and nighttime ecosystem water vapor fluxes; (2) partitioning ecosystem evapotranspiration into evaporation and plant transpiration using the Shuttleworth and Wallace (SW) energy partitioning model; and (3) identifying the most parsimonious predictors of water vapor fluxes using plant functional-trait-based metrics such as functional diversity and community weighted means. Daytime measured and modeled evapotranspiration were significantly higher in the higher plant diversity treatment, suggesting increased water acquisition. The SW model suggests that, at low plant species richness, a higher proportion of the available energy was diverted to evaporation (a non-productive flux), while, at higher species richness, the proportion of ecosystem transpiration (a productivity-related water flux) increased. While it is well established that LAI controls ecosystem transpiration, here we also identified that the diversity of leaf nitrogen concentration among species in a community is a consistent predictor of ecosystem water vapor fluxes during daytime. The results provide evidence that, at the peak of the growing season, higher leaf area index (LAI) and lower percentage of bare ground at high plant diversity diverts more of the available water to transpiration, a flux closely coupled with photosynthesis and productivity. Higher rates of transpiration presumably contribute to the positive effect of diversity on productivity.

Key words: biodiversity–ecosystem functioning; ecosystem evaporation; ecosystem transpiration; Ecotron; evapotranspiration; functional traits; leaf area index; lysimeter; plant species richness; Shuttleworth and Wallace model; The Jena Experiment.

INTRODUCTION

The evidence that biodiversity loss reduces the functioning of ecosystems has grown over the last two decades (Cardinale et al. 2012, Hooper et al. 2012). Many experimental studies established that increasing plant species richness in a community generally leads to higher biomass

production, an easily measurable end-product of ecosystem functioning. However, only little is known about the ecosystem-level energy and mass fluxes underpinning the biomass production (Duffy 2003, Cardinale et al. 2012, Milcu et al. 2014). To date, the selection (Huston 1997) and complementarity (Tilman et al. 1997, Cardinale et al. 2007) effects are the main mechanisms put forward to explain the positive biodiversity–ecosystem functioning relationship. While the selection effect can lead to enhanced ecosystem functioning due to an increased probability of including a highly performing dominant species

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with increasing species richness, the complementarity hypothesis asserts that increasing plant diversity should lead to a more complete exploitation of resources. Complementarity is expected to arise in more species-rich communities due to increased probability of including species that exhibit (1) various forms of niche partitioning leading to complementary resource capture in space and time or (2) interspecific facilitative/ positive interactions that enhances the capture of resources. In particular, ecosystem evapotranspiration (ET) and transpiration (T), two productivity-related fluxes strongly coupled with photosynthesis, are expected to increase with plant diversity due to its well-documented positive effect on biomass production and leaf surface area per ground area (the leaf area index [LAI]; Obrist et al. 2003, Hu et al. 2009). Belowground, complementarity in rooting patterns (von Felten and Schmid 2008) could also potentially lead to increased water acquisition and hence increased ET and T .

To our knowledge, the importance of plant species richness for water vapor fluxes has only been investigated in a few studies. With some notable exceptions (Stocker et al. 1999, Leimer et al. 2014), indications of more complete water use as well as increased water use efficiency have been found at higher diversity levels (Caldeira et al. 2001, Van Peer et al. 2004, Lemmens et al. 2006, and Verheyen et al. 2008). However, it is unclear whether these results can be generalized since most of these studies included experimental constraints related to the use of relatively small containers (Van Peer et al. 2004, De Boeck et al. 2006), short establishment phase (Stocker et al. 1999, Van Peer et al. 2004, De Boeck et al. 2006) and indirect estimates of evapotranspiration (ET) using water balance models (Verheyen et al. 2008, Leimer et al. 2014). Furthermore, no attempt has been made to partition the ecosystem ET into evaporation (E), a non-productivity related flux, and T . In addition to being controlled by different biological and physical processes, by not partitioning the ecosystem water vapor fluxes in E and T one cannot disentangle the direct (water acquisition-related) effects of species richness on T from canopy structure-mediated effects on ecosystem E . Consequently, we only have an incomplete understanding of the underlying mechanisms influencing non-productive (E) and productive (T) water vapor ecosystem fluxes, which could potentially play an important role in explaining the biodiversity-ecosystem function relationship (Verheyen et al. 2008).

