

High plasticity in germination and establishment success in the dominant forest tree *Fagus sylvatica* across Europe

Lena Muffler^{1,2}  | Jonas Schmeddes¹  | Robert Weigel²  | Adrià Barbeta³  | Ilka Beil¹  | Andreas Bolte⁴  | Constanze Buhk⁵  | Stefanie Holm¹ | Geoffrey Klein^{6,7}  | Marcin Klisz⁸  | Magnus Löf⁹  | Josep Peñuelas^{10,11}  | Léonard Schneider^{7,8}  | Yann Vitasse¹²  | Juergen Kreyling¹ 

¹Experimental Plant Ecology, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

²Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, University of Goettingen, Goettingen, Germany

³BEECA, Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Catalonia, Spain

⁴Thünen Institute of Forest Ecosystems, Eberswalde, Germany

⁵Geoeiology/Physical Geography, Institute for Environmental Science, University of Landau, Landau, Germany

⁶Institute of Geography, University of Neuchatel, Neuchatel, Switzerland

⁷WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Neuchatel, Switzerland

⁸Department of Silviculture and Genetics of Forest Trees, Forest Research Institute, Raszyn, Poland

⁹Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU), Alnarp, Sweden

¹⁰Global Ecology Unit CREAF-CSIC-UAB, CSIC, Bellaterra, Catalonia, Spain

¹¹CREAF, Cerdanya del Vallès, Catalonia, Spain

¹²WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

Correspondence

Lena Muffler, Plant Ecology, Albrecht-von-Haller-Institute for Plant Sciences, University of Goettingen, Goettingen, Germany.

Email: lena.muffler@uni-goettingen.de

Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: research training group RESPONSE (RTG 2010); Forest Research Institute in Poland; European Research Council Synergy Grant, Grant/Award Number: ERC-SyG-2013-610028 IMBALANCE-P

Editor: Lesley Lancaster

Abstract

Aim: Distribution ranges of temperate tree species are shifting poleward and upslope into cooler environments due to global warming. Successful regeneration is crucial for population persistence and range expansion. Thus, we aimed to identify environmental variables that affect germination and seedling establishment of Europe's dominant forest tree, to compare the importance of plasticity and genetic variation for regeneration, and to evaluate the regeneration potential at and beyond the southern and northern distribution margins.

Location: Europe.

Time period: 2016–2018.

Major taxa studied: European beech (*Fagus sylvatica* (L.)).

Methods: We investigated how germination, establishment and juvenile survival change across a reciprocal transplantation experiment using over 9,000 seeds of beech from 7 populations from its southern to its northern distribution range margins.

Results: Germination and establishment at the seedling stage were highly plastic in response to environmental conditions. Germination success increased with warmer

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Global Ecology and Biogeography* published by John Wiley & Sons Ltd

and declined with colder air temperature, whereas establishment and survival were hampered under warmer and drier conditions. Germination differed among populations and was positively influenced by seed weight. However, there was no evidence of local adaptation in any trait.

Main conclusions: The high plasticity in the early life-history traits found irrespective of seed origin may allow for short-term acclimatization. However, our results also indicate that this plasticity might not be sufficient to ensure the regeneration of beech in the future due to the low survival found under dry and hot conditions. The future climatic conditions in parts of the distribution centre and at the rear edge might thus become limiting for natural regeneration, as the likelihood of extreme heat and drought events will increase. By contrast, at the cold distribution margin, the high plasticity in the early life-history traits may allow for increasing germination success with increasing temperatures and may thus facilitate natural regeneration in the future.

KEY WORDS

climate change, European beech, fitness traits, forest ecology, germination, life-history traits, local adaptation, range margin, range shift, reciprocal transplant experiment

1 | INTRODUCTION

Distribution ranges of species are projected to shift polewards or upwards in elevation (Lenoir et al., 2008; Parmesan, 2006; Sykes et al., 1996), whereas populations at the rear edge are threatened due to global warming (Thomas et al., 2004; Thuiller et al., 2005). However, these predictions from species distribution models generally neglect the potential for *in situ* responses of organisms to changing environmental conditions through phenotypic plasticity, local genetic adaptation and demographic processes (Aitken et al., 2008; Savolainen et al., 2007; Scherrer et al., 2020; Valladares et al., 2014). Local genetic adaptation results in highest fitness of populations at their origin compared to non-local genotypes of the same species at the same location (Kawecki & Ebert, 2004). Thus, genetic differences can explain variation in traits between populations. However, certain traits might also be strongly affected by the environment and thus respond plastically to changing environmental conditions.

Local adaptation is expected to be particularly important in marginal populations due to stronger selective pressure of the environment at range margins than in the distribution centre and due to a probably limited genetic mixing caused by geographic isolation (Choler et al., 2004; Kawecki, 2008; Paul et al., 2011). In the case of strong local adaptation, assisted gene flow within a species range, that is the transplantation of genotypes from origins climatically similar to the expected future conditions of a given site, or assisted migration, that is the transplantation of genotypes outside of a species range, might be considered as an adaptation strategy by forest managers to ensure sustainable forest ecosystem services under rapid change in climatic conditions (Aitken & Bemmels, 2016; Williams & Dumroese, 2013). In contrast, plastic responses to changing

environmental conditions could allow for short-term acclimatization and thus might buffer the impact of climate change. These *in situ* plastic responses play an important role especially for plant species with limited migration potential due to low seed dispersal capacity and a long life span (Benito Garzón et al., 2019). This is especially true for trees, as they are long-living organisms and can hardly compensate the consequences of ongoing rapid climate change through migration (Jump & Peñuelas, 2005).

Successful regeneration plays an essential role in the persistence of populations, in particular for climax forest tree species. Therefore, germination and establishment of young trees are critical bottlenecks for the persistence of the population, especially as young trees respond more sensitively to changing climatic conditions than adult trees (Jackson et al., 2009). Moreover, germination and establishment are under strong natural selection and might favour rapid local adaptation (Donohue et al., 2010; Petit & Hampe, 2006). However, knowledge about plasticity and local adaptation in the early life-history traits is still scarce, though these processes are critical to better predict the potential of natural regeneration, for projecting distribution range shifts, and for conservation strategies in times of climate change.

