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High phenotypic variation found within the offspring of each mother tree in *Fagus sylvatica* regardless of the environment or source population

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Abstract

Aim: Climate change challenges temperate forest trees by increasingly irregular precipitation and rising temperatures. Due to long generation cycles, trees cannot quickly adapt genetically. Hence, the persistence of tree populations in the face of ongoing climate change depends largely on phenotypic variation, that is the capability of a genotype to express variable phenotypes under different environmental conditions, known as plasticity. We aimed to quantify phenotypic variation of central Europe's naturally dominant forest tree across various intraspecific scales (individuals, mother trees (families), populations) to evaluate its potential to respond to changing climatic conditions.

Location: Europe.

Time Period: 2016–2019.

Major Taxa Studied: European beech (*Fagus sylvatica* L.).

Methods: We conducted a fully reciprocal transplantation experiment with more than 9000 beech seeds from seven populations across a Europe-wide gradient. We compared morphological (Specific Leaf Area), phenological (leaf unfolding) and fitness-related (growth, survival) traits across various biological scales: within single mother

trees, within populations and across different populations under the contrasting climates of the translocation sites.

Results: The experiment revealed significant phenotypic variation within the offspring of each mother tree, regardless of geographic origin. Initially, seedling height growth varied among mother trees and populations, likely due to maternal effects. However, the growth performance successively aligned after the first year. In summary, we observed a consistent growth response in different beech populations to diverse environments after initial maternal effects.

Main Conclusions: The study strikingly demonstrates the importance of considering intraspecific variation. Given the surprisingly broad spectrum of phenotypes each mother tree holds within its juvenile offspring, we conclude that *Fagus sylvatica* might have the potential for medium-term population persistence in face of climate change, provided that this pattern persists into later life stages. Hence, we also suggest further investigating the inclusion of passive adaptation and natural dynamics in the adaptive management of forests.

1 | INTRODUCTION

Organisms have three fundamental mechanisms to persist under changing environmental conditions: phenotypic plasticity or, more broadly, phenotypic variation, genetic adaptation and, migration (Aitken et al., 2008; Berg et al., 2010; Chevin et al., 2010; Hoffmann & Sgrò, 2011; Lenoir & Svenning, 2015). Sessile organisms like trees, with long generation times and limited dispersal capacities, depend strongly on phenotypic variation (Benito Garzón et al., 2019). Phenotypic variation, the ability of a genotype to express variable phenotypes under different environmental conditions (Whitman & Agrawal, 2009), buffers against short term environmental variability. In times of accelerating extinction rates due to climate change (Urban, 2015), it is crucial for species persistence (Chevin et al., 2010; Ghalambor et al., 2007).

Exploring the sources and limits of phenotypic variation and understanding what it entails for evolution, population dynamics and range shifts becomes increasingly urgent for a realistic forecast of species persistence under future conditions (Reed et al., 2011). Previous research has focused on the adaptive character of phenotypic plasticity and its buffering function in the face of changing environmental conditions (Chevin & Hoffman, 2017; Draghi & Whitlock, 2012), its transmission across generations (Auge et al., 2017) and its implementation in mechanistic or hybrid species distribution models (Benito Garzón et al., 2019; Bush et al., 2016). Unfortunately, the foundation of phenotypic variation, that is the genotype, is inconsistently addressed across studies (Forsman, 2015; Forsman & Wennersten, 2016), ranging from genetically identical clones or (half-) siblings to populations or even

whole species. Yet, phenotypic variation may vastly differ among these intraspecific levels of organization (Forsman, 2015; Nussey et al., 2007; Violle et al., 2012). Understanding these patterns and sources of variation is crucial to avoid drawing false conclusions in ecological experiments.

Here, we quantified the phenotypic variation in European beech (*Fagus sylvatica* L.), the naturally dominant forest tree species in Western and Central Europe (Leuschner & Ellenberg, 2017), in a novel way across several levels of intraspecific organization, that is within mother trees, populations and the whole species. We conducted a fully reciprocal transplantation experiment across a range-wide gradient, spanning from the dry and warm (Spain) to the moist and cold (Sweden, Poland) distribution edge of the species. Seeds were collected from seven sites and transplanted to the same seven plus one sites within and, additionally, to three sites beyond the current distribution range of the species, using a total of >9000 seeds. For the first time, we compared the phenotypic variation of key functional and fitness-related traits within the progeny of individual mother trees, within populations (i.e. among mother trees) and within the species (i.e. among populations) under the contrasting climates of the transplantation sites. Genetic differentiation among populations of European Beech is reported but overall weak (Buiteveld et al., 2007; Cuervo-Alarcon et al., 2018; Vornam et al., 2004). Genetic diversity within populations, however, is high (Cuervo-Alarcon et al., 2018; Vornam et al., 2004) and phenotypic plasticity is assumed to play a major role in the variation of key functional traits of the species (Gárate-Escamilla et al., 2019). Studies comparing the phenotypic variation across several intraspecific scales, including maternal half-sib

families, are scarce so far. Understanding the source of phenotypic variation, however, is missing so far but crucial for estimating population persistence in face of climate change and the need and type of management actions.

