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Beyond the tree-ring: challenges and opportunities of using wood anatomy to track tree-growth responses to environmental fluctuations.

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Corresponding Author:	Valentina Buttò, Ph.D. Universite du Quebec en Abitibi Temiscamingue Rouyn-Noranda, Québec CANADA
First Author:	Valentina Buttò, Ph.D.
Order of Authors:	Valentina Buttò, Ph.D.
Abstract:	<p>Wood traits are regarded as promising functional indicators for evaluating tree responses to environmental fluctuations, with their variability often viewed as a more profound marker of climatic signals compared to tree-ring width and density. Despite the growing popularity of wood traits studies in ecology, there hasn't been an up-to-date diagnostic portrait of the way in which this proxy is used nowadays, in what contexts, and what kind of information has been gained by using it. To fill this gap, I gathered empirical evidence from recent literature (2019-2023) regarding the relationship between wood traits that are measured at the microscopic scale and environmental factors. Information about the goal and experimental design for each study, together with the significance and direction of the relationship between each wood trait and environmental factors, has been collected to compare results that might come from different contexts. It emerged that during the last 5 years, wood traits have been measured in 16 biomes, 29 countries, and more than 60 species. Drought has been the most studied ecological driver used to conceive the experimental designs, and conduit diameter the most frequently studied trait. Results of the relationship between wood traits variability and the environmental drivers not only highlight strong site- and species-specific response patterns, but also high intra-annual variability. Taken together, these elements give rise to some epistemological reflections on where and how we study and measure wood trait, and on the drivers of their plasticity. These efforts might enable opportunities to produce predictive relationships aimed at assessing tree productivity and vulnerability face to climate change. Results from this review point to the need of increasing accessibility of measurements of traits related to carbon allocation pathways in trees, such as phloem, fiber, pits, and parenchyma rays. Furthermore, gaining insights into the dynamic changes in trees' wood traits as influenced by their environment, given their strong interdependence, could be effectively achieved by employing statistical analysis to investigate cause-and-effect relationships within the data. This approach holds promise for identifying the ecological factors driving variability in wood traits and predictive relationship to assess tree responses to climate change. It's also important to measure the inner workings of trees, like their metabolism and physiology to nourish the reflection about climate change mitigation and adaptation strategies.</p>
Suggested Reviewers:	<p>Antoine Cabon antoine.cabon@wsl.ch Expertise in Tree growth, ecology, eco-physiology, ecological modelling, wood anatomy, wood phenology</p> <p>Kiyomi Morino kiyomi@arizona.edu Expertise in wood anatomy, dendrochronology, dendroclimatology</p>
Opposed Reviewers:	

Dear Editor,

Please consider my paper: « Beyond the tree-ring: challenges and opportunities of using wood anatomy to track tree-growth responses to environmental fluctuations” for publication in “Dendrochronologia”. In this work, I carry out a systematic review covering the last five years (2019-2023) of literature studying the relationship between wood traits and environmental factors. The idea behind this study was not only to present the most recent findings on the topic but also to delve into the context in which these studies took place and the experimental designs chosen by researchers to conduct them. The last five years have been taken as a period reference period for this review in order to provide a diagnostic of the current practices in the topic, and to consider traits that has been measured according to similar standards, whose foundations are relatively recent considering also the technological improvements.

These results allowed me to share some epistemological considerations about how we study variability in wood traits in response to environmental factors, along with possible avenues for future research.

In my knowledge, the topic has not been reviewed during the last years, and my systematic review might nourish interesting reflections about the way we study the relationship between wood anatomy and environmental factors for researchers working on the topic, but also for the ones that would like to start doing it.

Kind Regards

Valentina Buttò, PhD (elle/she/her) – Professor

Institut de recherche sur les forêts (IRF) | Campus Rouyn-Noranda

Tel. 819 762-0971 poste 2153 | Bureau F-215 | uqat.ca

Beyond the tree-ring: challenges and opportunities of using wood anatomy to track tree-growth responses to environmental fluctuations.

Author: Valentina Buttò*

Affiliation: Institut de recherche sur les forêts (IRF), Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC, Canada

*Corresponding author: Valentina.butto@uqat.ca

2 **Abstract:**

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4 to environmental fluctuations, with their variability often viewed as a more profound
5 marker of climatic signals compared to tree-ring width and density. Despite the growing
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7 portrait of the way in which this proxy is used nowadays, in what contexts, and what kind
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11 and experimental design for each study, together with the significance and direction of the
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23 review point to the need of increasing accessibility of measurements of traits related to
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25 Furthermore, gaining insights into the dynamic changes in trees' wood traits as influenced
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32 **Keywords:** functional traits, experimental design, climate-growth relationship, quantitative wood
33 anatomy, ecological drivers, environmental factors

1. Introduction:

Originally initiated before global warming gained widespread attention, tree-ring science was designed to enhance our understanding of climate and weather variability by exploring seasonal patterns influencing tree-ring growth in diverse biomes (Büntgen, 2023). Over time, its focus evolved to include the examination of tree growth responses to climatic events, driven by raising concerns related to climatic change and the imperative to preserve the ecosystem services provided by forests.

Wood anatomy expands the frontiers of tree-ring research, enabling the study of wood growth divorced from tree-ring presence. This is facilitated by increasingly affordable techniques for observing and measuring wood traits (Pearl et al., 2020). In the quest for indicators of climate change effects on plant growth, the anatomical traits of wood show great promise due to their functional characteristics (Chave et al., 2009; Kattge et al., 2011). Chave et al. (2009) identify three main wood properties related to the major plant ecological functions: water transport and storage, mechanical properties, and defense properties. Finding the relationship between environmental fluctuations and these properties might thus provide timely information on the capacity of trees to respond to climate change.

From an evolutionary perspective, the environment significantly influences the development of certain anatomical features, and biogeographic distribution serves as strong evidence for this connection (Liu et al., 2021; Wheeler et al., 2019). With deciduousness, ring porosity is a trait strongly related with seasonal climates, where trees synchronize their growth with periods featuring favourable temperatures and high water availability (Wheeler et al., 2019). Research into environmental signals within wood anatomical features is a relatively recent endeavor, beginning with a year-to-year exploration of traits associated with water properties (Fonti et al., 2010). Xylem cell size, wall thickness and wall thickness are often studied to understand how trees respond to their environment. However, these traits can be strongly influenced by certain rules, making it easy to misinterpret their relationship with environmental changes (De Micco et al., 2019). This is especially true for conduit diameter, a commonly studied trait, which is mainly affected by the size of the plant and has limited variability due to the physical

requirements for water transport (Carrer et al., 2015). Compared to hydraulic traits, parenchyma traits are less studied, although there is a growing interest within the scientific community in researching them, particularly regarding the renewed focus on carbon storage (Plavcová et al., 2023). In recent years, anatomical traits have been studied across various ecosystems and species relevant to ecology and forestry. However, there remains a lack of comprehensive reporting on how these traits are utilized to investigate the effects of climate on tree growth, as well as the methods and analysis employed in such studies. The latter aspect is crucial when comparing different findings and exploring the potential of extrapolating predictive relationships for tree growth in the context of climate change. The aim of this review is thus to provide a synthesis of the most recent efforts (2019-2023) to assess climatic influences on wood anatomical features in different biomes. This exercise begins with the hypothesis that indeed the study of anatomical trends may reveal a climatic signal in intra-annual growth, but it aims to delve deeper, drawing insights from fundamental questions: 1) where, why, and what is measured when wood traits are utilized to assess tree responses to climate; 2) what has been discovered thus far, and whether there are common response patterns in the relationship between wood traits and environmental fluctuations. For this purpose, I compiled a database where I reported the main findings of each study focusing on the afore mentioned topic, together with useful information that was amassed for discussing all results in the wider context of the most current literature. To provide a diagnostic of current practices in the topic and to consider traits measured according to similar standards, the review has taken the last five years as a reference period.

Material and methods:

Research protocol and literature search:

A systematic literature review was conducted following guidelines that were proposed by Atkinson and Cipriani (2018) and Foo et al. (2021). Accordingly, a first query on the specialized search engines Scopus (www.scopus.com) and Web of Science (www.webofscience.com) has been produced using the keywords for this study. For both search engines, a query was refined by: Document Type (Article); Year of publication (2019- 2023); and Language (English). The following Scopus syntax was employed:

TITLE-ABS-KEY ((wood* AND anatom* AND trait*) AND (environment OR climate) AND (forest* OR tree*)) AND PUBYEAR > 2018 PUBYEAR <2024 AND (LIMIT-TO (DOCTYPE , "ar")) AND (LIMIT-TO (LANGUAGE , "English"))

where wildcards (*) are used to account for multiple spellings of the keywords.

