



## Tansley insight

# Having the right neighbors: how tree species diversity modulates drought impacts on forests

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## Summary

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Droughts are a rising concern for terrestrial ecosystems, particularly for forests where drought-induced reductions in tree growth and survival are reported. Biodiversity has long been acknowledged as an important component modulating ecosystem functions, including mitigating their vulnerability to climate-related stresses. Yet the impact of tree diversity on forest vulnerability to drought is unclear. In this review, consistent mechanisms are identified by which tree diversity could reduce vulnerability to drought and emerging evidence is revealed that tree diversity is not systematically positively related to drought resistance in forests. A path is suggested to further increase our knowledge on this subject in the face of climate change, proposing standardization of methods to quantitatively establish diversity impacts on the drought resistance of forests.

## I. Introduction

Droughts are expected to set in more rapidly, last longer and be more intense with global warming (Trenberth *et al.*, 2014). Because of rising concerns associated with the recent drought-induced reductions in forest growth and survival (e.g. Allen *et al.*, 2015), mitigation processes that buffer forest drought vulnerability have become a major research frontier in ecology, ecophysiology and forest management (e.g. Sohn *et al.*, 2016; Grossiord *et al.*, 2017). While knowledge on fine-grained physiological responses to drought is continuously progressing and contributing to improved

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predictions (e.g. McDowell *et al.*, 2013), the vast majority of empirical studies and climate-vegetation models does not account for community-level processes that could mediate drought impacts on individual trees and on a forest as a whole.

Over the last 3 decades, findings in community ecology have led to the widespread agreement that species diversity plays a critical role in plant performance (Hooper *et al.*, 2005), including reducing plants' susceptibility to drought (Isbell *et al.*, 2015). Forests represent some of the richest biological areas on Earth, with more than two-thirds being 'mixed' ecosystems (that is where at least two tree species interact in a given forest community) (FAO, 2016). As such, one might also expect tree species diversity to be a critical factor shaping drought impacts on forest communities, interactions that could become increasingly significant with the exacerbation of drought events in the future. Nevertheless, despite



**Fig. 1** Examples of mixed forests in various climatic regions composed of tree species with contrasting physiological responses to drought. (a) In temperate beech and oak forests, beech (*Fagus sylvatica* L.) rooting system is less effective in exploring deep soil layers than oak (*Quercus petraea* (Matt.) Liebl.), indicating that species rely on different water sources in the soil (Zapater *et al.*, 2011). Beech is able to maintain a relatively stable midday leaf water potential ( $\Psi_{MD}$ ) as soil moisture conditions change, while oak tracks fluctuations in water availability, with no discernible threshold of minimum  $\Psi_{MD}$  (Zang *et al.*, 2012), pointing to differences in water flux regulations during drought. (b) In semiarid piñon–juniper woodlands, piñon (*Pinus edulis* Engelm.) is known to rely mostly on shallow soil moisture sources while juniper (*Juniperus monosperma* Engelm.) takes water from deeper soil layers (Grossiord *et al.*, 2017). Among other well known functional differences related to their stomatal regulation strategy (Garcia-Forner *et al.*, 2016), juniper and piñon also present different mycorrhizal associations, impacting their water and nutrient uptake and use (Allen *et al.*, 2010). (c) In mixed birch (*Betula pendula* Roth.), pine (*Pinus sylvestris* L.), and spruce (*Picea abies* (L.) Karst.) forests in boreal regions, interacting coniferous and broadleaved trees obviously distinguish themselves in their phenology, with pine and spruce starting most physiological processes earlier in the growing season. Furthermore, spruce relies on a superficial rooting system, pine an intermediate one, and birch a deep rooting system (Grossiord *et al.*, 2014a). Trees in all three forest types experience spatial (that is stratification of water sources in the soil) and temporal (that is different timing in phenology and stomatal regulations) partitioning of resources, as well as facilitative processes (that is mycorrhizal associations improving soil moisture and nutrient status).

extensive evidence of the importance of species diversity for multiple forest functions (Jactel & Brockerhoff, 2007; Morin *et al.*, 2011), the role of tree species diversity on forest responses to drought is largely missing from earlier research (Ammer, 2019).

