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Research Article

Exploring the effects of the assisted transfer of European beech (*Fagus sylvatica* L.) provenances in the Romanian Carpathians

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Abstract

The genetic inheritance of a tree species is fully expressed in the phenotype only when its ecological requirements are accomplished. Therefore, genetic tests provide the opportunity to simulate the change in the environment and determine the most suitable site conditions for specific populations. In light of the unpredictable climate conditions resulting from rapid environmental changes, the current study investigated possible signs of adaptation and productivity of European beech in the Romanian Carpathian region. For this purpose, the tree growth and stability performances, as well as the transfer effect, were examined in 17 international beech provenances tested in two different environments for 27 years. Growth and stability performances were evaluated using tree height (Th), breast height diameter (DBH), and survival (S). In the case of the transfer analyses, the ecodistance approach was applied. According to the results, the average of S was 13% higher in the Carbunari provenance trial, and DBH was higher in the Sacele trial by 15%, while no noticeable differences were registered for Th. The best-performing provenances were those originating from similar site conditions to the Romanian test sites, and the transfer function detected the sensitivity of beech provenances to increasing temperature. The general transfer response of provenances revealed a similar performance across sites and suggested that provenances exhibited adaptation and acclimation to the test environments from Romanian Carpathians.

Keywords: assisted transfer; ecodistances; forest; growth and stability performances; provenance trials

Introduction

The current trend of environmental changes amplifies concerns about the ability of forest tree species to adapt to reshaped site conditions (Dulamsuren *et al*., 2017; Knutzen *et al*., 2017; Muller *et al*., 2019; Cortés *et al*., 2020; Schuldt *et al*., 2020). The process of adaptation for each tree species is particular, and due to the

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multiple factors involved, it is challenging to provide a definite answer for their adaptive capacity (Aitken *et al.*, 2008; Isabel *et al.*, 2020; Royer-Tardif *et al.*, 2021).

European beech (*Fagus sylvatica* L.) is one of Central Europe's most successful plant species (Leuschner *et al.*, 2006). It has a wide range of distribution, spanning from lowlands to high elevations in mountainous regions (Magri, 2008; Şofletea and Curtu, 2008; von Wühlisch, 2008), thus being considered a forest tree species of high importance (Peters, 2013; Leuschner and Ellenberg, 2017). The beech tree's ability to compete effectively with other species (Pretzsch *et al.*, 2021), its high tolerance for shade, and its natural ability to regenerate (Peters, 1997) have enabled it to persist over time across large areas. These capabilities have also allowed it to continue to dominate other species in certain parts of its distribution range (Dyderski *et al.*, 2018).

In Romania, European beech is the most widespread tree species, covering over 30% of the entire forest land (IFN, 2024). This represents 10% of all beech forests in Europe (Biriş, 2014). The largest beech forests are found in the Carpathian Mountains and hilly areas, with particular occurrences in plain regions (Milescu *et al.*, 1967; Şofletea and Curtu, 2008).

During the last decades, the negative effects of environmental changes have caused growth decline and mortality in beech stands at the European scale (Jump *et al.*, 2006; Piovesan *et al.*, 2008; Lakatos and Molnár, 2009; Zimmermann *et al.*, 2015; NW-FVA, 2019; Meyer *et al.*, 2022; Obladen *et al.*, 2021; Walthert *et al.*, 2021). These problems were also reported in Romania and Moldova (Chira *et al.*, 2003; Budeanu *et al.*, 2016; Roibu *et al.*, 2017, 2022), where, in future, beech may lose territories in competition with high drought-tolerant tree species (Kasper *et al.*, 2022). In front of these disturbances, predicted for the future, beech may adapt to harsh site conditions or migrate to new environments (Aitken *et al.*, 2008).

European beech populations are characterized by high intrapopulation genetic and phenotypic variability (Vettori *et al.*, 2004; Jump and Peñuelas, 2007; Kraj and Sztorc, 2009; Gömöry *et al.*, 2010; Král *et al.*, 2010; Cuervo-Alarcon *et al.*, 2018;), which can allow this species to adapt to future site conditions through evolution (Ciocîrlan and Şofletea, 2013). Besides these, the high phenotypic plasticity recorded in many studies (Meier and Leuschner, 2008; Stojnić *et al.*, 2015a; Frank *et al.*, 2017; Müller *et al.*, 2020; Besliu *et al.*, 2024) can ensure better adaptations of beech to new environments (Bradshaw, 1965, 2006; Crispo, 2008). Therefore, testing the performance and the adaptive capacity of different populations is crucial in the battle of adaptations and can be done by using provenance tests, which brings the possibility of capturing the reaction of the different provenances through the change of the environment (Matyas, 1996; White *et al.*, 2007).

Whereas the performance of local populations may be lower than that of the non-local ones, it becomes the opportunity to transfer valuable provenances in order to increase the productivity and the stability of local populations (White *et al.*, 2007). Thereby, the assisted transfer of provenances is a complex process that needs extensive studies to prove the benefits that the transfer can provide (Mátyás, 2021) because this practice, if not sufficiently studied, may cause ecosystem imbalances such as invasions, maladaptation of the transferred provenances, or economic and ecologic damages (Hewitt *et al.*, 2011; Benito-Garzon *et al.*, 2013). However, the environmental conditions, which are in a rapid transformation, reveal the necessity of changing the perspective regarding the transfer of reproductive material from a local scale to a regional one, providing the opportunity for a macroclimatic overview of the movement of population (Mátyás *et al.*, 2009a).

In view of the actual needs, finding potential adapted and productive beech provenances, along with the analyses of the transfer impact, are important steps for future implementation of assisted migration practices that could be a solution for the mitigation of the predicted disturbances that will affect the species distribution. Based on the identified research needs, the present survey aimed to assess the performance and adaptive response of European beech in the Romanian Carpathians region by analyzing two international provenance trials. We set out to identify the most valuable provenances that could be the subject of forward selection for the establishment of seed orchards or for afforestation on lands with similar environmental conditions.

