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Drought responses by individual tree species are not often correlated with tree-species diversity in European forests

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Summary

1. Drought frequency and intensity are predicted to increase in many parts of the Northern Hemisphere and the effects of such changes on forest growth and tree mortality are already evident in many regions around the world. Mixed-species forests and increasing tree-species diversity have been put forward as important risk reduction and adaptation strategies in the face of climate change. However, little is known about whether the species interactions that occur in diverse forests will reduce drought susceptibility or water stress.

2. In this study, we focused on the effect of drought on individual tree species (n=16) within six regions of Europe and assessed whether this response was related to tree-species diversity and stand density, and whether community-level responses resulted from many similar or contrasting species-level responses. For each species in each plot, we calculated the increase in carbon isotope composition of latewood from a wet to a dry year ($\Delta\delta^{13}C$) as an estimate of its drought stress level.

3. When significant community-level relationships occurred (3 of 6 regions), there was only one species within the given community that showed a significant relationship (3 of 25 species-region combinations), showing that information about a single species can be a poor indicator of the response of other species or the whole community.

4. There were many two-species mixtures in which both species were less water stressed compared with their monocultures, but also many mixtures where both species were more stressed compared with their monocultures. Furthermore, a given species combination responded differently in different regions.

5. *Synthesis and Applications*: Drought stress may sometimes be reduced in mixtures but this is not a general pattern, and even varies between sites for a given combination. The management or prediction of drought stress requires consideration of the physiological characteristics of the mixed species, and how this complements the water-related climatic and edaphic features of the site, rather than species richness.

Keywords: carbon isotopes, climate change, competition, complementarity, European mixed-species forest; facilitation, species interaction, water stress

Introduction

Mixed-species forests are viewed as an important component of risk reduction and adaptation strategies for forest ecosystems in the face of global change (Messier, Puettmann & Coates 2013). Many studies have shown that mixed-species forests can be more productive than monocultures (Paquette & Messier 2011; Zhang, Chen & Reich 2012; Forrester & Bauhus 2016) and some have also shown that they can be more resistant and resilient to climate extremes (Lebourgeois *et al.* 2013; Pretzsch, Schütze & Uhl 2013). However, faster growing forests generally have greater evapotranspiration than slower growing forests (Law *et al.* 2002). Similarly, when the growth of a given species increases in mixtures compared with monocultures, the transpiration of that species also increases in the mixtures (Forrester 2015). If evapotranspiration is greater in mixtures it could potentially lead to greater water stress of some or all species during drought periods (Schume, Jost & Hager 2004; Grossiord *et al.* 2014b), which conflicts with the strategic use of mixtures to reduce forest water stress. To understand and to use these dynamics it is necessary to consider two factors that can be influenced by species interactions and potentially affect the intensity of drought stress.

The first is that, for a given stand density (basal area, sapwood area, leaf area etc), the species interactions may help reduce water stress, such as via facilitative processes including hydraulic lift and more favourable canopy micro-climates, or via a reduction in competition due to temporal or spatial stratification in soil water uptake and use (Forrester & Bauhus 2016). These can be broadly referred to as species complementarity. However, a second factor relates to the fact that these species interactions could result in an increase in growth and evapotranspiration in mixtures (Kunert *et al.* 2012; Forrester 2015), which could potentially result in greater water stress during hot or dry periods if soil water is depleted. The water stress of a given species may then be expected to increase with stand density (in terms of basal area, biomass, leaf area index), which is likely to be higher in mixtures if they are growing faster than monocultures, unless thinning intensities are also greater in mixtures. It is noted that many mixtures are not more productive than the respective monocultures, but when mixtures are more productive (and with greater evapotranspiration) this density effect might be expected.