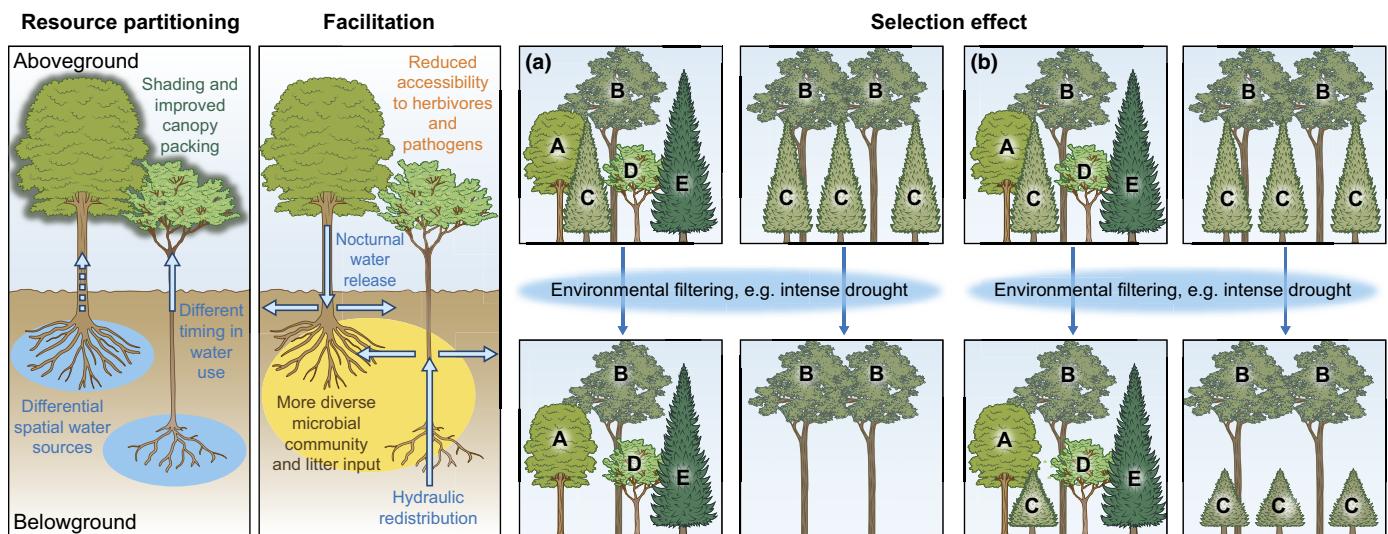
Recent findings from this emerging field are reviewed here and a pathway proposed to further advance our knowledge on the importance of tree species diversity in a climate change context. Within the different sections of this review, the primary goal was to address the underlying mechanisms by which higher tree species diversity could mitigate drought impacts on forests; the current knowledge on tree diversity effects on forests reaction to drought; and opportunities for advancing our knowledge of the role of tree diversity in modulating climate change impacts for forests.

## II. Mechanisms of tree species interactions mitigating drought impacts on trees

Consensus that species richness and/or functional diversity mediates ecosystem functioning has been widely accepted (Hooper *et al.*, 2005; Tilman *et al.*, 2014). Therefore, we can expect that tree species richness, trait means and the diversity of functional strategies related to drought in a given forest community will help to determine drought impacts on trees. A wide spectrum of strategies to deal with drought exists in trees, from strictly ‘drought-avoiding’ to ‘drought-tolerant’ species (Kramer, 1983). A tree’s response to drought is driven by structural and physiological adaptations, including xylem anatomy (e.g. vessel/tracheid area and length, number of pits), plant allometry (e.g. the ratio between evaporative/conductive and aboveground/belowground structures), stomatal behavior (often ranked along a gradient from isohydric to anisohydric strategies, but see Martínez-Vilalta &

Garcia-Forner, 2017), and rooting strategy (e.g. rooting depth, rooting forms, mycorrhizal associations). Many cohabiting tree species in natural ecosystems exhibit contrasting functional traits and strategies to deal with drought such as broadleaved forests in temperate climates (e.g. beech-oak stands), coniferous mixtures in semiarid regions (e.g. piñon-juniper woodlands), coniferous-broadleaved forests in boreal regions (e.g. spruce-pine-birch stands) (Fig. 1), and the obvious ‘hyperdiverse’ tropical forests.