There is mounting evidence that consideration of plant morphological, biochemical, behavioral, and phenological traits known to affect performance and fitness can improve our understanding of ecosystem functioning (Díaz et al. 2007, Cadotte et al. 2009, Milcu et al. 2014). To date, the most common community-level functional predictors/metrics derived from plant functional traits include the community weighted mean trait value (CWMs) and functional diversity (FD). CWMs, computed as the average of the trait values weighted by the

relative abundances of each species, can be used to identify the relative importance of a functional trait in driving ecosystem processes. Theoretically, this metric is related to the mass ratio hypothesis of Grime (1998) stating that ecosystem functioning is primarily determined by trait values of the dominant contributors to plant biomass (Díaz et al. 2007). In contrast, FD metrics quantifies the variety, range and evenness of the functional traits present in communities, and have been proposed to be linked to niche complementarity hypothesis since a greater range of trait-values is generally considered to indicate less niche overlap (Díaz et al. 2007). However, while functional trait-based metrics have been extensively used to predict biomass production, the role of functional traits for water vapor fluxes has not been yet explored despite evidence that this approach may help to achieve a better predictive framework for ecosystem functioning (Wright et al. 2004, Violle et al. 2007, Reiss et al. 2009). Based on our current understanding, we would expect the ecosystem water vapor fluxes to be best predicted by plant functional traits affecting the LAI and the rooting patterns (Reichstein et al. 2014).

To address the aforementioned knowledge gaps, we used 12 large lysimeters in a controlled environment facility for ecosystem research (Ecotron) hosting intact vegetation–soil monoliths from a long-term biodiversity experiment (The Jena Experiment; Roscher et al. 2004). This was combined with a modeling approach, based on the Shuttleworth and Wallace (1985) energy partitioning model (henceforth SW), which allowed to separately quantify the proportion of energy that is dissipated in T , E , and sensible heat flux (H). In order to derive a mechanistic and predictive understanding of plant diversity effects, in addition to species richness we also tested several predictors based on above- and belowground vegetation properties and functional trait-based indices (Appendix S1). Specifically, our goals were (1) quantifying the effect of plant diversity on day- and nighttime ecosystem water fluxes during the peak of the growing season; (2) partitioning the ecosystem ET in E and T using a modeling approach to test the importance of plant species richness (four vs. 16 species) on the partitioned fluxes; and (3) identifying the most parsimonious statistical models of water vapor fluxes using above- and belowground vegetation properties and functional trait-based metrics (CWMs and Rao's quadratic entropy index of functional diversity [FD_Q]).

MATERIALS AND METHODS

The Ecotron facility

The experiment was conducted in the Montpellier European Ecotron, an experimental infrastructure developed by the Centre National de la Recherche Scientifique (CNRS, France), to study the response of ecosystems to global environmental changes. The lysimeters (2 m², circular with a diameter of 1.6 m, weighing

7 to 8 Mg) were located in 12 controlled environment units of the macrososms platform. Each unit consists of a 30-m³ dome-shaped chamber situated on top of a dedicated lysimeter room (see Milcu et al. [2014] and Appendix S2 for more information on the macrososms platform of the Ecotron facility). The soil surface and canopy of the lysimeters were exposed to natural sunlight within each dome as a highly transparent material to light and UV radiation (250 μ m thick Teflon-FEP film, DuPont, Wilmington, Delaware, USA) was used as cover. Automatically controlled feedback loop algorithms based on industrial-grade proportional-integral-derivative (PID) controllers were used to achieve the desired set-points for air temperature, air humidity, and air percent CO₂.

Plant communities

The soil monoliths containing the plant communities originated from the long-term Jena Experiment (50°57.1' N, 11°37.5' E, 130 m above sea level; mean annual temperature 9.3°C, mean annual precipitation 587 mm). The site is located on the floodplain of the Saale River (Jena, Germany), and was a former arable field until 2000, then kept fallow before 82 large plots (20 × 20 m) varying in plant species richness (1–60 species), plant functional groups (one to four; grasses, small herbs, tall herbs, and legumes) and plant species composition were established in May 2002 (Roscher et al. 2004). Twelve plant communities from two sown diversity levels (four and 16 species) with six independent replicates per diversity level (Appendix S3), were selected according to the following criteria: (1) at least three functional groups (legumes, grasses, and herbs) were present; (2) realized species numbers were close to sown species richness; and (3) plots were equally distributed across the experimental blocks of the field site to account for the variability in soil texture. The monoliths were selected to be representative (as percentage of vegetation cover and standing biomass) of the plots they originate from. The monoliths were sampled and placed in lysimeters in December 2011 following an established non-compacting extraction method (see supplementary methods in Appendix S6 for more information on the procedure used to extract the soil monoliths). At the end of March 2012, the lysimeters were transported to the Ecotron facility in Montpellier.