The research was performed in January 2024, with Web of Science and Scopus detecting 294 and 160 records, respectively (Figure 1). An initial screening of title, abstract and keywords from both databases allowed for the exclusion of 10 methods papers, and 17 papers that were related to botanical groups other than trees (*e.g.*, ferns, grasses, etc.) and not containing climate data. After removing duplicates, 316 records remained (Figure 1). A full-text screening was performed to focus the research on studies explicitly reporting the relationship or correlation between anatomical traits and climate or other environmental variables. Among the 118 records that were included at this step, the top 10 most cited references have been used as landmark papers for forward and backward research, to avoid missing important references for the domain (Foo et al., 2021). A new database record was constructed from citing papers (forward research) and reference lists (backward research) of the 10 landmark papers using Scopus. This step allowed for the integration of 13 new records into the main collection. I thus gathered a collection of 131 papers for a second full-text screening where I only retained: 1) studies computing anatomical traits with quantitative wood anatomy techniques, *i.e.*, traits are measured using digital images of anatomical sections (von Arx et al., 2016); and 2) studies where the effects of each climate and environmental factor on wood anatomy are quantified for each trait (Figure 1).

To provide an up-to-date portrait of the research that was performed on the relationship between wood anatomical traits and environmental fluctuations, I compiled a new dataset with information that was extracted from the 97 retained records. The dataset was structured to extract the following information from each study:

- Trait type: *i.e.*, tracheid, vessel, fiber, ray, pit.
- anatomical trait (cell type or structure) [unit]:
- area (fiber, cell, tracheid) [μm^2];
- diameter and wall thickness (fiber, vessel, tracheid) [μm];

- 123 • number (xylem, phloem, parenchyma rays' cells) [No.];
- 124 • width, length (radial parenchyma) [μm];
- 125 • frequency and density (axial and radial parenchyma, vessel, tracheid) [no./mm
- 126 and no./mm²];
- 127 • grouping index (vessel) [unitless] (von Arx et al., 2013);
- 128 • fraction (axial parenchyma [mm²]: radial parenchyma [mm²]; vessel lumen,
- 129 axial or radial parenchyma [mm²]: ring area [mm²]) [% or unitless].
- 130 • Other derived metrics (conductivity, hydraulic diameter), theoretical hydraulic
- 131 conductance were also reported in the database (von Arx et al., 2016).

132 Wood trait measurements can be averaged and associated with a dated tree-ring
 133 series; or they can be computed across tree-ring sectors, when each tree-ring is split
 134 into sectors (10 sectors, in most of the cases) to assess the relationship between
 135 environmental factors and tree-ring sections allegedly developed in different moment
 136 of the growing season.

- 137 • ecological driver: it is the climate or environmental factor that is posited to drive
 138 the main variability of wood traits and the effects of which are the target of the
 139 experimental design. For example, gradient studies are always characterized by a
 140 main environmental factor affecting trait variability, such as altitude, latitude and
 141 drought;
- 142 • environmental factor: *e.g.*, temperature, precipitation and soil moisture deficit,
 143 where the last factor encompasses drought indices, SPEI (Standardized
 144 Precipitation Evapotranspiration Index) and comparisons between drought years
 145 and non-drought years, together with moisture (soil moisture and related proxies)
 146 and nutrient content;
- 147 • effect of the environmental factor on wood anatomical trait: positive, negative, no
 148 effect. “Negative–positive” and “positive–negative” are used when the effect
 149 changes across the tree ring, in absence of a precise assessment of earlywood and
 150 latewood;
- 151 • species and group: species of the study and group (angiosperm or gymnosperm)

- study duration: climate (> 30 years); weather (< 30 years); treatment (refers to studies where the experiment is conducted over one or two growing seasons); perturbation (refers to studies where time is defined by perturbation dynamics);
- study type: field study, field study with treatment (encompassing pot studies, common garden and research under controlled conditions), gradient studies;
- study population: natural stand or plantation, the latter including common gardens and pot experiments;
- biome where observations were made, and measurements were performed;
- country of the study area.

Correspondence analysis has been employed to assess: 1) which traits have been measured when studying a specific environmental factor, and 2) what responses have been detected when these traits are correlated with the most frequently measured environmental factors. Correspondence analysis has been performed using the CA function from Husson et al. (2016).

2. Results and discussion:

Picture a study on wood traits – climate relationships: where, why, what:

Wood anatomical traits were measured in 9 biomes, 29 countries, and more than 60 species (Figure 2, Table 1). Most studies have been realized on angiosperms in the temperate deciduous forest (23) and in the tropical rain forest (11), while other biomes, such as tropical dry forest, savanna, desert and alpine are less represented (Figure 2). The most common experimental design was the gradient study, where the most investigated ecological drivers of the climate-wood anatomy relationship were drought and climate, *i.e.*, average temperature and precipitation conditions over a period longer than 30 years (Figure 2). Wood traits variability have been studied in relationship to 14 environmental factors, including not only climatic factors (e.g. temperature, precipitation, moisture deficit), but also several perturbations like outbreaks, hurricanes, fire and flooding (Figure 2, Table 1).

Tracheid and vessel diameter or area were the most studied wood traits (Table 1). While studies measuring conifer traits always measured wall thickness along with cell diameter, only eight studies measured or computed vessel or fiber wall thickness in

angiosperms. Fiber or and wall thickness have been directly measured in five studies (Angélico et al., 2021; Câmara et al., 2020; Liu et al., 2022; Manvailer and Scremin-Dias, 2020; Prendin et al., 2019), and they have been computed by subtracting lumen diameter from the fiber diameter measured with the two cell walls in two studies (Maidana et al., 2022; Moulin et al., 2022). Other measuring strategies were used by Chambi-Legoas et al. (2023); Euring et al. (2021), who computed a cell wall fraction and by Arnaud et al. (2019), who indirectly assesses wall thickness by measuring wood's stiffness with the modulus of elasticity.

Other vessels-related traits measured were vessel grouping and pits (Table 1). Vessel grouping was measured variable in diffuse porous and semi-ring porous species, such as *Fagus sylvatica* L. (European beech), *Nothofagus pumilio* (Poepp. & Endl.) Krasser (lenga beech), *Inga vera* Willd. (ice-cream-bean, pois doux, churimo, guamo), *Enterolobium contortisiliquum* (Tamboril) and species within tribe Diosmeae (Rutaceae) (Akinlabi et al., 2022; Angélico et al., 2021; Garcia-Cervigon et al., 2020; Manvailer and Scremin-Dias, 2020; Tomasella et al., 2019). Pit diameter has been measured in three studies, where the authors were investigating the effect of fertilisation, drought and flooding on growth of *Eucalyptus grandis* W. Hill (rose or flooded gum), *I. vera* and *Enterolobium contortisiliquum* (Angélico et al., 2021; Manvailer and Scremin-Dias, 2020; Moulin et al., 2022).

Parenchyma traits are represented by measures performed on parenchyma rays and axial parenchyma, which are usually measured in frequency and density *i.e.* ray per mm in Akinlabi et al. (2022); Mundo et al. (2019), ray per mm² in Balzano et al. (2020b); da Silva et al. (2021); De Mil et al. (2019); Kotowska et al. (2020), number of axial parenchyma per mm² in Balzano et al. (2020a). Attributes of parenchyma cells that are usually only measured for rays cells are rays frequency over the entire tree-ring (De Mil et al., 2019); rays height and number of rays (Maidana et al., 2022; Manvailer and Scremin-Dias, 2020). Due to the contrasting functions of axial and ray parenchyma, the ratio between these two structural types was sometimes assessed to compare growth responses in different taxonomic groups and environments (Kotowska et al., 2020). During the last five years,

phloem traits have been measured just one time in Balzano et al. (2020b), who measured phloem cells per mm².

Overall, the correspondence analysis shows that perturbation and climate studies focused on different traits when assessing the relationship between environmental factors and wood traits (Figure 3a). The first and the second dimension of the correspondence analysis explained respectively 59.4% and 22.3% of the variability in the data. Accordingly, perturbation studies tended to focus on less frequently measured traits, such as those related to parenchyma, pit, and fibers. This choice might be related to different aspects and strategies related to the study of the effect of perturbations on wood traits. First, in general, relying on a limited literature about the effect of perturbation on wood traits, researchers might increase their chances of finding a climatic signal encompassing multiple traits. Second, the scoped studies were interested in the mechanisms underlying perturbation resilience, which might be related to their storage capacity and traits that could enhance their resistance (Manvailer and Scremin-Dias, 2020)

Studied worldwide, complex everywhere: the varied responses of wood traits to environmental fluctuations.