The few studies on germination and establishment of forest trees in the face of climate change so far had a local to regional focus (e.g. Arana et al., 2016; Dulamsuren et al., 2013). Successful tree regeneration is obviously important for the expansion of the distribution range at the leading edge. Limited, but still existing success of regeneration at the rear edge, however, is potentially as important because the strong selection during the earliest life stages may determine surprisingly quick genetic adaptation (Jump, Hunt, Martínez-Izquierdo, et al., 2006) and thereby mitigate range

contraction. Studies accounting for the whole distribution range from the rear to the leading edge are therefore necessary to better understand population dynamics under climate change (Rumpf et al., 2018).

European beech (*Fagus sylvatica* L., hereafter called beech), the dominant native forest tree in Central Europe, grows under a wide range of climatic and environmental conditions (Bolte et al., 2007; Fang & Lechowicz, 2006; Leuschner et al., 2006). The potential distribution range of beech is limited by late frost events as well as severe winter frost towards the north in Sweden and north-east in Poland, and by heat and drought towards the rear edge in Greece, Italy and Spain (Bolte et al., 2007; Giesecke et al., 2007; Jump, Hunt, & Peñuelas, et al., 2006; van der Maaten et al., 2017). Beech is absent or hardly grows in regions with an Ellenberg's climate quotient [average July temperature (°C)*1000/average annual precipitation (mm)] above 30°C/mm (Leuschner & Ellenberg, 2017).

Under rapid global warming, the high plasticity found in phenology and fitness-related traits like growth in beech could help in mitigating range contractions (Gárate-Escamilla et al., 2019; Kramer et al., 2017; Vitasse et al., 2010). Genetic diversity of beech populations was found to be lower in the centre and towards the leading edge of its distribution, whereas it becomes higher toward the rear edge of its distribution due to the post-glacial recolonizations from glacial refugia (Magri et al., 2006). This might favour local adaptations at the rear edge, which is supported by findings of local adaptation of dry-marginal populations to drought (Bolte et al., 2016; Thiel et al., 2014). However, the reported lower genetic diversity towards the north is valid at population level, whereas the genetic variation within populations may remain quite high across the whole range of the species (Vornam et al., 2004). Adaptive traits and performance of beech under drought are genetically determined (Cuervo-Alarcon et al., 2021), arise from both local genetic adaptation and phenotypic plasticity (Bolte et al., 2016; Stojnić et al., 2018), and are also moderated by other ecological factors like light availability (Wang et al., 2021). To better understand the population dynamics of this species across its whole distribution range, it is therefore crucial to consider the increasing likelihood of drought events in large parts of the distribution of beech with climate change (Kovats et al., 2014) and its projected distribution range shift towards the north (Kramer et al., 2010; Saltre et al., 2015). For this, studies that focus on the potential and limits of local adaptation and plasticity at the recruitment stage are urgently needed, as germination and juvenile establishment are crucial life-history traits for successful natural regeneration.

Here, we used a unique, fully reciprocal transplantation experiment of European beech along a large climatic gradient from its southern distribution margin in Spain to its northern margin in Sweden and Poland as well as beyond its current distribution range, in order to assess the potential for plasticity and local adaptation to the environment during its early life stages. We transplanted more than 9,000 seeds, harvested and sowed in the same year at all sites, and determined the germination success as well as the success of

establishment after the first year and survival after the second year as fitness traits for the earliest life stages. We aimed: (a) to identify which environmental variables of the transplant site or the population origin affect these earliest life stages; (b) to directly compare the importance of plasticity and genetic variation for germination, seedling establishment and survival of juvenile trees. Here, we expected local environmental conditions to dominate the outcome, that is a prevalence of plasticity over genetic adaptation; and (c) to explicitly evaluate the potential for regeneration at and beyond the southern and northern distribution margins.

2 | MATERIAL AND METHODS

2.1 | Experimental design and trait measurements

We conducted a fully reciprocal transplantation experiment across and beyond the distribution range to evaluate the importance of plasticity and local adaptation on germination and establishment success of beech (Figure 1, Table 1). The sites have diverse winter cold and summer drought conditions (Table 1, Figure 1a, see Supporting Information Table S1 for the climatic characteristics of the population origins) as these are important variables that limit the distribution range of beech (Bolte et al., 2007; Giesecke et al., 2007; Jump et al., 2006; van der Maaten et al., 2017). All sites within the range were beech dominated. The external sites beyond the distribution range were surrounded by deciduous trees and they were dominated by oak in Poland (*Quercus robur* L.) and Spain (*Quercus pyrenaica* Willd.) and by mountain ash (*Sorbus aucuparia* L.) in Sweden. The canopy cover at the experimental sites was comparable between all sites (approx. 60%–70% canopy closure). The soil texture of all sites varied little from poor silty sand to sandy silt (Supporting Information Table S2). The litter layer was removed before planting the seeds.

In autumn 2016, open-pollinated seeds of all populations were collected with a slingshot (Notch BIG SHOT Standard Kit, SHERRILLtree) from four mother trees in close proximity (in a range of not more than 250 m) to the experiment unit at each population site. Beech regeneration is strongly driven by mast events, during which enormous amounts of seeds are produced that can exceed 7 million seeds per hectare (Øvergaard et al., 2007). In conjunction with the widespread pollination of many trees during those mast years, a high number of seeds with a high genetic diversity are available (Tachiki & Iwasa, 2010). Thus, our seed collection during a continental-wide mast event (Ascoli et al., 2017) ensured high quantity and quality of seeds from all sites except for the Swedish sites, where poor fructification was observed. The Swedish sites would have represented cold populations, however, the Polish population GD remained representative of cold populations in our data set. We checked the initial seed quality by discarding empty and infested beech nuts after examining each seed carefully and verifying with multiple destructively opened samples per site. A good initial viability of the seeds is supported by a relatively high germination success of more than 50% at some

