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

Alexandru Milcu, Werner Eugster, Dörte Bachmann, Marcus Guderle, Christiane Roscher, Annette Gockele, Damien Landais, Olivier Ravel, Arthur Gessler, Marcus Lange, Anne Ebeling, Wolfgang W. Weisser, Jacques Roy, Anke Hildebrandt & Nina Buchmann

1CNRS, Ecotron (UPS-3248), Campus Baillarguet, F-34980, Montferrier-sur-Lez, France
2Centre d’Ecologie Fonctionnelle et Evolutive, CEFE-CNRS, UMR 5175, Université de Montpellier – Université Paul Valéry – EPHE, 1919 route de Mende, F-34293, Montpellier Cedex 5, France
3Institute of Agricultural Sciences, ETH Zurich, Universitaetsstrasse 2, 8092, Zurich, Switzerland
4Friedrich Schiller University Jena, Institute of Geoscience, Burgweg 11, 07749 Jena, Germany
5Albert-Ludwigs-Universität Freiburg, Institut für Biologie II – Geobotanik, Schänzlestr. 1, D-79104 Freiburg, Germany
6UFZ, Helmholtz Centre for Environmental Research, Department Community of Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany
7Max Planck Institute for Biogeochemistry, Hans-Knoell-Str. 10, 07745, Jena, Germany
8Swiss Federal Research Institute WSL, Zürcherstr. 111, 8903 Birmensdorf, Switzerland
9Friedrich Schiller University Jena, Institute of Ecology, Dornburger Str. 159, 07743, Jena, Germany.
10Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany.

Corresponding author: Alexandru Milcu, CNRS, Ecotron - UPS 3248, Campus Baillarguet, 34980, Montferrier-sur-Lez, France, email: alex.milcu@cnrs.fr, phone: +33(0)467-613-243.
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 modelling approach. We aimed at (1) quantifying the impact of plant species richness (4 vs. 16 species) on day- and night-time 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. Day-time measured and modeled evapotranspiration were significantly higher in the higher 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 day-time. The results provide evidence that, at the peak of the growing season, higher 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.
Keywords: biodiversity-ecosystem functioning, evapotranspiration, functional traits, plant species richness, ecosystem evaporation, ecosystem transpiration, leaf area index, Shuttleworth and Wallace model, lysimeter, The Jena Experiment, Ecotron.

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-performant dominant species with increasing species richness, the complementarity hypothesis is asserting 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: (i) various forms of niche partitioning leading to complementary resource capture in space and time; or (ii) 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
their well-documented positive effect on biomass production and leaf surface area per ground area (the 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

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 took advantage of twelve 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, alongside species richness we also tested several predictors based on above- and belowground vegetation properties and functional trait-based indices (Appendix A). Specifically, we aimed at (1) quantifying the effect of plant diversity on day- and night-time 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 (4 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 (FDQ)].

MATERIALS AND METHODS

The Ecotron facility

The experiment was conducted in the Montpellier European Ecotron (http://www.ecotron.cnrs.fr), 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 tonnes) were located in 12 controlled environment units of the macrocosms 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 B for more information on the macrorocosms 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 (250µm thick Teflon-FEP film, DuPont, 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 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 to 60 species), plant functional groups (1 to 4, 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 (4 and 16 species) with six independent replicates per diversity level (Appendix C), 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 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 D 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-minute 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 night-time 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 also, as 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 E). This allowed achieving similar soil moisture conditions (Appendix F). 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 six days with undisturbed water vapor fluxes (28th of June to 3rd of July, 2012), the continuous environmental conditions (air RH, air temperature, VPD and radiation) during this period are presented in Fig. 1ab).
**Water vapor flux measurements**

Ecosystem ET was measured as lysimeter weight changes over time. Four shear beam load cells per lysimeter (CMI-C3, Precia-Molen, France), with an accuracy of ± 200 g, were used to measure the changes in weight. The raw weight 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) 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 weight 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 (28th of June to 3rd of July, 2012). This period was also close to the final harvest of the plant communities (17th-20th of 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\text{day}) and night-time (ET\text{night}) ecosystem evapotranspiration as well as the evapotranspiration over 24h (ET\text{24h}). For more information on the measurement and sampling methodology, see Milcu et al. (2014) and Appendix F.

**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 (a) for the top of the vegetation canopy, (b) for the soil surface below the canopy, and (c) for bare ground 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 F 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 bare ground (%bare-ground). The functional–trait based metrics included functional diversity indices (FD) and community weighted means (CWM) calculated from ten plant functional traits that have been previously shown to be linked to plant transpiration, photosynthetic rates and light interception (see Appendix A 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; µmol m⁻² s⁻¹), specific leaf area (SLA; mm² mg⁻¹), leaf
greenness (dimensionless measure of foliar chlorophyll content), leaf dry matter content (LDMC; mg g\(^{-1}\)), leaf N concentration (% N in leaf DW), species-specific plant height (cm) and specific leaf nitrogen (SLN; g N m\(^{-2}\) leaf). See Appendix D for further details on the sampling and procedure. 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 2010) available through the R (Team 2013) statistical package version 3.1.2.