Experimental conditions

During the four months when the lysimeters were hosted in the Ecotron, we aimed to simulate the average climatic conditions at the Jena Experiment field site since 2002. As the recorded spring and summer climatic conditions of the year 2007 were very close to the average temperature and precipitation regimes in Jena for the period 2002–2010, they were used as set points (at 10-min intervals). The average air temperature achieved was close to the set point (14.0°C vs. 14.9°C in Jena). The achieved average air humidity (RH) however, was somewhat lower

(58.9% RH vs. 73.4% RH in Jena) because during nighttime the humidifying system in the Ecotron had to be stopped occasionally to prevent wetting the vegetation when the set points were higher than 80% RH. Because of this and since the monoliths were exposed to slightly higher temperatures during transport and prior to installation in the Ecotron, we opted for increasing the precipitation by +28% relative to 2007 (Appendix S4). This allowed achieving similar soil moisture conditions (Appendix S5). The precipitation was applied by manual watering using a hose equipped with a sprinkler and a flowmeter. As the incoming short-wave radiation estimated from the HelioClim-1 database (Blanc et al. 2011) was on average 37% lower in Jena than in Montpellier between April and July, a black shading mesh was added on the inside of each dome, which reduced the incoming radiation by 44%. Unwanted plant species (weeds) were removed every three weeks to maintain the targeted diversity levels. To recreate the mowing management of the Jena Experiment, the aboveground biomass was mown at the end of April and at the end of July. The final harvest took place at the time of the July mowing and included destructive vegetation and soil sampling. As the modeling exercise relied on a period of 6 d with undisturbed water vapor fluxes (28 June to 3 July 2012), the continuous environmental conditions (air RH, air temperature, vapor pressure deficit [VPD], and radiation) during this period are presented in Fig. 1a,b).

Water vapor flux measurements

Ecosystem ET was measured as lysimeter mass changes over time. Four shear beam load cells per lysimeter (CMI-C3, Precia-Molen, Privas CEDEX France), with an accuracy of ± 200 g, were used to measure the changes in mass. The raw mass changes were corrected for temperature effects on the sensitivity of the beam load cells, with correction factors provided by the manufacturer. The resulting data were then smoothed using a symmetric loess smoothing function with a span of 0.1 (as available in the R 3.1.2 software environment [R Development Core Team 2013]) to reduce the impact caused by minute differential pressure changes between the dome and the lysimeter chamber where the beam load cells are installed. Since not all mass changes can be associated with water vapor fluxes (e.g., during activities that add or remove mass from the lysimeter such as sampling, weeding, or when a measuring device is placed on the lysimeter), we restricted our analysis to a time period with the highest lysimeter data quality obtained during six consecutive undisturbed days (28 June to 3 July 2012). This period was also close to the final harvest of the plant communities (17–20 July) when all plant traits and vegetation properties were measured. The lysimeter measured ET for this period is presented in Fig. 1c. These measurements were used to estimate average day- (ET_{day}) and nighttime (ET_{night}) ecosystem evapotranspiration as well as the evapotranspiration over 24 h (ET_{24h}). For more

FIG. 1. (a,b) Ecotron environmental conditions during the selected 6 d averaged for the two plant diversity levels (four vs. 16 species). RH represents the air relative humidity and VPD the vapor pressure deficit. (c) Lysimeter measured evapotranspiration (ET) in the Ecotron.

information on the measurement and sampling methodology, see Milcu et al. (2014) and Appendix S6.

The Shuttleworth and Wallace model

Probably the most widely used model for ecosystem-scale ET simulations is the Penman (1948) model with Monteith (1981) extension to include stomatal resistance as a term that allows one simulate the plant control of ET, today known as the Penman-Monteith equation (PM). Shuttleworth and Wallace (1985) further developed a canopy model based on PM to allow partitioning of the radiative energy in sensible heat flux (H) and ecosystem evapotranspiration (ET) which can be further partitioned in evaporation (E) and transpiration (T).

This is done by expressing PM (1) for the top of the vegetation canopy, (2) for the soil surface below the canopy, and (3) for bare ground and considering that in any canopy there is a certain fraction of projected surface area that is not entirely covered by the plant community. PM uses available energy, air temperature, atmospheric moisture, and a series of transfer resistances, including the stomatal resistance of vascular plants to predict ET (see Appendix S6 for equations and full model details).

Vegetation properties and functional trait-based metrics

We measured the following vegetation properties: shoot biomass (ShootBM), root biomass (RootBM), root biomass and length by soil volume and depth (0–5,

5–10, 10–20, 20–30, 30–60 cm), total biomass (TotalBM), shoot biomass of legumes (LegBM), shoot biomass of grasses (GrassBM), shoot biomass of herbs (HerbBM), leaf area index (LAI), leaf biomass (LeafBM), and percentage of bare ground (% bare ground).

