

## **Accounting for trait variability and coordination in predictions of drought-induced range shifts in woody plants**

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## Summary

Functional traits offer a promising avenue to improve predictions of species range shifts under climate change, which will entail warmer and often drier conditions. Although the conceptual foundation linking traits with plant performance and range shifts appears solid, the predictive ability of individual traits remains generally low. In this review we address this apparent paradox, emphasizing examples on woody plants and traits associated with drought responses at the species' rear edge. Low predictive ability reflects the fact that range dynamics tend to be complex and multifactorial, as well as uncertainty in the identification of relevant traits and limited data availability, but also that trait effects are scale- and context-dependent. [The latter results from the complex interactions among traits \(e.g., compensatory effects\) and between them and the environment \(e.g., exposure\), which ultimately determine persistence and colonization capacity. To confront this complexity, a more balanced coverage of the main functional dimensions involved \(stress tolerance, resource use, regeneration and dispersal\) is needed, and modelling approaches must be developed that explicitly account for \(i\) trait coordination in a hierarchical context, \(ii\) trait variability in space and time and its relationship with exposure, and \(iii\) the effect of biotic interactions in an ecological community context.](#)

**Key words:** colonization, drought tolerance, environmental context, modelling range dynamics, persistence, species distributions, trait coordination, trait variability.

## I. Introduction

Predicting future range shifts\* (Box 1) under climate change has become a central goal of research in ecology and conservation science (Lenoir & Svenning, 2015; Taheri *et al.*, 2021). Because temperature and water availability are primary determinants of plant species distributions (Woodward, 1987), ongoing climate change has the potential to cause mismatches between a species current geographical range and the environmental conditions that support long-term population persistence\* (the Hutchinsonian niche) (Parmesan & Yohe, 2003; Pecl *et al.*, 2017). Warmer conditions are increasing atmospheric water demand to plants, compounded in many cases by a reduction in soil water availability. Hotter droughts and associated disturbances (biotic agents, wildfires) are thus expected to have an increasingly important role in driving plant responses to climate change (Allen *et al.*, 2015; Brodribb *et al.*, 2020). Therefore, drought is likely to be a critical stress factor determining range dynamics, particularly at the dry margin (rear edge, lower latitude/altitude) of species distributions (Hampe & Petit, 2005), where new climatic conditions may push populations beyond their drought tolerance limits (Wiens, 2016).

The classic approach to forecasting the impacts of climate change on species distributions uses Species Distribution Models\* (SDMs, Box 1) (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). These models assume that species are in equilibrium with their environment and that climate strongly controls their distributions via species-specific physiological tolerance limits, so that spatial climate effects can be used to estimate the impact of changing climate (space-for-time substitution; Blois *et al.*, 2013). It is well known, however, that a wide variety of environmental, ecological and historical factors, from small-scale environmental variability to dispersal limitations and disturbance regimes, determine the presence and abundance of a species at the local scale (*e.g.*, Lenoir *et al.*, 2010). Because such factors are highly variable (and may be decoupled) in space and time (Damgaard, 2019; Kling *et al.*, 2020), plant responses to environmental change show strong scale and location dependency (McLaughlin *et al.*, 2017; Vilà-Cabrera *et al.*, 2019; Oldfather *et al.*, 2020), limiting the predictive ability of classic SDMs (Vesk *et al.*, 2021; Lee-Yaw *et al.*, 2022). As a result, substantial effort has been put into developing modelling approaches to forecast range shifts that are more process-based\* (Schurr *et al.*, 2012; Briscoe *et al.*, 2019). A central feature of many of those is that they characterize environmental conditions (*e.g.*, exposure to drought\*) and use continuous attributes (functional traits\*) to describe relevant plant features that underlie demographic responses to the environment (Kearney & Porter, 2009; Snell *et al.*, 2014).

Because functional traits are commonly defined as features having an impact on fitness through their effect on demographic rates (Violle *et al.*, 2007) (Box 1), they provide a natural basis to simulate plant responses to environmental changes (Lavorel & Garnier, 2002; Westoby & Wright, 2006; Funk *et al.*, 2017) and forecast range shifts (Estrada *et al.*, 2016) (Fig. 1). Traits have been used successfully to predict demographic rates (Poorter *et al.*, 2008), life history strategies (Adler *et al.*, 2014), competitive interactions (Kunstler *et al.*, 2016), and even to reconstruct past climates in paleoecological studies (Birks, 2020). At the same time, however, there are many counterexamples showing that the ability of traits to explain plant demographic responses is low (Yang *et al.*, 2018; Swenson *et al.*, 2019), and relatively few studies have found strong effects of traits on plant range shifts (Buckley & Kingsolver, 2012; MacLean & Beissinger, 2017; Beissinger & Riddell, 2021). Resolving this apparent paradox has become a priority in trait-based ecology\* (Chacón-Labela *et al.*, 2023).

In this review, we aim at reconciling the solid theoretical basis for using trait-based approaches with the relatively modest empirical results obtained thus far. We first present the rationale and evidence for using functional traits as predictors of drought-induced range shifts in woody plants (section II), and then focus on ways forward to increase the predictive ability of trait-based approaches by accounting for trait coordination\* (section III) and variability\* within species (section IV). Finally, we discuss some implications for modelling range shifts (section V). Box 1 provides definitions of the key concepts used throughout the manuscript (marked with an '\*' on their first use) and Table 1 summarizes the main outstanding questions and proposed ways forward. In contrast to other recent reviews (*e.g.*, Beissinger & Riddell, 2021) we focus on woody plants and take a bottom-up, trait-centric perspective (Fig. 1) emphasizing traits associated with drought responses\* at the species' rear edge. We do not explicitly cover other important climate change-induced disturbances with the potential to induce range shifts, such as insect pests and wildfires (Hill & Field, 2021; Lecina-Diaz *et al.*, 2021). However, because these disturbances are frequently associated with drought and predicting their impacts implies similar challenges and solutions, we expect this review will contribute towards improving our general ability to forecast climate change-induced range shifts.

## **II. Rationale and evidence for using plant traits as predictors of drought-induced range shifts**

Range dynamics depend on the balance between persistence and colonization\* (or movement rate) throughout the geographical distribution of a species (Lenoir & Svenning, 2015). Because persistence and colonization capacity reflect different ecological processes, they are likely to be associated with different traits and plant functions\*. Four of those functions appear

particularly relevant: (i) stress tolerance, which determines adult and seedling survival; (ii) regeneration, which controls the capacity to recover after a disturbance causing adult mortality (Clarke *et al.*, 2013; Martínez-Vilalta & Lloret, 2016); (iii) resource use, which is an indicator of individual growth potential, [competitive ability](#) and shade tolerance, and may determine the chances of establishment and proliferation in new areas (*sensu* Estrada *et al.*, 2016), as well as local recovery after disturbance; and (iv) dispersal, which drives the capacity to colonize empty habitat patches and hence expand the range. The relative importance of these functions is likely to change along the species range, and there is evidence that range dynamics at rear *versus* leading range margins are predicted by different sets of traits (Stahl *et al.*, 2014; Kunstler *et al.*, 2021). [Because climate change will induce hotter and frequently drier conditions, it seems reasonable to hypothesize that traits related to drought tolerance and regeneration may be key determinants of persistence in the rear edge, where species may be closer to their physiological limits to drought \(Hampe & Petit, 2005\). On the other hand, traits related to resource use and dispersal may be particularly important determinants of colonization capacity at the leading edge \(Fig. 2a\).](#)

We know many of the traits involved in the functions described in the previous paragraph (Fig. 2b). Drought tolerance is largely determined by plant hydraulics and water relations (Choat *et al.*, 2018; Volaire, 2018; McDowell *et al.*, 2022), including traits such as the turgor loss point (TLP), rooting depth ( $R_{depth}$ ) and the vulnerability to xylem embolism (usually characterized as the water potential causing 50% loss of hydraulic conductivity,  $P_{50}$ ), as well as by plant size, [allocation and phenology \(e.g., drought-deciduousness; see section III below\)](#). Key regeneration traits include the ability to resprout from surviving tissues (RP) and seed longevity (SL), which determines the capacity to generate a persistent seed bank; as well as clonality (CL), which promotes vegetative reproduction when stressful conditions hinder seed production or seedling establishment (Ottaviani *et al.*, 2017). Traits related to the economy of resource use have been widely studied, and those involved in the leaf economics spectrum\* (LES) are best characterized (Wright *et al.*, 2004). Key LES traits include specific leaf area (SLA), leaf nitrogen concentration (LN), and leaf lifespan (LLS). The root economics space has been less studied, but it appears to involve two main dimensions, one of them tightly linked to the LES (including traits such as root tissue density, RTD, and nitrogen concentration, RN) (Weigelt *et al.*, 2021). Lastly, dispersal capacity depends on plant height ( $H_{max}$ ), [phenology](#) and seed (e.g., seed mass, SM) or fruit traits, depending on the dispersal vector (DV) (Thomson *et al.*, 2010; Tamme *et al.*, 2014).

In practice, however, few of the previous traits have been linked directly with range shifts, as evidenced by earlier reviews and data syntheses (Buckley & Kingsolver, 2012; MacLean & Beissinger, 2017; Beissinger & Riddell, 2021). We summarize available evidence for plants in Table S1 (Supporting Information). An important conclusion from this table is that only one of the 19 studies considered uses stress tolerance or regeneration traits as defined here, compared to 12 assessing dispersal or 13 including broad life form characterizations or habitat preference indices. The latter would not be considered functional traits according to standard definitions (*sensu* Violle *et al.*, 2007) and are challenging to implement in process-based models. However, the fact that habitat preferences regarding temperature and (to a lesser extent) moisture arise as significant predictors in several cases (*e.g.*, Rumpf *et al.*, 2018) underlie the importance of stress tolerance in observed range shifts. The evidence summarized in Table S1 reflects a disconnect between the functional dimensions more frequently covered in trait-based ecology, largely focused on resource use and the LES; those included in studies of range shifts, which tend to **emphasize** dispersal and establishment capacity (Estrada *et al.*, 2016); and those likely to be relevant (Fig. 2b). We posit here that trait-based approaches to predict range shifts require a more balanced coverage of the main functional dimensions involved, and a stronger focus on stress (**drought**) tolerance and regeneration capacity as determinants of persistence (Table 1, i). **The fact that hydraulic traits have been understudied in the context of predicting range shifts was also stressed by Beissinger & Riddell (2021), and** represents a challenge in terms of data availability, as key traits determining tolerance to drought ( $P_{50}$ , TLP,  $R_{depth}$ ) are available for <1000 **plant** species, an order of magnitude less than for many LES, dispersal and regeneration traits (TRY v. 5, Kattge *et al.*, 2020).

A second (and related) conclusion from Table S1 is that there are very few studies linking individual plant traits directly with drought-induced range shifts, and a similar conclusion applies for trait-enabled, process-based models (Supporting Information Table S2). This reflects difficulties in attributing range shifts to specific drivers but also the fact that many more studies focus on the colder and wetter leading edge (12 of the 19 studies listed in Table S1) than on the rear edge (only five), where drought effects are predicted to be strongest (Hampe & Petit, 2005). It is more common to find studies that relate functional traits to demographic responses to drought, and particularly to drought-induced mortality (Anderegg *et al.*, 2019). **Note, however, that adult mortality may or may not result on a range shift, depending for instance on ensuing regeneration dynamics (Martínez-Vilalta & Lloret, 2016).** Anderegg *et al.* (2016) showed that hydraulic traits related to the vulnerability of the water transport system were significant predictors of mortality risk at the global scale, and similar

results have been obtained at the local level (Martínez-Vilalta *et al.*, 2002; Rowland *et al.*, 2015). This is consistent with the key role of hydraulic failure in drought-induced mortality (Choat *et al.*, 2018; McDowell *et al.*, 2022) and with hydraulic traits shaping species distribution patterns in different biomes (Engelbrecht *et al.*, 2007; Laughlin *et al.*, 2020a). Other studies have shown that [easier to measure traits, such as wood density \(more generally referred as stem-specific density, SSD\) or SLA, are also](#) related to drought-induced mortality (albeit weakly) at the global scale (Greenwood *et al.*, 2017). [But there are also many examples of studies that have failed to find a relationship between individual traits and mortality, even for ‘mechanistic’ hydraulic traits \(Johnson et al., 2018; Chen et al., 2021\); and the capacity of hydraulically-enabled models to predict drought-induced mortality remains low at regional scales \(Rowland et al., 2021; Trugman et al., 2021\).](#)

A complementary approach to assess trait effects on demographic outcomes involves identifying traits that increase or decrease in abundance in plant communities after a severe drought, reflecting their net impact on demographic [growth](#). Again, changes towards more drought-tolerant communities appear common (Clark *et al.*, 2016; [Swenson et al., 2020](#); Wilcox *et al.*, 2021). This is frequently reflected in lower hydraulic vulnerability (Barros *et al.*, 2019; Trugman *et al.*, 2020), whereas for other traits, drought-induced changes appear highly context-dependent ([e.g., Madsen-Hepp et al., 2023](#)). A dominant pattern in forests is that taller tree species tend to be more susceptible to water scarcity, resulting in increased abundance of shorter species after drought (Bennett *et al.*, 2015; Rowland *et al.*, 2015). A recent global synthesis by Batllori *et al.* (2020) confirms this pattern and shows that replacement of forest and woodland species by low statured shrubs is common, and that species with resprouting capacity tend to increase after drought.