To understand how tree species diversity could contribute to reduced vulnerability to drought and to provide process knowledge for the implementation of climate-vegetation models, elucidating the underlying mechanisms of species interactions are a key starting point. These beneficial interactions can be divided into three classes, mechanisms related to resources partitioning, facilitation and selection effects. Classes 1 and 2, which are often difficult to distinguish without direct experimental observations (Forrester & Bauhus, 2016) and consequently are often grouped together (Loreau & Hector, 2001), refer to biological mechanisms that modify the environment and the degree of stress experienced by trees. Mechanisms related to resources partitioning (Class 1) imply that dissimilarities in functional traits reduce competition for resources, as species use different resources in space and time, they are less likely to compete for them (Hooper, 1998). For instance, resource partitioning may involve mechanisms such as root stratification (e.g. Schwendenmann *et al.*, 2015) or differential stomatal regulation strategies (e.g. West *et al.*, 2012) (Fig. 2) that can improve species-specific soil moisture status by reducing competition for water among species. The occurrence of these mechanisms does not systematically imply reduction in drought impacts for trees (e.g. soil water partitioning may be insufficient to fully overcome moisture reduction during extreme droughts,



**Fig. 2** Conceptual representation of the three classes of mechanisms: resource partitioning, facilitation, and selection effect. For resource partitioning and facilitation, two tree species characterized by contrasting traits related to their water and nutrient acquisition and use (that is canopy structure, phenology, tree height, rooting depth and mycorrhizal associations) are shown, highlighting the physical and biological mechanisms of resource partitioning (Class 1) and facilitation (Class 2) taking place in mixed forests (that is resulting from tree species interactions in aboveground and belowground compartments). The conceptual representation of selection effects (Class 3) includes an example (a) highlighting how a given forest community hosting a higher number of tree species (species A, B, C, D and E) is more likely to have an increased number of species surviving an environmental or climatic filtering event (e.g. intense drought) than a forest community hosting the same number of individuals but fewer tree species (species B and C). In this example, species C is particularly vulnerable to drought stress and suffers complete drought-induced mortality at the community level following the filtering event. The second example (b) highlights how a given forest community hosting a higher number of tree species is more likely to have an increased number of drought-tolerant species maintaining major functions (e.g. growth) during an environmental or climatic filtering event than a forest community hosting the same number of individuals but fewer tree species. In this example, species C is particularly vulnerable to drought stress and suffers strong growth reductions following the filtering event.

Grossiord *et al.*, 2018) and trait plasticity resulting from climate variability may alter their occurrence and impact (e.g. plants can modify their water sources during droughts, resulting in altered resource partitioning, Grossiord *et al.*, 2018).

Facilitation (Class 2) refers to mechanisms occurring when one species has a positive effect on the functioning of cohabiting species (Callaway, 1995). Examples of biotic and abiotic facilitative mechanisms can involve active hydraulic redistribution (e.g. Zou *et al.*, 2005), nocturnal water release (e.g. Prieto *et al.*, 2012) and reduced accessibility to herbivores and pathogens (e.g. Jactel & Brockerhoff, 2007) (Fig. 2), resulting in improved soil moisture and reduced biotic damages during drought (Fig. 2).

Selection effects (Class 3) arise from selective processes within an initial species pool that cause dominance of species with particular traits (Loreau, 2000) (Fig. 2). In the context of diversity–drought vulnerability relationships, we can for example interpret selective processes in higher diversity forests as an increased chance of initially containing and/or becoming dominated by particularly drought-tolerant species (e.g. deep-rooted anisohydric species) relative to lower diversity communities. Selection can occur at the expense of other species (referred to as ‘competitive dominance’) or not (Fox, 2005). One may expect this mechanism to be more relevant for ‘hyperdiverse’ ecosystems such as tropical forests compared with boreal, temperate, and dryland forests, which typically harbor between two and six tree species. Nevertheless, whether tropical forests are more prone to selection effects than other forest types, or whether a given threshold of species richness is needed in order for selection effects to occur, remains untested.

### III. Observed impacts of tree species diversity on forest response to drought

A review of the literature revealed that 28 studies, including 151 tree species (Supporting Information Fig. S1), have investigated drought effects in forests in relation to tree species diversity. These studies were conducted in temperate, boreal, Mediterranean, mountainous, and tropical forests, with the majority of studies in relatively low-diversity temperate regions (Table 1). The earliest work was published in 2010, but the majority was published over the last 3 yr (Table 1), demonstrating an explosion in research on this topic and a growing interest of the scientific community.