Specifically, we quantified the phenotypic variation of Europe's naturally dominant forest tree in a novel way across various intraspecific scales in order to draw a broader picture on the species capacity to cope with different environmental conditions – among and within populations, across a wide geographical and environmental gradient. The observed variation among the seedlings could demonstrate the immediate capacity to adjust to changing environments. However, successful establishment and juvenile growth are also necessary prerequisites for long-term adaptive processes.

Based on the high genetic variation within single stands (Vornam et al., 2004), we hypothesized a high phenotypic variation already within the progeny of each mother tree.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We carried out a reciprocal transplantation experiment (RTE) with European beech (*Fagus sylvatica* L.). RTE's have been developed as a method to study local adaptation of different populations as well as their phenotypic plasticity (Kawecki & Ebert, 2004; Palacio-López et al., 2015). They allow an appropriate comparison of different populations and even the detection of local adaptation by placing each at all environments of interest.

European beech is the dominant natural tree species in Western and Central Europe. This shade-tolerant species can form pure stands under a large variety of environments and thus is of high ecological and economical importance (Leuschner et al., 2006; Leuschner & Ellenberg, 2017).

Our RTE, detailed in Muffler et al. (2021), was conducted along a gradient from Spain towards Poland and Sweden (Figure S2), reflecting two key factors that affect the species' growth and distribution: winter cold and summer drought (Bolte et al., 2007; Kramer et al., 2010; Muffler et al., 2020; Weigel et al., 2018). At eight different forest stands dominated by beech along this gradient, we collected beechnuts from four mother trees, respectively, within a 250 m radius. The beechnuts were collected directly from the tree with a sling shot (Bigshot, Sherrill Inc) to ensure the correct maternity. Empty or mould-infested beechnuts were sorted out. Seed collection was carried out in autumn 2016 during a continental-wide masting event (Ascoli et al., 2017), which ensured a large quantity of seeds expressing the full genetic diversity (Tachiki & Iwasa, 2010) at all sites except for Sweden where poor fructification took place. The Swedish site within the current species distribution range (VI) was still used as a transplantation site, but not as a seed source. To allow for natural cold stratification, the beechnuts were planted within 3 weeks after collection in experimental plots that were established

at all transplantation sites. In addition to the eight sites that were located within the current distribution range of European beech, we also installed three sites beyond the natural distribution range. Two sites were established further north and east in Sweden and Poland (sites MO & NR, Figure S2) and one site further south in Spain (site PM, Figure S2). These sites represent areas into which beech is expected to expand in the future (Sweden and Poland) or dry and warm conditions that existing beech populations are expected to face in the near future due to climate change (Saltré et al., 2015).

The plots were placed in beech-dominated forests near the mother trees of the specific forest stand. It was taken care that all sites had a comparable canopy closure of approx. 60%–70%. The three sites outside of the natural distribution range were located in oak dominated forests in Spain (*Quercus pyrenaica* WILLD.) and Poland (*Quercus robur* L.) and a mountain ash stand in Sweden (*Sorbus aucuparia* L.). For detailed site information, see Table S1.

The beechnuts were planted in ten cages (true replicates) at each transplantation site, each protected by a 5 mm mesh on all sides except the bottom, inserted several cm into the ground, to prevent seed predation, seed removal and contamination by seeds from surrounding trees. All plots were protected by additional fences to prevent the intrusion of wild game. Before planting the beechnuts, the natural litter layer potentially containing local seeds and seeds from the soil surface were removed. Beechnuts do not form any soil seed bank and do not survive more than one winter. Each cage (110×50 cm) contained three seeds per single mother tree, planted as nested replicates on a 10×10 cm area. In total, this amounts to 30 seeds per mother tree of all seven populations at each transplantation site. This results in $n = 11$ sites × 10 replicates × 7 populations × 4 mother trees × 3 seeds = 9240 seeds. Thus, each installed cage contained 84 planted seeds replicated 10 times per site. The position of the seeds of the different origins and mother trees was systematically interspersed and altered per cage and marked. After planting, we covered the seeds with the same standardized, seed-free beech litter at all sites. After 1 year, the top covers of the cages were removed. In the first year of the experiment, all germinated and established seedlings were registered and labelled individually, and most non-germinated beechnuts were successfully retrieved. The seedlings and seeds were found at the very same location where they were planted, and no additional seeds indicating uncontrolled input from local seed sources were observed.