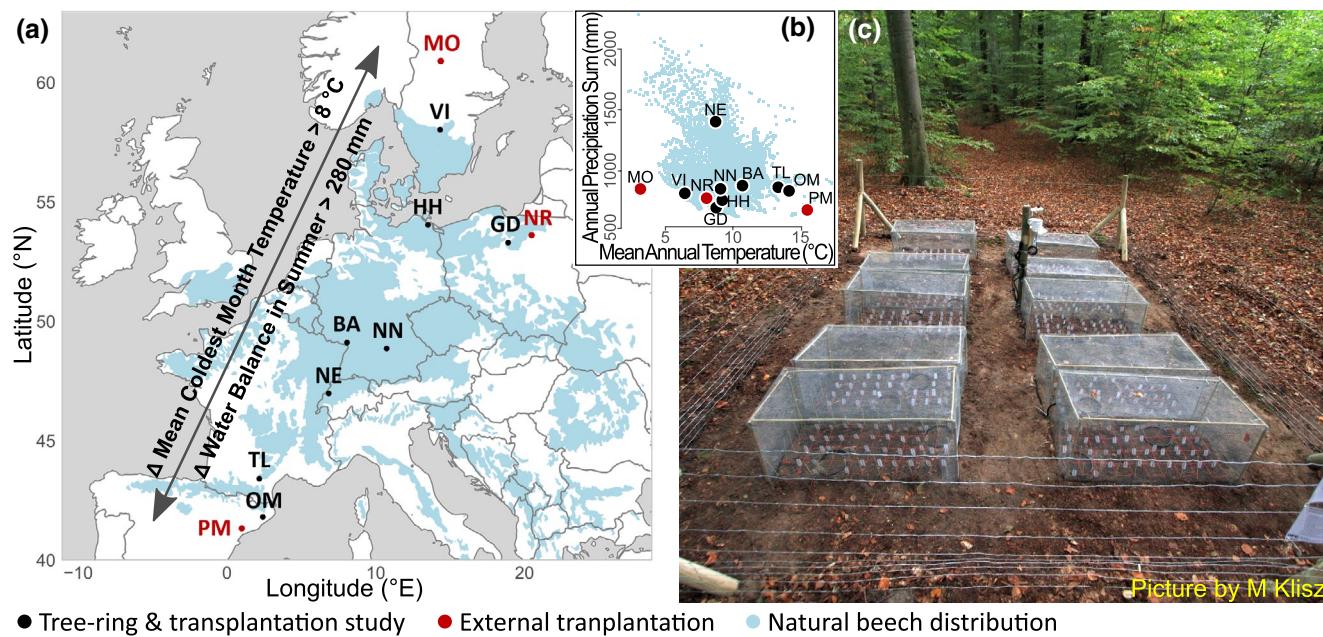


FIGURE 1 (a) Site locations within (black dots) and beyond (red dots) the distribution range of *Fagus sylvatica* (blue area), source: <http://www.euforgen.org>. The climatic gradient is based on differences between the warmest and coldest site in winter and between the driest and wettest site in summer; water balance is calculated by precipitation – potential evapotranspiration, the climatic parameters were averaged over the 30-year period 1986–2015 (Harris et al., 2014, CRU TS v. 4.03), (b) climatic distribution range of *F. sylvatica* (extracted and calculated from CRU TS v. 4.03, Harris et al., 2014) and (c) experimental unit (19 m²) of 10 replicate blocks as it was set up identically at each study site (picture: site GD, Poland). See Table 1 for site ID codes used in (a) and (b). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Site characteristics following the south-west – north study gradient.

Site ID	Country	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Mean annual temp. (°C)	Mean coldest month temp. (°C)	Mean warmest month temp. (°C)	Volumetric water content
PM	Spain	41.33	1.01	1,060	10.9	3.1	21.0	.15
OM	Spain	41.81	2.41	1,041	10.7	3.0	19.8	.17
TL	France	43.41	2.18	709	10.3	2.7	18.6	.14
NE	Switzerland	46.98	6.84	707	9.2	-2.4	18.9	.16
BA	Germany	49.11	8.07	181	11.0	0.2	20.1	.07
NN	Germany	48.87	10.74	565	9.2	-2.4	17.9	.18
HH	Germany	54.05	13.51	44	9.3	-0.3	17.9	.24
GD	Poland	53.30	18.90	113	8.9	-2.5	18.3	.31
NR	Poland	53.61	20.47	173	8.1	-3.1	18.2	.19
VI	Sweden	58.03	14.33	135	7.4	-1.6	17.6	.15
MO	Sweden	60.89	14.38	206	4.0	-7.5	17.2	.17

Note: Geographic position [longitude degree (°E), latitude degree (°N)], elevation (above sea level), mean annual air temperature, mean coldest month air temperature, mean warmest month air temperature, and the volumetric soil water content measured at each site and averaged over the observation period (winter 2016/2017 to autumn 2018).

of our sites (Supporting Information Table S3, compare Bartsch et al., 2020; Barna, 2011). At each site, the experiment was replicated in 10 blocks into which seeds of each population and mother tree were systematically sown in autumn 2016 ($n = 11$ sites \times 10 replicate blocks \times 7 populations \times 4 mother trees \times 3 seeds = 9,240 seeds in total, i.e. 120 seeds per population at each site, Figure 1). Seeds to be sown in each replication block were drawn at random for each population. We planted the seeds maximally 3 weeks after harvest to allow for the important natural cold

stratification of beech seeds (Barna, 2011; Suszka et al., 1996). The seeds were covered by standardized seedless beech litter to simulate natural and comparable seed bed conditions at each site. The seeds in each block were protected against predation by rodents and against potential incoming falling seeds using cages with small-meshed (5 mm) wire (Figure 1c) and larger fences protected against deer and wild boar intrusion. Still, three blocks in Poland (site GD) were affected by rodents and had to be excluded from the analysis (252 seeds).

In autumn 2017, we measured the germination success after 1 year by counting all seeds that ever had germinated (i.e. also dead seedlings) by checking them for signs of germination (emergence of cotyledons). We measured establishment by counting all seedlings that were still alive when visually inspected in autumn (Supporting Information Tables S3 and S4). The survival of seedlings was assessed again in the second year (autumn 2018). As response variables, we calculated the germination success (the ratio of germinated seeds to planted seeds after 1 year) as well as the establishment in the first year (the ratio of established seedlings in 2017 to germinated seeds) and the survival in the second year (the ratio of established seedlings in 2018 to established seedlings in 2017). The site OM within the distribution range in Spain had to be excluded for the survival in 2018, as the young beech trees were completely buried under litter after removing the cage covers in autumn 2017. Moreover, the average seed weight of 50 seeds per population was measured to account for potential maternal effects by seed provisioning (Donohue, 2009; Zas et al., 2013; Supporting Information Table S1).

