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Abstract

Motivation: Trait variation within species can reveal plastic and/or genetic responses to environmental gradients, and may indicate where local adaptation has occurred. Here, we present a dataset of rangewide variation in leaf traits from seven of the most ecologically and economically important tree species in Europe. Sample collection and trait assessment are embedded in the GenTree project (EU-Horizon 2020), which aims at characterizing the genetic and phenotypic variability of forest tree species to optimize the management and sustainable use of forest genetic resources. Our dataset captures substantial intra- and interspecific leaf phenotypic variability, and provides valuable information for studying the relationship between ecosystem functioning and trait variability of individuals, and the response and resilience of species to environmental changes.

Main types of variable contained: We chose morphological and chemical characters linked to trade-offs between acquisition and conservation of resources and water use, namely specific leaf area, leaf size, carbon and nitrogen content and their ratio, and the isotopic signature of stable isotope ^{13}C and ^{15}N in leaves.

Spatial location and grain: We surveyed between 18 and 22 populations per species, 141 in total, across Europe.

Time period: Leaf sampling took place between 2016 and 2017.

Major taxa and level of measurement: We sampled at least 25 individuals in each population, 3,569 trees in total, and measured traits in 35,755 leaves from seven European tree species, i.e. the conifers *Picea abies*, *Pinus pinaster* and *Pinus sylvestris*, and the broadleaves *Betula pendula*, *Fagus sylvatica*, *Populus nigra* and *Quercus petraea*.
Software format: The data files are in ASCII text, tab delimited, not compressed.

KEYWORDS
European forests, intraspecific variability, leaf economics spectrum, leaf functional traits, phenotypic variation, tree species

1 | INTRODUCTION

Leaves are the primary site for photosynthesis in terrestrial ecosystems, generating resources and underpinning ecosystem functions. Nitrogen uptake and carbon assimilation by plants are the basis of trophic interactions and, together with leaf decomposability, drive the terrestrial biogeochemical cycling. These essential roles imply the simultaneous performance of multiple functions, for example light interception, water and nutrient transport, gas exchange and heat dissipation, in addition to deploying defence mechanisms against herbivores and pathogens and physical damage. Trade-offs among these functions exist such that under different environmental pressures, shape, anatomy and chemical composition of leaves exhibit great diversity arising from phylogenetic and adaptive processes over evolutionary time (Ackerly & Reich, 1999; Nicotra et al., 2011). Wright et al. (2004) examined 2,548 plant species and found a comprehensive global pattern, suggesting that the trade-offs span a leaf economics spectrum (LES). This spectrum shows a strong relationship among leaf traits related to the growth potential versus construction costs, going from plants with low photosynthetic rates and slow return on investment of leaf dry matter and nutrients (long life span), to plants with high rates and a rapid return (short life span). The LES concept led to the adoption of leaf trait syndromes being widely used to define species strategies, as they describe how species manage resources (Garnier et al., 2016) from a whole-plant perspective (Poorter et al., 2014).

Traits are measured at the individual plant level and can thus reflect the individual resource use and plant–plant interactions beyond the species averages (McGill et al., 2006). It has been shown that 25% of the estimated trait variation in plant communities occurs at the intraspecific level (Siefert et al., 2015), highlighting the importance of this component of variation for ecosystem functioning (Crutsinger et al., 2006; Pérez-Ramos et al., 2019; Siefert et al., 2012) and warning us against neglecting it. In fact, datasets such as LEDA (Kleyer et al., 2008), TRY (Kattge et al., 2011) and BROT (Tavsanoglu & Pausas, 2018), amongst others, that compile functional traits from different species, biomes and traits incorporate data at the individual level. This variation arises from phenotypic plasticity, genetic diversity and their interaction, driven by adaptation to different local environments (Leimu & Fischer, 2008) and to environmental gradients at different scales (Messier et al., 2010). Nevertheless, a large effort is required to quantify and collate trait variation within species, and accordingly it is frequently under-represented with data from a limited number of individuals per species.

