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Integrating multi-trait selection and climate associations to identify climate-resilient seed sources: insights from a beech provenance trial over four decades

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Research Article

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Posted Date: August 5th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-10592471/v1

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Additional Declarations: The authors declare no competing interests.

Integrating multi-trait selection and climate associations to identify climate-resilient seed sources: insights from a beech provenance trial over four decades

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Abstract:

European beech (*Fagus sylvatica* L.) is a dominant temperate forest species, yet its adaptive potential under changing climates remains uncertain. We evaluated 30 provenances of *F. sylvatica* and *F. orientalis* in the long-term provenance trial Malente (northern Germany), established in 1986, monitoring basal area, survival, phenology, and stem form over four decades. Mixed linear models quantified provenance effects, and best linear unbiased predictors (BLUPs) were integrated into a multi-trait selection framework using the genotype-ideotype distance index (MGIDI).

Significant provenance differentiation was observed for basal area (up to 55% of variance), bud burst phenology (up to 75%), and survival (up to 55%), whereas stem form showed comparatively weak genetic control (up to 20%). Multi-trait selection identified six superior provenances (Schmallenberg 1, Ebrach 4, Sovaenger, Reichensachsen, Seesen 1, and Fuerstenberg), combining high productivity, stable survival, and acceptable stem form. Variation in performance was not explained by Euclidean climatic distance to the trial, despite the clear separation of provenance climatic clusters. Climatic variables regressions however, revealed highly significant control of performance. MGIDI was primarily associated with mean coldest month temperature (MCMT, R^2 = 0.64) and growing degree days above 5 °C (GDD5, R^2 = 0.40), indicating superior multi-trait performance of provenances originating from colder climates with lower heat accumulation. Basal area showed similarly strong associations with MCMT (R^2 = 0.56) and GDD5 (R^2 = 0.44), while survival was strongly related to MCMT (R^2 = 0.63) and climatic continentality (TD, R^2 = 0.43). Stem form exhibited generally weak climatic associations, with only MCMT showing a significant relationship (R^2 = 0.18).

These results highlight substantial genetic differentiation among beech provenances and demonstrate that combining multi-trait selection with trait and specific climatic variables analyses enables identification of climatically adapted provenances with superior productivity and survival. The findings provide practical guidance for breeding, conservation, and climate-resilient forestry strategies.

Keywords: *Fagus sylvatica*, provenance differentiation, multi-trait selection, MGIDI, climatic drivers, climate adaptation

1 INTRODUCTION

Climate change is increasingly reshaping the functioning, stability and distribution of forest ecosystems worldwide. Across Europe, rising temperatures, altered precipitation regimes and an increasing frequency of extreme weather events, particularly prolonged heatwaves and droughts, have already caused severe impacts on forest vitality and productivity (Lindner *et al.*, 2010; Dey *et al.*, 2019; Vacek *et al.*, 2023; Intergovernmental Panel on Climate Change (IPCC), 2023; Knutzen *et al.*, 2025). The summer of 2024 was reported as the hottest on record both globally and across Europe (European Environment Agency, 2025), highlighting the accelerating trajectory of climatic change. Among the most important drivers of forest degradation, drought plays a central role worldwide (Kogan, 1997; Tao *et al.*, 2022; Quiroga-González *et al.*, 2025; Han *et al.*, 2025). As climatic conditions continue to shift, many species (Muluneh, 2021), including forest trees (Buras & Menzel, 2019; Chakraborty *et al.*, 2021; Mauri *et al.*, 2022) are undergoing range contractions or shifts toward higher elevations and latitudes, long-lived forest trees however, are often unable to track suitable habitats at the pace required due to landscape fragmentation and anthropogenic barriers (McLachlan *et al.*, 2005; Ortiz *et al.*, 2021). These developments underline the need for adaptive forest management strategies that maintain ecosystem functioning, biodiversity and carbon sequestration under future climates (Lindner *et al.*, 2010; Berrang-Ford *et al.*, 2015; Demant *et al.*, 2019).

European beech (*Fagus sylvatica* L.), is the dominant broadleaved tree species across large parts of temperate Europe and one of the most ecologically and economically important forest trees in Central Europe (Leuschner, 1998; Leuschner & Ellenberg, 2017; Leuschner *et al.*, 2023). Its natural range extends from the Iberian Peninsula and southern Italy to southern Scandinavia, and from western Europe to the Carpathian and Balkan mountain systems (Eaton *et al.*, 2016; Kasper, 2023). Within this broad distribution, beech occupies lowland environments in the north and montane zones in the south (Alexandrov *et al.*, 2011). Although highly competitive and ecologically versatile with respect to soil conditions, the species is generally associated with humid temperate climates characterized by mild winters and sufficient summer moisture (Ellenberg, 1988; Bolte *et al.*, 2007). Consequently, prolonged summer drought and high temperatures represent key limiting factors at its xeric distribution margins (Czúcz *et al.*, 2011).

Evidence increasingly suggests that European beech is under growing climatic stress not only at its southern range limits but also within its central distribution area. Growth declines linked to recent warming and recurrent drought episodes have been reported across Central Europe (Knutzen *et al.*, 2017; Martinez del Castillo *et al.*, 2022; Diers *et al.*, 2023). The extreme drought and heat events of 2018 and 2019, in particular, triggered widespread canopy decline, early leaf senescence and partial dieback in mature stands (NW-FVA, 2019; Arend *et al.*, 2022; Frei *et al.*, 2022; Rukh *et al.*, 2023). In southern Europe, repeated drought stress has further been associated with beech decline and increasing replacement by more drought-tolerant competitive species (Mazza *et al.*, 2024). Together, these trends raise concerns about the long-term stability and silvicultural reliability of European beech under future climate conditions.

Against this background, Oriental beech (*Fagus orientalis* Lipsky) has gained increasing attention as a complementary genetic resource for climate-adaptive forestry. Its natural distribution spans southeastern Europe, Asia Minor and the Caucasus, from the Rhodope Mountains to northern Iran (Kandemir & Kaya, 2009; Felbermeier & Mohadjer, 2014). Compared with European beech, it is typically associated with warmer, drier and more continental climates and is therefore considered more drought- and heat-tolerant (Felbermeier & Mohadjer, 2014; Elzami, 2018; Avila *et al.*, 2021). Despite these differences, both taxa share key ecological traits, including shade tolerance, strong competitive ability and similar silvicultural properties (Sagheb-Talebi *et al.*, 2014; Willner *et al.*, 2017). Experimental evidence from cultivation trials indicates high survival and stable growth performance of Oriental beech even under drought-prone conditions and during extreme climatic years such as 2018 and 2020 (Frischbier *et al.*, 2019, 2021). As a result, the use of Oriental beech in Central Europe is increasingly discussed within the framework of assisted migration and assisted gene flow as proactive adaptation

strategies to climate change (Aitken & Whitlock, 2013; Aitken & Bemmels, 2016) and considered as a potential substitute or complement to European beech on dry sites (Avila *et al.*, 2021; Liesebach *et al*., 2021).

These approaches aim to enhance adaptive capacity by introducing pre-adapted genetic material suited to projected future climates. Genetic and phylogeographic evidence further suggests historical and ongoing gene flow between both taxa in their contact zones (Papageorgiou *et al.*, 2008, 2014; Müller *et al.*, 2019; Budde *et al.*, 2023), and that European beech may have originated from ancestral Oriental beech lineages during the Quaternary (Magri *et al.*, 2006; Gömöry *et al.*, 2018). On this basis, Oriental beech may represent assisted gene flow within a closely related species complex, potentially enhancing adaptive genetic diversity in European beech (Kurz *et al.*, 2023).

