



Trait dimensions of abiotic stress tolerance in woody plants of the Northern Hemisphere

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Abstract

Aim: Trade-offs among tolerances to different abiotic stressors limit polytolerance in woody plants. However, the general trait syndromes that underlie large-scale tolerance patterns of woody plants remain controversial. Here, we tested if the leading trait dimensions that define the global spectrum of plant form and function capture the underlying trait trade-offs limiting woody plant polytolerance.

Location: Northern Hemisphere.

Time Period: Present.

Major Taxa Studied: Woody plants.

Methods: We used a dataset of 779 species to link the trait dimensions defining the global spectrum of plant form and function with two dimensions summarizing tolerance syndromes to drought, shade, cold and waterlogging. Stress tolerance dimensions were a trade-off between drought and cold/waterlogging tolerance strategies, and a shade tolerance spectrum. Relationships among trait and stress tolerance dimensions were evaluated using general additive models separately for deciduous and evergreen angiosperms, and evergreen gymnosperms.

Results: Drought-tolerant angiosperms showed greater specific stem density (SSD) and seed mass (SM), and lower specific leaf area (SLA) and leaf nitrogen content per mass (LN), compared to the cold/waterlogging-tolerant species. Shade-tolerant angiosperms displayed greater SSD and SM and lower SLA and LN compared to intolerant angiosperms. Highly contrasting trait adaptations also distinguished drought- (greater SSD, SM and lower SLA, LN) from shade-tolerant evergreen gymnosperms.

Main Conclusions: The 'SSD–SM' and the 'SLA–LN' dimensions mainly distinguish cold or drought-tolerant woody angiosperms and shade- or drought-tolerant gymnosperms. Our results also support a conservative trait strategy for shade-tolerant compared to shade-intolerant species, with some differences between plant functional types probably due to contrasting leaf lifespans. Overall, our findings identify some leading functional constraints on polytolerance in woody plants and provide a framework to integrate additional trait dimensions to fully elucidate such constraints.

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KEYWORDS

abiotic stress, cold tolerance, drought tolerance, functional traits, leaf economics spectrum, polytolerance, shade tolerance, trait adaptations, woody plants

1 | INTRODUCTION

Natural systems worldwide are facing high rates of climate change and anthropogenic disturbance (Smith et al., 2022). These impacts will alter the relative importance of different stresses experienced by plants (Craine et al., 2012; Zhang et al., 2018). For example, warming can increase the relative importance of drought/heat over other stresses, such as shade (Craine et al., 2012; Zhang et al., 2018). Unfortunately, the lack of a systematic understanding of plant adaptations to multiple stresses hinders our ability to predict how plants will endure future multi-stress scenarios of increasing severity and duration. Filling this knowledge gap is particularly relevant for woody plants as they contain the bulk of standing forest biomass, a key component of terrestrial carbon storage (Bonan, 2008), and they consistently thrive under multiple abiotic stresses in all forested ecosystems worldwide (Niinemets, 2010a).

The search for general patterns of species' adaptations to the environment is a long-standing goal of ecology (Westoby, 1998). The effort put into defining such general patterns has consolidated the idea that there are trade-offs among adaptations to contrasting habitat conditions (Laughlin, 2023). Analyses of such trade-offs at the cross-species level allow for defining major axes of ecological specialization (Grime, 1977), and the trait-based approach (sensu Westoby & Wright, 2006) has been used intensively for this purpose. As a result, the trait-based approach has already uncovered basic axes of trait variation summarizing vascular plant adaptations to the environment, such as those axes underlying the leaf economics spectrum (Lambers & Poorter, 1992; Lichstein et al., 2021; Niinemets, 1999, 2001; Reich et al., 1997; Westoby et al., 2002; Wright et al., 2004) or the fine-root economics space (Bergmann et al., 2020; Carmona, Bueno, et al., 2021; Weigelt et al., 2021).

Across habitats and on a large scale, Díaz et al. (2016) showed that combinations of plant height, seed mass, specific stem density, specific leaf area, leaf nitrogen content on a mass basis and leaf area can summarize key energetic trade-offs and mechanical constraints shaping aboveground global plant functional diversity. This trait space is called the Global Spectrum of Plant Form and Function (GSPFF; Díaz et al., 2016). Trait combinations within the GSPFF are summarized by two leading and orthogonal trait dimensions. One trait dimension is a 'plant-seed size' trade-off axis that loosely resembles the r-K continuum (Pianka, 1970). The second dimension is the Leaf Economics Spectrum (LES, Wright et al., 2004) that aligns leaf-level adaptations of the global flora along a continuum of strategies from acquisitive (low-carbon and high-nitrogen leaves) to conservative (high-carbon and low-nitrogen leaves) (Wright et al., 2004). Since its formulation, the GSPFF is a reference trait-based framework to explore aboveground plant functional diversity at different spatial scales and across levels of biological organization.

The trait-based approach has been dominating the understanding of species' resistance to abiotic stressors (e.g., Hallik et al., 2009; Puglielli, Laanisto, et al., 2021, 2023; Sack, 2004; Stahl et al., 2013),

defined here as a species' ability to tolerate adverse abiotic conditions in its natural environment (ecological tolerance, sensu Niinemets & Valladares, 2006, 2008). Most previous research has followed the hypothesis that adaptations to tolerate a given stress prevent species from simultaneously enduring other stresses. This idea was based on the *shade-drought trade-off* theory (Smith & Huston, 1989), thought to explain plant co-existence dynamics at different scales. This theory assumed that if a given amount of carbon is allocated to roots to have a more extensive and deeper root system to tolerate drought, the same carbon cannot simultaneously be allocated to leaves to enhance light interception and increase shade tolerance (Laanisto & Niinemets, 2015). However, a recent global analysis (Puglielli, Laanisto, et al., 2021) suggests that carbon partitioning among leaves and roots is not necessarily the mechanism underlying the shade-drought trade-off, as allocation patterns can converge between shade and drought-tolerant species.

Many other studies investigating the functional basis of the shade-drought trade-off yielded contradictory results. Some found contrasting whole-plant (Stahl et al., 2013) or leaf trait syndromes (Hallik et al., 2009) between shade- and drought-tolerant temperate woody plants of the Northern Hemisphere, while studies in ecosystems with a longer growing season did not (Markestijn & Poorter, 2009; Sack, 2004; Sack et al., 2003; Sack & Grubb, 2002). Valladares and Niinemets (2008) proposed that a longer growing season could reduce the strength of the shade-drought trade-off by favouring enough carbon fixation during favourable periods of season to survive when stresses occur, possibly favouring adaptations to multiple stressors. Nevertheless, accounting for the length of the growing season only partly improved the interpretation of the shade-drought trade-off (Laanisto & Niinemets, 2015). The different adaptive responses of woody plants to gain shade tolerance add uncertainty to understanding the functional basis of the shade-drought trade-off. Some studies hypothesized that traits improving carbon gain can explain shade tolerance (e.g., Givnish, 1988), but others found that trait combinations that enhance resource conservation at the expense of carbon gain favour shade tolerance (Kitajima, 1994; Lusk, 2004; Lusk et al., 2008; Sack & Grubb, 2002). A recent meta-analysis involving many traits could not fully resolve this matter (Poorter et al., 2019). Similar discrepancies to that on the shade-drought trade-offs indeed extend to other tolerance combinations (Grubb, 2016). For example, a recent work reviewed the convergence in traits underlying freezing and drought tolerance in angiosperms (Folk et al., 2020), but another study did not find such convergence (Fernández-Marín et al., 2020). In summary, despite consistent evidence for trade-offs among tolerance to multiple stressors (Laanisto & Niinemets, 2015; Niinemets & Valladares, 2006; Puglielli, Hutchings, et al. 2021), the functional basis of such trade-offs in woody plants is not yet clarified (Grubb, 2016; Valladares et al., 2016; Valladares & Niinemets, 2008; Wang & Wang, 2023).