**Statistical analyses**

Statistical analyses were performed in R (version 3.1.2.). T-tests were used to compare measured and modeled water vapor fluxes. 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 with 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 six days for each predictor as well as available soil texture-related covariates (see Appendix A) on the averaged water vapor fluxes of the selected six days. The resulting models were then simultaneously run through a model averaging procedure (dredge function in MuMIn package) which computes Akaike weights (AICw), 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 AICw ≤ 0.95) were
selected and simultaneously included in a multivariate linear fitting regression model using the R 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 AICc (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, 2b as averages for the two plant species richness levels. Although over 24h the modeled ET slightly underestimated the measured ET (Fig. 2c), when restricted to only day-time, the model agreed well with the measured data (Fig. 2d), with average day-time ET over six days within ± 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. T-tests based on average daily ET showed that there was no significant difference between measured and modeled day-time (t = -0.58, P = 0.568) and 24h ET (t = 1.33, P = 0.197).

As expected, modeled night-time evapotranspiration (ET$_{\text{night}}$) values were lower than day-time values (Fig. 2a). However, we found that the modeled ET$_{\text{night}}$ 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 discrepancy between the measured and modeled ET$_{\text{night}}$ is likely related to the controlled environment in the Ecotron (see Appendix F), we restricted the further assessment of the effect of species richness and functional diversity on the modeled T and E to day-time only.

Species richness effects
Measured day-time ecosystem evapotranspiration (ET\textsubscript{day}) was significantly higher in the lysimeters hosting monoliths from communities sown with 16 species relative to 4 species (+16.6% \(F_{1/10} = 0.049, \text{Fig. 2a}\)). This is also visible in Fig. 1c with exception of the last day after the rainfall/irrigation of 20mm. However, no significant difference in ET\textsubscript{day} was found between species richness during night-time (\(F_{1/20} = 0.25, P = 0.625\)), or when the ET was integrated over 24h (\(F_{1/10} = 2.84, P = 0.122, \text{Fig 2a}\)).

Modeled ET\textsubscript{day} was also significantly higher in the treatment with 16 species relative to 4 species richness (+14.5% \(F_{1/10} = 6.86, P = 0.026; \text{Fig. 3b}\)), a result in accordance with the measured results. Averaged over 24h, modeled ET was also significantly higher in the treatment 16 sown species richness (+14.6% \(F_{1/10} = 6.62, P = 0.028\), while no diversity effect was found for ET\textsubscript{night}.

Modeled ecosystem transpiration during day-time (T\textsubscript{day}), either expressed as fraction of the available energy (+65.2% \(F_{1/10} = 6.77, P = 0.026, \text{Fig. 2c}\) or mean water vapor loss per day (+68.4% \(F_{1/10} = 6.79, P = 0.026, \text{Fig. 2d}\)) was significantly higher in the monoliths with higher plant species richness (Table 1). Furthermore, T\textsubscript{day} correlated well with the total plant biomass at the final harvest (\(r^2 = 0.72, P < 0.001; \text{Fig. 3f}\)). In contrast, modeled day-time evaporation (E\textsubscript{day}) was significantly lower at high species richness expressed as both fraction of available energy (-22.2% \(F_{1/10} = 6.09, P = 0.033, \text{Fig. 2d}\)) and mean water vapor loss per day (-15.9% \(F_{1/10} = 6.45, P = 0.029, \text{Fig. 2d}\)). Consequently, the ratio of day-time ecosystem transpiration to evaporation (T\textsubscript{day}/E\textsubscript{day}) was also significantly affected by sown plant species richness, with a significantly higher ratio in the monoliths with 16 sown species (\(F_{1/10} = 7.28, P = 0.022, \text{Fig 2c}\)). The proportion of total energy dissipated as sensible heat flux (H\textsubscript{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\textsubscript{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\textsubscript{day}, E\textsubscript{day} and H\textsubscript{day}. Higher LAI also led to higher measured ET\textsubscript{24h} and ET\textsubscript{day} (Table 1). Alongside LAI, the percentage of bare ground was retained in the most parsimonious models for all of the modeled variables and influenced positively the E\textsubscript{day} and H\textsubscript{day} and negatively the T\textsubscript{day} and the T\textsubscript{day}/E\textsubscript{day} ratio.

The minimal adequate models for water vapor fluxes that directly focused on functional trait based metrics 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\textsubscript{Q-leafN\%}) stood out as a consistent predictor of ecosystem water vapor fluxes; increasing FD\textsubscript{Q-leafN\%} was correlated with an increase in measured and modeled fluxes. The relationships between FD\textsubscript{Q-leafN\%}, LAI, percentage bare ground and modeled daytime ecosystem transpiration (T\textsubscript{day}) are depicted in Figure 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 so far used in experiments...
addressing the role of biodiversity for ecosystem functioning. Here, we applied the SW model to plant communities of contrasting species richness (4 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 six days 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 the 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 experiment in the Ecotron showing a 37.6% increase in water use efficiency in
communities with 16 plant species relative to 4 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 filed site from where the soil monoliths of our study have been 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) fund 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 ET in 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 calibrated/ 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%) predicted best the water vapor fluxes and was strongly correlated to the LAI (Fig. 4). Moreover, it was a better predictor of measured day-time 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 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 day-time, at least at the peak at the growing season. More novel, 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 day-time 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 $T_{\text{day}}$ 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 (Seneviratne et al. 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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References


Tables: 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. ET$_{24h}$, ET$_{day}$ and ET$_{night}$ represent lysimeter measured evapotranspiration values during 24h, day-time and night-time, respectively. T$_{day}$, E$_{day}$ and H$_{day}$ represent the day-time transpiration, evaporation and sensible heat flux, respectively. Vegetation properties (LAI = leaf area index, Bare = % bare ground, hrGR = biomass of grasses) and functional trait-based predictors (FDQ-leafN% = diversity of leaf N concentration, CWM-height = community weighted means of species height) were separately analyzed in different models. Non-significant effects are marked as “ns”. See Appendix A for the list of all predictors included in the initial models before the AICc-based model simplification.