Despite growing interest, substantial uncertainties remain regarding adaptive differentiation, growth performance and phenotypic stability across provenances of both species. Local populations are not necessarily optimally adapted to future climates, and significant genetic variation among provenances has repeatedly been demonstrated (Alberto *et al.*, 2013; Rau *et al.*, 2015; Boshier *et al.*, 2015). Accordingly, the identification of suitable provenances has become a central objective in forest genetics and silviculture. Provenance trials remain the most powerful empirical approach for quantifying adaptive variation, phenotypic plasticity and long-term performance under contrasting environments (Mátyás *et al.*, 2009; Robson *et al.*, 2018). However, long-term trials combining European and Oriental beech are still rare, despite their particular value for evaluating climate adaptation and assisted migration strategies.

Recent methodological developments in multi-trait selection, such as the Multi-trait Genotype-Ideotype Distance Index (MGIDI), now allow simultaneous assessment of adaptive, productive and qualitative traits (Olivoto *et al.*, 2019; Olivoto & Lúcio, 2020; Olivoto & Nardino, 2021). Although their use in forest tree research remains limited, application in European beech has demonstrated its potential for integrated provenance evaluation (Liepe *et al.*, 2024).

In this context, we focus on a long-term provenance trial established in Malente (northern Germany), which represents a rare experimental system including both European and Oriental beech provenances from a wide climatic gradient. This trial provides a unique opportunity to assess adaptive differentiation and growth performance under northern Central European conditions and to evaluate the suitability of different provenances under ongoing climate change. Recent multisite analyses have further indicated relatively stable provenance rankings across environments in European beech (Liepe *et al.*, 2024), reinforcing the relevance of well-designed single-site trials for detecting consistent adaptive patterns.

Here, we evaluated long-term provenance differentiation in European and Oriental beech using growth, productivity, survival, phenology, and stem form traits measured in the Malente provenance trial. Basal area, survival, and stem form were respectively included as indicators of productivity, adaptive performance, and timber quality. To integrate overall provenance performance across traits, we applied the multi-trait genotype-ideotype distance index (MGIDI). The objectives of this study were to (1) quantify provenance differentiation across major growth, survival, phenological, and structural traits, (2) identify superior provenances through multi-trait selection, and (3) examine whether provenance performance is related to climatic conditions at the site of origin and reflects specific patterns of climate-driven adaptive differentiation.

2 Materials and Methods

2.1 Study Site and Plant Material

The Malente provenance trial (Figure 1) was established in 1986 in northern Germany (54.19° N, 10.59° E). The trial included two beech species: *Fagus sylvatica* (41 provenances) and *F. orientalis* (8 provenances). Provenances are indicated by colored shapes in Figure 1, detailed provenance information is provided in Table S1. Geographic

provenance information was spatially referenced using latitude and longitude data provided in the provenance database. Coordinates were projected and overlaid with a spatial climate region shapefile of Germany to assign German provenances (DE_810xx) to their corresponding climatic regions (Figure S1). This spatial join was performed in R using the sf package, allowing classification of provenances along a gradient from oceanic to more continental climate conditions. The resulting regional assignments were used for visualization and interpretation of geographic origin (Figure 1). Seedlings aged 1 to 3 years were planted in an incomplete block design with up to three replicates per provenance, with each plot of 10 × 10 m being initially planted with 100 seedlings (spacing 1.0 x 0.5 m).

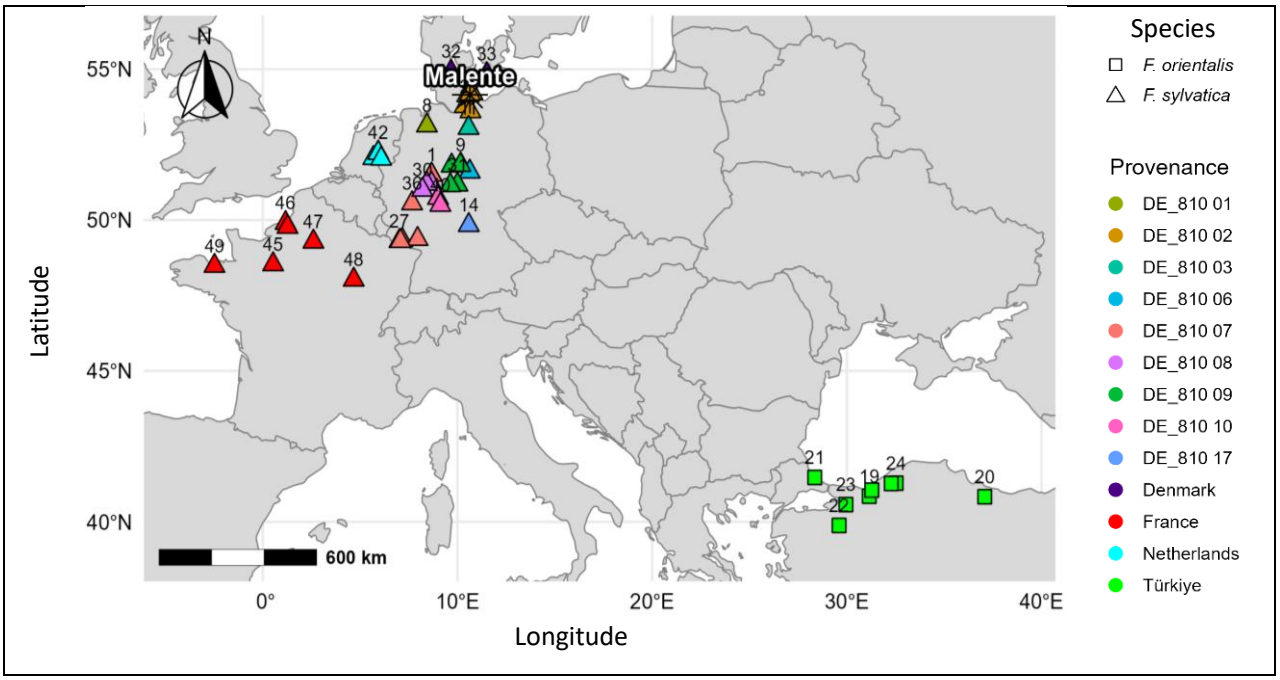


Figure 1. Geographic origin of *Fagus sylvatica* and *F. orientalis* provenances planted in the Malente provenance trial. Colors represent individual provenances, with German (DE_810xx) grouped by region of provenance, representing contrasting climatic regions from oceanic to more continental environments. Shapes indicate species (*F. sylvatica* triangles; *F. orientalis* squares). The Malente site is marked with an asterisk and labelled. Note: The country name Türkiye follows the official United Nations nomenclature (formerly Turkey).

2.2 Field Measurements and Trait Derivation

Trees were monitored over several decades for growth, phenology, structural traits, and survival:

- Tree growth: Tree height was measured in 1988, 1991, 1994, 1998, and 2013. Diameter at breast height (DBH) was measured in 2004, 2008, 2013, 2020, and 2024.
- Basal area: Basal area (m^2) per tree was determined from DBH for all measurement years using the formula $BA = \frac{\pi}{4} * DBH^2$, then plot-level sums in m^2/ha were derived.
- Phenology: Bud burst was recorded once per spring on 9/5/1989, 4/5/1990, 14-15/5/1991 and 24/4/2000. Scores (0 to 5) were converted to a binary trait (folded/unfolded), with scores 0 to 2 classified as folded and 3 to 5 as unfolded. The percentage of unfolded trees per plot was calculated, reflecting provenance differences in spring phenology.
- Stem form and straightness: Assessed in 1998 and 2013. In 1998, stem form and branching type were classified using categorical codes ranging from normal (0) to strong deviation (3). Trees were classified as having acceptable stem form when both stem form and branching were scored as normal or showed only slight deviations (combinations 0/0, 0/1, or 1/1). In 2013, stem form was rated on a four-class

quality scale (1 = straight, 2 = slight to moderate bends, 3 = strong bends, 4 = no straight stem); trees rated with 1 or 2 were considered acceptable. The percentage of trees with acceptable stem form was calculated for each plot.