The functional-trait based metrics included functional diversity indices (FD) and community weighted means (CWM) calculated from 10 plant functional traits that have been previously shown to be linked to plant transpiration, photosynthetic rates, and light interception (see Appendix S1 for an overview of tested predictors). Rao's quadratic entropy (FD_Q; Botta Dukát 2005) was preferred as an index of functional diversity as it incorporates information about functional distance as well as functional evenness (abundance weighted) of a community. Species-specific aboveground biomass was used for abundance weighting. For each available plant species, the following traits were measured in situ in each dome before the final destructive harvest: stomatal conductance (gs; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), specific leaf area (SLA; mm^2/mg), leaf greenness (dimensionless measure of foliar chlorophyll content), leaf dry matter content (LDMC; mg/g), leaf N concentration (% N in leaf dry mass), species-specific plant height (cm), and specific leaf nitrogen (SLN; g N/m^2 leaf). See Appendix S6 for further details on the sampling methodology. Literature surveys were used for seasonality of foliage (ordinal, 1 = summer green, 2 = partly evergreen, 3 = evergreen), rooting type (ordinal, 1 = long-living primary root system, 2 = secondary fibrous roots in addition to the primary root system, 3 = short living primary root system, extensive secondary root system), and rooting depth (cm) as used by Roscher et al. (2004). FD_Q was calculated for each of the ten functional traits separately, all available traits simultaneously (FD_Q-all) and only leaf-related traits (FD_Q-leaf). FD_Q and CWM were calculated using the FD package (Laliberté and Shipley 2011) available through the R (R Development Core Team 2013) statistical package version 3.1.2.

Statistical analyses

Statistical analyses were performed in R (version 3.1.2.). To compare measured and modeled water vapor fluxes, we used *t* tests. To test for plant species richness effects, we used repeated-measures analysis of variance (ANOVA) on daily averaged data with dome as a random factor and a temporal autocorrelation function (corAR1) for individual domes as available through the "lme" function. To identify the most important predictors, we fitted simple linear regression models on fluxes averaged over 6 d for each predictor as well as available soil texture-related covariates (see Appendix S1) on the averaged water vapor fluxes of the selected 6 d. The resulting models were then simultaneously run through a model averaging procedure ("dredge" function in MuMIn package) which computes Akaike weights (AIC_w), that represent the probability that a particular

model is the best fit to the observed data (Burnham and Anderson 2001). The predictors found within the 95% confidence interval (cumulative AIC_w $\leq$ 0.95) were selected and simultaneously included in a multivariate linear fitting regression model using the lm function. The resulting regression models were then simplified to reach the most parsimonious models by using the automatic model simplification "step" procedure based on Akaike information criterion corrected for sample size (AIC_c; Venables and Ripley 2002).

RESULTS

Results of the Shuttleworth and Wallace model

Time traces of ecosystem soil evaporation (*E*) and plant transpiration (*T*) fluxes modeled with the SW model are displayed in Fig. 2a and b as averages for the two plant species richness levels. Although over 24 h the modeled ET slightly underestimated the measured ET (Fig. 2c), when restricted to only daytime, the model agreed well with the measured data (Fig. 2d), with average daytime ET over 6 d within $\pm 10\%$ of measured values for most of the lysimeters ($r^2_{\text{modeled,measured}} = 0.79$) and a Root Mean Square Error of Approximation (RMSEA) of 1.45. The *t* tests based on average daily ET showed that there was no significant difference between measured and modeled daytime ($t = -0.58$, $P = 0.568$) and 24 h ET ($t = 1.33$, $P = 0.197$).

As expected, modeled nighttime evapotranspiration (ET_{night}) values were lower than daytime values (Fig. 2a). However, we found that the modeled ET_{night} values were on average 52% lower ($t = 6.37$, $P < 0.001$) than the values measured with the lysimeters (Fig. 2b). Since we argue that the discrepancy between measured and modeled ET_{night} is likely related to the controlled environment in the Ecotron (see Appendix S6), we restricted the further assessment of the effect of species richness and functional diversity on the modeled *T* and *E* to daytime only.

Species richness effects

Measured daytime ecosystem evapotranspiration (ET_{day}) was significantly higher in the lysimeters hosting monoliths from communities sown with 16 species relative to four species (+16.6%, $F_{1,10} = 0.049$; Fig. 3a). This is also visible in Fig. 1c with exception of the last day after the rainfall/irrigation of 20 mm. However, no significant difference in ET_{day} was found between species richness during nighttime ($F_{1,20} = 0.25$, $P = 0.625$), or when the ET was integrated over 24 h ($F_{1,10} = 2.84$, $P = 0.122$; Fig. 3a).

Modeled ET_{day} was also significantly higher in the treatment with 16 species relative to four species richness (+14.5%, $F_{1,10} = 6.86$, $P = 0.026$; Fig. 3b), a result in accordance with the measured results. Averaged over 24 h, modeled ET was also significantly higher in the treatment

FIG. 2. Time trace of ecosystem evaporation (E) and transpiration (T) fluxes as modeled by the SW model in communities with (a) 16 and (b) four plant species. T (gray area) and E (black area) are plotted additively so that their sum represents total evapotranspiration (ET). Comparison of averaged modeled and lysimeter ET (c) with and without (d) nighttime values. The gray band shows range of $\pm 10\%$ agreement; dashed lines show $\pm 15\%$. LAI, leaf area index.

with 16 sown species richness (+14.6%, $F_{1,10} = 6.62$, $P = 0.028$), while no diversity effect was found for ET_{night} .

