

Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change

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Abstract: The integration of functional traits into vulnerability assessments is a promising approach to quantitatively capture differences in species sensitivity and adaptive capacity to climate change, allowing the refinement of tree species distribution models. In response to a clear need to identify traits that are responsive to climate change and applicable in a management context, we review the state of knowledge of the main mechanisms, and their associated traits, that underpin the ability of boreal and temperate tree species to persist and (or) shift their distribution in a changing climate. We aimed to determine whether current knowledge is sufficiently mature and available to be used effectively in vulnerability assessments. Marshalling recent conceptual advances and assessing data availability, our ultimate objective is to guide modellers and practitioners in finding and selecting sets of traits that can be used to capture differences in species' ability to persist and migrate. While the physiological mechanisms that determine sensitivity to climate change are relatively well understood (e.g., drought-induced cavitation), many associated traits have not been systematically documented for North American trees and differences in methodology preclude their widespread integration into vulnerability assessments (e.g., xylem recovery capacity). In contrast, traits traditionally associated with the ability to migrate and withstand fire are generally well documented, but new key traits are emerging in the context of climate change that have not been as well characterized (e.g., age of optimum seed production). More generally, lack of knowledge surrounding the extent and patterns in intraspecific trait variation, as well as co-variation and interaction among traits, limit our ability to use this approach to assess tree adaptive capacity. We conclude by outlining research needs and potential strategies for the development of trait-based knowledge applicable in large-scale modelling efforts, sketching out important aspects of trait data organization that should be part of a coordinated effort by the forest science community.

Key words: vulnerability assessment, drought tolerance, fire tolerance, migration ability, intraspecific variation in trait, species persistence.

Résumé : L'utilisation des traits fonctionnels dans l'évaluation de la vulnérabilité est une approche prometteuse pour intégrer de manière quantifiable les différences de sensibilité des espèces et leur capacité d'adaptation aux changements climatiques, améliorant ainsi les modèles de répartition des arbres. Afin d'identifier dans un contexte d'aménagement les traits clés qui sont affectés par les changements climatiques, nous examinons l'état des connaissances sur les principaux mécanismes – ainsi que leurs traits associés — qui régissent la capacité des arbres des forêts boréales et tempérées à persister ou à migrer. Nous avons tenté de déterminer si les connaissances actuelles sont suffisamment matures et disponibles pour être utilisées efficacement dans le contexte des évaluations de vulnérabilité. En synthétisant les avancées conceptuelles les plus récentes et en évaluant la disponibilité des données, nous avons comme objectif principal de guider les modélisateurs et autres intervenants dans la sélection de traits fonctionnels pouvant servir à caractériser les différences dans la capacité des espèces à persister et à migrer face à un climat en changement. Par exemple, malgré que l'on comprenne assez bien les mécanismes physiologiques qui déterminent la sensibilité aux changements climatiques (ex.,

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cavitation induite par la sécheresse), un grand nombre de traits associés à ces mécanismes n'ont pas été systématiquement documentés pour les arbres d'Amérique du Nord. Nous constatons également des différences dans les méthodologies utilisées pour mesurer ces traits (ex., capacité de rétablissement des xylèmes), ce qui nuit à l'intégration des traits dans l'évaluation de la vulnérabilité. Pour leur part, les traits traditionnellement associés à la capacité de migrer et de résister au feu sont généralement bien documentés; cependant, de nouveaux traits clés émergent dans le contexte des changements climatiques demeurent peu documentés (ex., l'âge de la production optimale de graines). De façon générale, le manque de connaissance entourant la variabilité intraspécifique des traits, ainsi que sur la covariation et l'interaction entre traits, est limitant dans nos évaluations de la capacité adaptative des arbres. Nous concluons en soulignant des besoins précis en matière de recherche et en identifiant certaines avenues possibles pour le développement des connaissances liées aux traits applicables dans des projets de modélisation à grande échelle. Nous soulignons finalement l'importance de certains aspects de la gestion de données de traits qui devraient faire partie de tout effort coordonné de documentation par la communauté scientifique du milieu forestier.

Mots-clés : évaluation de la vulnérabilité, tolérance à la sécheresse, tolérance au feu, capacité de migration, variabilité intraspécifique des traits, persistance de l'espèce.

1. Introduction

Recent years have seen a marked increase in efforts to assess potential effects of climate change on the distribution and abundance of forest plant species (Thuiller et al. 2006; Iverson et al. 2008; McKenney et al. 2011; Price et al. 2013; Berteaux et al. 2014; Périé et al. 2014). Vulnerability assessments in the context of climate change are frequently based on bioclimatic envelope modelling techniques (Guisan and Zimmermann 2000). These models help identify species requiring particular attention, as well as target zones where conservation and management efforts may be most effectively focused (Dawson et al. 2011). However, there are concerns as to whether bioclimatic envelope models can adequately reflect actual changes in distributions (Pearson and Dawson 2003; Hampe 2004; Hijmans and Graham 2006). Interpretation of model results remains limited, notably because two major components of vulnerability are rarely considered: sensitivity (i.e., the degree to which a species is affected by, or responds to, specific changes), and adaptive capacity (i.e., the ability of a species to accommodate these changes; Glick and Stein 2010; Iverson et al. 2011).

The inclusion of functional traits in vulnerability assessments could permit a more quantitative assessment of species-specific sensitivity and adaptive capacity to climate change (Angert et al. 2011; Iverson et al. 2011; Matthews et al. 2011; McMahon et al. 2011; Foden et al. 2013; Prasad et al. 2013). Functional traits are morphological, physiological, and phenological attributes that determine an organism's functional response to a given environmental filter (Violle et al. 2007). In situ measurements capture both inherited local adaptation and plastic response to the environment (Willson et al. 2008; Paquette et al. 2015). Because functional traits are by definition linked to ecological functions (Violle et al. 2007), identification of the traits that allow plants to stay in place and tolerate climate change — or to move to new suitable habitats — opens up the possibility of a more mechanistic approach to vulnerability assessment.

Recently, several statistical approaches have been developed to incorporate traits into bioclimatic envelope models (Angert et al. 2011), including post-hoc modification of niche-based vulnerability ratings using a suite of species traits (Matthews et al. 2011) and habitat-niche models that modify trait-based demographic processes (Midgley et al. 2010; Fordham et al. 2012; Talluto et al. 2016). However, relatively low gains in predictive power were reported from adding traits. This has been attributed to several factors, including poor data quality (Angert et al. 2011) and the challenge of scaling trait information to higher levels of organization (Violle et al. 2007; Suding and Goldstein 2008). One additional explanation may be related to trait selection. Not all traits are climate-sensitive (i.e., likely to be involved in species' response to environmental change), and responsive traits vary with the specific environmental factor under study (Mlambo 2014). It is paramount to select traits that are mechanistically associated

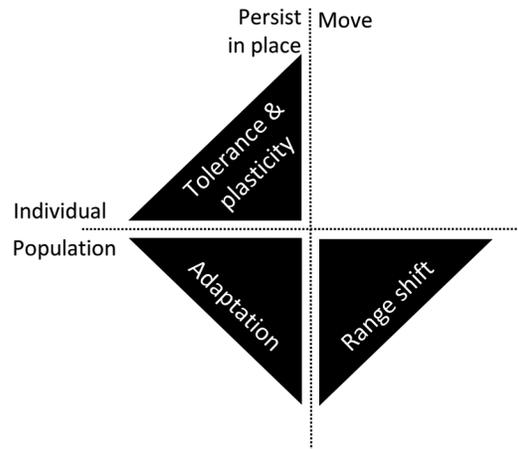
with specific selective agents of climate change, and which respond at the appropriate scale.

Climate change is likely to change the frequency, duration, and severity of drought, flooding, pest, and heat wave events (Lemprière et al. 2008; Allen et al. 2010; Reyer et al. 2013). In both temperate and boreal forests, there have already been reports of climate-driven tree mortality due to drought and heat stress (van Mantgem et al. 2009; Allen et al. 2010; Michaelian et al. 2011). It is therefore imperative to ascertain the mechanisms that induce mortality in regional communities and define their thresholds to improve predictions (McDowell et al. 2011; Anderegg et al. 2015). A second main axis of climate change effects is related to the frequency and intensity of natural disturbance (Dale et al. 2001). Current forecasts for North American boreal forest fire regimes include longer fire seasons and increased fire frequency and severity, with the latter being more likely under the continental climate of western Canada (Flannigan et al. 2009; de Groot et al. 2013; Girardin et al. 2013; Boulanger et al. 2014). More extreme weather events (e.g., winds, hurricanes, and ice storms) are also more probable in the temperate forest zones (Lindner et al. 2010), and outbreaks of insect and fungal pests are likely to be more frequent and persistent (Dukes et al. 2009; Bentz et al. 2010).

Individual species response to these changes could be negative (widespread mortality, or reproductive failure), positive (alleviation of biophysical limitations or opportunistic response to reduced competition), or neutral, with potentially different responses throughout a species' range (Chuine and Beaubien 2001). Species sensitivity and adaptive capacity to climate change are complex phenomena that reflect mechanisms operating at different biological, spatial, and temporal scales. We review here key mechanisms and their associated traits related to species' ability to persist in place or to migrate to a more suitable habitat (synthesized in Fig. 1). We limit this review to broad-scale abiotic filters of plant community assembly (i.e., climatic, dispersal, and disturbance filters) and mechanisms operating at the individual or population level. We do not cover biotic filters and community level mechanisms (e.g., complementarity; Ettinger and Hille Ris Lambers 2013), nor synergistic effects of cumulative stresses (e.g., drought and pests; Hogg et al. 2002; Niinemets and Valladares 2006), which can also drive species persistence and migration capacity.

This synthesis aims to provide assistance to modellers and practitioners in selecting trait information for vulnerability assessments. We consolidate knowledge of the major mechanisms and traits that allow boreal and temperate tree species to either persist in place or move in response to the main climate change drivers. We outline issues currently limiting the effective use of traits, point out practical challenges, and offer ideas to help resolve these issues. We pay particular attention throughout this review to the question of whether existing knowledge is sufficient to conduct trait-based assessments of temperate and boreal tree species to a changing climate.