2.2 | Environmental data and statistical analyses

We analysed climatic effects (long-term average climate variables over 30 years, see Supporting Information Table S5) and maternal effects (seed weight for germination and establishment in the first year) of the seed populations and effects of the transplant site (meteorological data from winter 2016/2017 to autumn 2018, see Supporting Information Table S5; soil properties: pH_{CaCl₂}, C/N ratio, soil hydraulic properties) on the life-history traits germination, establishment in the first and survival in the second year by random forest regressions (Breiman, 2001; see Supporting Information for detailed methodology of explanatory soil, climate, and meteorological variables). For meteorological data, we considered winter 2016/2017 to spring 2017 for germination, spring 2017 to summer 2017 for establishment in the first year, and autumn 2017 to summer 2018 for survival in the second year. We summarized germination, establishment, and survival across the replication blocks for each site and population (average of 120 sown seeds) to obtain robust results. For each response variable, we built an initial maximal model containing all our environmental data as explanatory variables. After a variable reduction procedure (see Supporting Information), a final model ($n_{\text{tree}} = 500$) with the reduced set of explanatory variables was fit in order to compute partial response plots for each of the four most important variables. We had a closer look at the four most important variables, because this was the smallest number of variables explaining one of the response variables. Here, just four variables explained establishment in the first year. The prediction accuracy was tested by k -fold cross-validation (over all combinations $k = 11$ sites \times 7 populations = 77). We used the correlation coefficient (Pearson's r) of all $k = 77$ predicted values with the corresponding averaged true values as a measure of the prediction accuracy.

For cases in which both the population origin (representing genetic differences between populations) and transplant site

(representing plasticity) variables were important model predictors, we fitted a quasi-binomial generalized linear model to test for significant effects (F -test, $p < .05$) of each factor (population origin, transplant site, and their interaction). If a factor was significant, we performed post-hoc comparisons between groups (least-squares means). A significant interaction between population origin and transplant site would indicate local adaptation.

In addition, the importance of local adaptation was evaluated by regressing (F -test on quasi-binomial model fit with $p < .05$, pseudo- $R^2 = 1 - \text{model deviance}/\text{null deviance}$, Faraway, 2006) the life-history trait responses against the climatic transfer distances. This analysis was again just applied for the life-history traits explained by population origin as well as transplant site in the random forest model, which was only the case for germination. The climatic transfer distance (climatic conditions at the transplant site – 30-years average climate at the population origin) is by definition a direct measure of how far a seed has been moved away from its native climatic origin and constitutes a powerful quantitative variable to test for local adaptation (Bansal et al., 2015; Sáenz-Romero et al., 2017). The effect of climatic transfer distance was computed for winter cold (mean February air temperature), late frost (minimum air temperature in May), and water balance (CRU TS v. 4.03, Harris et al., 2014). We aggregated water balance during winter (December to February), because water balance in winter was better at explaining germination in the random forest model than water balance in spring.

All analyses were executed with R 3.6.2 (R Core Team, 2019; <https://www.R-project.org/>). For R packages, see the Supporting Information.

3 | RESULTS

3.1 | Germination increased under warmer and drier conditions – establishment and survival positively affected by cooler and moister conditions

Environmental variables related to both transplant sites and origin of population were important predictors for germination [model accuracy (coefficient of correlation): $r = .63$; Figures 2 and 3, Supporting Information Table S6]. In detail, populations originating from regions with wetter winters (Figure 3a,d) had a higher germination success. Looking at the importance of the meteorological conditions at the transplant sites, germination increased when spring was warmer (more degree hours above 5°C) and with increasing soil temperature in winter (Figure 3b,c). Our analyses revealed temperature thresholds above which a sharp increase in germination was observed, that is, at soil temperature of 1°C in winter and more than 10,000 degree hours above 5°C in spring.

Establishment in the first year and survival in the second year were best predicted by variables related to the current site-specific meteorological conditions only, whereas climate of the origins did not play any important role (model accuracy: $r = .43$ for establishment in the first year and $r = .60$ for survival in the second

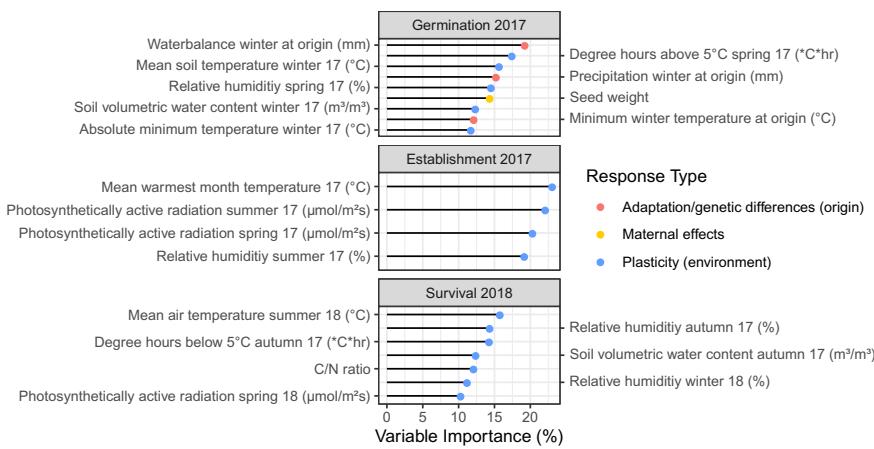


FIGURE 2 Variable importance (% increase in mean squared error) of the random forest predictors explaining germination in 2017 (germinated seeds/planted seeds), establishment in 2017 (established seeds in 2017/germinated seeds) and survival in 2018 (established seeds in 2018/established seeds in 2017). The predictors are related to the climatic origin of a population (climate average 1986–2015) or originated from meteorological data directly measured at the transplant sites. Climate and meteorological data were summarized to quarterly data for winter (December to February), spring (March to May), summer (June to August) and autumn (September to November). The influence of climatic origin is an indicator for local adaptation or genetic differences, the influence of seed weight indicates maternal effects, and the influence of the meteorological data and thus of the environment is an indicator for plasticity [Colour figure can be viewed at wileyonlinelibrary.com]

year; Figures 2, 3, Supporting Information Tables S7 and S8). Establishment in the first year (2017) increased towards sites with a cooler and moister summer (Figure 3e,h) and more radiation input from spring to summer (Figure 3f,g). Establishment and survival decreased sharply with a mean warmest month temperature above 17°C in 2017 and average summer temperatures above 18°C in 2018 (Figure 3e,i).