Modeled ecosystem transpiration during daytime (T_{day}), either expressed as fraction of the available energy (+65.2%, $F_{1,10} = 6.77$, $P = 0.026$; Fig. 3c) or mean water vapor loss per day (+68.4%, $F_{1,10} = 6.79$, $P = 0.026$; Fig. 3d), was significantly higher in the monoliths with higher plant species richness (Table 1). Furthermore, T_{day} correlated well with the total plant biomass at the final harvest ($r^2 = 0.72$, $P < 0.001$; Fig. 3f). In contrast, modeled daytime evaporation (E_{day}) was significantly lower at high species richness expressed as both fraction of available energy (−22.2%, $F_{1,10} = 6.09$, $P = 0.033$; Fig. 2d) and mean water vapor loss per day (−15.9%, $F_{1,10} = 6.45$, $P = 0.029$; Fig. 3d). Consequently, the ratio of daytime ecosystem transpiration to evaporation ($T_{\text{day}}/E_{\text{day}}$) was also significantly affected by sown plant species richness, with a significantly higher ratio in the monoliths with 16 sown species ($F_{1,10} = 7.28$, $P = 0.022$;

Fig 3c). The proportion of total energy dissipated as sensible heat flux (H_{day}) was significantly lower (−28.4%; $F_{1,10} = 7.30$, $P = 0.022$) in the monoliths with 16 compared to 4 sown plant species (Table 1).

Vegetation properties and functional trait-based metrics as predictors for water vapor fluxes With one exception (ET_{night} , which was best predicted by the community weighted means of the height of the species), among the vegetation properties, LAI proved to be the most consistent predictor of water vapor fluxes (Table 1). Fig. 3e depicts the role of LAI in the modeled partition of the available energy in T_{day} , E_{day} and H_{day} . Higher LAI also led to higher measured $ET_{24\text{h}}$ and ET_{day} (Table 1). In addition to LAI, the percentage of bare ground was retained in the most parsimonious models for all of the modeled variables and positively influenced the E_{day} and H_{day} and negatively the T_{day} and the $T_{\text{day}}/E_{\text{day}}$ ratio.

The minimal adequate models for water vapor fluxes that directly focused on functional trait based metrics

TABLE 1. ANOVA results for the effect of sown species richness (Sdiv, i.e., 4 vs. 16 species) alongside the most parsimonious multiple regression models.

Response variables	Best model, based on							
	Sdiv		Canopy, root, and soil texture			Functional-trait predictors		
	<i>P</i>	<i>r</i> ²	<i>P</i>	<i>r</i> ²	Model	<i>P</i>	<i>r</i> ²	Model
Measured								
ET _{24 h}	ns		<0.001	0.78	2.788 + 0.342 × LAI	ns		
ET _{day}	0.049	0.34	<0.001	0.93	2.138 + 0.344 × LAI	0.015	0.46	2.46 + 0.67 × FD _Q -leafN%
ET _{night}	ns		0.094	0.26	0.700 – 0.002 × grBM	0.015	0.46	0.883 – 0.111 × CWM-height
Modeled								
<i>T</i> _{day}	0.026	0.04	<0.001	0.99	1.109 + 0.28 × LAI – 0.017 × Bare	0.040	0.36	0.893 + 0.918 × FD _Q -leafN%
<i>E</i> _{day}	0.029	0.39	<0.001	0.97	1.642 – 0.101 × LAI + 0.006 × Bare	0.076	0.29	1.706 – 0.295 × FD _Q -leafN%
<i>T</i> _{day} / <i>E</i> _{day}	0.022	0.42	<0.001	0.99	0.597 + 0.276 × LAI – 0.011 × Bare	0.034	0.37	0.541 + 0.769 × FD _Q -leafN
<i>H</i> _{day}	0.022	0.42	<0.001	0.98	0.319 – 0.032 × LAI + 0.002 × Bare	0.054	0.32	0.357 – 0.111 × FD _Q -leafN%

Notes: ET_{24 h}, ET_{day} and ET_{night} represent lysimeter measured evapotranspiration values during 24 h, daytime and nighttime, respectively. *T*_{day}, *E*_{day}, and *H*_{day} represent the daytime transpiration, evaporation, and sensible heat flux, respectively. Vegetation properties (LAI, leaf area index; Bare, percentage of bare ground; grBM, biomass of grasses) and functional trait-based predictors (FD_Q-leafN%, diversity of leaf N concentration; CWM-height, community weighted means of species height) were separately analyzed in different models. Nonsignificant effects are labeled “ns”. See Appendix S1 for the list of all predictors included in the initial models before the Akaike information criterion corrected for sample size (AIC_c)-based model simplification.

had generally a weaker predictive power than those based on the LAI (Table 1). However, the diversity of leaf N concentration in the canopy (FD_Q-leafN%) stood out as a consistent predictor of ecosystem water vapor fluxes; increasing FD_Q-leafN% was correlated with an increase in measured and modeled fluxes. The relationships between FD_Q-leafN%, LAI, percentage of bare ground, and modeled daytime ecosystem transpiration (*T*_{day}) are depicted in Fig. 4.