<table>
<thead>
<tr>
<th>Response variables</th>
<th>Sdiv (ANOVA)</th>
<th>Best model based on canopy, root and soil texture</th>
<th>Best model based on functional-trait predictors</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Measured</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ET$_{24h}$</td>
<td>ns</td>
<td>2.788 + 0.342*LAI</td>
<td>ns</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P &lt; 0.001, $r^2 = 0.78$</td>
<td></td>
</tr>
<tr>
<td>ET$_{day}$</td>
<td>P = 0.049</td>
<td>2.138 + 0.344*LAI</td>
<td>2.46 + 0.67*FDQ-leafN%</td>
</tr>
<tr>
<td></td>
<td>$r^2 = 0.34$</td>
<td>P &lt; 0.001, $r^2 = 0.93$</td>
<td>P = 0.015, $r^2 = 0.46$</td>
</tr>
<tr>
<td>ET$_{night}$</td>
<td>ns</td>
<td>0.700 - 0.002*grBM</td>
<td>0.883 - 0.111*CWM-height</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P = 0.094, $r^2 = 0.26$</td>
<td>P = 0.015, $r^2 = 0.46$</td>
</tr>
<tr>
<td><strong>Modeled</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T$_{day}$</td>
<td>P = 0.026</td>
<td>1.109 + 0.28<em>LAI – 0.017</em>Bare</td>
<td>0.893 + 0.918*FDQ-leafN%</td>
</tr>
<tr>
<td></td>
<td>$r^2 = 0.40$</td>
<td>P &lt; 0.001, $r^2 = 0.99$</td>
<td>P = 0.040, $r^2 = 0.36$</td>
</tr>
<tr>
<td>E$_{day}$</td>
<td>P = 0.029</td>
<td>1.642 – 0.101<em>LAI + 0.006</em>Bare</td>
<td>1.706 – 0.295*FDQ-leafN%</td>
</tr>
<tr>
<td></td>
<td>$r^2 = 0.39$</td>
<td>P &lt; 0.001; $r^2 = 0.97$,</td>
<td>P = 0.076, $r^2 = 0.29$</td>
</tr>
<tr>
<td>T$<em>{day}$/E$</em>{day}$</td>
<td>P = 0.022</td>
<td>0.597 + 0.276<em>LAI – 0.011</em>Bare</td>
<td>0.541 + 0.769*FDQ-leafN</td>
</tr>
<tr>
<td></td>
<td>$r^2 = 0.42$</td>
<td>P &lt; 0.001, $r^2 = 0.99$</td>
<td>P = 0.034, $r^2 = 0.37$</td>
</tr>
<tr>
<td>H$_{day}$</td>
<td>P = 0.022</td>
<td>0.319 – 0.032<em>LAI + 0.002</em>Bare</td>
<td>0.357 – 0.111*FDQ-leafN%</td>
</tr>
<tr>
<td></td>
<td>$r^2 = 0.42$</td>
<td>P &lt; 0.001, $r^2 = 0.98$</td>
<td>P = 0.054, $r^2 = 0.32$</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. (a) Ecotron environmental conditions during the selected six days averaged for the two plant diversity levels (4 vs. 16 species). RH represents the air relative humidity and VPD the vapor pressure deficit. (b) Lysimeter measured evapotranspiration (ET) in the Ecotron.

Figure 2. Time trace of ecosystem evaporation (E) and transpiration (T) fluxes as modeled by the SW model in (a) communities with 16 and (b) 4 plant species. T (grey area) and E (black area) are plotted additively so that their sum represents total ET. Comparison of averaged modeled and lysimeter ET with (c) and without (d) night-time values.

Figure 3. Plant diversity (4 vs. 16 species) effects on day-time, night-time and 24h 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. (e) LAI and plant diversity effects on modeled E (squares), T (circles) and H (triangles). (f) Relationship between modeled day-time T and plant biomass.

Figure 4. Scatterplot and correlation matrix depicting the relationships between the most important predictors (FDQ-leafN% = diversity of leaf N concentration, LAI, % 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.
Figure 1

(a) Air RH [%] and Temperature

(b) Radiation [W m⁻²] and VPD [kPa]

(c) Measured ET [mm 12 min⁻¹]

Day of the year
Figure 2
Figure 3

(a) Measured Evapotranspiration [mm]

Day-time: 4 species
Night-time: 16 species

P = 0.049

ns

(b) Modeled Evapotranspiration [mm]

Day-time

P = 0.026

Night-time

P = 0.028

(c) Modeled Fraction of available energy

T: P = 0.026
E: P = 0.036
H: P = 0.022

(d) Modeled Day-time water flux [mm]

P = 0.026

P = 0.029

(e) Modeled Fraction of available energy vs. LAI

T: r² = 0.95
E: r² = 0.96
H: r² = 0.93

(f) Modeled Total biomass [g DW m⁻²] vs. Modeled day-time T [mm]

r² = 0.72
Figure 4
Appendices (A to F)

Appendix A. Overview table presenting the mean ± 1*SD of the tested predictors and covariates for the two levels of sown species richness. FDQ abbreviation indicates a functional diversity index estimated using Rao’s quadratic entropy index (Botta Dukát 2005). CMW indicates a community weighted means estimated for the respective functional trait.