Fig. 1. Conceptual synthesis of the main mechanisms and traits underlying differential species response to climate change (indicated at individual [ind.] or population [pop.] scales). A question mark (?) indicates a lack of information on associated traits for a given mechanism.



Strategy	Mechanism	Scale	Main traits
PERSIST IN PLACE (Section 2.)			
Via tolerance			
- Drought (2.1.)			
Avoidance	Efficiency of water uptake Mitigation of water loss	Ind. Ind.	Rooting depth Stomatal sensitivity, Leaf mass area, Xylem conductance
Resistance	Resistance to cavitation	Ind.	Index of xylem resistance to embolism
Recovery	Resumption of water transport Vegetative reproduction	Ind. Pop.	Xylem recovery capacity? Resprouting ability
- Change in temperature regime (2.2.)			
	Mitigation of heat-related physiological impacts	Ind.	Heat shock proteins induction?
	Morphological plasticity	Ind.	Branching pattern variability
	Accelerated phenology	Ind.	Bud burst timing
- Change in fire regime (2.3.)			
Resistance	Mechanical and architectural protection Fuel potential	Ind. Ind.	Bark thickness, Height to live crown Leaf and bark flammability
Recovery	Reproduction by seeds Vegetative reproduction	Pop. Ind./Pop.	Seed bank, seed production, seed dispersal distance Resprouting ability
Via response to elevated CO₂ (2.4.)			
	Efficiency under high CO ₂	Ind.	?
Via adaptation (2.5.)			
- Phenotypic plasticity	Physiological and morphological plasticity	Ind.	Amplitude of intraspecific trait variability
- Genetic diversity	Micro-evolution and local adaptation	Pop.	Age at sexual maturity, heritable traits quantification, adaptive variation, seed and pollen dispersal
- Epigenetic	Epigenetic control over environmental tolerance	Ind.	?
RANGE SHIFT (Section 3.)			
	Reproductive capacity of source population (3.1.)	Pop.	Age of optimum seed production, seed production and seed viability
	Dispersal ability (3.2.)	Pop.	Seed dispersal vector and distance
	Colonisation potential of the advancing front (3.3.)	Pop.	Veg. reproduction, self-pollination, seed bed requirement

Table 1

Table 2

2. Mechanisms and traits to persist in place

The ability of species to persist in their current location is frequently neglected in predictions of tree response to climate change; instead, the focus is on species' ability to migrate (Thuiller et al. 2008; Lavergne et al. 2010; Hof et al. 2011). In the short term, the ability to persist is determined by a species' capacity to tolerate environmental change (temperature, drought, or CO₂) through innate genetic capacity and (or) phenotypic plasticity, which in some cases can translate into a greater capacity to take advantage of new growing conditions (Park et al. 2014). Over longer timescales, a different suite of mechanisms can also allow adaptation to a novel climate. A species' ability to withstand changes in fire, pest, and disease regimes will also affect its ability to persist in place. In this section, we review research areas where a trait approach could bring significant additional insight (i.e. when there is a generalizable relationship between variation in trait value and the environmental filter). While this is a reasonable assumption with respect to drought and heat filters, it is less likely to be valid with respect to pests and diseases, where interactions seem to be the result of individual "evolutionary arms race" (Red Queen Hypothesis) between particular and taxonomically limited plant defenses and specific herbivores or pathogens (Berryman 1988; Gilbert 2002).

2.1. Drought tolerance

2.1.1. Tree survival under drought

As a result of shifting weather patterns, drought stress is expected to be an increasingly important factor constraining plant growth and survival over the coming century (Allen et al. 2010; IPCC 2013). During a drought, a complex set of mechanisms involving trade-offs between carbon gain and water loss act within an individual tree to either avoid (i.e., maintain water potential and allow sap circulation) or resist (i.e., cope with low water potential and momentary failure in sap circulation) water stress (Fig. 1). Intense drought events can kill trees via xylem cavitation and loss of hydraulic conductance, while prolonged drought may cause carbon starvation due to prolonged stomatal closure and discontinuation of sap transport (Chaves et al. 2002; Meinzer et al. 2009; Hartmann et al. 2013; Anderegg et al. 2015). Studies indicate that species with deep root systems, rapid stomatal control, xylem resistant to cavitation, and abundant carbohydrate reserves are likely to exhibit higher drought tolerance and reduced mortality (Chaves et al. 2002; Allen et al. 2010; Choat et al. 2012; West et al. 2012; O'Brien et al. 2014). At the population level, species with resprouting ability — which confers a higher capacity for recovery following drought — are also more likely to maintain their population and persist in place (Table 1).

As expected, as long as the water table remains reachable, deep roots ensure continued access to existing ground water reserves (Nepstad et al. 1994; Tyree 2007). Despite being recognized as a crucial trait for drought avoidance (Allen et al. 2010; Choat et al. 2012; Oliveira et al. 2014) and being widely available (87% of North American tree species available in the TRY database; Table 1), **rooting depth** remains difficult to characterize. This is due in large part to the importance of the local environment in driving intraspecific variability (Bréda et al. 2006; Garnier and Navas 2013): individuals are plastic and will tend to root at greater depth in deep soil, providing them with greater drought tolerance (Tague et al. 2013). Location may outweigh species traits in determining individual capacity to tolerate drought (Tobner et al. 2013). While general descriptive information capturing coarse interspecific differences in rooting depth and architecture is available (e.g., deep tap root versus shallow rooting habit; Table 1), the rarity of screening programs, common garden or reciprocal transplant experiments has resulted in only a few quantitative datasets being available for formal comparisons among species.

One further hurdle for interspecific comparison is the technical difficulty of accurately measuring rooting depth in particular and root traits in general (Schenk and Jackson 2005). Because only a small number of deep roots can be sufficient to ensure continued water supply, the tendency of field measurements to underestimate true rooting depth may impair our ability to predict drought tolerance based solely on rooting measurements (Schenk and Jackson 2005).

Numerous rooting depth metrics are routinely measured, used, and recommended, but their functional importance need to be formally established. Which metric between maximum root depth, mean root depth, or the depth of the deepest 10% of roots best captures the functional importance of roots in the context of drought tolerance? Much remains poorly understood at the interface of moisture stress physiology and belowground architecture: can a single small but deep root sustain an entire mature tree crown? Are there minimal conduit dimensions? How do trees integrate, sample, or avoid variation in the soil moisture profile? Technical refinements have been developed to overcome some of these issues, from stable isotope techniques (Ehleringer et al. 2000) to satellite-based information (Ichii et al. 2009). However, it remains to be seen exactly how these new techniques may be implemented cost-effectively to complement and refine field measurements. Furthermore, because much of belowground uptake in temperate and boreal forests occurs through mycorrhizae (Marschner and Dell 1994) that can extend many metres away from the tree roots, rooting depth may only provide us with a rough estimate of the ability of any particular individual to capture below-ground resources (Lehto and Zwiazek 2011).

Drought tolerance also depends on the ability to acquire CO₂ through stomata and solubilise it into the cellular stroma, while limiting water loss through transpiration. The propensity to close stomata to limit water loss is expressed through **stomatal sensitivity**, a critical characteristic for drought avoidance (Marron et al. 2002; Bréda et al. 2006). However, stomatal closure also prevents CO₂ diffusion to carboxylation sites and therefore limits photosynthesis, affecting growth (Chaves et al. 2002). Because of its high interspecific variability, stomatal sensitivity is a good indicator of this trade-off and allows us to distinguish species' relative drought sensitivity (Klein 2014). Drought-tolerant species are capable of supporting continued photosynthesis, and therefore biomass accumulation, while simultaneously reducing their water consumption (i.e., increased water use efficiency, Monclus et al. 2006; Table 1). Because the ratio of these two processes is difficult to assess over the entire plant, more easily measurable proxies have been developed, such as **intrinsic water use efficiency** (Table 1; Farquhar et al. 1989). However, the relationship between these metrics and plant drought tolerance is neither well understood nor well documented (3% of North American trees, Table 1).

Indeed, water loss can also be controlled by other mechanisms acting at different levels: (i) at the leaf level, by changing stomata density (Haworth et al. 2011), or increasing leaf thickness and tissue density, resulting in higher **leaf mass area** (leaf dry weight per unit leaf area; Poorter et al. 2009); (ii) at the stem level, by adapting xylem conductance, generally associated with **wood density** (Meinzer et al. 2009); and (iii) at the individual level by reducing total leaf area through **leaf or branch shedding**, or by preferential allocation of resources to the roots (Bréda et al. 2006). Wood density and leaf mass area (and its inverse, the ratio of leaf area to leaf mass; specific leaf area) have been measured widely and are generally available (31% and 77% of North American species, respectively, in TRY; Table 1), following relatively standard protocols (Pérez-Harguindeguy et al. 2013). However, because leaf shedding and branch dieback are dynamic and continuous mechanisms, standardization of their measurement remains difficult, and therefore are not yet included in trait databases (Table 1).

When water demand remains constant as supplies decline, hydraulic tension in the stem becomes a deciding factor in differentiating tolerance to water deficit. Risk of xylem cavitation has been

Table 1. Synthesis of key traits involved in the main mechanisms for tree species' tolerance to drought.