Survival in the second year (2018) was also favoured by higher autumn moisture availability in the first autumn in 2017 (Figure 3j,l). However, survival in 2018 was negatively affected by too moist soil conditions in autumn 2017 (Figure 3l). Moreover, survival was hampered at sites where the seedlings experienced the lowest number of cold days in their first autumn compared to the other sites (threshold at about 1,500 degree hours below 5°C in autumn 2017, Figure 3k).

3.2 | Plasticity as well as genetic differences determine germination, whereas plasticity alone drives establishment and survival

Plasticity as well as genetic differences were important for germination, as the environmental conditions of both the population origin and the transplant site had an effect on germination (Figure 2). Seed weight as a proxy for maternal seed provisioning was not amongst the four most important variables, but remained in the model with an increase in mean squared error of 14.3% and had a positive impact on germination (Figure 2, Supporting Information Figure S8).

Furthermore, we found that the environmental conditions at the transplant site and the climatic conditions at the population's origin

had comparable variable importance for germination (33% and 25% of residual deviance), respectively, but their interaction was not significant (Table 2). The missing interaction between site and population indicates a lack of local adaptation.

Moreover, germination success of all populations generally increased when transplanting seeds from their origin to environments with warmer winters, with less frost risk in spring and with drier winters (Figure 4). Thus, germination success was not the highest at the population origin, which also indicates a lack of local adaptation for the germination process and highlights the importance of environmental conditions and plasticity.

The environment of the transplant sites could explain the major part of variation in the establishment as well as survival success (Figure 2), which indicates high plasticity in these traits. Seed weight had no relevant effect on the establishment in the first year (% increase in mean squared error < 5%).

3.3 | High germination at and beyond the southern range margin, but low germination of marginal populations

Across all sites, the populations from the driest winters, that is from Poland (GD) and Spain (OM), showed by far the lowest germination success (Figures 3a,d and 5a,c, Supporting Information Tables S4 and S6). Remarkably, the site beyond the dry distribution margin in the south (PM) had significantly the highest germination success and the Polish sites within and beyond the cold distribution margin had the lowest germination success (Figure 5b,d). Moreover, germination success increased for all populations towards the warmer transplant sites (Figure 5d, Supporting Information Tables S3 and S6).