<table>
<thead>
<tr>
<th>Functional trait-based metrics</th>
<th>Description</th>
<th>Type of trait / source</th>
<th>Unit</th>
<th>4 species (mean ± SD)</th>
<th>16 species (mean±SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FDQ-leafN%</td>
<td>based on leaf N%</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.40 ± 0.28</td>
<td>0.79 ± 0.42</td>
</tr>
<tr>
<td>CWM-leafN%</td>
<td>based on leaf N%</td>
<td>continuous / measured in situ</td>
<td>mg N g⁻¹ leaf DW</td>
<td>2.55 ± 0.67</td>
<td>2.36 ± 0.35</td>
</tr>
<tr>
<td>FDQ-SLN</td>
<td>based on N specific leaf area</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.17 ± 0.25</td>
<td>0.54 ± 0.34</td>
</tr>
<tr>
<td>CWM-SLN</td>
<td>based on N specific leaf</td>
<td>continuous / measured in situ</td>
<td>g N m⁻² leaf</td>
<td>1.50 ± 0.25</td>
<td>1.26 ± 0.34</td>
</tr>
<tr>
<td>FDQ-SLA</td>
<td>based on specific leaf area</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.14 ± 0.14</td>
<td>0.49 ± 0.22</td>
</tr>
<tr>
<td>CWM-SLA</td>
<td>based on specific leaf area</td>
<td>continuous / measured in situ</td>
<td>g N m⁻² leaf</td>
<td>16.91 ± 2.25</td>
<td>19.77 ± 2.77</td>
</tr>
<tr>
<td>FDQ-GS</td>
<td>based on stomatal conductance</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.57 ± 0.72</td>
<td>0.77 ± 0.67</td>
</tr>
<tr>
<td>CWM-GS</td>
<td>based on stomatal conductance</td>
<td>continuous / measured in situ</td>
<td>µmol m⁻² s⁻¹</td>
<td>469 ± 155</td>
<td>557 ± 167</td>
</tr>
<tr>
<td>FDQ-greenness</td>
<td>based on leaf greenness</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.16 ± 0.24</td>
<td>0.60 ± 0.29</td>
</tr>
<tr>
<td>CWM-greenness</td>
<td>based on leaf greenness</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>37.56 ± 7.36</td>
<td>34.86 ± 3.41</td>
</tr>
<tr>
<td>FDQ-LDMC</td>
<td>based on leaf dry matter content</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.42 ± 0.30</td>
<td>0.92 ± 0.35</td>
</tr>
<tr>
<td>CWM-LDMC</td>
<td>based on leaf dry matter content</td>
<td>continuous / measured in situ</td>
<td>mg g⁻¹</td>
<td>231.55 ± 41.38</td>
<td>229.38 ± 31.47</td>
</tr>
<tr>
<td>FDQ-height</td>
<td>based on recorded species height</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>0.25 ± 0.35</td>
<td>0.58 ± 0.50</td>
</tr>
<tr>
<td>CWM-height</td>
<td>based on recorded species height</td>
<td>continuous / measured in situ</td>
<td>cm</td>
<td>15.7 ± 10.48</td>
<td>16.6 ± 4.02</td>
</tr>
<tr>
<td>FDQ-rootdepth</td>
<td>based on rooting depth</td>
<td>continuous / literature</td>
<td>dimensionless</td>
<td>0.73 ± 0.88</td>
<td>0.67 ± 0.56</td>
</tr>
<tr>
<td>CWM-rootdepth</td>
<td>based on rooting depth</td>
<td>continuous / literature</td>
<td>cm</td>
<td>3.51 ± 0.74</td>
<td>3.70 ± 0.35</td>
</tr>
<tr>
<td>FDQ-typeroot</td>
<td>based on rooting type</td>
<td>ordinal / literature</td>
<td>dimensionless</td>
<td>0.40 ± 0.17</td>
<td>0.74 ± 0.32</td>
</tr>
<tr>
<td>CWM-typeroot</td>
<td>based on rooting type</td>
<td>ordinal / literature</td>
<td>NA</td>
<td>2.55 ± 0.30</td>
<td>2.37 ± 0.31</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Type of variable / source</td>
<td>source</td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------</td>
<td>------------------------------------------</td>
<td>---------------------------------</td>
<td>--------------</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td><strong>FDQ-leaf</strong></td>
<td>based on all six leaf related traits</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>2.05 ± 1.15</td>
<td>4.77 ± 1.76</td>
</tr>
<tr>
<td><strong>FDQ-all</strong></td>
<td>based on all ten functional traits</td>
<td>continuous and ordinal / in situ</td>
<td>dimensionless</td>
<td>3.44 ± 1.73</td>
<td>6.77 ± 2.41</td>
</tr>
<tr>
<td><strong>Vegetation properties</strong></td>
<td><strong>Description</strong></td>
<td><strong>Type of variable / source</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sdiv</td>
<td>sown species richness</td>
<td>categorical (4 and 16 species) / in situ</td>
<td>counts</td>
<td>4 ± 0</td>
<td>16 ± 0</td>
</tr>
<tr>
<td>Rdiv</td>
<td>realized species richness at July harvest</td>
<td>counts / measured in situ</td>
<td>counts</td>
<td>3.16 ± 0.75</td>
<td>11.3 ± 1.5</td>
</tr>
<tr>
<td>LAI</td>
<td>leaf area index</td>
<td>continuous / measured in situ</td>
<td>dimensionless</td>
<td>1.46 ± 0.97</td>
<td>2.78 ± 0.84</td>
</tr>
<tr>
<td>%bare</td>
<td>percentage bare ground</td>
<td>percentage / measured in situ</td>
<td>%</td>
<td>26.83 ± 20.50</td>
<td>6.25 ± 9.23</td>
</tr>
<tr>
<td>ShootBM</td>
<td>shoot biomass</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>148.71 ± 61.07</td>
<td>193.01 ± 43.31</td>
</tr>
<tr>
<td>RootBM</td>
<td>total root biomass</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>100.52 ± 39.87</td>
<td>154.07 ± 37.77</td>
</tr>
<tr>
<td>RootBM/L</td>
<td>root biomass per layer (0-5, 5-10, 10-20, 20-30, 30-40, 40-60cm)</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>layer dependent</td>
<td>layer dependent</td>
</tr>
<tr>
<td>RootS/V</td>
<td>root surface per volume soil (by layer)</td>
<td>continuous / measured in situ</td>
<td>cm²/cm³</td>
<td>layer dependent</td>
<td>layer dependent</td>
</tr>
<tr>
<td>TotalBM</td>
<td>total biomass (shoot + root biomass)</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>249.24 ± 93.34</td>
<td>347.08 ± 55.75</td>
</tr>
<tr>
<td>LegBM</td>
<td>biomass of legumes</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>18.24 ± 24.65</td>
<td>42.86 ± 40.27</td>
</tr>
<tr>
<td>Leaf biomass</td>
<td>biomass of leaves</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>93.89 ± 50.93</td>
<td>124.21 ± 28.62</td>
</tr>
<tr>
<td>Leaf-to-ShootBM-ratio</td>
<td>ratio of leaf to shoot biomass</td>
<td>ratio / measured in situ</td>
<td>dimensionless</td>
<td>0.63 ± 0.14</td>
<td>0.67 ± 0.09</td>
</tr>
<tr>
<td>HerBM</td>
<td>biomass of herbs</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>83.15 ± 71.47</td>
<td>95.58 ± 54.15</td>
</tr>
<tr>
<td>GraBM</td>
<td>biomass of grasses</td>
<td>continuous / measured in situ</td>
<td>g DW m⁻²</td>
<td>34.12 ± 61.66</td>
<td>36.81 ± 52.14</td>
</tr>
<tr>
<td><strong>Covariates</strong></td>
<td><strong>Description</strong></td>
<td><strong>Type of variable / source</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil sand %</td>
<td>soil sand content at 0-20 cm depth</td>
<td>percentage / measured in situ</td>
<td>%</td>
<td>21.16 ± 17.63</td>
<td>17.87 ± 15.89</td>
</tr>
<tr>
<td>Soil clay %</td>
<td>soil clay content at 0-20 cm depth</td>
<td>percentage / measured in situ</td>
<td>%</td>
<td>26.09 ± 7.09</td>
<td>24.42 ± 6.25</td>
</tr>
<tr>
<td>Soil silt %</td>
<td>soil silt content at 0-20 cm depth</td>
<td>percentage / measured in situ</td>
<td>%</td>
<td>52.74 ± 10.94</td>
<td>57.70 ± 12.28</td>
</tr>
</tbody>
</table>
Appendix B. Top image: simplified schematic of one controlled environment unit (macrocosm) of the CNRS Ecotron facility. Red arrows represent the direction of airflow (image by Marc Saubion). Bottom image: closeup of the vegetation from dome no. 1 at the July harvest (photo by Alexandru Milcu).
### Appendix C