- Dominant trees: Within each plot, the mean diameter at breast height (DBH) of the top ten largest trees was identified for each measurement year to evaluate growth of the dominant trees.
- Survival: Survival was recorded at each measurement year and summarized per plot as the percentage of surviving trees.

Prior to analysis, the dataset was checked for completeness and consistency. Provenances represented by a single replicate were excluded, leaving 30 provenances from the original 49 for subsequent analyses. The distribution of all traits, including growth, basal area, structural traits, phenology, and survival, was inspected using quantile-quantile plots to ensure suitability for multi-trait evaluation.

2.3 Statistical Analysis

2.3.1 Quantification of Provenance and Random Effects

Phenotypic data were analyzed using mixed linear models to account for genetic and experimental design effects. For each trait, provenance (genotype) and replicate effects were fitted using the following model:

$$Y_{ij} = \mu + G_i + B_j + e_{ij}$$

where Y_{ij} is the phenotypic observation of the i-th provenance in the j-th replicate, μ is the overall mean, G_i is the random effect of provenance, B_j is the fixed block effect, and e_{ij} is the residual error. Models were fitted using restricted maximum likelihood (REML) as implemented in the R package *metan* (Olivoto & Lúcio, 2020).

From these models, best linear unbiased predictors (BLUPs) for each provenance were extracted and used as input for all downstream analyses. Model accuracy and assumptions were evaluated through diagnostic checks and likelihood-based tests provided by the same framework.

To investigate relationships among traits, genetic correlations, phenotypic correlations, and partial correlations were obtained from the fitted mixed model. Genetic correlations were derived from the genetic covariance matrix, while phenotypic correlations were obtained from the phenotypic covariance matrix. Partial correlations were derived from the model-based precision matrix and represent conditional associations between pairs of traits after accounting for all other traits. This approach allowed characterization of the multivariate trait structure among growth, productivity, structural, and survival traits. Results were visualized using correlation heatmaps to highlight patterns of trait interdependence.

2.3.2 Multi-trait Selection

For multi-trait selection, a subset of traits representing economically and silviculturally relevant performance was selected: basal area (as a proxy for productivity), stem form (tree quality), and survival (stand stability). All of these traits were assessed simultaneously in 2013, which represented the most complete and balanced measurement campaign, corresponding to approximately 27 years after establishment, when trees had reached early maturity. The spatial block design of the trial, including provenance allocation and tree diameter distribution at the 2013 assessment, is shown in Figure S2. Importantly, this was prior to a later thinning intervention that occurred in a non-systematic and spatially heterogeneous manner.

Multi-trait selection was performed using the multi-trait genotype-ideotype distance index (MGIDI) after Olivoto and Nardino (2021) implemented in the R package *metan*. The MGIDI is defined as:

$$MGIDI_i = \left[\Sigma_{j=1}^{f} (\gamma_{ij} - \gamma_j)^2\right]^{0.5}$$

where $MGIDI_i$ is the multi-trait genotype-ideotype distance index for the i-th provenance, γ_{ij} is the score of the i-th provenance in the j-th factor, and γ_j is the j-th score of the ideotype.

The procedure consists of four steps: (i) rescaling BLUPs to a 0-100 range to account for trait directionality, (ii) factor analysis with varimax rotation to reduce dimensionality and account for correlation structure among traits, (iii) definition of an ideotype with maximum values for all selected traits, and (iv) computation of the Euclidean distance between each provenance and the ideotype in the reduced factor space. Since the goal of tree improvement with beech is the selection for increasing adaptability and growth rates, we have designed the ideotype as having a higher survival rate, a greater basal area and better stem quality. Lower MGIDI values indicate higher similarity to the ideotype and thus superior multi-trait performance. A selection intensity of 20% was applied.

2.3.3 Associations with Climatic Environmental variables

Climatic data for the trial site as well as all provenances were obtained with the ClimateEU v5.01b software package, available at http://tinyurl.com/ClimateEU, based on methodology similar to Marchi *et al.* (2020) and Mahony *et al.* (2022). Climatic variables were downloaded using longitude, latitude, and elevation of the seed source locations in addition to the trial site. The obtained dataset covered annual climate records from 1950 to 2013 and included monthly temperature and precipitation variables, standard bioclimatic variables (BIOCLIM), and climatic moisture and heat indices.

Since the focus is to characterize the climatic conditions under which the source populations developed prior to seed collection and establishment of the trial, climatic variables for individual provenances were averaged across the 1951-1980 normal period. This period was selected because it represents the historical climatic conditions experienced by the parent stands before seed collection and therefore reflects the long-term selective environment underlying provenance adaptation. For the trial site however, the period selected to compute relevant environmental distances was averaged across 1986-2013 representing the observation period.

From the extracted and averaged climate dataset, a subset of biologically relevant climatic variables was selected or calculated for multivariate analyses based on their ecological importance for beech. The variables included climatic moisture deficit (CMD), annual heat-moisture index (AHM), annual precipitation (MAP), precipitation at growing season (PGS), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), growing degree days above 5 °C (GDD5), and continentality expressed as the temperature difference between the warmest and coldest month (TD). Together, these variables describe major climatic gradients related to water availability, drought stress, thermal adaptation, growing season length, and continental versus oceanic climatic conditions.

To summarize climatic differentiation among provenance origins, principal component analysis (PCA) was performed using standardized climatic variables. Prior to PCA, variables were centered and scaled to unit variance (mean = 0, variance = 1). Provenance scores along the principal climatic axes were extracted and used to visualize climatic relationships among provenances and species.

To quantify climatic transfer distance, Euclidean climatic distance (Perez-Navarro *et al.*, 2022; Villoutreix *et al.*, 2025) between each provenance and the Malente trial site was calculated in the reduced PCA space using the first two principal components:

$$D_i = \sqrt{(PC1_i - PC1_r)^2 + (PC2_i - PC2_r)^2}$$

where D_i represents the climatic distance of the i-th provenance to the reference trial site, and $PC1_r$ and $PC2_r$ denote the PCA coordinates of the Malente site. Lower values indicate greater climatic similarity between provenance origin and trial site, whereas larger values represent stronger climatic transfer distances.

Associations between provenance performance and climate were evaluated using regression models at two complementary levels. First, Euclidean climatic distance derived from PCA was used as an integrated measure of climatic transfer between provenance origin and the Malente trial site. Second, individual climatic variables were analyzed to identify specific environmental components associated with variation in performance. Analyses were based on best linear unbiased predictors (BLUPs) of the assessed traits.
All climatic analyses, multivariate procedures, regressions, and graphical visualizations were conducted in R using functions implemented in the packages tidyverse, ggplot2, psych, and stats.