Here, we present a dataset of inter- and intraspecific variation in leaf traits from seven ecologically and economically important tree species, evaluated from materials collected in populations across Europe. These data were collected as part of the European research project GenTree (http://www.gentree-h2020.eu), which aims to characterize phenotypes (see also Martínez-Sancho et al., 2020) and genetic variation in a set of European tree species. The final dataset will be of interest to study the relationships between ecosystem functioning and trait variability, to evaluate the relative extents to which genetic variation and plasticity contribute to intraspecific phenotypic variation, to assess the association between genetic and phenotypic variation, and ultimately to estimate the adaptive potential and resilience of species to environmental changes.

2 | METHODS

2.1 | Data source

We study leaf traits in seven European tree species in populations across their distributions. The species list comprised the conifers Norway spruce (*Picea abies* (L.) Karst), maritime pine (*Pinus pinaster* Aiton) and Scots pine (*Pinus sylvestris* L.), and the broadleaves silver birch (*Betula pendula* Roth), European beech (*Fagus sylvatica* L.), European black poplar (*Populus nigra* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.).

Between 18 and 22 populations per species (141 populations in total) were selected in pairs across Europe (Table 1, Supporting Information Table S1; Figure 1) to represent the range of environmental variation experienced by the species but excluding stands disturbed by intense or very recent natural or anthropogenic actions. Locally, population pairs were sampled along an environmental gradient (such as elevation, water availability or day length), but they were close enough to be connected by gene flow. A paired design offers increased statistical power to detect signatures of selection, whilst minimizing the confounding effect of population genetic

TABLE 1 Geographical and altitudinal ranges across sampled species, and sample sizes for leaf trait estimation. For each species, the table gives the number of study populations (Npop), surveyed trees (Ntrees), subsampled trees for chemical leaf trait assessment ($Ntree_{ch}$) and leaves measured to assess morphological leaf traits ($Nleaf_{morp}$)

Species	Latitudinal range (° N)	Longitudinal range (° E)	Elevational range (m a.s.l.)	Npop	Ntrees	$Ntree_{ch}$	$Nleaf_{morp}$
Betula pendula	41.9689–66.3663	−3.6645–29.2824	14.6–1,552.1	20	505	280	5,053
Fagus sylvatica	40.5484–59.3843	−1.0280–23.7195	75.4–1,626.2	22	558	308	5,574
Populus nigra	40.1605–51.1556	−4.4065–22.8203	5.2–764.9	18	471	279	4,709
Quercus petraea	38.1406–58.4150	−3.0298–23.7577	10.0–1,619.9	20	500	280	4,999
Picea abies	41.4808–66.4354	6.4809–58.8777	81.8–2,029.1	20	499	272	5,060
Pinus pinaster	36.8246–44.9702	−5.1238–11.3479	10.7–1,084.3	20	500	280	5,000
Pinus sylvestris	40.1907–66.4371	−5.3659–29.3002	18.7–1,857.4	21	536	298	5,360

