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Woody plant adaptations to multiple abiotic stressors: Where are we?[☆]

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ABSTRACT

Interacting abiotic stresses exert a fundamental selective pressure on the adaptive syndromes of long-living organisms such as woody plants. However, general patterns and mechanisms describing woody plant adaptations to tolerate multiple abiotic stressors are yet to emerge. This hampers our ability to build predictive frameworks foreseeing species responses to stochastic changes in abiotic stress regimes due to climate change. With this Virtual Special Issue (VSI), we aimed to summarize what we know, and what we do not know, about woody plant adaptations to achieve tolerance to multiple abiotic limitations. To this end, we brought together studies exploring ecological or ecophysiological perspectives on woody plant adaptations to tolerate multiple abiotic stresses. Ecological studies suggest patterns associating trait trade-offs, climate, and biotic interactions with woody plants' multi-stress tolerance. Ecophysiological studies point to traits and conceptual frameworks that might explain some processes underpinning woody plant multi-stress tolerance. Here, we first revised the definitions of stress and stress tolerance used in ecological and ecophysiological research, providing a nomenclature of tolerance that could be used to unify definitions across research fields. Then, we summarized the main theories and evidence on woody plant adaptations to tolerate multiple abiotic stresses. Finally, we introduced the ecological and ecophysiological perspectives on this matter and placed the contributions to this VSI within the current state of the art. Altogether, this VSI allowed us to identify the lack of large-scale integration of patterns and processes describing woody plant adaptations to multiple abiotic stresses as a major gap in this field.

1. Introduction

Abiotic stressors are ubiquitous factors and exert fundamental constraints on species' distribution, form, and function. Such constraints are particularly relevant for sessile organisms, such as plants, especially woody ones. These are long-lived, perennial organisms continuously adjusting their resource acquisition, use, and conservation strategies to environmental and resource alterations (Smith and Huston, 1989; Niinemets and Valladares, 2006; Puglielli et al., 2021a). As a result, their adaptations to abiotic stress regimes in their natural habitat are reflective of different long-term environmental limitations, making woody plants important models for studying plant adaptation to multiple abiotic stressors (Niinemets, 2010a).

Habitats can be usually defined as having one overarching abiotic limitation that mainly constraints plant performance (i.e., the law of the minimum). However, despite absolute polytolerance to two stressors is generally low for woody plants (Niinemets and Valladares, 2006), more recent evidence (Laanisto and Niinemets, 2015; Puglielli et al., 2021b) has shown that the degree of polytolerance to two stressors is influenced by the interaction with other stressors, meaning that polytolerance strategies cannot be defined in terms of absolute, but relative polytolerance (Puglielli et al., 2021b). Multiple abiotic (and biotic) limitations always act in concert in a single habitat, and, as a result, plant performance is co-limited by the interaction of multiple environmental limitations (Niinemets and Valladares, 2008). For instance, in several ecosystems (e.g., Mediterranean / savanna shrublands, bogs, and seasonally dry tropical forests), multiple abiotic stressors characterized by different severity and timing during a growing season differently

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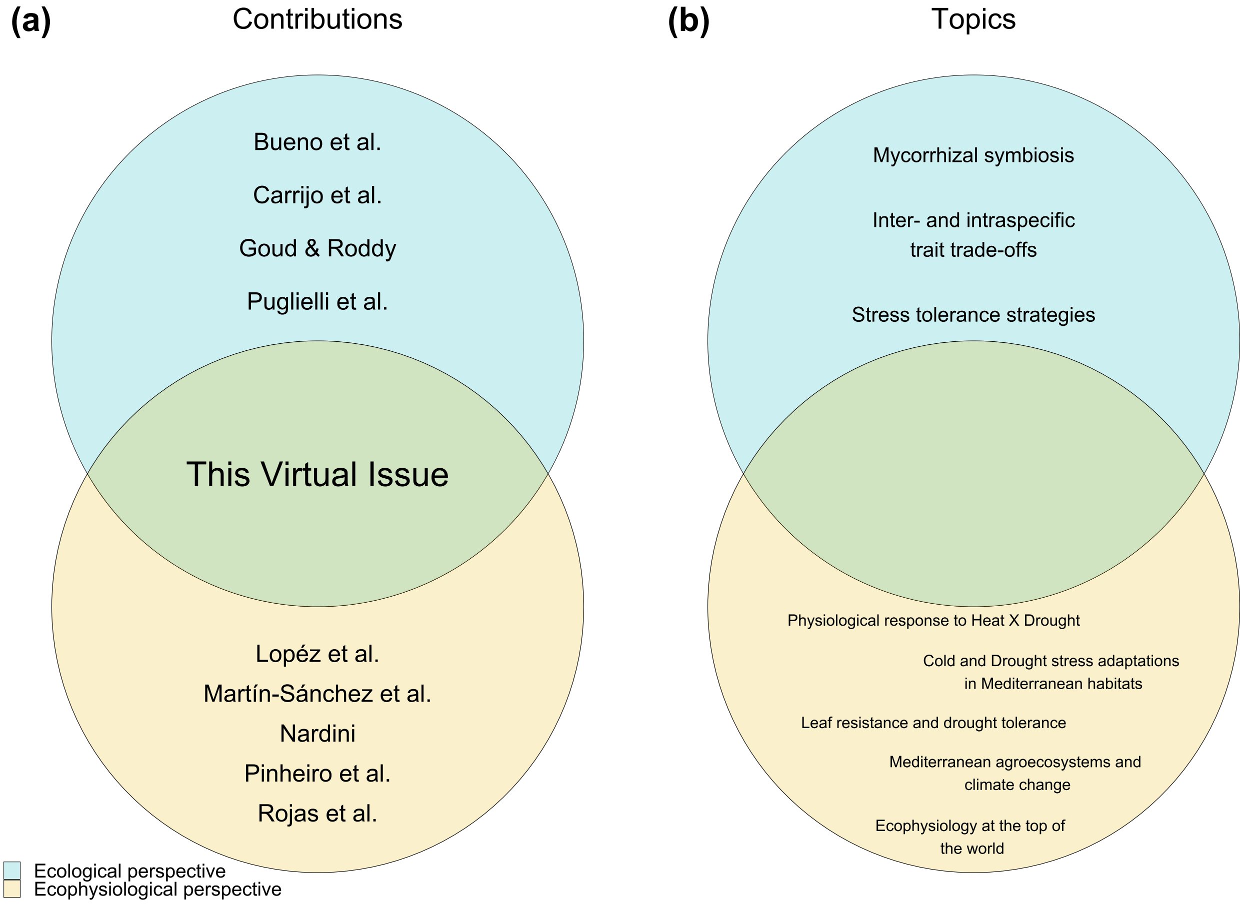