Table with sown species richness (Sdiv) and functional group (G = grasses, H = herbs and L = legumes) composition of the twelve selected plots from the Jena Experiment. The species present at the final harvest are marked in bold.

<table>
<thead>
<tr>
<th>Plot ID</th>
<th>Sdiv</th>
<th>G</th>
<th>H</th>
<th>L</th>
<th>Species composition</th>
<th>Ecotron dome</th>
</tr>
</thead>
<tbody>
<tr>
<td>B2A22</td>
<td>16</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>(Cc, Fp, Tf, Pp, Pt, Cj, Ra, So, Am, CAp, Th, Lc, Vlc, Tr, Lp, Ov)</td>
<td>1</td>
</tr>
<tr>
<td>B4A04</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>(Ae, Pl, As, Tc)</td>
<td>2</td>
</tr>
<tr>
<td>B1A01</td>
<td>16</td>
<td>4</td>
<td>8</td>
<td>4</td>
<td>(AVp, Pp, Ao, Bh, Pl, To, Ar, Rr, As, Gp, TRp, CAc, Tc, Vlc, Lp, Lc)</td>
<td>3</td>
</tr>
<tr>
<td>B1A04</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>(Fp, Pl, CAp, Ov)</td>
<td>4</td>
</tr>
<tr>
<td>B3A23</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>(Bh, Rr, Lc, TRf)</td>
<td>5</td>
</tr>
<tr>
<td>B2A18</td>
<td>16</td>
<td>4</td>
<td>8</td>
<td>4</td>
<td>(Ap, Bh, Pp, Cc, Rr, Pm, Ar, Pv, CAp, Gp, As, Cp, Ml, Tr, Td, Tc)</td>
<td>6</td>
</tr>
<tr>
<td>B4A18</td>
<td>16</td>
<td>4</td>
<td>8</td>
<td>4</td>
<td>(Cc, LUC, Ap, Bh, La, Pm, Vc, To, Ch, CAc, Plm, Hs, Th, Tc, Lp, Ov)</td>
<td>7</td>
</tr>
<tr>
<td>B2A01</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>(Ao, Pv, Ka, Tp)</td>
<td>8</td>
</tr>
<tr>
<td>B3A22</td>
<td>16</td>
<td>4</td>
<td>8</td>
<td>4</td>
<td>(PHp, Fr, Ao, Be, Rr, Ar, Bp, Vc, Gp, Cb, Ra, Gm, Vlc, Ov, TRf, Td)</td>
<td>9</td>
</tr>
<tr>
<td>B2A16</td>
<td>4</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>(Pm, La, Ka, Vlc)</td>
<td>10</td>
</tr>
<tr>
<td>B3A24</td>
<td>16</td>
<td>6</td>
<td>5</td>
<td>5</td>
<td>(Fp, Bh, Ap, Ao, Pt, Ae, To, Rr, Ar, Pv, Gh, Lc, Tp, Tr, Vlc, Ms)</td>
<td>11</td>
</tr>
<tr>
<td>B4A11</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>(Tf, TRp, Hs, Ms)</td>
<td>12</td>
</tr>
</tbody>
</table>