What has so far prevented the identification of general trait syndromes underlying abiotic stress tolerance trade-offs in woody

plants? Trait–tolerance relationships have so far been investigated through analyses focused on (i) relatively few species (e.g., Markesteijn & Poorter, 2009; Sack, 2004), (ii) species from specific habitats (e.g., Hallik et al., 2009; Markesteijn & Poorter, 2009; Sack, 2004) and/or (iii) species from a specific geographic location (e.g., Rueda et al., 2018; Stahl et al., 2013). Furthermore, different studies often use different tolerance scoring systems and/or trait-based frameworks. Altogether, these aspects have hampered any generalization attempt, and consistent multivariate patterns of plant adaptations to abiotic stressors remain controversial.

Recently, using published species-specific tolerance data (Laanisto & Niinemets, 2015; Niinemets & Valladares, 2006) for 799 woody plants from the Northern Hemisphere, Puglielli, Hutchings, et al. (2021) examined multivariate trade-offs in woody species' ecological tolerances of four major abiotic stresses (cold, shade, drought and waterlogging). Two leading tolerance dimensions were identified. The first dimension reflects a trade-off between drought and tolerance to cold/waterlogging. The second dimension is a shade

tolerance spectrum, from low- to high-shade tolerance. Within these two dimensions, species form a triangular trade-off space, called the Stress Tolerance Space (henceforth STS, Figure 1a,b), defined by three end-point strategies: shade, drought and cold/waterlogging tolerance specialists. The boundaries of this triangle represent 'boundary line trade-offs' (sensu Grubb, 2016) setting the limits to polytolerance in woody plants of the Northern Hemisphere (Puglielli, Hutchings, et al., 2021, Figure 1c). Thus, the triangular STS can be interpreted as a two-dimensional stress tolerance landscape (Puglielli et al., 2022) containing pairs of coordinates that reflect species-specific multi-stress tolerance strategies. These coordinates can be used to map different aspects of species biology within the STS, including functional traits and their combinations, and therefore to establish general multivariate trait–tolerance patterns in a two-dimensional stress tolerance landscape (Puglielli et al., 2022).

The objective of this study was to test whether the variation along the trait dimensions defining the GSPFF, for which we can establish a putative link with abiotic stress (Table 1), can be used to

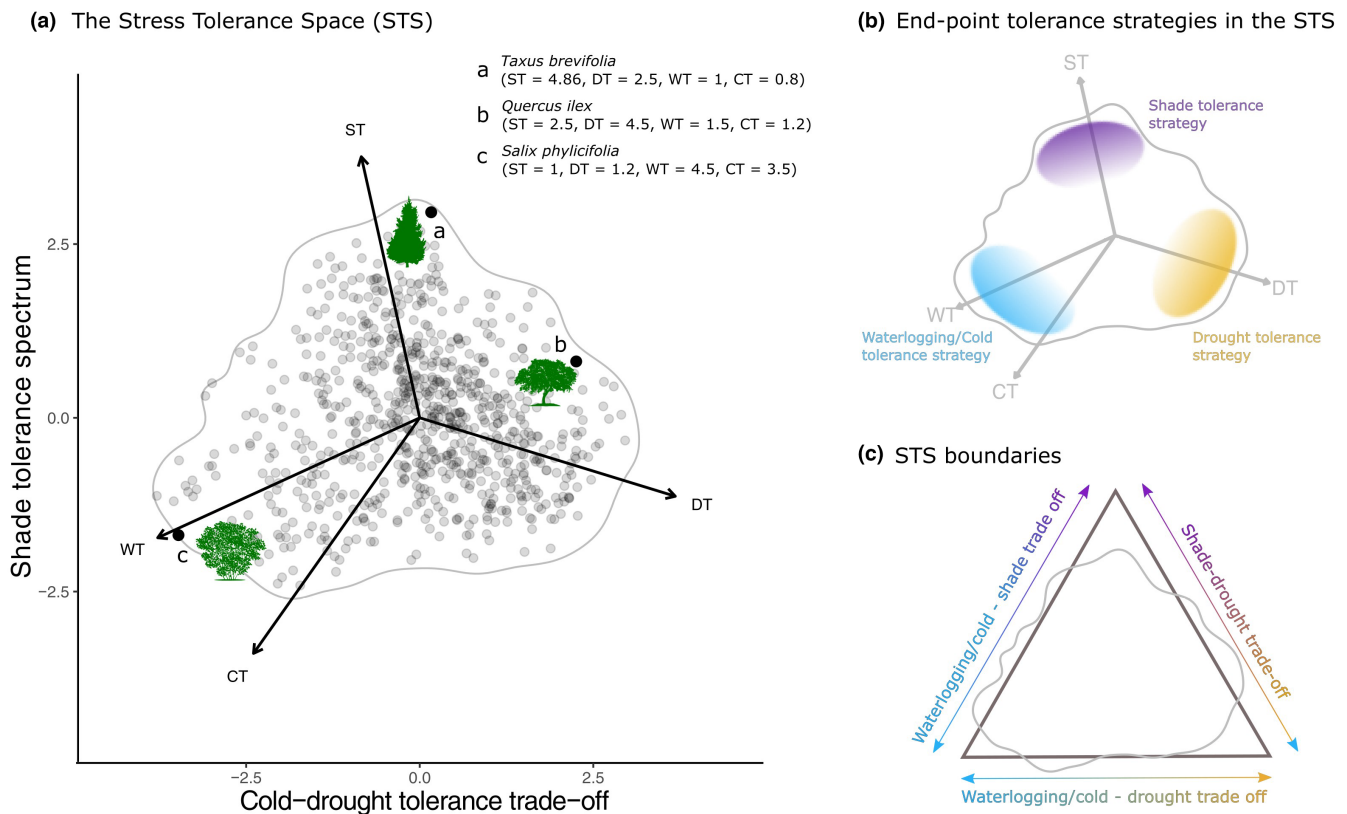


FIGURE 1 The triangular Stress Tolerance Space (STS) of woody plants. (a) STS is defined by combinations of tolerance to drought (DT), shade (ST), waterlogging (WT) and cold (CT) for 799 species in the Northern Hemisphere. The first axis reflects a trade-off between drought and cold/waterlogging tolerance, while the second axis is a shade tolerance spectrum, from low to high-shade tolerance. The irregular grey polygon represents the actual border of the STS as defined by Puglielli, Hutchings, et al. (2021) (see Section 2). Each data point represents a tolerance strategy as defined by the relative contribution of WT, CT, ST and DT to the overall strategy as shown for three species: a—evergreen conifer *Taxus brevifolia*; b—broad-leaved evergreen angiosperm *Quercus ilex*; and c—deciduous angiosperm *Salix phylicifolia*. (b) Three end-point tolerance strategies can be identified, which should correspond to contrasting trait syndromes underlying drought, shade and cold/waterlogging tolerance. A list of the species that are associated with each of the three end-point tolerance strategies is reported in Appendix S1 of the Supporting Information (Table S1.1). (c) The STS boundary sets the limits on the abiotic stress tolerance strategies of woody plants from the Northern Hemisphere, and it is defined by three trade-off axes that culminate in either one of the three end-point tolerance strategies. The black triangular polygon is a simplified representation of the space defined by the three trade-off axes that set the limits of the STS.