DISCUSSION

Ecosystem ET is an important process for water and energy balance, and is closely linked to ecosystem productivity (Hu et al. 2008, Verheyen et al. 2008). The Shuttleworth and Wallace’s (SW) energy partitioning model has been widely used with good performance to partition the ET in its component water vapor fluxes (*T* and *E*), in crops (Shuttleworth and Wallace 1985, Brisson et al. 1998) and natural grasslands (Hu et al. 2009), but it has not been used so far in experiments addressing the role of biodiversity for ecosystem functioning. Here, we applied the SW model to plant communities of contrasting species richness (four vs. 16 species) in a controlled environment facility (Ecotron) equipped with lysimeters. This setup allowed us to compare the performance of the SW model with the lysimeter measured fluxes. Considering the large daily variability of environmental variables, and particularities

of the Ecotron environment (e.g., top down air flow), the overall agreement of measured and modeled ET during the 6 d of our study was good (*r*² = 0.79), and within the range found by previous studies (Brisson et al. 1998, Tourula and Heikinheimo 1998, Kato et al. 2004).

Overall, our results show an increase of water acquisition in the high diversity treatment (16 plant species) as indicated by higher ET_{day} as well as higher modeled *T*_{day}. Although speculative, since we provide no direct evidence for complementarity, increased water acquisition can be interpreted as an indicator of complementarity, however, the jury is still out on the importance of complementarity for grassland water acquisition (Verheyen et al. 2008, Bachmann et al. 2015). In parallel with the higher modeled *T*_{day}, the productive fraction of the ET, communities with 16 species also exhibited lower proportions of energy diverted into non-productive water and energy fluxes (*E*_{day} and *H*_{day}) and an increase in the ratio of energy diverted to transpiration over evaporation during daytime (*T*_{day}/*E*_{day}; Table 1). This suggests that plant diversity effects mediated by the structure of the canopy (by the LAI as indicated by Table 1) occurred by reducing the propensity to dissipate the energy via the non-productive evaporative process. Since *T*_{day} occurs only during the period of photosynthetic activity, a higher proportion of *T* implies that more of the ET water was used to acquire carbon, which would increase the water use efficiency (C gain/ET). Indeed, this is consistent with the results of Milcu et al. (2014) from same

FIG. 3. Plant diversity (four vs. 16 species) effects on daytime, nighttime, and 24-h evapotranspiration fluxes (a) measured in lysimeters and (b) modeled by the SW model. (c) Plant diversity effects on modeled partition of the available radiative energy in evaporation (*E*), transpiration (*T*), and sensible heat flux (*H*). (d) Modeled *E* and *T* as affected by plant diversity. Values are mean $\pm$; ns, not significant. (e) LAI and plant diversity effects on modeled *E* (squares), *T* (circles), and *H* (triangles). (f) Relationship between modeled daytime *T* and plant biomass.

FIG. 4. Scatterplot and correlation matrix depicting the relationships between the most important predictors (diversity of leaf N concentration [FD_Q-leafN%], LAI, percentage of bare ground) of water vapor fluxes and modeled daytime ecosystem transpiration (T_{day}). The line in the scatterplots represents a locally weighted scatter-plot smoother (loess) fitting.

experiment in the Ecotron showing a 37.6% increase in water use efficiency in communities with 16 plant species relative to four species. These findings are also in line with several previous studies (Van Peer et al. 2004, De Boeck et al. 2006, Lemmens et al. 2006) documenting an increase in ET and water use efficiency with increasing plant diversity. However, our results are not in agreement with the findings of Leimer et al. (2014), which indirectly estimated ecosystem ET using a simple soil water balance model in the same field site from where the soil monoliths of our study were extracted (the Jena Experiment). By modelling ecosystem ET from fluctuations in soil water content measured in two soil layers (0.0–0.3 m and 0.3–0.7 m), the study of Leimer et al. (2014) found no plant diversity effects on modeled ET with monthly resolution from 2005 to 2008. This is different from our results which showed significantly higher modeled ET as well as a tendency of higher measured ET. While not fully comparable due to very different methodology and temporal resolution, it is worth noting that the Leimer et al. (2014) study was only tested against the results of a hydrological model and not against measured ET. Another possible explanation for the discrepancy could be that, by using a controlled environment approach and direct measurements of ET, we were able to reduce more confounding factors. Alternatively, we cannot discount the possibility that the study of Leimer et al. (2014), which presented monthly aggregated data for four years, also incorporated longer-term processes that are not included in our study. For example, unaccounted potential discrepancies in the phenology of plant

development throughout the growing season might alter the differences in water use between the communities with low and high diversity.