Materials and Methods

Trials design and tested provenances

The great importance of European beech and the need for new information about its adaptive capacity at the scale of the entire distribution range were the reasons that proved the necessity of installing the series of common garden experiments across Europe. Therefore, in the spring of 1995 and 1998, a network of 49 provenance trials was established (Figure 1) (von Wuehlisch, 2004). In the first series (1995), two of the seventeen international provenance trials were installed in Romania at Sacele, Brasov County, and Carbunari, Maramures County (Mihai, 2009; von Wuehlisch, 2004).

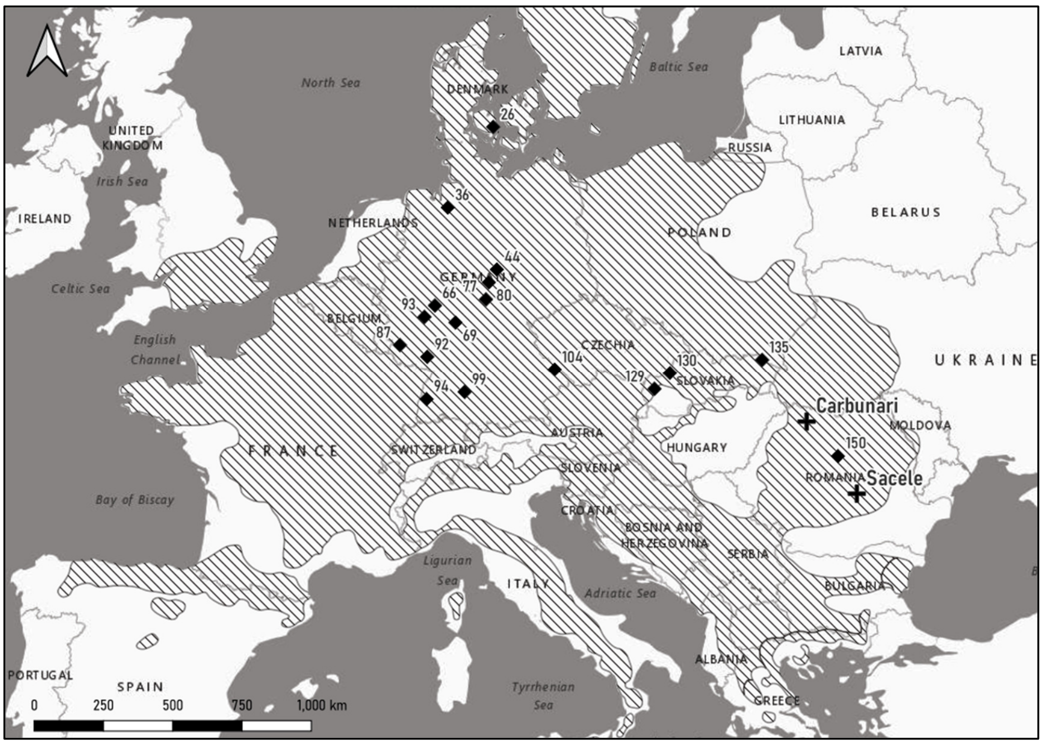

Figure 1. The natural distribution range of *Fagus sylvatica* [hatch (Caudullo *et al*., 2017)], locations of Romanian trials [black crosses (Robson and Garzón, 2018)], and provenances [black diamonds (Robson and Garzón, 2018)]

In the Sacele trial, 44 provenances were planted. The Carbunari trial had 26 provenances, with 16 of them common in both trials (Robson and Garzón, 2018). Two of the Romanian provenances, Sovata (no 150 and 151), were planted as different provenances in the two trials. Because they originate from the same Carpathian region with similar environmental conditions, they were considered one provenance in the present study, playing the role of local provenance (Table 1).

Table 1. Description of the location of the provenances and trials

Provenance number		Provenance origin	Country	Altitude (m)
1	26	Glorup	Denmark	70
2	36	Osterholz	Germany	28
3	44	Oderhaus	Germany	710
4	66	Dillenburg	Germany	500
5	69	Budingen	Germany	198
6	77	Eisenah	Germany	615
7	80	Ebeleben	Germany	315
8	87	Osburg	Germany	540
9	92	Elmstein	Germany	405
10	93	Montabaur	Germany	313
11	94	Ettenheim	Germany	445
12	99	Ehingen	Germany	620
13	104	Zwiesel	Germany	755
14	129	Smolenice	Slovakia	420
15	130	Trencin	Slovakia	350
16	135	Medzilaborce	Slovakia	400
17	150	Sovata	Romania	1018
Trials name		**Location of the trials**	**Country**	**Altitude (m)**
1	Sacele	Brasov County	Romania	873
2	Carbunari	Maramures County	Romania	294

The experiments were conducted using a complete randomized block design with three replications. Each plot contained 50 trees, planted at a spacing of 2 by 1 meter between them (von Wuehlisch, 2004; Liesebach, 2017).

Work methodology and environmental conditions

The growth and stability traits measurements were done in the spring of 2022 when the trees reached the age of 29 (27 years after planting plus 2 years in the nursery). Fifteen trees from each provenance were randomly selected, which means five trees per provenance in each replication. The minimum number of selected trees was determined in relation to the survival and the age of the provenances. Trees were chosen using a pre-established scheme to allow random selection. For the selected trees, total height (TH) and breast height diameter (DBH) were measured. The number of living trees for each provenance was counted, and the survival (S) was calculated as the percentage of living trees out of the initial number of trees planted.

The Sacele trial is located in the Curvature region of the Carpathian Mountains, at an elevation of 873 m (a.s.l.). The site is situated in a high meadow, with a plane surface, and the soil is a dystric cambisoil (Anonymous, 2024). The Carbunari trial is located in a hilly area near the Maramures Mountains, at a low elevation of 294 m (a.s.l.). It is placed on a slope with a 15° inclination, with southwestern expositions and an undulated surface. The soil is a mollic eutricambosoil (Anonymous, 2004).

To capture the trial site climatic conditions (Figure 2), the temperatures and precipitations were downloaded using the Climate downscaling tool (Marchi *et al*., 2024; B4EST, 2024). Moreover, data loggers were installed in each trial to test climatic data accuracy.