It should be clear from the previous text that some traits offer promise in predicting demographic responses to drought and resulting range shifts. However, finding general relationships between individual traits and range shifts is difficult because the relationships between traits and demographic rates and range dynamics are highly scale- and context-dependent ([in a mechanistic sense, sensu Catford et al., 2022](#)). By this we mean [that the effects of a given trait on fitness depend on environmental factors \(including biotic interactions\) and also on the values of the other traits of the target species \(Yang et al., 2018; Fontana et al., 2021\).](#) In addition, analysing the different vital rates in isolation (or for a single life stage; Oldfather *et al.*, 2021) can be misleading due to the presence of demographic tradeoffs (Laughlin *et al.*, 2020b) and compensations across populations (Villellas *et al.*, 2015).

In the following sections we explore how an improved characterization of how traits covary (*i.e.*, trait coordination\*), and a better understanding of trait variability within species ranges and its relationship with exposure, including the effects of biotic interactions\*, could help increase the predictive ability of trait-based approaches. Most of our examples focus on traits conferring tolerance to drought at the species' rear edge, as this aspect remains understudied in the literature on plant range shifts.

### III. From plant functions to trait spectra: accounting for trait coordination

The effects of traits cannot be considered in isolation, as they are frequently masked or compensated by the influence of other traits and depend on overall plant strategies (the integrated phenotype). This makes the standard definition of functional trait (*sensu* Violle *et al.*, 2007) problematic in the sense that a given trait may be related to fitness (and hence considered 'functional') in some situations but not in others (but see Sobral, 2021). It also complicates the link between individual traits and broad plant functions such as those identified in Fig. 2b, as those typically result from the coordinated action of many traits acting together. At the same time, the fact that traits covary allows us to summarize the potentially unlimited number of traits that could be considered into a reduced number of functional axes or trait spectra\* (*e.g.*, the LES). The relevant question is: how much trait coordination is there within and between different plant functions and how is it structured?

The lower the number of relatively independent trait axes required to describe plant function (Laughlin, 2014; Mouillot *et al.*, 2021), the lower also the number of traits needed to characterize meaningful trait syndromes\* or, more broadly, plant strategies. There have been several attempts to define these strategies quantitatively based on traits, such as the LHS scheme (Westoby, 1998) or the fast *versus* slow plant economics spectrum (Reich, 2014), the latter based on a generalization of the LES (but see Zhou *et al.*, 2022). However, the complexities of plant range responses to changes in climate (Lenoir & Svenning, 2015; Parmesan & Hanley, 2015) suggests that simple (low-dimensional) functional classifications are unlikely to hold great predictive power, as already shown in section II.

An important issue is how to connect the broad plant functions identified in Fig. 2 (drought tolerance, regeneration, resource use and dispersal) to relatively independent trait spectra that summarize the relevant variability. For some of these functions, our understanding appears reasonably robust, and allows for instance using LES traits to characterize resource use strategies (Reich, 2014; Zhou *et al.*, 2022). In other cases, however, we are on less solid

ground. Although a lot is known about the traits that confer drought tolerance (Choat *et al.*, 2018), decades of ecophysiological research have not been able to produce a classification of plant water use and drought tolerance strategies that is general and predictive (Kannenberg *et al.*, 2022). Classic categorizations such as the dehydration (drought) escape-avoidance-tolerance scheme have proven difficult to quantify, and when this quantification has been attempted (e.g., the iso/anisohydry framework to characterize the regulation of plant water status), the mechanistic link with drought-induced mortality has been difficult to establish (Martínez-Vilalta & García-Forner, 2017; Li *et al.*, 2019). A key reason for this are compensatory changes in other traits (e.g., rooting depth), which can modulate exposure to drought (see section IV below).

At a higher level, an equally challenging issue is establishing the extent to which different plant functions (and the traits underlying them) covary with each other. It is well known that individual traits may contribute to multiple functions (Sack & Buckley, 2020). Tree height, for instance, is related to traits associated to different functions, including seed size (Moles *et al.*, 2009), stem hydraulics and wood density (Liu *et al.*, 2019), but is largely independent from the LES at the global scale (Díaz *et al.*, 2016). Wood density (or SSD) is associated with stem mechanical properties and construction costs (resource use), capacitance and hydraulic vulnerability, at least across species, and has been considered a central trait defining the wood economics spectrum (Chave *et al.*, 2009). Even more important for predictions of range shifts are traits having opposite effects on different functional dimensions. For example, larger seeds tend to be associated with higher seedling survival under drought (Lloret *et al.*, 1999) and may thus promote regeneration, but they typically have lower dispersal capacity (Moles & Westoby, 2006). Other examples of trade-offs among different functions include the fact that species that lack resprouting capacity tend to be more resistant to embolism, at least in the Mediterranean biome (Pausas *et al.*, 2016); or the hypothesized association between conservative resource use at the leaf level and drought tolerance, mediated by hydraulic traits (Reich, 2014; Oliveira *et al.*, 2021) (see Box 2).

### ***The scales of trait coordination***

Trait coordination occurs at different levels (Fontana *et al.*, 2021), but it has been mostly studied across species, in the context of characterizing plant strategies. An important practical limitation at this level is that sample size (number of species with data) declines dramatically when several traits are combined, even in the most comprehensive databases such as TRY (Kattge *et al.*, 2020). A promising avenue to improve trait data availability at the species-level

is the use of phylogenetic information to impute missing values (Anderegg *et al.*, 2022) (Table 1, ii). This approach takes advantage of the fact that many relevant traits show high phylogenetic conservatism, and hence closely related species tend to show similar values (see Sanchez-Martinez *et al.* (2020) for hydraulic traits and Anderegg *et al.* (2022) for LES traits and wood density). Importantly, not only trait values but also trait correlations may show evolutionary conservatism (Sanchez-Martinez *et al.*, 2020), and thus evolutionary correlations can also be used to incorporate evolutionary dependencies between traits and constrain trait estimation in phylogenetic imputation methods.

Importantly, predicting range shifts requires addressing trait coordination within species and its changes in space and time (see section IV), as much as trait coordination across species. The fact that many empirical trait relationships are scale-dependent (Donovan *et al.*, 2011; Anderegg *et al.*, 2018) and in some cases species-dependent (*e.g.*, Supporting Information Fig. S1) suggest that they do not correspond to fundamental trade-offs, and may simply reflect the effect of third variables (*e.g.*, current environmental conditions) on the traits involved.

Therefore, different covariation structures may be expected if conditions change (Zhou *et al.*, 2022). Genetic correlations between traits within species indicate a shared genetic basis, and hence a potential constraint to microevolutionary responses (Etterson & Shaw, 2001), but they have been rarely assessed for traits outside the LES (Donovan *et al.*, 2011). Clearly, more ecoevolutionary work is needed to disentangle the nature of the constraints (biophysical, evolutionary, ecological) underlying trait relationships (Agrawal, 2020) and limiting the selection of certain trait combinations under climate warming.

A promising methodological approach to address the multidimensional nature of trait relationships and their effects on plant performance\* in empirical studies is the use of trait networks (He *et al.*, 2020). These networks can be used to characterize the importance of individual traits, which can be assessed through their connectivity (degree) or centrality (betweenness) in the network (Messier *et al.*, 2017; Kleyer *et al.*, 2019). Properties describing the overall topology of the network, such as its modularity, may be particularly useful to identify trait spectra (Supporting Information Fig. S2), and their dependency to the environmental context (Flores-Moreno *et al.*, 2019). An important limitation of current trait network approaches is that they do not reflect the hierarchical nature of trait-performance relationships (Fontana *et al.*, 2021) or incorporate information on the direction of effects. A way forward is the combination of network approaches with structural equation models to establish causal networks (Grace & Irvine, 2020), so that the coordination of individual traits

into trait spectra, and their directional effects on demographic rates and of those on range dynamics (*cf.* Fig. 1) can be formally tested (Table 1, iii). This will require careful experimental designs that assess traits (encompassing the main functional dimensions identified above) and demographic rates concurrently, both under controlled experimental conditions and in the field (Moles, 2018).

### ***Taking a whole-plant perspective***

Plants are whole functional units and should be considered as such, particularly when aiming at predicting organismal-level outcomes. Allocation traits\* are particularly relevant in that regard, as they frequently hold the key to understand trait coordination at the whole-plant (phenotypic) level (Table 1, iv). For instance, traits such as the sapwood-to-leaf area ratio (the Huber value, Hv) or the root:shoot ratio (RS) are key components of drought tolerance strategies, as they determine the balance between water demand, supply and transport capacity (Mencuccini *et al.*, 2019b). At the same time, allocation traits are essential to reveal the coordination of organ-level traits between each other and with fitness (Yang *et al.*, 2018) (see Box 2 for an example using hydraulic traits). A whole-plant perspective may also help simplify important issues related to trait differences among organs. It is well known, for instance, that hydraulic traits show substantial variability within plants, reflecting tip-to-base xylem conduit widening (Olson *et al.*, 2021), the influence of extra-xylary pathways in leaves and roots (Scoffoni *et al.*, 2017), and hydraulic segmentation protecting more valuable (resource-rich) organs (Johnson *et al.*, 2016). However, most species comparisons and modelling exercises use only stem hydraulic traits, potentially missing relevant differences in the way these traits scale to the whole plant (McCulloh *et al.*, 2019; Mencuccini *et al.*, 2019a). A promising alternative would be to estimate hydraulic traits ( $K_s$ ,  $P_{50}$ ) directly at the whole-plant level from the relationship between plant water use and leaf water potentials, taking advantage of the fact that time series of these variables are becoming increasingly available (Poyatos *et al.*, 2021; Novick *et al.*, 2022).

An additional aspect that remains understudied is the role of the tightness of trait coordination in itself (*i.e.*, the amount of trait covariation present, regardless of how it is structured), which at the whole-plant level can be understood as a measure of the degree of phenotypic integration (Armbruster *et al.*, 2014). Because proper plant functioning involves the coordinated expression of many traits, it has been hypothesized that phenotypic integration in itself has adaptive value (Damián *et al.*, 2020). It has been shown that trait coordination tends to be tighter in more stressful environments imposing strong multidimensional trait

constraints, and for trait spectra that are stronger determinants of local performance (*e.g.*, drought-tolerance traits at the distribution's rear edge) (Dwyer & Laughlin, 2017; Benavides *et al.*, 2021; but see Matesanz *et al.*, 2021). It could thus be hypothesized that species or populations with more tightly coordinated drought-tolerance traits may be more able to cope with declining water availability and hence would show higher persistence under more arid conditions. Trait network indices such as edge density and modularity (He *et al.*, 2020) can be directly used as measures of the tightness of trait coordination, and may be considered traits in themselves and included as explanatory variables in predictive models (Table 1, iv).

#### **IV. From species-level traits to local performance and range dynamics: accounting for trait variability and exposure**

Traits vary in space and time and across different levels of organization (Siefert *et al.*, 2015). Trait variability within and among populations has a genetic component that underpins local adaptation and acts in concert with different responses to the environment of a given genotype (phenotypic plasticity) to influence species responses to changes in climate (Valladares *et al.*, 2014). The fact that traits tend to adjust to local environmental conditions implies that species means may not provide an adequate description of a specific population. In many tree species, for instance, drier populations tend to have higher sapwood-to-leaf area ratios (Hv) and lower (more negative) turgor loss point (TLP) than populations from wetter areas (Rosas *et al.*, 2019; Anderegg *et al.*, 2021; López *et al.*, 2021). Because these adjustments tend to make populations at the drier range edge more tolerant to drought (Fig. 3), predictions using species trait means would misrepresent hydraulic risk (Challis *et al.*, 2022) and underestimate species persistence.