Temperature and precipitation were the most studied environmental factors (Figure 2). Temperature exerts contrasting effects on wood anatomy, depending upon the study, the site, the time span being considered (during or beyond the growing season), and the sector of the tree-ring (Figure 2, Figure 3b). Correspondence Analysis revealed that dimension 1 and dimension 2 explained 43.1% and 30% of variability in the association between measured traits and the effect of temperature (Figure 3b). Variability is driven by intra-annual response pattern detected for the different traits, with density being associated with a positive-negative response pattern, while conductivity and grouping are associated with a negative-positive pattern. Overall, positive effects of temperature on tracheid or vessel diameter and area are recorded along ecological gradients or at the treeline (Camarero et al., 2021; Jiang et al., 2021; Seftigen et al., 2022). In most cases, temperature had a positive and a negative effect on earlywood and latewood xylem cell diameter and area, respectively (Babushkina et al., 2019; Babushkina et al., 2021a; Balzano et al., 2020a; Balzano et al., 2019; Björklund et al., 2020; Cuny et al., 2019; Dinella et al., 2021; Farooq et al., 2023;

Han et al., 2023; Huang et al., 2021; Puchi et al., 2020; Seftigen et al., 2022; Stirbu et al.,
 2022b). In Mediterranean environments, autumn precipitation was related to the formation
 of earlywood-like cells, leading to intra-annual density fluctuations in *Pinus pinaster* Aiton
 (maritime pine) (Balzano et al., 2020a). Wall thickness was positively correlated with
 temperature in 8 studies, where the strongest correlation was recorded in latewood cells
 (Babushkina et al., 2019; Babushkina et al., 2021b; Björklund et al., 2020; Cuny et al.,
 2019; Farooq et al., 2023; Huang et al., 2021; Seftigen et al., 2022; Stirbu et al., 2022a).
 Fluctuations in temperature seem to consistently influence the xylem cell number
 (D'Andrea et al., 2023; Dinella et al., 2021; Nola et al., 2020; Puchi et al., 2020; Rodríguez-
 Morata et al., 2022; Stirbu et al., 2022b). The stability of this correlation is tied to the strong
 dependency of xylem cell number on cambial activity, which itself is influenced by
 temperature. Indeed, evidence from different biomes points to temperature as the main
 driver of cambial reactivation, with strong indications demonstrating a relationship
 between onset of cambial activity and xylem productivity (Begum et al., 2013; Deslauriers
 et al., 2008). Once cambial activity has been restored, the effect of temperature can vary
 depending on the specific phase of the growing season under investigation. These
 individual sample events would correspond to different stages of xylem differentiation,
 namely enlargement, and secondary wall deposition and lignification (Butto et al., 2021).
 In cold and wet environments, water availability is hardly a limiting factor especially early
 during the growing season, thereby explaining the positive correlation between temperature
 and earlywood trait sizes (Björklund et al., 2020; Cuny et al., 2019; Guada et al., 2021; Zhu
 et al., 2020). More generally, temperature has a positive influence on wood traits in
 environments or growing periods where moisture conditions are not limiting (Balzano et
 al., 2020a; Balzano et al., 2019; Björklund et al., 2020; Camarero et al., 2021; Cuny et al.,
 2019; Dinella et al., 2021; Fajardo et al., 2022; Farooq et al., 2023; Garcia-Cervigon et al.,
 2020; Guada et al., 2021; Huang et al., 2021; Rodríguez-Morata et al., 2022; Seftigen et
 al., 2022; Vicente et al., 2022; Zhu et al., 2020). For the closely scrutinized records, only
 five studies reported negative local relationships between temperature and a wood trait. In
 most of these cases, sites were prone to drought periods (Belokopytova et al., 2018;
 Björklund et al., 2020; Dinella et al., 2021; Hong et al., 2023; Huang et al., 2021). Indeed,
 with moisture deficits or under water-limited conditions, conduit size and wall thickness

are reduced with increasing temperature (Balzano et al., 2020a; Belokopytova et al., 2018; Björklund et al., 2020; Guada et al., 2021; Hong et al., 2023; Huang et al., 2021; Islam et al., 2019; Puchi et al., 2020; Song et al., 2022; Stirbu et al., 2022b).

Vessels seems the most associated traits to studies measuring moisture, while studying moisture deficit was more closely associated with both tracheid and vessel measurements (Table 1). Soil moisture deficit had a negative effect in almost all studies, except for latewood tracheid wall thickness in *Picea abies* (L.) H. Karst (Norway spruce) and tracheid diameter in *Larix kaempferi* (Lamb.) Carr. (Japanese larch, karamatsu) (Huang et al., 2021). The same authors reported no effect of moisture deficit on tracheid diameter and wall thickness on other species that were growing in the same common garden (Huang et al., 2021). To date, drought is the most obvious environmental driver to be targeted for investigation in warmer regions, where angiosperms are the taxa that are being most frequently targeted. Skewed taxonomic selections might explain the high frequency of negative correlations that have been observed between vessel size and temperature, and which researchers have reported over the last five years. Conversely, gymnosperms are target species that are favoured in altitudinal and latitudinal studies, which results in a high number of positive correlations between tracheid size and temperature; the coldest sites at high elevations and latitudes are considered to be strongly growth-limited (Paulsen and Körner, 2014). The outcome of the correlations between temperature and wood anatomy traits would thus be related to an interaction between water availability and temperatures, which remains a response that is very difficult to untangle in field and gradient studies. Yet, moisture deficit might be considered as an environmental factor resulting from the interaction of water availability and temperature, especially where drought spells exhibit seasonal patterns.

When investigating the response patterns of wood traits to precipitation, correspondence analysis dimensions explain 50.6% and 24.1% of variability within the patterns (Figure 3c). Correspondence analysis suggests that conductivity, density and vessel frequency undergo a positive effect of precipitation at the beginning of the growing season, and a negative effect of precipitation at the ending of the growing season. On the other size, number of cells, diameter and area, can be both positively and negatively

affected by precipitation. For this factor, correlation between xylem cell area and diameter is positive in twelve studies investigating *Pinus pinea* L. (Stone pine), *Pinus halepensis* Mill., (Aleppo Pine), *Pinus pinaster* Aiton (maritime pine, during fall), *Arbutus unedo* L. (Strawberry tree); *Pinus cembra* L. (Swiss pine), *Pinus sylvestris* L. (Scots pine), *Picea mariana* (Mill.) BSP (black spruce), multiple deciduous species of *Quercus*, *Larix decidua* Mill. (European larch), *Abies durangensis* Martinez (Durango fir), *Pinus engelmannii* Carr. (Apache pine), *P. cembroides* Zucc. (Mexican pinyon), the evergreen *Quercus boissieri* (= *Q. infectoria* Oliver; Boissier or Aleppo oak), Eucalyptus species, *Fraxinus angustifolia* Vahl. (Narrow leaves ash) (only in earlywood cells) and *Toona ciliata* Roem. (Australian red cedar, Indian mahogany, previous year precipitation) (Babushkina et al., 2021a; Balzano et al., 2020a; Balzano et al., 2019; Câmara et al., 2020; Camarero et al., 2021; Castagneri et al., 2020a; Guan et al., 2023; Islam et al., 2019; Pacheco et al., 2020; Puchi et al., 2020; Stirbu et al., 2022b). In contrast, the correlation between wood traits and precipitation is negative in studies investigating wood anatomy variability in *Quercus ilex* L. (holm oak), *Pinus pinaster* Aiton (maritime pine, during spring) and *Pinus sylvestris* L. (Scots pine) (Balzano et al., 2020a; Balzano et al., 2020b; Dinella et al., 2021). In *Pinus tabuliformis* Carr. (Manchurian or Chinese red pine) and *P. sylvestris*, tracheid diameter and area were positively correlated with precipitation across earlywood and negatively across latewood (Han et al., 2023; Song et al., 2022). Other studies have reported no effect of precipitation on xylem cell diameter and area (García-Cervigón et al., 2021; Guan et al., 2023; Hietz et al., 2022; Rodríguez-Ramírez et al., 2022b). Along moisture-limited size or precipitation gradients, the correlation between wall thickness and temperature was positive (Babushkina et al., 2021a; Belokopytova et al., 2018; Puchi et al., 2020), but changed in sign and intensity across the gradient and time period under study (Puchi et al., 2020). These results suggest that correlation between precipitation and wood traits has a more erratic patterns in literature, with high site-specific and specie- specific connotations.