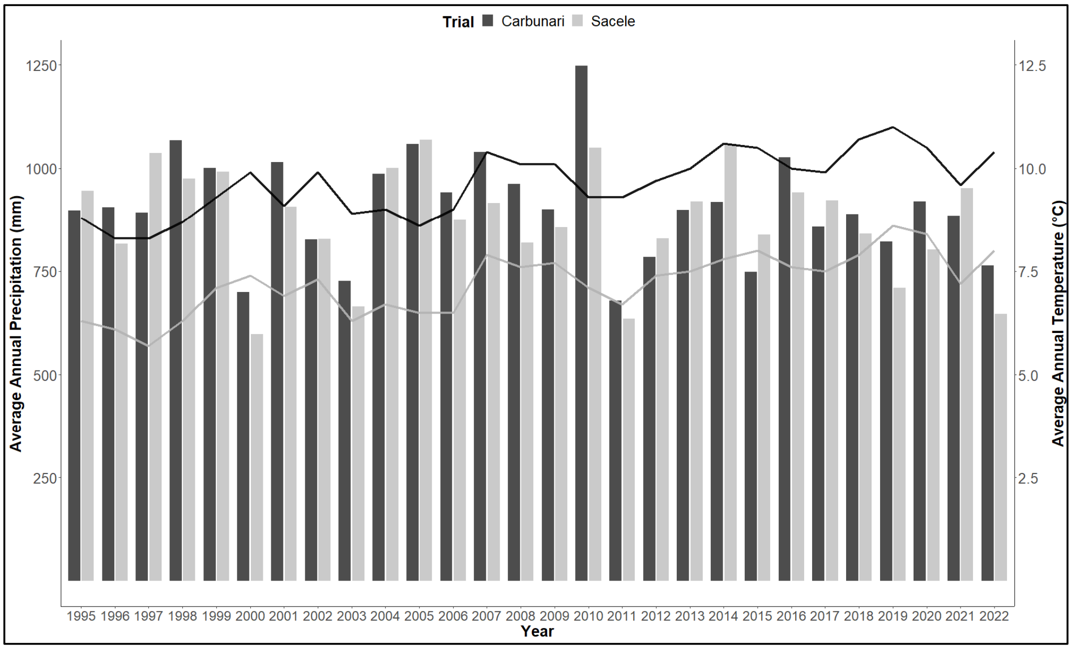

Figure 2. The climate conditions at the trial sites
The bars describe the amount of precipitations, and the lines are the mean temperature per year

For the 27 growing seasons, similar values for the annual precipitation amount were observed in the two environments. The average annual precipitation in the Sacele trial was 873 mm, and in the Carbunari trial, 906 mm. The differences between sites, regarding the climatic conditions, appear in the case of temperatures. Thus, in the Carbunari trial, the mean annual temperature (9.6 °C) was higher by 2.4 °C than in the Sacele trial (7.2 °C). Therefore, the two sites can be classified as humid and warm (Carbunari) and humid and cold (Sacele).

Data analyses

In order to test the variations between the provenances and the two environments, a linear model was used, with the following equation:

$$Y_{ij} = \mu + Pi + Tj + \varepsilon ij \quad (1)$$

where: Y_{ij} is the response variable (TH, DBH, and S); μ is the grand mean; Pi is the provenance effect; Tj is the trial effect and εij is the random error. The blocks were not included in the model due to their lack of influence on the studied traits at this level. Residual plots were used to verify the model's accuracy, and a t-test analysis was conducted to highlight significant differences in the graphs.

The best-performing provenances from the two sites were identified using a graphical approach. This method relied on the average values of provenances for S and the average of TH. The TH increment was selected as an indicator of growth performance instead of DBH because significant differences between provenances at the trial level were obtained only for this trait. Provenances that achieved values for these traits above the trial average were selected as the best-performing ones.

In the transfer analysis, the ecodistance (ecological distance) approach was applied (Mátyás and Yeatman, 1992; Mátyás *et al*., 2009a). This method is based on the presumption that the phenotypic response of provenance is also influenced by the distance of transfer, not only by the climatic conditions of the testing sites. Thus, this approach enables an overview of the macroclimatic adaptations of different provenances by comparing the climatic conditions between the origins of provenances and testing sites (Mátyás *et al*., 2009a).

In this analysis, Ellenberg's climate quotient (EQ) was used as an independent variable that characterised the climatic favourability for beech growth (Ellenberg, 1988). Thus, the ecodistance (ΔEQ) was calculated as the difference between the EQ of the test site and the EQ of the origin of provenances (Mátyás *et al*., 2009a). To calculate the EQ of the origin of provenances, the climate data of the last 27 years before the installation of the trials (before 1995) was used. After these, the regression equation between the average values of ΔEQ and the values of the measured traits (TH, DBH and S) was computed to test the transfer's magnitude. A polynomial function was used in the regression equation, which was fitted using a linear model. The local populations adapted to the test sites took the value of 0. To eliminate the additive test site effect, the trait averages of the provenances were corrected using the difference between their averages and the grand average of both sites for each measured trait, as was described by Mátyás *et al*., (2009a). All these analyses were computed in the R environment (R Core Team, 2023).

Results

Significant differences were revealed between the two test sites for S and DBH, but no significant differences for TH. At the trial level, significant differences between provenances were obtained only for TH in both trials (Table 2).

Table 2. The variation of the selected traits between provenances and testing sites

Interactions	Trial	S	Th	DBH
Between provenances	Carbunari	0,658	0,006**	0,925
	Sacele	0,965	0,003**	0,504
Between test sites		0,000***	0,858	0,000***

The black stars represent the level of significance (* at $p < 0.05$, ** at $p < 0.01$, *** at $p < 0.001$).