2.2 | Trait measurement

We quantified key functional and fitness-related traits of the transplanted beech seedlings over three growing seasons.

Specific leaf area (SLA) is an important functional trait that contributes to the regulation of plant photosynthesis, growth and productivity at scales from leaf to ecosystem (Reich et al., 1997). It is highly influenced by the availability of light and water and, therefore, considered to be very plastic (Ackerly et al., 2002; Ramírez-Valiente et al., 2010). To determine SLA, we collected leaf samples ($n = 1246$)

at the end of the first growing season in September. Sampling was carried out late in the vegetative period to avoid impairing the photosynthetic activity of the young trees with their few leaves. The samples were immediately pressed for further usage. After pressing, we scanned the surface area at 400 dpi with a scanner (Perfection V800 Photo, ScanMaker 1000XL Plus, Mikrotek) and measured the leaf surface area with the software ImageJ 1.5 2a (Rasband, National Institute of Health, USA). Afterwards we dried the leaves for at least 24 h at 60°C in a drying oven (UF 110, Memmert) and weighed them with a fine scale (Entris 124i-1S, Sartorius ALC-210.4, Acculab). To obtain the SLA, we then divided the leaf area in cm^2 by its dry weight in g. In total, the SLA of 1246 seedlings was measured.

Spring phenology, expressed here as the day of leaf unfolding, is a key functional trait for the plants' fitness (Chuine & Beaubien, 2001) and, therefore, subject to natural selection. Earlier leaf-out timing allows to explore resources (water, nutrients) before other species or individuals, providing a competitive advantage, especially in regions with unfavourably dry summer conditions (Robson et al., 2013). However, too early leaf-out exposes the leaves to eventual late spring frost events and herbivory which can severely affect tree growth and competitive abilities, in particular at juvenile ages (Gömöry & Paule, 2011; Vitasse et al., 2014). Spring phenology is highly sensitive to environmental conditions, especially temperature and is, therefore, used as 'fingerprint of global warming' (Parmesan & Yohe, 2003; Vitasse et al., 2021). We recorded leaf unfolding dates of 2 years old seedlings (i.e. at the beginning of the third growing season), at the three sites having the highest number of remaining seedlings (Site MO, VI & TL; Figure 1) using phenocams (HomeVista, SecaCam) positioned at 1 m height above the seedlings that took three pictures each day. For each individual ($n = 394$), leaf unfolding was defined as the date at which green leaves became visible on the respective picture.

Survival rate and seedling height served as fitness-relevant measures for the seedlings' performance and, respectively, their seed family and source population. Both traits can be proxies for overall adaptation or maladaptation in the respective environments. The height was measured every year at the end of each growing season (2017: $n = 1528$; 2018: $n = 656$; 2017: $n = 570$). Survival rate was defined as the ratio of living individuals after 3 years in relation to established seedlings in the first year. Note that survival and growth (of the previous year) were positively correlated in our experiment (generalized linear mixed model with transplantation site and time as random effects: $p < 0.0001$; slope = 0.45). Some sites were highly impacted by summer droughts in 2018 and 2019 (see Table S2). Site NL (Southern Germany) was excluded from statistical analyses due to low seedling numbers. Site OM (Spain) was excluded from analysis after 2017 due to a thick layer of beech leave litter causing the death of all seedlings due to light deprivation. We assume, that it happened because of the specific location at a slope, at which leaves of the surrounding trees accumulated and then got trapped inside our fence. No comparable problems with leave litter occurred at any other site. In GD (Poland) three cages were affected by seed predation and had to be excluded.

Here, we deliberately focus on early life stages, with our experimental setup including seed stratification, germination and establishment at the transplantation sites, which are crucial for successful regeneration (Muffler et al., 2021) and potential genetic adaptation by strong selection through environmental conditions at this age (Donohue et al., 2010; Petit & Hampe, 2006). We consider successful establishment and juvenile growth as crucial prerequisites for longer-term natural adaptive processes.