In the last five years, the effect of perturbations on wood trait variability has been the subject of eight studies (Anadon-Rosell et al., 2021; Byers et al., 2020; Castagneri et al., 2020b; da Silva et al., 2021; Manvailer and Scremin-Dias, 2020; Mundo et al., 2019; Özden Keleş et al., 2021; Prendin et al., 2019) (Table 1). Perturbations in these studies were insect outbreaks (Castagneri et al., 2020b; Prendin et al., 2019), fire (Byers et al., 2020; Mundo

et al., 2019), flooding (Anadon-Rosell et al., 2021; Manvailer and Scremin-Dias, 2020), fungal pathogens (Özden Keleş et al., 2021), and pollution (da Silva et al., 2021). In general, perturbations negatively affected all wood traits, while carry-over effects were observed in case of insect outbreaks (Castagneri et al., 2020b; Prendin et al., 2019). On flooded sites, wood displayed not only shorter and smaller fibers, but also smaller vessels (Manvailer and Scremin-Dias, 2020). Conversely, fungal disease has been related to greater conduit size (Özden Keleş et al., 2021), and fire to increased vessel frequency (Mundo et al., 2019). Less frequently, researchers have studied parenchyma-associated traits (Akinlabi et al., 2022; da Silva et al., 2021; De Mil et al., 2019; Kotowska et al., 2020; Maidana et al., 2022; Manvailer and Scremin-Dias, 2020; Mundo et al., 2019) and phloem traits (Balzano et al., 2020b). The number of rays and parenchyma density were positively correlated with precipitation and fire, respectively (Akinlabi et al., 2022; Mundo et al., 2019), while parenchyma density was negatively correlated with pollution (da Silva et al., 2021). Effects of nutrients were neither detected on parenchyma fractions nor on ray width and height when investigating effects of fertilization on soil-fertility gradients (Kotowska et al., 2020; Maidana et al., 2022). Similarly, precipitation and flooding seem to exert no effect upon parenchyma fraction or upon ray width and height, independent of the ecosystem and species (De Mil et al., 2019; Manvailer and Scremin-Dias, 2020). Wood traits can be thus affected by perturbations, but more studies are needed to understand the general patterns of these responses.

Blessing and curse of wood trait co-dependency when studying tree responses to environmental factors.

To understand the highly variable nature of the relationship between wood traits and climatic factors, various considerations can be made, starting from the method used to study these relationships, while also considering the nature of these traits. Relationships between environmental factors and wood anatomy variables were assessed with Pearson's correlations (36% of the cases), linear mixed model (27% of the cases), ANOVA (15% of the cases), linear regressions (5% of the cases), structural equation models (3% of the cases) and Spearman's correlations (3% of the cases). In 7% of the cases, relationships between environmental factors and wood anatomy have been assessed with other nonparametric

methods (Wilcoxon test and Kruskal-Wallis), Generalized partial least squares regressions, generalized mixed models (other than linear mixed models) and MANOVA. In 4% of the cases, traits variability in relationship with climate is analysed by visual interpretation of their patterns. The prevalence of correlational analyses or, more generally, analytic frameworks with assumptions of linearity between variables can lead to occasional contradictory patterns in the results. Response patterns may sometimes appear counterintuitive or suggest inconsistent effects of climate on traits, even within the same species. However, these changing correlations between wood traits and environmental factors over space and time might be considered as indirect indicators of non-stationarity, which is an emergent property of the physiological and ecological processes underlying trait variability. Evidence for non-linear relationships between wood traits and environmental fluctuations not only arises from dendrochronological studies, but also from investigations into the relationship between wood phenology and wood traits (Buttò et al., 2021; Cuny and Rathgeber, 2016). Using wood anatomy as a proxy for assessing a tree's capacity to survive climate change cannot be summarily omitted from a process-based interpretation of trait variability, given that environment is just one of the many factors that shape wood traits plasticity.

In creating a predictive model or identifying potential vulnerabilities to climate change in a species, it's crucial to consider the mechanisms underlying the ecological responses of different traits. The strong correlation between wood traits, influenced by functional and geometrical constraints as well as carbon trade-offs, presents a double-edged sword when examining their function and ecological drivers (Preston et al., 2006). On one hand, utilizing one trait as a proxy for another can be particularly advantageous when measuring a specific trait is challenging. For example, wood density serves as a proxy measure for hydraulic and mechanical properties, which typically require destructive or time-consuming techniques to assess directly (Lachenbruch and McCulloh, 2014). On the other hand, when a proxy trait is used to make correlations with environmental factors, causality of this relationship must be carefully evaluated, since it might lead to misleading explanations (Lachenbruch and McCulloh, 2014; Preston et al., 2006). Conduit diameter offers a clear example of this last insidious risk, since it is possible to find a correlation between P_{50} i.e. the xylem pressure inducing 50% loss of hydraulic conductivity and

conduit diameter. However, causality of this correlation, especially for angiosperms has not been sustained by empirical studies (Hacke and Sperry, 2001). The correlation between P_{50} , serving as a proxy for drought resistance, and conduit diameter likely stems from conduit diameter's inverse relationship with wood density. Wood density, in turn, correlates with wall thickness, a functional trait mechanistically linked to drought resistance. Specifically, the negative pressure induced by drought stress prompts increased deposition of secondary walls, leading to cells with thicker walls that are more resistant to implosion under negative pressure (Hacke et al., 2001). The upregulation of secondary wall deposition due to negative pressure may interact with cell enlargement by affecting wall elasticity, thereby impeding cell distention and ultimately resulting in smaller cells (Dünser and Kleine-Vehn, 2015). Applying statistical techniques such as moderator and mediation analyses, along with structural equation models, could enhance our understanding of the relationship between wood traits and environmental factors. This approach has the potential to advance our knowledge of the ecological drivers behind wood trait variability and provide mechanistic insights into these responses. Among the available tools for modeling, R packages like lavaan, piecewiseSEM, and psych offer valuable resources for testing models based on process-based assumptions (Lefcheck, 2016; Revelle and Revelle, 2015; Rosseel, 2012).

Process-based perspectives might enhance the detection of the relationship between climate variables and general tree growth patterns.

The relationship between environmental factors and wood traits plasticity is normally mediated by other components, such as metabolism e.g. non-structural sugars, osmotic regulators, hormones (Aloni, 2014; Buttò et al., 2020; Carteni et al., 2018; Dünser and Kleine-Vehn, 2015), morphology e.g. tree height (Anfodillo et al., 2012; Anfodillo et al., 2013; Lechthaler et al., 2019; Petit and Anfodillo, 2009), and development e.g. duration of enlargement, duration of secondary wall deposition and lignification (Buttò et al., 2020; Buttò et al., 2021; Cuny et al., 2019; Cuny and Rathgeber, 2016) (Figure 4). At the individual scale, exposure to environmental conditions affect wood traits inducing acclimative responses. These responses are driven by wood traits plasticity reaction norms, and plasticity normally declines with ontogeny (De Kroon et al., 2005) (Figure 4). Repeated exposure to environmental factors leads to adaptive responses, that finally define the entire

spectrum of phenotypic plasticity at population levels. From this perspective, in order to understand and predict wood traits variability, multiple proxy approaches are necessary to study the potential mechanisms underlying traits sensitivity and its temporal patterns (Peltier and Ogle, 2020).

In last few years, combining non-structural sugars and wood trait measurements has provided insightful information regarding tree acclimation to environmental modifications at the community level (Fajardo and Piper, 2021; Tomasella et al., 2019). On the short term, it has been observed that wood trait variability is directly linked acclimative responses related to adjustments in carbon dynamics occurring at the whole-plant scale in response to environmental fluctuations (Rademacher et al., 2022). Under stress conditions, non-structural carbohydrate dynamics promote stress-induced acclimation by modulating growth resource availability, ultimately affecting tree growth (Piper and Paula, 2020). It is again through drought studies that we find very insightful examples of the potential for integrating carbon allocation when investigating stress-induced acclimation responses in wood traits. Studying the relationship between growth and non-structural sugar dynamics, Fajardo and Piper (2021) observed starch-to-sugar conversion at the entire community level in response to a brief moisture deficit, which explained the unchanged tree-ring growth of the species under study following periods of drought.