Growth and stability analyses

The stability of the tested populations was indicated by the survival capacity (S%) of provenances in the two trials. While no distinct variations were reported at the trial level, there were significant differences observed in S of the provenances between the two sites. In the Carbunari trial, the average value of S was 13% higher compared to Sacele. This suggests that the stability of the provenances was more affected by the site conditions from the Sacele trial. The highest S values were recorded in the Carbunari trial, where the German provenances 80 (Ebeleben - 63%) and 44 (Oderhaus - 62%), along with the Slovakian provenance 135 (Medzilaborce - 59%), performed the best. On the other hand, the lowest values for S were observed in the Sacele trial, where the Romanian provenance 150 (Sovata - 23%), and Slovakian provenances 135 (Medzilaborce - 24%) and 129 (Smolenice - 29%) recorded the lowest stability performance. Most of the tested provenances showed higher values for S in the Carbunari trial, except for three German provenances - 36 (Osterholz), 77 (Eisenah), and 94 (Ettenheim), which achieved almost the same S in both trials. Provenance 77 (Eisenah, Germany) obtained a low S in both tests (37% and 38%). The provenance that achieved similar S and averaged over the trials in both tests was 69 (Budigen, Germany). Some of the provenances obtained different values for S in the two experiments. For instance, the Slovakian provenances 129 (Smolenice), 130 (Trencin), and 135 (Medzilaborce) obtained values for S that were 18% to 35% higher in the Carbunari trial compared to the Sacele trial. Similarly, the German provenances 92 (Elmstein) and 93 (Montabaur) obtained 24% higher S in the Carbunari trial. On the other hand, the Romanian provenance 150 (Sovata) obtained values for S below the trial mean in both sites. However, in the Carbunari experiment, the S was 20% higher than in the Sacele.

No provenances were recorded clearly higher S in the Sacele test, which means that the environmental conditions of this site narrowed the survival capacity (Figure 3).

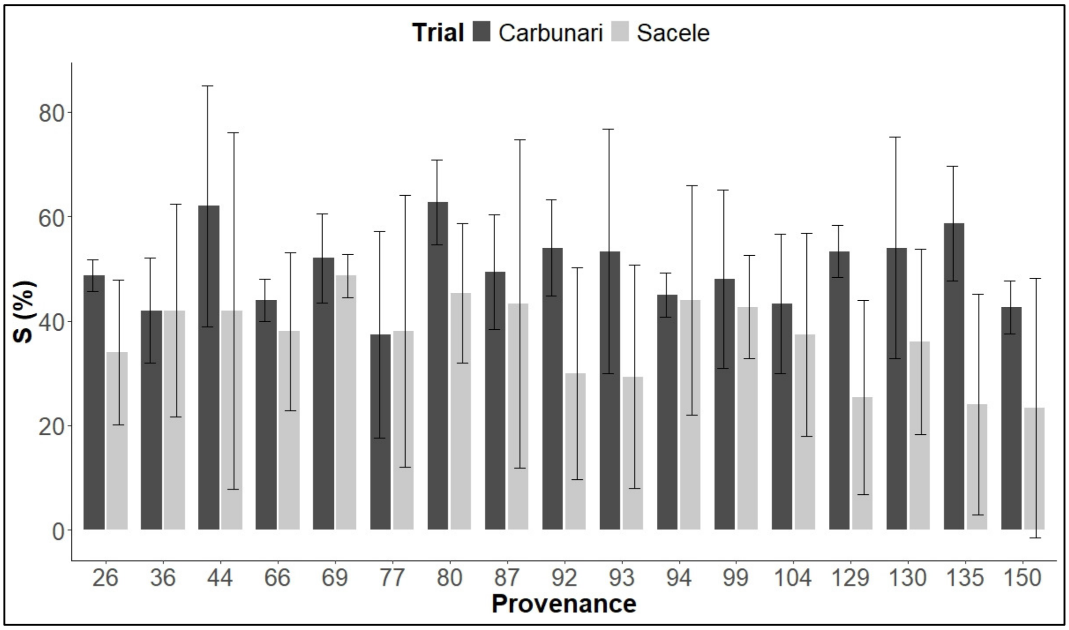

Figure 3. The survival (S%) of the tested provenances in the two trials
The black lines that are positioned above the bars in the graph are the error bars

At the age of 29 years, different behaviours of the tested provenances were recorded in the case of growth traits (TH and DBH). Significant differences among provenances were recorded only for TH (p<0,05). On the other hand, while no noticeable differences were observed across the testing sites for TH, highly significant differences were revealed for DBH (p<0,001). Thus, the site conditions had a different influence on the phenotypic response of provenances.

Even if the differences between the testing sites were not significant, in the particular cases of Dutch provenance 26 (Glorup) and German provenances 66 (Dillenburg) and 69 (Budingen), significantly higher values for Th were registered in the Sacele trial (10 to 16%). On the contrary, the Romanian provenance 150 (Sovata) and German provenance 92 (Elmstein) achieved a 12 to 13% higher Th in the Carbunari trial. The German provenance 69 (Budingen) had the highest average for this trait, while the lowest Th was obtained by the German provenance 104 (Zwiesel), both in the Sacele trial.

In the DBH matter, significant differences were only observed between experiments that achieved an average of 15% in favour of the Sacele trial. The highest mean values for DBH were recorded in the Sacele trial by German provenances 44 (Oderhaus) and 66 (Dillenburg) and by the Romanian provenance 150 (Sovata). Besides, the majority of the provenances recorded higher DBH in the trial installed at Sacele. In the Carbunari trial, the Slovakian, German and Dutch provenances 129 (Smolenice), 66 (Dillenburg), and 26 (Glorup) reached the lowest DBH from all tested provenances. The performance of these provenances was significantly lower than in the Sacele trial (Figure 4). Similar performance for DBH was registered in both experiments by the German provenances 80 (Ebeleben), 93 (Montabaur), and 104 (Zwiesel).

The provenances 26 (Denmark) and 66 (Germany) recorded significantly higher values for the growth traits under the Sacele trial's environmental conditions, which enabled their genotypes to exhibit a performant phenotype.