Reducing stand density by thinning can initially increase the availability of water for the remaining trees and has been discussed as an option to mitigate drought impacts (Cescatti & Piutti 1998; Laurent, Antoine & Joel 2003; Martín-Benito *et al.* 2010; Sohn *et al.* 2013). For instance, many studies have shown that increases in drought-induced mortality can be related to increases in stand density (Allen *et al.* 2010), however drought-related mortality was also found to be unrelated to differences in stand density (van Mantgem & Stephenson 2007). The mitigation effects of density control by thinning are also not straight forward and appear to depend on the time since thinning as well as the resulting stand structure and tree hydraulic architecture (Sohn *et al.* 2013). These contrasting effects of stand density and thinning

110 indicate that stand density in relation to tree-species diversity is important to consider when
111 examining the drought stress of forests.
112
113 Direct measurements of water pools and fluxes are labour intensive or require intensive
114 instrumentation, which restricts the number of sites and species included in studies comparing
115 these pools and fluxes in mixtures and monocultures (Forrester 2015; Volkmann *et al.* in
116 press). Therefore, complementary studies have used indirect methods to estimate the effect of
117 drought on tree water status, particularly stable carbon isotope composition ($\delta^{13}C$). The
118 variation in $\delta^{13}C$ of tree rings between a wet and a dry year ($\Delta\delta^{13}C$) can be used as a proxy
119 for tree water stress (Saurer, Siegenthaler & Schweingruber 1995) and used to examine
120 whether water stress increases or decreases along gradients of tree-species diversity and/or on
121 different sites (Grossiord *et al.* 2014a; Grossiord *et al.* 2014b; Metz *et al.* 2016). A European-
122 wide study that included sixteen species showed that water stress at the community level
123 declined with increasing tree-species diversity in two forest types (Temperate Beech forests
124 and Thermophilous deciduous forests), increased with diversity in Boreal forests, while there
125 was no relationship in three other forests types including Hemi-Boreal, Mountainous Beech
126 and Mediterranean forests (Grossiord *et al.* 2014a; Grossiord *et al.* 2014b). This study
127 concluded that there does not appear to be any general relationship between community-level
128 drought stress and diversity, so drought stress will often not be reduced by increasing the
129 diversity of forests. Rather than simply increasing species diversity, it appears to be more
130 important to combine species with complementary characteristics, in terms of their water-
131 related interactions, and that also suit the climatic and edaphic conditions at the site (Forrester
132 2014).
133
134 In contrast, a study focusing on *Fagus sylvatica* L. suggested that this species was less
135 stressed when growing in mixtures than in monocultures (Metz *et al.* 2016). Most of the

mixtures had lower stand densities (competition indices) than the monocultures, so it was not clear whether this was a species mixing effect or a density effect. Metz *et al.* (2016) concluded that "the systematic formation of mixed stands tends to be an appropriate silvicultural measure to mitigate the effects of global warming and droughts on growth patterns of *Fagus sylvatica*.". This is a strong and potentially very useful conclusion for foresters. However, it contrasts with those of other studies with *F. sylvatica* in Central Europe that indicated that *F. sylvatica* may actually suffer more drought stress when mixed with species that exhaust water reserves early in the summer (e.g., *Tilia* sp. or *Quercus* sp. Gebauer, Horna & Leuschner 2012; Mölder and Leuschner 2014), or found that *F. sylvatica* may cause other species (e.g., *P. abies* (L.) Karst.) more water stress during droughts (Schume, Jost & Hager 2004) thereby reducing the stability and productivity of the mixtures compared with the monocultures. Another study showed that *F. sylvatica* trees were more resistant and resilient to drought (in terms of growth response) in mixtures with *Quercus petraea* or *Picea abies*, while the resistance and resilience of those species was not significantly different in mixtures with *F. sylvatica* compared with monocultures (Pretzsch, Schütze & Uhl 2013). These contrasting responses indicate that to predict the drought susceptibility of forests it is important to know whether all species are likely to benefit from the mixture or whether only some benefit (e.g., *F. sylvatica*) at the expense of other species. Similarly, it is important to know whether the whole community (total or mean of all species) will be less stressed as a mixture or a monoculture, as opposed to only a single species within the community (e.g., *F. sylvatica*).