Fig. 1. Venn diagram mapping the contributions and the topics included in this Virtual Special Issue according to their ecological or ecophysiological perspective on woody plant adaptations to tolerate multiple stressors.

alter species ability to grow and reproduce (Niinemets, 2010a). Even drought spans a combination of multiple abiotic limitations besides water deficit stress (Volaire, 2018). These interacting and/or alternating abiotic limitations, which often have non-additive effects on plant performance, have shaped the adaptive evolution of woody plants (Larcher, 1987; Niinemets, 2010a), eventually defining their adaptive and acclimation potentials. Identifying the general patterns of woody plant adaptations to multiple abiotic stressors and disentangling the underlying processes (*sensu* Volaire et al., 2020) is necessary to pave the path towards generalization and predictions. This herculean task is particularly needed in the context of global climate change where long-term plant adaptations to the major abiotic stress, as well as their acclimation limits, have been, and will likely continue to be, challenged by novel and often unpredictable abiotic stress combinations.

In this Virtual Special Issue (VSI), we aimed at bringing together multi-taxon evidence on woody plants' adaptations to complex environmental matrices, where multiple abiotic stressors occur. We also brought together opinions and review articles to suggest how future research alleys on this topic should be built from the current knowledge. Importantly, the contributions that constitute this VSI span ecological and ecophysiological perspectives on woody plants' adaptations to achieve multi-stress tolerance (Fig. 1), increasing the possibility of directly comparing how different and yet interconnected fields of research try to address similar questions.

In this mini-review, we first revise the classical definitions of plant stress and stress tolerance to summarize how 'stress' and 'stress tolerance' are differently perceived by ecologists and ecophysiologists. In doing that, we highlight 'time' as an important addition to the definition of stress to better define the differences in which ecologists and ecophysiologists define stress (see Volaire et al., 2020 for an extensive review on this topic). When revising the concept of stress tolerance, we focus on the distinction between 'physiological tolerance' and 'ecological tolerance' (*sensu* Niinemets and Valladares, 2008), as we argue this to be one of the major obstacles in generalizing the concept of tolerance across different research fields. Second, we briefly review evidence supporting the existence of a single stress tolerance syndrome in woody plants. Finally, in the last two sections, we present the contributions of our VSI in the context of the more general research trends and approaches that have so far characterized the ecological and ecophysiological research on woody plant adaptations to tolerate multiple abiotic stressors. This mini-review introduces our VSI and does not provide a detailed review of the literature on woody plant adaptations to multiple abiotic stressors. For this we refer to the extensive review by Niinemets (2010a), and to the context introduced by the contributions in our VSI.

1.1. Some definitions of 'plant stress' and 'stress tolerance'

Levitt (1972) defined stress as a reduction in individual plant performance as environmental conditions become unfavorable on a (relatively) short timescale (see also Larcher, 1987 and Lichtenthaler, 1996 for similar definitions). This definition is easily interpreted from an acclimation perspective, as it suggests a dynamic response of plant performance in relation to varying abiotic factors. For this reason, this definition was promptly adopted by plant (eco)physiologists, who often build dose–response curves or temporal trends of how physiological / morphological traits dynamically adjust when the level of the abiotic limitation changes during a short time scale (Volaire, 2018; Volaire et al., 2020). In this context, tolerance can be interpreted as the breadth of a dose–response curve, or of a temporal trend, set by the upper and lower levels of a given abiotic factor either corresponding to a minimum

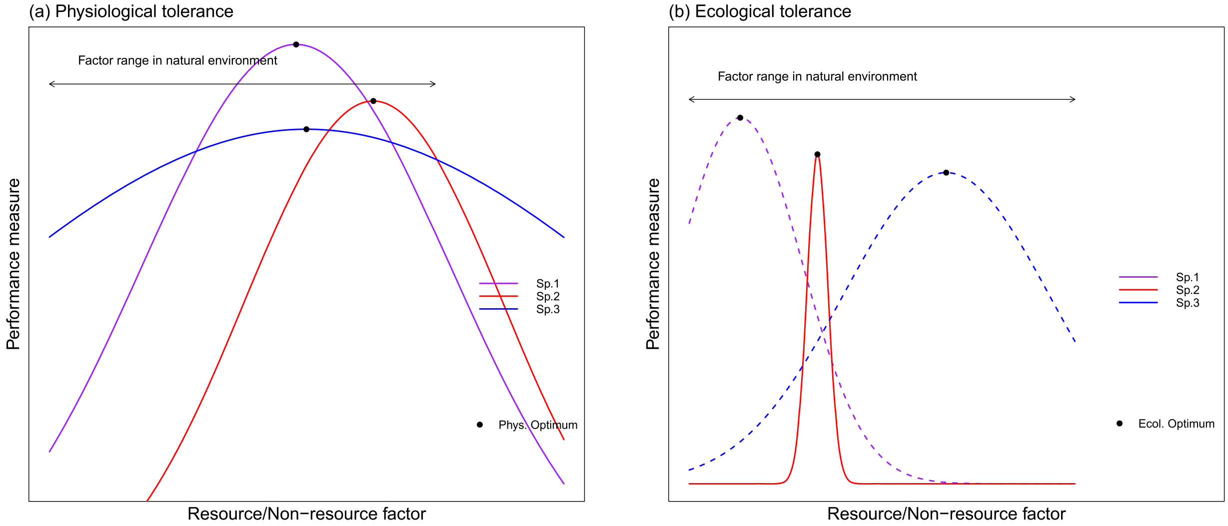

Fig. 2. Conceptual difference between **(a)** physiological tolerance, and **(b)** ecological tolerance. Performance curves for three virtual species (Sp.1–Sp.3) along a resource/non-resource gradient of an abiotic factor are shown. The black dots in each panel correspond to the physiological or ecological tolerance optimum for each species (i.e., where the performance function is maximized). The theoretical range of resource/non-resource factor in the natural environment is also shown to highlight the conceptual difference between physiological and ecological tolerance. Dashed lines represent truncated tolerance functions for species in the field (see main text). Curves were drawn following Niinemets and Valladares (2008) with permission.

or disrupted plant performance. This is what is usually referred to as 'physiological tolerance', and the maximum of this function is then called the 'physiological optimum' (Niinemets and Valladares, 2008; Fig. 2a). Comparing 'physiological tolerance' curves between species allows interpreting the adaptive value of plant acclimation limits to given abiotic factors (Lichtenthaler, 1996; Poorter et al., 2010; Garnier et al., 2015).

