

Tree diversity does not always improve resistance of forest ecosystems to drought

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Climate models predict an increase in the intensity and frequency of drought episodes in the Northern Hemisphere. Among terrestrial ecosystems, forests will be profoundly impacted by drier climatic conditions, with drastic consequences for the functions and services they supply. Simultaneously, biodiversity is known to support a wide range of forest ecosystem functions and services. However, whether biodiversity also improves the resistance of these ecosystems to drought remains unclear. We compared soil drought exposure levels in a total of 160 forest stands within five major forest types across Europe along a gradient of tree species diversity. We assessed soil drought exposure in each forest stand by calculating the stand-level increase in carbon isotope composition of late wood from a wet to a dry year ($\Delta\delta^{13}C_s$). $\Delta\delta^{13}C_s$ exhibited a negative linear relationship with tree species diversity in two forest types, suggesting that species interactions in these forests diminished the drought exposure of the ecosystem. However, the other three forest types were unaffected by tree species diversity. We conclude that higher diversity enhances resistance to drought events only in drought-prone environments. Managing forest ecosystems for high tree species diversity does not necessarily assure improved adaptability to the more severe and frequent drought events predicted for the future.

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Biodiversity plays an important role in ecosystem functioning by promoting a wide range of functions and services (1–3). This beneficial effect of biodiversity is determined by mechanistic processes directly under the influence of species interactions: complementarity among species for resource use through ecological niche partitioning and/or facilitation processes increase ecosystem performance because resources are better shared among neighboring species and are thus potentially more available (4). Previous studies have demonstrated that, apart from enhancing performance, diverse terrestrial ecosystems may also be more resilient and more resistant to biotic stresses such as insect pests or diseases (5, 6). However, it remains unclear whether higher biodiversity also leads to improved resistance of terrestrial ecosystems to the more frequent droughts expected in temperate regions (7). The rare case studies published thus far have shown contrasting results. Two reported that species in more diverse ecosystems could be more resistant to drought stress (8, 9), whereas another suggested that enhanced biodiversity could trigger higher exposure to drought (10). Improving our understanding of how species diversity influences the resistance of terrestrial ecosystems to a fluctuating climate is crucial.

More frequent and intense droughts will greatly affect the carbon and water cycles of the terrestrial biosphere (11), in particular in forested ecosystems (12). Many societies around the world rely on forests for essential services such as wood production, hunting, or watershed protection. We therefore urgently need to improve our knowledge of the physiological response of these ecosystems to drier climatic conditions to propose new climate-smart management options. Forests, although influenced by local environmental conditions, play a major role in the global carbon and water balance as they release into and assimilate from the atmosphere huge amounts of CO₂ while losing water vapor through transpiration. Tree species are known to vary widely in the ecological strategies they use to deal with drought stress. It could therefore be expected that in highly diverse forests composed of tree species with contrasting functional traits, limited water resources could be better partitioned among the neighboring species as a result of complementarity and facilitation processes (4). Such forests should be more resistant to deal with drought stress because the trees should be able to maintain better access to diminishing water resources as the drought

Significance

In the context of climate change, expected drier and warmer environmental conditions will have drastic consequences on forest functions and services and may bring about important drought-induced die-off events. Biodiversity promotes forest ecosystem performance and resistance to insect pests and diseases, but whether or not diverse forests are also better adapted to deal with drought stress remains unknown. Within our study network of 160 forest stands across Europe, we found that mixed species forests are less exposed to drought stress in some regions only. Therefore, managing forest ecosystems for high tree species diversity does not necessarily assure improved resistance to the more severe and frequent drought events predicted for the future.

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progresses. In contrast, if the interacting species in a diverse forest have similar functional traits (i.e., functional redundancy), ecological niche overlap (13) may lead to more stressful conditions during drought than in pure stands due to lower water availability for each species.

Carbon isotope composition in C_3 plant tissues ($\delta^{13}C$) provides an integrated record of the ratio of intercellular to atmospheric CO_2 concentrations during the period when the carbon was fixed and thus reflects the balance between net CO_2 assimilation and stomatal conductance (14). Plants typically react toward drought stress by closing their stomata and reducing carbon assimilation rates. However, leaf stomatal conductance is affected to a greater extent than assimilation, causing a concomitant increase in $\delta^{13}C$ (14, 15). Therefore, under soil drought conditions, $\delta^{13}C$ from organic material has been widely accepted as an indicator of the intensity of drought exposure in plants (16, 17) (*SI Text*). If complementarity for water use is occurring among species, $\delta^{13}C$ values should increase less between wet and dry soil conditions with increasing tree species diversity (i.e., a negative relationship). Inversely, if tree species occupy redundant ecological niches, $\delta^{13}C$ values should either have a similar or higher increase between wet and dry conditions with increasing tree species diversity (i.e., a null or positive relationship).