TABLE 1 List of traits used in this study, their function and their putative link with abiotic stress.

Trait (Abbreviation)	Unit	Function ^a	Putative link with abiotic stress
Specific stem density (SSD)	mgmm ⁻³	Trade-off between growth rate and mortality risk due to biomechanical failure (elastic buckling), mechanical damage due to falling debris or wind or hydraulic failure	Greater SSD is associated with slower growth and enhanced survival and may favour tolerance to abiotic stressors (Chave et al., 2009). SSD could be greater for drought- (Šimová et al., 2017) and shade-tolerant species (Poorter et al., 2019) compared to intolerant ones, but SSD could still be greater for drought-tolerant than shade-tolerant species. Wood density decreases in habitats with a shorter growing season (Moles, 2018), and cold-tolerant species might display lower SSD compared to drought- and shade-tolerant species
Seed mass (SM)	mg	Trade-off between seedling survival versus colonization ability in space and time	Greater SM may favour seedling emergence and survival in chronically light- or water-limited environments (Leishman et al., 2000). Therefore, a greater SM is expected to be linked to shade and drought tolerance. SM is known to decrease where the growing season shortens due to strong seasonality of temperature and rainfall (Moles, 2018). Cold-tolerant species could have lower SM compared to shade- and drought-tolerant species. A similar link to abiotic stress might contribute to explain the empirical positive relationship usually observed between SM and SSD
Leaf nitrogen content (LN) ^b	mg g ⁻¹	Trade-off between the benefits of high photosynthetic capacity and enhanced light harvesting by pigment-binding protein complexes and the costs of acquiring nitrogen and vulnerability to herbivory	Lower LN is expected to be favoured where the cost of leaf production is high and leaf turnover is slow (Wright et al., 2004) Thus, lower LN might be favoured under different abiotic stress regimes. However, contrasting N allocation patterns within the leaves can happen without changes in the overall LN (e.g., nitrogen allocation between photosynthetic vs. non-photosynthetic leaf components in shade-tolerant vs. intolerant species, Niinemets, 2010b). Finally, LN might be related to fertility at a given site (Niinemets, 2015) and depends on the plant functional type. Where the growing season shortens, a greater LN might be favoured to maximize plant performance under short-time favourable environmental conditions (Šimová et al., 2017)
Specific leaf area (SLA) ^b	mm ² mg ⁻¹	Trade-off between leaf carbon gain and longevity	Lower SLA is expected where the cost of leaf production is high and leaf turnover is slow (Wright et al., 2004), always showing a great degree of covariation with LN. Therefore, a lower SLA may always favour abiotic stress tolerance, and this is expected to be particularly evident when comparing drought-tolerant versus drought-intolerant species (Moles, 2018). However, such response might differ between functional types, especially regarding leaf-level adaptations to achieve shade tolerance (Lusk et al., 2008; Niinemets, 2010b), for which there is considerable uncertainty on the extent to which shade-tolerant species adaptations follow the 'carbon gain maximization' or the 'stress tolerance' hypothesis (Poorter et al., 2019). Where the growing season shortens, a higher SLA might be favoured to maximize plant performance under short-time favourable environmental conditions (Reich & Oleksyn, 2004)

^aFunction is defined according to Díaz et al. (2016). For plant height and leaf area see Appendix S6.

^bLarge trait databases often miss information on the light conditions at which leaf traits were measured, and most of leaf traits measurements globally are sampled at least under some partial shade (Niinemets & Keenan, 2016). This generates a source of uncertainty when analysing leaf-level adaptations underlying shade tolerance since tolerant and intolerant species cannot be compared in a common light (Lusk & Warton, 2007). However, Niinemets and Keenan (2016) also noted that the shading effect on leaf traits is much less pronounced for traits expressed on a mass basis, especially LN, than for traits expressed on an area basis. For this reason, they also found an overall little effect of growth irradiance in modifying the relationship LMA (or 1/SLA) -LN, with a slope for the high- versus low-light environment of -0.79 ± 0.20 and -0.77 ± 0.22 . Additionally, Niinemets et al. (2015) found that LMA saturates at relatively low values of irradiance ($\approx 30\%$ of above-canopy light levels), while LN is one of the least sensitive traits in responding to changes in integrated quantum flux density. Altogether, this indicates that combinations of these traits can be safely used to explore the leaf-level adaptations associated with shade tolerance mostly irrespective of the growth irradiance in which the traits were originally determined.

evaluate the adaptations underlying abiotic stress tolerance strategies to shade, drought, cold and waterlogging in woody plants from the Northern Hemisphere. For this purpose, we explored general multivariate patterns of trait-tolerance relationships by linking the trait dimensions defining the GSPFF with those defining the STS. Given that tolerance strategies in the STS are defined by three trade-off axes that culminate in either one of the three end-point

tolerance strategies (Figure 1a-c), we expected to identify contrasting trait syndromes around the tips of the STS, that is where species with highly specialized tolerance strategies live (Table S1.1). We used a data set of 779 woody plants that span all major forested ecosystems of the Northern Hemisphere (Appendix S1 of the Supporting Information, Figure S1.1), and three broad functional types (deciduous and evergreen angiosperms and evergreen gymnosperms).

2 | METHODS

2.1 | Abiotic stress tolerance data

The species-specific estimates of shade (ST), drought (DT), cold (CT) and waterlogging tolerance (WT) defining STS were obtained from the datasets of Niinemets and Valladares (2006) and Laanisto and Niinemets (2015), which include stress tolerance scores for 799 woody species.

In the original data compilation (Niinemets & Valladares, 2006), ST, DT and WT were independently estimated by cross-calibrating multiple tolerance scales reported in the literature where multiple measurements for one species were available across different tolerance scales. CT is expressed as a species-specific average of USDA plant hardiness data gathered from multiple sources (Laanisto & Niinemets, 2015 for further details). The derived stress tolerance scores assume continuous values between 1—very intolerant and 5—very tolerant (Laanisto & Niinemets, 2015; Niinemets & Valladares, 2006). The species are also classified according to their broad taxonomic division (angiosperms, gymnosperms) and leaf type (deciduous, evergreen) (Niinemets & Valladares, 2006).

The formalization of the STS (Puglielli, Hutchings, et al., 2021) revealed that two dimensions (principal components) capture ~80% of the variance in species-specific combinations of ST, DT, CT and WT. Each pair of coordinates in the STS corresponds to a species-specific combination of tolerances to the four stressors, that is, abiotic stress tolerance strategy (Figure 1). One STS axis scales positively with DT and negatively with WT and CT. The second STS axis is positively correlated with ST and represents a *shade tolerance spectrum*. Hereafter, we refer to STS axis 1 as the *cold–drought tolerance trade-off* where cold stands for a short growing season (see Appendix S2, Figure S2.1 for details, and Puglielli, Tordoni, et al., 2023 for a similar interpretation). Species coordinates in the STS are available in Puglielli, Hutchings, et al. (2021). Species nomenclature follows The Plant List v.1.1, updated using the R package Taxonstand (Cayuela et al., 2012). We also tested the effect of the phylogenetic relationship of species on the STS to conclude that this factor does not alter the STS shape and properties (Appendix S2 S2.2, Table S2.2).