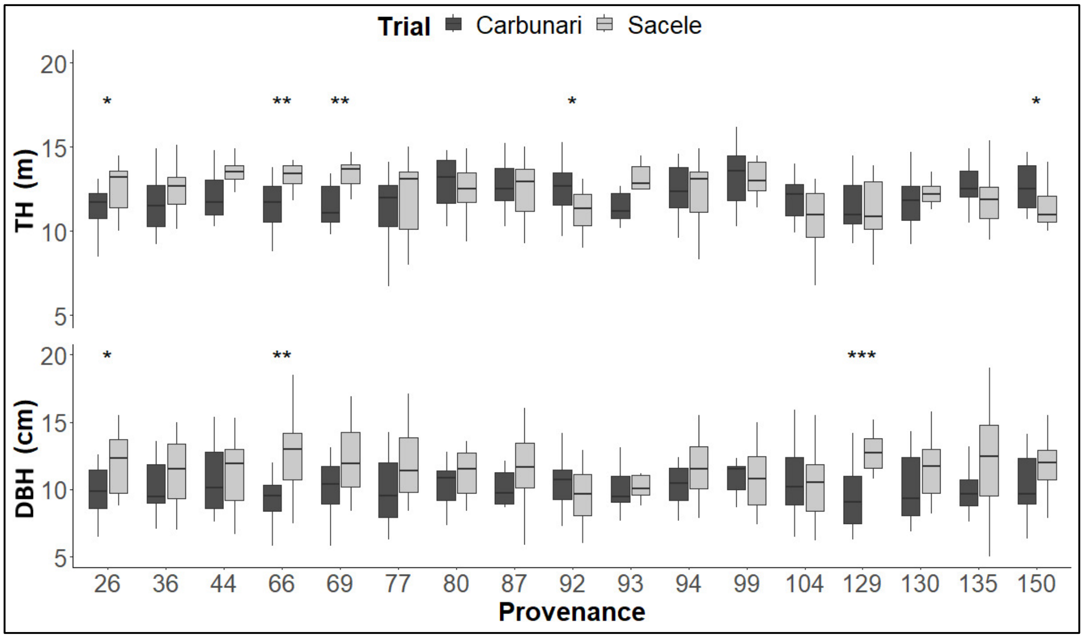

Figure 4. The growth traits of the tested provenances in the two trials
In the boxplot are presented the minimum, first quartile, median, third quartile, and maximum value.
The symbols above the boxplots indicate the level of significance determined by the t-test between the two test sites (* at $p < 0.05$, ** at $p < 0.01$, *** at $p < 0.001$)

Best-performing provenances

The international beech provenances manifest various reactions in the case of performance.

In the Sacele trial, the German provenances 69 (Budingen), 66 (Dillenburg), 44 (Oderhaus), and 99 (Ehingen) were in the front of the best-performing rank, while in the other trial (Carbunari), only three German provenances 80 (Ebeleben), 92 (Elmstein-Germany), 44 (Oderhaus) and one Slovak provenance 135 (Medzilaborce) were selected as the best-performing ones (Figure 5).

The German provenances 80 (Ebeleben) and 44 (Oderhaus) achieved similar and high performance in both sites. Conversely, the German provenance 104 (Zwiesel) and the Slovakian provenances 129 (Smolenice) and 130 (Trencin) recorded low performance in the two trials.

Several provenances performed oppositely in the two trials. The provenances 66 (Dillenburg) and 36 (Osterholz) had high performance in the Sacele trial but very low performance in the Carbunari trial. However, the provenances 92 (Elmstein-Germany) and 135 (Medzilaborce) recorded high performance in the Carbunari experiment but low performance in the other trial. The Romanian provenance 150 (Sovata) was not included in the rank of the best-performing provenances in any of the two trials because it recorded lower values, in special for S, than other provenances. Still, the height increment was higher in the environmental conditions of the Carbunari trial (Figure 5).

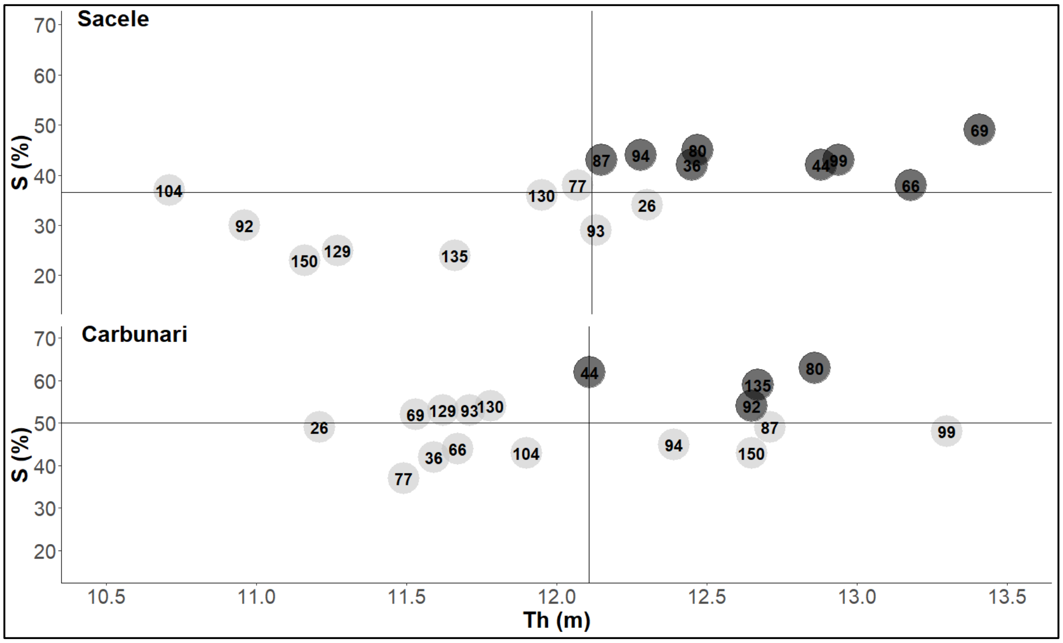

Figure 5. The best-performing provenances from the two trials
In the figure, the black circles mark the best-performing provenances, and the lines are the average values for the selected traits

Transfer analyses

The general response of the tested provenances to the transfer in the Romanian sites does not suggest a clear trend in significance between the mean ΔEQ and the mean of the analyzed traits. This result suggests that provenances had a similar reaction across the testing sites. However, there were provenances that recorded close values for the studied traits even if they originate from different site conditions. For example, the German provenance 104 (Zwiesel), which was transferred from colder and more humid site conditions, obtained only a 1% higher average of S and slightly lower DBH and TH than the Slovak provenance 129 (Smolenice), which originates from a drier and warmer area. The provenances with values for the average ΔEQ appropriate to 0 are transferred from site conditions similar to those of the test sites. In this category were included German provenances 44 (Oderhaus), 66 (Dillenburg), and Slovak provenance 135 (Medzilaborce). It is important to mention that provenances transferred from similar site conditions also achieved high performance in the Carpathian region of Romania. The Romanian provenances 150 (Sovata), which originate from a high-altitude site (1018 m) with colder and wetter conditions than in the trials, obtained very low S but high DBH. So, the transfer to drier and warmer conditions, in the case of this provenance, leads to a decrease in the S (Figure 6).