**Grasses (G):** \(Ae = Arrhenatherum elatius\) L. (J. et C. PRESL), \(Ao = Anthoxantum odoratum\) L., \(Ap = Alopecurus pratensis\) L., \(AVp = Avenula pubescens\) HUDS. (DUM.), \(Be = Bromus erectus\) HUDS., \(Bh = Bromus hordeaceus\) L., \(Cc = Cynosurus cristatus\) L., \(Dg = Dactylis glomerata\) L., \(Fp = Festuca pratensis\) HUDS., \(Fr = Festuca rubra\) L., \(HL = Holcus lanatus\) L., \(Lc = Luzula campestris\) (DC.), \(PHp = Phleum pratense\) L., \(Pp = Poa pratensis\) L., \(Pt = Poa trivialis\) L., \(Tf = Trisetum flavescens\) L. (P. BEAUV.);

**Herbs (H):** \(Am = Achillea millefolium\) L., \(Bp = Bellis perennis\) L., \(Cb = Crepis benis\) L., \(CAc = Carum carvi\) L., \(CAp = Campanula patula\) L., \(Cj = Centaurea jacea\) L., \(Co = Cirsiun oleraceum\) L., \(Cp = Cardamine pratensis\) L., \(Dc = Daucus carota\) L., \(Gm = Galium mollugo\) L., \(Gh = Glechoma hederacea\) L., \(Hs = Heracleum spondylium\) L., \(Ka = Knautia arvensis\) L., \(La = Leontodon autumnalis\) L., \(Lh = Leontodon hispidus\) L., \(Lv = Leucanthemum vulgare\) Lam., \(Plm = Pimpinella major\) L. (HUDS.), \(Pl = Plantago lanceolata\) L., \(Pm = Plantago media\) L., \(PRv = Primula veris\) L., \(Pv = Prunella vulgaris\) L., \(Ra = Rumex acetosa\) L., \(To = Taraxacum officinale\) WEBER, \(TRp = Tragopogon pratensis\) L., \(Vc = Veronica chamaedrys\) L;

**Legumes (L):** \(Lp = Lathyrus pratensis\) L., \(Lc = Lotus corniculatus\) L., \(Ml = Medicago lupulina\) L., \(Ms = Medicago x varia\) MARTYN, \(Ov = Onobrychis viciifolia\) SCOP., \(Td = Trifolium dubium\) SIBTH., \(TRf = Trifolium fragiferum\) L., \(Th = Trifolium hybridum\) L., \(Tr = Trifolium repens\) L., \(Tp = Trifolium pratense\) L., \(Vlc = Vicia cracca\) L.
Appendix D. Comparison of cumulative precipitation (mm) recorded in the “Jena Experiment” field site in 2007 and simulated in the Ecotron in 2012.
Appendix E. Comparison of the soil moisture achieved in the Ecotron and the “Jena Experiment” field site in 2007 at similar depths for the period with available Ecotron data form 2012.
Appendix F - Supplementary Methods

Extraction of soil monoliths

Soil monoliths were extracted by UMS GMBH (München, Germany) following a proprietary non-compacting extraction method. Using a hydraulic press, steel cylinders with cutting edges were pressed down to 2 m depth (to include the average depth of the water table in summer known from previous hydrological field investigations) while simultaneously digging out the soil 60 cm around the cylinder. The created space around the cylinders allowed to cut the bottom of the soil monolith and to insert a sealing plate in order to be able to lift the monolith and to create a water tight container/ lysimeter. The lysimeters were then extracted with a crane, and after inspection, were buried to the surface level near the experimental field after extraction in order to facilitate the recovery after the extraction disturbance, while being exposed to the same environmental conditions as the field plots. At the end of March 2012 the lysimeters were transported to the Ecotron facility in Montpellier.

Measurements of environmental variables

Air temperature and relative humidity were measured with the DT269 digital sensor (Michell Instruments Ltd, Ely, UK). The soil moisture was measured with a Trime-Pico 32 time domain reflectometry sensor (IMKO GmbH, Ettlingen, Germany). Solar radiation was measured with a BF5 Sunshine Sensor (Delta-T Devices, Cambridge, UK).