In a previous study, we analyzed the influence of drought on the relationship between tree species diversity and the increase in stand-level carbon isotope composition between a wet and dry year ($\Delta\delta^{13}C_S$) in boreal forests (10). Species diverse forests were shown to be more affected by drought stress than less diverse ones (i.e., a positive relationship between $\Delta\delta^{13}C_S$ and tree species diversity). In the present study, we extend our research to five major forest types across Europe, which extends from northern hemiboreal forests to southern Mediterranean forests (Table S1). Our objective was to test whether the relationship between $\Delta\delta^{13}C_S$ and tree species diversity would be consistent across a large range of climatic and edaphic conditions. At each of the five study sites, we selected a set of representative canopy trees (Table S2) in 21–42 forest stands varying in tree species diversity. For each site, we used a water balance modeling approach to select 1 y within the last 14 y with high drought stress and 1 reference y when no drought occurred (Figs. S1 and S2). We measured the $\delta^{13}C$ in the tree rings of the selected canopy trees and calculated $\Delta\delta^{13}C_S$ for each stand.

Results

Within a given forest type, there was a large variability among species in $\Delta\delta^{13}C$ values (Fig. S3), pointing out that drought response highly varied across tree species. Nevertheless, whatever the forest type, $\Delta\delta^{13}C$ always displayed positive values (Fig. S3),

which is consistent with the considerable literature on the impact of drought on tree- or species-level $\delta^{13}C$ (16, 17). This result confirmed that the tree rings selected for the targeted dry year coincided with years when all tree species clearly suffered from a severe and long-lasting water shortage.

Mean site $\Delta\delta^{13}C_S$ values were highly variable across the different forest types (Fig. 1). This variability can be partly explained by the large differences in the intensity of drought stress during the selected dry years across forest types (Table S3). We found a wide variability in $\Delta\delta^{13}C_S$ among forest stands within a given forest type (Fig. 2). The observed range of values (typically around 2‰) suggested highly contrasting ecosystem-level carbon and water tradeoffs among stands indicating highly contrasting soil water availability during the dry year. Among the confounding factors that were included in the $\Delta\delta^{13}C_S$ statistical model (competition intensity, light interception levels, microclimate, and soil nutrient availability), in the hemiboreal and mountainous beech forest types only competition intensity explained part of the large variability (Fig. S4), the other factors being nonsignificant (Table S4). In the temperate beech and thermophilous deciduous forest types, variations in $\Delta\delta^{13}C_S$ were only significantly correlated with tree species diversity (Fig. 2 and Table S4). Variations observed in the Mediterranean forest were not explained by tree diversity nor by any of the confounding factors (Table S4).

Discussion

The positive relationship between $\Delta\delta^{13}C_S$ and tree species diversity that had been previously observed for boreal forests (10) indicated a higher drought exposure in the more diverse stands. This previous study suggested that drought stress could exacerbate competition for water among neighboring tree species. However, in the present study, we found evidence that such a detrimental effect of tree species diversity cannot be generalized to European forest types. Indeed, we observed either no relationship (hemiboreal, mountainous beech, Mediterranean forests) or negative relationships (temperate beech, thermophilous deciduous forests) between $\Delta\delta^{13}C_S$ and tree species diversity (Fig. 2).

The negative relationship between $\Delta\delta^{13}C_S$ and tree species diversity that we observed for temperate beech and thermophilous deciduous forests implies that water availability was higher in diverse stands than in pure ones under drought conditions. These observations are consistent with other studies in which tree species diversity was found to reduce drought stress (8, 9). Higher water availability in more diverse stands suggests niche partitioning and/or facilitation processes among the interacting species. Below-ground partitioning may occur when species that extend their root systems toward deeper soil layers coexist with

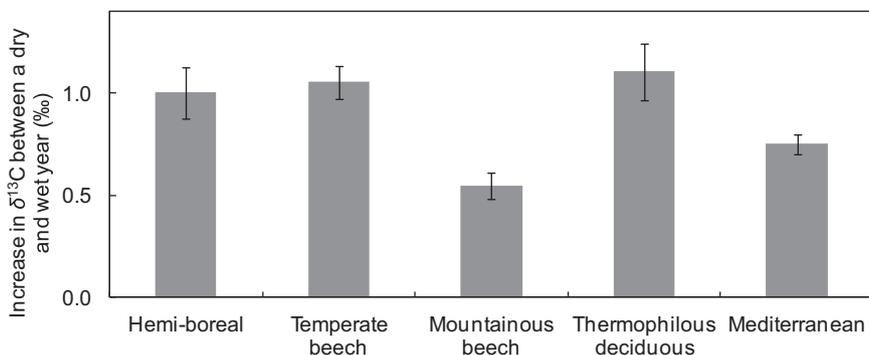


Fig. 1. Intensity of the physiological response to drought stress during the targeted dry year. Mean \pm SE of the increase in stand-level carbon isotope composition ($\Delta\delta^{13}C_S$, ‰) between the dry year and the year without water stress are shown for all stands with all tree species diversity levels for a given forest type. The increase in $\Delta\delta^{13}C_S$ between dry and wet conditions characterizes the intensity of drought stress to which the ecosystems were subjected.