2.3 | Statistical analysis

We (1) characterized phenotypic variation at different intraspecific levels (i.e. within the species among populations, within populations among mother trees and within the progeny of single mother trees) of European beech by displaying the trait values for each individual offspring. We then (2) tested for differences in variation among the intraspecific levels by applying Levene's tests at the population and mother tree levels. We (3) analysed the proportion of trait variation contributed by each intraspecific level and the environment (represented by the different transplantation sites) using linear mixed models following the methods of Albert et al. (2010) and Rosas et al. (2019). We set up one model per trait with all sources of variation (environments, populations, mother trees and residuals – the latter accounting for the variation within the progeny of each mother tree) as nested random factors and the intercept as the only fixed effect, yielding the explained variance per source of variation.

Additionally, we (4) analysed the relative importance of different levels of intraspecific organization and the environment on height growth over the 3 years of the experiment using a linear model with fixed effects 'population', 'mother tree' and 'environment' (the different transplantation sites). The height measurements of the seedlings were averaged for each cage per site. Finally, we also (5) tested for genetic differences in mean trait expression of the populations and genotype × environment interactions in linear mixed models (SLA, leaf unfolding, height growth) and generalized linear mixed models (survival rate). The nesting of the mother trees within the population was introduced as random effects to account for the nested structure in the experimental design. Homoscedasticity and normal distribution of the residuals were checked visually in residuals-versus-fitted and qq-plots. For the variance analysis (4) leaf unfolding and survival rate did not fulfil the parametric assumptions, therefore they were rank-transformed, rendering the analysis a non-parametric model. Specific leaf area and plant height did not require transformations. For the test of genetic differences among populations (5), the traits height growth and leaf unfolding were rank-transformed. A significant population x environment interaction would indicate differential responses of specific populations in specific environments. The analyses were conducted in R 3.5.3 (R Core Team, 2019) and the additional packages lmerTest v.3.0 (Kuznetsova et al., 2017), ggplot2 v.3.3.2 (Wickham, 2009) and car v.3.0 (Fox & Weisberg, 2019).
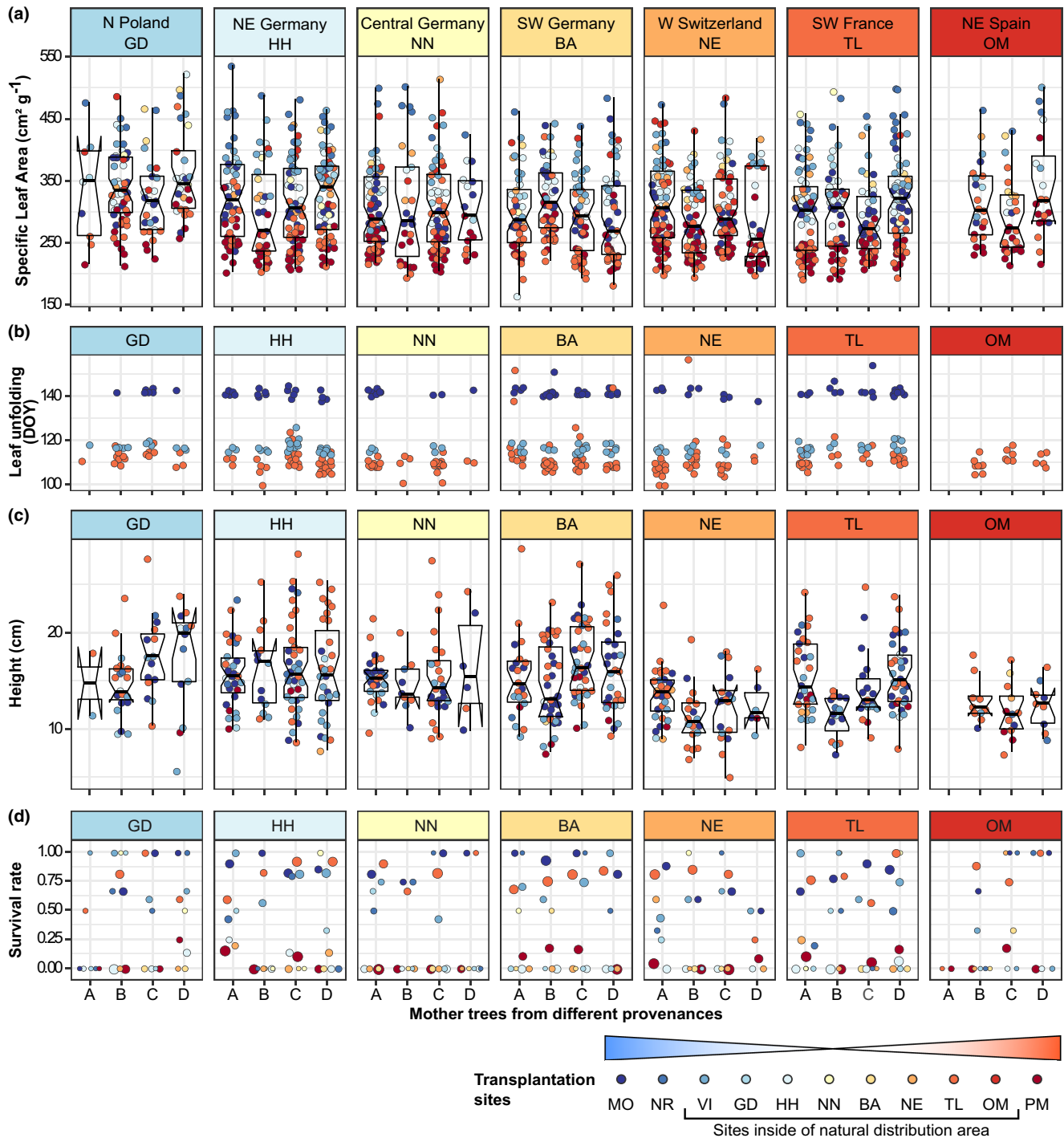
FIGURE 1 Phenotypic variation within the offspring of each mother tree. Phenotypic variation of beech seedlings stemming from four mother trees per source population and transplanted to eleven sites representing different environmental conditions for the functional traits specific leaf area (SLA) (a) and day of leaf unfolding (b) and the fitness traits height (c) and survival rate (d) after three growing seasons. Each panel represents one population, organized from the cold Northeast of Europe (left) to the warm Southwest (right). Each panel contains four dot plots representing four mother trees, that is half-sib families (a–d), summarized by a boxplot showing the median and quartiles with the whiskers extending to 1.5 inter-quartile distance. If the notches of two boxplots do not overlap this is 'strong evidence' that the two medians differ (Chambers, 2018). Each dot represents one seedling, except for the trait survival rate for which the size of a single dot depicts the number of seedlings per mother tree per environment that were still alive after 3 years (min: 1, max: 22). All dots are coloured according to the eleven environments the seeds were transplanted to. Blue colours represent transplantation to the cold north-eastern European sites, red colours represent the warm south-western European sites. The legend also indicates the transplantation sites outside the current species distribution range beyond the cold edge (MO in Central Sweden, NR in Eastern Poland) and the dry edge (PM in Eastern Spain).