In the Sacele trial, no significant trend was observed in the regression analyses of the transfer function. The German provenances 44 (Oderhaus) and 66 (Dillenburg), which originate from homogeneous site conditions as those from the trial (ΔEQ ≤ 0), recorded a high performance. On the other hand, four German provenances obtained opposite performances in this trial, even if the transfer distance was equivalent. Thus, provenances 69 (Budingen) and 80 (Ebeleben) showed higher values for all traits compared to provenances 92 (Elmstein) and 93 (Montabaur), indicating different climate receptivity of provenances that originates from similar site conditions (Figure 7).

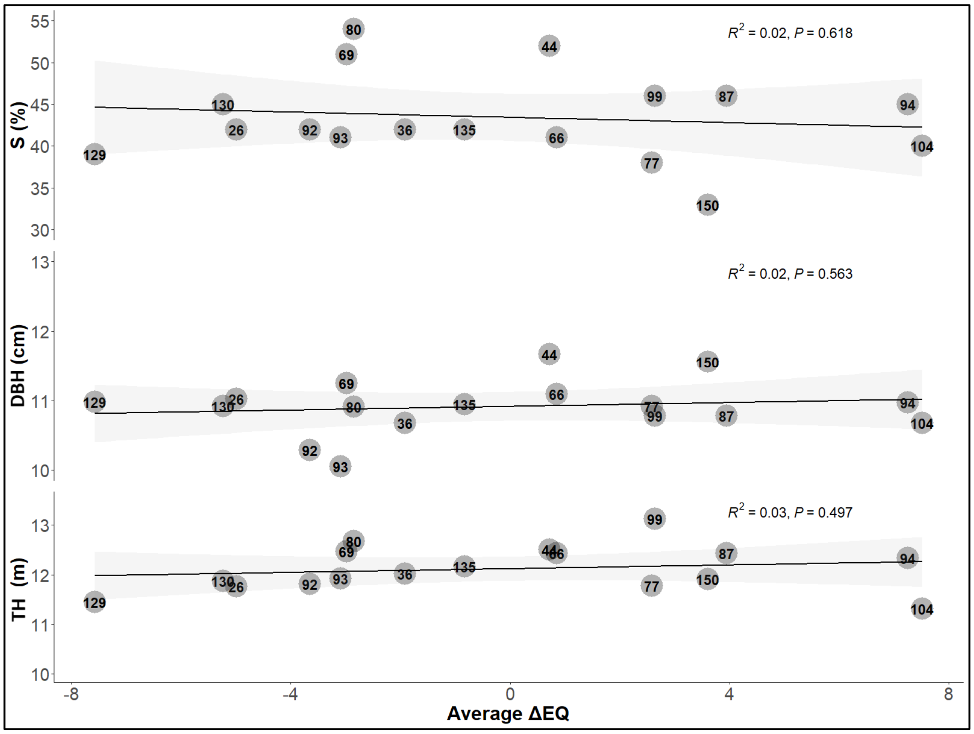

Figure 6. The provenance average ecodistances for both trials
The P values represent the level of significance ($p < 0.05$ = significant correlation)

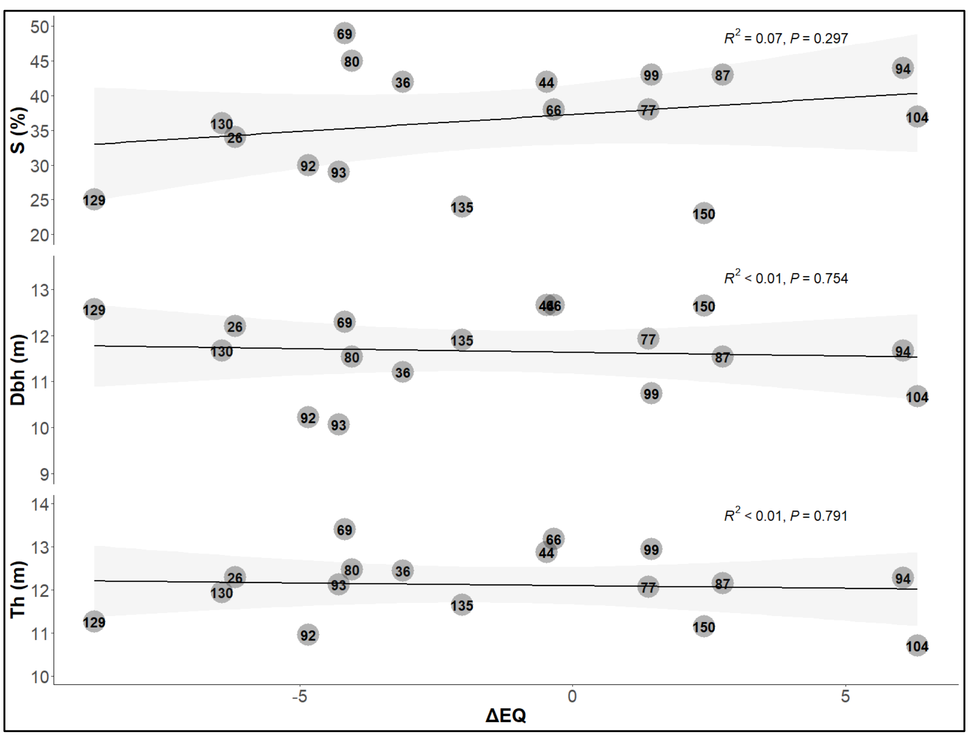

Figure 7. The provenance ecodistances for the Sacele trial
The P values represent the level of significance ($p < 0.05$ = significant correlation)

The regression analyses for the Carbunari trial reveal a low but significant correlation between the ΔEQ and two traits (S and DBH). For S, a significant decreasing trend ($p<0.05$) was observed with an increase in the transfer distance. These results revealed that the S decreases when provenances are transferred from a drier and warmer site to a cold and wet site. An opposite trend was observed for DBH. For this trait, the increase in the transfer distance leads to higher DBH performance, meaning that the transfer from dry and warm site conditions to colder and wetter sites significantly increases the DBH growth. A similar but not significant trend was recorded for TH. The provenances that obtained values for ΔEQ close to 0 were 36 (Osterholz-Germany) and 135 (Medzilaborce –Slovakia), registered contrary performances for all traits, suggesting once again the different climate receptivity of provenances (Figure 8).