Strategy	Mechanism	Main trait	Relationship with drought tolerance	Definition, standard, and variability issues	Availability†	
Avoidance	Efficiency of water uptake	Rooting depth	↑ Bréda et al. 2006; Markewitz et al. 2010	Large variation in methodology used: from expert-based categories to DNA analysis (Jackson et al. 1999) and uprooting of stumps (Nicoll and Ray 1996). For quantitative data: variation in standards and units, creating dataset compatibility issues. Large variations with local edaphic conditions (Larcher 2003) and with ontogeny. Species may be only present in restricted conditions along gradients. Seedling stage and some species remain poorly documented. Field measurements of true rooting depth tend to be underestimated (Schenk and Jackson 2005). Need for common garden experiments.	TOPIC* USDA* TRY* 87% (126) FEIS* Silvics*	
		Economy of water	Water supply to demand ratio	↓ Meinzer et al. 1997	Proportion of conductive to evaporative tissue. Variation in metric used: e.g. leaf area: sapwood ratio (McDowell et al. 2002), Huber value (Ewers and Zimmermann 1984; Sperry and Tyree 1988). Some variation in standards and units creating compatibility issues. Variation with tree age and sample location on the tree (Ewers and Zimmermann 1984).	TOPIC TRY 39% (189)
	Mitigation of water loss	Stomatal conductance		↓ Raven 2014	Variation in stomatal conductance to limit water loss. Regulated by stomatal aperture changes and stomatal density, which are measured following standard protocols (Hogg and Hurdle 1997; Bond and Kavanagh 1999). Speed of aperture changes could be assessed via stomatal size, because these are negatively correlated (Drake et al. 2013; Raven 2014). A more easily standardized metric of overall stomatal control is the length of guard cells, which is less affected by environmental factors than stomatal density and well documented among angiosperms (Hetherington and Woodward 2003; Beaulieu et al. 2008; Drake et al. 2013).	TRY 11% (45)
			Water use efficiency	Monclus et al. 2005; Monclus et al. 2006	The ratio of biomass accumulation to water consumption. Difficult to measure at a whole plant scale. Proxy: the intrinsic water use efficiency (W _i ; ratio between net assimilation rate; Monclus et al. 2006) and stomatal conductance (Δ; the carbon isotope discrimination ratio during CO ₂ capture; Monclus et al. 2005). Relationship is still unclear with many plant internal mechanisms.	TRY 3% (27)
		Stomata density	↑ Hetherington and Woodward 2003	Number of stomata per unit leaf area. Standardized protocol. Variation with local environmental conditions and plant form (Larcher 2003), for angiosperms (Abrams 1990) and for gymnosperms (Helmers 1943).	TOPIC TRY 6% (25)	
		Leaf morphology	↑ Valladares and Sánchez-Gómez 2006; Wright et al. 2004; Poorter et al. 2009	Generally expressed by the ratio of dry mass per leaf area (leaf mass area, LMA). Standard protocol widely available (Pérez-Harguindeguy et al. 2013). Variation with local environmental conditions, with ontogeny, and with sample location in the canopy (Poorter et al. 2009). Some issues remain with measurements for compound leaves and conifer needles (Brand 1987). It is the reverse of the specific leaf area (1/LMA), which is well documented.	TOPIC TRY 77% (10470)	

Table 1 (continued).

Strategy	Mechanism	Main trait	Relationship with drought tolerance	Definition, standard, and variability issues	Availability†
		Xylem conductance	↑ Lens et al. 2011 ; Brodrribb 2009	Water transport ability of vascular tissues. Variation in metric used: hydraulic conductance (G , $\text{gMPa}^{-1}\text{s}^{-1}$), stem-specific xylem hydraulic conductivity (K_s ; $\text{kgm}^{-1}\text{s}^{-1}\text{MPa}^{-1}$; Melcher et al. 2012), sapwood area conductivity (K_s and K_{sa} ; $\text{mgs}^{-1}\text{kPa}^{-1}\text{mm}^{-1}$; Lens et al. 2011), hydraulic conductivity (K_h ; $\text{mm}^2\text{kPa}^{-1}\text{s}^{-1}$). Need to be in accordance with foliage transpiration. Depends on the diameter of the conducting elements and type of perforation.	TRY 31%*(212)
		Leaf area control: Branch dieback and leaf shedding	↑ Rood et al. 2000	Propensity to sacrifice leaves or branches in response to drought to save water at the organism level. No standard methodology (Rood et al. 2000). Based on field observations of the occurrence and patterning of branch senescence at different times in the growing season.	TRY n/a
Resistance	Xylem resistance to cavitation	Resistance to embolism	↓ Maherali et al. 2004	Most frequently used index is Ψ_{50} (i.e., xylem pressure at which 50% of the xylem conductivity in the stem is lost through cavitation; Choat et al. 2012). Techniques used differ in the way cavitation is induced (e.g., bench dehydration, centrifugation, or air injection) and in the way cavitation is measured (e.g., percentage loss of conductivity or acoustic emission), creating dataset compatibility issues (Cochard et al. 2013), though relative rankings among species tend to hold true. Ψ_{50} co-varies with wood density and other xylem parameters (Sperry et al. 2006 ; Choat et al. 2012), which can be used as easily measurable proxies. Ψ_{50} has a high degree of conservatism (Willson et al. 2008), allowing use of closely related species to infer values for undocumented species.	TOPIC TRY 41% (1279)
Recovery	Resumption of water transport	Xylem recovery capacity	↑ Brodersen and McElrone 2013	Capacity to resume conductivity of embolised tissue (Pugnaire and Valladares 2007 ; Brodersen and McElrone 2013). Occurrence and mechanisms for post-cavitation xylem recovery remain debated. Large variation in methodologies creates dataset compatibility issues: from dye infiltration to nuclear magnetic resonance imaging and genetic screening of xylem sap (Brodersen and McElrone 2013)	TRY n/a
	Individual recovery	Carbohydrate storage	↑ McDowell et al. 2008	Concentration of non-structural carbohydrates in roots (Dietze et al. 2014). Relationship with drought-induced mortality is complex and remains to be elucidated (Becker et al. 2000 ; McDowell et al. 2011 ; O'Brien et al. 2014). Variations in sampling and lab methods creating dataset compatibility issues, though relative rankings among species tend to hold true (Quentin et al. 2015). Data available is primarily for seedlings.	TRY 6% (7)
	Population recovery	Resprouting ability	↑ Pérez-Harguindeguy et al. 2013	Relative ability to form new shoots after destruction of above-ground biomass (Pérez-Harguindeguy et al. 2013). Variation in method used creates dataset compatibility issues. Documentation remains anecdotal. Commonly categorized as sprouters versus non-sprouters and rare quantitative assessment.	USDA* TOPIC* TRY* 87% (144)

Table 1 (continued).

Strategy	Mechanism	Main trait	Relationship with drought tolerance	Definition, standard, and variability issues	Availability†
	Induced fruiting		↑ Bréda et al. 2006	Whether or not a species can react to prolonged drought by having a higher than average reproductive effort (most year).	TRY n/a
	Seed resistance to desiccation		↑ Greene and Johnson 1998	Proportion of seeds that remain viable under water-stressed conditions (Tweddle et al. 2003). Standard methods exist for quantitative assessment although generally documented categorically (Tweddle et al. 2003; Pérez-Harguindeguy et al. 2013). Seed size commonly used as proxy.	USDA* TOPIC TRY n/a
	Seedling root allocation		↑ Markesteijn and Poorter 2009	Generally expressed by the ratio of maximum rooting depth to leaf area, root-to-shoot ratio, and rooting depth per leaf area. Methods are well defined.	TRY 0%

Note: Tolerance to a given environmental stressor can arise through avoidance (i.e., the extent to which an individual limits its own exposure to the stressor), resistance (i.e., ability of an individual to withstand the stress), and recovery strategies (i.e., ability of an individual or a population to recover after the stress). The arrow indicates the relationship between the described trait and drought tolerance (upward pointing arrow, higher trait values indicate increasing tolerance; downward pointing arrow, higher trait values indicate decreasing drought tolerance; no arrow, lack of clear directional relationship). n/a indicates that no data are available for that trait. Total number of entries for North American species considered is indicated in parentheses. Database and literature references: TOPIC (Aubin et al. 2012), USDA (USDA 2015), FEIS (FEIS 2015), Silvics (Burns and Honkala 1990).

*At least some data is available as qualitative.

†Percentage of native North American tree species documented in TRY database (www.try-db.org; Kattge et al. 2011).

‡Value for sapwood area conductivity.

successfully used to differentiate drought-adapted from mesic species (Maherali et al. 2004; Lambers et al. 2008; Meinzer et al. 2009; Urli 2013). The index of **resistance to embolism** (Ψ_{50}), defined as the xylem pressure at which 50% of conductivity is lost, is inversely related to a species' ability to tolerate internal water deficit (Choat et al. 2012). This index is widely used and provides values that can be compared among species-specific studies (Brodribb and Holbrook 2004; Maherali et al. 2004; Choat et al. 2012). However, recent studies point out inconsistencies among the vulnerability curves derived from different Ψ_{50} measurement techniques (Sperry et al. 2012; Wheeler et al. 2013; Wang et al. 2014). Additionally, Ψ_{50} has been shown to overestimate drought sensitivity in species capable of restoring conductivity to embolised tissue, such as many angiosperms. Less conservative indices like Ψ_{88} have been put forward as an alternative (Urli 2013). A recent initiative seeks to better understand plant hydraulics by developing a standardized methodology for data collection and aggregation (Jansen et al. 2015), promising a solid basis for future surveys of drought tolerance traits.

The **capacity to resume conductivity** in embolised tissue, and recovery of hydraulic conductance (e.g., production of new xylem to replace cavitated conduits; Kappen and Valladares 2007; Klein et al. 2014) can become critical under extreme events (Sperry et al. 1994; Taneda and Sperry 2008; Johnson et al. 2012). While questions remain as to the physiological mechanisms responsible for this capacity (Klein et al. 2014; Rockwell et al. 2014), more fundamental objections have also been raised on its relative importance for tree survival (Cochard et al. 2013; Sperry 2013; Delzon and Cochard 2014; Rockwell et al. 2014). No metric or proxy (Table 1) has yet been identified that captures this drought recovery mechanism in a format useful for vulnerability assessments.