In addition to trait differentiation among populations, trait variability within populations can also be substantial and has an important role in plant responses to global change (Bolnick *et al.*, 2011; Moran *et al.*, 2016). If the individual-level relationship between a given trait and a demographic rate is non-linear, which is common, the population mean of the trait would be a poor predictor of population-level performance (due to Jensen's inequality, Ruel & Ayres, 1999). For instance, if the relationship between a given trait and mortality is non-linear, the 'average plant' could be predicted to survive even if a large proportion of the individuals in the population (potentially >> 50%) actually crossed the mortality threshold. Similar issues arise for within-individual trait variability, which can be large and has profound consequences for fitness (Herrera, 2017), as discussed in section III for hydraulic traits. In addition, the modular nature of plants implies that organ loss (*e.g.*, stem or partial canopy dieback) may not be a

reliable indicator of individual mortality or population-level persistence, particularly for resprouting species (*e.g.*, Lloret *et al.*, 2004).

Trait adjustments also occur over time. Although there are examples of rapid trait evolution in response to fluctuations in water availability (Franks *et al.*, 2007; Anstett *et al.*, 2021), in most cases genetic adaptation is unlikely to compensate for the expected rates of climate change (Jump & Peñuelas, 2005; Franks *et al.*, 2014). Phenotypic plasticity, on the other hand, can be very fast in plants (Nicotra *et al.*, 2010). Our understanding of the factors determining (and limiting) phenotypic plasticity within species ranges is increasing (Stotz *et al.*, 2021; Solé-Medina *et al.*, 2022), including trait adjustments in response to drought (Rowland *et al.*, 2023). Plastic adjustments typically reduce the likelihood or anticipated magnitude of range shifts relative to a constant-traits scenario (Hoffmann & Sgrò, 2011; Razgour *et al.*, 2019), although cases of maladaptive plasticity have been recorded (Zettlemyer & Peterson, 2021). An important example of the latter are legacy\* effects resulting from previous disturbances, which may induce long-term shifts in trait values. For instance, accumulated hydraulic damage over time, a process known as cavitation fatigue, increases tree vulnerability to future drought stress and has been associated to drought-induced forest mortality (Anderegg *et al.*, 2013).

The importance of spatiotemporal trait variability within species has been increasingly recognized, but most studies aiming at relating functional traits with demographic rates (or range shifts) still use species-level means based on limited sample size and spatial coverage. Clearly, improving the predictive ability of trait-based approaches requires trait data at increased spatial and temporal resolution, reflecting variability within species ranges (*e.g.*, Rosas *et al.*, 2021). A way to deal with within-species variability is to progressively replace the focus on species' trait means with trait distributions and characterize them and their changes in space and time as accurately as possible from empirical measurements, accounting for trait covariation (Table 1, vi) (Laughlin *et al.*, 2012; Laughlin & Messier, 2015).

### ***Accounting for environmental variability and local exposure***

The spatial configuration of a species' geographical distribution determines the distance among populations (geographical marginality; Vilà-Cabrera *et al.*, 2019) and between them and suitable habitat patches, and it is thus an important determinant of effective dispersal and metapopulation dynamics, potentially affecting both colonization rates and persistence (rescue effect) (*e.g.*, Fordham *et al.*, 2012). This is particularly important for populations located at the geographical margins of species distributions, because they tend to be smaller

and more isolated from one another than those located in the core of the range (Hampe and Petit, 2005; Sexton *et al.*, 2009). Importantly, however, environmental conditions vary in complex ways within species ranges, not necessarily conforming to the simplistic expectation of higher climatic or ecological marginality towards (geographic) range margins (McLaughlin *et al.*, 2017; Vilà-Cabrera *et al.*, 2019; Oldfather *et al.*, 2020) (Fig. 3).

The need to account for fine-scale environmental variability is especially clear for stress tolerance traits determining persistence, which cannot be interpreted at the local level without considering exposure to the relevant environmental factors (Anderegg & HilleRisLambers, 2016; Trugman *et al.*, 2021) (Table 1, viii). Because plants growing under identical environmental conditions can differ markedly in the degree of water shortage they experience (*e.g.*, if they differ in rooting depth), it is useful to distinguish between external exposure (as determined by hydroclimatic conditions) and internal exposure (the stress actually experienced by plant tissues). In the context of drought vulnerability assessments, the latter is usually estimated as the minimum water potential experienced by a species/population in the field ( $\Psi_{min}$ ) (Bhaskar & Ackerly, 2006; Martínez-Vilalta *et al.*, 2021). This variable is particularly convenient because the difference between  $\Psi_{min}$  and the water potential causing 50% loss of hydraulic conductivity ( $P_{50}$ ) is a measure of the hydraulic safety margin (HSM) (Choat *et al.*, 2012; Delzon & Cochard, 2014). Despite its limitations (Martínez-Vilalta *et al.*, 2021), this metric provides a conceptually robust measure of hydraulic risk and vulnerability to drought and has been related successfully to drought-induced mortality (Table 1, ix; see also section II above).

In the context of persistence under increased drought stress, a critical question remains whether (and for what species and populations) plasticity in hydraulic vulnerability will be able to compensate for increases in tissue-level exposure, which is only partially controlled by the plant (Martínez-Vilalta & García-Forner, 2017). Several studies have shown limited plasticity for xylem vulnerability traits ( $P_{50}$ ) for some species groups (*cf.* Lamy *et al.*, 2014; López *et al.*, 2016 for Pinaceae), suggesting that hydraulic safety margins will become narrower as conditions become more arid. Identifying mismatches between the plant's capacity to limit exposure to low water potentials and its capacity to adjust hydraulic traits should improve our ability to detect particularly vulnerable species and populations (Table 1, vii).

In many applications, it is more practical to estimate external exposure to drought using climatic or hydroclimatic indices than tissue-level exposure. This can be done using

standardized indices such as the Standardized Precipitation Evapotranspiration Index (SPEI) (Slette *et al.*, 2019) or absolute measures of water availability (Zang *et al.*, 2020). The complex temporal patterns associated with plant performance at range limits and the limited resolution of relevant environmental data at regional to global scales complicate the representation of local conditions and climatic extremes in range shifts studies (Germain & Lutz, 2020). However, new tools are being developed to estimate present and future microclimate at unprecedented resolution, which will greatly improve hydroclimatic characterization (Zellweger *et al.*, 2019; Lembrechts & Lenoir, 2020). Improving soil characterization should be the next priority (Fatichi *et al.*, 2020), as soil attributes are extremely important determinants of plant exposure to drought and their huge spatial variation makes estimation particularly challenging. Improving the coverage and availability of soil (and plant) water potential data is an obvious step in this direction (Novick *et al.*, 2022).

Finally, exposure to drought has to be considered in the context of the complexity of species life-cycles (Buckley & Kingsolver, 2012). Phenology drives reproductive success and exposure to biotic and abiotic stress factors such as frost and drought, and hence affects several of the functional axes highlighted in Fig. 2 and needs to be accounted for when predicting range dynamics (Chaine, 2010). Because transpiration and water demand from the canopy are largely determined by the amount of evaporating surface, tissue-level exposure to drought is controlled, to an important extent, by the dynamics of leaf area (Wolfe *et al.*, 2016; Sabot *et al.*, 2022). A classic example is drought-deciduousness, which is common in species inhabiting arid environments and may be more effective than traits conferring hydraulic safety in enabling persistence under extreme drought (Pivovarov *et al.*, 2016). In general, an improved characterization of the timing of drought within the seasonal phenological cycle (and its plasticity) is thus essential to properly assess exposure, and it is likely to improve the predictive ability of process-based models (Charrier *et al.*, 2021).

### ***The role of biotic interactions***

Drought-driven species range shifts will also depend on alterations to species interactions and co-existence (HilleRisLambers *et al.*, 2013; Alexander *et al.*, 2015), as changes in water availability modify the balance between competition and facilitation in plant communities (Ploughe *et al.*, 2019). The effect of biotic interactions (including competition, predation/herbivory and pathogens) tends to be more important at the species' warm versus cool range edges (Paquette and Hargreaves, 2021). There is in fact ample evidence, for instance, that biotic agents (primarily insect pests, but also fungal pathogens) are involved in

many episodes of drought-induced forest mortality (McDowell *et al.*, 2022), and that the complexities of host-pathogen interactions explain why these mortality events tend to be so hard to predict from plant traits alone (Trugman *et al.*, 2021).

In addition, plant-plant interactions are significant determinants of exposure to drought at the local level and, as a result, plants can display different responses to a given level of climatic exposure depending on their trait values relative to the traits of co-existing species (Uriarte *et al.*, 2016; De Cáceres *et al.*, 2021) (Fig. 4). Under increased aridity, species with the most stress-tolerant traits in a given community may have an additional ecological advantage (Vilà-Cabrera *et al.* 2019) due to increased niche availability following reduced demographic performance of other, less drought-tolerant co-existing species (Lloret *et al.*, 2012) (Fig. 4). In addition, community reorganization can alter competitive interactions even in the absence of changes in local exposure, as in situations when the effect of novel competitors on the target species is explained by the degree of functional similarity between current and novel competitors (Alexander *et al.*, 2015). Therefore, the value of a given species trait relative to the values of the other species in the community may be as informative as its absolute value (Table 1, xi).

Importantly, disturbance legacies may also modify trait distributions at the community level, influencing vegetation responses to subsequent conditions (Foster *et al.*, 2003; Johnstone *et al.*, 2016). During an El Niño-related combination of extreme drought and fires in Amazonian forests, tree mortality was higher in secondary forests and forests previously affected by burning and logging activities than in undisturbed primary forests, and this was mediated by shifts in wood density and bark thickness as legacy effects of previous human disturbance (Berenguer *et al.*, 2021). At the landscape scale, addressing the interaction of habitat configuration (*e.g.*, fragmentation) with dispersal and resource-use traits represents a powerful approach to capture the effects of disturbance legacies on the functional reorganization of communities (Arasa-Gisbert *et al.*, 2022).

The recognised need to account for biological interactions and ensure that species distribution modelling is better rooted in ecological reality has contributed to the development of joint Species Distribution Models (jSDMs) (Pollock *et al.*, 2014; Ovaskainen & Abrego, 2020). These models combine classic species distribution modelling with co-occurrence analyses that originate from community ecology, and typically estimate species interactions from the residual variance unexplained by abiotic factors (Pollock *et al.*, 2014). Although these models

capture key aspects of ecological interactions, they have also important limitations, as they are based on observed species associations (*i.e.*, interactions are not modelled explicitly but inferred from co-occurrence data) and are very sensitive to missing biotic or abiotic variables (Dormann *et al.*, 2018; Zurell *et al.*, 2018). Species traits, and particularly those related to resource use and stress tolerance (Fig. 2), offer a promising avenue to simulate species interactions explicitly in models (Dormann *et al.*, 2018; Tikhonov *et al.*, 2020) (Table 1, x; see next section).

## V. Implications for modelling range shifts

It should be clear from the preceding sections that, in most cases, improving our capacity to predict range shifts using traits requires the use of process-based niche models. Most current models, however, do not account for many of the aspects highlighted above. In many cases, for instance, trait coordination is either excluded or, at best, imposed *a priori* based on first principles (*e.g.*, LES relationships, seed size *versus* number tradeoff) (Table S2). An alternative and powerful approach is to let trait coordination emerge from the modelling exercise itself, for example when it involves exploring the trait parameter space during the calibration phase and employing the resultant likelihood function to select the trait combinations maximizing model performance (Table 1, v). This approach is still rare (Table S2), but there is great potential to expand it to trait-enabled models in general. Similarly, models incorporating optimality principles have shown a remarkable ability to constrain trait coordination at different levels (Deans *et al.*, 2020; Harrison *et al.*, 2021).