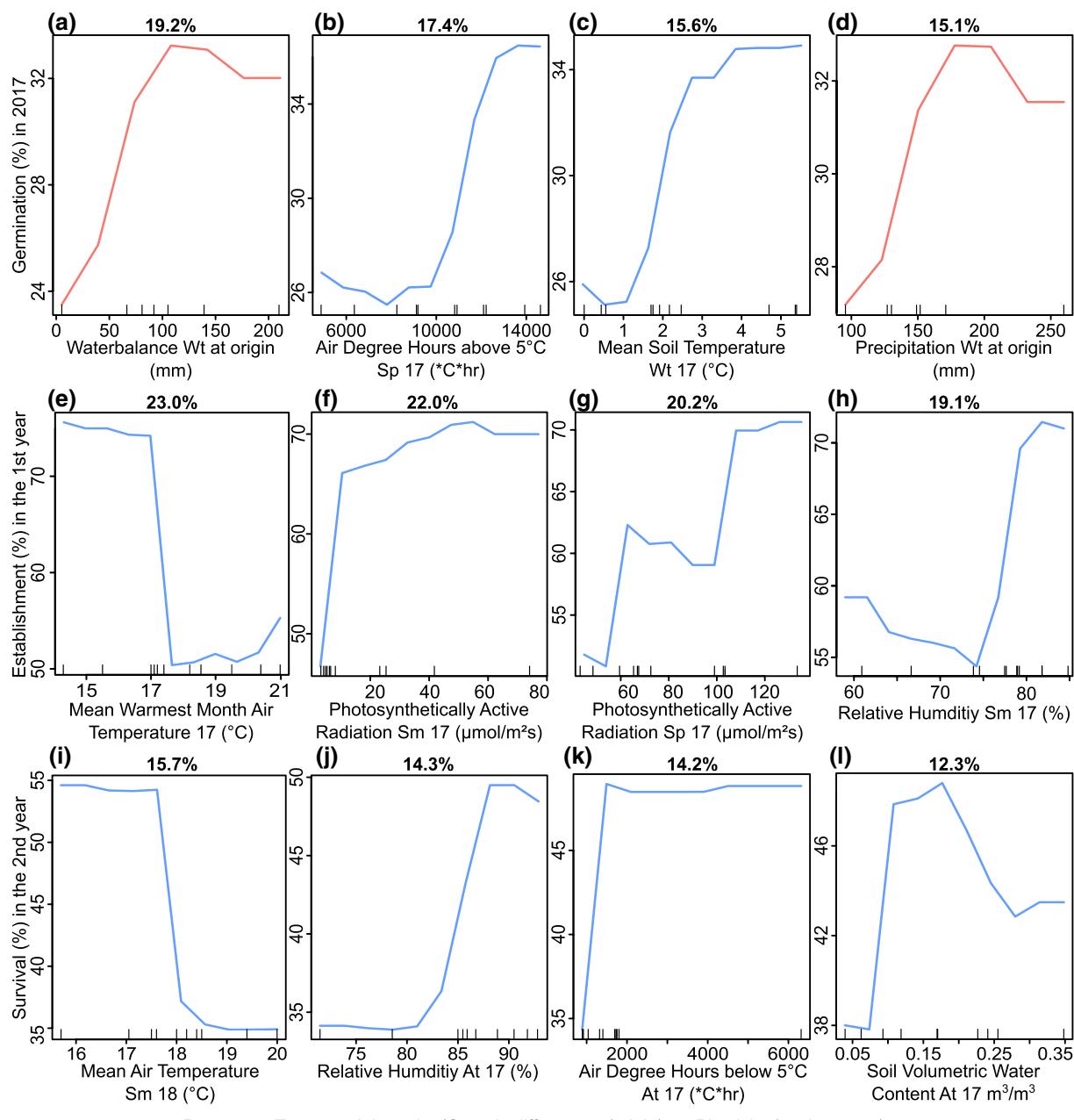


FIGURE 3 Partial plots of the four most important random forest predictors explaining (a-d) germination (%) in 2017 (germinated seeds/planted seeds), (e-h) establishment (%) in the first year (established seeds in 2017/germinated seeds) and (i-l) survival (%) in the second year (established seeds in 2018/established seeds in 2017). Please note that each partial plot only displays the mean response to one environmental factor separately, which does not represent the full range of germination /establishment /survival. The range of the y axis in each panel corresponds to the response range when only varying one predictor, while all other predictors are held constant. Colour of the response curves is according to Figure 2 [red: Adaptation/genetic differences (origin), blue: plasticity (environment)]. The importance of each predictor (% increase in mean squared error) is given on top of each panel. The predictors are related to the climatic origin of a population (climate average 1986–2015) or originated from meteorological data directly measured at the transplant sites. Climate and meteorological data were summarized to quarterly data for winter (December to February, Wt), spring (March to May, Sp), summer (June to August, Sm) and autumn (September to November, At). Climate and meteorological data at the site origin and at the transplant site are shown in Supporting Information Tables S6-S8. Upward facing ticks along the x axis display the population origins or transplant sites [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Environmental parameters affecting the earliest life stages of beech

Germination success increased with moister winter conditions at the population origin as well as with warmer winter and spring conditions at the transplant site. Moist winters may result in a higher risk of seeds being damaged by pathogens such as fungi, which is known to increase with moisture in winter at least for grass species (Mordecai, 2012; Schafer & Kotanen, 2003; Wagner & Mitschunas, 2008). Thus, moist winter conditions at the origin could possibly trigger an investment into seeds that are more resistant against pathogens and lead to higher germination success at all sites compared to the seeds originating from dry winter conditions. The increased germination success at transplant sites with warmer spring conditions follows basic biological expectations of temperature enhancing physiological processes. However, the lower germination success with cooler soils might also be induced by a higher number of freeze-thaw cycles in the seeds, as freezing events occur more

TABLE 2 Germination success explained by each factor: transplant site, population origin, and their interaction (quasi-binomial generalized linear model fit).

Factor	Degrees of freedom	Residual deviance	F	p
Null model	748	2,988.3		
site	10	2027.0	51.6	<.001
population	6	1521.2	45.2	<.001
site:population	60	1,373.7	1.3	.059

often at these sites than at sites with a soil temperature of more than 1°C in winter (Supporting Information Figure S9).

Establishment in the first and survival in the second year were only driven by the meteorological conditions at the transplant site and not by the climate of the origins. Average air temperature in summer was the most important parameter affecting the establishment and survival in the first and second year, respectively. In hotter summers, a high evapotranspiration demand might cause limited establishment and survival due to drought stress. Higher temperatures increase the vapour pressure deficit, which results in stomata closure to reduce the transpiration and hence, reduces photosynthesis and increases the risk of xylem cavitation if the tension becomes too high (Choat et al., 2018; Ruehr et al., 2016; Yuan et al., 2019). This corresponds well with our findings indicating a high importance of atmospheric moisture deficit in summer (first year) and autumn (second year) for the establishment and survival of beech. It appeared that dry conditions particularly in autumn 2017 strongly decreased survival of beech seedlings in the following year. This might be related to drought-induced reduction of carbohydrate assimilation or depletion of carbohydrate reserves (McDowell et al., 2008), which likely causes higher mortality risk for the young seedlings in the next year given their limited amounts of reserves compared to adult trees. Further, the survival in the second year improved remarkably with increasing number of cold days in autumn of the previous year. Decreasing air temperatures in autumn initiates a change from growth to storage of carbohydrates (Skomarkova et al., 2006) and hence storage of carbohydrates might be hampered by warm air temperatures in autumn. Moreover, cold temperatures during autumn are required to build up cold hardiness and thus lower autumn temperatures may better prepare young trees for the coming winter (Larcher, 2005).

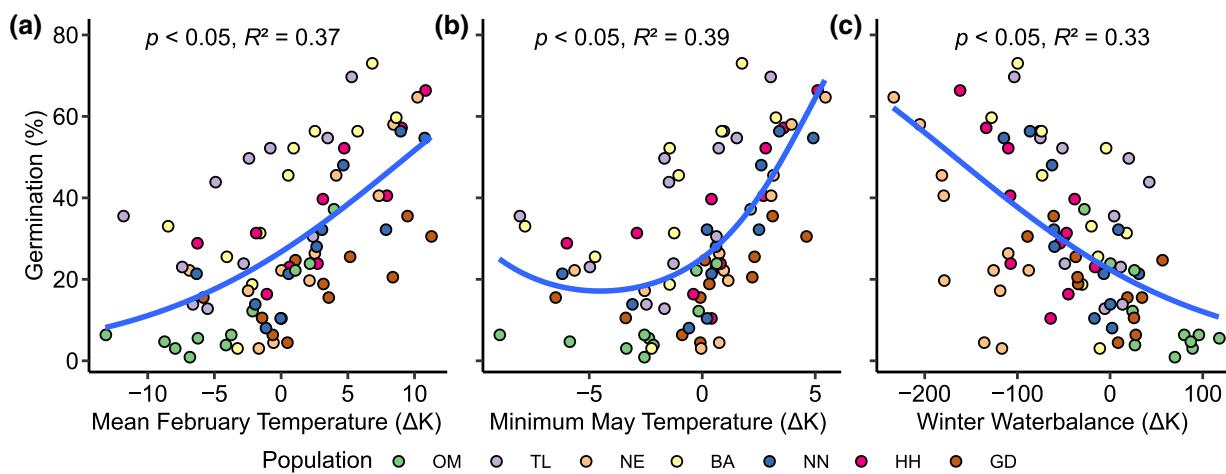


FIGURE 4 Effect of climatic transplantation (climatic transfer distance calculated for the 11 × 7 pairs of all site × population combinations) on germination in 2017. Positive values along the x axis indicate transplantation to warmer (a & b) or wetter (c) sites, negative values indicate transplantation to colder or drier sites, and the zero position represents growth at the seed origin. Populations are ordered from the southern to the north-eastern distribution margin (see Supporting Information Table S1 for population ID codes). The p-values and pseudo- R^2 were calculated from univariate regression (quasi-binomial generalized linear model) [Colour figure can be viewed at wileyonlinelibrary.com]