Carbon allocation might help explain cell wall thickness variability in response to environmental fluctuations. When drought stress occurs, an increasing concentration of sugars that are derived from starch degradation, together with new photo-assimilates, allows the maintenance of water in the xylem, by adjusting cell osmotic potential (Traversari et al., 2020). The carbon that is being used to stabilize tree metabolism may underlie the lack of a positive correlation between wall thickness and water deficit, which could be expected when discussing acclimation strategies that are aimed at increasing hydraulic safety. Interestingly, recent literature analysing drought effects on secondary wall construction revealed modifications to its chemical composition, which might stiffen the cell wall against negative sap pressures, without necessarily make it thicker (Euring et al., 2021; Liu et al., 2022; Moulin et al., 2022). These modifications might act upon the ultrastructure of the secondary wall, since resistance to drought-induced embolism is

mainly related to pit features, particularly in gymnosperms (Lens et al., 2013). In angiosperms, fiber and vessel cell wall thickness could also play a fundamental role in drought resistance, but its contribution is rarely assessed since this variable remains difficult to measure in a rapid, repeatable, and inexpensive manner. The latter may explain why only eight studies measured or computed fiber wall thickness in the last five years.

3. Conclusions

Over the last five years, wood trait variability has been recorded in a very large number of species and environments. Relationships or correlations that emerge between wood trait variability and environmental factors are strongly site and species-specific, except for moisture deficit. Yet, this last factor is typically studied in very precise contexts, *i.e.*, drought sites or drought and precipitation gradients, where plant size might undergo adaptation to a seasonal water deficit, eventually leading to changing conduit sizes. Lumen diameter was the most measured trait, probably because it is among the more rapid and easy to measure, in contrast to vessel and fiber wall thickness, whose measurements are time-consuming and less standardized. Yet, these traits display information providing great insight into the ecological drivers of carbon allocation in the stem and hydraulic safety in angiosperms. Similar observations might be made for parenchyma cells, for which the types of measurements are disparate and poorly standardized in current practice. Statistical and mechanistic modelling, including multiproxy approaches are promising avenues for the discipline, in the perspective of using wood traits to predict tree performances and vulnerability to climate change.

475 *Table 1 Articles measuring wood traits and environmental factors in the last 5 years.*

476

Environmental factor	Fiber	Parenchyma	Phloem	Pit	Tracheid	Vessel
Fire		(Mundo et al., 2019)			(Byers et al., 2020)	(Mundo et al., 2019)
Flooding		(Manvailer and Scremin-Dias, 2020)	(Manvailer and Scremin-Dias, 2020)	(Manvailer and Scremin-Dias, 2020)		(Anadon-Rosell et al., 2021; Manvailer and Scremin-Dias, 2020)
Iso-thermality						(Akinlabi et al., 2022)
Hurricane		(Ziemińska et al., 2023)				(Ziemińska et al., 2023)
Latitude					(Zheng et al., 2022)	
Moisture	(Chambi-Legoas et al., 2023; Liu et al., 2022)				(Han et al., 2023; Rita et al., 2022; Seo et al., 2020; Song et al., 2022)	(Câmara et al., 2020; Didion - Gency et al., 2021; García-Cervigon et al., 2020; García-Cervigón et al., 2021; Guada et al., 2021; Li et al., 2021; Liu et al., 2022; Moulin et al., 2022; Rodríguez-Ramírez et al., 2020; Tomasella et al., 2019; Vander Mijnsbrugge et al., 2020; Weithmann et al., 2022; Zimmermann et al., 2021)
Moisture Deficit	(Moulin et al., 2022)			(Moulin et al., 2022)	(Huang et al., 2021; Petit et al., 2022; Seo et al., 2020)	(Barigah et al., 2021; Câmara et al., 2020; Chambi-Legoas et al., 2023; Fajardo and Piper, 2021; Garcia-Cervigon et al., 2020; García-Cervigón et al., 2021; Jupa et al., 2021; Li et al., 2021; Liu et al., 2022; O'Brien et al., 2020; Rodríguez-Ramírez et al., 2022a; Rodríguez-Ramírez et al., 2022; Rodríguez-Ramírez et al., 2022b; Tomasella et al., 2019; Weithmann et al., 2022)

Nutrient	(Angélico et al., 2021; Arnaud et al., 2019; Maidana et al., 2021)	(Kotowska et al., 2020)	(Angélico et al., 2021)	(Seo et al., 2020)	(Chambi-Legoas et al., 2023; Euring et al., 2021; Li et al., 2021; Maidana et al., 2021; Zhang et al., 2020; Zhang et al., 2022)
Outbreak	(Özden Keleş et al., 2021)			(Castagneri et al., 2020b; Özden Keleş et al., 2021)	
PDO				(Lange et al., 2020)	(García-Cervigón et al., 2021)
Pollution		(da Silva et al., 2021)			
Precipitation		(Akinlabi et al., 2022; De Mil et al., 2019)	(Balzano et al., 2020b)	(Babushkina et al., 2019; Babushkina et al., 2021a; Balzano et al., 2020a; Belokopytova et al., 2018; Câmara et al., 2020; Dinella et al., 2021; Han et al., 2023; Hong et al., 2023; Pacheco et al., 2020; Puchi et al., 2020; Rita et al., 2022; Stirbu et al., 2022b)	(Balzano et al., 2020a; Balzano et al., 2019; Camarero et al., 2021; Castagneri et al., 2020a; Fajardo et al., 2020; Fajardo et al., 2022; García-Cervigón et al., 2021; Guan et al., 2023; Hietz et al., 2022; Islam et al., 2018; Islam et al., 2019; Julio Camarero and De Micco, 2019; Nola et al., 2020; Rodríguez-Ramírez et al., 2022b)
Temperature				(Babushkina et al., 2019; Babushkina et al., 2021a; Balzano et al., 2020a; Balzano et al., 2019; Belokopytova et al., 2018; Björklund et al., 2020; Cuny et al., 2019; Dinella et al., 2021; Farooq et al., 2023; Han et al., 2023; Hong et al., 2023; Huang et al., 2021; Julio Camarero and De Micco, 2019; Puchi et al., 2020; Seftigen et al., 2022; Seo et al., 2020; Song et al., 2022; Stirbu et al., 2022b; Unterholzner et al., 2024; Ziaco et al., 2023)	(Balzano et al., 2020a; Camarero et al., 2021; D'Andrea et al., 2023; Fajardo et al., 2022; Garcia-Cervigon et al., 2020; García-Cervigón et al., 2021; Guada et al., 2021; Guan et al., 2023; Islam et al., 2018; Islam et al., 2019; Jiang et al., 2021; Miranda et al., 2022; Nola et al., 2020; Rodríguez-Morata et al., 2022; Rodríguez-Ramírez et al., 2022b; Vicente et al., 2022; Zhu et al., 2020)
VPD				(Puchi et al., 2020)	