During prolonged drought events, **non-structural carbon** (NSC) storage in stems and roots may play an important role for drought survival (O'Brien et al. 2014). Indeed, species with rapid stomatal closure should require higher NSC reserves to avoid starvation (Chaves et al. 2002), a prediction corroborated by experimental results (McDowell et al. 2008; Galvez et al. 2011; Johnson et al. 2012). Despite these advances, however, the complex role played by NSC storage in tree survival after drought has not been fully elucidated (McDowell et al. 2011; Dietze et al. 2014). The link with survival is complex and several mechanisms are still poorly understood, including drought effects on NSC transport, use, and depletion within the plant (Tague et al. 2013; O'Brien et al. 2014). Several issues have been reported with NSC data, including the lack of information available for adult trees and variation in data collection methodology (Table 1).

2.1.2. Regeneration establishment and survival under drought

Seedling establishment and survival during (or immediately following) drought are necessary for population persistence (Padilla and Pugnaire 2007; Poorter and Markesteijn 2008). Although seedling tolerance to drought depends on a suite of traits similar to those important for adult trees, trait values (and therefore sensitivity) vary considerably among life history stages. For example, Tobner et al. (2013) found **specific root length** (the ratio of root length to dry mass of fine roots, Pérez-Harguindeguy et al. 2013) to be higher in juveniles of *Abies balsamea* and *Acer rubrum* than in adults, independent of soil conditions. Quality and availability of trait information also vary considerably between seedlings and adults. Traits easier to measure on small individuals (e.g., **root-to-shoot** ratio and NSC) have been routinely measured on seedlings, while other traits typically associated with mature trees are rarely measured in seedlings (e.g., wood density). Yet, databases do not consistently specify the life stage for which the information was gathered.

During the establishment stage, **seed size** is a good proxy of seedling survival (Moles and Westoby 2004). Seedlings of small-

seeded species, such as *Betula* spp. are very sensitive to drought because their radicles do not have access to soil moisture located under thick organic layers. Such species are thus restricted to litter-free microsites with relatively high water availability (Bolton and D'Amato 2011; Lambert et al. 2015). Other seed characteristics, such as **resistance to desiccation**, are considered important factors in population-level recovery after drought (Joët et al. 2013), and can be inferred from seed size (Table 1). In temperate and boreal tree species, propensity for **vegetative reproduction** also appears to be a critical strategy. For instance, some shallow-rooting species, such as *Populus tremuloides*, can experience severe dieback as a result of drought. It is their important bud bank that allows populations to recover rapidly through vegetative reproduction, making the species relatively drought tolerant at the population level, if not at the individual level (Steneker 1974; Man and Rice 2010). In seedlings of Mediterranean woody species, root-to-shoot ratio, **rooting depth**, **rooting depth per leaf area**, **relative growth rate**, **net assimilation rate**, and **transpiration rate** were also found to be correlated with drought survival (Padilla and Pugnaire 2007; Lopez-Iglesias et al. 2014). In particular, root allocation and morphology are crucial to a seedling's ability to reach water (Paz 2003). The ratio of **maximum rooting depth to total leaf area** and the root-to-shoot ratio have been found to be strong predictors of seedling performance under water deficit (Lloret et al. 1999; Paz 2003).

2.2. Changes in temperature regime

In addition to exacerbating water-related stress, temperature increases predicted under climate change are likely to have strong and varied consequences for trees, including changes ranging from physiological processes (i.e., photosynthesis and respiration; Chmura et al. 2011) to bud/leaf and cambium phenology and growth patterns (Chmielewski and Rotzer 2001; Morin and Chuine 2014; Pretzsch et al. 2014). These consequences are expected to vary along latitudinal gradients (De Frenne et al. 2013).

Despite their extensive use in climate envelope modeling, changes in mean annual temperatures are expected to have limited direct negative impacts on trees. Instead, subtle changes early and late in the growing season that influence the interplay between chilling requirements, heat sum thresholds, and temperature stress are likely to have much more important impacts (Burton and Cumming 1995; Parmesan 2006; Morin et al. 2007, 2010; Caffarra and Donnelly 2011). The ability of many species to adjust to shifting spring conditions — such as flexible **bud burst requirements** and shallow dormancy — also exposes them to unusual weather events. The selective balance between protection against temperature stress, its seasonality, and effective use of growing conditions complicates the identification of a defined set of traits related to temperature. Trees experience unseasonably high or low temperatures differently according to their phenological stage and previous conditioning (Cannell and Smith 1986). Depending on temperature-adapted traits and individual histories of acclimations, temperatures of only $-2\text{ }^{\circ}\text{C}$ in early summer can kill buds, flowers, and new growth. Once fully acclimated, however, some trees can survive mid-winter temperatures as low as -80 or $-85\text{ }^{\circ}\text{C}$ for boreal and subalpine species, such as *Betula papyrifera* and *Pinus contorta* var. *latifolia* (Sakai 1983).

Meaningful progress has already been made towards this goal: Burton and Cumming (1995) and Cumming and Burton (1996) successfully modelled the temperature response of trees based in part on physiological determinants of **bud burst heat sums**, **chilling requirements**, and **freezing tolerances** of seedlings. Remaining steps involve the documentation of species parameters at wider scales to improve calibration, but the basic framework for the incorporation of these traits into range-prediction models is operational.

Adaptations to extreme temperatures have been evaluated for a number of commercial tree species. For example, both interspe-

cific and interpopulation variability has been observed for **thresholds for the induction of heat shock proteins** and other stress responses that reduce the physiological impacts of high temperatures (Colombo et al. 1995). The **presence of antifreeze proteins** and **supercooling mechanisms** that reduce membrane damage from ice crystal formation (Pearce 2001) and the thresholds for their induction and their effectiveness have yet to be widely investigated for boreal and temperate species. Although promising, none of these traits are sufficiently documented to be used in vulnerability assessments. **Branching pattern modifications** (number of branches and allocation to long versus short axes) are recognized as a morphological response to limit excessive light and heat in arid ecosystems and may also manifest to a lesser extent in temperate and boreal forests (Norman and Jarvis 1974; Valladares and Pugnaire 1999; Guo et al. 2007). Indeed, avoidance of excessive radiation through self-shading is both biomechanically and biochemically cheaper than the “normal” enhanced light harvesting tree architecture and often copes adequately with excessive light or water-limited environments (Valladares and Pearcy 1998; Falster and Westoby 2003; Paquette et al. 2007).

The importance of **cold hardiness** and **dormancy** traits in the face of a warming climate may seem counterintuitive. However, milder winters and earlier springs can result in incomplete chilling requirements affecting tissue development (Caffarra and Donnelly 2011). These conditions may provoke maladaptive growth, resulting from early bud break (which depends on the accumulation of degree-days), followed by dieback when a late frost occurs. Species requiring warmer temperatures to initiate bud burst have shown to be more susceptible to late spring cold periods than those that leaf-out earlier on average (Vitasse et al. 2014). Damage to forests from early bud break followed by killing frosts and dieback has occurred more frequently in recent years (Marino et al. 2011; Augspurger 2013; McKenney et al. 2014). Conversely, the **timing of bud set** and the acquisition of **cold tolerance** are mainly under the control of photoperiod (Kayal et al. 2011; Pelgas et al. 2011; Dhont et al. 2012), which is unaffected by changes in climate. Early frost in the fall is consequently less damaging than late frost in the spring, except perhaps for multiple flush species, such as *Quercus rubra* (Cline and Harrington 2007). However, high temperatures in the fall may delay bud burst the following spring (Heide 2003).

Interestingly, cold tolerance in roots is not necessarily tied to that of shoots. For example, a comparison of *Q. rubra*, *Betula alleghaniensis*, and *Acer saccharum* seedlings showed that roots hardened more slowly in the winter, were less tolerant to cold temperatures, and broke dormancy earlier in the spring than aerial shoots (Calmé et al. 1994). This is perhaps because soil temperature fluctuates less than air temperature. Fine root death associated with colder soils, resulting from recent reductions in the depth of insulating snow packs, has been responsible for *Callitropsis nootkatensis* decline in coastal Alaska (Hennon et al. 2010) and is believed to be at least partly responsible for major dieback events of northern hardwoods of eastern North America (Auclair et al. 1996).

For commercial tree species, considerable information exists on adaptive traits (e.g., timing to bud burst, timing to bud set, etc.) from common garden experiments (where seedlings of multiple geographic sources are grown under relatively uniform conditions) and from the nursery management literature. Such traits were documented for major commercial species, with the potential to inform models of differential species/provenance abilities to acclimate to altered temperature regimes (e.g., Schreiber et al. 2013). Again, a large proportion of these data have yet to be compiled, standardized, and made available to potential users.

2.3. Increased fire frequency or intensity

Adaptations of trees to fire include post-fire recovery capacity and mechanical protection to avoid severe physiological damage. These adaptations tend to be different in the North American boreal forest (characterized by high-intensity crown fires) compared to the temperate forest (historical adaptation to low-intensity fires). For example, de Groot et al. (2003) group *B. papyrifera* and *P. tremuloides* as “fire endurers” because of their ability to resprout after severe fires, which is typical of the boreal forest. At the other extreme, large, mature *Pinus strobus* individuals in the eastern temperate forest are characterized as a “fire resisters” because of their thick, protective bark and their tall live crown (FEIS 2015). Similar traits are found in *Pinus ponderosa* and *Pseudotsuga menziesii* of the western temperate forest. Since European settlement in eastern North America, fire suppression has shifted the balance towards fire-intolerant temperate species such as *A. saccharum* (Nowacki and Abrams 2015). Altered fire regimes and (or) intensity will likely influence which species can penetrate the temperate-boreal ecotone.

2.3.1. Post-fire recovery capacity

Fire and other large-scale disturbances break the inertia associated with stable plant communities, which makes the habitat more permeable to new species colonization. The distinction between post-disturbance succession and colonization by migration is blurred, but interrupting successional pathways favours species with traits amenable to rapid establishment, potentially speeding up their colonization of new areas or providing a competitive advantage. Some traits responsible for post-fire population recovery are similar to those involved in species migration (see Sect. 3), while other traits are fire-specific, and therefore important in the context of changing fire regimes. It is worth noting that more severe fire regimes may shift abiotic conditions outside local tree species' niche, leading to regeneration failure and important impacts on forest structure (Gauthier et al. 2015b).