Most mechanistic models use hydroclimatic variability to estimate exposure, but the spatial resolution of this data is usually limited and microenvironmental variability is seldom considered, particularly regarding soil attributes (Table S2). Representing within-species variability in traits is also rare (Table S2), despite the growing understanding of trait variation along environmental gradients (O'Sullivan *et al.*, 2022) and the fact that some models explicitly account for local adaptation and phenotypic plasticity (*e.g.*, Garzón *et al.*, 2019). Within-population variability in traits can be represented using individual- or cohort-based models (Christoffersen *et al.*, 2016; Fisher *et al.*, 2018; De Cáceres *et al.*, 2021), but parameterizing these models remains a challenge, both in terms of data and computational needs. However, using a probabilistic approach in which multivariate trait distributions are estimated efficiently from measurements and used to simulate variability among populations and individuals (and within, if needed) is becoming increasingly feasible (Laughlin *et al.*, 2012; Laughlin & Messier, 2015; Mencuccini *et al.*, 2019a). Similar approaches could be used to simulate temporal

adjustments in traits, but even relatively simple responses such as drought-deciduousness are currently only incorporated by a handful of models (Table S2). Hydraulically-enabled, process-based models have already been used to assess the impact of biotic interactions on the drought responses of coexisting species (De Cáceres *et al.*, 2021). This approach has the advantage of building explicitly on community theory and hence allowing greater generalization than approaches based solely on species associations (Table 1, x).

A key limitation to incorporate many of the previous considerations is the corresponding increase in model complexity. In this regard, the incorporation of eco-evolutionary optimality principles offers a promising way forward (Table 1, xii). Those principles allow predicting trait variation and covariation without explicitly simulating the complexities of the underlying evolutionary, physiological and ecological mechanisms (Franklin *et al.*, 2020; Harrison *et al.*, 2021). So far, optimality principles have been applied mostly to leaf- and canopy-level process, particularly to the modelling of photosynthesis and gas exchange. However, recent developments show the potential to apply these principles to derive trait spectra such as the LES from first principles and to address carbon allocation and plasticity at the whole-plant level (Harrison *et al.*, 2021). The use of optimality principles has also been suggested to improve predictions of tree mortality (and hence persistence) (Meir *et al.*, 2015), and has been applied to model species competition and coexistence under drought (Lindh *et al.*, 2014). Despite the potential of optimality approaches for modelling many of the underlying processes, including biotic interactions, their ability to predict species range shifts remains to be evaluated.

## VI. Conclusion

Individual functional traits are weak predictors of species range shifts. While this conclusion is frustrating, we have a growing understanding of why this is the case. The conceptual framework linking traits with species performance and range shifts (Fig. 1) is not disputed. However, the link is more complex than often assumed. This is in part due to the nature of range shifts themselves, which tend to be multifactorial and involve complex spatial patterns at different scales, but also because the effects of traits on plant performance are highly scale- and context-dependent (Fontana *et al.*, 2021). Improving the ability of trait-based approaches to predict range shifts requires a more balanced consideration of the functional dimensions determining persistence and colonization rates (Fig. 2), and will be facilitated by rapidly growing data availability (both for traits and for range shifts: *e.g.*, the BioShifts database, Lenoir *et al.*, 2020) and improved imputation methods. However, addressing context-dependency also requires new, hypothesis-driven empirical research (Moles, 2018) and

analytical approaches that explicitly account for trait covariation and trait variability in space and time in relation to exposure, including biotic interactions.

There are still many challenges ahead (Table 1), and it is clear that more empirical approaches, from classic SDMs to vulnerability assessments based on past and present climatic suitability (*e.g.*, Margalef-Marrassé *et al.*, 2020), will continue to provide insights and useful predictions. However, empirical methods are not able to deliver the levels of generality needed in many applications aimed at forecasting vegetation responses under altered abiotic and biotic conditions, particularly when non-analogue conditions are involved. To an important extent, progress will depend on our ability to develop more refined process-based models that incorporate the subtleties of trait coordination and trait-environment interactions. Existing models include many of the relevant processes (Table S2), but computational and parameterization constraints preclude considering them all at the same time. The use of optimality principles should facilitate doing so without falling in the so called ‘complexity trap’. We are thus optimistic that trait-based approaches will help us predict species range shifts as our understanding of the drivers and implications of trait variation and co-variation, and the context-dependency of trait effects, increase over the near future.

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### **Author’s contributions**

JMV, RGV, AJ, MM and AVC conceived the ideas and structure of the review; JMV led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### **Data availability**

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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## Supporting Information

The following Supporting Information is available for this article:

**Table S1** Studies assessing the effect of plant traits on contemporary range shifts.

**Table S2** Examples of different model types using plant traits (broadly defined) to predict species range shifts.

**Figure S1** Trait relationships within- and among-species (N = 6 Fagaceae and Pinaceae species) along a water availability gradient in Catalonia, NE Spain.

**Figure S2** Idealized trait network structures describing different relationships among traits.

**Figure S3** Standardised Major Axis (SMA) regressions between specific leaf area (SLA, as a proxy for the leaf economics spectrum) and hydraulic traits.

**Box 1** Glossary (terms are marked with an ‘\*’ on their first appearance in the text).

**Allocation trait:** a ratio describing the relationship between the size of two plant parts (*e.g.*, two different organs) in terms of mass, volume or area (Weiner, 2004).

**Biotic interaction:** the effect that a pair of organisms living together in a community have on each other.

**Colonization:** the process by which a species spreads to new areas.

**Drought responses:** the ways by which plants react to low water availability.

**Drought tolerance (*sensu lato*):** the ability to function and survive under low water availability.

We note that some definitions consider drought tolerance more narrowly as a particular mechanism to achieve resistance to drought (typically involving the ability to endure low water potentials in plant tissues), but we prefer to use a more general definition here, which is consistent with much of the recent literature on plant drought responses.

**Exposure to drought:** the degree of water shortage experienced by a plant. It can be assessed externally, in which case it is determined by environmental factors, or internally (at the tissue level), in which case it is jointly determined by environmental factors and plant traits (*e.g.*, rooting depth).

**Function:** A process that contributes to species performance. Dispersal, stress tolerance, regeneration, and resource use are examples of different functions or functional dimensions.

**Functional trait:** any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism, which impacts fitness indirectly via its effects on performance (Violle *et al.*, 2007).

**Leaf economics spectrum (LES):** a continuum of leaf functional strategies involving a set of multivariate correlations that confine the global diversity of leaf resource-use traits onto a single axis of variation, running from quick (acquisitive) to slow (conservative) return on investments of nutrients and dry mass in leaves (Wright *et al.*, 2004).

**Legacy:** the persistence of the influence of an event (*e.g.*, a disturbance) over a given time period.

**Performance:** the ability to grow, reproduce and survive, including the capacity to move into new areas.

**Persistence:** the capacity of a species to continue to exist in a given area.

**Process-based (or mechanistic) model:** a model that specifies underlying processes or mechanisms (*e.g.*, physiological, phenological, or demographic processes), as well as the relevant environmental conditions.

**Range shift:** a change in the geographic distribution of a species over time.

**Species distribution model (SDM):** a numerical tool that relates species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations.

**Trait-based ecology:** a research program aimed at using functional traits to gain a more mechanistic understanding of community dynamics and vegetation responses to environmental change (Westoby & Wright, 2006).

**Trait coordination:** the way different traits covary (*i.e.*, their covariation structure). From a functional perspective this is commonly understood as the way different traits work together to perform some function (Armbruster, 2014). The tightness of trait coordination refers specifically to the degree by which different traits covary with each other, and can be quantified as the total (sum) or average covariation, or using different trait network metrics (see section III in main text).

**Trait spectrum:** a continuous range of plant properties in the space defined by a set of phenotypic traits that have a disposition for covariation and are complementary in performing some function. The LES is a classic example of a functional trait spectra; but trait spectra have also been proposed for wood/stems (Chave *et al.*, 2009), roots/mycorrhizas (Bergmann *et al.*, 2020) and seeds (Moles & Westoby, 2006).

**Trait syndrome:** a set of trait values shared by a group of species. Trait syndromes frequently reflect trait covariation, but this is not necessarily the case.

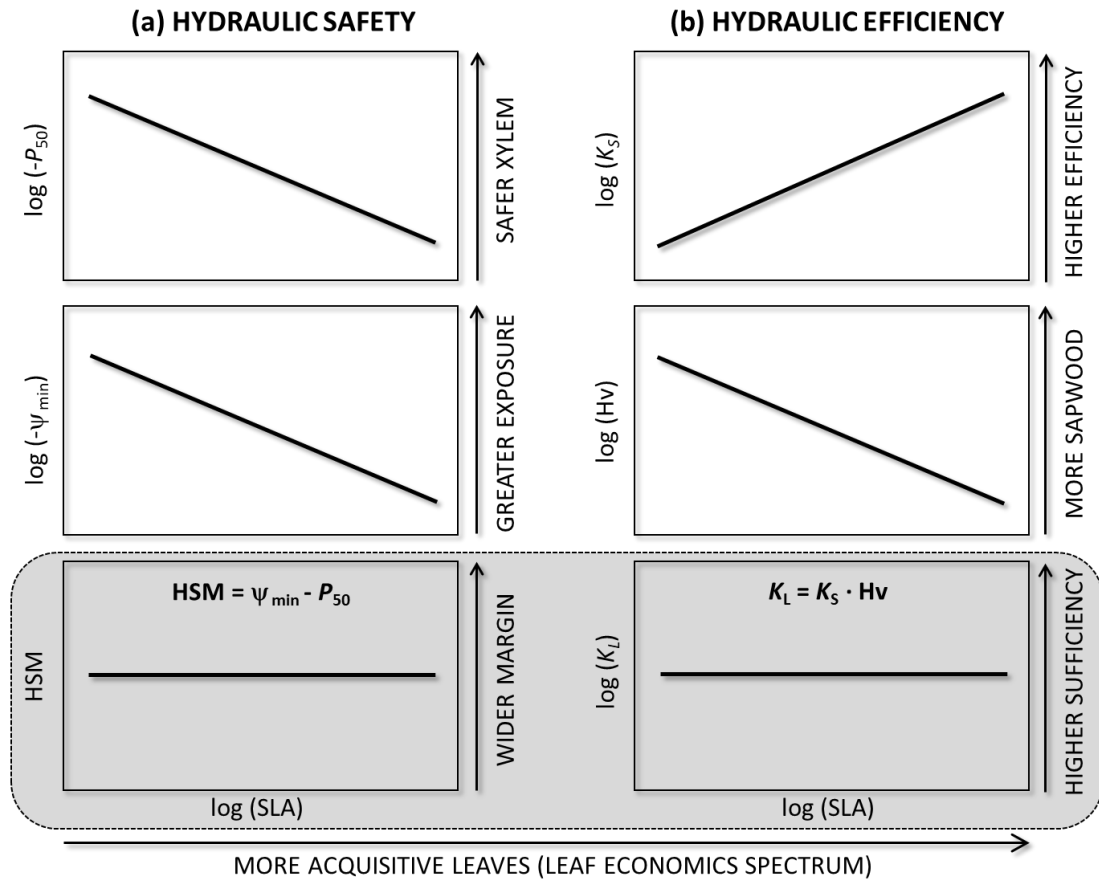
**Trait variability:** the amount of trait variation at different ecological scales, from within-individuals to among-species.

## **Box 2** The relationship between hydraulic traits and the leaf economics spectrum (LES)

As a part of the ‘fast–slow’ plant economics spectrum, it has been hypothesized that there is an association between conservative resource use at the leaf level and drought tolerance, mediated by hydraulic traits (Reich, 2014; Oliveira *et al.*, 2021). There is indeed clear evidence that SLA and xylem hydraulic conductivity per unit of sapwood ( $K_s$ ) tend to be positively correlated across species at the global scale, implying that acquisitive leaves with higher resource-use rates are associated with greater hydraulic transport capacity in the xylem (Reich, 2014). At the same time, species with high SLA also tend to be less resistant to embolism (higher  $P_{50}$ ) at the global scale, implying that higher resource-use at the leaf level is associated with higher hydraulic vulnerability (Oliveira *et al.*, 2021).