This requires information about all species within the mixture, and also the separation of the effects of species composition from potentially related factors that can influence drought stress, such as stand density, which is likely to increase with diversity if productivity increases with diversity. In this study, we used data of individual species tree-ring $\delta^{13}C$ from six regions

in Europe and sixteen species to test whether these forests show any general relationships between the water stress of a given species, species composition and stand density.

Specifically, our objectives were to determine whether: (i) significant relationships at the community level between drought stress and diversity are associated with similar species-level relationships by all, several or only a single species within the community; (ii) if there is no relationship at the community level, are all species-level relationships also insignificant, or do they contrast and counterbalance each other to result in a neutral community-level relationship. Lastly, while stand density (basal area) was only weakly related to diversity at each region, density did vary between plots, therefore, we also examined whether (iii) the drought stress of each species was related to stand density.

Materials and Methods

Experimental sites

The study was done in a European permanent plot network that was established in 2011 (FunDivEUROPE; Baeten *et al.* 2013). The network includes six regions that are representative of major European forest types (Table 1). Within each region, 21 to 42 plots (30 m × 30 m) were established, resulting in a total of 184. A total of 16 different target tree species occurred within the plots. Some species occurred in more than one region, but none occurred in all regions (Table 1). The tree-species richness of the plots ranged from 1 to 3 in Finland and Spain, 1 to 4 in Romania and Germany and 1 to 5 in Italy and Poland. The target species were the most common species within the given region. Within each region, each target tree species was represented at all richness levels, and when possible there were two replicates per species combination per region. There were only weak or no relationships

between tree-species richness and stand basal area in each region (Fig. S7 in Jucker, Bouriaud & Coomes 2015).

Three additional criteria were used when establishing the plots (FunDivEUROPE; Baeten *et al.* 2013). Firstly, all plots were in mature forests that had received minimal management during the past decade or longer. Secondly, within a region, all plots were at a comparable developmental stage and had similar topography, soil and bedrock properties. Thirdly, the relative abundance of each target species within a given plot was as similar as possible, while the presence of non-target species was usually restricted to < 5% of the total plot basal area.

Stand characteristics

This study focuses on the species-level responses using the same data that were used to examine community-level responses in two previous studies (Grossiord *et al.* 2014a; Grossiord *et al.* 2014b), where additional detail about the methodology is provided. The stem diameter at 1.3 m was measured for all trees with diameter ≥ 7.5 cm in 2011 and 2012. These were used to calculate the basal area (m^2 ha^{-1}) of each species (*i*) in each plot (BA_i) and hence the total plot basal area (BA_T). Tree-species richness was simply the number of target tree species within a given plot. Tree-species diversity was quantified using Shannon's index (Shannon 1948) based on the basal area of each target species within a plot using Equation 1.

$$\text{Tree-species diversity} = -\sum_{i=1}^{n} \frac{BA_i}{BA_T} \ln\left(\frac{BA_i}{BA_T}\right) \quad (1)$$

where *n* is the number of target tree species in the plot. While the relative abundance of each target species within a given plot was as similar as possible, there was still some variability. Therefore, Shannon's index was used to account for the evenness of the species mixing.

To account for the effects of irradiance, soil nutrient availability and soil moisture on $\delta^{13}C$, the effects of irradiance were approximated using plot leaf area index (LAI) and those of soil nutrient availability were approximated using soil C/N ratio. In addition, stand basal area was used to approximate competition for all resources. Stand basal area and LAI were also used to check that species richness and diversity were not confounded with stand density, which can influence the productivity (and possibly related ecosystem functions) more than richness and diversity in European forests (Vilà *et al.* 2013). The measurements of LAI and soil C/N ratio are described in Appendix 1.