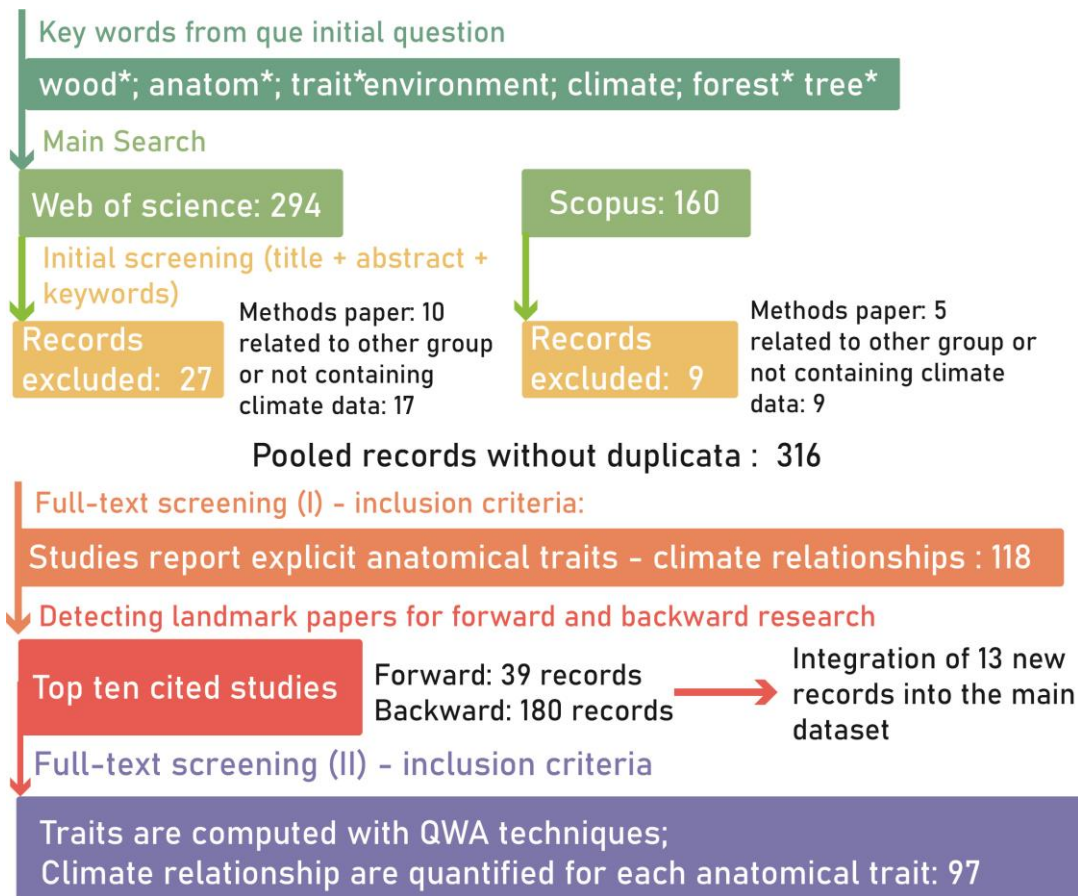


Figure 1: PRISMA diagram of the systematic review with all main steps and inclusion criteria for the full-test screenings

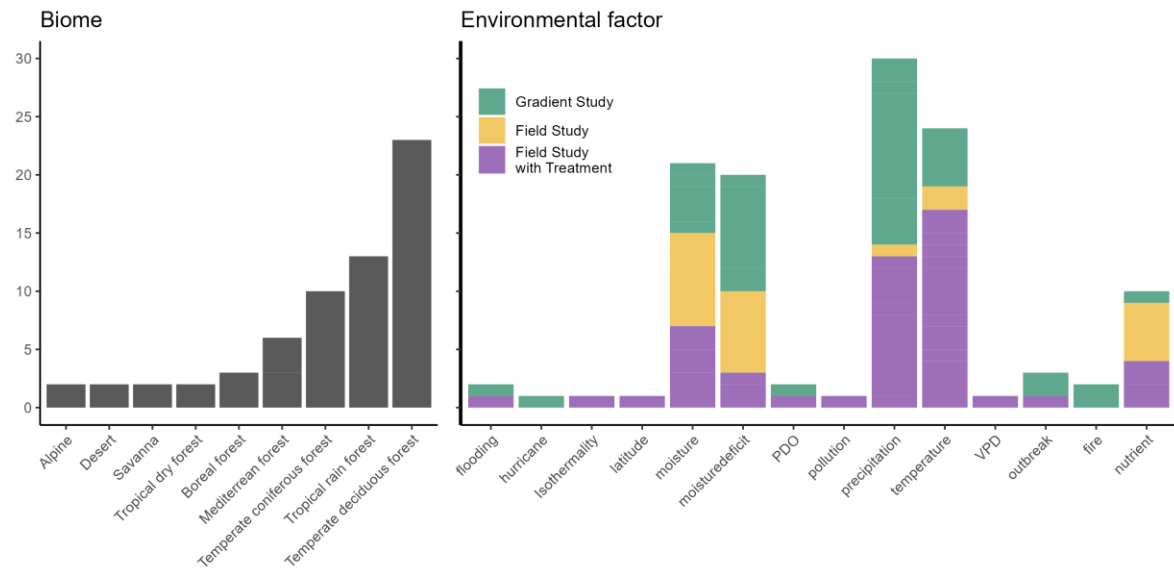


Figure 2: Main biomes (right panel) and environmental factors (left panel) that have been studied when assessing the relationship or correlation with wood anatomical trait for each experimental design (studies are cited in table 1).

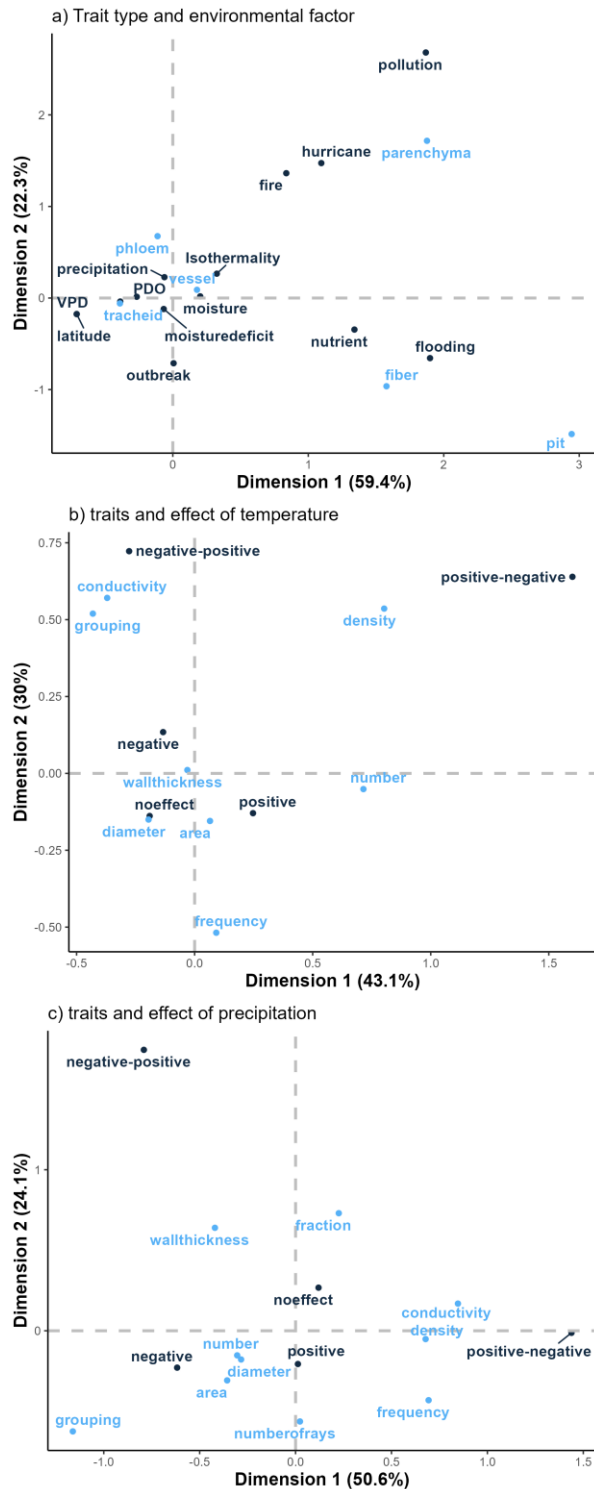


Figure 3: association between trait type and environmental factor studied (a), trait measured and direction of the effect of the environmental factor for temperature (b) and precipitation(c). Direction of the effect can be negative or positive (in earlywood,

496 latewood, or both), but also negative-positive and positive-negative (from the first to the
497 last tree-ring sector or from earlywood to latewood)