Resprouting ability is a key trait for post-fire recovery (Bond and Midgley 2001; Paula and Pausas 2006; Clarke et al. 2013), at the scale of both the individual and the population. Commonly divided between resprouters and non-resprouters, this trait actually represents a continuum that can be assessed quantitatively as the proportion of plants, at different life stages or sizes, that resprout after a disturbance (Paula et al. 2009; Paula and Pausas 2013). Qualitative information on tree resprouting ability is easily found in the literature (for example, Burns and Honkala 1990) and in databases (TRY, 87% of North American species; Table 1). Despite readily available information, quantitative assessments of tree resprouting ability are rare and performed with varying methods, while the influence of factors, such as the location of the bud bank (aerial, underground), is rarely assessed (Clarke et al. 2013). Additionally, a survey of temperate trees noted that resprouting ability tended to decrease with age and (or) size (Del Tredici 2001). **Root carbon reserves** also influence recovery capacity. Higher NSC reserves generally enhance resprouting capacity and viability as well as recovery of damaged crowns (Landhäusser and Lieffers 2002; Bond and Midgley 2003; Pérez-Harguindeguy et al. 2013); however, for *P. tremuloides*, Schier and Zasada (1973) and Landhäusser and Lieffers (2002) found that early growth of sprouts was related to reserves while sprout initiation was not. Hence, more species-specific information needs to be synthesized (e.g., Frey et al. 2003).

The formation of a **seed bank** and **seed heat tolerance** facilitate recruitment and population recovery after fire (Paula and Pausas 2008). Some tree species possess aerial seed banks, characterized by **serotiny** (e.g., *Pinus banksiana* and *Picea mariana* in boreal North America), a trait that is well documented (Gauthier et al. 1996; Goubitz et al. 2002; Talluto and Benkman 2013). Under increased fire frequency, **age to reproductive maturity** may become critical for the development of the aerial seed bank in the

limited time between recurrent fire events (Lavoie and Sirois 1998); in the preceding example, *P. banksiana* is favoured over *P. mariana* under short fire intervals, because *P. banksiana* is more precocious in cone and seed production. Under increased fire severity, wind-dispersed seeds may be advantaged in colonizing exposed mineral substrates (e.g., favoring *Populus spp.* and *Betula spp.*; de Groot et al. 2013); the convection column of a fire may also promote long-distance dispersal for wind-dispersed seeds (Whelan 1986). These traits must be considered in relation to different axes of the fire regime. For example, Buma et al. (2013) convincingly illustrate that serotinous species may be either favoured or not depending on changes in fire return interval, increased variability of this interval, or compound disturbances.

While few boreal tree species appear to have a long-lived soil seed bank (with the exception of *Prunus pensylvanica*), many temperate species with hard seed coats (e.g., in the Rosaceae family) can reliably buffer year-to-year variability in seed crops and environmental conditions by maintaining viable seeds over several years (Hille Ris Lambers et al. 2005). Although **seed persistence** has been widely studied (Walck et al. 2005; Santos et al. 2010; Wijayratne and Pyke 2012), variation in local site conditions and a lack of consistent methodology make it difficult to aggregate information from multiple studies. **Propagule size and shape** may be used as proxies instead (Thompson et al. 1993, 1998; Pérez-Harguindeguy et al. 2013) with species that produce small (<3 mg), spherical seeds being more likely to form permanent seed banks.

2.3.2. Mechanical protection

Bark thickness and architectural traits are key traits associated with tree mechanical protection against physiological damage (McAlpine and Hobbs 1994; van Mantgem and Schwartz 2003) and affecting canopy fuel potential. Information on these traits is widely available from large databases (e.g., FEIS 2015; <http://www.feis-crs.org/beta/>). Conversely, some architectural traits, such as **height to live crown base** are not commonly reported as field measurements, but can be predicted using allometric relationships (Jenkins et al. 2004), typically as a species-specific function of stand density (Rijal et al. 2012). Root tolerance to fire is mainly expressed by rooting depth. Deep roots are protected from lethal temperatures (Brown and Smith 2000) and smaller or finer roots, usually located in the organic horizon, are more sensitive to heat damage. However, **rooting depth** is likely less important in crown fire ecosystems. Also, soil depth of buds and rhizomes in relation to fire severity is likely to be more critical than maximum rooting depth (Pausas et al. 2004; Clarke et al. 2013).

2.4. Response to elevated CO₂

Persistence can also hinge on a species' ability to take advantage of new growing conditions, including an increase in CO₂ (Bonan 2008; IPCC 2013). With CO₂ serving as the basic feedstock for biomass, boreal and temperate trees, as C3 species, therefore have the potential to show an increase in photosynthetic capacity in the presence of elevated atmospheric CO₂. However, as individual plants adapt and grow with a given concentration of CO₂ in the environment, their respiration rate typically follows their photosynthetic rate. While the expected CO₂ fertilization effect is widely observed (Wullschlegel et al. 1995), there is not always a net, sustained increase in tree growth or carbon sequestration (Norby and Zak 2011; Franks et al. 2013). Experimental exposure of trees to elevated CO₂ over several years typically shows that trees eventually achieve a new metabolic equilibrium that balances CO₂, moisture, and nutrient availability, “down-regulating” to non-elevated levels of photosynthesis and growth (Ainsworth and Long 2005). Elevated photosynthesis often results in progressive nitrogen limitations to tree growth, which can sometimes be offset by enhanced fine root production (Luo et al. 2004; Norby et al. 2010). On the other hand, the correlation of reduced longevity

with faster growth may signal more rapid tree population turnovers and a cancellation of any net increase in carbon sequestration (Bugmann and Bigler 2011).

A main consequence of increased CO₂ concentration for plants is the potential increase in **water use efficiency**, either by a reduction in transpiration with unchanged photosynthesis rates or by increased photosynthesis rates. Improved water use efficiency has the potential to reduce the sensitivity of trees to drought events. Accordingly, dendrochronological evidence for a CO₂ fertilization effect is strongest for trees growing in semi-arid environments (Huang et al. 2007). The reduced **stomatal density** and **stomatal conductance** that tend to characterize long-term growth under elevated CO₂ could have strong implications for local and regional water balance. It is notable that the plasticity of these traits varies considerably among species and with tree age; for example, young *P. tremuloides* stands exhibit the typical increases in productivity that accompany reduced stomatal conductance and transpiration under elevated CO₂, but older stands experience increased conductance and water loss (Uddling et al. 2009).

These traits have been measured abundantly for trees and data are available in the literature and databases (e.g., LeafWeb, <http://leafweb.ornl.gov/Pages/LeafWeb.aspx>, Gu et al. 2010; BETY, <http://www.betydb.org>, LeBauer et al. 2010; TRY, <http://www.try-db.org>, Kattge et al. 2011). But the long-term response of plants to elevated CO₂ is still poorly understood, with many instances of increased growth by some species in particular habitats in a manner that still defies generalization (Körner et al. 2005; Körner et al. 2007; Bader et al. 2010). As an interim observation, it is noted that the presence and persistence of a CO₂ fertilization effect is generally stronger on water-limiting, nutrient-rich sites (McMurtrie et al. 2008), and that there are no reliable differences among species (Gedalof and Berg 2010).

2.5. Persist in place via adaptive capacity

The greatest uncertainty in our current assessments may be understanding species' capacity to adapt (Hof et al. 2011) and the mechanisms through which they might achieve this (Chmura et al. 2011). Adaptive capacity is the ability of organisms, populations, and ecosystems to maintain viability and persist in spite of environmental change, while adaptive variation represents the range of traits that, in combination, form an organism's adaptive capacity (Scotti 2010). Adaptive capacity covers a wide range of ecological, physiological, and genetic phenomena that act at multiple levels of organisation and time scales, including short-term phenotypic plasticity within individuals (physiological tolerance, acclimation), genetic diversity within populations and species (microevolution, local adaptation), and epigenetic controls that respond to changes in local conditions (Meyers and Bull 2002). Given the pace of projected change, it is likely that adaptive capacity will be an important determinant of species persistence, making it critical in forest management practices (Pedlar et al. 2012; Park et al. 2014; Nadeau et al. 2015). In the short term, the ability of individuals to acclimate through phenotypic plasticity is likely critical, while natural selection may be the driver of long-term persistence.

2.5.1. Phenotypic plasticity

Phenotypic plasticity, the capacity of a single genotype to produce a range of different phenotypes in response to varying environmental conditions (Sultan 2010), is the most rapid mechanism of response to environmental change (Meyers and Bull 2002; Matesanz et al. 2010). Tolerance, discussed earlier, is achieved in part by plasticity at the individual level, ranging from quickly reversible physiological adjustments to lasting morphological changes (Valladares et al. 2012). Plastic responses play a key role in tree species persistence in the face of climate change. Not only is there great variation in trait plasticity, with certain traits having

inherently more intraspecific variability than others, but in many cases the amplitude of this variability is itself more informative of a species' capacity to adapt and persist than the mean trait value. For instance, plasticity in a phenological trait, such as timing of bud set, can confer increased fitness under a range of climate conditions (Reed et al. 2011). Phenological plasticity has been suggested as an indicator of species capacity to adapt to climate change, with species that have shown accelerated phenology in the last decades performing better under warmer conditions (Cleland et al. 2012).

2.5.2. Genetic diversity

The persistence of a population at a site will ultimately depend on the presence of individuals that can survive and reproduce under prevailing environmental conditions. Natural selection sifts through expressed phenotypic variation, which, in combination with genetic diversity, increases the likelihood of finding a phenotype tolerant to the new environmental conditions. This could happen with no visible change in the species population structure or dynamics. Under strong selective pressure, natural selection can direct microevolutionary shifts within a few generations (Franks et al. 2013). Thus, species with high genetic variation (as is generally the case for species with large distributions) are expected to be better able to persist in the face of environmental change (Bussotti et al. 2015).