Sampling methodology

Shoot biomass was estimated by clipping the vegetation at ground level in a rectangle of 0.8 x 1.0 m per plot and drying at 65°C for three days. Root biomass was estimated from three cores of 3.5 cm diameter and 60 cm depth. The soil cores were separated into six layers (0-5, 5-10, 10-20, 20-30 and 40-60cm) before they were pooled per layer, washed with tap water and dried following the same procedure as for shoot biomass. Leaf area index (LAI) was estimated using a portable LAI-2000 plant canopy analyzer (LI-COR, Lincoln, USA). LAI was measured in the evening under diffused light conditions with one measurement above the canopy as a reference.
and the average of five measurements near ground level positioned at different places in the
center of each lysimeter. The zenith angle was restricted to 0-43\(^\circ\) in order to minimize the edge
effect (Hyer and Goetz 2004) inherent to a canopy with a surface of 2m\(^2\). In lysimeters with a
high proportion of one rosulate species (\textit{Plantago media}) with leaves laying very close to the
ground, the values measured with the LAI-2000 were replaced with the average value of two leaf
area measurements using a LI-3100 leaf area meter (LI-COR, Lincoln, USA) leaf area meter)
from two rectangles of 0.2 \times 0.5 m per plot. Percentage vegetation cover and bare ground as well
species specific percentage cover were visually estimated for the whole lysimeter (2 m\(^2\)).

Stomatal conductance was measured at midday using a portable porometer (SC-1 Leaf
porometer, Decagon Devices, Pullman, USA). Leaf greenness was estimated with a hand-held
chlorophyll meter (SPAD-502, Konica-Minolta, Osaka, Japan), which enables non-destructive
assessment of leaf greenness by measuring the absorbance by the leaf of two different
wavelengths (650 nm and 940 nm). The SPAD values were calibrated \(r^2 = 0.69\) against
spectrophotometrically determined chlorophyll concentrations from leaf extracts following the
method of Moran (1982). Leaf dry mater content (LDMC) is defined as the ratio of leaf dry mass
to saturated fresh mass according to Vile et al. (2005). LDMC was determined with the partial
rehydration method following the protocol of Wilson et al. (1999). Samples were put sealed
plastic bags promoting rehydration by storing leaves overnight between sheets of moistened
tissue paper. Then, samples were blotted dry using tissue paper to remove any surface water and
immediately weighed. Samples were oven-dried (65°C, 3 days) and reweighed to get values for
dry mass. This procedure gives a good approximation in comparison to the complete rehydration
method (Vaieretti et al. 2007).

\textit{The Shuttleworth and Wallace model}

Evaporation and transpiration were modeled with the approach by Shuttleworth and Wallace
(1985). This approach is a further development of the Penman-Monteith model,

\[
\lambda E_x = \frac{\Delta \cdot (Rn_x - G') + c_p \cdot \rho_a \cdot \frac{e_{sat} \cdot x - e_x}{r_a^x}}{\Delta + \gamma \cdot \frac{r_a^x + r_s^x}{\rho_a^x}},
\]  

(1)
where \( x \) denotes the plant canopy compartment of interest. \( \lambda_{E_x} \) is parameterised once for the canopy top (\( \lambda_{E_c} \)), once for the soil surface below canopy (\( \lambda_{E_s} \)), and once for the fraction of bare soil not covered by the canopy (\( \lambda_{E_b} \)). Total evapotranspiration \( \lambda E \) is expressed as the sum of transpiration from the plant canopy and evaporation from the soil weighted by their respective surface cover fractions \( f_c, f_s \) and \( f_b, \lambda E = f_c\lambda_{E_c} + f_s\lambda_{E_s} + f_b\lambda_{E_b} \), with \( f_s = f_c \), and \( f_c = 1–f_b \). Thus, transpiration \( T = \lambda_{E_c} \) and evaporation \( E = \lambda_{E_s} + \lambda_{E_b} \). \( R_n \) is net radiation (at canopy top \( R_{n_c} \) or soil surface \( R_{n_s} \)), \( G \) is ground heat flux, \( \Delta \) is the mean rate of change of saturated vapor pressure with temperature, \( \gamma \) is the psychrometric constant, \( c_p \) is specific heat at constant pressure \( (1005.5 \text{ J kg}^{-1} \text{ K}^{-1}) \), \( \rho_a \) is the density of air, \( e \) and \( e_{\text{sat}} \) are the actual and saturation vapor pressure, and \( r_a \) and \( r_s \) are aerodynamic and surface (stomatal) resistances, respectively.

We used the mass flux of water vapor in our analysis, which is the simple conversion from energy flux densities modeled by the Shuttleworth and Wallace (1985) model to mass flux densities, with plant transpiration \( T = \lambda_{E_c}/L_v \), and soil evaporation \( E = \lambda_{E_s}/L_v \), with \( L_v \) being the latent heat of vaporisation \( (L_v = 2.501\cdot10^8 – 2370\cdot T_{\text{air}} \text{ J kg}^{-1}) \). Saturation vaporpressure \( e_{\text{sat}} \) was determined via the Magnus equation for nonfreezing conditions at air temperature \( T_{\text{air}} \) measured in °C in each dome \( (e_{\text{sat}} = 610.7\times 10^{7.5T_{\text{air}}/(235+T_{\text{air}})}, \text{ in Pa}) \), and actual vapor pressure \( e=RH/100\cdot e_{\text{sat}} \), with relative humidity \( RH \) in %. Density of air was computed from \( T_{\text{air}} \) and atmospheric pressure \( P \) [in Pa], \( \rho_a = P/(T_{\text{air}}+273.15)/R \), with the gas constant for dry air \( R = 287.05 \text{ J kg}^{-1} \text{ K}^{-1} \). \( \Delta \) was approximated as \( L_v\cdot e_{\text{sat}}/R_v/(T_{\text{air}}+273.15)^2 \) with the gas constant for water vapor \( R_v = 461.5 \text{ J kg}^{-1} \text{ K}^{-1} \).