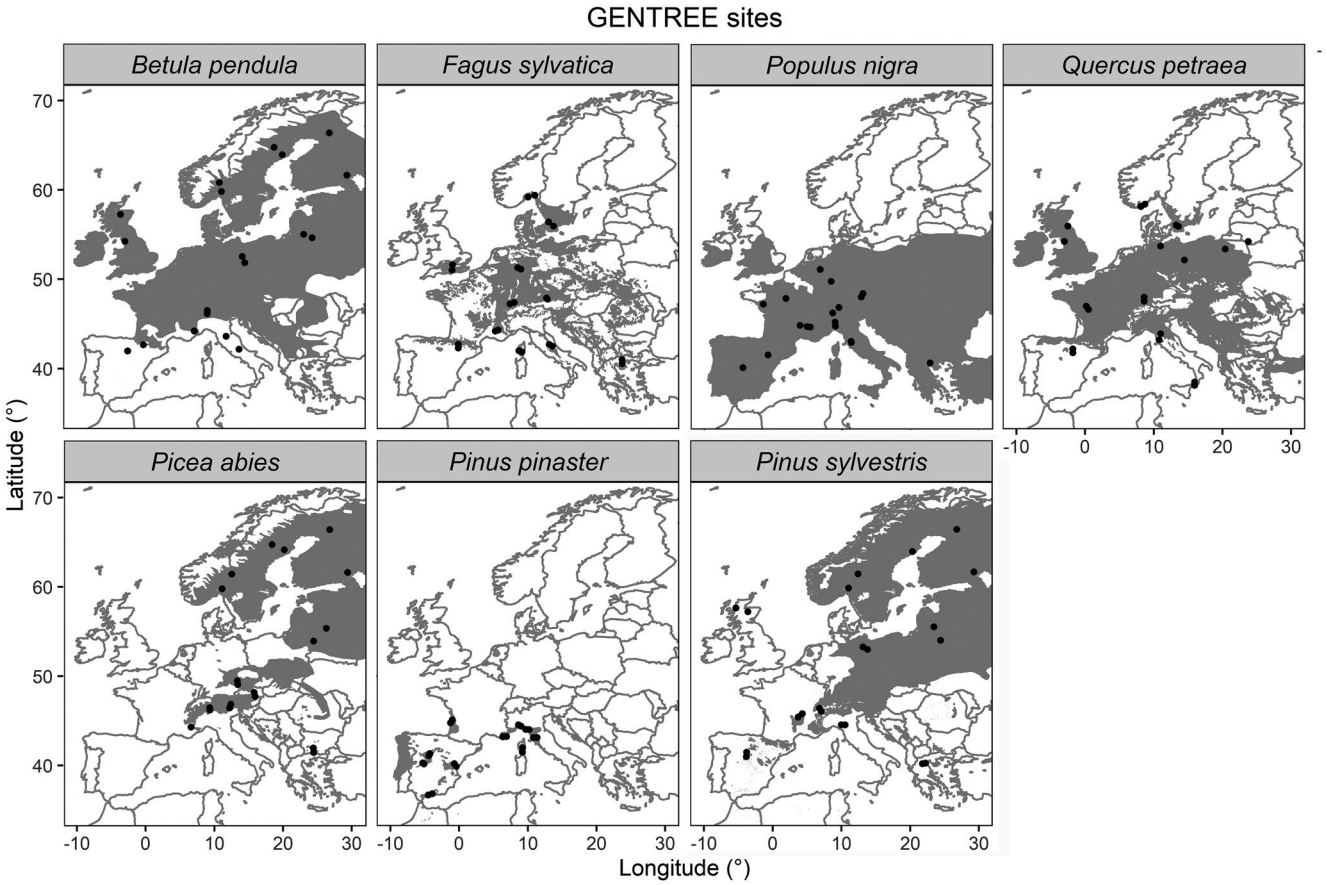

FIGURE 1 Distribution maps and site locations of the seven study tree species. Distribution information was downloaded from European Forest Genetic Resources Programme (http://www.euforgen.org)

structure (Lotterhos & Whitlock, 2015). In the north, where it is mostly flat and the gradient was often day length, distance within a pair was sometimes large. Nevertheless, site selection was done considering genetic estimates of gene flow and differentiation of the species there, which showed that distances under *c.* 100 km do not prevent gene flow and are not sufficient to yield significant differentiation among populations (Robledo-Arnuncio et al., 2004; Rusanen et al., 2003; Tollesfrud et al., 2009). Further details about

the selection of populations can be found at https://ec.europa.eu/research/participants/documents/downloadPublic?documentIds=080166e5b2f16f3e&appId=PPGMS

2.2 | Variables

The specific leaf area (SLA, the area of an individual fresh leaf divided by its dry mass; mm^2/mg) is one of the most frequently used traits in functional ecology. This is partly due to its ease of measurement, but also because it can be used to estimate the position of a species along the acquisition–conservation continuum on the leaf economics spectrum (Garnier et al., 2016). Very sensitive to variation in resource availability, high SLA is common in nutrient rich or shady environments (i.e. acquisitive value) and low SLA in nutrient poor and exposed environments (i.e. conservative value) (Pérez-Harguindeguy et al., 2013). The area of a leaf (LA; mm^2) is linked to the energy balance and water-use during photosynthesis. Small leaves can easily maintain favourable temperature and photosynthetic water-use efficiency under stressful conditions such as low water availability and high solar radiation compared to large leaves (Parkhurst & Loucks, 1972). LA varies at the interspecific and intraspecific levels, and it is influenced by different factors at different scales including phylogeny, climate, geology, altitude, latitude and allometry (Ackerly et al., 2002).