Quantification of tree water stress

The stomatal response of plants to soil water deficit is related to the molar ratio of the two naturally occurring C isotopes ($^{13}C/^{12}C$) in the plant material that was produced during the period of water deficit (Dupouey *et al.* 1993; Warren, McGrath & Adams 2001; Ferrio *et al.* 2003), expressed as $\delta^{13}C$ (‰). The variation in $\delta^{13}C$ of plant material that was produced during a given wet period (i.e. reference year) and a drought period can therefore be used as an index of the physiological response to soil drought. We used the difference in the $\delta^{13}C$ of latewood within growth rings of the tree stems between a year with very wet summer conditions and a year with extreme drought conditions (Grossiord *et al.* 2014a; Grossiord *et al.* 2014b). This variation, $\Delta\delta^{13}C$ (‰), was calculated for each species in each plot as $\delta^{13}C_{dry}$ - $\delta^{13}C_{wet}$. While $\delta^{13}C$ can be influenced by any factors that influence stomatal conductance, including radiation, soil fertility (Farquhar, Ehleringer & Hubick 1989; Warren, McGrath &

236 Adams 2001; Ferrio, Voltas & Araus 2003), and genetics (Brendel *et al.* 2002), it was
237 assumed that the main factor that varies between the wet and dry year is the water-related
238 stress (see (Grossiord *et al.* 2014a; Grossiord *et al.* 2014b) for more details). A higher $\Delta\delta^{13}C$,
239 and hence a greater increase in $\delta^{13}C$ in the dry year, indicates a stronger stomatal response and
240 thus a higher level of drought stress; a $\Delta\delta^{13}C$ of zero would indicate that there was no change
241 in $\delta^{13}C$ in response to drought, and hence no drought-induced stress. The latewood was
242 sampled because the $\delta^{13}C$ of earlywood can be influenced by the remobilization of
243 photosynthates from previous growing seasons (Offermann *et al.* 2011) or favourable spring
244 weather, whereas the latewood is more likely to be affected by droughts that occur in the later
245 part of the growing season. While $\delta^{13}C$ analyses are sometimes performed on the cellulose
246 fraction of the wood, cellulose and bulk material produce highly correlated signals (Loader,
247 Robertson & McCarroll 2003) and the latter was used in this study.
248
249 Wood cores for $\delta^{13}C$ measurements were collected by randomly selecting six trees per species
250 in monocultures and three trees per species in mixed-species plots from the ten largest-
251 diameter trees to ensure that only dominant and co-dominant trees were selected. The larger
252 size classes were used to avoid the confounding effects of shading on the $\delta^{13}C$ of suppressed
253 trees (Ferrio, Voltas & Araus 2003). A total of 1,390 trees were sampled across the six
254 regions and one 5-mm-diameter core was extracted from the southern side of each tree at a
255 height of 1.3 m. For each core the latewood for the selected years (wet vs. dry) was separated
256 from the earlywood using a scalpel. The latewood samples for a given year (wet or dry), a
257 given species and a given plot, were bulked to obtain enough material for carbon isotope
258 analysis to ensure sample homogeneity and to reduce the cost of the analyses. While this is a
259 relatively low sample number, the replication is adequate due to the strong imprint of
260 environmental signals on tree-ring carbon isotope composition (Peñuelas *et al.* 2008). This
261 procedure is described in detail by Grossiord *et al.* (2014a) and Grossiord *et al.* (2014b).

The growing seasons with non-limiting soil water conditions and those with severe soil drought were selected using a water balance model to estimate the daily relative extractable water for each region between 1997 and 2010. The dry year used for $\delta^{13}C_{dry}$ was randomly selected from the three driest years between 1997 and 2010. The wet year used for $\delta^{13}C_{wet}$ was randomly selected from the years with a low water stress index. This procedure is described in detail in Appendix 1.

Statistical analyses

The effect of stand variables on $\Delta\delta^{13}C$ was examined using linear regression analyses. Stand variables included tree-species richness, tree-species diversity, stand basal area, LAI and soil C/N ratio. The labour intensive aspect of the data collection and the number of regions, species and tree richness levels did not allow for a high level of replication. While multiple linear regression could be used to account for all stand variables in a single model for each given species, we avoided fitting multiple regressions because this would result in low ratios of sample sizes to the number of variables (often ratios of less than 10) (Clarke & Wheaton 2007; Bolker *et al.* 2009). We therefore examined the effects of each variable separately. All statistical analyses were carried out using R software version 3.2.1 (R Core Team 2015).