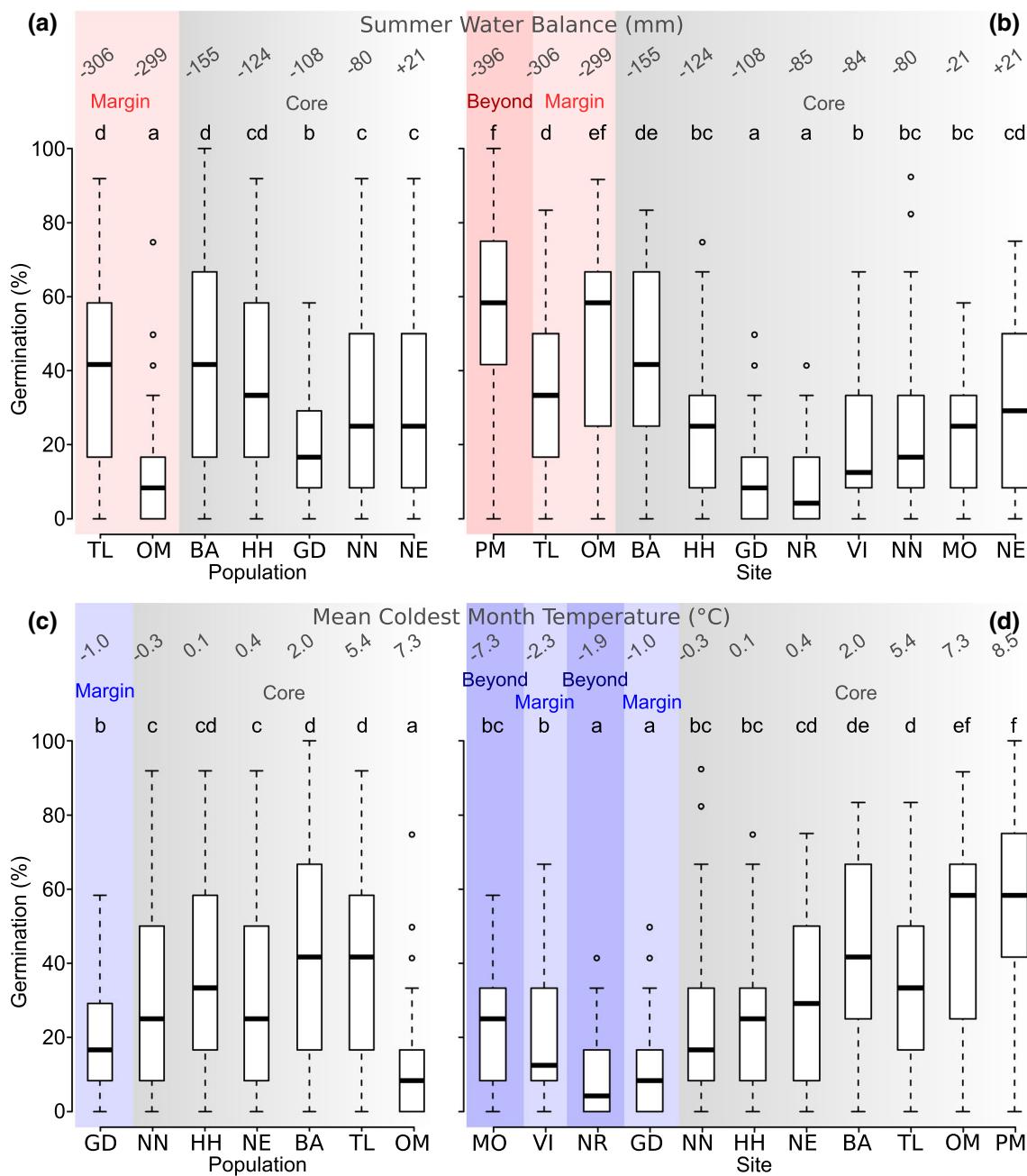


FIGURE 5 Differences in germination success in 2017 (germinated seeds/planted) between population (effect of the population origin) and transplant sites (effect of the environment). Populations and sites are ordered from the margin and beyond the margin to the core with respect to drought (a,b) and winter cold (c,d). The lower-case letters above the graphs represent significantly different groups in a least-squares means post-hoc test over a quasi-binomial generalized linear model fit including population and site (without interaction) as model predictors. See Table 1 for site ID codes and Supporting Information Table S1 for population ID codes [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Importance of plasticity, genetic differentiation, and local adaptation in early life-history traits

We found that the germination success differed among populations. The variation among populations could potentially be explained by genetic differences between the populations or by maternal effects, as germination was positively affected by seed weight. A positive influence of seed weight on germination was

also found in *Pinus* and *Quercus* species in Spain (Gómez, 2004; Urbieta et al., 2008; Zas et al., 2013). Seed provisioning is of high importance for the heterotrophic growth of seedlings. However, also other maternal effects (i.e. epigenetic modifications) could possibly influence the germination of beech (Donohue, 2009). Studies on maternal effects on germination in trees are scarce and should be increasingly conducted to better understand the mechanisms explaining the differences in germination success between populations.

No sign of local adaptation in germination success was detected as the germination success did not increase with a shorter climate transfer distance and no significant interaction between population and transplant site occurred. Likewise, establishment in the first and survival in the second year were only affected by the environment at the transplant sites and not by the population origin, revealing a high plasticity and no indications of local adaptations in these traits. This finding corresponds to our expectations that local environmental conditions, and thus plasticity, mainly shape the natural regeneration of beech. A high plasticity in beech was also found by other studies for growth, young tree survival, phenology, and in root traits (Gárate-Escamilla et al., 2019; Kramer et al., 2017; Meier & Leuschner, 2008; Vitasse et al., 2010). However, it is important to note that high plasticity is not inherently positive for local population persistence (cf. Kreyling et al., 2019), as it implies large differences in survival with changing environmental parameters, that is, limited survival under certain conditions.