Leaf nitrogen and carbon contents (LNC, LCC; %) are indicative of variation in resource acquisition (nitrogen and carbon assimilation). Leaf N constitutes the proteins involved in the photosynthesis, especially RuBisCO, which fixes CO_2 inside the leaf (Lambers et al., 2008). Thus, photosynthetic capacity (A_{max}, the photosynthetic rate per unit leaf mass) correlates linearly with LNC (Field & Mooney, 1986). Nutrient rich environments favour the allocation of an important fraction of leaf N to the photosynthetic machinery, instead of to defensive compounds or supporting tissue, which is more typical in poor environments (Berendsen et al., 2007). LCC is the structural basis and constitutes a rather stable 50% of plant dry mass, and its usefulness lies in its relationship with other nutrients (leaf stoichiometry) that can be indicative of life history strategies, such as responses to stress (Zhang et al., 2017). For instance, an increase in the C : N ratio in plant tissues can reflect a shift from photosynthetic to structural tissue allocation under harsher conditions (Ågren, 2008).

The estimation of stable isotope abundance in leaves can provide information about the physical, chemical and metabolic processes (Griffiths, 1991; and references therein). Plant photosynthesis discriminates against the stable ^{13}C isotope (Faquhar et al., 1989) until stomata close and intercellular CO_2 concentration drops. Consequently, the isotopic signature $\delta^{13}C$ (‰; Equation 1) is linked to plant's water use efficiency (WUE), with higher levels of $\delta^{13}C$ achieved under prompt stomatal closure. In this way, higher $\delta^{13}C$ is observed in drier sites and during drier years (Marshall et al., 2007).

$$\delta\text{isotope} = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}}\right) \times 1{,}000, \quad (1)$$

where R is the ratio between the amount of the heavy isotope of an element to the amount of the light isotope in a sample, in reference to a ratio of a given standard material.

The isotopic signature of stable isotope ^{15}N in leaves ($\delta^{15}N$; ‰; Equation (1)) varies among species, ecosystems and climatic gradients, and thus it can reveal spatial and temporal patterns of N cycling (Craine et al., 2009, and references therein). For example, at large scales and under cool and wet conditions, there is a trend towards increasing losses of the heavier ^{15}N in soils resulting in ^{15}N-depleted forms of NO_3, N_2O and other N-containing compounds, and hence lower $\delta^{15}N$ in plants (Amundson et al., 2003). Contrastingly, rain events after dry periods cause a larger proportional loss of ^{14}N and increased $\delta^{15}N$ in N compounds in ecosystems (Ogaya & Peñuelas, 2008). Hence, $\delta^{15}N$ can reflect time-integrated measures of N storage and terrestrial N cycling (Amundson et al., 2003).

2.3 | Data collection and trait estimation

We selected at least 25 healthy adult individuals within each population, totalling 3,569 trees. Ten young but fully expanded leaves were taken from a fully exposed branch – from the top of the crown – without visible herbivory or other damage. They were scanned within 48 hr and LA of each leaf was assessed using WinFOLIA (Regent Instruments Inc., Canada). All samples were then oven-dried at 60 °C for 72 hr and each leaf weighed for dry mass with an electronic balance to the nearest 0.1 mg (Kern ALS 120-4N, Balingen, Germany) to assess SLA. Leaf collection, storage, processing and morphological trait measurement followed Pérez-Harguindeguy et al. (2013). This resulted in 35,755 leaves being used for leaf morphological trait assessment (Supporting Information Table S2, Figures S1, S2).

For a subset of 14 trees out of 25 alternatively selected in each population, together with the whole set from two populations (see below for details), a sample composed of several leaves was oven-dried and ground. Then, 3–3.5 mg of the ground material was weighed and sealed in tin foil capsules. These samples from 1,997 trees were shipped to the UC Davis Stable Isotope Facility, where the chemical analyses were carried out with an elemental analyser interfaced to a continuous flow isotope ratio mass spectrometer (IRMS; see the website for details https://stableisotopefacility.ucdavis.edu/). The final δ isotope values are expressed relative to international standards Vienna Pee Dee Belemnite (VPDB) and Air for carbon and nitrogen, respectively (Supporting Information Table S2, Figures S3, S4, S5, S6, S7).