Grime (1977) defined stress as the constraint imposed by the chronic (i.e., long-term) lack of resources over biomass production in a habitat. The term 'chronic' brings a clearer adaptive perspective to this definition compared to Levitt's one. That is plants adapted to chronically resource-limited habitats have an inherent slow biomass accumulation compared to plants adapted to resource-rich habitats, even if it were to grow them under the same environmental conditions. Grime's definition of stress, usually referred to as '*resource stress*', is the most common definition of stress used in plant ecological research. Later, Chapin (1991) nuanced Grime's definition of stress to accommodate the '*non-resource stress*', referring to the stress imposed by environmental factors that are not resources for a plant (e.g., temperature). Despite the distinction between resource and non-resource stress is still in use in the field of functional ecology (see Craine et al., 2012 for a review), the two stress types constantly interact in natural environments because non-resource stress directly alters a plant's demand for resources (Craine et al., 2012). Therefore, multiple stressors interact to shape a species' realized tolerance strategy to both resource and non-resource stress (Puglielli et al., 2021b).

Given these considerations, the concept of tolerance in ecological research (hereafter ecological tolerance, *sensu* Niinemets and Valladares, 2008) refers to a curve that has both a breadth and an 'ecological optimum' that might differ from the physiological one (Niinemets and Valladares, 2008; Fig. 2b). This is because in their natural environment, species do not only chronically face a narrower range of a resource compared to the ones supplied when building physiological response curves (Niinemets and Valladares, 2008), but they also compete interspecifically for that resource (Fig. 2b). Additionally, interacting non-resource stresses further alter a species ability to use a given resource, contributing to shape a species' ecological tolerance. In other words, multiple long-term selective pressures at a given habitat have shaped a species' ecological tolerance.

To clarify the difference between 'physiological' and 'ecological' tolerance definitions, we can try to re-express them by using the dichotomy 'fundamental' *vs*. 'realized' niche (*sensu* Hutchinson, 1957). The fundamental niche is loosely defined as the potential set of environmental conditions where a species can grow, survive, and reproduce, while the realized niche is where a species thrives in the presence of other species and dispersal barriers. In other words, the realized niche is the shrunk/skewed/truncated version of the fundamental niche. Similarly, we can define 'physiological tolerance' as the potential plants' performance to a given abiotic factor, and it can be interpreted as a measure of 'fundamental tolerance'. On the other hand, the 'ecological tolerance' for a given abiotic factor reflects how the fundamental tolerance is shrunk / skewed / truncated in the real world – i.e., where other species, abiotic and biotic factors have shaped, during evolution, the tolerance breadth and the ecological optimum of a given species (Niinemets and Valladares, 2008). Therefore, we define ecological tolerance as a measure of 'realized tolerance'. As such, the physiological and the ecological optima will represent a measure of potential and realized niche position for a given abiotic stress factor, when optima are compared across species.

Overall, it is evident that physiological and ecological tolerance of a given species are subject to different biological interpretations. As a result, there is no general agreement on the definition of tolerance, and ecologists and ecophysiologists inherently rely on different definitions. To this purpose we have provocatively used the differentiation 'fundamental' *vs*. 'realized' stress tolerance, highlighting the similarities with the 'fundamental' *vs*. 'realized' niche concepts, as these concepts are, on the contrary, rarely confused. Similar conceptual differences can also be found in other research fields, such as biogeography, where differences between 'potential' *vs*. 'realized' range size are often defined following Hutchinson's concept of 'fundamental' *vs*. 'realized' niche (e.g., Nogués-Bravo et al., 2014). Here we call for a switch towards the 'fundamental' *vs*. 'realized' tolerance definition to set immediately the conceptual similarities between definitions while stressing their different biological interpretation. By building on the universal niche nomenclature, our proposal to redefine tolerance has the potential to unify the concept of tolerance across research fields.

Finally, we want to point the attention to an important limitation of the above-described approaches: they rarely account for the effect of ontogeny, which is necessary to compare tolerances across species (Niinemets, 2010a). However, Niinemets and Valladares (2006) argued

Table 1
The main adaptations of stress-tolerant plants defining the stress tolerance syndromes proposed by Grime (1977) and by Chapin et al. (1993).

Adaptation	Grime (1977)	Chapin et al. (1993)
Enhanced nutrient retention	Yes	
Evergreen habit	Yes	–
Growth rate	Slow	Slow
Photosynthesis	Low	Low
Organ longevity	Long	Long
Secondary metabolites concentration	High	High
Stomatal conductance	–	Low
Tissue N	–	Low
Tissue turnover	Slow	Slow
Transpiration	–	Low
Water conservation	High	High

(and partly tested) that despite ecological and physiological tolerance values changing with ontogeny (e.g., Niinemets, 2006; Sendall and Reich, 2013; Sendall et al., 2015), relative differences among species are going to remain largely constant in a comparative context. As of today, we still miss large cross-species data on ontogenetic changes in species tolerances, hindering our ability to test for the ontogenetic effect explicitly and conclusively (Puglielli et al., 2021a). Thus, the 'ontogenetic assumption' remains reasonable because it is the only one possible at this stage.

1.2. A single syndrome to tolerate them all?

The definition of a single, general stress tolerance syndrome that is valid for all plants is a long-standing goal of ecological and ecophysiological research on plants' abiotic stress tolerance (e.g. Grime, 1977; Chapin et al., 1993; Table 1). The predictions reported in Table 1 are quite clear and point to the idea that a single stress tolerance syndrome must be inherently linked to traits favoring slow growth, slow acquisition of resources, and slow organ turnover. Despite some criticism of this idea (Grubb, 1998), as of today, we know that traits linked to a conservative acquisition and use of resources are found in unproductive, harsh habitats (Wright et al., 2004, 2005; Moles, 2018; Yang et al., 2019), and this is usually referred to as the 'slow' strategy of stress tolerators. The identification of trait trade-offs reflecting plant strategies in relation to habitat characteristics is a major advancement provided by the advent of trait-based ecology (*sensu* Westoby and Wright, 2006).