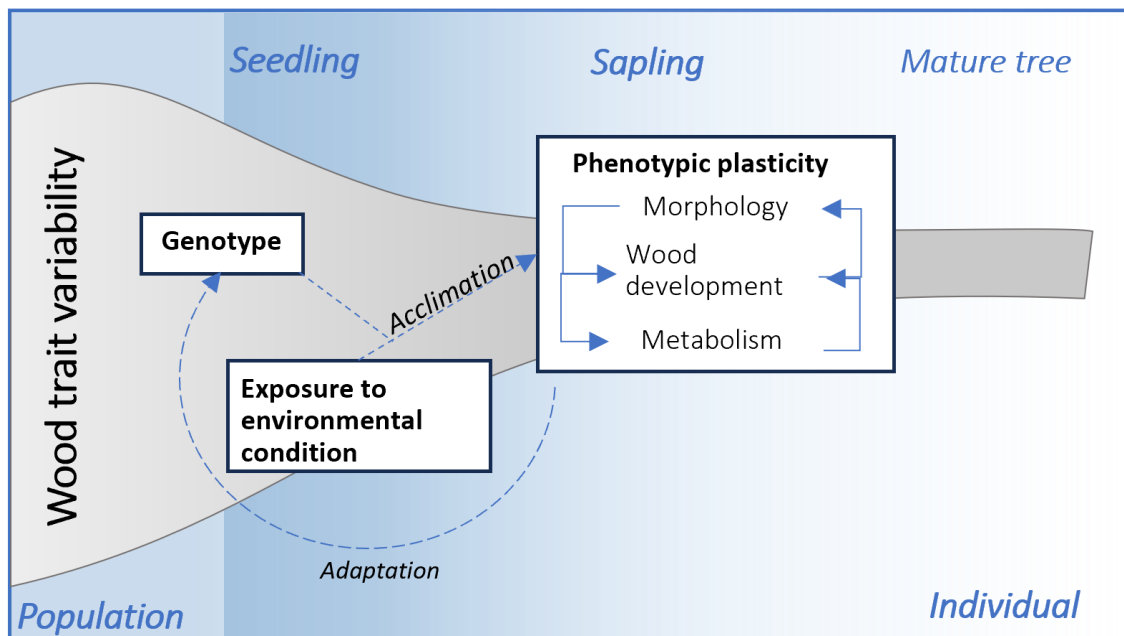


Figure 4: sources of wood trait variability from population to individual scales. The grey area represents the decrease in wood traits plasticity from population to individual scales, and at individual scales, from seedling to mature stage.

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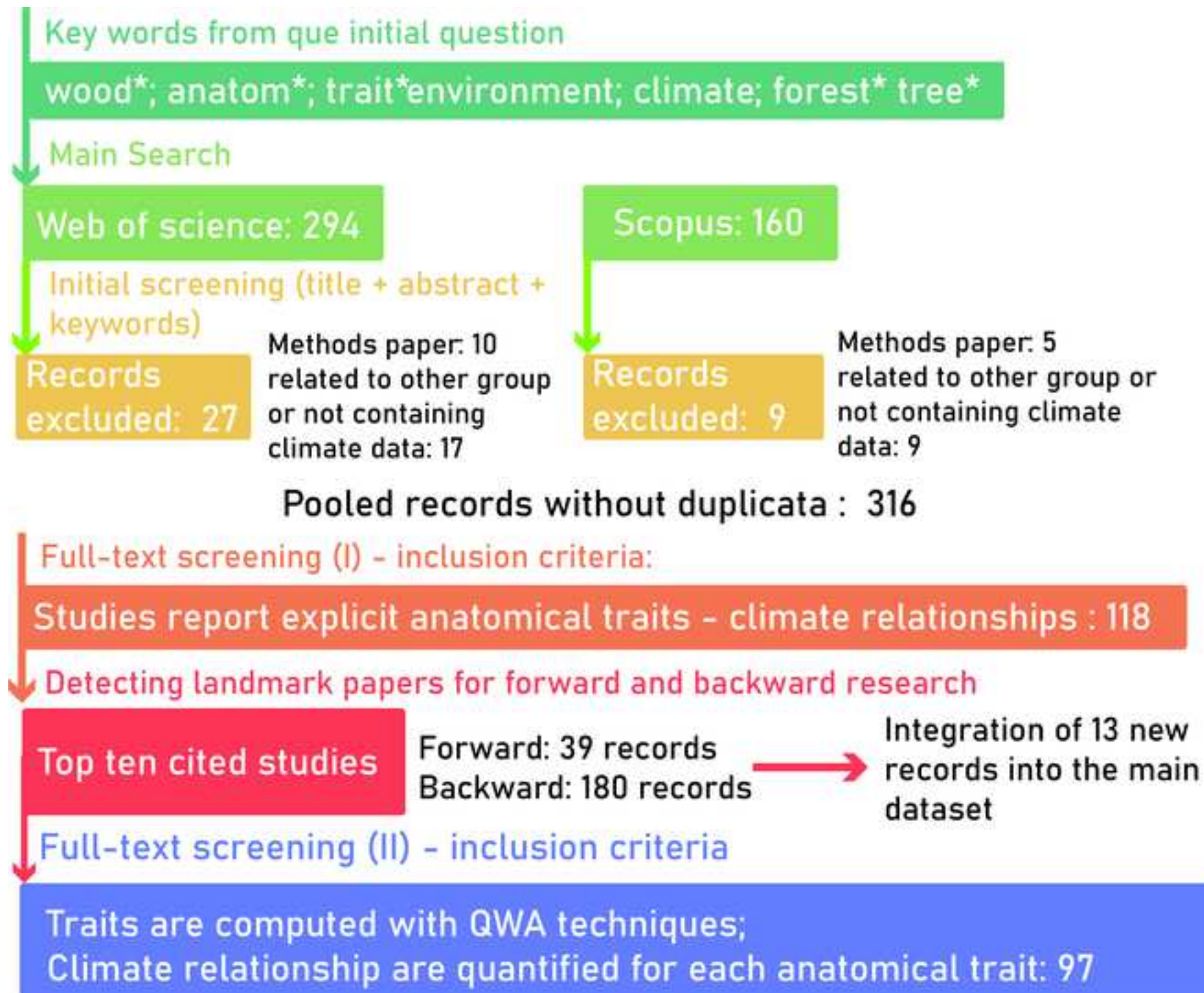