This systematic review highlights emerging evidence that tree diversity regulates drought impacts in forests (only 8% of studies found no effects of diversity; Fig. 3). However, it is impossible to draw general conclusions on how tree diversity affects the directionality of forest responses to drought (positive *vs.* negative effects). Although positive effects of diversity – in other words, instances in which high tree species diversity was related to lower reductions in functions during drought, relative to low-diversity situations – are more commonly observed than negative effects, only 42% of studies found strictly positive effects (Fig. 3). The underlying mechanisms driving tree diversity effects were not assessed, limiting our mechanistic understanding of these responses, but several studies have suggested that differences and/or overlap in soil water sources and hydraulic lift could contribute to these positive or negative patterns (e.g. Lebourgeois *et al.*, 2013; Pretzsch *et al.*, 2013). Moreover, these findings suggest that,

**Table 1** List of studies investigating how tree species diversity modulates drought impacts on forests.

Ecosystem	Developmental stage	Forest type <sup>a</sup>	Country/Continent	Levels of species richness <sup>b</sup>	Scale	Studied function(s)/trait(s)	Mixture effect	Drought type	Source
Positive effects									
Plantation	Adult	Tr.	Australia	1, 2	Ecosystem	Transpiration, WUE <sup>c</sup>	+	Natural	Forrester <i>et al.</i> (2010)
Plantation	Young	Tr.	Panama	1, 2, 3, 4, 5	Ecosystem	Transpiration	+	Natural	Kunert <i>et al.</i> (2012)
Natural forest	Adult	Mo.	France	1, 2, 3	Tree	Growth	+	Natural	Lebourgeois <i>et al.</i> , 2013;
Natural forest	Adult	Tp.	Germany	1, 2	Tree	Growth	+	Natural	Pretzsch <i>et al.</i> (2013)
Natural forest	Adult	Tp.	Germany	1, 2, 3	Tree	Growth	+	Natural	Del Río <i>et al.</i> (2014)
Natural forest	Adult	Tp.	Germany	1, 2, 3	Tree	Mortality	+	Natural	Neuer <i>et al.</i> (2015)
Natural forest	Adult	Md.	Spain	1, 2, 3	Tree	Growth	+	Natural	De-Dios-García <i>et al.</i> (2015)
Greenhouse	Seedling	Tp.	-	1, 2	Tree	Growth	+	Experimental	Fruléux <i>et al.</i> (2016)
Natural forest	Adult	Tp.	Spain	1, 2, 3, 4, 5, 6	Tree	Growth	+	Natural	Gazol & Camarero (2016)
Natural forest	Adult	Tp.	Germany	1, 2, 3, 4, 5	Tree	Growth, δ <sup>13</sup> C	+	Natural	Metz <i>et al.</i> (2016)
Natural forest	Adult	Tp., M., B.	Europe	1, 2, 3, 4, 5, 6	Ecosystem	Growth, Mortality	+	Natural	Ruiz-Benito <i>et al.</i> (2017)
Neutral effects									
Natural forest	Adult	Tp.	France	1, 2	Tree	Growth	=	Natural	Merlin <i>et al.</i> (2015)
Natural forest	Adult	Tp., Md., Mo., B.	Europe	1, 2, 3, 4, 5	Ecosystem	Growth	=	Natural	Jucker <i>et al.</i> (2016)
Greenhouse	Seedling	Tp.	-	1, 3, 5	Ecosystem	Transpiration	=	Experimental	Lübbe <i>et al.</i> (2016)
Natural forest	Adult	Tp.	France	1, 2	Tree	δ <sup>13</sup> C	=	Natural	Bonal <i>et al.</i> (2017)
Negative effects									
Natural forest	Adult	B.	Finland	1, 2, 3	Ecosystem	δ <sup>13</sup> C	-	Natural	Grossiord <i>et al.</i> (2014a)
Natural forest	Adult	Tp., Md., B.	Spain, Canada	1, 2, 3, 4, 5	Ecosystem	Growth	-	Natural	Paquette <i>et al.</i> (2018)
Mixed effects									
Natural forest	Adult	Tp., Md., Mo.	Europe	1, 2, 3, 4, 5	Ecosystem	δ <sup>13</sup> C	= +	Natural	Grossiord <i>et al.</i> (2014b)
Natural forest	Adult	Tp.	Germany	1, 2, 3, 4	Tree	Growth	= +	Natural	Mölder & Leuschner (2014)
Natural forest	Adult	Tp.	France	1, 2	Tree	Growth, wood density	= +	Natural	Toigo <i>et al.</i> (2015)
Natural forest	Adult	Tp.	Italy	1, 2	Tree	Transpiration	= -	Natural	Grossiord <i>et al.</i> (2014c)
Natural forest	Adult	Md.	Spain	1, 2, 3, 4	Ecosystem	Growth	= -	Natural	Jucker <i>et al.</i> (2014)
Natural forest	Adult	Md.	Spain	1, 2, 3	Tree	Transpiration, WUE	+ -	Natural	Grossiord <i>et al.</i> (2015)
Natural forest	Adult	Tp., Md., Mo., B.	Europe	1, 2, 3, 4, 5	Tree	δ <sup>13</sup> C	= + -	Natural	Forrester <i>et al.</i> (2016)
Natural forest	Adult	Tp., Md.,	Spain	1, 2	Tree	Growth, WUE	+ -	Natural	González de Andrés <i>et al.</i> (2017)