The key parameters used to model \( \lambda_{E_c}, \lambda_{E_s} \) and \( \lambda_{E_b} \) are the short-wave albedo of canopy \( (\alpha_c) \) and bare soil \( (\alpha_s = \alpha_b) \), the fractions of vegetated \( (f_c) \) and unvegetated \( (f_s) \) ground surface, the wind speed above the canopy \( (u) \), the fraction of that wind speed observed in mid-canopy \( (\xi_c) \) and at the ground surface \( (\xi_s, \xi_b) \); where soil evaporation takes place; we assumed that \( \xi_b = \xi_c \), but \( \xi_s \ll \xi_c \), and the soil surface resistance \( (r_s) \). The albedo was used to compute \( R_n \) from available global radiation \( (R_g) \) measurements as \( R_n = (1–\alpha) R_g \). It was assumed that 10% of \( R_n \) is dissipated to \( G \) under a vegetation canopy, and 30% on the bare-soil component. Since...
experiments were done inside a controlled environment facility, we assumed that the dome temperature is not very different from the soil temperature and thus the net longwave component of Rn is negligible.

The stomatal resistance of plants ($r_s^c$) was modeled according to Wesely (1989) and Erisman et al. (1994),

$$r_s^c = r_i \cdot \left[ 1 + \left( \frac{200}{Rg + 0.1} \right)^2 \right] \cdot \left[ \frac{400}{T_s(40 - T_s)} \right],$$

where $r_i$, the minimal stomatal resistance, and $T_s$, leaf surface temperature in °C in the range 0–40°C. The values for $r_i$ were determined from $r_s^c$ measurements carried out for each relevant species of each dome at midday (see sampling methodology). The weighted average of $r_s^c$ was used to parameterize $r_i$. Weighting was by the proportion of leaf biomass of each plant species, individually for each of the twelve plant communities.

Wind speed posed some challenges since the conditions in the domes of the Ecotron facility do not represent the typical relationships between horizontal wind speed and mechanical turbulence as the Penman-Monteith model implicitly assumed. The air condition systems of the Ecotron’s domes created a turbulent environment, where wind speed varied between between 0.7–2.5 m s$^{-1}$ in a fraction of a second, and with averaged (during a few seconds) anemometer readings (Almemo 2890-9, Coalville, UK) of 0.9-1 m s$^{-1}$. Video records however clearly showed that the turbulent motion of the plants in the domes rather corresponded to the turbulence observed at a higher wind speed. Hence, horizontal wind speed was set to 2 m s$^{-1}$. The wind speed above bare soil patches was set to the value specified above plant canopies. Wind speed inside the canopy at mid-height was set to 35% of the above-canopy wind speed, and the wind speed at ground level inside the plant canopy was set to 4%. These optimum values were determined iteratively via minimization of deviations of the total ET from lysimeter measurements (nonlinear least-squares fitting procedure).

While the parameters in the physically-based model by Shuttleworth and Wallace (1985) are given, the search for the best model fit to experimental data obtained from the lysimeters in each Ecotron unit was done with an iterative least squares fitting procedure to find best parameter estimates for which no measurements were available. The free parameters for which
best estimates were searched for were: albedo of the plant canopy; albedo of the bare soil fraction; relative proportion of available energy partitioned to ground heat flux under plant canopy and on the bare soil part; fraction of above-canopy wind speed inside the plant canopy and at the ground surface (a) below plants and (b) over the bare soil fraction; soil surface resistance against evaporation. This procedure was however partially restricted to not overfit the model in such a way that one parameter estimate was searched for all twelve Ecotron domes/experimental units to not introduce artificial differences between the domes for parameters that conceptually should be the same in the Shuttleworth and Wallace (1985) model for all of the Ecotron’s domes. To model E and T separately with the SW model, additional model parameters were introduced to characterize the canopy structure and plant species specific contributions to T, which were quantified using the best available empirical measurements (see below). Where no direct measurements were available (soil resistance to evaporation, wind speed, albedo of plants and of soil), a best estimate for the respective model parameter was made under the premise that the Ecotron provides controlled conditions and hence the same parameter estimate can be used for all replicates. Since the soil monoliths stem from the same soil extracted from the Jena experiment, we argue that this assumption is justified, but acknowledge that it does not include potential indirect feedbacks to soil density and structure.

There are intrinsic limitations in the simulation of the night-time environmental conditions in the Ecotron. The intensive air mixing of the atmosphere in the domes prevents night-time stratification of air, which means that the air, soil surface and the soil will quickly arrive at similar temperatures. In a natural setting however, the soil surface would be considerably cooler than the soil below or the atmosphere above, which would reduce evaporation from the cool nocturnal soil surface. In addition, due to the air-humidifying system, the air relative humidity during night-time was limited at 65% which may increase evaporation in the Ecotron. Presumably, these limitations explain the discrepancy between the modeled and measured night-time ET. However, the day-time evaporative flux is the predominant component of water vapor loss over 24h since the night-time fluxes typically represent only 10-15% (Caird et al. 2007) of day-time fluxes. Therefore, we restricted our analyses of plant diversity effects on the modeled E and T for the day-time period where the environmental conditions simulated in the Ecotron match closely the field conditions at the “Jena Biodiversity Experiment” site. In
addition, there was good agreement between the day-time measured and modeled ET (see results).

**Supplementary References**