Results

Relationships between richness or diversity and $\Delta\delta^{13}C$

Tree-species richness and diversity generally had similar effects on the species-level $\Delta\delta^{13}C$. $\Delta\delta^{13}C$ decreased with increasing diversity or richness for *C. sativa* in the Thermophilous

deciduous forests of Italy (Fig. 1 and Fig. S1, Tables S1 and S2 in Supporting Information). It also decreased with increasing diversity (but not richness) for *F. sylvatica* in the Temperate Beech forests of Germany. In contrast, $\Delta\delta^{13}C$ increased for *P. abies* with richness and diversity in the Boreal forests of Finland (Fig. 1 and Fig. S1). $\Delta\delta^{13}C$ also increased with richness for *F. sylvatica* in the Mountainous Beech forests in Romania (Fig. S1d), which is the opposite pattern for *F. sylvatica* in Germany (Fig 1c). There were no significant relationships between $\Delta\delta^{13}C$ and diversity in the other two forest types, Hemiboreal forests in Poland and Mediterranean forests in Spain.

To indicate why there were so few significant relationships with richness and diversity (3 of 25 species-region combinations), Fig. 2 compares the $\Delta\delta^{13}C$ of each species in its monoculture with the $\Delta\delta^{13}C$ of the same species when it was in a two-species mixture. While there is no statistical power to test for the significance of the differences, the rankings are used here to interpret the relationships between $\Delta\delta^{13}C$ and diversity or richness. For many species, the monocultures were not the most stressed stands, and in the Boreal forests of Finland, all species were actually less stressed in monocultures. The variability in the ranking of monocultures and two-species mixtures for different species within a given region indicates that correlations between $\Delta\delta^{13}C$ and richness or diversity will be reduced because the positive effects on water stress in some mixtures are often offset by negative effects on water stress in other mixtures.

The two species for which drought stress declined with increasing diversity (*F. sylvatica* in Germany and *C. sativa* in Italy) were also examples where monocultures were more stressed than all two-species mixtures containing those species (Fig. 2). However, this situation was not enough to result in a general positive diversity effect because there were also other species where monocultures were more stressed than all two-species mixtures, but there was no

diversity effect (e.g. *B. pendula* in Poland or *Q. cerris* in Italy). Fig. 2 also shows that there were no single species that were consistently more stressful to all other species within a given site.

Relationships between basal area, leaf area index or soil C/N and $\Delta\delta^{13}C$

The other stand characteristics often varied widely between plots within a given region, but they were rarely correlated with $\Delta\delta^{13}C$. Stand basal area was negatively correlated with $\Delta\delta^{13}C$ for *B. pendula* in the Hemiboreal forests of Poland (Fig. S2, Table S3). In the same forests, the $\Delta\delta^{13}C$ was negatively correlated with LAI for *Q. robur* (Fig. S3, Table S4). This indicates that these species actually became less stressed as stand basal area or LAI increased. The C/N of soil was positively correlated with $\Delta\delta^{13}C$ for *B. pendula* in the Boreal forests of Finland, while it was negatively correlated with the $\Delta\delta^{13}C$ of *P. abies* in the Mountainous Beech forests of Romania (Fig. S4, Table S5). There were no other significant relationships between stand variables and $\Delta\delta^{13}C$ for the other species in any region.