3 | RESULTS

3.1 | High phenotypic variation among individuals

The progeny of each single mother tree, regardless of their source population, exhibited consistent variation in the functional trait specific leaf area (SLA = leaf area/leaf dry weight) across the different environments (Figure 1, Levene's test for homogeneity of variances: $p = 0.57$ among all mother trees and $p = 0.51$ among all populations). This suggests that the full phenotypic variation of the whole species (comprising all seven populations and 27 mother trees) was already expressed in the progeny of each mother tree. The majority of the variance in SLA was attributed to the environment (63.8%, Figure 2, Table S3), followed by the mother trees progeny (30.2%). Variance within populations (i.e. among the mother trees) (4.5%) and among the populations (1.5%) was negligible.

Likewise, variation in leaf phenology across the environmental conditions of the transplantation sites showed no significant differences within populations (i.e. among the mother trees) or among the populations (Figure 1; Levene's test for homogeneity of variances: $p = 0.49$ among all mother trees and $p = 0.78$ among all populations). Similar differences in leaf-out dates of 4 weeks between transplantation sites demonstrate the strong and equal phenotypic variation within the offspring of each single mother tree to environmental differences, irrespective of the populations' origin. The environment explained the majority of the variance in leaf unfolding, emphasizing the presumably high phenotypic plasticity in this trait (80.7%, Figure 2, Table S3). Inter-individual variation within the progeny of each mother tree contributed 16.1% to the overall variation in leaf unfolding. Less than one percent of the variation was found within

populations, that is among mother trees, or within the species, that is among the populations.

Thus, phenotypic variation within the progeny of each mother tree was as high as the variation at the mother tree and, even, the population level. Considering the large environmental gradient covered here (mean annual temperature 4–11°C) and the strong phenotypic variation in the studied traits (SLA site averages: 248.2–447.8 cm^2/g; about 4 weeks difference in leaf unfolding), it is remarkable that the observed range of phenotypic variation was already expressed in the progeny of each single mother tree. In summary, the offspring of each individual mother tree contains a similar capacity to adjust the observed functional traits to changing environmental conditions as the whole species.