Figure 2

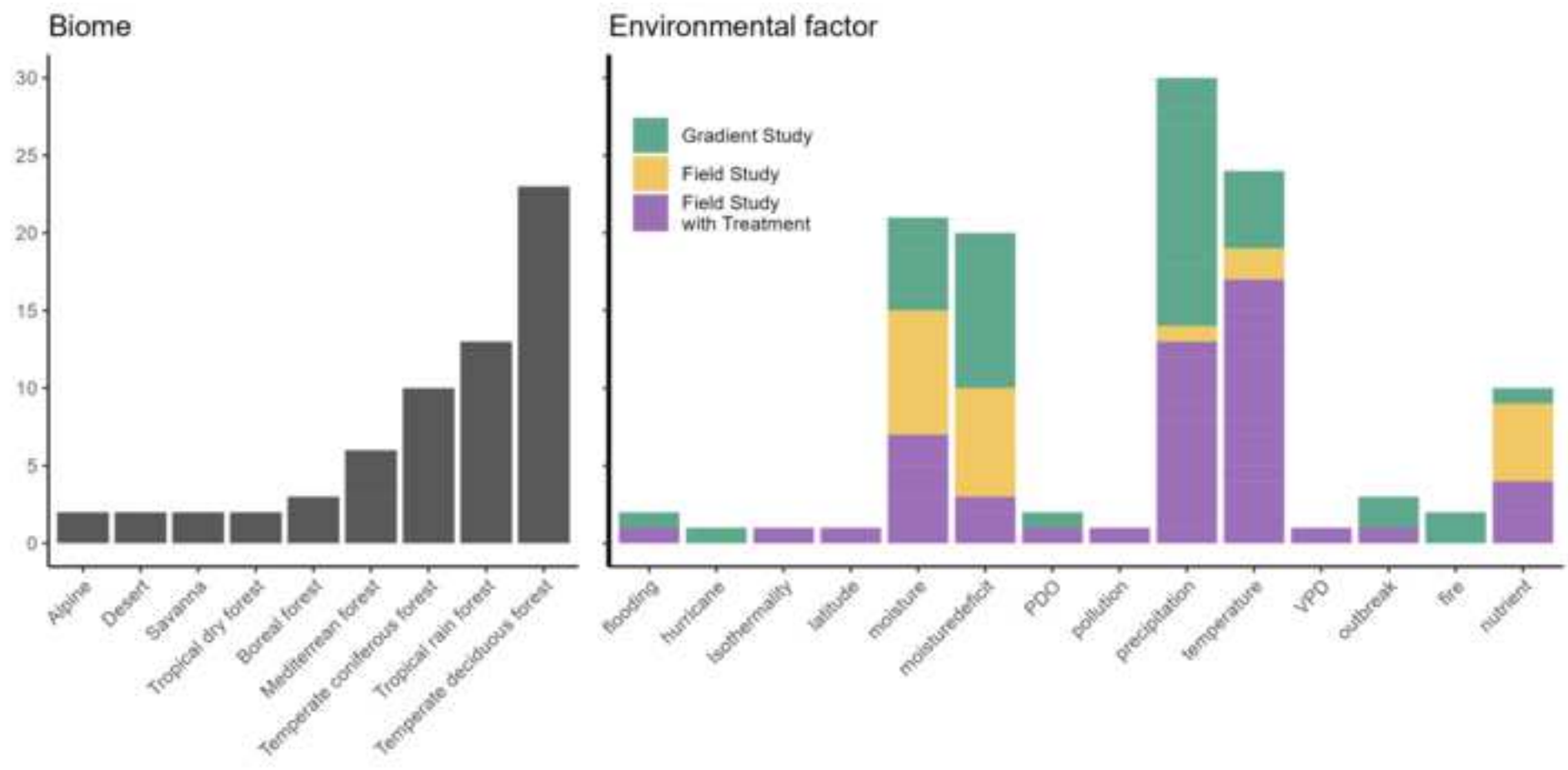
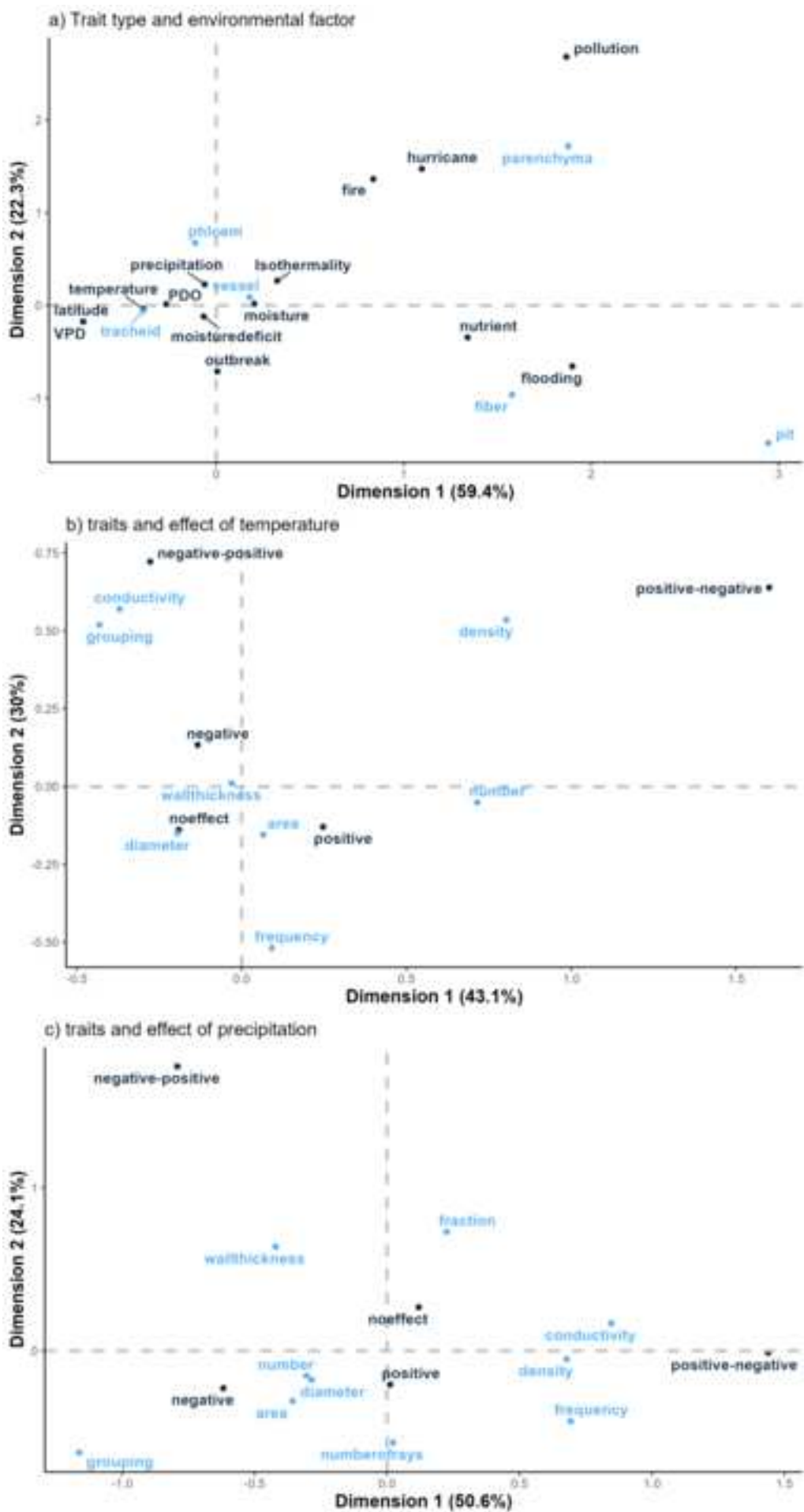
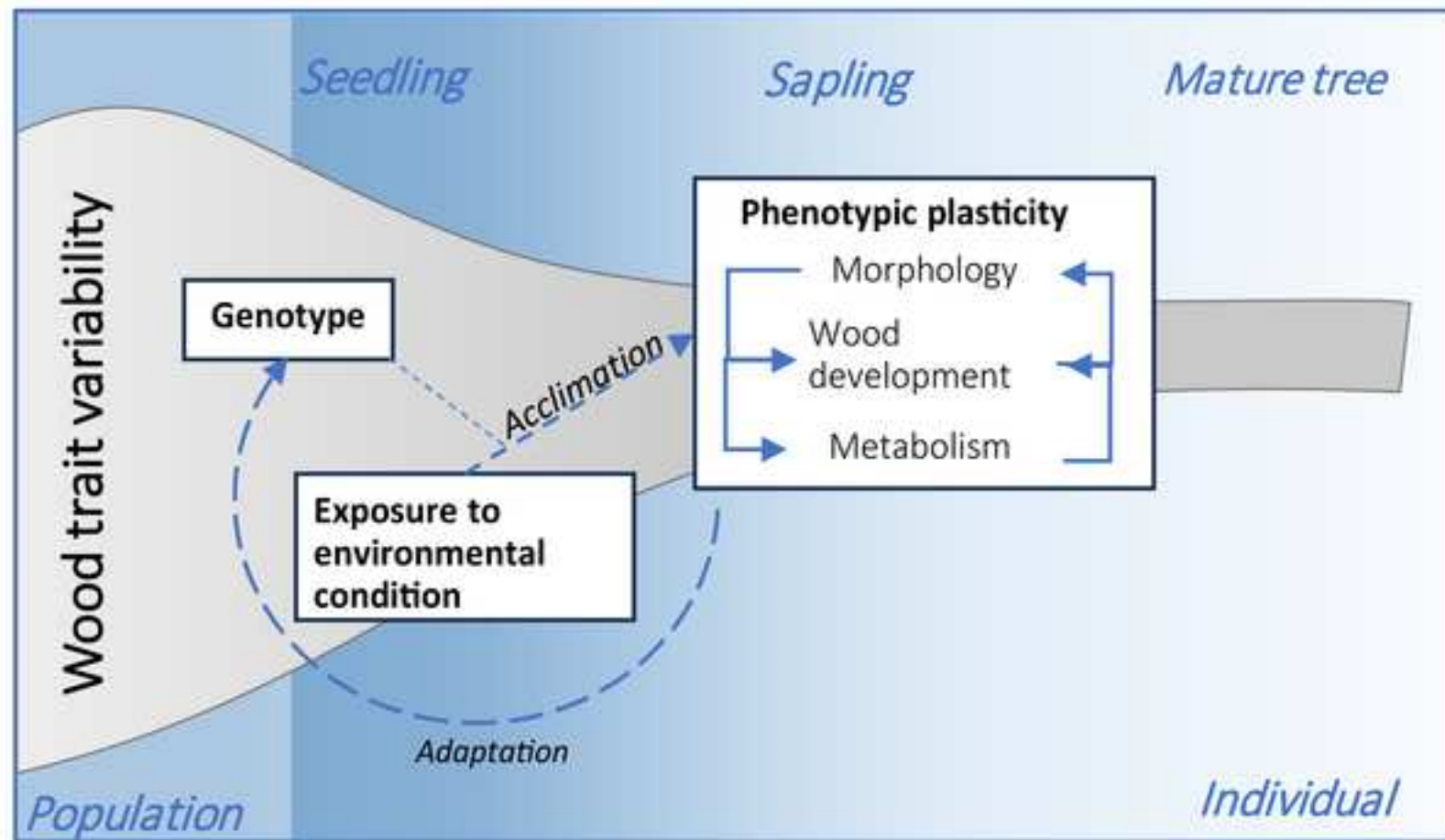


Figure 3





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5