Discussion

Species identity or species richness effects

This study shows that the community-level diversity patterns, which were significant in three of the six regions (Grossiord *et al.* 2014a; Grossiord *et al.* 2014b), were mirrored by only one of the species within each given community, and often the relationships for those species were not strong. In the Temperate Beech forests of Germany, water stress declined in mixtures only because *F. sylvatica* was less drought stressed. In the Thermophilous deciduous forests of Italy, stress declined in mixtures only because *C. sativa* was less stressed, and in the Boreal

340 forests of Finland stress increased in mixtures because *P. abies* was more stressed. There were
341 no community-level relationships in the Hemiboreal forests in Poland or the Mediterranean
342 forests in Spain because there were no significant relationships for any of the individual tree
343 species within those communities. There was also no community-level relationship in the
344 Mountainous Beech forests of Romania, despite a significant relationship for *F. sylvatica*,
345 because the other species showed no significant relationships.
346
347 This variability in species responses within a given stand is consistent with most previous
348 studies that directly measured water pools and fluxes in mixtures; the community-level
349 response is the average of different responses by each species within the community. For
350 example, in some stands there is no clear mixing effect for any species (Moore, Bond & Jones
351 2011; Grossiord *et al.* 2013), in others each species may have greater transpiration per tree
352 (Forrester *et al.* 2010; Kunert *et al.* 2012), and in others some species may have greater
353 transpiration or interception of precipitation at the expense of other species (Schume, Jost &
354 Hager 2004; Gebauer, Horna & Leuschner 2012). Even for a given species, the mixing effect
355 on water fluxes are the average response of different cohorts or size classes within the stand,
356 such that only some of the trees of that species may be responsible for its response (Forrester
357 2015).
358
359 One of the most general findings was that there is no common relationship between diversity
360 and $\Delta\delta^{13}C$ and that the majority of species were not most water stressed in their monocultures.
361 This reduced the probability of negative correlations between diversity and drought stress
362 ($\Delta\delta^{13}C$) within a given region because the response in mixtures, where there was a positive
363 effect, was offset by the response in other mixtures where there was a negative effect. The
364 two cases where water stress decreased with increasing diversity (i.e., *F. sylvatica* in Germany
365 and *C. sativa* in Italy) were also examples of species-region combinations for which a given

species was more stressed in monoculture than *all* two-species mixtures. It is also important to note that even within a given region there was no single species that was consistently more stressful to all others in that region.

With regards to management implications, while there were few significant relationships between $\Delta\delta^{13}C$ and diversity, there were many two-species mixtures where both species were less water-stressed in mixture than in monoculture (e.g., mixtures of *C. betulus* or *P. abies* with *P. sylvestris* in Poland; *Q. petraea* or *C. sativa* with *Q. cerris* in Italy etc., Fig. 2). Thus, for most species, drought stress changed with neighbour identity rather than with diversity. There is no data from this study to provide a process-based explanation for why these combinations worked for each species within the mixture, and it is likely that a combination of processes was responsible, some of which improved water availability and others that may have simultaneously had the opposite effect (Forrester & Bauhus 2016). For example, a conifer such as *P. abies* might reduce water availability by having higher interception rates than neighbouring broad-leaved species, such as *F. sylvatica*, but *P. abies* might also increase water availability by having a lower transpiration rate than *F. sylvatica* (Schume, Jost & Hager 2004).

Site and region effects

The design of this study allows an analysis of the relationship between diversity and species response to drought across major forest types in Europe and an indication of the generality of such relationships. Our results show that a given species combination can respond differently in different regions. For example, in Germany, *F. sylvatica* was less stressed in mixtures with all other species examined in that region, which is the same result that was found in another study in the same region (Metz *et al.* 2016). However, this was not the case in Romania,

where *F. sylvatica* was more stressed in mixture with *A. alba* than in monocultures. Also, in Romania *F. sylvatica* was least water stressed with *Acer pseudoplatanus*, which was actually the most stressful species towards *F. sylvatica* in Germany. Spatial changes in the interactions between a given combination of species in terms of growth have been found in many forests (Forrester 2014). This shows the risk of using data from a small part of a species distribution to generalise about a given combination (Forrester 2014). For example, the mixing effect on growth of *P. sylvestris* and *F. sylvatica* was found to decrease from 78% at a single site in Germany, to 17% when averaged across seven sites in Germany and Poland, to 9% when averaged for 32 sites spread across a large proportion of the natural distribution of this species combination in Europe (Forrester & Pretzsch 2015). Furthermore, different provenances of a given species can vary in their hydraulic architecture (Poyatos *et al.* 2007) or other water-related traits (Ponton *et al.* 2002) and thus in their response to droughts (Taeger *et al.* 2013), thereby influencing the way a given species interacts with others.