Of all tested predictors of water vapor fluxes based on vegetation properties such as canopy structure and belowground rooting patterns, we found that the LAI and the percentage of bare ground on the soil surface were the two predictors retained in the most parsimonious models. While it has been long established that the LAI is a consistent driver of water vapor fluxes, and is actually factored into the SW energy partition model (Shuttleworth and Wallace 1985), here we show that plant diversity effects on ecosystem water vapor fluxes are mediated by the leaf area index (LAI). Furthermore, to our knowledge, this is the first study attempting to link ecosystem water vapor fluxes to plant functional trait-based metrics. By doing this, we found that of all functional trait-based metrics, the index of functional diversity based on leaf nitrogen concentration in the canopy (FD_Q-leafN%) best predicted the water vapor fluxes and was strongly correlated to the LAI (Fig. 4). Moreover, it was a better predictor of measured daytime ET than species richness. Previous studies from the same experiment showed that FD_Q-leafN% was an important predictor of C fluxes and community biomass (Roscher et al. 2012, 2013, Milcu et al. 2014), and it was suggested that it might capture the cumulative investment in light acquisition by the community represented by the LAI, and hence, indirectly affect the ecosystem-level plant transpiration. Alternatively, it has also been suggested that this index of diversity measuring the unevenness of N allocation in the canopy could be linked to a more optimal N distribution in the canopy (Field 1983, Hirose and Werger 1987, Milcu et al. 2014) and not necessarily with the LAI. However, additional manipulative experiments are needed to clarify the exact mechanism through which FD_Q-leafN% affects the water vapor fluxes.

To conclude, our results show higher water acquisition (higher ET) in more diverse communities during daytime, at least at the peak at the growing season. More novel is that we identified a plant functional diversity metric capturing the diversity of leaf N% in the canopy (FD_Q-leafN%) as a consistent predictor of several daytime ecosystem-level water and energy fluxes (ET, T , E , and H), presumably via its effect on LAI, a measure of the community investment in light acquisition. Furthermore, since the SW model is showing that higher plant diversity leads to a higher T rates, a flux closely coupled with photosynthesis and hence productivity related, this presumably contributes to the well-documented positive effect of diversity on productivity. This is also supported by the positive correlation between modeled T_{day} and total plant biomass (Fig. 3f). Allocating more of the available water to the productivity-related flux is likely going to become more important in the future, since extreme climatic events such as droughts and heatwaves are predicted to increase in intensity and frequency in many regions (IPCC 2012). Under these conditions, plant

communities containing more functionally diverse species will likely use more of the available water for growth and cooling.