3 RESULTS

3.1 Provenance Differentiation at the Malente Trial

Significant differences among provenances were detected for most assessed traits (Table 1). Provenance effects were particularly strong for juvenile height growth and bud burst phenology. Tree height assessed between 1988 and 1998 showed highly significant provenance differentiation ($p < 0.001$), with provenance accounting for 70-88% of the total phenotypic variance. Mean tree height increased from 64.4 cm in 1988 to 569.9 cm in 1998. Early differences among provenances may partly reflect variation in the initial age or size of seedlings at planting, which ranged from one to three years, in addition to genetic differences.
Basal area also showed significant provenance differentiation across all assessment years ($p < 0.001$). Provenance explained approximately 43-56% of the total variance, indicating moderate but consistent genetic differentiation in stand productivity. Mean basal area increased from 25.6 $m^2\ ha^{-1}$ in 2004 to 40.7 $m^2\ ha^{-1}$ in 2020 before declining to 33.4 $m^2\ ha^{-1}$ in 2024. The reduction after 2020 reflects a thinning intervention conducted between 2020 and 2024.

Significant provenance differences were detected for dominant trees throughout the observation period (2004–2024). The mean DBH of the ten largest trees per plot increased from 12.2 cm in 2004 to 19.8 cm in 2024, while provenance accounted for 26 to 34% of the total phenotypic variance. In contrast to other DBH based observation such as basal area or dominant trees, mean DBH itself showed little or no significant provenance differentiation. Provenance variance for DBH traits was close to zero in most assessment years, with residual variance accounting for nearly all observed variation.

Bud burst assessments conducted on 1989, 1990, and 1991 revealed strong and highly significant provenance effects ($p < 0.001$), with provenance explaining approximately 70-76% of the total variance. These results indicate substantial genetic differentiation in spring phenology among provenances, with *F. orientalis* generally flushing earlier than *F. sylvatica*. The relatively early assessment in April 2000, however, captured bud burst only in a few early-flushing *F. orientalis* individuals, while the majority of trees remained dormant, resulting in no detectable provenance effect. Overall, these observations highlight the strong genetic control of bud burst timing, despite limitations due to the single-date assessments.

Survival differed significantly among provenances throughout the observation period. Provenance explained approximately 31-55% of the phenotypic variance depending on assessment year, with the strongest differentiation observed during the early years of the trial. Mean survival declined continuously from 86.9% in 1988 to 12.7% in 2024.

Stem form showed comparatively weak provenance differentiation. No significant provenance effect was detected for stem form in 1998 or 2013, although the 2013 assessment indicated moderate phenotypic variation among plots.

Trait correlations revealed no significant relationship between bud burst and height growth, basal area, or survival for the measurement years corresponding to, or immediately following, the bud burst assessments (1989-1991 and 2000), suggesting no evidence of a growth/frost avoidance trade-off within the trial. In contrast,

bud burst timing showed a weak but positive association with stem form in 2013, indicating that phenological variation may be linked to structural quality rather than growth performance (Figure 2).

Table 1. Trait-specific variance components and genetic parameters across years

Trait	Year	LRT_P	V_P	V_R	MS B	Mean ± SD
Tree height	1988	79.73 ***	203.61 (87%)	28.29 (12%)	626.29 ***	64.42 ±14.31
	1991	71.85 ***	1194.12 (85%)	208.91 (14%)	2057.64 ***	171.38 ±43.8
	1994	55.96 ***	3071.65 (79%)	808.8 (20%)	4936.67 **	332.79 ±79.44
	1998	41 ***	5107.78 (70%)	2188.99 (29%)	5282.82 n.s.	569.91 ±124.1
	2013	0 n.s.	0 (0%)	12322.69 (100%)	54.07 n.s.	1621.4 ±131.5
Basal area	2004	22.48 ***	25.78 (55%)	20.36 (44%)	119.81 **	25.56 ±8.46
	2008	20.93 ***	45.42 (53%)	39.16 (46%)	181.56 *	31.35 ±11.06
	2013	17.53 ***	62.93 (49%)	64.82 (50%)	162.78 n.s.	34.77 ±13.51
	2020	17.43 ***	105.99 (48%)	111.18 (51%)	397.27 *	40.73 ±18.81
	2024	13.14 ***	84.52 (42%)	112.63 (57%)	1683.58 ***	33.44 ±16.37
Dominant trees	2004	5.91 *	0.52 (28%)	1.32 (71%)	12.41 ***	12.23 ±1.7
	2008	5.23 *	0.92 (26%)	2.52 (73%)	21.43 ***	14.81 ±2.31
	2013	6.64 **	1.39 (30%)	3.15 (69%)	22.76 **	16.83 ±2.62
	2020	8.44 **	2.04 (34%)	3.84 (65%)	24.4 **	19.95 ±3.14
	2024	5.52 *	2.05 (28%)	5.17 (71%)	63.1 ***	19.78 ±3.21
Diameter at breast height	2004	0.21 n.s.	0.03 (5%)	0.53 (94%)	3.83 **	8.16 ±0.85
	2008	0 n.s.	0.00024 (0.019%)	1.25078 (99%)	14.71 ***	10.47 ±1.35
	2013	0 n.s.	0 (0%)	1.9 (100%)	19.96 ***	12.7 ±1.91
	2020	0 n.s.	0 (0%)	4.13 (100%)	34.44 ***	16.74 ±2.45
	2024	0 n.s.	0.018 (0.26%)	6.906 (99%)	36.78 **	17.94 ±2.85
Bud phenology	1989	47.81 ***	0.03 (75%)	0.01 (24%)	0.23 ***	0.6 ±0.19
	1990	40.21 ***	0.0053 (69%)	0.0023 (30%)	0.03 ***	0.93 ±0.11
	1991	45.63 ***	0.05 (75%)	0.01 (24%)	0.18 ***	0.49 ±0.23
	2000	3.82 n.s.	0.0001 (24%)	0.0003 (75%)	0.004 ***	0.01 ±0.02
Stem form	1998	0 n.s.	0 (0%)	0.004 (100%)	0.07 ***	0.67 ±0.13
	2013	3.3 n.s.	0.009 (20%)	0.034 (79%)	0.12 *	0.38 ±0.2
Survival	1988	17.83 ***	0.006 (51%)	0.005 (48%)	0.03 **	0.86 ±0.14
	1991	19.26 ***	0.005 (53%)	0.005 (46%)	0.016 *	0.87 ±0.14
	1994	21.24 ***	0.007 (55%)	0.005 (44%)	0.016 n.s.	0.86 ±0.17
	2004	9.84 **	0.003 (36%)	0.006 (63%)	0.003 n.s.	0.44 ±0.13
	2008	10.53 **	0.003 (38%)	0.005 (61%)	0.01 n.s.	0.33 ±0.11
	2013	9.43 **	0.002 (35%)	0.004 (64%)	0.007 n.s.	0.25 ±0.1
	2020	11.12 ***	0.001 (38%)	0.003 (61%)	0.001 n.s.	0.17 ±0.09
	2024	7.31 **	0.001 (31%)	0.002 (68%)	0.022 ***	0.12 ±0.07

Variance components and genetic parameters for all measured traits across years. Columns: likelihood ratio test of provenance effects (LRTP), variance attributable to provenance (VP) and residual variance (VR), mean square of Block effects (MS B), and trait means with standard deviation (Mean ± SD). Variance components are presented as absolute values, with relative contributions in parentheses. Significance levels are indicated as *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and n.s. = not significant.