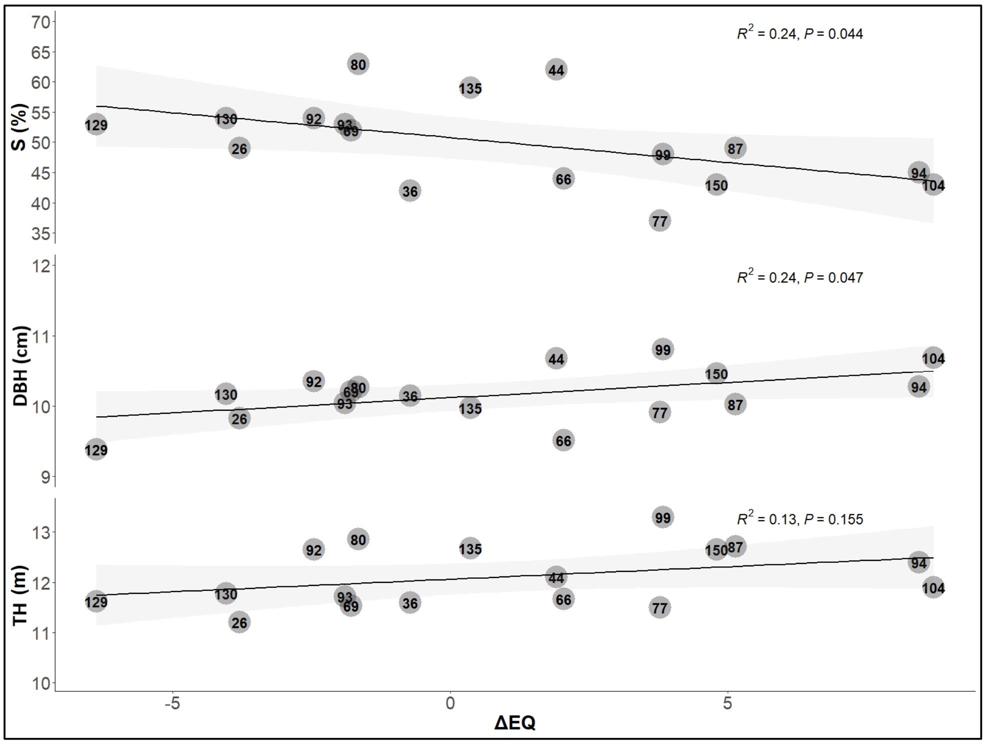

Figure 8. The provenance ecodistances for the Carbunari trial
The P values represent the level of significance ($p < 0.05$ = significant correlation)

Discussion

Growth and stability analyses

A genotype's genetic inheritance is fully transmitted in the phenotype only in case of favourable environmental conditions; if not, the phenotype will be less performant even if the genetic inheritance is higher (Enescu, 1972). Testing the phenotypic variations between different tree species populations, along with examinations of the capacity to grow in different site conditions, are some of the benefits of using the provenance tests (Matyas, 1996; Mátyás, 2021).

Environmental conditions significantly influenced the stability of provenances. The test site, characterized by a humid and warm climate (Carbunari trial), had a significantly higher S than the other site (Sacele), where the climate was colder. This suggests the sensitivity of beech to lower temperatures, which was previously reported by other studies (Leuschner and Ellenberg, 2017; Peters, 2013). Furthermore, Chmura et al., (2024) observed that the climate conditions from the test sites significantly influenced the performance of beech provenances, which revealed the plastic response of this species populations. The highest stability in the two trials was recorded by the German provenances 80 (Ebeleben), 44 (Oderhaus) and 69 (Budingen), which were mentioned as one of the top rankings regarding stability and growth traits in a previous study (Mihai, 2009). The native beech provenance 150 (Sovata), originating from a high-elevation site, exhibited low S in both test sites. This finding is consistent with the results obtained by Mihai et al., (2008). Besides, this provenance was reported by Hofmann et al., (2015) as having a low resistance to frosts in a trial from Germany.

Other research studies focused on beech genetic tests pointed out the high performance of the German provenances in terms of growth traits (Thiel *et al*., 2014; Müller and Finkeldey, 2016; Müller *et al*., 2020). In Romania, the German provenance Dillenburg obtained a high performance only in favourable environmental conditions (Besliu *et al*., 2024). On the contrary, Stojnić et al., (2015b) observed that the German provenances were less adapted to the environmental conditions of southern Europe, which was also proved in the Bulgarian provenance trials (Petkova *et al*., 2019). Of the Slovakian provenances tested in the Romanian trials, only provenance 135 (Medzilaborce) achieved a high performance in the Carbunari trial, and the Dutch provenance 26 (Glorup) was not selected as a performant one in any of the trials. The German provenances 66 (Dillenburg) and 69 (Budingen) and Dutch provenance 26 (Glorup) achieved significantly higher values for the growth traits in the environmental conditions from the Sacele trial, where the temperatures were 2.4 °C lower than in the other trial. This emphasises the need to test the provenance capabilities in different environments in order to select the most appropriate site conditions where provenances can be transferred (Hewitt *et al*., 2011; Benito-Garzon *et al*., 2013; Capdevielle-Vargas *et al*., 2015; Besliu *et al*., 2024).