3.2 | No signs of genetic differences for any trait – Annual growth performance converges over time

Height growth mostly varied among the progeny of each single mother tree and strikingly little at higher levels of intraspecific organization and across environments (Figures 1 and 2). The majority of growth variation in the first growing season was attributed to the progeny of the individual mother trees (70.0%) and this share increased for the subsequent 2 years of growth (80.2%; 79.4%; Figure 2, Table S3). Variation attributed to the population and mother tree levels decreased considerably over the 3 years, while the importance of environmental conditions (i.e. the effect of the transplantation sites) increased over time (Table 1). The initial seedling growth also significantly correlated with the mother trees' average seed weight ($f = 77.2$, $p < 0.001$, marginal $r^2 = 0.26$, Figure S1),
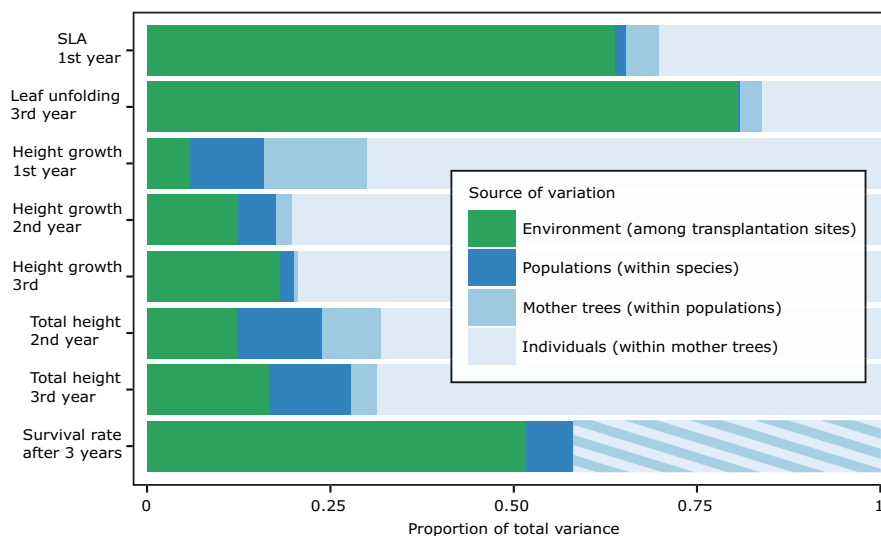

FIGURE 2 Partitioning of the variance explained by the three level of genetic organization and the environment. Sources of variation in the functional traits specific leaf area (SLA = leaf area/leaf dry weight) and leaf unfolding date, and fitness-related traits according to a variance partitioning based on mixed models with only random effects (Albert et al., 2010). The height increment of the first year equals the total height of the first year. Survival rate is calculated over the offspring of each mother tree and, hence, results in just one number per mother tree and transplantation site. The analysis can, therefore, not differentiate between the variation of mother trees and individuals (displayed in stripes of both categories).

Factor	2017		2018		2019	
	F value	*p* value	*F* value	*p* value	*F* value	*p* value
Populations	40.3	**<0.001**	4.2	**<0.001**	1.1	0.350
Mother trees	9.3	**<0.001**	1.5	0.085	1.3	0.162
Environment	11.4	**<0.001**	12.9	**<0.001**	17.4	**<0.001**

TABLE 1 Effect of populations and mother trees on the seedlings' height growth over time.

Note: Provided are ANOVA results based on linear models with populations and mother trees together with environmental effects as fixed effects. Significant ($p < 0.05$) values are in bold.

Trait	Factor	DF	*F* value	*p* value
Specific leaf area	Population	6	0.9	0.499
	Environment	9	220.2	**<0.001**
	Population × environment	53	1.3	0.054
Leaf unfolding	Population	6	0.3	0.934
	Environment	2	410.4	**<0.001**
	Population × environment	10	0.9	0.526
Growth 2019	Population	6	0.7	0.620
	Environment	2	30.9	**<0.001**
	Population × environment	12	1.0	0.486
Survival until 2019	Population	6	2.3	0.063
	Environment	8	40.3	**<0.001**
	Population × environment	48	0.6	0.066

TABLE 2 The seedlings did not show significant genetic (main population effect) or genotype by environment interaction (population x environment interactions) in the functional traits SLA and leaf unfolding as well as in the fitness traits survival and growth.

Note: Provided are ANOVA results based on linear mixed models (SLA, leaf unfolding, growth) and generalized linear mixed models (survival) with populations and environment as fixed effects and individual mother trees nested within the populations as random effects. Significant ($p < 0.05$) values are in bold.

suggesting that maternal seed provisioning influenced the first-year fitness of beech seedlings. In summary, the results highlight a remarkably homogeneous growth response of diverse beech origins to various environments after initial and temporary maternal effects.