2.2 | Trait data

We selected the six traits defining the GSPFF (Díaz et al., 2016, Table 1): maximum plant height (PH), specific stem density (SSD), seed mass (SM), individual leaf size (LA), leaf nitrogen content per unit of leaf mass (LN) and specific leaf area (SLA). Combinations of these traits are known to reflect fundamental trade-offs constraining aboveground vascular plant functional strategies at the global scale, and they are relevant to define trait syndromes underlying woody species' abiotic stress tolerance strategies (Table 1).

Trait data for the STS species were obtained from Carmona, Bueno, et al. (2021) and Carmona, Tamme, et al. (2021) that compiled trait data from public datasets in the TRY Plant Trait Database

(version 5.0, <https://www.try-db.org/TryWeb/Prop2.php>, Kattge et al., 2020). Our trait data consisted of 706 observations for PH (completeness=89.3%), 377 for SSD (47.7%), 619 for SM (78.3%), 502 for LA (63.5%), 449 for LN (56.6%) and 484 for SLA (61.2%). The main summary statistics for each trait used in the analyses are reported in Appendix S3, Table S3.3.

Carmona, Bueno, et al. (2021) and Carmona, Tamme, et al. (2021) also used an imputed version of the trait dataset for their analysis (see Appendix S4 S4.1, S4.2 for details on the imputation procedure). We performed data analysis both on the original and on the imputed dataset to conclude that imputation did not alter the main trait dimensions that define the trait space nor the modelling results (Appendix S4 S4.1–4.3, Figures S4.2 and S4.3, Tables S4.4 and S4.5). To increase the power of our statistical modelling, we performed all subsequent analyses using the imputed dataset that included 779 species with complete trait information.

Since our dataset spans broad- and needle-leaved species, we expected the relationship between SLA and LN to partly depend on interspecific differences in LA (e.g., Niinemets & Kull, 1994). Similarly, since our dataset included both trees and shrubs, we expected both SSD and SM to depend on PH (e.g., Díaz et al., 2016; Fajardo et al., 2022). Scaling of traits with a size-related trait (such as LA or PH) can challenge the identification of trait trade-offs reflecting meaningful ecological strategies, especially considering that PH and LA varied widely in our dataset (range=0.04–72.66 m and 3–721,004.8 mm²). With this in mind, prior to the data analysis, we wanted to control for (i) the covariance between both SLA and LN with LA; and (ii) the covariance of both SSD and SM with PH. To do that, we run simple log–log linear models using either SLA, LN, SSD or SM as the response variable, and LA or PH as the independent variable depending on the considered group of traits (i.e., leaf vs. whole-plant traits). Then, we extracted the residuals from these models and used these residuals as the new set of traits for subsequent analyses. In summary, in our final dataset, SLA and LN were expressed as the residual variance of the trait that is not explained by interspecific differences in LA. SSD and SM are expressed as the residual variance that is not explained by interspecific differences in PH.

2.3 | Data analysis

We identified two main axes of trait covariation in our dataset: the first dimension was positively related to LN (loading=0.70) and SLA (0.68). The second dimension was positively related to SSD (0.69) and SM (0.68) (Appendix S4 S4.1, Figures S4.2 and 4.3, Table S4.4 for all the methodological steps related to the definition of the trait space). We interpret the first axis as a 'leaf economics spectrum' (sensu Wright et al., 2004). The second PCA axis was a 'stem density/seed mass spectrum'.

We used Generalized Additive Models (GAMs) with a bivariate soap film smoother to map how trait combinations (i.e., trait space axes) vary within the STS. The soap film smoother was preferred

over other smoothers because it allows evaluating model predictions inside user-defined boundaries (Wood, 2011) – that is, STS boundaries. We defined the outer boundaries of the STS using the 99th quantile of the multivariate probability distribution of combinations of stress tolerance (Figure 1). STS boundaries were calculated using a multivariate kernel density estimate with unconstrained bandwidth selectors using the 'ks' R function (Duong, 2007). We fitted GAMs using the 'mgcv' R package by setting a trait syndrome (either PC1 or PC2 of the trait space) as the response variable, and the STS axes as the bivariate explanatory variable. The model's goodness of fit was evaluated using the proportion of the null deviance explained by each model, which is equivalent to the proportion of variance explained (i.e., R^2) when using Gaussian models estimated as GAMs (Wood, 2017).

Model predictions were mapped in the STS separately per each plant functional type (PFT) since they occupy different and not always overlapping portions of the STS and of the trait space (Appendix S4 S4.4, Figure S4.4, Table S4.6). PFTs considered were deciduous angiosperm ($n=540$), evergreen angiosperm ($n=132$) and evergreen gymnosperm ($n=102$). Deciduous gymnosperms were excluded from the analysis due to a lack of data for modelling ($n=14$). GAM predictions per each PFT were generated only within the portion of the STS occupied by each PFT to avoid the GAM smoother extrapolating model predictions outside the STS regions occupied by each group (Carmona et al., 2023). The whole analysis was also applied to single traits (see Appendix S5, Figure S5.5a–l). The same approach was employed to evaluate how the *cold-drought trade-off axis* and the *shade tolerance spectrum*—that is, the STS axes—are distributed within the functional trait space defined by the leaf economics spectrum and the stem density/seed mass spectrum (Figure S4.2b). All statistical analyses were performed in R 4.0.5 (R Core Team, 2021).

Finally, to evaluate how size-related traits (PH and LA) associated with stress tolerance strategies, following Brunbjerg et al. (2018), we used GAMs with a step-wise selection approach (detailed in Appendix S6). This approach allowed us to quantify the amount of variation (expressed in terms of proportion of deviance explained) in stress tolerance strategies (i.e., STS axes) that is explained by the combinations of 'leaf economics spectrum' and 'stem density/seed mass spectrum' (i.e., PC1 and PC2 of the trait space) and by size-related traits (i.e., PH–LA) (Appendix S6; Figures S6.6a–f, S6.7a–l).

3 | RESULTS

3.1 | Trait syndromes in the STS

For each PFT, all the traits and trait syndromes were significantly related to the position of the species in the STS, with the proportion of explained deviance ranging between 0.04 and 0.31 depending on the trait/trait syndrome and PFT (p always <0.001 ; Figure 2a–f, Figure S5.5a–l, Table S5.7). Across PFTs, at the single trait level, species positioning in the STS explained more variance for SSD and SM (mean proportion of explained deviance \pm SD = 0.23 ± 0.08) than

for leaf traits (i.e., LN and SLA, mean proportion of explained deviance = 0.17 ± 0.09) (Figure S5.5; Table S5.7).

The same pattern was also true for the trait syndromes considered—that is, when comparing LES traits (Figure 2a–c, mean proportion of explained deviance = 0.19 ± 0.09 ; p always <0.001) versus the stem density/seed mass spectrum (Figure 2d–f, mean proportion of explained deviance = 0.26 ± 0.03 ; p always <0.001). At this level of analysis, for deciduous angiosperms, we found greater SLA and LN (hot spot in Figure 2a) at the WT/CT tip of the STS compared to the lower SLA and LN values towards the DT tip of the STS (cold spot in Figure 2a). For shade-tolerant deciduous angiosperms, we found intermediate SLA and LN values compared to drought and waterlogging/cold-tolerant species (Figure 2a). For evergreen angiosperms, we found the lowest SLA and LN values in the shade–drought trade-off region of the STS (cold spot in Figure 2b). Leaf-level strategies were shifted towards the faster return end of the LES towards the WT/CT tip for evergreen angiosperms (Figure 2b). However, for some evergreen angiosperms, the DT strategy was also associated with greater SLA and LN values (hot spot in Figure 2b). Evergreen gymnosperms showed the greatest SLA and LN values towards the ST tip, whereas the smallest values of these traits were found at the DT tip of the STS (hot and cold spots in Figure 2c, respectively).