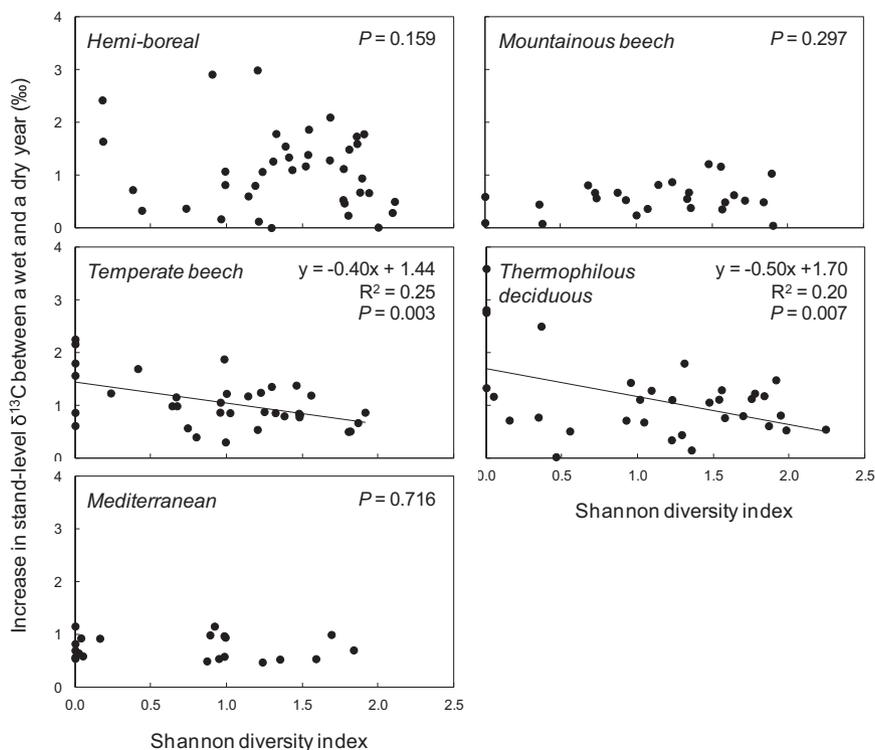


Fig. 2. Increase in stand-level carbon isotope composition in relation to tree species diversity for each forest type. Relationship between the increase in stand-level carbon isotope composition ($\Delta\delta^{13}\text{C}_s$, ‰) and the Shannon diversity index for the hemiboreal, mountainous beech, temperate beech, thermophilous deciduous, and Mediterranean forest types. Solid lines show the statistically significant relationships ($P < 0.05$). Corresponding equations, R^2 , and P values are given for each significant relationship.

others that occupy the superficial layers. Facilitation mechanisms such as hydraulic lift whereby deeper rooting tree species take up water and redistribute it via their root system to drier superficial soil layers are also known to take place in mixed forest ecosystems (18). Higher functional diversity of the fungal community could also partially improve water availability in more diverse stands (19). These underlying processes nevertheless remain speculative and future research is needed to shed light on the relative contribution of these potential processes (20).

For the three other forest types (hemiboreal, mountainous beech, and Mediterranean), the relationship between $\Delta\delta^{13}\text{C}_s$ and tree species diversity was nonsignificant (Fig. 2), suggesting that no net resource partitioning or facilitation processes were occurring. For these three forest types, tree species diversity did not play an important role in modulating ecosystem-level response to drought stress, despite strong functional differences among species in their response to drought (Fig. S3). Intraspecific and interspecific interactions therefore seem to have an equal influence on the level of drought exposure in these ecosystems. The tree species that compose these forests may be “ecological equivalents” (21) that use similar competitive strategies to deal with drought stress. However, for both the hemiboreal and mountainous beech forests, the variability among stands in $\Delta\delta^{13}\text{C}_s$ was partly explained by competition intensity (i.e., basal area; Fig. S4). Stands with higher basal area showed the greatest increase in $\Delta\delta^{13}\text{C}_s$ and thus the strongest soil water limitation. In these forest types, silvicultural practices controlling stand basal area may therefore be one management option to improve resistance to drought.