No significant genotype (population) effect or genotype-environment interaction was detected in fitness (growth, survival rate) and functional traits (SLA, phenology) (Table 2).

The seedlings were affected by Europe-wide droughts in 2018 and 2019, leading to high mortality at some experimental sites (Figure 1, Table S2). However, the beech populations did not exhibit significant differences in their survival rate (Table 2). In fact, only 6.4% of the total variation in seedling survival was attributed to the populations (Figure 2, Table S3).

4 | DISCUSSION

4.1 | High phenotypic variation within the progeny of each mother tree

Our results reveal a remarkably high phenotypic variation in key functional traits of a major forest tree species at the individual scale, that is in the offspring of each mother tree, rather than at higher intraspecific levels of organization such as populations. This phenomenon appears to be independent of the trees geographic and environmental origin. The prevalence of phenotypic plasticity over genetic adaptation as the main source of variation in key functional traits of European beech is supported by other recent studies (Gárate-Escamilla et al., 2019; Muffler et al., 2021). However, local genetic adaptation has been reported for continental (Aranda et al., 2015; Gárate-Escamilla et al., 2019) and even regional scales (Frank et al., 2017) and some provenance trials indicate small differences in leaf traits among beech populations (e.g. Sánchez-Gómez et al., 2013). Additionally, for other traits, such as frost tolerance or hydraulic architecture, small indications of local differences have been reported (Aranda et al., 2015; Hofmann et al., 2015; Kreyling et al., 2014). Yet, many observed phenotypic and genetic differences lack consistent geographic or environment-related patterns, which indicates that both neutral genetic drift in small populations in glacial refugia (de Lafontaine et al., 2013) and directed genetic selection towards local adaptation might be drivers of the reported differences among populations. Moreover, previous studies often focused on phenotypic differences by comparing population means. While providing valuable insights into large-scale differences, this approach inevitably masks inter-individual variation, that is variation at the level where

selective processes are ultimately effective (Forsman, 2015; Forsman & Wennersten, 2016; Nussey et al., 2007). A few existing studies have already considered intra-populational trait variation in common garden experiments (Aranda et al., 2017; Bresson et al., 2011). While these studies do not include all intraspecific levels of our study, they do highlight that intra-populational variation is systematically higher than inter-populational variation. Our study even suggests that the lowest intraspecific level, that is the variation within offspring of each mother tree is the main source of variation in our target species. Ultimately, the high phenotypic variation found within the progeny of each mother tree (Figures 1 and 2) and the absence of significant genetic differences in mean trait expression (Table 2) hint at a high capacity for acclimating to environmental changes at any given local tree stand, that is to a high potential for population persistence.

Yet, it is important to note that the studied traits might not be the only ones involved in the response to climate variation. Rooting intensity and depth, as well as frost tolerance, for instance, are likely crucial for resisting drought and temperature variability, respectively, although they are not often quantified in studies requiring large sample sizes. High phenotypic plasticity in functional traits is supposed to be beneficial in temporally variable environments and is likely to enhance species' persistence under rapidly changing climatic conditions (Chevin & Hoffman, 2017; Gárate-Escamilla et al., 2019). Nevertheless, it is also intensively discussed whether high phenotypic plasticity of functional traits might either delay or facilitate genetic adaptation by buffering selective processes (Fox et al., 2019; Oostra et al., 2018; Reed et al., 2011). Still, it has been demonstrated that directional and, for trees, surprisingly quick natural selection due to warming is also possible in long-lived temperate tree species (Jump et al., 2006).

4.2 | Initial differences in growth diminish over time

Overall, the growth performance and survival of the seedlings highlight a remarkably homogeneous response across different beech populations to highly contrasting environments (from Spain to Sweden and Poland). This consistency follows the initial and transient maternal effects due to seed provisioning or other maternal environmental effects (e.g. epigenetics, see Donohue, 2009 and Rico et al., 2014). In contrast to a few other European beech provenance trials (e.g. Robson et al., 2013; Wang et al., 2021), we found no significant differences in growth increment among the populations after 3 years of experiment and no sign of significant genetic differences (all main effects of population and interactions between transplantation site and population being non-significant in Table 2). This suggests that, when excluding the potential effect of maternal effects, these tested populations exhibited equal fitness along our extensive environmental gradient and at an early recruiting stage. The alignment of growth also contradicts a presence of strong competition effects within our experimental timeframe, as we would

have otherwise expected increasing differences in height growth. However, intraspecific competition may become a concern when experimental set ups like ours are excessively prolonged.