**Table 1** (Continued)

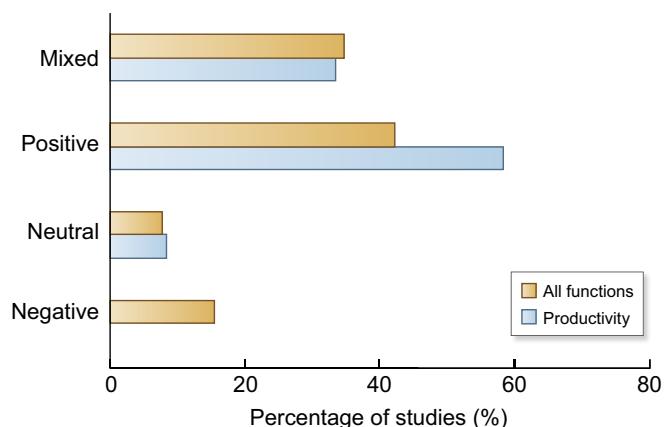
Ecosystem	Developmental stage	Forest type <sup>a</sup>	Country/Continent	Levels of species richness <sup>b</sup>	Scale	Studied function(s)/trait(s)	Mixture effect	Drought type	Source
Natural forest	Adult	Md.	Spain	1, 2	Tree	Growth, Mortality	+ –	Natural	Condés & del Río (2015)
Natural forest	Adult	Tp	Germany	1, 2, 3	Tree	Growth	–	Natural	Vitali <i>et al.</i> (2018)

Publications are classified based on resulting effects of higher tree species diversity on vulnerability to drought: positive effects (that is reduced vulnerability to drought), neutral effects (that is no effect on vulnerability to drought), negative effects (that is increased vulnerability to drought) and mixed effects (that is positive, negative or neutral effects occur in the same study but for different tree species or ecosystems).

<sup>a</sup>Tr., tropical forests; Tp., temperate forests; Mo., mountainous forests; Md., Mediterranean forests; B., boreal forests.

<sup>b</sup>Number of tree species in the studied forest stands.

<sup>c</sup>WUE, water-use efficiency.



**Fig. 3** Percentage of studies finding mixed, positive, neutral and negative effects of diversity on tree responses to drought for all studies (orange bars represent all functions,  $n = 28$ ) or for studies that only used productivity as an indicator of drought impacts at the tree-level (blue bars,  $n = 12$ ).

contrary to observations in other ecosystems such as grasslands (e.g. Isbell *et al.*, 2015), tree diversity is not systematically a positive modulator of drought impacts in forests. Therefore, relationships between diversity and drought impacts may be more context dependent in forests than in other ecosystems and/or experimental inconsistency across studies may complicate the comparisons of their findings.

Environmental conditions are known to play a significant role in diversity effects as the interactions between any given pair of species are dynamic, changing as resource availability or climate conditions change (Belote *et al.*, 2011). It is not unusual for ‘positive’ interactions that enhance functions to turn into ‘negative’ interactions under different biotic and abiotic conditions (e.g. shift from positive to negative diversity effects on tree growth during wet vs dry conditions in Iberian forests, Jucker *et al.*, 2014). Studies conducted across large geographical scales have suggested an important context dependency in tree diversity effects (Ratcliffe *et al.*, 2017). As environmental conditions (both biotic and abiotic) are highly variable among the studies considered in this review, it is likely that local site characteristics, climate conditions, management practices and species composition (that is functional traits) are interacting and adding complexity to the ‘diversity signal’ in forest ecosystems.