2.4 | Technical validation

The assessment of morphological leaf traits is relatively simple but sample processing needs to be transparent and repeatable to avoid mistakes. Hence, we generated a sampling protocol followed by all project partners to ensure that samples of each surveyed tree could be tracked (https://ec.europa.eu/research/participants/docum

ents/downloadPublic?documentIds=080166e5b2f16f3e&appId=PPGMS).

Morphological trait assessment and sample preparation for chemical analyses were conducted entirely at the Museo Nacional de Ciencias Naturales (Consejo Superior de Investigaciones Científicas, Madrid). After recording weights and leaf area values, we examined the outliers within each population and checked their credibility by examining the samples and images. We kept these values as long as they were not identified as typos or mixed-up samples. This process was repeated after the estimation of SLA.

The validation technique used for the chemical analysis can be found on the UC Davis Stable Isotope Facility website (https://stableisotopefacility.ucdavis.edu/).

3 | DATA STRUCTURE

3.1 | Data tables

The dataset comprises three files. The first file (morpho_leaf_traits.csv) provides the morphological traits (i.e. SLA and LA) at leaf level, meaning a dataset with 35,755 observations. The second file (chemical_leaf_traits.csv) contains the chemical composition (LNC, LCC, and isotope signatures) in a subset of 14 trees of each population and the whole batch from two populations of *Populus nigra* (FR_PO_04 and FR_PO_06), totalling 1,997 observations. In both files, each population has its own code, composed of two letters indicating the country, another two letters indicating the species and a two-digit number (from 01 to 22) to indicate the population. For example, ES_FS_01 is the code of a population located in Spain (ES) of *Fagus sylvatica* (FS), numbered 01. Moreover, each sampled tree has a unique identifier, which includes the population code with an additional two-digit number indicating the order of survey (from 01 to 25). Country acronyms are: AT: Austria, CH: Switzerland, DE: Germany, ES: Spain, FI: Finland, FR: France, IT: Italy, GB: Great Britain, GR: Greece, LT: Lithuania, NO: Norway, PL: Poland, RU: Russia, SE: Sweden. Species acronyms are: BP: *Betula pendula*, FS: *Fagus sylvatica*, PA: *Picea abies*, PO: *Populus nigra*, PP: *Pinus pinaster*, PS: *Pinus sylvestris*, QP: *Quercus petraea*.

A third file (sites_leaves.csv) contains information about sites (target species, population code, site name, country, geographical coordinates and elevation).

3.2 | Format type

Each data file is in ASCII text, semicolon delimited, not compressed.

3.3 | Header information

Header information includes the population code (population), the tree identifier (treeID), the leaf identifier (leafID) in the file with data at the leaf level, and the acronyms of the variables: specific leaf area (SLA), leaf size (LA), leaf carbon content (LCC), leaf nitrogen content (LNC), ratio between carbon and nitrogen (C:N), isotopic signature of stable ^{13}C isotope ($\delta^{13}C$), isotopic signature of stable ^{15}N isotope ($\delta^{15}N$).

3.4 | Row information

Each row represents a single measurement.

3.5 | Variable definition

All variables measured in the seven species are detailed in the Methods section.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

RB, BF, FV, BC and CCB wrote the leaf sampling protocol, coordinated the leaf sampling, received, and stored all images and samples collected by the different groups.

RB, BC, CCB, DLQ and AM measured morphological leaf traits and prepared samples for the chemical analyses.

RB checked the data quality, wrote the manuscript and prepared the data files.

All the authors contributed to the field sampling, leaf scanning and commented on earlier versions of the manuscript and approved the current version.

DATA AVAILABILITY STATEMENT

We stored the dataset in a repository (Benavides et al., 2020) and it can be freely downloaded at https://doi.org/10.6084/m9.figshare.12044370.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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