In the case of the stem density/seed mass spectrum (Figure 2d–f), the results were similar between deciduous and evergreen angiosperms (Figure 2d,e). Species with the highest SSD and SM values were positioned towards the DT tip of the STS (hot spots in Figure 2d–f), while those species with the smallest SSD and SM towards the WT/CT tip of the STS (cold spots in Figure 2d–f). Evergreen gymnosperms displayed the highest values of SSD and SM values at the DT tip of the STS (hot spot in Figure 2f), and the smallest values towards the ST tip (cold spot in Figure 2f).

3.2 | Stress tolerance syndromes in the GSPFF

Stress tolerance strategies were significantly related to species positioning in the trait space independently of PFT (Figure 3a–f). The proportion of explained deviance in these relationships ranged between 0.11 and 0.45 (p always <0.001 ; Figure 3a–f; Table S5.7). In particular, always independently of the PFT, more cold/waterlogging-tolerant species were consistently associated with the lowest SSD and SM values compared to drought-tolerant species (cold and hot spots in Figure 3a–c, respectively), which displayed the highest values of both traits (Figure 3a–c).

Shade-tolerant deciduous angiosperms were associated with greater SSD and SM than intolerant species (hot vs. cold spot in Figure 3d, respectively). Although this holds for evergreen angiosperms as well, for this PFT, the leaf-level strategy becomes important as well in distinguishing shade-tolerant and -intolerant species (hot vs. cold spots in Figure 3d), with shade-tolerant species displaying a lower SLA and LN than shade-intolerant species. Evergreen gymnosperms showed a completely reverse pattern compared to the other PFTs (Figure 3f).

The amount of variation in stress tolerance strategies (i.e., the STS axes) explained by the 'leaf economics spectrum' and the 'stem density/seed mass spectrum' was always higher than that explained by size-related traits (mean proportion of explained deviance 0.18 and 0.12, respectively) independently of the PFT, except for species sorting along the shade tolerance spectrum in deciduous and evergreen angiosperms (Table 2; Appendix S6; Figures S6.6a–f; S6.7a–f).

4 | DISCUSSION

We tested if trait variation along the axes defining the GSPFF could capture general patterns of woody plants' trait adaptations underlying different abiotic stress tolerance strategies. The results show that, for all the considered PFTs: (i) different trait combinations generally underlie extreme tolerance strategies in the STS (that is, STS vertices) (Figure 2a–f); (ii) the STS end-point strategies always occupy different positions in the GSPFF (Figure 3a–f). Thus, we uncovered general patterns of trait adaptation that discriminate tolerance strategies in woody plants and identified some of the leading functional constraints to their polytolerance.

4.1 | 'SSD–SM dimension' and abiotic stress tolerance strategies

The drought tolerance strategy of angiosperms was associated with larger SSD and SM values compared to the other tolerance strategies (Figures 2d,e and 3a,b). From an adaptive standpoint, denser wood generally favours xylem resistance to drought stress (Jacobsen et al., 2007; Pratt et al., 2007; Šímová et al., 2017) and drought tolerance (Guillemot et al., 2022), while larger seeds favour seedling establishment and survival in habitats where drought is the major stress imprint (Leishman et al., 2000). Conversely, light wood and small seeds underlie the waterlogging/cold tolerance strategy of angiosperms. Wood density and seed mass decrease with decreasing mean annual temperature and increasing temperature seasonality (Moles, 2018), thus in habitats where the growing season shortens. Wood with a lower density of wider vessels can favour high water transport when species are metabolically more active during a short growing season (Reich & Oleksyn, 2004). Similar patterns were observed by Šímová et al. (2017) for North American woody plants. In summary, contrasting SSD and SM adaptations underlie species positioning at the extremes of the cold–drought trade-off axis in woody angiosperms.

Evergreen gymnosperms did not extend to the waterlogging/cold tolerance tip of the STS despite some species (e.g., *Picea mariana*, *Pinus serotina*) having relatively high waterlogging tolerance. However, these species are not waterlogging tolerance specialists, and their tolerance strategy involves some degree of tolerance to other stressors, constraining their distribution within the STS. This stresses the importance of multifactorial instead of single-factor analyses when defining the trait dimensions underlying abiotic stress tolerance. At any rate, contrasting SSD and SM underlie

gymnosperms tolerance towards shade or drought (Figures 2c,f and 3c,f). Drought-tolerant species (e.g., *Juniperus*, *Pinus* and *Cupressus* species, Table S1.1) display denser wood and larger seeds compared to shade-tolerant species (e.g., *Abies*, *Picea* and *Tsuga* species, Table S1.1). Our results generalize previous evidence on contrasting trait adaptations underlying the selective tolerance strategy towards shade or drought, and possibly the distribution, of North American gymnosperms (Rueda et al., 2017).

4.2 | 'SLA–LN dimension' and abiotic stress tolerance strategies

At the leaf level, the drought tolerance strategy always involved the lowest SLA and LN values compared to the other tolerance strategies. This was particularly evident when comparing DT versus WT/CT strategies. SLA and LN are known to be higher for species from cold habitats with a short growing season (Cates & Orians, 1975; Royer et al., 2012; Šímová et al., 2017; Wright et al., 2004), supporting our results. Contrasting SLA and LN values between CT/WT and DT strategies were observed for deciduous angiosperms as well. Drought-tolerant deciduous species from warm-temperate/temperate regions generally display tougher leaves than species from cool-temperate climates, widening their growing season beyond drought periods compared to drought-intolerant species (Hallik et al., 2009). The pattern for evergreen gymnosperms again reflected contrasting adaptations to gain ST or DT (Figures 2c,f and 3c,f).

Evergreen angiosperms had the lowest SLA and LN along the shade–drought trade-off region of the STS (Figure 2b). This region of the STS (i.e., along the right side of the triangular space) includes species from habitats with a longer growing season where relative polytolerance to shade and drought is maximized (e.g., evergreen oaks from Mediterranean climate, Laanisto & Niinemets, 2015; Puglielli, Hutchings, et al., 2021, Table S1.1). Since this region is mostly populated by evergreen angiosperms compared to the other PFTs (note the region near the right side of the triangular STS, Figure 2), it might also reflect a different distribution of this PFT across habitats/biomes where shade and drought tolerances can coexist (e.g., wet sites with seasonal droughts where drought-tolerant evergreen angiosperms can survive under more shaded conditions). Evergreen angiosperms placed towards the WT/CT tip of the STS (e.g., some *Erica* species, Table S1.1) showed relatively greater SLA and LN compared to those in the shade–drought trade-off region (Figure 2b), compatible with the pattern observed for deciduous angiosperms. Finally, a group of evergreen angiosperms showed great SLA and LN values towards the DT tip of the STS. Hallik et al. (2009) observed a similar pattern. This can probably be explained by stress avoidance strategies, such as greater rooting depth, which could sustain leaves with greater SLA and LN. This is supported by drought-tolerant evergreen angiosperms that have a relatively higher PH and LA than intolerant ones (Appendix S6).