1.2.1. The importance of plant phenology

Despite the idea of a general stress tolerance syndrome represents a successful framework in a broad comparative context, some considerations need to be made. At the leaf level, for instance, the 'slow' strategy of stress tolerators might be more reflective of evergreen broad- and needle-leaved species' strategies. This is because of the long leaf-life span of evergreen leaves, which allows sorting of clear large-scale interspecific differences in leaf trait–environment relationships. In other words, a longer leaf-life span means probably more year-to-year exposure to adverse environmental conditions, marking more evident leaf morpho-functional local adaptations along broad gradients in evergreens (Wright et al., 2005).

On the other hand, deciduousness represents an equally successful alternative strategy for temporally avoiding, and therefore surviving, highly stressful periods (Zanne et al., 2014, 2018). For instance, deciduous species become particularly successful in highly seasonal environments – e.g., seasonally dry tropical forests (e.g., Poorter and Markesteijn, 2008), or where the growing season becomes particularly short. Deciduousness can decouple the leaf trait–environment relationships for the species belonging to this functional type, as the leaves are formed under favorable environmental conditions, potentially missing leaf-level adaptations to the stress imprint in their natural habitat. Therefore, it is of uttermost relevance considering how the leaf types (or more generally functional types), as well as their related phenological events (Volaire et al., 2020), integrate in the trait syndromes that woody plants have evolved under regimes of multiple abiotic stressors. For instance, plant functional type is considered the main determinant of biomass allocation in relation to shade or drought tolerance in woody plants globally (Puglielli et al., 2021a). Contrasting strategies between functional types, or time-dependent processes, can blur the emergence of patterns trying to link traits and tolerances across species. Numerous previous studies have in fact already pointed out the constraints imposed by differences among plant functional types in generalizing trait–tolerance and trait–environment relationships (e.g., Lusk et al., 2008; Hallik et al., 2009; Markesteijn and Poorter, 2009; Stahl et al., 2013; Tomlinson et al., 2013a, 2013b; Rueda et al., 2018; Puglielli et al., 2021a).

Other studies have stressed the need to account for time-dependent processes to disentangle patterns of plant adaptations to abiotic stress (Volaire, 2018; Volaire et al., 2020). This aspect is highly relevant forchoosing the right trait framework depending on the timescale of the analysis, and this is indeed the most striking difference between the ecological and the ecophysiological approach. According to Volaire (2018), the ecological approach uses functional traits or ecological tolerances to describe species ecological strategies, but these might fail to reveal plant adaptations to short-term fluctuations in resource and non-resource stressors. In line with this, a recent meta-analysis by Wang and Wang (2023) showed that the acclimation responses of woody plants to the interacting effect of shade and drought are more evident in terms of process traits compared to functional traits (*sensu* Volaire et al., 2020). On the other hand, functional traits better characterized the adaptive value of the differences in the acclimation responses of shade or drought tolerant *vs.* intolerant species in response to the same shade × drought treatment. Thus, ecophysiological adaptive strategies of woody plants, that is the group of mechanisms that operate at the temporal scale of multiple abiotic stress fluctuations (e.g., during a growing season; Volaire, 2018), represent an additional adaptive dimension requiring urgent integration in the research agenda on woody plant adaptations to tolerate multiple stressors.

1.2.2. The search for a shade tolerance adaptive syndrome

The identification of a general shade tolerance syndrome for woody plants is another important obstacle in identifying a single stress tolerance syndrome, as being shade-tolerant does not necessarily imply embracing the previously described 'slow' strategy. On the contrary, the evidence is quite heterogeneous when coming to plants' adaptations to low light environments (see Valladares and Niinemets, 2008; Niinemets, 2010b; Valladares et al., 2016; Poorter et al., 2019 for extensive reviews on this topic). One interesting aspect is that plants' responses to low light seem to display opposite patterns when comparing acclimation and adaptive responses (e.g., Lusk et al. 2008 for leaf mass per area; Puglielli et al. 2021a for biomass allocation to leaves, stems, and roots), and this aspect deserves further research.

While for plant morpho-physiological acclimation responses to low-light (and their adaptive value) we recommend reading Poorter et al. (2019), here we report the two main competing hypotheses on the achievement of shade tolerance from a purely adaptive perspective: (i) the 'carbon-gain hypothesis', and (ii) the 'stress tolerance hypothesis'. The carbon gain hypothesis (Givnish, 1988) predicts that shade-tolerant species enhance net energy capture in low light, mainly by allocating carbon to leaf production to maximize leaf area compared to intolerant species. The second hypothesis assumes high stress tolerance in shade and lower carbon losses (Kitajima, 1994), and predicts that shade-tolerant species construct more robust leaves with greater dry mass per unit leaf area compared to intolerant species. Currently, there is no consensus on the general (trait) syndrome (Poorter et al., 2019), or on biomass allocation patterns (Puglielli et al., 2021a), associated with high shade tolerance in woody plants. However, the available evidence (e.g., Lusk et al., 2008; Hallik et al., 2009; Puglielli et al., 2021a)