Environmental conditions are highly variable along the north-south gradient considered in this study and could account for the inconsistency of the response among the different forest types. Negative relationships occurred in the temperate beech and

thermophilous deciduous forests, the two sites that showed the highest mean drought stress intensity and the highest drought stress frequency over the last 14 y (Table S3). In contrast, drought events in the boreal and hemiboreal forests were moderate and rather rare (Table S3), and these are the sites where we observed positive relationships (10) or no effect of species interaction. Thus, overall, the global pattern we found seems consistent with the “stress-gradient hypothesis” (22, 23), although our study was not designed to test this hypothesis. This hypothesis indeed suggests that facilitation and complementarity processes should occur more frequently and should be more important under drier conditions, whereas competition should dominate under favorable ones. The Mediterranean forest was also characterized by high drought stress intensity and frequency (Table S3), but we found no effect of species interactions. We suspect that the very shallow soils found at this site prevented any chance for the establishment of below-ground complementarity processes such as root stratification.

We conclude that higher tree species diversity offers a greater resistance to drought events in some forest types but that this pattern cannot be generalized to all forest ecosystems. Forest response is likely to be context dependent. Local tree species associations are probably interacting with local environmental conditions, and this would explain the complexity of the relationship between biodiversity and forest resistance to drought stress we observed across Europe. Managing forest ecosystems for high tree species diversity does not necessarily assure improved resistance to the more severe and frequent drought events predicted for the future.

Materials and Methods

Experimental Sites. The sites used in this study are included in a permanent network of stands established in 2011–2012 in existing mature forests in five European countries (Germany, Poland, Romania, Italy, and Spain) within the

framework of the FP7-FunDivEurope project (24). The study areas include highly variable climatic conditions and host Europe's most important broadleaved and coniferous tree species (*SI Text*). In each site, 21–42 forest stands (30 × 30 m) were selected for a total of 160 stands covering a gradient of tree species diversity, from pure to the local maximum of between three and five species per stand (*SI Text*). Each level of tree species diversity was replicated approximately 10 times, but with different species compositions: the experimental setup was not designed to separate the effect of the presence of particular species or particular combinations of species from the effect of tree species diversity. To minimize confounding factors among stands within a given site, stands were selected for similar developmental stage, soil characteristics, slope, altitude, past management practices, and canopy structure characteristics (24). This selection focuses the study on rather average site conditions and is not suited to assess the influence of species diversity across a wider range of environmental factors. With this design we aimed, however, to eliminate other local factors that could have affected ecosystem functioning as much as tree species diversity. Nevertheless, some variability among stands within a given site could not be avoided, and stand characteristics were included in the statistical analyses as confounding factors. A detailed description of stand selection and characteristics can be found in *SI Text* and ref. 24. To characterize each stand's tree species diversity, we calculated the Shannon diversity index of each stand with species basal area as a surrogate for abundance in the equation (*SI Text*).

Selection of Target Years. To select a year with nonlimiting soil water conditions during the growing season and a year with severe soil drought during the growing season, we used the water balance model BILJOU (25) to estimate the daily REW (unitless) for each site during the period from 1997 to 2010 (Fig. S1). Based on REW, a water stress index (25) was calculated and used to select the 2 y (Fig. S2).

Wood Sample Preparation and Analyses. We selected a subsample of dominant and codominant trees per species and per stand to avoid confounding factors related to light interception (*SI Text*). For each tree, we extracted one wood core at breast height and carefully extracted the latewood for each selected year. Latewood sections from a given species, a given year, and a given stand were bulked and analyzed for $\delta^{13}\text{C}$ with a mass spectrometer. By selecting only the latewood, whose $\delta^{13}\text{C}$ mainly characterizes the functioning of the

trees during the second part of the growing season, we avoided potential effects related to the remobilization of stored photosynthates from the previous growing season (26) or to a favorable spring climate.

Stand-Level Carbon Isotope Composition. We calculated the stand-level $\delta^{13}\text{C}$ for each year using species-level $\delta^{13}\text{C}$, with the sum of basal area of each species in each stand as the weighting factor for the contribution of each species (*SI Text*). $\Delta\delta^{13}\text{C}_5$ was then defined as the increase in stand-level $\delta^{13}\text{C}$ between the dry and the wet conditions and therefore characterizes the ecosystem-level physiological response to soil drought.

Characterization of Confounding Factors. The following stand characteristics were measured to take them into account in the statistical model: leaf area index (i.e., light regimes), soil C/N (i.e., nutrient availability), stand basal area (competition intensity), and altitude (local climatic conditions).

Data Analyses. For each site, linear mixed models were used to determine the fixed effects of the Shannon diversity index and the confounding factors on $\Delta\delta^{13}\text{C}_5$ (Table S4). Interactions between the Shannon index and the confounding factors were initially integrated into the model but then were removed because none were significant.

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