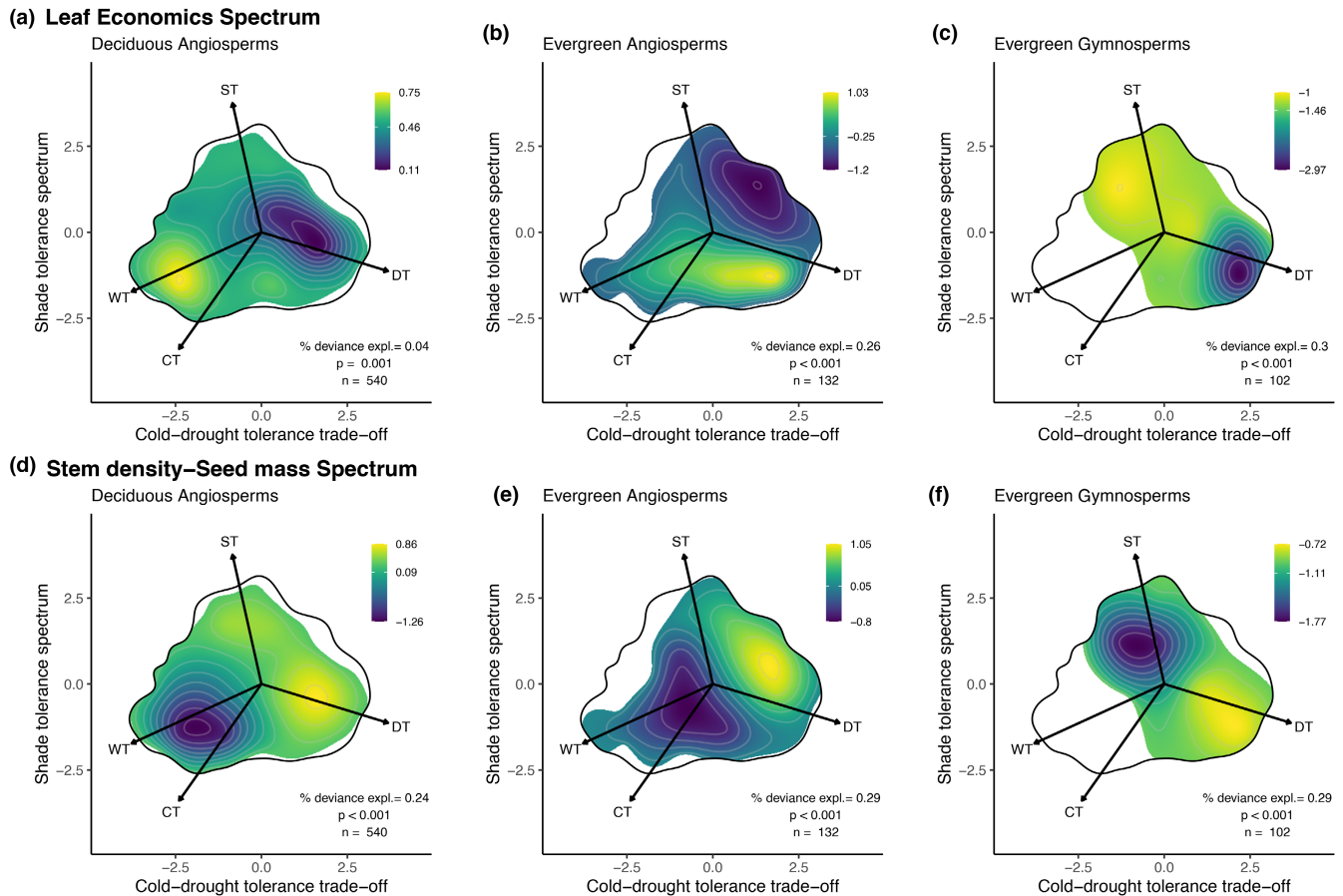


FIGURE 2 Trait syndromes in the Stress Tolerance Space (STS) by plant functional type (PFT). (a–c) Leaf economics spectrum; (d–f) Specific stem density/Seed mass spectrum. The proportion of null deviance explained, the sample size and the p -value of each model are shown. Full model statistics are reported in Table S5.7. The black contour represents the outer boundary of the STS defined across all species and PFTs. Different areas per PFT reflect their actual distribution in the STS. CT, cold tolerance; DT, drought tolerance; ST, shade tolerance; WT, waterlogging tolerance. A list of the species placed towards the tips of the triangular space by plant functional type can be found in Table S1.1. Note that heat maps refer to the values corresponding to the individual scores along PC1 and PC2 in Figure S4.2b. Hot and cold spots refer to the greatest and the lowest values of traits defining either (a–c) the leaf economics spectrum (hotspots indicate greater specific leaf area and leaf nitrogen content on a mass basis) or (d–f) the specific stem density–seed mass spectrum (hotspots indicate greater values of both traits). Also note that the trait scale is different between PFTs, as the range of values markedly differs between PFTs, in turn reflecting their relative positioning along the considered trait spectra. We preferred to keep relative scales to clearly show the differences in trait combinations underlying tolerance strategies within each PFT.

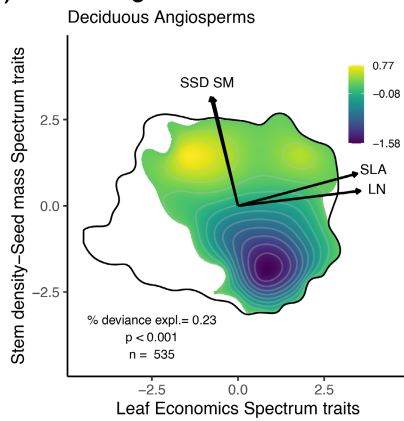
4.3 | The trait dimensions of the shade tolerance strategy

Plant adaptations to low light have been generally explained through two competing hypotheses. The ‘carbon gain hypothesis’ (Givnish, 1988) predicts that shade-tolerant species improve net energy capture in low light mainly by maximizing leaf area compared to intolerant species. The ‘stress tolerance hypothesis’ (Kitajima, 1994) predicts a smaller SLA for shade-tolerant than shade-intolerant species. As of today, there is no consensus on the trait adaptations of the shade tolerance adaptive syndrome (Poorter et al., 2019).

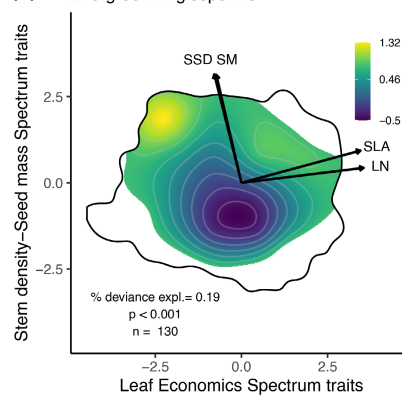
We found that shade-tolerant woody angiosperms displayed denser wood and larger seeds than shade-intolerant species (Figure 3d,e). Denser wood might favour mechanical resistance and be associated with a longer lifespan of plant organs, an expected

adaptive difference between shade-tolerant and shade-intolerant woody plants (Poorter et al., 2019). Larger seeds in shade-tolerant species guarantee a larger initial size that enhances seedling survival, conferring an adaptive advantage in low light compared to intolerant species (Niinemets & Valladares, 2006). At the leaf level, shade-tolerant angiosperms (e.g., *Acer*, *Cornus*, *Ardisia*, *Castanopsis* species, Table S1.1) generally had lower SLA and LN compared to intolerant species (Figure 3d,e; Poorter et al., 2019). Interestingly, the relevance of the LES-related traits in distinguishing shade-tolerant and shade-intolerant woody angiosperms was greater for evergreen than for deciduous angiosperms (relative position of hot and cold spots in Figure 3d,e), possibly due to their different leaf longevities. For deciduous angiosperms, the SSD–SM dimension was much more relevant in differentiating shade-tolerant and shade-intolerant species than the SLA–LN dimension. A smaller difference in the magnitude of the adaptive response of leaf-level