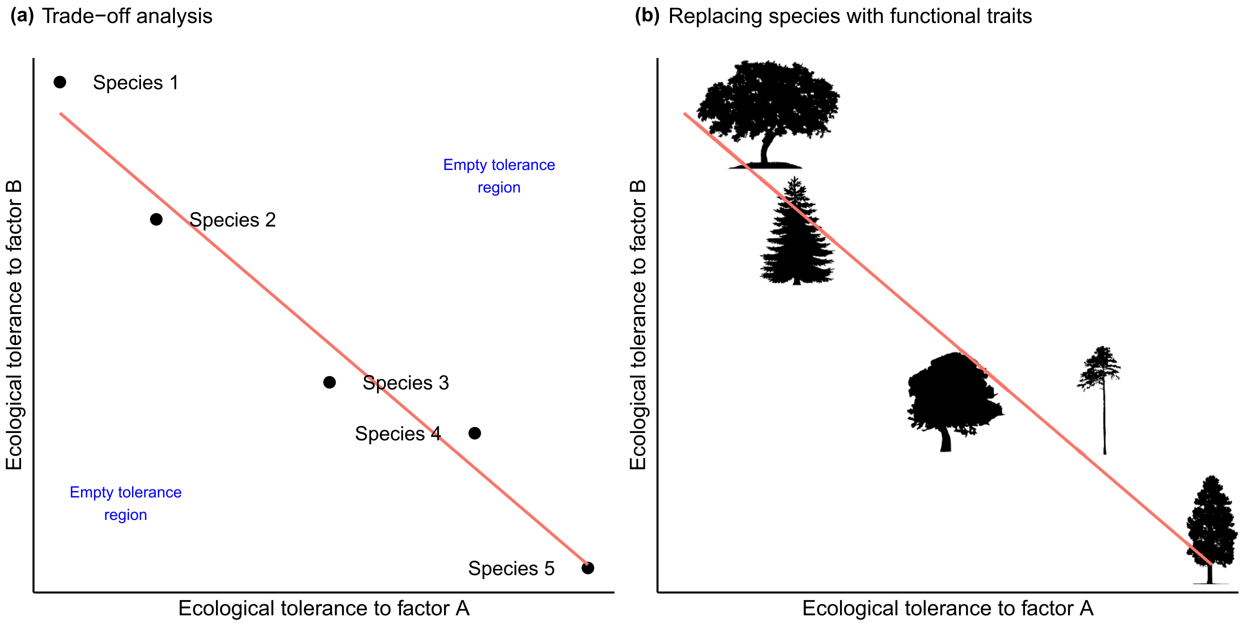

Fig. 3. Main approaches used in the ecological research on plant abiotic stress tolerance. **(a)** Identifying the tolerance patterns through trade-off analyses involving ecological tolerances. This approach identifies not viable tolerance combinations – i.e., empty tolerance regions. **(b)** Replacing species with their traits (usually done through a trait-based approach) to identify the trait combinations underlying the pattern.

suggests that to finally disentangle the trait syndrome(s) of shade-tolerant *vs.* -intolerant woody plants in the field, we need to consider the interaction between the biome/ecosystem (e.g., tropical *vs.* temperate) where a species occurs and the plant functional type it belongs. This further stresses the previous considerations on the importance of accounting for plant functional type's effect when studying plant adaptations to abiotic stresses. Another important body of evidence suggests that the traits linked to shade tolerance can display pronounced changes with ontogeny (Delagrange et al., 2004; Niinemets, 2006; Lusk et al., 2011; Sendall and Reich, 2013; Sendall et al., 2015; Puglielli et al., 2021a), which is likely to interact with the above-mentioned determinants (Puglielli et al., 2021a). In this context, however, the same previous considerations on the lack of large-scale ontogenetic data on stress tolerance apply as well.

1.2.3. The need for multiple trait dimensions

The search for general adaptive syndromes evolved by woody plants to tolerate multiple co-occurring or subsequent abiotic stressors is of uttermost importance to foresee species responses to current and future climatic changes (Niinemets, 2010a). Some patterns such as the Leaf Economics Spectrum (Wright et al., 2004) are largely accepted, and, for instance, the Leaf Economics Spectrum was already shown to be linked, weakly though, to species ecological tolerance to shade and drought (Hallik et al., 2009). However, new patterns have emerged – i.e., the Global Spectrum of Plant Form and Function (Díaz et al., 2016). Others, instead, have been only envisioned, such as the Whole-Plant Economic Spectrum (Reich, 2014), predicting that a 'fast–slow' traits trade-off can explain all the trait combinations for above- and belowground plant organs, including the hydraulic trait dimension. These new patterns have never been analyzed alongside species tolerance towards multiple abiotic stresses.

Nevertheless, there is evidence that the hydraulic dimension (e.g., Li et al., 2015) and the fine-root two-dimensional space (Carmona et al., 2021) are independent of the Leaf Economics Spectrum and of the Global Spectrum of Plant Form and Function, respectively, requiring an integration of the idea of a 'Whole-Plant Economic Spectrum' (Reich, 2014). Independent trait dimensions can, in fact, result in much more trait combinations than those expected based on trait trade-offs (Laughlin, 2014), possibly resulting in unpredictable trait syndrome–tolerance relationships. Overall, we call for more analyses linking measures of abiotic stress tolerance to multiple pattern and process trait dimensions (*sensu* Volaire et al., 2020) carefully selected from independent trait planes / axes in order to more efficiently identify general tolerance syndromes (see Laughlin, 2014 for a discussion on the importance of trait independence for identifying plant strategies). This endeavor is strongly needed to finally tackle the inherent multidimensional nature of multi-stress tolerance in woody plants.

2. Ecological perspective on woody plant multi-stress tolerance

The ecological perspective on stress in woody plants has typically been focusing on two broad directions: trade-offs, especially between different abiotic stress factors; and functional trait correlations with and within different stress levels (Fig. 3). The first direction is best described as a top-down theoretical approach, presuming strict trade-offs between woody plant's capability of tolerating different stress factors (e.g. Smith and Huston, 1989) due to physicochemical constraints restricting adaptations and acclimatizations (Laanisto and Niinemets, 2015; Puglielli et al., 2021b). The second direction has emerged more from local scale case studies trying to assess how much different stress factors affect various functional traits. This approach rapidly developed over time into global assessments of economic spectra describing the functional spaces of above- and below-ground plant organs to assess the full functionality of plants (Wright et al., 2004; Diaz et al., 2016; Carmona et al., 2021; Weigelt et al., 2021).

Trade-offs have traditionally been defined through negative relationships between two traits (or features or parameters, etc.) of living organisms. The constraint of having just two traits against each other limits the potential insightfulness of such analyses due to the multifaceted nature of stress and its tolerance and effect patterns (Puglielli et al., 2021b). In this context, another significant aspect is the nature of the trade-off relationship (Grubb, 2016). While the earlier conceptual trade-off models of abiotic stress tolerance expected a strict "boundary line" type (*sensu* Grubb, 2016) of trade-offs, the analysis with empirical data have shown high variability of polytolerance patterns of abiotic stress tolerance (e.g. Niinemets and Valladares, 2006; Laanisto and

Niinemets, 2015), with the trade-off type clearly being “trend line” (*sensu* Grubb, 2016).