One could conclude from the previous paragraph that species with acquisitive leaves tend to have a more efficient water transport but are also more vulnerable to drought. Things, however, are a bit more complicated. It turns out that allocation to sapwood relative to leaves (the Huber value,  $H_v$ ) increases with declining SLA, in such a way that fully compensates for the positive effect of SLA on  $K_s$  (Mencuccini *et al.*, 2019). As a result, the xylem hydraulic conductivity per unit leaf area ( $K_L$ ), which is the product of  $K_s$  by  $H_v$  and quantifies the hydraulic sufficiency of leaves (*i.e.*, the supply capacity of the stem per unit of leaf area demanding water), is unrelated to SLA (Rosas, 2019) (Box figure). The situation is analogous when we look at the ‘safety’ side of xylem function: species with higher SLA (more acquisitive leaves) tend to show higher  $\psi_{min}$  (lower exposure to drought), so that hydraulic safety margins (HSM, the difference between  $\psi_{min}$  and  $P_{50}$ ) are invariant with SLA (Rosas, 2019) (Box figure).

The previous results are important for at least three reasons. Firstly, as HSM and  $K_L$  are likely to be stronger determinants of plant performance under drought than  $P_{50}$  and  $K_s$ , they show that even when there is substantial trait coordination between organs, the relevant axis of variation to predict plant responses to stress may be independent from this coordination. Secondly, because they illustrate that allometric relationships and allocation (to leaves *versus* stems, in this case) hold the key to understanding trait coordination (or lack thereof) among organs, and how it translates into whole-plant performance (Armbruster *et al.*, 2014; Yang *et al.*, 2018). Finally, because they highlight the importance of accounting for exposure to drought (in this case  $\psi_{min}$ ) in determining hydraulic risk.

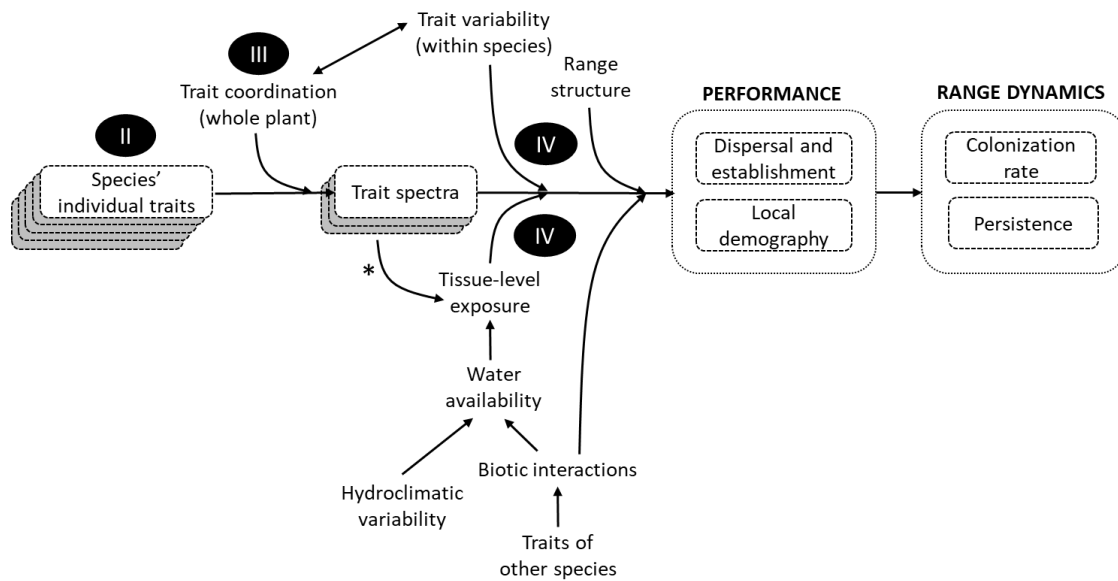


**Box 2 Fig. 1** Directional global relationships between specific leaf area (SLA, as a proxy of the leaf economics spectrum, LES) and key hydraulic traits across species, showing that even if traits are coordinated at the tissue-level, whole-plant hydraulic function is largely decoupled from the LES (bottom row). For hydraulic safety (a, left column) species with more acquisitive leaves (higher SLA) tend to be more vulnerable to xylem embolism (less negative pressure inducing 50% loss of xylem conductivity,  $P_{50}$ ) but also less exposed to low tissue water potentials (less negative minimum water potential,  $\psi_{min}$ ), so that the hydraulic safety margin (HSM) becomes independent of SLA. Similarly, for hydraulic efficiency (b, right column) species with more acquisitive leaves tend to have a more conductive sapwood (higher hydraulic conductivity per unit of sapwood area,  $K_s$ ) but also more leaves per unit of sapwood (lower Huber value,  $Hv$ ), so that again these relationships compensate each other and result in invariant hydraulic sufficiency of leaves (hydraulic conductivity per unit of leaf area,  $K_L$ ) as a function of SLA. See Fig. S3 (Supporting Information) for the empirical data supporting these relationships across species at the global scale.

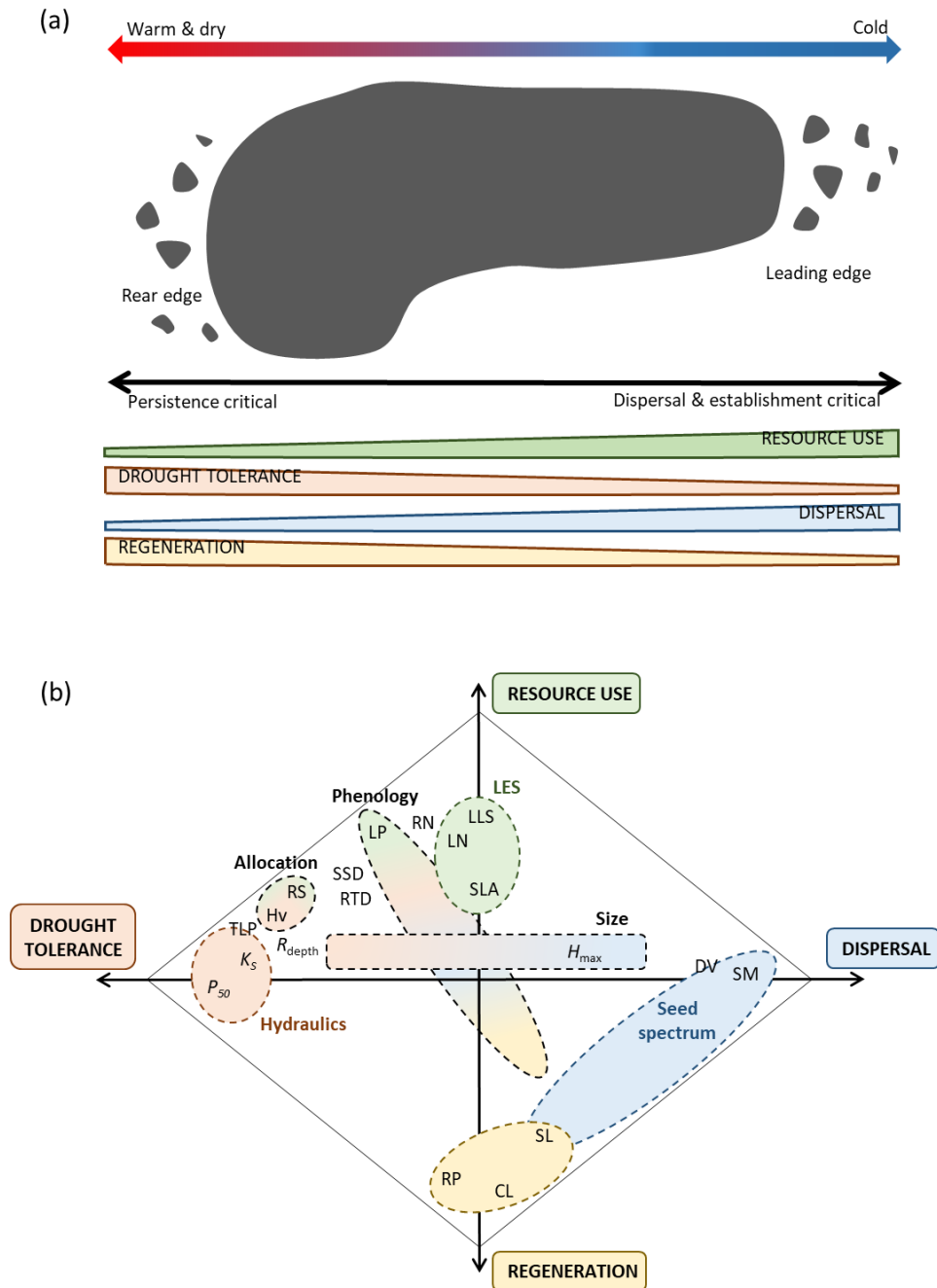
**Table 1** Some outstanding questions, challenges and proposed ways forward in the prediction of drought-induced species range shifts using trait-based approaches. Proposed ways forward are identified with their corresponding number (i, ii, ...) on their first appearance in the text.

| Outstanding question                                                                                                     | Key challenges                                                                                                                                                                                                                                                                                                                | Proposed way forward                                                                                                                                                                                                                                                                                                                                                                               |
|--------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| a. How can we increase the functional relevance of measured traits and their linkage to range dynamics?<br>[section II]  | <ul style="list-style-type: none"> <li>Uncertainty on what are the key traits.</li> <li>Limited data availability.</li> <li>Trait syndromes for drought tolerance and regeneration capacity not well defined.</li> </ul>                                                                                                      | (i) Use a more balanced coverage of traits, focusing on stress tolerance and regeneration capacity as determinants of persistence.                                                                                                                                                                                                                                                                 |
| b. How can we increase trait coverage at the species level (in addition to gathering more data)?<br>[section III]        | <ul style="list-style-type: none"> <li>Data availability, as sample size declines dramatically when several traits are combined.</li> </ul>                                                                                                                                                                                   | (ii) Use phylogenetic methods and evolutionary correlations among traits to improve trait imputation.                                                                                                                                                                                                                                                                                              |
| c. How should we define trait spectra that are functionally relevant to the prediction of range shifts?<br>[section III] | <ul style="list-style-type: none"> <li>Characterizing the complex hierarchy of trait interactions that determines whole-plant performance.</li> </ul>                                                                                                                                                                         | (iii) Use causal networks to test alternative trait covariation structures at the whole-plant level (including measured of phenotypic integration) and their effect on performance in empirical studies.<br>(iv) Take a whole-plant perspective and increase the importance given to allocation traits and phenotypic integration.<br>(v) Use process-based models to constrain trait covariation. |
| d. How to account for fine-scale trait variability in space and time (and their limits)?<br>[section IV]                 | <ul style="list-style-type: none"> <li>Limited data availability on trait variability within species, which results in uncertain parameterization of trait distributions, even when efficient Bayesian approaches are used.</li> <li>Limited data available to constrain the rate and the limits of trait changes.</li> </ul> | (vi) Use trait distributions (instead of mean values) in predictive models, and constrain them (and their variation along environmental gradients) using empirical data and known trait covariation structures.<br>(vii) Characterize the drivers of phenotypic plasticity along environmental gradients, accounting for the coordination of trait plasticity.                                     |
| e. How can we deal with the effect of environmental variability and local exposure?<br>[section IV]                      | <ul style="list-style-type: none"> <li>Characterization of exposure to drought at the relevant spatiotemporal scale.</li> <li>Limited knowledge of belowground factors determining exposure to drought.</li> </ul>                                                                                                            | (viii) Use hydrometeorological data and models to characterize the local environmental context, including phenology and belowground attributes (from soils and plants) and the effect of biotic interactions.<br>(ix) Whenever possible, combine traits with exposure indicators using robust metrics (e.g., the hydraulic safety margin, HSM,                                                     |

|                                                                                       |                                                                                                                                                                                                                                                                   |                                                                                                                                                                                   |
|---------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                                                       |                                                                                                                                                                                                                                                                   | in the characterization of vulnerability to drought).                                                                                                                             |
| <i>f.</i> How can we address biotic effects on range dynamics?<br>[section IV]        | <ul style="list-style-type: none"> <li>• Parametrization of multi-species trait values (or distributions) very costly in terms of data needs.</li> <li>• Belowground interactions and the mechanisms underlying legacy effects are still poorly known.</li> </ul> | (x) Simulate interactions explicitly using trait-enabled, process-based models.<br>(xi) Use community-level trait distributions to contextualize the traits of the focal species. |
| <i>g.</i> How can we avoid the 'complexity trap' in predictive models?<br>[section V] | <ul style="list-style-type: none"> <li>• Optimality principles that regulate long-term persistence and biotic interactions remain poorly known.</li> </ul>                                                                                                        | (xii) Apply optimality principles whenever possible.                                                                                                                              |