However, there are several noteworthy caveats to this assertion. First, it is hypothesized that genes flow outward from central, highly fecund populations to peripheral populations (García-Ramos and Kirkpatrick 1997). As a result, populations at the rear edge may receive cold-adapted alleles that are generally considered maladaptive for persistence under climate change (Hampe and Petit 2005; Aitken et al. 2008), while the leading edge of a distribution may receive pre-adapted alleles to warmer conditions from central populations, thus providing genetic variation that is advantageous for climate warming. Furthermore, the expected genetic responses depend on the genetic architecture of functional traits (number of genes involved and their effects on phenotypes (Kayal et al. 2011; Pelgas et al. 2011; Prunier et al. 2011). Indeed, if two traits are genetically correlated through pleiotropy or physical linkage, the genetic variability observed at the species level may not act as expected (e.g., trade-off between timing of bud set and growth duration (Pelgas et al. 2011) or between chemical defense and drought tolerance (Alsdurf et al. 2013)), and consequently neither may evolve (Etterson and Shaw 2001). Finally, the long generation times associated with trees (up to several decades) and large population size (thousands of individuals) mean that hundreds of years may be required to realize significant shifts in allele frequencies for many species.

In boreal and temperate tree species, genetic and phenotypic variation have been characterized for a number of commercially important boreal tree species; most are wind-pollinated and show high intra-population genetic variability and low inter-population divergence because of high levels of gene flow (Hamrick et al. 1992). In spite of this low population divergence, several experiments have revealed clines (continuous phenotypic variation along a latitudinal or elevational gradient) in growth-related traits and phenology in a number of boreal tree species, suggesting that local, potentially adaptive variations do exist (Howe et al. 2003; Prunier et al. 2011). This information has rarely been made available through trait databases, and species other than commercially important boreal trees remain insufficiently documented.

Intraspecific variation in traits is a direct expression of both genetic variation and the phenotypic plasticity of those traits within a species and its component populations. The relative contribution of these two phenomena to plant responses to climate change remains an open question (Gienapp et al. 2008; Nadeau and Jiggins 2010). However, studies on mammals and annual plants have reported that the majority of observed phenotypic

change to date is related to plasticity (Réale et al. 2003; Reed et al. 2011); this is likely also the case for trees, given the long generation times noted earlier. Several recent technological advances now make resolution of this issue more tractable. Both genetic and nongenetic variation can be measured through provenance trials or reciprocal transplant experiments (e.g., Li et al. 1997; Neale and Ingvarsson 2008; Morin et al. 2010; Sultan 2010), but measuring adaptive phenotypic plasticity will further require distinguishing between adaptive plasticity (i.e., responses conferring a fitness benefit) and non-adaptive responses (Van Kleunen and Fischer 2005). Careful dissection of fitness responses under controlled environmental conditions will be necessary as adaptive changes in physiological pathways are often complex, involving trade-offs among different interacting traits (Mykles et al. 2010).

2.5.3. Epigenetics

Epigenetic pathways have recently been singled out as potentially important mechanisms through which trees may adapt more rapidly to climate change. Epigenetic controls refer to stable, heritable phenotypes that result from changes in genetic expression without alterations to the DNA sequence (Berger et al. 2009). Maternal environment temperature during conifer zygotic embryogenesis and seed maturation may shift the developmental trajectory of embryos, resulting in significant changes to the growth cycle of the progeny (Johnsen et al. 2005; Yakovlev et al. 2012). Some studies showed that translocated *Picea abies* individuals produced offspring with phenological traits closely resembling those of populations at the translocation site, as opposed to populations at the site of origin (Skårøppa et al. 2007, 2010).

This phenomenon has important implications for a species' ability to persist in place under climate change. If warmer temperatures at the time of seed maturation result in offspring that are better adapted to warmer conditions, this may help successive generations keep pace with climate change at a given location. In *Picea abies*, epigenetic treatments produced a phenotypic differentiation similar to that observed between provenances separated by 4–6 degrees of latitude (Kvaalen and Johnsen 2008); however, the extent to which these findings are generalizable across species and environmental gradients remains to be tested (Bräutigam et al. 2013; Loo et al. 2014).

3. Mechanisms and traits to move: migration

The movement of species in response to climate has been the concern of paleoecologists and biogeographers for decades (e.g., Reid 1899; Davis 1976; Huntley 1996), and theory concerning tree species migration continues to develop. Bioclimatic envelope models project substantial shifts in the location of suitable climatic habitat for tree species populations over the coming century (e.g., McKenney et al. 2007; Iverson et al. 2008; Périé et al. 2014), but the ability of trees to track these changes remains highly questionable (Boisvert-Marsh et al. 2014; Nadeau et al. 2015). The velocity of range shifts depends on traits that affect each species' ability to produce and disperse seeds, as well as establish viable populations under local site conditions (Thuiller et al. 2008; Angert et al. 2011; Araújo and Peterson 2012; Boulangeat et al. 2012; Beauregard and de Blois 2014). Specifically, three broad ecological mechanisms that drive species population movement are recognized: (i) reproductive capacity of the source population, (ii) dispersal ability, and (iii) colonization potential at the advancing front (Clark 1998; Thuiller et al. 2008; Corlett and Westcott 2013; Table 2). We examine each of these broad mechanisms in this section and review relevant underlying traits.

The role and importance of certain traits can vary within a species' area of distribution. While the previous sections focused on traits and mechanisms important at the core of a species distribution, traits related to migration focus on individuals at the leading edge. Traits that have differentiated in the past along latitudinal or altitudinal gradients may be impacted differently

under future climate change, with varying consequences for range expansion (Kremer et al. 2014). As a caveat to this review, we note that while unassisted movement of species is an intuitive and popular phenomenon to consider in climate change vulnerability assessments, it may play a relatively minor role for trees because of their slow dispersal rates in relation to the velocity of climate change. Recipient systems may also exhibit a certain inertia to incoming species (Leak and Smith 1996) in the form of recalcitrant litter layers, shade, or allelopathic chemicals (e.g., Hewitt and Kellman 2004; Kellman 2004).

3.1. Reproductive capacity of the source population

Successful migration is first dependent on the reproductive capacity of the source population, which is influenced by generation time, seed crop production, and seed viability (Farmer 1997; Clark 1998; Aitken et al. 2008; Hampe 2011). Generation time is determined by **age of sexual maturity** and varies substantially among species (Moles et al. 2004), from as young as 4 years for *P. banksiana* and *A. rubrum*, to greater than 30 years for members of the Fagaceae family (Burns and Honkala 1990). Age to sexual maturity is particularly important in the context of climate change, given the rapid pace of climate envelope shifts projected over the coming century and the long generation time of tree species (Corlett and Westcott 2013; Burrows et al. 2014). Species that can reproduce earlier are likely to increase their chances of successful dispersal and colonization, especially under the increased disturbance frequencies that can be expected under a warming climate (Dale et al. 2001; Angert et al. 2011). **Age of optimum seed production** is a related metric that is generally harder to document (Table 2), but may be of particular importance in the context of climate change.

Seed crop production also has a strong influence over migration potential because species capable of producing large quantities of seed increase their likelihood of successful recruitment locally and at their advancing front (Clark 1998; Hampe 2011; Nathan et al. 2011). Most trees, however, are not capable of producing their maximum potential seed crop each year, varying by as much as 80% annually (e.g., Gross et al. 1968). **Maximum seed production** and periodicity of peak seed production years (**mast years**) vary substantially among species. Animal-dispersed tree species generally produce fewer seeds than wind-dispersed species (e.g., *Quercus spp.* species with a maximum of 5–6 thousand seeds per year per tree while *Populus spp.* and *Betula spp.* can have yields as high as 5–10 million seeds per year per tree; Burns and Honkala 1990). Controls on masting in trees are a matter of debate, but genetic control is considered to be important, with strong influence from environmental conditions. For instance, mast year onset in *Q. rubra* appears strongly affected by the previous growing season's summer temperatures and soil moisture levels (Farmer 1997). Increased seed production and frequency of masting events are possible (Allen et al. 2014), particularly in areas where temperature was previously limiting (e.g., leading edge). However, other species (e.g., *Populus spp.* and *A. rubrum*) show little to no periodicity in seed production, producing relatively constant yields from year to year; such differences should be accounted for in the assessment of species' ability to migrate (FEIS 2015; Burns and Honkala 1990).

Seed production mechanisms in trees have been thoroughly studied for North American commercial species, especially conifers grown for timber production (e.g., ODLF 1966). However, fewer data are available for deciduous tree species or conifers of lesser economic importance. Predictably, information remains scarce primarily in the case of traits that require data to be collected throughout tree lifespan, or that vary significantly across a species' range, such as age of optimum seed production (e.g., not documented in TRY; Table 2).

Table 2. Synthesis of key traits involved in the main mechanisms for tree species' ability to shift their geographical range (displacement).