The dispersion around both sides of the trade-off line clearly indicates a larger, if not dominant, role of adaptation and acclimatization in shaping the trade-offs (which are still present, just not as omnipresent as traditionally thought) in woody species abiotic stress tolerance patterns. Trend line trade-off suggests that adapting to further tolerance might still be possible, but that would depend on the attainability of favorable combinations of functional traits; while boundary line trade-off indicates the absolute tolerance limit. Thus, further studies on this topic discovering that tolerating multiple stress factors at the same time, or polytolerance, in woody species sometimes tends to cross some trend lines and have to pay more attention to the nature of the trade-off line. Such crossings can only happen in a trend line trade-off space, not in a boundary line one (Puglielli et al., 2021b).

This VSI includes two perspective studies that describe two broad directions to approach this new perspective. The first one is treating the advancement of knowledge from within the abiotic stress tolerance space (Puglielli et al., 2022 this issue). These authors point out the need for a more comprehensive and holistic approach in stress tolerance trade-off studies, and they say that studying species tolerance or adaptations to multiple stressors is highly complicated because of the inherent multidimensionality of plants’ strategies in coping with multiple stresses. This is why they propose a potential roadmap towards the development of a “periodic table” for abiotic stress tolerance of woody plants. The roadmap is based on a theoretical framework of Winemiller et al. (2015), where five key ecological dimensions are selected (habitat, strategy, trophic, defense, and metabolic dimensions) that ought to provide sufficient wholesome insight for describing an organism’s position in a virtual “periodic table” of stress tolerance. Using this approach dramatically reduces the number of biological dimensions to tackle the multidimensional nature of woody plant adaptations to tolerate abiotic stresses (*sensu* Puglielli et al., 2021b), where the limits of abiotic stress tolerance strategies of woody plants were defined on a global scale.

The second perspective brings into play the biotic interactions for explaining tolerance towards multiple stresses (Bueno et al., 2022 this issue). Their review provides a short evolutionary timescale on when and how mycorrhiza developed on woody species and then provides more detailed accounts of how this symbiotic relationship helps mitigate different abiotic stress factors (drought, cold, heat, nutrient deficiency, and shade). They present key mechanisms for how mycorrhiza can help tolerate a specific abiotic stress factor, but also the crucial trade-offs related to mitigation processes (e.g., from limitations related to fungal life strategies and growth forms to concurring nutrient dynamics and biogeographical constraints related to stress mitigation).

Bueno et al. (2022 this issue) also provide a useful theoretical framework on how the symbiosis between mycorrhiza and woody species could function in multiple abiotic stress situations. They point out that such experimental and observational research is scarce, which is why they lay out the first steps to take toward understanding the complexity of plant responses to multiple stress factors and their mediation strategies by mycorrhizal fungi. According to their conclusions, the first step would be to identify how severely different combinations of abiotic stress can limit the set of mitigation resources available to mycorrhiza. Thus, this complex and underexplored topic would require a geographically and environmentally diverse approach.

Tolerating abiotic stress is one of the countless research areas that have been dominated by functional ecology in recent decades. On a larger spatial scale, the effect of abiotic stress on plant functional traits is relatively well known on the main climatic gradients and is linked to plant strategies (Wright et al., 2004; Reich, 2014; Díaz et al., 2016; Carmona et al., 2021), while local scale variations both within and between species are largely unknown (Goud and Roddy, 2022 this issue). Local-scale variations in intra- and interspecific trait variability of the most frequently used functional traits on both leaf and plant level in contrasting environmental conditions are presented in two papers in this VSI.

Carrijo et al. (2021 this issue) studied functional traits in Brazilian savanna within the framework of the global spectrum of plant form and function (Díaz et al., 2016) – one habitat was characterized by old lowland alluvial soils with low fertility and low water-holding capacity, and the other one by upland areas in the interfluvial zone with fertile and water-holding soils. They sampled six functional traits (leaf area, leaf thickness, specific leaf area, stem-specific density, relative bark thickness, and maximum plant height) of 101 species. They found, expectedly, that stress tolerance strategies of species depend on the water deficit and fire regime of the habitat. An interesting aspect of their result was that the same response patterns were found for both between communities and within species analysis – indicating that if local conditions are specific enough, they can act as dominating selective agents at multiple levels of biological organization simultaneously. This knowledge provides us another potential angle for synthesizing together the two traditionally contrary approaches (trade-offs vs. trait correlations) used in understanding the stress tolerance of plants.

At the same time, another study in our VSI (Goud and Roddy, 2022 this issue) showed that the trait–trait and trait–environmental patterns can also depend on the considered level of biological organization. This research was carried out in a Pine barrens (rare temperate forest ecoregion in coastal areas of northeastern North America) gradient from lowland bog to upland forest, where the authors studied leaf functional traits (SLA, LDMC and leaf thickness) on three dominant shrub species. Their results suggest that the between- and within-species trait variations along environmental gradients form a complex set between adaptations, acclimatization and micro-environmental variations. This knowledge brings forth a somewhat forgotten concept in functional ecology according to which plants, and especially woody plants, are structurally modular organisms (Watson, 1986; de Kroon et al., 2009; Herrera, 2017), and that different parts of the same plant, which can range in size from leaves to whole branches or root systems, can respond differently to variation in abiotic and biotic conditions. There are so far very few studies that have analyzed how environmental factors specifically affect the intraspecific variability of different plant parts of the same organism (see Herrera, 2017, for review). Thus, the approach by Goud and Roddy (2022 this issue) is an important step toward disentangling the reactions and mechanisms at work along complex environmental gradients.

3. Ecophysiological perspective on woody plant multi-stress tolerance

A plant’s ability to survive stressful environments strongly relates to a number of tolerance mechanisms, ranging from molecular to physiological and ecological level. Understanding plant stress responses and associated tolerance mechanisms is crucial to both basic biology as well as to improve predictions of plant impacts of climate change, thus enabling greater societal awareness and mitigation planning.

In this VSI, we host five ecophysiological-oriented review articles that survey a series of studies covering the main responses of woody plants to a multitude of abiotic stressors. Briefly, these reviews focus on:

(i) The main stressors of two relevant woody species in their native environments – i.e. *Quercus ilex* L. (an evergreen oak that dominates the landscape of several Mediterranean forests) and *Polylepis tarapacana* Phil. (a tree characteristic of the Altiplano, one of the highest elevation forest stands on Earth) (Martín-Sánchez et al., 2022 this issue; Rojas et al., 2022 this issue).