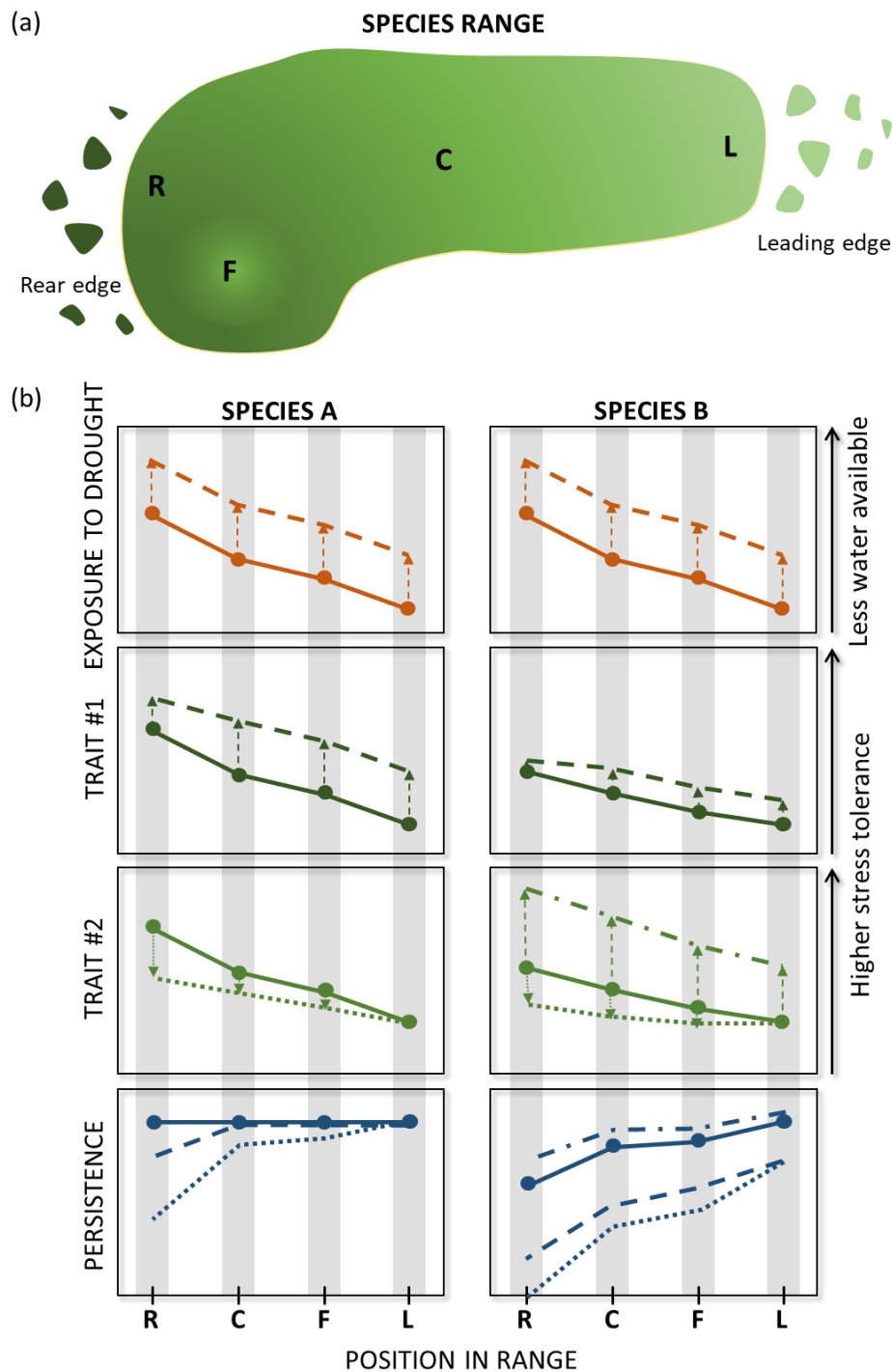


**Fig. 1** Conceptual framework linking plant functional traits and trait spectra with local demography and expected range shifts under increased drought, mediated by exposure. Hydroclimate refers to the combination of hydrological and climatic conditions influencing water availability to plants. Note that we explicitly distinguish between external exposure (water availability) and internal (tissue-level) exposure (Box 1), which is partially determined by plant traits and trait spectra (\*), including rooting depth, allocation and phenology. Range structure refers to the spatial structure of the species' geographical distribution, which affects for example the distance between populations and hence the likelihood of effective dispersal and metapopulation dynamics. Local demography includes growth, mortality and regeneration. Numbers in black circles indicate the main areas covered in this review and correspond to different manuscript sections.



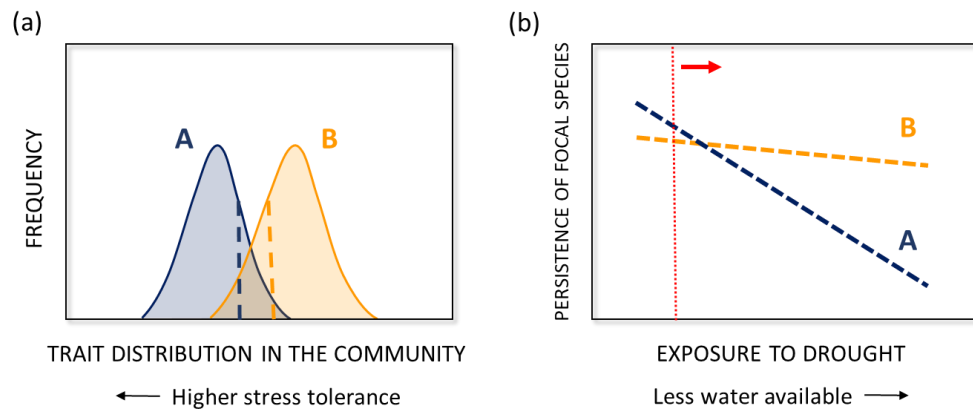
**Fig. 2** (a) Varying importance of plant functional dimensions involved in drought-induced species' range shifts along a species range, with particular reference to rear (typically warm and dry and lower latitude/altitude) and leading (typically cold and higher latitude/altitude) edges. (b) Main functional dimensions involved, which are not meant to be necessarily orthogonal (see section III in the main text). Examples of relevant traits according to our current understanding (see section II in the main text) are also provided, with their position across the axes reflecting their relative importance for different functions, and their position along the axes their linkage with the underlying mechanisms (with more 'mechanistic' traits

located towards the axes end). Some traits are grouped into different spectra or typologies (e.g., Hydraulics, LES, Seed spectrum), and the colour of the corresponding ellipse and text label reflect the functional axes they are expected to mostly relate to. When these trait groups are expected to be strongly linked to more than one functional axis (Size, Allocation, Phenology), the text label is shown in black, and the colour of the ellipse reflects that of the corresponding functional axes. Traits: CL – Clonality, DV – Dispersal vector,  $H_{\max}$  – Maximum plant height, Hv – Huber value,  $K_s$  – Specific hydraulic conductivity, LP – Leaf phenology (including drought-deciduousness), LLS – Leaf life-span, LN – Leaf Nitrogen concentration,  $P_{50}$  – Pressure causing 50% loss of xylem conductivity,  $R_{\text{depth}}$  – Rooting depth, RN – Root Nitrogen concentration, RS – Root:Shoot ratio, RTD – Root tissue density, RP – Resprouting capacity, SL – seed longevity, SLA – Specific leaf area, SM – Seed mass, SSD – Specific stem density, TLP – Turgor loss point. LES: leaf economics spectrum.



**Fig. 3** Some trait-related factors determining species persistence under drier environmental conditions at different range positions (L: leading edge; C: distribution centre; R: rear edge; F: Refugia). (a) Even if spatial variation in environmental conditions typically implies greater climatic exposure to drought towards the rear edge (R), indicated as darker tones of green in the figure, finer-scale environmental variability may generate complex patterns, exemplified here by an altitudinal gradient that reduces exposure in an area close to the rear edge (local refugia, F), minimizing the risk for the corresponding populations. (b) Variation in (external)

exposure to **drought**, two different traits conferring stress tolerance and expected changes in persistence for different positions along the range and under different hypothesized scenarios of trait variability. Temporal changes in **external** exposure and traits are indicated by arrows running from current to future **conditions** (the latter marked by dashed or dotted lines). Two idealized species are compared: species A shows high capacity to adjust the values of trait #1 in space and time, so that increased exposure **is associated with higher stress tolerance, and the impact on performance is low**; species B, on the other hand, shows limited capacity to adjust trait #1 and hence it is expected to experience substantially lower persistence under future conditions **characterized by** greater exposure (everything else being equal). The impact of a second trait (trait #2) that may show maladaptive plasticity (dotted lines) **and hence** reduce future stress tolerance and persistence relative to the constant trait #2 scenario is also illustrated for both species. Finally, the possibility that variation in trait #2 may compensate for the lack of plasticity in trait #1 is also illustrated (dot-dash lines, species B only), in which case the persistence of this species may even increase (due to increased drought tolerance) in **future scenarios**. Future environmental conditions are assumed to induce **lower water availability (i.e., greater external exposure to drought)**, and spatiotemporal variations in exposure are assumed similar between species for simplicity.



**Fig. 4** Impact of the trait distribution at the community level on the performance of a focal species. (a) Differences in the community-level trait distribution between two communities (A and B), both containing the focal species. Vertical dashed lines of the colour corresponding to the community indicate the trait value of the focal species in each community. Although in absolute terms, the target species is more stress tolerant in community A than in B, relative to the other species in the community the target species is more stress tolerant in community B. (b) Expected change in the persistence probability of the focal species as a function of **external exposure to drought (water shortage)** in the two communities represented in (a), showing potentially lower reductions in persistence when the focal species is found in a less stress-tolerant community (B), due to increased niche availability following reduced demographic performance of other, less stress-tolerant co-existing species (see section IV in main text). Note that communities A and B can correspond to different locations within the current species range or to temporal shifts due to the appearance of novel competitors, and may have similar exposure to climatic stress. The vertical red line in panel (b) indicates the current level of **(external) exposure to drought** and the red arrow the direction of the expected change in exposure.

## ***New Phytologist* Supporting Information**

Article title: Accounting for trait variability and coordination in predictions of drought-induced range shifts in woody plants

Authors: Jordi Martínez-Vilalta, Raúl García-Valdés, Alistair Jump, Albert Vilà-Cabrera, Maurizio Mencuccini

Article acceptance date: [Click here to enter a date.](#)

The following Supporting Information is available for this article:

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| Reference                      | Scope               | Taxon or species group | N species | Type of shift | Part of the range | Plant functions | Traits showing significant effects                                                       | Traits showing no effect                                                                          |
|--------------------------------|---------------------|------------------------|-----------|---------------|-------------------|-----------------|------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------|
| Abella <i>et al.</i> (2019)    | Mojave Desert (USA) | Desert plants          | 159       | Elevation     | Overall           | ST, OT          |                                                                                          | <b>Drought tolerance, Disturbance-affinity</b>                                                    |
| Angert <i>et al.</i> (2011)    | Switzerland         | Alpine plants          | 133       | Elevation     | Leading           | DI, OT          |                                                                                          | Seed shed height; Seed shed duration; SM; DV; N floristic zones; N oceanic zones; Breeding system |
| Bergamini <i>et al.</i> (2009) | Switzerland         | Bryophytes             | 61        | Elevation     | Overall           | OT              | Soil acidity pref.: +<br>Light pref.: +<br>Temperature pref.: -<br>Temperature optima: - | Soil moisture pref.                                                                               |
|                                |                     |                        |           | Elevation     | Leading           |                 | Temperature optima: -                                                                    |                                                                                                   |
|                                |                     |                        |           | Elevation     | Rear              |                 |                                                                                          | Temperature optima                                                                                |