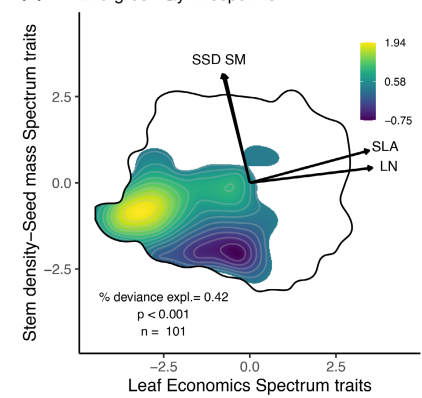
(a) Cold–drought tolerance trade-off



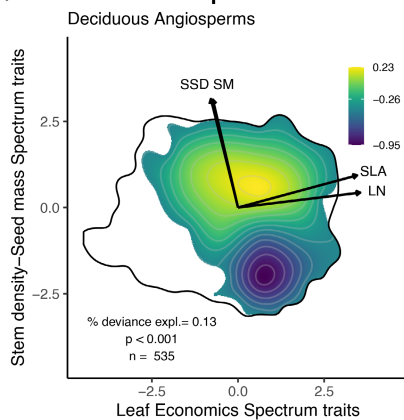
(b) Evergreen Angiosperms



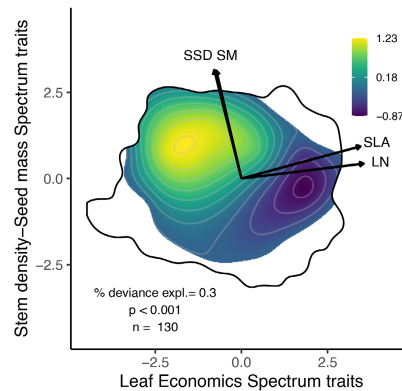
(c) Evergreen Gymnosperms



(d) Shade tolerance spectrum



(e) Evergreen Angiosperms



(f) Evergreen Gymnosperms

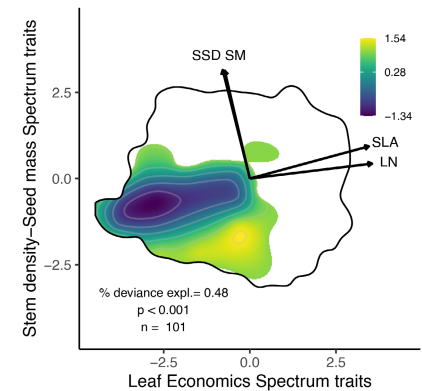


FIGURE 3 Stress tolerance strategies in the global spectrum of plant form and function by plant functional type (PFT). (a–c) The cold–drought tolerance trade-off axis, and (d–f) the shade tolerance spectrum (see Figures 1 and 2) in the global spectrum of plant form and function. The proportion of null deviance explained, the sample size and the p -value of each model are shown. Full model statistics are reported in Table S5.7. The black contour represents the outer boundaries of the trait space defined by the PCA across all species and PFTs (Figure S4.2b). Different areas per PFT reflect their distribution in the trait space. LN, leaf nitrogen content on a mass basis; SLA, specific leaf area; SM, seed mass; SSD, specific stem density. Hot and cold spots in (a–c) refer to the drought and the cold/waterlogging tolerance strategy, respectively. Hot and cold spots in (d–f) refer to the shade-tolerant and shade-intolerant species, respectively. Note that the trait scale is different between PFTs (see Figure 2 for an explanation).

traits between shade-tolerant and shade-intolerant deciduous compared to evergreen angiosperms agrees with previous studies (Lusk et al., 2008; Niinemets, 2010b; Walters & Reich, 1999). However, shade-tolerant angiosperms always display lower SLA than intolerant ones, and this guarantees a longer leaf lifespan but at the expense of short-term carbon gain (Poorter et al., 2019). Similar findings were obtained by Poorter et al. (2019) when comparing shade-tolerant and shade-intolerant plants under common light conditions.

Evergreen gymnosperms showed a reverse pattern. Shade-tolerant species (e.g., *Abies*, *Picea* and *Tsuga* species, Table S1.1) showed greater SLA and LN, and smaller SSD and SM, compared to shade-intolerant species (e.g., *Juniperus* and *Pinus* species, Table S1.1, Figure 3f). Evergreen gymnosperms differ from angiosperms in multiple features including type of vascular conduits (Sperry et al., 2006) and biomass allocation (Puglielli, Laanisto, et al., 2021). Our results are consistent with the evidence suggesting that shade-tolerant evergreen gymnosperms form flat shoots with

lower foliage clumping to increase leaf area index and maximize light interception (Niinemets, 2010b). However, leaf lifespan can still be longer for shade-tolerant than for shade-intolerant gymnosperms (Warren et al., 2012), possibly due to relative adjustments of SLA components (leaf density and thickness, Poorter et al., 2009; Puglielli et al., 2019), or inherently low photosynthesis (Warren et al., 2012), thus decoupling SLA and leaf longevity in shade-tolerant gymnosperms.

Altogether, our results suggest that the two hypotheses expected to explain plant adaptations to low light are not mutually exclusive. Woody angiosperms show adaptive responses that are compatible with the stress tolerance hypothesis (low SLA, greater SSD and SM). On the other hand, gymnosperms display adaptations aimed at enhancing light capture, and possibly carbon gain, but their inherently long leaf lifespan might constrain this response. The leaf traits included in this study can be safely used to compare adaptations between shade-tolerant and shade-intolerant woody plants irrespective of the growth light environment (Table 1). However, we

TABLE 2 The amount of variation in stress tolerance strategies explained by the multiple trait dimensions addressed in this study.

PFT	Response	Predictor	Proportion of deviance explained
Deciduous angiosperms	Cold-drought trade-off	SSD/SM-LES traits	0.21
		PH-LA	0.06
	Shade tolerance spectrum	SSD/SM-LES traits	0.14
		PH-LA	0.18
Evergreen angiosperms	Cold-drought trade-off	SSD/SM-LES traits	0.20
		PH-LA	0.18
	Shade tolerance spectrum	SSD/SM-LES traits	0.03
		PH-LA	0.26
Evergreen gymnosperms	Cold-drought trade-off	SSD/SM-LES traits	0.21
		PH-LA	0.03
	Shade tolerance spectrum	SSD/SM-LES traits	0.28
		PH-LA	0.08

Note: The table shows General Additive Models results obtained using abiotic stress tolerance strategies (i.e., the cold-drought trade-off or the shade tolerance spectrum, Figure 1) as the response variable and two bivariate smoothers, one expressing the interaction between SSD/SM and the LES (that is, the trait space axes in Figure 3), and a second expressing the interaction PH-LA (left out from the trait space, see Data analysis), as the independent variables. The proportion of deviance explained by each term was calculated following the method explained in Appendix S6.