At some sites, droughts in 2018 and 2019 had a significant impact on the seedlings, leading to high mortality rates. While these selective events could have accentuated the fitness advantages of seed origins presumably adapted to drought, we did not observe any differences in the survival rate among the tested populations (again all interactions between transplantation site and population being non-significant). This lack of differentiation does not necessarily negate the potential existence of drought adaptations and fitness advantages in some populations of the species. It is important to note, that we did not study populations from the southeast of the species' distribution range (Balkan) and only covered the seedling stage. Robust estimations of fitness throughout the extensive life cycle of trees require long-term provenance trials with known family structures of the individual trees. Nonetheless, our experiment sheds light on a crucial stage of selection, namely, seedling growth and survival, which is relevant for population dynamics (Jackson et al., 2009).

4.3 | Potential implications for species persistence and management

In the light of recent droughts in 2018 and 2019 and anticipated changes in environmental conditions, there is growing concern regarding the future of beech forests in Western and Central Europe (Engel et al., 2023; Gessler et al., 2007; Saltré et al., 2015). Consequently, the necessity of passive and/or active adaptive forest management practices has been a topic of debate (Jandl et al., 2019; Lindner et al., 2010). Assisted migration, which involves the organized transfer of presumably pre-adapted genotypes or species from warmer and drier origins to colder and wetter regions with the aim of growing trees better adapted to future climatic conditions, has been recently advocated in forestry (Bolte et al., 2009; Gömöry et al., 2020) and species conservation (Hoegh-Guldberg et al., 2008; Peterson & Bode, 2021; Weeks et al., 2011). However, the transfer of allochthonous genetic material may also lead to unintended long-term consequences, such as outcrossing depressions (Whitlock et al., 2013), the emergence of undesirable genetic properties (Benito-Garzón et al., 2013; Weeks et al., 2011) or uncertainty about environmental conditions (Pachauri et al., 2014) to select the genetic material for.

In light of the extensive phenotypic variation observed within the juvenile offspring of individual mother trees in our study, we conclude that autochthonous European beech populations might already possess substantial potential for phenotypic adjustments. This potential is apparent even in the face of dramatic climate change, exemplified by our wide climatic gradient of transplantation sites (7°C difference in mean annual temperature between the warmest and coldest transplantation site). We found consistently high phenotypic variation within the juvenile offspring of individual mother trees,

while the variance among populations was minimal, as indicated by the lack of significant main and interaction effects of population on mean trait expression (Table 2). We assume that the observed high phenotypic variation, provided that this pattern persists in later life stages, might be advantageous for medium-term population persistence under changing climatic conditions. It ensures the presence of well-performing individuals in the progeny of every mother tree, adjusting to various environmental conditions encountered in our transplantation sites.

When assessing species persistence, however, it is also crucial to consider shifts in interspecific competition. For example, phenological studies at the south-western distribution edge of our species suggest that climatic changes, such as the advancement of leaf flush and prolonged vegetative periods, may favour competitors like *Quercus petraea* over beech (Vitasse et al., 2011).

Phenotypic variation is an obligatory prerequisite but not a direct proof of (genetic) adaptive potential. High phenotypic variation across all families is a precondition for adaptive and selective processes. Further studies with known family structures are needed to explore the combined potential of genetic adaptation and phenotypic plasticity in our target species and other forest trees throughout their full life cycle.

Taking into account the substantial number of seeds produced by each mature tree during its lifetime and the positive relationship between growth and survival found in our study, our findings suggest potential for phenotypic acclimatization even in the face of significant climate change. Therefore, the potential of natural regeneration in Adaptive Forest Management (AFM; Jandl et al., 2019) warrants further exploration also in mature trees. To derive well-founded implications for forest management, we recommend including additional key functional and fitness-related traits and focusing on longer-term effects beyond the seedling stage. Nevertheless, high phenotypic variation during the seedling stage and successful establishment, as shown in our study, are prerequisites for any natural, longer-term adaptive process.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available in the supplementary material of this article. All analyses were carried out with the functions and additional packages specified in the methods section in the free and open-source environment R.

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BIOSKETCH

Jonas Schmeddes is an ecologist interested in population dynamics in forest ecosystems and the adaptive potential of trees. In his PhD project he uses a European-wide transplantation experiment to investigate the phenotypic plasticity and genetic adaptation within and among populations of European beech (*Fagus sylvatica* L.). His aim is to study the potential and limits of the species to respond to changing environmental conditions and the consequences for the species' persistence in future.

SUPPORTING INFORMATION

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