Stand density

With few exceptions, $\Delta\delta^{13}C$ was not correlated with stand density (basal area or LAI) for any species in any of the six regions. As shown in previous studies at these sites, density was also only weakly correlated with tree-species richness in each region (Jucker, Bouriaud & Coomes 2015). The weak or absent correlation between stand density (basal area or LAI) and species-level $\Delta\delta^{13}C$ may be due to unmeasured variables, such as differences in the hydraulic architecture of a given species in different plots. For example, a stand that was thinned several decades ago (via management or a natural disturbance) may now have a similar community basal area and LAI to stands that were less intensively thinned, but the trees of a given species within that stand could now have larger mean tree leaf areas and hence different hydraulic architectures. While the forests used in this study have not been recently managed, they are

mature forests and all previous management during the first decades of stand development will have influenced the current stand structures and hydraulic architectures, which can influence the response of trees to droughts (McDowell *et al.* 2006; Sohn *et al.* 2013). Confounding effects of stand structure or hydraulic architecture may have caused the variable (and usually absent) effects of stand density on $\Delta\delta^{13}C$. It should also be noted that while there were not enough data to test for interactions between diversity and stand density, this may be important to examine in future studies.

Management considerations and conclusions

Diversity was often a poor predictor of the water stress response of individual species and all significant relationships at the community level were mirrored by the response of only one species within the community. This indicates that information about only a single species within a mixture provides very little information about the potential mixing effect on that community or all other species within the community. However, while species diversity does not appear to be a good predictor of community- or species-level water stress response, species identity is clearly important and there were many two-species mixtures in which both species were less water stressed compared with their monocultures. It is also important to note that there were also two-species mixtures where one or both species were more water stressed than in their monocultures (e.g., all mixtures in Finland). Therefore, while mixed-species forests may sometimes result in reduced water stress, this will certainly not always be the case. Furthermore, the mixing effect on water stress also varied between regions, and a species that benefited from mixing in one region (e.g., *F. sylvatica* with *P. abies* in Germany) did not always benefit, even when mixed with the same species, in another region (e.g., in Romania). These mixing effects are likely to result of several simultaneously occurring water-related interactions, some of which may have positive effects and others negative effects

(Forrester & Bauhus 2016). Further investigation of these processes and how they can be influenced by species interactions and forest management will be necessary to improve the process-based understanding of these dynamics. This will be required in order to more confidently predict which combinations of species, sites, climatic conditions, stand ages and stand structures will be most beneficial for reducing water stress of forests.

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Data Accessibility

FunDivEUROPE online data portal (http://fundiv.befdata.biow.uni-leipzig.de/)

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Quantification of soil water availability, leaf area index and soil C/N

Fig. S1. Relationship between $\Delta\delta^{13}C$ and tree-species richness

Fig. S2. Relationship between $\Delta\delta^{13}C$ and stand basal area

Fig. S3. Relationship between $\Delta\delta^{13}C$ and leaf area index

Fig. S4. Relationship between $\Delta\delta^{13}C$ and soil C to N ratio

Table S1. Statistics for relationship between $\Delta\delta^{13}C$ and tree-species diversity

Table S2. Statistics for relationship between $\Delta\delta^{13}C$ and tree-species richness

Table S3. Relationship between $\Delta\delta^{13}C$ and stand basal area

Table S4. Relationship between $\Delta\delta^{13}C$ and leaf area index

Table S5. Relationship between $\Delta\delta^{13}C$ and soil C to N ratio