Mechanism	Main trait	Relationship with migration ability	Definition, standard, and variability issues	Availability†
Fecundity of source population	Age at sexual maturity	↓ Aitken et al. 2008; Angert et al. 2011	Minimum age (years) required to start producing seeds. Variations exist with geography and local environment. Expresses an extreme and not an average.	TOPIC TRY 8% (17) FEIS
	Age of optimum seed production	↓ Angert et al. 2011	Age after which tree yearly seed production reaches its normal mature production level. Variations depending on the source, the definition of a good seed crop, and geographic location of the study.	TOPIC TRY n/a Silvics
	Maximum (mast year) and average seed production	↑ Aitken et al. 2008; Angert et al. 2011	Number of seeds released by a mature individual on average each year or during mast year. Generally provided in seeds per year per individual, although seed rain studies are more common for commercial tree species (seeds per year per hectare). Important variation with local conditions past and present.	TOPIC* TRY 2% (2) Silvics FEIS
	Periodicity of mast years	↑ Aitken et al. 2008; Angert et al. 2011	Frequency of years of above-average seed yields. Quantitative variable averaging 2–6 years for most species. High variation with geographic location.	TOPIC TRY n/a FEIS
	Seed fecundity	↑ Aitken et al. 2008; Angert et al. 2011	Number of seeds needed to produce one seedling, which encompasses loss of fertility, predation, and seedling establishment mechanisms in “natural conditions”. Most easily measurable as the ability of seeds to grow to seedling size in ideal conditions (MacKay 1972) for which methodology is simple and standardized (MacKay 1972). Mostly available for commercial species as germination rate (e.g., Burns and Honkala 1990).	TRY 15% (55) Silvics
Dispersal ability of source population	Seed dispersal distance	↑ Vittoz and Engler 2007	The average distance from the parent tree reached by propagules. Hard to express through a simple quantitative index. Methodologies vary widely depending on dispersal vector. Proxies used for wind dispersion: seed terminal velocity (Greene and Johnson 1993; Wright et al. 2008) and seed release height.	TRY‡ 12% (35) Silvics FEIS
	Dispersal vector	Koike 2001; Ozinga et al. 2004; Vittoz and Engler 2007	Main seed dispersal mode. Categories are well standardized (Vittoz and Engler 2007; Pérez-Harguindeguy et al. 2013), though some vectors are more difficult to document than others. Absence of information does not mean that a species is not dispersed via a certain vector.	TOPIC* TRY* 87% (531) FEIS* Silvics*
	Seed mass	Westoby 1998; Swenson and Weiser 2010	Number of seeds per kilogram, or milligram per seed. Widely documented. The relationship of seed mass with dispersal distance remains debated (Lavorel et al. 2007). Methodological questions remain, such as whether green or dry weight should be preferentially used, and whether measurements should include epicarp structures.	USDA TOPIC TRY 91% (1993)
Colonization potential after dispersal	Clonal propagation	↑ Pérez-Harguindeguy et al. 2013	Plant ability to reproduce vegetatively via clonal organs. Broadly accepted categorical system, though variations exist (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Documentation remains anecdotal (presence or absence of clonal organs) (Cornelissen et al. 2003) though widely available (e.g., flora descriptions). Quantitative assessments are rare.	USDA* TOPIC* TRY* 14% (20) Silvics* FEIS*
	Self-pollination	↑ Pannell and Barrett, 1998	Propensity for self-pollination. Well standardized categories. Basic indications present in flora descriptions, but information on self-pollination for monoecious species is more difficult to confirm.	TOPIC* TRY* 13% (33) Published flora
	Seed dormancy requirement	Baskin and Baskin 1998	Necessary period of time under which seed is not able to germinate under otherwise suitable conditions. Well standardized categories. Generally well documented for trees (Baskin and Baskin 2004).	TOPIC* TRY* 87% (163) Silvics*

Table 2 (continued).

Mechanism	Main trait	Relationship with migration ability	Definition, standard, and variability issues	Availability†
Seedbed preferences		Munier et al. 2010	Whether a species requires a specific environment to germinate (e.g., nurse logs). Generally known for commercial species, but documentation is anecdotal.	TRY n/a FEIS* Silvics*
Seedling root:shoot ratio		↑ Markesteijn and Poorter, 2009	Methods are well defined (Paz 2003).	TRY 0%

Note: The arrow indicates the relationship between the described trait and migration ability (upward pointing arrow, higher trait values indicate higher migration ability; downward pointing arrow, higher trait values indicate decreasing migration ability; no arrow, lack of clear directional relationship for categorical traits). n/a indicates that no data are available for trait. Total number of entries for North American species considered indicated in parentheses. Database and literature references: TOPIC (Aubin et al. 2012), USDA (USDA 2015), FEIS (FEIS 2015), Silvics (Burns and Honkala 1990).

*At least some data is available as qualitative.

†Percentage of native North American tree species documented in TRY database (www.try-db.org; Kattge et al. 2011).

‡Value indicated is for seed terminal velocity.

3.2. Dispersal ability

Dispersal is the primary mechanism through which species expand their distribution (Clark 1998; Broennimann et al. 2006; Corlett and Westcott 2013), but is often oversimplified in bioclimatic envelope models (Araújo and Peterson 2012). Recent reviews suggest most seeds are dispersed no further than 10–1500 m from the parent plant, with only a small number of seeds (<2–10%) dispersing beyond this distance (e.g., Hewitt and Kellman 2002; Kinlan and Gaines 2003; Corlett 2009). However, there have been relatively few quantitative assessments of actual **seed dispersal distance** (Vittoz and Engler 2007). Information is primarily inferred from seed characteristics, spatial patterns of seedlings, or seed rain observations. This information is typically measured in open fields or after forest harvest, but rarely measured in closed forest stands (Greene and Johnson 1995; Clark 1998; but see Hewitt and Kellman 2002). In the absence of quantitative estimates of seed dispersal distance for most species, **seed dispersal vector** is widely used as a proxy of dispersal ability (documented for 87% of North American trees in TRY, Table 2). Nonetheless, the relationship between seed dispersal mode and transport distance can vary substantially (Pons and Pausas 2007; Thomson et al. 2011). The quality and availability of seed dispersal information varies significantly among taxa, region, and dispersal vector (see Table 2). To accurately capture dispersal potential, one should aggregate information from a set of experiments specifically designed for each of the species' main seed dispersal vectors (Pérez-Harguindeguy et al. 2013).

In the case of boreal and temperate trees, wind and animal dispersal are the predominant modes of transport, with wind-dispersed species typically travelling further than acorn-bearing trees (Bussotti et al. 2015). **Terminal velocity** in a still column of air and **seed release height** have frequently been used to model tree seed dispersal by wind (Greene and Johnson 1989; Askew et al. 1997; Kuparinen 2006; Wright et al. 2008; Thomson et al. 2011). Potential for dispersal via animal transport (zoochory) could be assessed from vector species abundance and habitat attractants, although such estimates should also account for predation (e.g., Pons and Pausas 2007). **Seed mass** has also been used as a readily available trait (91% of North American trees in TRY, Table 2), informative both about species dispersal ability and germinant survival (Harper et al. 1970; Westoby 1998; Garnier and Navas 2013). Small seeds tend to travel farther (Weiher et al. 1999; Swenson and Weiser 2010) and are produced in larger numbers, but also generally have fewer reserves available for the germinant (Westoby 1998; Rees et al. 2010). Again, there is significant variation within this trend; some large, wind dispersed seeds with wings or pappi, or dispersed from greater heights, will travel longer distances than smaller seeds (Thomson et al. 2011).

While paleo-ecological studies of prehistoric climate changes show post-glacial tree migration patterns exceeding those projected from typical dispersal patterns, rare long-distance dispersal events as well as the presence of small outlier populations in micro-refugia have been identified as critical drivers of species range expansion (Clark 1998; Clark et al. 2003; Feurdean et al. 2013). Such events are fundamentally difficult to predict (Corlett and Westcott 2013; Feurdean et al. 2013) and may only be loosely related to seed traits, if at all. Overall, the difficulty in expressing dispersal ability through a simple quantitative index (Clark 1998; Moles and Westoby 2004; Angert et al. 2011; Zhu et al. 2012), coupled with dispersal stochasticity, has resulted in low predictive power for modelling efforts.

3.3. Colonization potential of the advancing front

As shown by the invasion literature, the ability of individuals to germinate, survive, and reproduce upon reaching new sites will

largely determine which species can successfully colonize (Godoy et al. 2012). Upon colonizing a new site, a species' ability to tolerate inbreeding and successfully reproduce in small populations will play a critical role in its migration success. Species with a propensity for **self-pollination** and **vegetative spread** are more likely to develop viable populations from only a few individuals. While breeding system information is well known for trees and can easily be found in published floras (although only 13% of North American tree species are documented in TRY; Table 2), clonal propagation capacity is more difficult to quantify (Table 2).

Several additional controls on colonization come into play at the germination stage. Species dependent on the coincident migration of a specific symbiotic species for their establishment are likely to be less successful colonisers under climate change (Bonte et al. 2012). For example, *Pinus albicaulis* is almost exclusively dispersed by Clark's nutcracker (*Nucifraga columbiana*), making any range expansion by *P. albicaulis* highly co-dependent on the bird's response to climate change (Tomback 1982; McLane and Aitken 2012). In general though, such co-dependencies should only play a minor role in boreal and temperate forests where trees are typically wind pollinated and either dispersed abiotically or by generalist fauna, with associations to generalist mycorrhizal species.

A more significant constraint on germination for many temperate and boreal tree species may be the availability of particular environmental conditions on which they depend, such as particular moisture and cold temperature regimes to break **seed dormancy** (Baskin and Baskin 1998). Such environmental requirements act at fine scales and are not typically captured by climatic envelope models; there is, however, little doubt that these may be affected by localized differences in climate warming. Similarly, the **seedbed preferences** of some temperate (e.g., *B. alleghaniensis* on *Tsuga canadensis* logs, Marx and Walters 2008) and boreal tree species (e.g., *Picea glauca* on unburied decaying logs, Simard et al. 2003), are critical to their development; their migration could be impeded by the low availability of appropriate substrate on which to establish. While seed dormancy information is widely available, seedbed preference is only documented for the main commercial tree species, notably through formal experiments (e.g., Simard et al. 2003), and remains largely anecdotal for many other species (Table 2).

At the seedling stage, morphological and physiological traits, such as root-to-shoot ratio and **photosynthetic nitrogen-use efficiency**, can also be highly informative as to the likelihood of establishment success (Godoy et al. 2012). Phenological plasticity has also been evoked as a characteristic that could confer invasiveness (Daehler 2003; Davidson et al. 2011; Drenovsky et al. 2012; Godoy et al. 2012), and favour range expansion.

4. Using functional traits in vulnerability assessments: strengths and limitations

Our aim in this review is to provide guidance on the selection of ecologically relevant traits for forest vulnerability assessments in the context of a rapidly changing climate. We hope to ease the integration of ecological knowledge into the biophysical predictions currently used to prioritise management actions for conservation under climate change. Our review also identifies knowledge gaps in trait-based understanding of species response, and highlights disparities among research domains.