Figure 2. Phenology and its correlations with growth and quality traits. Growth traits include tree height measured in 1991, 1994 and 1998 (H91, H94, H98) and diameter at breast height measured in 2004, 2008 and 2013 (BHD04, BHD08, BHD13), survival is represented by assessments in 1988, 1991 and 1994 (Surv88, Surv91, Surv94), and quality-related trait is represented by stem form in 2013 (Form13). Phenology is represented by bud burst assessments in 1989, 1990 and 1991 abbreviated (Bud89, Bud90, Bud91). Above the diagonal, the figure displays correlation coefficients with color shading indicating their strength. Below the diagonal, stars denote the statistical significance of each correlation (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

3.2 Selection of Suitable Provenances

Applying a selection intensity of 20% to the 30 evaluated provenances, six were identified as most suitable based on the MGIDI index: Schmallenberg 1 (17), Ebrach 4 (14), Sovaenger (33), Reichensachsen (31), Seesen 1 (9), and Fuerstenberg (34) (Figure 3, Figure S1, S3). Schmallenberg 1 exhibited the lowest MGIDI value (0.266), indicating the highest combined performance and stability across traits, while Fuerstenberg had the highest MGIDI among the selected provenances (1.232) but still fell within the top 20% selection threshold.

Most selected German provenances clustered in the central upland regions (81008, 81009, 81017), whereas Sovaenger represented the northern provenance group from Denmark (Figure S1, S3). Overall, MGIDI-based selection identified provenances that combine superior multi-trait performance with stability, providing a focused set of candidates for reforestation, potential breeding and conservation strategies.

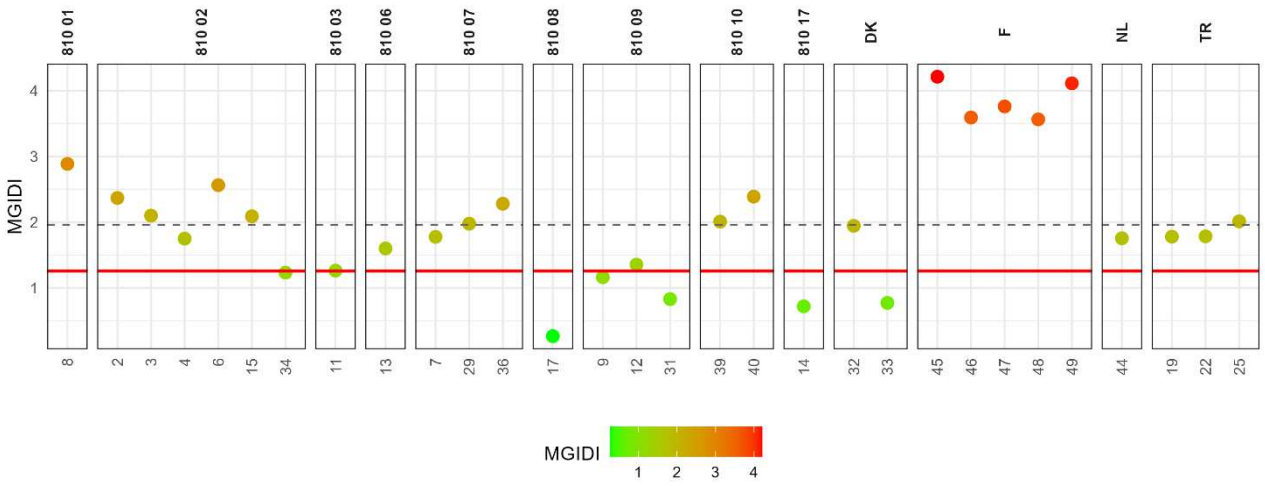


Figure 3. Multi-trait selection of beech provenances based on MGIDI index. MGIDI values for European and Oriental beech provenances grouped by origin. Each point represents a provenance, with German provenances grouped according to the regions of provenance (810xx codes) and non-German provenances grouped by country of origin (DK = Denmark, F = France, NL = Netherlands, TR = Türkyie). Lower MGIDI values indicate a lower distance to the defined ideotype, i.e. a higher overall multi-trait performance. The dashed line indicates the mean MGIDI, and the red line shows the 20% selection threshold. Colors represent MGIDI magnitude (green = superior performance, red = lower performance).

3.3 Provenance Clustering in Multivariate Climate Space

A principal component analysis (PCA) revealed distinct climatic differentiation among provenance origins. Turkish *F. orientalis* provenances clustered mainly in the lower-right quadrant and were associated with higher mean warmest month temperature (MWMT) and climatic moisture deficit (CMD). French provenances were distributed primarily in the upper-right quadrant and were associated with higher mean coldest month temperature (MCMT) and annual heat-moisture index (AHM). Several German *F. sylvatica* provenances from more continental inland regions (81006, 81009, 81010, and 81017), together with the Turkish provenances, were positioned along the positive PC2 axis in the direction of the temperature difference between the warmest and coldest month (TD), indicating an association with greater climatic continentality. Central European provenances occupied more intermediate positions, reflecting comparatively moderate climatic conditions (Figure 4).

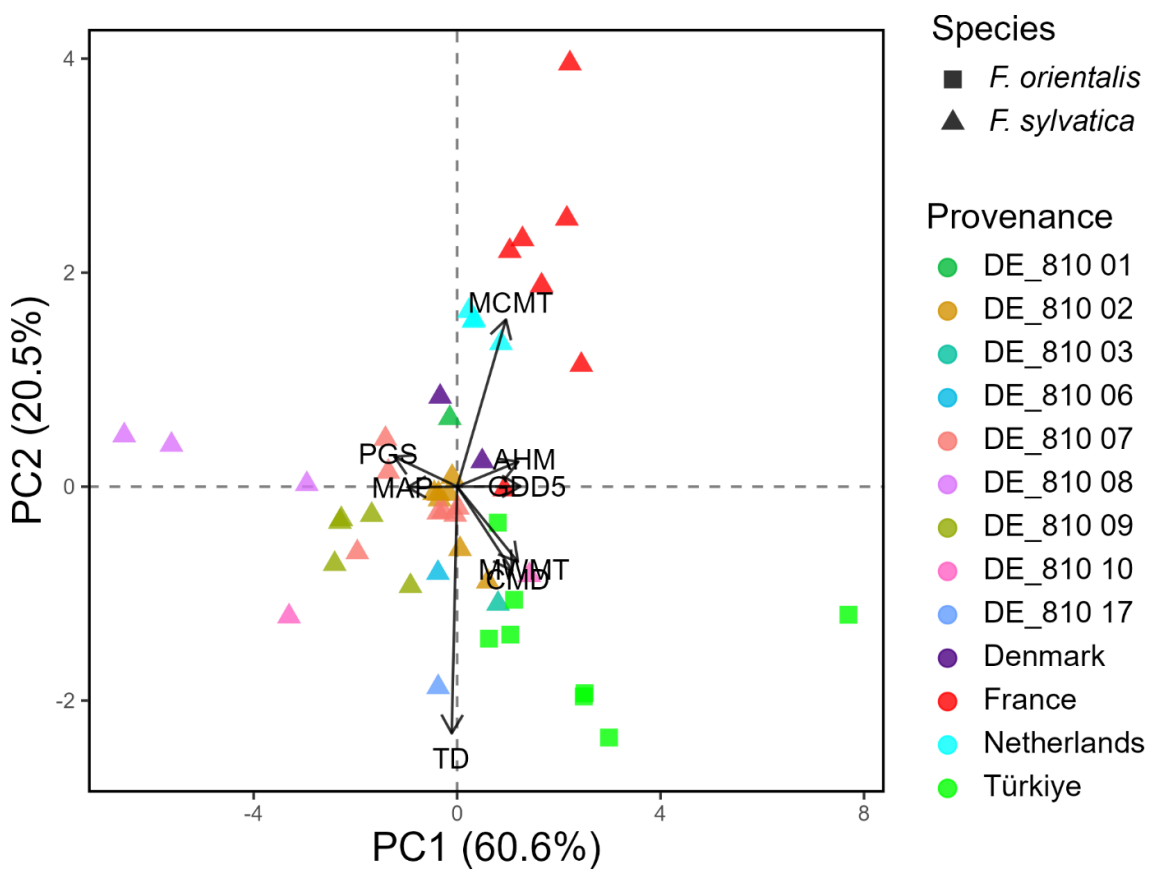


Figure 4. Principal component analysis (PCA) of climatic variables for *Fagus sylvatica* and *F. orientalis* provenances in the Malente trial. All 49 available provenances are shown in the PCA, including those that were excluded from subsequent analyses. Points represent provenances colored by geographic origin and shaped by species. Arrows indicate the direction and contribution of climatic variables to the ordination space. PC1 (60.4%) primarily separated French provenances associated with higher MCMT and AHM from Turkish *F. orientalis* provenances associated with higher MWMT and CMD, whereas PC2 (20.3%) reflected thermal continentality (TD). Several German (81006, 81009, 81010, and 81017) and Turkish provenances clustered along the positive PC2 axis.