|                               |                  |                 |     |           |         |            |                                                                                                                                                                                                      |                                                                                                                                                                                                 |
|-------------------------------|------------------|-----------------|-----|-----------|---------|------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Bodin <i>et al.</i> (2013)    | France           | Trees           | 175 | Elevation | Overall | DI, OT     | Light pref.: +<br>Temperature pref.: +<br>SM: +<br>Life form: +<br>(phanerophytes and woody chamaephytes)<br>Woodiness: +<br>Deciduousness: +<br>Height: +<br>DV: + (anemochory)<br>Pioneer habit: + | Soil moisture pref.;<br>Continentality; Soil reaction pref.; Nitrogen availability pref.; Soil dispersion pref.; Humus content pref.; Biogeographic affinity                                    |
| Crimmins <i>et al.</i> (2011) | California (USA) | Vascular plants | 64  | Elevation | Overall | ST, DI, OT |                                                                                                                                                                                                      | <b>Life form; Physiognomy; DV; Fire adaptation</b>                                                                                                                                              |
| Felde <i>et al.</i> (2012)    | Norway           | Vascular plants | 106 | Elevation | Overall | DI, OT     | Snow cover pref.: +<br>Elevation pref.: +<br>DV: + (boleochory)                                                                                                                                      | Temperature pref.; Functional type; Woodiness; Life-form; Light pref.; Soil moisture pref.; Soil reaction pref.; Nutrients pref.; Grazing pressure pref.                                        |
|                               |                  |                 |     | Elevation | Leading |            | Snow cover pref.: +<br>Elevation pref.: +<br>Temperature pref.: -                                                                                                                                    | DV; Functional type; Woodiness; Life-form; Light pref.; Soil moisture pref.; Soil reaction pref.; Nutrients pref.; Grazing pressure pref.                                                       |
|                               |                  |                 |     | Elevation | Rear    |            |                                                                                                                                                                                                      | Snow cover pref.; Elevation pref.; Temperature pref.; DV; Functional type; Woodiness; Life-form; Light pref.; Soil moisture pref.; Soil reaction pref.; Nutrients pref.; Grazing pressure pref. |
| Geppert <i>et al.</i> (2020)  | European Alps    | Orchids         | 44  | Elevation | Overall | OT         | Habitat pref.: +<br>(grasslands, subalpine and wetlands)                                                                                                                                             |                                                                                                                                                                                                 |

|                                 |                     |                                     |      |           |         |        |                                                                                                                                                            |                                   |
|---------------------------------|---------------------|-------------------------------------|------|-----------|---------|--------|------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------|
|                                 |                     |                                     |      | Elevation | Leading |        | Habitat pref.: +<br>(grasslands, wetlands<br>and generalist)                                                                                               |                                   |
|                                 |                     |                                     |      | Elevation | Rear    |        | Habitat pref.: +<br>(grasslands, subalpine<br>and wetlands)                                                                                                |                                   |
| Grytnes <i>et al.</i> (2014)    | Europe              | Alpine plants                       | 565  | Elevation | Leading | OT     | Temperature pref.: -<br>Moisture pref.: -<br>Snow-bed pref.: +<br>DV: - (endochory)                                                                        | Nitrogen pref.                    |
| Holzinger <i>et al.</i> (2008)  | Switzerland         | Vascular plants                     | 133  | Elevation | Leading | DI     | DV: + (anemochory)                                                                                                                                         | Dispersal timing; Diaspore length |
| Le Roux & McGeoch (2008)        | Marion Island       | Native sub-Antarctic vascular flora | 21   | Elevation | Leading | OT     |                                                                                                                                                            | Habitat pref.                     |
| Lenoir <i>et al.</i> (2008)     | Europe              | Forest plants                       | 171  | Elevation | Overall | OT     | Habitat pref.: +<br>(mountainous);<br>Life-form: + (herbs,<br>ferns, and mosses)                                                                           |                                   |
| O'Sullivan <i>et al.</i> (2021) | Taiwan              | Trees                               | 75   | Elevation | Overall | OT     | Elevation pref.: +                                                                                                                                         |                                   |
| Parolo & Rossi (2008)           | Italian Alps        | Vascular plants                     | 166  | Elevation | Leading | DI     |                                                                                                                                                            | Diaspore weight and morphology    |
| Powney <i>et al.</i> (2014)     | Britain and Belgium | Vascular plants                     | 1075 | Aggregate | Overall | DI, OT | Plant height: ~<br>Light pref.: -<br>Nitrogen pref.: ~<br>pH pref.: ~<br>Moisture pref.: +<br>Habitat breadth: +<br>Life cycle: + (biennial and perennial) | Salt tolerance                    |

|                                  |                        |                  |             |           |         |        |                                   |                                                                                                                                                                                           |
|----------------------------------|------------------------|------------------|-------------|-----------|---------|--------|-----------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Rumpf <i>et al.</i> (2018)       | European Alps          | Mountain plants  | 183         | Elevation | Overall | DI, OT |                                   | Nutrient pref.; Temperature pref.; SM; Seed terminal velocity; Seed retention in fur; Seed gut survival; Seed release height; Life span; N vegetative offspring; Dominance; Life strategy |
|                                  |                        |                  |             |           | Leading |        | Temperature pref.: +              | Nutrient pref.; SM; Seed terminal velocity; Seed retention in fur; Seed gut survival; Seed release height; Life span; N vegetative offspring; Dominance; Life strategy                    |
|                                  |                        |                  |             |           | Rear    |        | Temperature pref.: -              | Nutrient pref.; SM; Seed terminal velocity; Seed retention in fur; Seed gut survival; Seed release height; Life span; N vegetative offspring; Dominance; Life strategy                    |
| Schmidtlein <i>et al.</i> (2013) | Northern (German) Alps | Mountain plants  | 1103        | Elevation | Leading | DI     | Habitat pref.: + (forest species) | SM                                                                                                                                                                                        |
| Sittaro <i>et al.</i> (2017)     | Canada                 | Temperate trees  | 16          | Latitude  | Leading | DI     | Seed spread rate: -               | Seed size                                                                                                                                                                                 |
| Wolf <i>et al.</i> (2016)        | California (USA)       | California flora | 4426 (taxa) | Elevation | Overall | DI     | Seed size: +                      | Life-form                                                                                                                                                                                 |
| Zhu <i>et al.</i> (2012)         | USA                    | Forest plants    | 92          | Latitude  | Leading | DI     |                                   | Seed size; Seed spread rate                                                                                                                                                               |
|                                  |                        |                  |             | Latitude  | Rear    |        |                                   | Seed size; Seed spread rate                                                                                                                                                               |

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**Table S2** Examples of different model types using plant traits (broadly defined) to predict species range shifts. For each model, we indicate its main characteristics and the way it accounts for the key aspects covered in this review, as summarized in Fig. 1 (main text). The five models are chosen to highlight major model types, from trait-based correlative approaches to trait-based representation of detailed physiological processes. Overall, few trait-based models have been employed to predict range shifts.

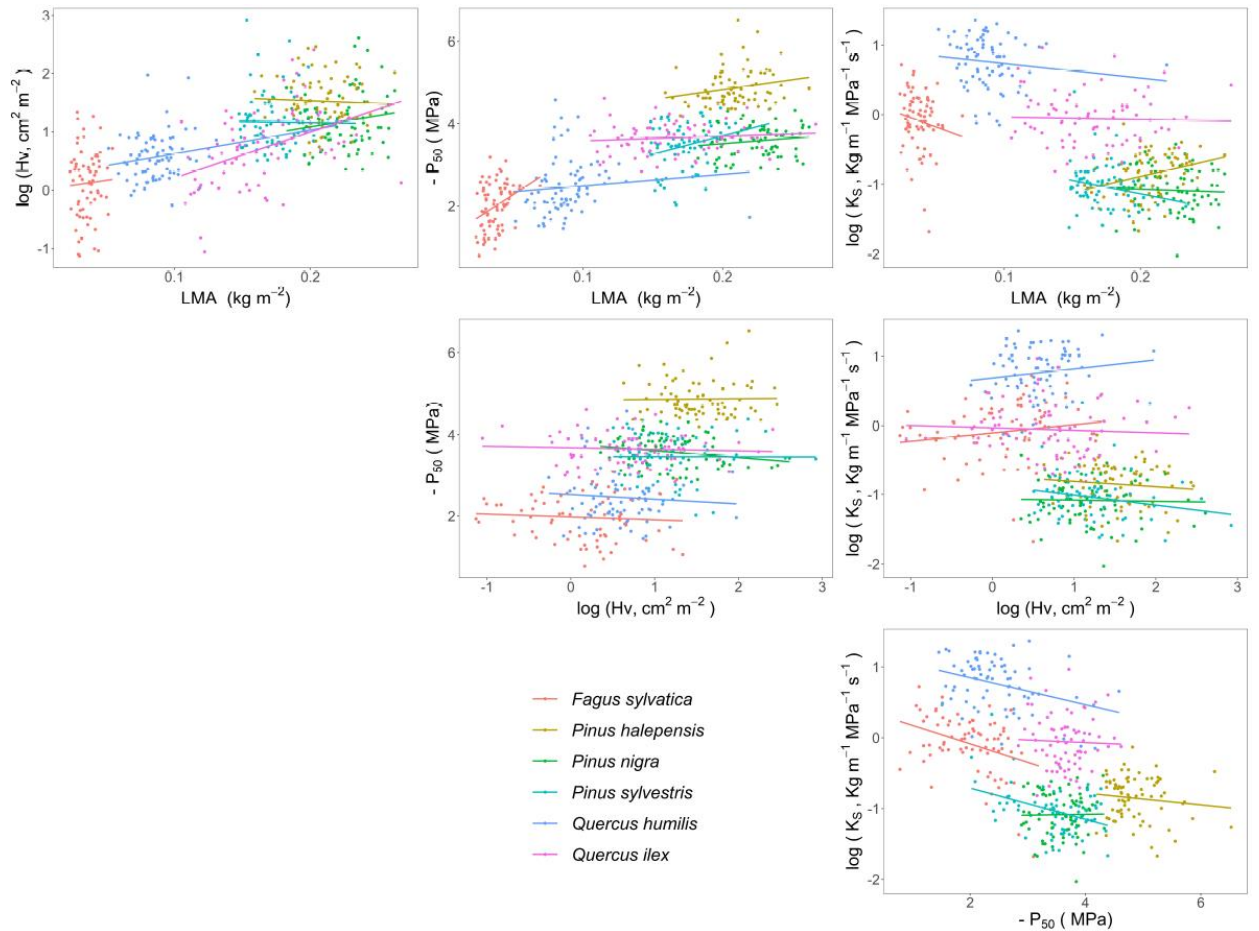
| Model type                        | Model example / Key references                                                   | Characteristics                                                                                             | Outputs                                                                                                                      | Traits                                                                                                                                                                  | Trait coordination                                                                                                                         | Within-species trait variability                    | Hydro-climatic variability and exposure                                  | Biotic Interactions and legacies                                                                                                                           | Local demography                                                                                                        | Dispersal and establishment                                              |
|-----------------------------------|----------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------|--------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|
| Dynamic Vegetation Model          | <b>ForClim</b><br>Gutiérrez <i>et al.</i> (2016)                                 | Simulates independent forest patches where trees establish, grow and compete for light, and eventually die. | Equilibrium forest composition for each of the simulated patches across the entire region.                                   | Not in the strict sense. Species-specific climatic tolerances (degree-day requirements, minimum and maximum winter temperature, drought tolerance) control tree growth. | Emerges from parameter selection giving best fit to regional presence / absence distribution maps.                                         | Not included, but see Chauvet <i>et al.</i> (2017). | Uses data from local weather station and regional maps of soil features. | Competition among species for light. Legacies can be included by improving spatially-explicit representations of disturbances and species-specific traits. | Seed production, dispersal, seedling establishment are represented within the patch.                                    | Assumes unlimited seed dispersal (occupancy dynamics are not simulated). |
| Process-based Forest-Growth Model | <b>CASTANEA</b><br>Cheaib <i>et al.</i> (2012);<br>Stéfanon <i>et al.</i> (2015) | Simulates photosynthesis and growth of individual trees as well as entire forest stands.                    | Growth, gross and net primary production. Growth threshold used as a proxy for the capacity to survive in given environment. | Numerous physiological and phenological traits.                                                                                                                         | Not directly. Emerges from a comparison of presence / absence distribution records from inventory data against predictions of tree growth. | Could easily be included, if data available.        | Uses data from local weather station and regional maps of soil features. | Not represented. Mostly mono-specific stands.                                                                                                              | Not explicitly represented. Focus on growth during the growth cycle of a forest (including allocation to reproduction). | Not represented.                                                         |
| Species Distribution Model        | <b>PHENOFIT</b><br>Morin <i>et al.</i> (2008)                                    | Simulates survival and reproductive success as a function of                                                | Mean probability of presence of an adult tree in a grid cell over several years, based on                                    | Species-specific parameters linked to leafing, flowering, fruiting and leaf                                                                                             | Only for phenological phases.                                                                                                              | Included for phenological phases.                   | Uses data from local weather station. Soil water availability from       | Not included.                                                                                                                                              | Not represented.                                                                                                        | Species-specific migration rates from pollen records set                 |