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LITERATURE CITED

- Bachmann, D., A. Gockele, J. M. Ravenek, C. Roscher, T. Strecker, A. Weigelt, and N. Buchmann. 2015. No evidence of complementary water use along a plant species richness gradient in temperate experimental grasslands. *PLoS ONE* 10:e0116367.
- Blanc, P., B. Gschwind, M. Lefèvre, and L. Wald. 2011. The HelioClim project: surface solar irradiance data for climate applications. *Remote Sensing* 3:343–361.
- Botta Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16:533–540.
- Brisson, N., B. Itier, J. C. L'Hotel, and J. Y. Lorendeau. 1998. Parameterisation of the Shuttleworth-Wallace model to estimate daily maximum transpiration for use in crop models. *Ecological Modelling* 107:159–169.
- Burnham, K., and D. R. Anderson. 2001. Model selection and multimodel inference: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65:23–35.
- Cadotte, M., J. Cavender-Bares, D. Tilman, and T. Oakley. 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE* 4:e5695.
- Caldeira, M. C., R. J. Ryel, J. H. Lawton, and J. S. Pereira. 2001. Mechanisms of positive biodiversity-production relationships: insights provided by $\delta^{13}\text{C}$ analysis in experimental Mediterranean grassland plots. *Ecology Letters* 4:439–443.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences USA* 104:18123.
- Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, and D. A. Wardle. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- De Boeck, H. J., C. Lemmens, H. Bossuyt, S. Malchair, M. Carnol, R. Merckx, I. Nijs, and R. Ceulemans. 2006. How do climate warming and plant species richness affect water use in experimental grasslands? *Plant and Soil* 288:249–261.
- Díaz, S., S. Lavorel, F. de Bello, F. Quétier, K. Grigulis, and T. M. Robson. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences USA* 104:20684–20689.
- Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecology Letters* 6:680–687.
- Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56:341–347.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:891–899.
- Hirose, T., and M. J. A. Werger. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72:520–526.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108.
- Hu, Z., G. Yu, Y. Fu, X. Sun, Y. Li, P. Shi, Y. Wang, and Z. Zheng. 2008. Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China. *Global Change Biology* 14:1609–1619.
- Hu, Z., et al. 2009. Partitioning of evapotranspiration and its controls in four grassland ecosystems: application of a two-source model. *Agricultural and Forest Meteorology* 149:1410–1420.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460.
- IPCC. 2012. Managing the risks of extreme events and disasters to advance climate change adaptation. Pages 109–230 in C. B. Field et al. editors. Special report of working groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Kato, T., R. Kimura, and M. Kamichika. 2004. Estimation of evapotranspiration, transpiration ratio and water-use efficiency from a sparse canopy using a compartment model. *Agricultural Water Management* 65:173–191.
- Laliberté, E., and B. Shipley. 2011. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0.9.
- Leimer, S., Y. Kreuziger, S. Rosenkranz, H. Beßler, C. Engels, A. Hildebrandt, Y. Oelmann, W. W. Weisser, C. Wirth, and W. Wilcke. 2014. Plant diversity effects on the water balance of an experimental grassland. *Ecophysiology* 1391:1378–1391.
- Lemmens, C. M. H. M., H. J. De Boeck, B. Gielen, H. Bossuyt, S. Malchair, M. Carnol, R. Merckx, I. Nijs, and R. Ceulemans. 2006. End-of-season effects of elevated temperature on ecophysiological processes of grassland species at different species richness levels. *Environmental and Experimental Botany* 56:245–254.
- Milcu, A., et al. 2014. Functional diversity of leaf nitrogen concentrations drives grassland carbon fluxes. *Ecology Letters* 17:435–444.
- Monteith, J. 1981. Evaporation and surface temperature. *Quarterly Journal of the Royal Meteorological Society* 107:1–27.
- Obrist, D., P. S. J. Verburg, M. H. Young, J. S. Coleman, D. E. Schorran, and J. A. Arnone. 2003. Quantifying the effects of phenology on ecosystem evapotranspiration in planted grassland mesocosms using EcoCELL technology. *Agricultural and Forest Meteorology* 118:173–183.
- Penman, H. L. 1948. Natural evaporation from open water, bare soil, and grass. *Proceedings of the Royal Society. Series A, Mathematical and Physical Sciences* 193:120–145.
- R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>
- Reichstein, M., M. Bahn, M. D. Mahecha, J. Kattge, and D. D. Baldocchi. 2014. Linking plant and ecosystem functional biogeography. *Proceedings of the National Academy of Sciences USA* 111:13697–13702.

- Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* 24:505–514.
- Roscher, C., J. Schumacher, J. Baade, W. Wilcke, G. Gleixner, W. W. Weisser, B. Schmid, and E. D. Schulze. 2004. The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology* 5:107–121.
- Roscher, C., J. Schumacher, M. Gubsch, A. Lipowsky, A. Weigelt, N. Buchmann, B. Schmid, and E. Schulze. 2012. Using plant functional traits to explain diversity–productivity relationships. *PLoS ONE* 7:e36760.
- Roscher, C., J. Schumacher, A. Lipowsky, M. Gubsch, A. Weigelt, S. Pompe, O. Kollé, N. Buchmann, B. Schmid, and E. Schulze. 2013. A functional trait-based approach to understand community assembly and diversity–productivity relationships over 7 years in experimental grasslands. *Perspectives in Plant Ecology, Evolution and Systematics* 15:139–149.
- Shuttleworth, W. J., and J. S. Wallace. 1985. Evaporation from sparse crops—an energy combination theory. *Quarterly Journal of the Royal Meteorological Society* 111:839–855.
- Stocker, R., C. Körner, B. Schmid, P. Niklaus, and P. Leadley. 1999. A field study of the effects of elevated CO₂ and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology* 5:95–105.
- Tilman, D., D. Tilman, C. L. Lehman, C. L. Lehman, K. T. Thomson, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences USA* 94:1857–1861.
- Tourula, T., and M. Heikinheimo. 1998. Modelling evapotranspiration from a barley field over the growing season. *Agricultural and Forest Meteorology* 91:237–250.
- Van Peer, L., I. Nijs, D. Reheul, and B. De Cauwer. 2004. Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. *Functional Ecology* 18:769–778.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*. Fourth Edition. Springer, New York, New York, USA.
- Verheyen, K., H. Bulteel, C. Palmborg, B. Olivie, I. Nijs, D. Raes, and B. Muys. 2008. Can complementarity in water use help to explain diversity–productivity relationships in experimental grassland plots? *Oecologia* 156:351–361.
- Violle, C., M. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional!. *Oikos* 116:882–892.
- von Felten, S., and B. Schmid. 2008. Complementarity among species in horizontal versus vertical rooting space. *Journal of Plant Ecology* 1:33–41.
- Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.

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