3.4 Trait Performance in Response to Climate Transfer Distance

Euclidean climatic transfer distance derived from the PCA space showed no significant relationship with any of the evaluated performance traits (MGIDI, basal area, stem form and survival), suggesting that broad-scale climatic similarity alone does not capture the drivers of provenance adaptation (Figure 5).

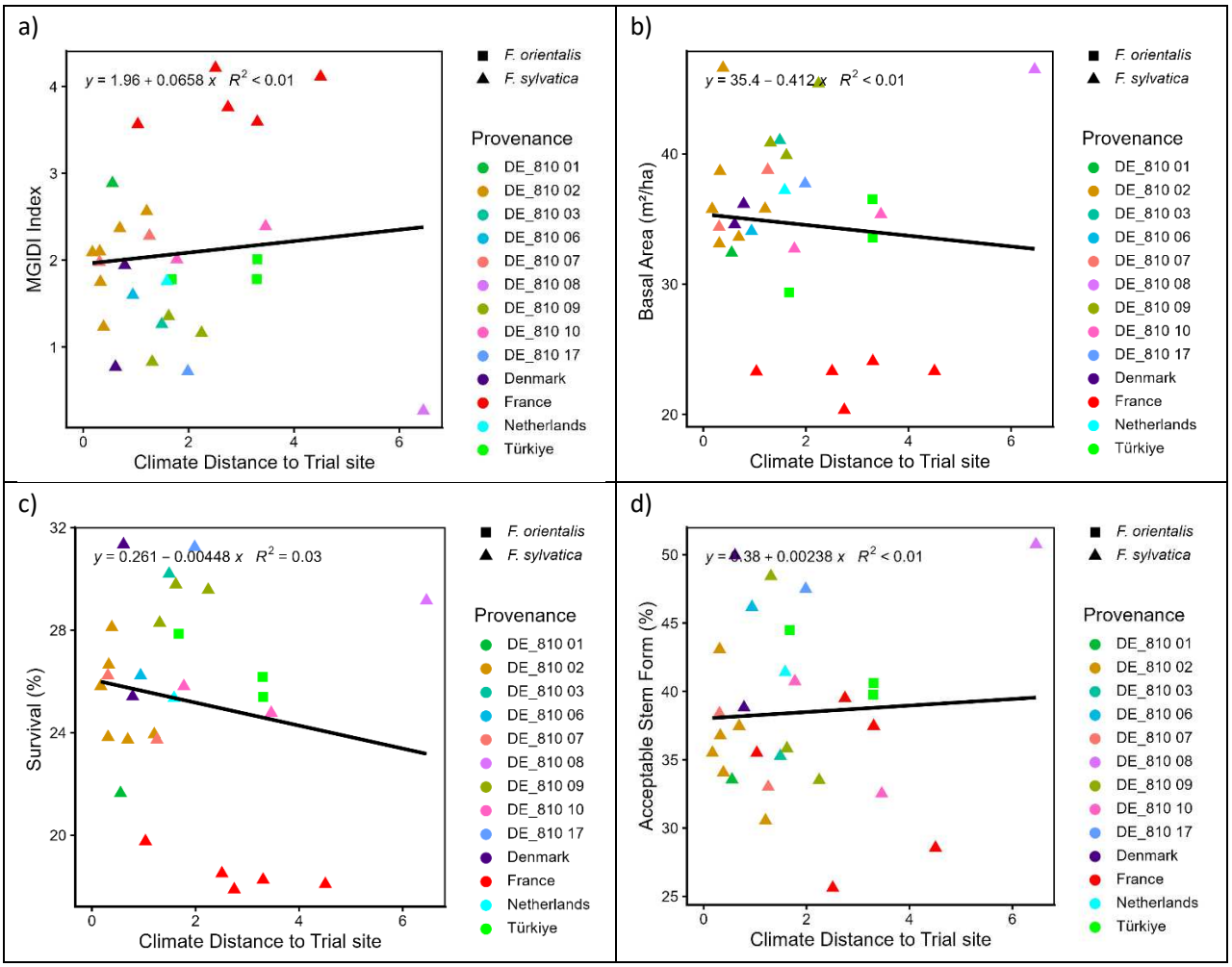


Figure 5. Trait responses to climatic distance across provenances. Relationships between Euclidean climatic transfer distance and provenance performance traits assessed in 2013: (a) MGIDI index, (b) basal area (m^2 ha^{-1}), (c) survival (%), and (d) acceptable stem form (%). Symbols distinguish *Fagus sylvatica* and *F. orientalis*, and colors represent individual provenances. Solid lines show fitted linear regressions for each relationship.

Importantly, the patterns observed in the PCA biplot, including provenance clustering and the orientation of environmental arrows, highlighted key climatic variables that were subsequently explored in regression analyses and later identified as the main drivers of trait-specific provenance performance.

3.5 Climatic Drivers of Trait Variation

MGIDI was strongly associated with winter temperature and climatic seasonality. MCMT showed the strongest relationship (R^2 = 0.64, $p < 0.001$), (Figure 6.a), followed by GDD5 (R^2 = 0.40, $p < 0.001$) and TD (R^2 = 0.38, $p < 0.001$). Lower but significant relationships were observed for growing season precipitation (MWMT) (R^2 = 0.15, p = 0.040), mean warmest month temperature (PGS) (R^2 = 0.14, p = 0.047), and annual heat-moisture index (AHM) (R^2 = 0.14, p = 0.047). Climatic moisture deficit (CMD) showed a weak marginal relationship (R^2 = 0.12, p = 0.08), whereas mean annual precipitation (MAP) was not significantly associated with MGIDI (Table S2).

Basal area showed the strongest overall relationships with climatic variables. Mean coldest month temperature (MCMT) exhibited the highest explanatory power (R^2 = 0.56, $p < 0.001$), (Figure 6.b), with decreasing basal area associated with warmer winter climates. Growing degree days above 5 °C (GDD5) also showed a strong negative relationship (R^2 = 0.44, $p < 0.001$). Moderate but significant relationships were observed for annual heat-moisture index (AHM) (R^2 = 0.28, p = 0.003), growing season precipitation (TD) (R^2 = 0.26, p = 0.004), temperature difference between the warmest and coldest month (PGS) (R^2 = 0.25, p = 0.005), and climatic moisture deficit

(CMD) (R^2 = 0.22, p = 0.011). Mean warmest month temperature (MWMT) was also significantly associated with basal area (R^2 = 0.21, p = 0.012), whereas mean annual precipitation (MAP) showed only a weak and non-significant relationship (R^2 = 0.10, p = 0.094) (Table S2).