Regarding inconsistencies among studies that impact their comparison, the most notable is how drought impacts were characterized and measured: most studies used changes in annual growth rates, but some used more complex functional traits such as transpiration and water-use efficiency (Table 1). A reduction in transpiration, however, or an increase in stomatal closure does not necessarily translate into a reduction in growth (Jucker *et al.*, 2017), leading to potentially contrasting conclusions from studies looking at different traits. Other noteworthy differences include the scale (tree-level vs ecosystem-level assessments) and approach (experimental vs observational studies). Regarding the scale, most studies only looked at tree-level responses (Table 1). As demonstrated by Forrester *et al.* (2016), however, in six different regions in Europe, findings at the tree level may differ substantially from the ecosystem level in a given forest community. Overall, these differences make it difficult to conduct a systematic meta-analysis or even draw conclusions on the relative effect of these approaches on studies’ outcomes. If only studies that used growth rates as indicator of drought stress in natural ecosystems are considered and at the tree level, then most results reported positive effects of diversity and none reported solely negative effects (Fig. 3). Nevertheless, 41% of studies still reported neutral and mixed effects when using growth rates as the indicator (Table 1), suggesting that differences in

experimental approaches only partially explained the absence of agreement across studies conducted in forests.

#### IV. Advancing tree diversity research in a climate change context

In light of the discrepancy among studies, it seems obvious that, in order to perform powerful comparisons among studies, approaches first need to be standardized. Identification of the best metrics for assessing tree species diversity controls over drought resistance and comparison of these metrics for each specific question would represent a uniform framework from which to ask these important questions. Studies using aboveground growth rates are currently the most represented (Table 1) and growth is a good indicator of integrated drought responses at the tree and ecosystem levels, as this metric sums most physiological processes related to resource acquisition and use. Furthermore, they often require less labor-intensive sampling and no heavy instrumentation. That said, changes to aboveground vs belowground allocation could complicate aboveground growth as a singular metric, and work to determine how allocation, as well as diversity-controlled changes to allocation at the forest scale, is affecting drought responses would be of interest.

More complex functional traits provide stronger indications of the underlying physiological mechanisms and impacts of species interactions that remain relatively unknown. Such traits should therefore be systematically investigated in conjunction with growth metrics when field characteristics allow (see Table S1 for a list of traits). Additionally, to improve our mechanistic understanding, field studies interested in forest responses to drought solely should systematically consider assessing tree species diversity, including the diversity of functional traits. This approach would allow subsequent diversity–drought responses syntheses to use such pre-existing data.

Most studies focus on a few sites and species at most (Fig. S1), making global predictions more complicated as models need to know whether all species benefit from diversity or whether only a few do (Forrester *et al.*, 2016). Increasing the number of global studies (at ecosystem or regional-scales) should be the next step by using approaches such as national inventories, global databases or remote sensing tools. This should be developed in combination with long-term comparative platforms along environmental gradients in which tree species diversity varies in a factorial combination with climate (e.g. FunDivEUROPE platform, Baeten *et al.*, 2013). Experimental approaches in which tree diversity is artificially manipulated in combination with climatic conditions (e.g. ORPHEE experiment, Castagnyrol *et al.*, 2014) should also be extended as they keep environmental conditions constant allowing for causal relationships between tree diversity and functions to be established. Developing global and long-term approaches will allow scientists to investigate the role of the background climate and context-dependency of tree species diversity effects in forests (Ratcliffe *et al.*, 2017).

#### V. Conclusions

Diversity has strong potential to help us understand how and why forests respond to drought. Over the last 10 yr, a burgeoning

number of studies has emerged and, although far from complete, the data that do exist highlight that tree species diversity may be a major determinant of drought impacts in forests. However, considering that these findings are often contradictory, the obvious next step should be to investigate the underlying physical and biological mechanisms of species interactions driving diversity effects during droughts. Furthermore, our knowledge is currently limited to low-diversity forests, mostly temperate ecosystems, highlighting our need to further explore the role of tree diversity in ‘hyperdiverse’ forests in tropical regions where the significance of diversity during drought remains almost untested. A unified approach to addressing critical unknowns in diversity–drought relationships offers a powerful way forward for forecasting and mitigating the higher frequency and intensity of droughts expected for our forests. Therefore, to provide mitigation approaches for a climate-smart management of forest ecosystems, future work will need to use standardized approaches, possibly covering large gradients of climatic and biotic conditions.

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** List of tree species included in drought-diversity studies.

**Table S1** List of physiological mechanisms resulting in beneficial diversity effects.

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