Abbreviations: LA, leaf area; LES, leaf economics spectrum; PH, plant height; SSD/SM, stem density-seed mass spectrum.

still call for cautiousness when generalizing the adaptive value of the described leaf trait syndromes underlying the shade tolerance strategy due to the ubiquitous uncertainty in the light level at which leaf traits were determined, and more studies in this direction are needed.

4.4 | The multiple trait dimensions of abiotic stress tolerance

Our results show that simultaneously accounting for the SSD-SM and the SLA-LN dimensions allows distinguishing the three endpoint strategies defining the STS, since extreme tolerance strategies hardly overlapped within the trait space (hotspots in Figure 3a-f). However, we want to stress that our models always explained <50% of the variance of trait syndromes and tolerance strategies (Figures 2a-f and 3a-f). This probably depends, at least in part, on the complex nature of the trait-tolerance relationships, other factors such as alternative designs to tolerate a given stressor (Pan et al., 2022), missing key trait dimensions, or on the use of databases with their inherent limitations.

Importantly, despite the above potential limitations, our results show that accounting for species' abiotic stress tolerance strategies can help explain some trait-trait relationships that are not so obvious when analysing trait dimensions alone. For example, relationships between SSD and SLA with other traits that define strategy schemes, such as SM, are generally weak and appear only under some circumstances (Moles, 2018). We found that despite SM and SSD belonging to an independent trait dimension compared to SLA, drought- and shade-tolerant species have a greater SM, SSD and lower SLA compared

to their intolerant counterparts (Figure 3a-f). Cold/waterlogging-tolerant angiosperms display larger SLA and lower SSD and SM compared to intolerant ones. Similarly, the positive SM-SSD relationship is generally expected to be driven by the positive relationship between PH and SSD that reflects the need for mechanical support. However, when analysed independently of PH, the SM-SSD relationship appears to be driven by species drought and shade tolerance when comparing tolerant and intolerant species. Similarly, Moles (2018) was able to reconcile the empirical positive SM-PH relationship (these traits were expected to be independent, Westoby, 1998) by integrating these traits into a broader life-history strategy via the fitness advantage that such a relationship could bring (see also Laughlin et al., 2020, 2023). Therefore, our results support that some trait-trait relationships might arise because they reflect species adaptations to long-term abiotic stress regimes.

Finally, despite the above-described trait dimensions explained most of the variation in abiotic stress tolerance strategies (Table 2), our results also indicate that the size-related traits (PH and LA) represent a trait dimension that is not negligible to further explain the large-scale patterns of abiotic stress tolerance strategies (Table 2). We observed a pattern compatible with a turnover in growth forms along the STS axes (Appendix S6), mostly ascribable to the presence of very short shrubs with smaller LA towards the cold/waterlogging tip of the STS for angiosperms, and towards the drought tolerance tip for gymnosperms. Additionally, it emerges that shade-tolerant species are on average taller and display a greater individual leaf size compared to intolerant ones (being drought- or cold-tolerant species, Appendix S6), as previously hypothesized (Niinemets & Valladares, 2008). However, higher resolution size and architectural traits might better explain

how size-related traits influence large-scale abiotic stress tolerance patterns in woody plants.

We call for the use of additional traits linked to multiple functions, possibly from trait dimensions that are independent of those used here (e.g., fine-root dimensions Carmona, Bueno, et al., 2021, or leaf hydraulic dimension, Li et al., 2015), to further clarify the adaptive value of trait syndromes that underlie the large-scale patterns of abiotic stress tolerance strategies of woody plants. Using independent trait dimensions can in fact improve the interpretation of plant strategies (Laughlin, 2014). Including intraspecific trait variability (ITV, including ontogenesis) in this research agenda remains a priority since ITV can alter empirically determined trait trade-offs (Fajardo et al., 2022; Kuppler et al., 2020; Niinemets, 2015; Puglielli, Cuevas Román, et al., 2017; Puglielli, Laanisto, et al., 2023; Zhou et al., 2022) and therefore trait dimensions, ultimately modifying trait-tolerance relationships. However, the current shortage of large-scale ITV data (Chelli et al., 2019; Kattge et al., 2020) hinders filling this gap.

5 | CONCLUSIONS

Overall, we identified trait dimensions that contribute to explaining the abiotic stress tolerance strategies of woody plants to drought, shade, cold and waterlogging and their trade-offs. The general patterns of trait adaptations that we found at the level of plant functional type were as follows:

- For woody angiosperms, the specific stem density-seed mass spectrum is a key trait dimension that distinguishes strategies towards the tips of the cold-drought trade-off axis. Drought-tolerant species always display denser wood and larger seeds compared to cold/waterlogging-tolerant species. The traits linked to the leaf economics spectrum were less relevant in differentiating these two tolerance strategies. However, drought-tolerant species consistently displayed lower SLA and LN compared to cold/waterlogging-tolerant species.
- For evergreen gymnosperms, the shade-drought trade-off is a key strategic tolerance axis of differentiation in trait adaptations. Both the stem density-seed mass and leaf economics spectrum distinguished drought and shade-tolerant species, mostly reflecting adaptations to maximize light interception capability in shade-tolerant compared to shade-intolerant species.
- For woody angiosperms, trait adaptations to gain shade tolerance agree with the expectation of a stress tolerance strategy. Shade-tolerant evergreen angiosperms displayed denser woods, larger seeds and lower SLA and LN than intolerant ones. The shade tolerance strategy of deciduous angiosperms was mostly associated with denser woods and larger seeds.

Our results identify contrasting forms and functions associated with tolerance of different stressors. However, this information cannot fully resolve the functional constraints of polytolerance in woody plants. We call for expanding the proposed framework by integrating

additional and independent trait dimensions to the ones defining the global spectrum of plant form and function.

AUTHOR CONTRIBUTIONS

Giacomo Puglielli conceived the idea. Nicola Pavanetto and Giacomo Puglielli planned the methodology and performed the data analysis. Carlos P. Carmona contributed to the trait data and conceptualization of the methodologies. Ülo Niinemets contributed part of the tolerance data, conceptualization of the study and interpretation of the results. Lauri Laanisto contributed part of the tolerance data and manuscript writing. Nicola Pavanetto and Giacomo Puglielli wrote the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Stress Tolerance Space data were obtained from Puglielli, Laanisto, et al. (2021, available as supporting information Table S1). Raw tolerance data were obtained from Niinemets and Valladares (2006) and available in figshare: Niinemets and Keenan (2016). Appendix A. A table showing shade, drought and waterlogging tolerance for 806 species of woody plants from the temperate Northern Hemisphere. Wiley. Dataset. <https://doi.org/10.6084/m9.figshare.3565671.v1> Data from 'Tolerance to Shade, Drought, and Waterlogging of Temperate Northern Hemisphere Trees and Shrubs' (Niinemets & Valladares, 2006 Ecological Monographs). Cold tolerance data were provided by Lauri Laanisto. Trait data were obtained from Carmona, Bueno, et al. (2021) and are available in figshare. Data (including cold tolerance data) and R code to reproduce the analyses are available at <https://figshare.com/s/16882b3e610e873638b7>.

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BIOSKETCH

Nicola Pavanetto is a PhD student exploring the trait–environment relationships shaping abiotic stress tolerance strategies of woody plants.

Giacomo Puglielli is a researcher seeking to understand the multiple dimensions of abiotic stress tolerance strategies of woody plants by linking ecophysiological theories, plant functional traits, biotic interactions, and biogeography.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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