Transfer analyses

The phenotypic response of provenances to different environmental conditions is considered to be conditioned not only by the adaptive capacity but also by the magnitude and direction of the transfer (Mátyás *et al*., 2009b). Analyzing provenances' reactions to the transfer in different site conditions may be a way to test the possibility of implementing assisted migration practices (König, 2005; Sansilvestri *et al*., 2015), which target increasing forest stability and productivity (Gray *et al*., 2011; Leech *et al*., 2011) along with preserving ecosystem services (Pedlar *et al*., 2012). The assisted transfer of provenances is a complex technique that involves studies about the climate sensitivity and performance of provenances in common garden experiments (Mátyás, 2021).

Testing the transfer effect of the international European beech provenances was done by applying the ecodistances approach (Mátyás and Yeatman, 1992; Mátyás *et al*., 2009a, 2009b; Mátyás, 2021). In this method, the Ellenberg quotient index was used, which is considered to be a proper indicator of beech environmental requirements (Czúcz *et al*., 2011) and was also used in another study focused on beech resistance in Romania (Budeanu *et al*., 2016).

Regarding the general transfer response of provenances to the test sites from the Carpathian region of Romania, no significant correlation was obtained between the transfer distance and analysed traits. This result indicates that international provenances revealed similar reactions and manifest macroclimatic adaptation to the tested environments. In accordance with these findings, Petkova et al., (2019) observed no correlation between transfer distances and survival or height increment in a comparative study between German and Bulgarian provenances, but the survival of the local provenances, which grow in the hard site conditions from the edge of the distribution range, were higher than those of the provenances from Central Europe. Additionally, Petrík et al., (2020) mention that international beech provenances manifest acclimation to site conditions of the Czech Republic and Slovakia after performing the transfer analyses for the stomatal density and potential conductance, which seems to be also influenced by the transfer to limiting conditions. On the other hand, provenances transferred from similar site conditions to those of the Romanian sites achieved high performance, sustaining thus the necessity of transferring populations only from related environments and precautions regarding the circulation of the forest reproductive material (Konnert *et al*., 2015). Nevertheless, the similar performance obtained by the provenances that were totally opposite in their ecodistance, together with the different reactions of the provenances that originate from related environments, express the various climate receptivity of European beech provenances and accentuate the high genetic diversity of beech populations across Europe (Konnert and Ruetz, 2001; Vettori *et al*., 2004; Gömöry *et al*., 2010; Stojnić *et al*., 2015b; Stojnić *et al*., 2016).

The analyses of the transfer impact separately on the two environments detected the sensitivity of the transfer to temperature increase. If no significant relations in the transfer distance were recorded in the humid and cold site (Sacele), in the other environment, humid and warm (Carbunari), the regression revealed significant correlations between the ecodistances and S and DBH. Therefore, if we consider that the precipitation amount was almost equal in the two sites, then the climatic factor that influenced the differentiation between provenances regarding the transfer function was the air temperature. The ecodistance function, performed in the Carbunari trial, revealed that the transfer from a dry site to a colder one could significantly affect the survival capacity of beech provenances, but contrarily, the DBH may increase. Thus, this finding emphasizes the necessity of testing the response to different environmental conditions, including those outside the natural distribution range, to better understand the ecological requirements of tree species (Benito Garzón *et al*., 2019). Mátyás et al., (2009b) accentuated by their study that the transfer of provenances to limited environments decreased their growth and stability performances after an analysis of the transfer influence of some provenances among three testing sites from Slovenia, Slovakia, and Hungary, with different environmental conditions. This finding is in accordance with the result of the present survey because the lower temperatures from the Sacele trial narrowed the performance of provenances. Besides, other studies focused on the transfer analyses of beech provenances pointed out the negative influence of extreme sites on the growth and stability performance and morphological leaf traits (Mátyás *et al*., 2009a; Horváth and Mátyás, 2016; Petrík *et al*., 2020, 2022).

Together with other results reported from the analyses of the beech provenance trials, this paper contributes to an overview of European beech adaptive capacity in Romanian Carpathians. The results of the tested provenances at the age of 29 years are representative because they reached half of the testing period that was proposed. Therefore, the interpretation of their reaction is reliable. Furthermore, the environmental conditions at the two test sites, which fall within the natural range of species, and the provenances that originate from a large part of the species distribution, allow for the generalization of results in the case of young beech stands. The reaction of provenances may be used as base information for the implementation of assisted migration practices in order to increase the stability and productivity of the Romanian beech stands. As was also previously proved in other studies (Mihai *et al*., 2008; Mihai, 2009; Besliu *et al*., 2024), part of the international beech provenances confirmed the acclimation and adaptation to the Romanian environment, and moreover, revealed higher performance in comparison with local beech populations.

In view of future research perspectives, phenological observations are truly needed to whole the adaptive answer of the international beech provenances in the Carpathian region of Romania. Modelling the capacity of beech provenances in future climate scenarios will be another important objective.

Conclusions

The performance of international European beech provenances over the past 27 years validates the macroclimatic adaptation to the environmental conditions of the Romanian Carpathians. The best-performing provenances were those originating from central Germany, where the environmental conditions were similar to the Romanian test sites. Nevertheless, the varying climatic suitability of the tested provenances underscored the importance of utilizing only the most well-adapted provenances in areas where they have been proven to perform under local conditions.

The transfer function detected the sensitivity of beech provenances to increasing temperature. Besides, assisted transfer of provenances between contrasting site conditions may affect their stability; thus, comprehensive studies are crucial before transferring beech populations.

In the face of uncertain climate conditions derived from the rapid environmental changes, identifying and promoting the most well-adapted populations, as well as exploring and implementing assisted migration practices, are central clues in adopting a smart management perspective in the forestry sector.

Authors' Contributions

Conceptualization: E.B., A.L.C., M.B.; Data curation: E.B., M.B.; Formal analysis: E.B.; Funding acquisition: M.B., E.N.A.; Investigation: E.B., M.B.; Methodology: E.B., A.L.C., M.B; Project administration: M.B., E.N.A.; Resources: E.B., M.B.; Software: E.B., M.I.C.C.; Supervision: A.L.C., M.B.; Validation: A.L.C., E.N.A., M.B.; Visualization: E.B., M.I.C.C.; Writing - original draft: E.B.; Writing - review and editing: E.B., A.L.C., E.N.A., M.B., M.I.C.C..

All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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