(ii) The morpho-anatomical and physiological adjustments against combined abiotic stressors (López et al., 2022 this issue; Nardini, 2022 this issue).

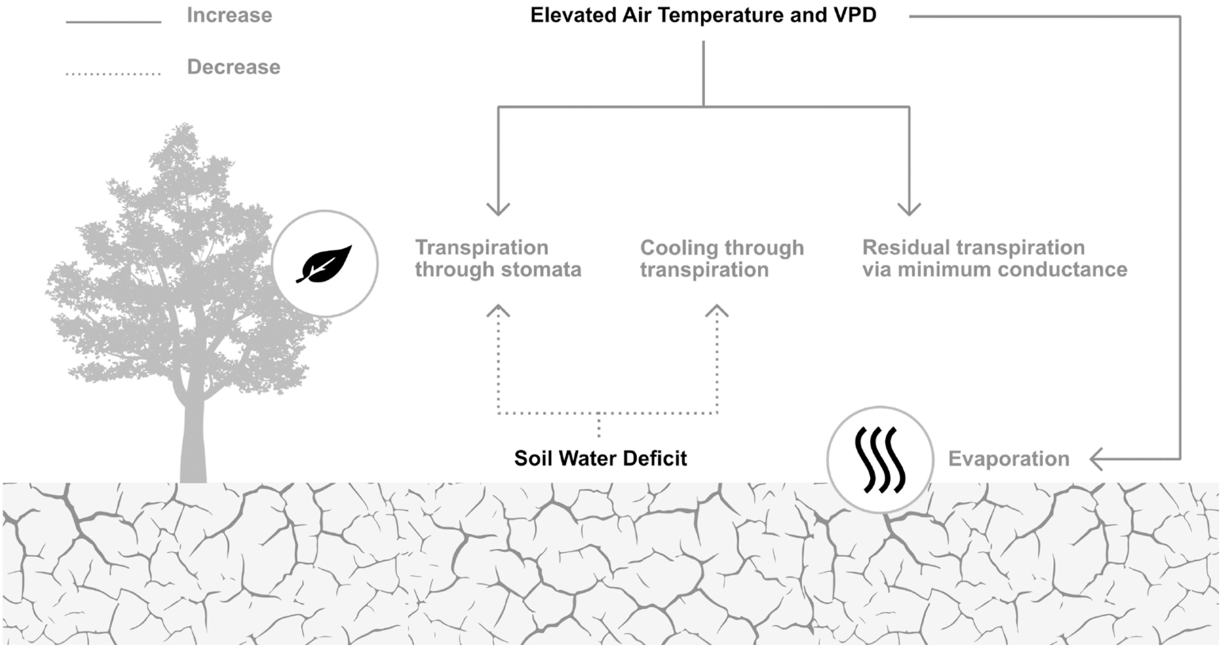

Fig. 4. The interaction between soil drought and elevated air temperature, and consequently vapor pressure deficit (VPD), aggravating plant stress. During soil drought, stomatal closure reduces transpiration and thus leaf cooling, potentially leading to extreme foliage temperatures, especially under a warming atmosphere. In parallel, elevated air temperature and VPD increase leaf water loss through both stomata and cuticle (represented by leaf minimum conductance) as well as evaporation from the soil, aggravating drought and potentially leading plants to lethal dehydration levels.

(iii) The importance of a comprehensive understanding of plant stress responses aiming at improving agroecosystem practices in a context of climate change (Pinheiro et al., 2022 this issue).

Interestingly, all ecophysiological-oriented reviews in this issue share a common interest regarding the effects of water scarcity on the studied species and describe recent advances in drought stress research – including the most common responses and tolerance mechanisms. This concern can be explained since drought consists of a major threat to both natural ecosystems and contemporary agriculture (Gupta et al., 2020), which has been intrinsically associated with increasing woody plant mortality across the globe over the last century (Allen et al., 2010; Choat et al., 2018), and is projected to increase in frequency and intensity in the future due to climate change (Trenberth et al., 2014).

It is worth mentioning that increasing air temperatures and elevated vapor pressure deficits (VPD) frequently accompany drought events and impose additional challenges to plant survival and growth (Grossiord et al., 2020; López et al., 2022 this issue; McDowell et al., 2022) (Fig. 4). One of the most interesting facts about the combination of drought and atmospheric warming (and thus elevated VPD) is how each of these stresses can exacerbate the other. On one hand, elevated temperatures increase water evaporation from soils aggravating soil water deficit (McDowell et al., 2018). On the other hand, drought-induced stomatal closure reduces transpirational cooling, thereby increasing leaf temperature and potentially threatening the integrity of leaves (Shirley, 1936; López et al., 2022 this issue). In this context, studies such as those presented by Martín-Sánchez et al. (2022 this issue) and Rojas et al. (2022 this issue) assessing the ecophysiology of woody species inhabiting environments where drought is often accompanied by extreme temperatures are of utmost importance.

From a physiological perspective, stress responses are often reflected in changes in carbon and water relations, which are particularly sensitive to both drought and heat (Choat et al., 2018). For instance, during drought, stomatal closure is one of the first mechanisms aiming at reducing water loss and plant dehydration (Cardoso et al., 2018; Creek et al., 2020), occurring around the leaf turgor loss point (Cardoso et al., 2020). This protective mechanism, however, directly results in reductions in photosynthesis which, if extended, might result in carbon starvation and leaf malfunctioning (McDowell et al., 2008). In any case, stomatal closure is crucial for the plant to avoid fast desiccation and to maintain healthy levels of hydration until rainfall resumes. Even after stomatal closure, though, plants continue to lose water at a much lower rate through the cuticle and partially open stomata (Duursma et al., 2019). This minimum transpiration rate can be rapidly exacerbated in case of elevated air temperatures and VPD, favoring plant dehydration and, ultimately, damage (López et al., 2022 this issue). Therefore, another important strategy often observed in woody plants during dry and warm conditions is leaf shedding, which although represents a direct loss of carbon and nutrients, restricts total tree transpiration in a more efficient manner than simple stomatal closure (Ruehr et al., 2019; López et al., 2022 this issue).