Survival was strongly associated with winter climatic conditions and climatic continentality. Mean coldest month temperature (MCMT) showed the strongest relationship (R^2 = 0.63, p < 0.001), (Figure 6.c), indicating higher survival among provenances originating from colder winter climates. Continentality (TD) was also strongly related to survival (R^2 = 0.43, p < 0.001), with higher survival associated with more continental provenance climates. Growing degree days above 5 °C (GDD5) additionally showed a significant negative relationship (R^2 = 0.34, p < 0.001). In contrast, MWMT, growing season precipitation (PGS), AHM, CMD, and MAP were not significantly associated with survival (Table S2).

Stem form showed generally weak relationships with climatic variables. Mean coldest month temperature (MCMT) was the only variable significantly associated with stem form (R^2 = 0.18, p = 0.021) (Figure 6.d), with slightly lower stem form values associated with warmer winter climates. Continentality (TD) showed only a marginal relationship (R^2 = 0.12, p = 0.060). All remaining variables, including GDD5, MWMT, PGS, AHM, MAP, and CMD, were not significantly related to stem form (Table S2).

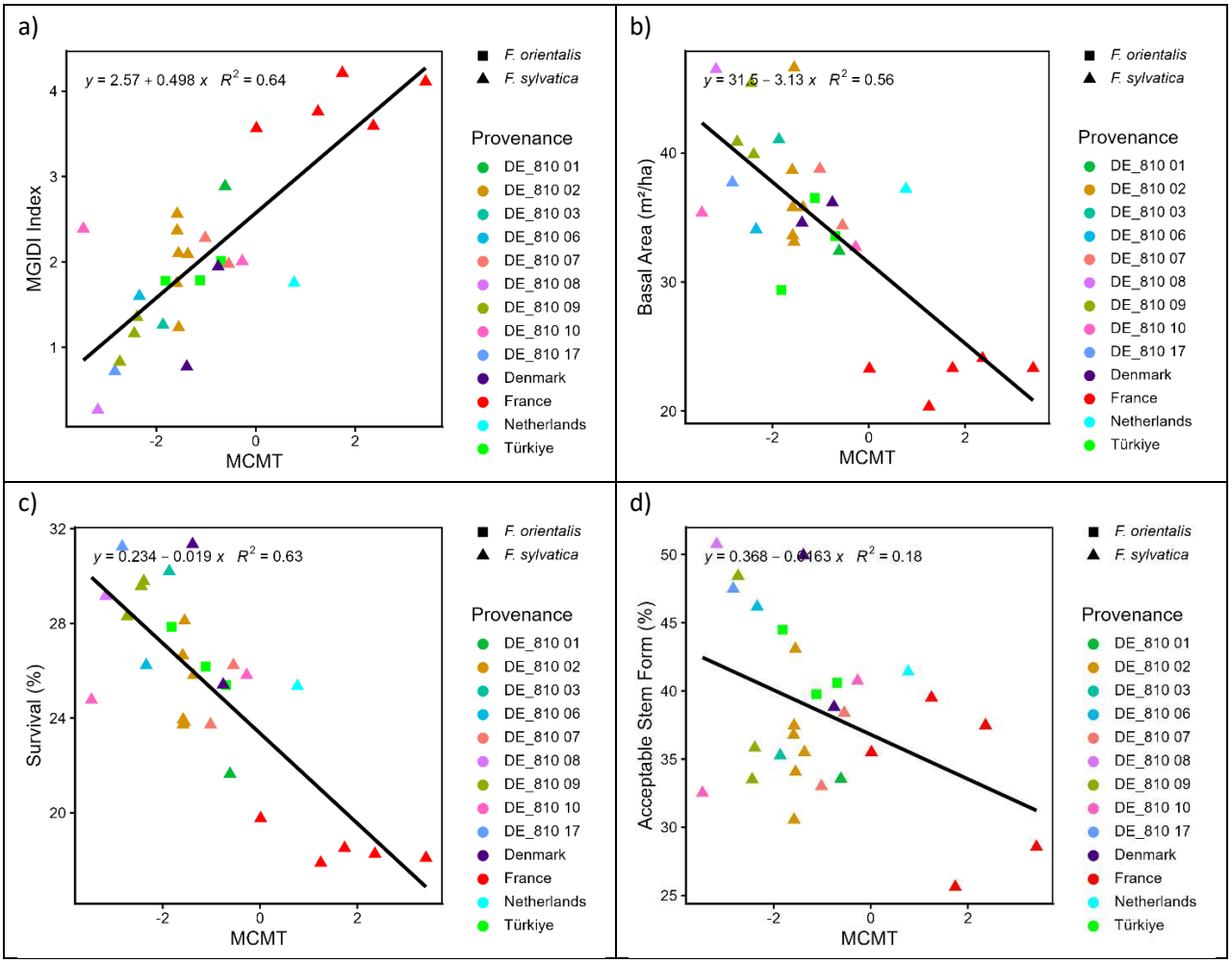


Figure 6. Trait-environment relationships with mean coldest month temperature (MCMT). Relationships between mean coldest month temperature (MCMT) and provenance performance traits assessed in 2013: (a) MGIDI index, (b) basal area (m^2 ha^{-1}), (c) survival (%), and (d) acceptable stem form (%). Symbols distinguish *Fagus sylvatica* and *F. orientalis*, and colors represent individual provenances. Solid lines show fitted linear regressions for each relationship.

4 DISCUSSION

4.1 Provenance differentiation and trait performance

Our single-site trial with 30 provenances revealed substantial differentiation for most traits, indicating strong genetic effects on early growth, productivity, and survival. Juvenile height growth (1988-1998) showed highly significant provenance effects, with provenance explaining up to 87% of phenotypic variance. Part of this variation may reflect initial differences in seedling size at planting, which can influence early growth trajectories. By 2013, however, provenance effects on height were no longer significant, suggesting a convergence of growth trajectories over time, potentially driven by increasing competition, stand dynamics, and environmental homogenisation within the trial site (Kurjak *et al.*, 2024).

Basal area, used here as a proxy for plot-level productivity, maintained significant provenance differentiation across all assessment years (2004-2024), explaining 42-56% of total variance. This indicates that genetic differences among provenances persist in terms of biomass accumulation and are less sensitive to environmental stochasticity than individual tree height. In contrast, mean DBH showed negligible provenance variation, likely because individual diameter growth is constrained by local plot conditions such as tree density and competition (Donfack *et al.*, 2023). Some provenances appear better able to maintain more living trees per plot, resulting in higher total basal area, even though the average diameter of individual trees remains similar across provenances.

Phenological traits, particularly bud burst, demonstrated significant early provenance differentiation (1989-1991), with 70-76% of variance explained by provenance (Kramer *et al.*, 2017). This indicates strong genetic control and suggests a role in local adaptation. Stem form, a key timber quality trait, showed weaker provenance differentiation than growth and productivity traits in the present trial. Similar patterns were reported by Liepe *et al.*, (2024) who found lower provenance differentiation for stem quality traits compared with basal area and growth performance. This likely reflects the strong influence of environmental heterogeneity, stand density, competition, and silvicultural management on stem architecture and quality development. In line with this interpretation, Besliu *et al.*, (2024) also emphasized that quality-related traits are highly responsive to local environmental conditions and management effects, which can partially mask underlying genetic differentiation.

Survival varied significantly among provenances throughout the effective observation period up to 2013 (before thinning). Provenances originating from cooler, more continental climates tended to show higher survival rates, highlighting the importance of historical climate adaptation in shaping stand persistence.