Much of the trait-mechanism associations we have on species' ability to shift their geographical distribution stem from the important theoretical and empirical work carried out on post-glacial tree range expansion and on forecasts of biological invasions, which provide a mechanistic basis upon which we can identify a set of traits associated with migration. However, early efforts to integrate migration potential into climate change response models have yielded only slight improvements in interpretive power (e.g., Zhu et al. 2012). While this may be because of the complexity

of expressing dispersal ability through a simple index, or the generally low quality of existing trait information (Angert et al. 2011; Stahl et al. 2014), it is also likely to be caused by our poor understanding of the relative importance of the different traits in this process. Mechanisms apparently unrelated to traits, such as rare long-distance dispersal events (Clark et al. 2003), availability of suitable edaphic conditions (Beauregard and de Blois 2014), fragmentation of the landscape matrix (Hewitt and Kellman 2002), and even the availability and quality of spatial data on the physical environment, are also likely to affect migration-related predictions.

We can confidently identify sets of traits that capture individual species' tolerance to fire. Here, the mechanisms are well understood, and the traits involved in species' response are clearly defined and well documented. Decades of research on fire prediction and fire control, provoked by the need to protect people and resources, have provided a solid knowledge base. Fire-related information has been aggregated in large databases (e.g., FEIS 2015) and used in numerous succession models. This allows for accurate characterisation of fire tolerance for temperate and boreal tree species.

Research on carbon sequestration has achieved similar advances for tree response to CO₂. The push to understand carbon sources and sinks in forests, particularly in boreal regions (Gauthier et al. 2015a), has improved our collective knowledge on potential drivers affecting carbon gains and losses in forest ecosystems under a changing climate. However, questions remain concerning our capacity to accurately predict long-term tree response to elevated CO₂ (Norby et al. 2010; Norby and Zak 2011; Walker et al. 2015). Published experiments have shown species responding idiosyncratically to elevated CO₂, with no evidence of trait-based patterns in these responses (Gedalof and Berg 2010). For now, it does not appear possible to capture tree response to elevated CO₂ using traits, particularly in the context of predicting community response to climate change, where uncertainties are necessarily scaled up and moisture and fertility gradient can play an important role.

Drought and extreme heat tolerances are difficult to characterize using a condensed set of traits. Significant effort has been put into elucidating the mechanisms involved, but debate remains over their relative importance. Variability in methods used to measure traits related to drought tolerance also creates data comparability issues and limits data aggregation (Table 1). As a result, drought tolerance indices currently used in models remain, for the most part, coarse classifications based on expert opinion or on current species distributions. Explicit quantitative assessments of tolerance, which encompass a complex set of physiological, morphological, and demographic traits, remain unavailable for the majority of North American flora (but see Valladares and Niinemets 2008). Although informative under current climate conditions, expert-based indices may not accurately represent true species tolerance (West et al. 2012; Bussotti et al. 2015) and may not be applicable to either extreme events or novel climatic regimes (Niinemets and Valladares 2006).

The greatest uncertainty in species' ability to cope with climate change resides in their adaptive capacity (Gienapp et al. 2008; Nadeau and Jiggins 2010; Hof et al. 2011). Until recently, the ability to persist in place via local adaptation or phenotypic plasticity has been somewhat overlooked, with greater emphasis put on species' ability to move (Jump and Penuelas 2005; Hof et al. 2011). The role of genetics in species' response to climate change is typically restricted to long-term adaptation potential via evolution (Jump and Penuelas 2005). Although well studied from both evolutionary and ecological perspectives, knowledge of local adaptation mechanisms and phenotypic plasticity remains underexploited in the context of climate change (Dawson et al. 2011). However, given the very large discrepancy between tree migration rates (McLachlan et al. 2005; Boisvert-Marsh et al. 2014) and projected

rates of climate change (Loarie et al. 2009), tolerance and short-term (or rapid) adaptive capacity may be key to tree species' responses to climate change. To tease apart differences in adaptive capacity among species, advances are needed at the interface of genetics, physiology, and ecology. Studies that focus on the limits of acclimation in place will be crucial, especially given the emphasis that is currently put on natural regeneration processes in forest management.

Another important factor limiting our ability to assess tree adaptive capacity is our lack of knowledge on intraspecific trait variation, including co-variation and interaction among traits. On the assumption that intraspecific variability is negligible compared to interspecific variability, these phenomena have been somewhat neglected by community ecologists (Albert et al. 2011; Violle et al. 2012). Thus far, few studies have systematically characterised the extent of intraspecific trait variability (e.g., Albert et al. 2011; de Bello et al. 2011; Auger and Shipley 2013) and we do not fully understand the ecological implications of such variation. The relative importance of environmental and genetic sources of variation, including epigenetic sources, remains unknown for most traits, as is the degree of niche conservatism within clades (Godoy et al. 2012; Lamy et al. 2014; Park et al. 2014). These knowledge gaps limit our capacity to understand how local populations will adapt to new climatic conditions and to estimate the risk of extinction (Jump and Penuelas 2005).

This review identifies data availability, accessibility, and quality as the main issues precluding widespread incorporation of trait-based analyses in species vulnerability assessments. Although the last century has seen the generation of vast amounts of ecological knowledge that could contribute to vulnerability assessments, most of the trait data currently available remain scattered and have not been collected with the purpose of characterising susceptibility to climate change. Thus, only a fraction of this information is both relevant in the context of climate change vulnerability and readily available for modelling purposes. Several aspects of trait data organization may help to improve this situation:

- **Consensus on methodological standards and terminology** is needed to promote dataset integration and compatibility. Although we note significant progress in protocol standardisation (e.g., Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013), dataset integration remains a challenge. To undertake true comparative ecology, a common core of standards should be developed, including descriptive language (ontology, e.g. Laporte and Garnier 2012), measurement, methodology, and sampling schemes, both within and among disciplines (Garnier and Navas 2013). Achieving this would improve both data quality in general and the predictive power of models using these traits.
- **Better taxonomic, geographic, and environmental coverage.** For many traits, only abundant species with commercial value are well documented, contributing to a cycle of research and application by which only these species are included in models, studied, and further documented. Systematic sampling of traits across a species' distribution is similarly lacking, despite its importance for understanding spatial and environmental structuring of trait response.
- **Dataset contextualisation.** Data are often presented in articles and databases without detailed methodological descriptions of the geographical or environmental range sampled and without distinction between measurements performed on seedlings and those performed on mature trees. Data contextualization in the form of thorough, standardized metadata should guide users to the dataset suitable for their specific question. This could be made available as an article appendix or as its own separate searchable database, among other options.
- **Extent, pattern, and ecological implications of trait variation.** Documentation of trait variation is needed to better un-

derstand underlying mechanisms in species' responses. To our knowledge, no single trait is currently sufficiently documented in databases to provide an accurate portrait of intraspecific trait variability (Tables 1 and 2; but see Poorter and Markesteijn 2008; Lamanna et al. 2014). The use of averaged data for a species, irrespective of its variability along environmental gradients, within a given species, or its ontogeny, substantially reduces the predictive power of models. Unfortunately, this is currently the only option available for most species. Traits should also be studied in combination, within a transdisciplinary framework, to understand trait co-variation, interactions, and adaptive variation.

Systematic and distribution range-level sampling, trait variation documentation, and data gap elimination appear to be arduous tasks without a large, coordinated, and, most crucially, expensive research effort. Current trends in funding are not likely to remedy this limitation. However, emerging support for collaborative science may provide some opportunities; one such type of initiative, which has contributed to global-scale research, is the aggregation of legacy datasets into databases (e.g., TRY, Kattge et al. 2011; TOPIC, Aubin et al. 2012). Significant data holdings remain scattered in older journal papers and grey literature, or are made unavailable by proprietary claims. Aggregating these legacy datasets represents a major challenge, because of the slow and intensive nature of collating data collected in different formats, and using varied methodologies at heterogeneous scales. In parallel, the initiation of a collaborative trait screening program would be an efficient way to document traits of strategic value. Such a program would ensure high dataset quality and limit methodological variability and compatibility issues, thus providing accurate documentation of trait variation. Similar programs of structured comparisons have been conducted elsewhere (e.g., for plant species common to the British Isles, Grime et al. 1988), although not with a focus on climate change response. Coordination of small, independent initiatives with different end-goals but using common standards and practices may be one way forward in the absence of important funding sources.

Complementary initiatives may focus on the measurement of specific traits in controlled environments (i.e., growth chambers, common garden experiments), to assess genetic and phenotypic sources of trait variation. According to Kremer et al. (2014), functional traits displaying congruence in phenotypic and genetic patterns along environmental gradients could be good candidates to predict phenotypic plasticity. A first step may be to use existing common garden experiments to identify traits exhibiting such congruence. Until adequate coverage of species, traits, and range can be achieved, proxies may be developed (from closely related species for traits with a high degree of conservatism or from easier to measure co-varying traits; Paquette et al. 2015), allowing research to carry on using the best available data.

The complexity and multidimensionality of climate change vulnerability has led us to develop new approaches in which data integration and cross-disciplinary collaboration are central. An accurate quantitative vulnerability assessment requires aggregation of knowledge across disciplines and scales. Therefore, in practice, the use of traits to assess vulnerability is a fundamentally interdisciplinary exercise (*sensu* Hicks et al. 2010) in which species-level genetic, ecophysiological, and morphological data are integrated and scaled from individuals to higher levels: plant communities, biomes, and evolutionary processes (Shipley 2007). With advances in conceptual understanding and knowledge, the next step should include integration of community-level mechanisms and synergistic effects on species ability to persist and migrate. As climate change proceeds, our ability to manage forests will certainly be challenged: adaptive management based on

quantitative assessments of all major vulnerability components will determine how effectively we meet this challenge. More than ever before, scientists are being asked to make their data available in a format suitable for easy archiving, discovery, and use by others. Researchers from traditionally isolated fields are connecting and developing cross-disciplinary communications. We believe that fostering the development of multidisciplinary research teams that can approach collaboration as an iterative process would support mutual understanding and create exciting research opportunities, toward predictive ecology.

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