In case more intense plant dehydration takes place, water status might drop below a threshold level at which air bubbles are pulled inside the xylem, expanding, and completely blocking the water transport in that particular conduit (i.e., embolism) (Tyree and Sperry, 1989). Widespread xylem embolism in turn, eventually results in a complete failure of the hydraulic system of plants, thus constituting the primary cause of drought-induced mortality (Choat et al., 2018). Therefore, the lower the water status threshold for embolism induction and spread, the higher the xylem resistance to embolism. This protective mechanism has been observed for a number of drought tolerant species (McAdam and Cardoso, 2019), including *Q. ilex* subsp. *ballota* that occurs in the driest parts of the Mediterranean region (Martín-Sánchez et al., 2022 this issue). Xylem embolism can also result from freeze–thaw cycles and trees of *Q. ilex* growing under a typical continental subtype of the Mediterranean-type climate, where cold winters are common, are likely also tolerant to freeze-induced embolism (Martín-Sánchez et al., 2022 this issue).

Plants occurring in water-limited environments often exhibit hard leaves with high mass per unit area (LMA), which leads to a compelling discussion about the coordination between leaf mechanical resistance and drought tolerance (Nardini, 2022 this issue). Combined tolerance to

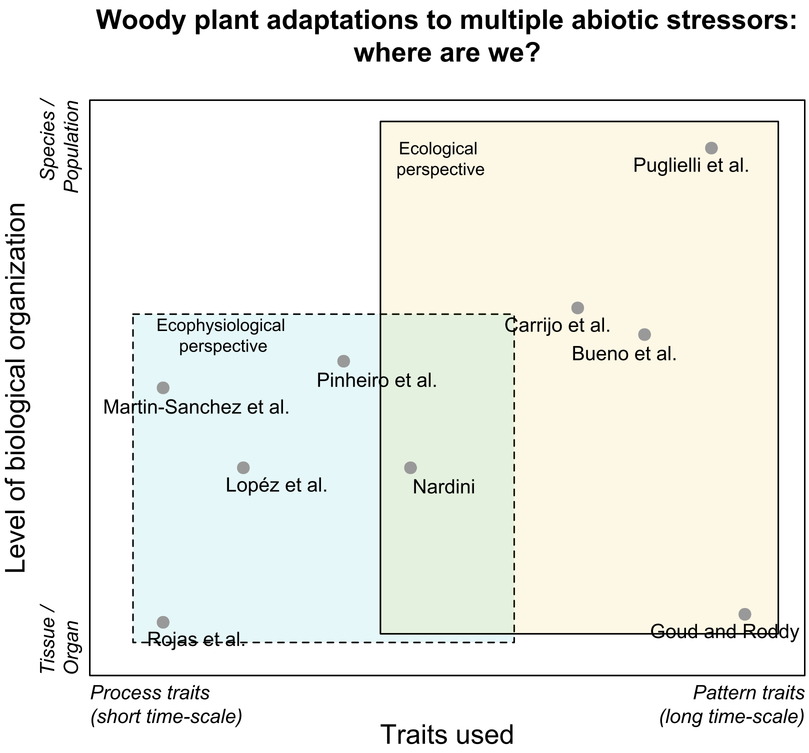

Fig. 5. Mapping the contributions included in this Virtual Special Issue within the conceptual framework provided by Volaire (2018) aimed to summarize the conceptual differences between ecological or ecophysiological perspective on plant adaptations to tolerate multiple stressors. The available ecological and ecophysiological evidence on the topic, reviewed here and summarized by the contributions to our Virtual Issue, spans shaded areas, with some overlaps between ecological and ecophysiological perspectives. Empty areas of the space identify major research gaps.

these stressors arises because some anatomical modifications observed in hard leaves (i.e., leaves with high LMA) – including thick cell walls, high major vein density, and narrow xylem conduits – are mechanistically correlated to physiological traits conferring tolerance to dehydration – such as low turgor loss point and high xylem resistance to embolism (Nardini, 2022 this issue). In fact, increases in drought tolerance (lower turgor loss point and higher xylem resistance to embolism), paralleled by increases in LMA (indicating higher leaf mechanical resistance), have been observed for sunflower plants exposed to drought conditions during growth (Cardoso et al., 2018). Further studies assessing variations in both drought tolerance and leaf mechanical resistance within woody species (e.g., da Silva Brito et al., 2022) and genotypes are thus necessary for a better understanding of whether trees can exhibit the same adaptive patterns as observed in herbaceous plants.

Uncertainties about the vulnerability of woody species in different ecosystems to multiple abiotic stressors are still large. Therefore, assessing how plants of different ecosystems respond to extreme abiotic stress factors is much needed, as acclimation and adaptation mechanisms can be then exploited to sustain agroecosystems and conserve biodiversity in the context of climatic change (Pinheiro et al., 2022 this issue).

4. Conclusion

With our VSI, we wanted to focus on the main advancements in the ecological and ecophysiological research on plant adaptations to tolerate multiple abiotic stresses to finally understand *where are we?* To better highlight how the contributions of this VSI locate in the broader context of current knowledge on abiotic stress tolerance, we mapped them within the conceptual framework proposed by Volaire (2018) (Fig. 5). It becomes evident that there remains a huge gap of knowledge on how patterns and process traits can be integrated to disentangle species/population level plant adaptations to multiple abiotic stresses (empty area in Fig. 5). Reaching such an integration requires combining extensive databases of process traits, first principles models, remote sensing/eddy covariance techniques, pattern traits and biotic interactions to finally bridge the scope of ecological and ecophysiological research on woody plant multi-stress tolerance. However, this matter is evidently complicated by the inherent difficulty of combining traits that reflect patterns and processes at different levels of biological organization and operating at different temporal and spatial scales. Unifying these approaches into a single framework is, therefore, the next challenge for (eco)physiological research.

We sincerely hope that the present VSI will provide part of the map to identify new routes toward new questions and tools to build a so much needed general predictive framework for woody plant adaptations to tolerate multiple stressors. We also hope that relatively few dimensions can be used to describe tolerance strategies toward all stressors because, quoting Field (1991): 'if species respond uniquely to every stress, and if every stress must be evaluated from a different perspective, the scaling problem is greatly complicated, perhaps beyond all hope of practical solution'.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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