|                                                    |                                                               |                                                                                                                                                                                               |                                                                                                                                                         |                                                                                                                                                                                                               |                                                                                                                              |                                                                                                                                                    |                                                                                              |                                                                                                                                                                                                          |                                                                                                                                                    |                                                                                                                                                                                    |
|----------------------------------------------------|---------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                    |                                                               | phenology, frost injury and drought stress.                                                                                                                                                   | probability to survive until next season and probability to produce viable seeds.                                                                       | senescence; frost hardiness.                                                                                                                                                                                  |                                                                                                                              |                                                                                                                                                    | Thonrthwaite equation.                                                                       |                                                                                                                                                                                                          |                                                                                                                                                    | long-distance dispersal distances across grid cells. Extinction and establishment from presence likelihood rules.                                                                  |
| Dynamic Landscape Model coupled to Ecosystem Model | <b>LANDIS-PRO + LINKAGES</b><br><br>Wang <i>et al.</i> (2019) | Simulates physiological effects of temperature, precipitation, terrain and soil on species-specific and age-specific establishment, growth, fecundity, dispersal, colonization and mortality. | Potential distribution obtained from species potential colonization probability and maximum growing space or carrying capacity over 300 years.          | Growth: Maximum growth rates, drought tolerance, shade tolerance, nitrogen tolerance, growing degree-day requirements. Demography: longevity, maturation age, fire tolerance, sprouting and dispersal traits. | Not included.                                                                                                                | Not included.                                                                                                                                      | Uses data from local weather station, maps of soil regional features and ecological regions. | Competition is represented via self-thinning rule. Legacies are explicitly included via spatially-explicit representation of disturbances (e.g., harvest), land-use changes and species-specific traits. | Tracks establishment, growth, fecundity, dispersal, colonization and mortality for each age cohort at each grid cell (distribution and abundance). | Dispersal depends on habitat connectivity (dispersal and colonization lags). Disturbances (fire, tree harvest) and land-use changes (e.g., urban expansion) represented spatially. |
| Dynamic Eco-Evolutionary Model                     | <b>NEMO</b><br><br>Cotto <i>et al.</i> (2017)                 | Simulates effects of temperature, precipitation and soil on species-specific and age-specific establishment, growth, fecundity, dispersal, colonization and mortality for                     | Potential distribution obtained from species potential colonization probability determined by demography traits, strength of evolutionary selection and | Not represented explicitly. Multiple quantitative polygenic traits containing mutating alleles potentially allow to include specific traits.                                                                  | Not included here, but can be included in the eco-evolutionary framework if covariance and heritability data were available. | Explicitly represented by evolutionary processes representing adaptation and maladaptation in response to mutations and environmental pressures on | Uses data from local weather station and regional maps of soil features.                     | Competition among individuals of different life stages. Evolutionary legacies are explicitly modelled.                                                                                                   | Tracks establishment, competition, fecundity, dispersal, colonization and mortality for each individual in each age cohort at each grid cell.      | Dispersal depends on habitat connectivity (dispersal rates / colonization lags).                                                                                                   |

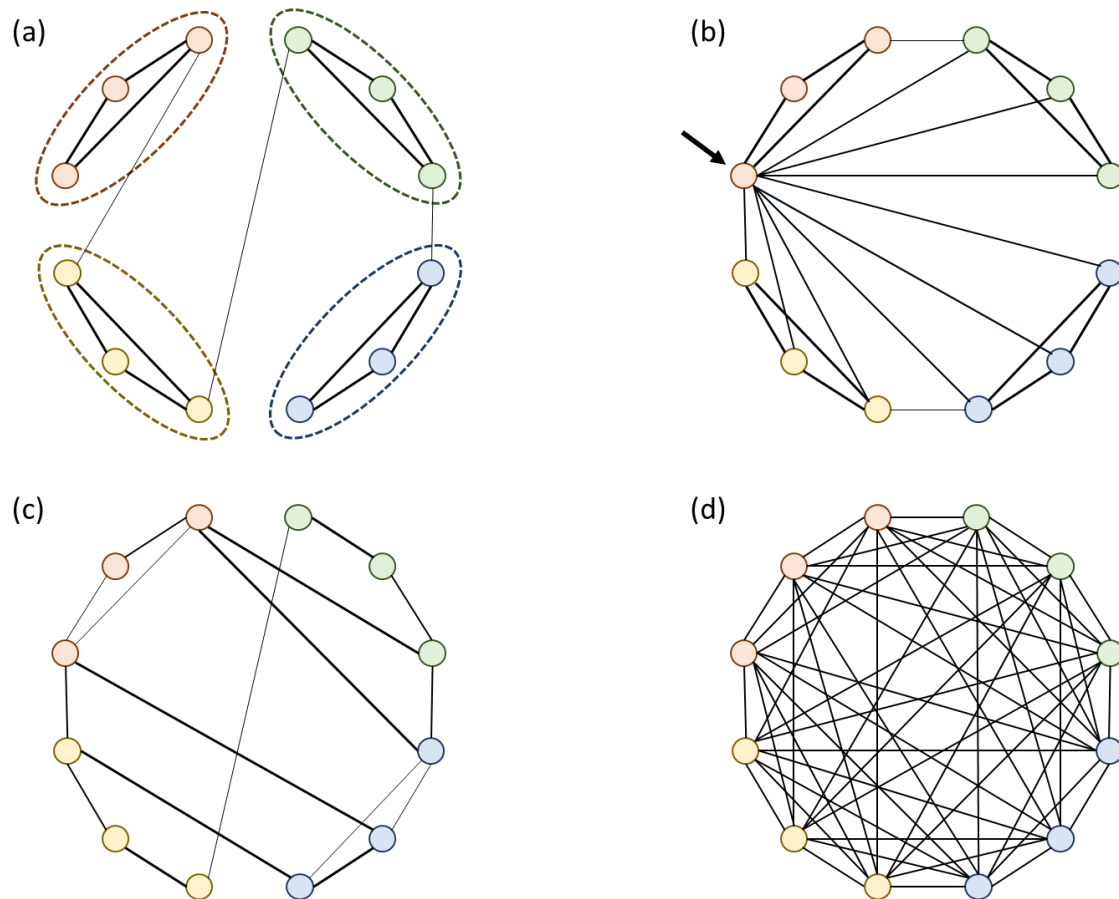
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|  |  | individual plants<br>(agents). | environmental<br>pressures. |  |  | each individual<br>phenotype. |  |  |  |  |
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**References for Table S2:**

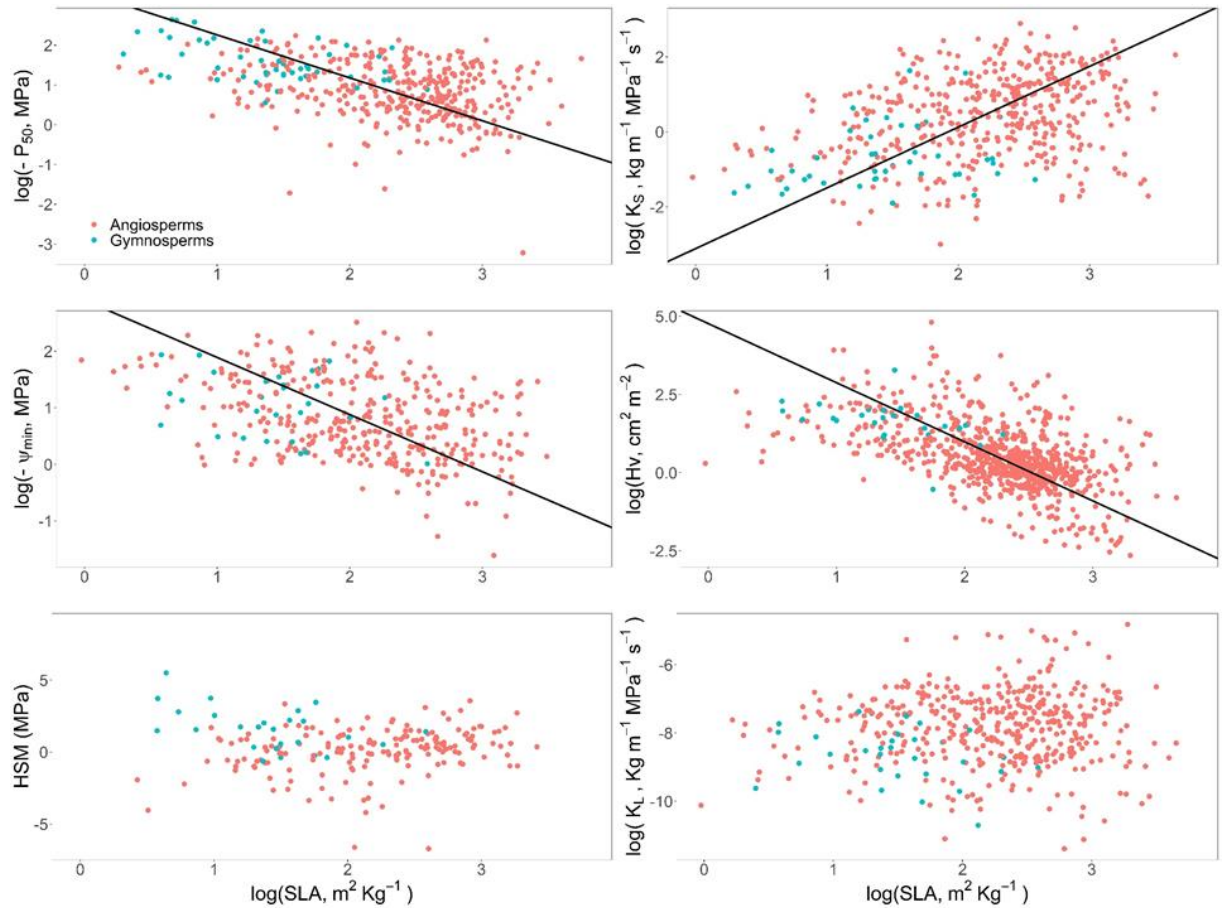
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**Fig. S1** Trait relationships within- and among-species ( $N = 6$  Fagaceae and Pinaceae species) along a water availability gradient in Catalonia, NE Spain. LMA, leaf mass per area; Hv, Huber value, sapwood to leaf area ratio;  $K_s$ , stem-specific xylem hydraulic conductivity;  $P_{50}$ , pressure causing 50% xylem embolism in the xylem. The original data and further methodological details can be found in Rosas *et al.* (2019).



**Fig. S2** Four idealized trait network structures describing different relationships among traits. Case (a) describes a clustered situation in which traits contributing to a given function (represented with the same colour) are tightly coordinated with each other and only loosely related to traits involved in other functions, and hence functional trait spectra can be clearly identified (marked with dashed ellipses). In case (b) functional trait spectra can still be identified but a single trait with a very high degree (marked with an arrow) is related to all other traits, potentially justifying its use as a synthetic functional predictor (unless compensation occurs among the effects of different traits on performance). In case (c) trait modules exist, but do not coincide with plant functions, complicating the definition of functional trait spectra. Finally, case (d) describes a highly connected network in which each trait is related to most other traits, in which identifying functional trait spectra is virtually impossible. Line width indicates the magnitude of the association between trait pairs.



**Fig. S3** Standardised Major Axis (SMA) regressions between specific leaf area (SLA, X axis) as an indicator of the leaf economics spectrum and hydraulic traits: water potential at 50% loss of hydraulic conductivity ( $P_{50}$ ), xylem minimum water potential ( $\psi_{min}$ ), hydraulic safety margin (HSM), stem-specific hydraulic conductivity ( $K_s$ ), Huber value (sapwood area to leaf area ratio,  $H_v$ ), and leaf-specific hydraulic conductivity ( $K_l$ ) for 1149 species covering all major biomes (HydraTRY database; Rosas, 2019; Sánchez-Martínez *et al.*, 2020). Symbol colour denotes species group (Angiosperms *versus* Gymnosperms). Regression lines across all species are shown only when statistically significant ( $P < 0.05$ ). All data are natural-log transformed with the exception of HSM. This data is the basis for the conceptual version of this figure presented in the main text (Box 2 Fig. 1).