4.2 Multi-trait selection and MGIDI performance

The multi-trait genotype-ideotype distance index (MGIDI) proved effective in identifying superior provenances across productivity, structural, and survival traits. Applying a 20% selection intensity, six provenances were identified as combining favorable performance across traits, with Schmallenberg 1 exhibiting the lowest MGIDI value and thus the closest proximity to the ideotype. The predominance of central German provenances among the selected entries may indicate favorable climatic matching between their regions of origin and the environmental conditions of the Malente trial. At the same time, the inclusion of the Danish provenance Sovaenger suggests that northern provenances may also possess adaptive characteristics conferring stable multi-trait performance under northern Central European conditions. The usefulness of MGIDI in integrating multiple traits into a single selection framework has previously been highlighted (Olivoto & Nardino, 2021; Alexandru *et al.*, 2023; Liepe *et al.*, 2024; Stoica *et al.*, 2025) emphasizing its ability to identify genotypes combining productivity, stability, and overall performance while avoiding undesirable trade-offs among traits (Mátyás *et al.*, 2009; Aitken & Bemmels, 2016).

In this context, MGIDI effectively combined partially correlated traits into a single selection criterion, allowing the identification of provenances that simultaneously achieved high productivity and acceptable levels of survival

and stem form, however, to our knowledge, previous applications of MGIDI have not explicitly combined multi-trait selection with environmental origin associations, an approach that may provide a more comprehensive understanding of the adaptive basis underlying provenance performance and strengthen ecological interpretations of selection results.

4.3 Climate adaptation and provenance performance

Our PCA-based climate analysis revealed clear climatic structuring among provenance origins. *Fagus orientalis* provenances clustered towards warmer and more moisture-limited climates (higher MWMT and CMD), whereas French provenances were associated with milder cold-season conditions and higher heat-moisture indices (AHM). Several German inland provenances together with Turkish material were positioned along the axis of climatic continentality (TD), indicating stronger temperature seasonality, while other central European provenances occupied more intermediate climatic positions. Despite this clear climatic differentiation in provenance origin space, Euclidean climatic distance to the Malente trial site was not significantly related to MGIDI, basal area, stem form, or survival, indicating that broad-scale climatic similarity alone is insufficient to fully capture the determinants of provenance adaptation in this trial.

Specific climatic variables, however, provided stronger explanatory power than PCA-derived climatic distance metrics, indicating that reducing climate space into composite axes may mask key adaptive gradients.

MGIDI was primarily driven by winter temperature (MCMT, $R^2 = 0.64$; positive slope), indicating higher multi-trait performance in provenances originating from colder winter climates (Aitken & Bemmels, 2016). Additional positive associations with growing degree days (GDD5, $R^2 = 0.40$) and climatic continentality (TD, $R^2 = 0.38$) further suggest that provenances from more continental climates with stronger seasonal temperature contrasts tend to perform better overall when transferred to Atlantic climates (Figure S1), as previously described in studies on climatic gradients and local adaptation in forest trees (Savolainen *et al.*, 2007). Weak but significant relationships with precipitation and heat-moisture variables indicate secondary modulation by moisture availability, but these effects were substantially less important than winter temperature and seasonality.

Basal area showed a clear and consistent climatic pattern similar to previous provenance trials in European beech (Liepe *et al.*, 2024), decreasing with increasing winter temperature (MCMT, $R^2 = 0.56$; negative slope) and growing degree days (GDD5, $R^2 = 0.44$), indicating lower productivity in provenances originating from warmer and thermally more favorable climates, such as several French provenances (Figure S1). In contrast, basal area increased with growing season precipitation (PGS, $R^2 = 0.26$) and climatic continentality (TD, $R^2 = 0.26$), indicating higher productivity in more continental and precipitation-favorable origin climates, consistent with ecodistance-based provenance productivity theory (Mátyás *et al.*, 2009). Accordingly, central German upland provenances such as Schmallenberg 1 (81008) as well as some Turkish provenances, were associated with higher continentality and comparatively higher productivity, whereas more oceanic, warm-origin provenances tended to perform less well.

Survival exhibited a similarly strong but more selective climatic response, increasing with decreasing winter temperature (MCMT, $R^2 = 0.63$; negative slope), indicating higher persistence of provenances originating from colder winter climates. Higher survival was also associated with greater climatic continentality (TD, $R^2 = 0.43$), while increasing growing degree days (GDD5, $R^2 = 0.34$; negative slope) reduced survival. In contrast, precipitation and moisture-related variables were not significant, indicating that winter temperature and climatic seasonality are the primary determinants of provenance persistence under the trial conditions. This pattern is consistent with evidence that frost and winter climate represent key selective pressures shaping fitness-related traits in forest trees (Aitken & Bemmels, 2016; Gömöry *et al.*, 2018).

Stem form showed generally weak climatic relationships. MCMT was the only significant predictor ($R^2 = 0.18$), with slightly lower stem quality observed in provenances originating from warmer winter climates. Continentality (TD) showed only a marginal effect, while all other climatic variables were non-significant, confirming that

structural quality traits are largely decoupled from broad-scale climatic origin and are more likely driven by stand-level competition and microsite conditions.

Overall, specific climatic drivers were substantially more informative than integrated climatic distance metrics for explaining provenance performance. Winter temperature and climatic seasonality consistently emerged as the dominant predictors of productivity and survival, with better-performing provenances generally originating from colder and more continental climates, whereas structural traits exhibited weak climatic structuring and appeared more influenced by local environmental conditions within the trial.

4.4 Implications for provenance selection and management

Provenance performance in this trial suggests that selection should prioritize material originating from colder and more seasonal climates (Figure S3), as these provenances combined higher productivity and survival under the Malente conditions. This supports climate-informed transfer strategies rather than reliance on geographic proximity alone. In particular, central German upland and similarly continental provenances appear well matched to current site conditions and represent suitable candidates for both deployment and breeding.

At the same time, the fact that one of the two Danish provenances was selected, provides a preliminary indication that cooler-origin populations may perform well under the environmental conditions of the Malente site. This observation should be interpreted cautiously, but it highlights the potential value of including a broader range of northern provenances in future provenance trials and assisted migration studies. Given the weak climatic control of stem form, management interventions such as spacing and thinning remain essential for controlling structural quality, indicating that silviculture and genetic selection act in a complementary rather than substitutive manner. Although this trial provides clear ranking of provenances under a single environment, transferability across contrasting environmental gradients cannot be assumed, reinforcing the need for multi-site validation when defining large deployment zones. Overall, combining multi-trait selection with climate-informed provenance choice offers a pragmatic framework for balancing productivity, stability, and adaptive potential in future forest management.

5 Conclusion

This study shows that beech provenance performance is strongly structured by climatic origin, with winter temperature and seasonality emerging as key determinants of productivity and survival. Multi-trait selection (MGIDI) effectively identified superior provenances that combine growth and stability, while quality traits were largely governed by stand-level processes rather than provenance. These results provide a transferable framework for provenance evaluation and adaptive management across forest tree species, while highlighting the value of a climate-informed, multi-trait selection strategy for identifying productive, stable, and potentially well-adapted forest material under changing environmental conditions.

Acknowledgements: We gratefully acknowledge the continuous measurements conducted by our technicians and nursery staff. The presented analysis is only possible through the long-term maintenance of the sites for which we thank Alexander Decius (Försterei Wüstenfelde, Schleswig-Holsteinische Landesforsten AöR).

Funding: This research was conducted during the project 'ORIENT-BUCHE' funded by the German Federal Ministry of Agriculture, Food and Regional Identity following a decision by the German Bundestag (Grant No. 2223NR082D).

Data and code availability: Data and code will be made available upon request.

Conflict of interest: The authors declare that they have no conflict of interest.

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