The conditions of our sites along the large climatic gradient were highly diverse. Thus, we were able to study the responses of the earliest life stages in beech to various climatic conditions that are representative of the whole species distribution range. Moreover, a continent-wide mast event occurred in 2016 (Ascoli et al., 2017) and ensured high seed quality and quantity for all sites. Here, we were not able to investigate the phenology of germination. Studies by Arana et al. (2016) and Varsamis et al. (2020) found an adaptation in the timing of germination to their local environment in populations of *Nothofagus* species and *Fagus sylvatica*, respectively. While we might have missed such a temporal differentiation in germination in our data, the net outcome of establishment and survival not being influenced by seed origins but by local conditions at the transplant sites emphasizes the importance of plasticity over genetic adaptation in the studied early life-history traits.

4.3 | Potential for regeneration across the distribution range from the south to the north

Germination was favoured by warmer and drier conditions and maximized even further south than the current contracting edge, but juvenile survival decreased strongly with heat and drought. Hence, germination and survival are driven by different, even opposite environmental factors. The lack of regeneration at the rear edge could exacerbate the range loss (Peñuelas et al., 2007).

Low survival was also found in parts of the distribution centre, as the year 2018 had been one of the driest and hottest years ever recorded in Switzerland and Germany (Buras et al., 2020; Schuldt et al., 2020). This indicates that marginality is not just induced geographically but rather ecologically (e.g. by climatic and soil characteristics; Bolte et al., 2016; Vilà-Cabrera et al., 2019). A vulnerability of beech to drought in the central part of its distribution was also found for adult trees during the summer drought in 2018 (Schuldt et al., 2020). This is supported by other studies that found that adult

beech trees were sensitive to drought in the centre of the distribution range (Cavin & Jump, 2017; Muffler et al., 2020). Thus, parts of the distribution range centre of beech, for example our site BA in south-western Germany, are likely becoming ecologically marginal for adult trees and for natural regeneration, as the likelihood of drought events in summer is expected to increase in the near future at mid latitudes in Europe (Kovats et al., 2014). In addition, species persistence at marginal sites likely also depends on the competition with better adapted species, such as the less drought sensitive evergreen tree species *Quercus ilex* L. at the southern distribution margin (Barbeta et al., 2019).

At cold marginal sites, the high plasticity in the early life-history traits may allow for increasing germination success with increasing temperatures and may thus facilitate natural regeneration even beyond the current cold margin in times of climate change. However, the potential for natural regeneration (survival) was three times higher at the northern than the north-eastern distribution margin in our study (Supporting Information Table S3). Water stress over summer and exceptionally moist conditions in autumn may explain the low survival at the north-eastern margin, as too moist soil conditions are stressful for beech growth (Leuschner & Ellenberg, 2017). These findings call for subsequent regional studies with more study sites ranging from cold-dry to cold-wet sites, in order to better explain the potential for natural regeneration for the projected expansion of beech beyond the current cold distribution margin (Kramer et al., 2010; Saltre et al., 2015).

4.4 | Implications and outlook

Although no sign of local genetic adaptation for early life-history traits was detected, we cannot exclude genetic moderation of the observed early-stage plasticity in beech. Genetic variation in plastic responses is suggested to be an important predictor of species vulnerabilities to climate change (Kelly, 2019). Plasticity in fitness traits may moderate and exceed the role of static local adaptation in adaptive processes during climate change in the centre of species distribution ranges, in particular for long-living trees (Benito Garzón et al., 2019; Stojnić et al., 2018). However, the interaction of evolutionary local adaptation and plasticity under extreme weather events still remains unclear (Cuervo-Alarcon et al., 2021) and should be subject of future research, in particular at species distribution margins with high selection pressure and strong evolutionary dynamics (Hampe & Petit, 2005).

Assisted gene flow and migration of pre-adapted non-local populations is currently discussed as a possible adaptation strategy to changing climatic conditions in forestry and nature conservation (e.g. Aitken & Bemmels, 2016). Our results, however, demonstrated a surprisingly high plasticity of local beech populations in the early life-history traits and thus an ability for short-term acclimatization, at least at the recruitment stage. At the same time, our results also indicate that this plasticity might not be sufficient under warm and

dry conditions considering the very low survival of beech seedlings after 2 years.

Overall, the insights of our study into natural regeneration patterns of beech under changing climatic conditions are a valuable contribution to improve species distribution models. The potential for natural regeneration under warmer and drier climatic conditions has so far been understudied and requires more experimental investigations. Moreover, increasing temperature and occurrence of drought are not only threats for beech but also for other tree species worldwide (Allen et al., 2010; Anderegg et al., 2013; Brodribb et al., 2020). Thus, we call for similar and long-term studies on other economically and ecologically important tree species that investigate the response of natural regeneration to changing climatic conditions. An ability for acclimatization or adaptation in the earliest life stages of a tree species could mitigate the effects of increasing heat and occurrence of drought by enabling local populations to persist under these conditions or by facilitating a range expansion.

ACKNOWLEDGMENTS

We thank Jörg Brunet, Xavi Buqueras, Christer Karlsson, Per Linder, Nicolas Manuel, the Bayerische Staatsforsten, the commune of Corcelles-Cormondrèche in Switzerland, the forest management of the University of Greifswald, Forstamt Annweiler, Forstbetrieb Kaisheim, Forstrevier Klingenmünster, the International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), the National Forest Holding of Poland's State Forests in Toruń, the National Property Board Sweden, the Office National des Forêts, the Parc Natural del Montseny, the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR), and the Tranemåla Foundation for assistance during site selection and access to the sites. We also thank Sören Kaack for his help during field sampling, and Anne Bohm, Sebastian Fuchs, Jennifer Gilles, Kai Hobritz and Sebastian Lorenz for the analysis of soil metadata. The study was funded by the DFG (Deutsche Forschungsgemeinschaft) Research Training Group RESPONSE (DFG RTG 2010). Fieldwork in Poland was also funded by the Forest Research Institute in Poland. Adrià Barbata and Josep Peñuelas were funded by a European Research Council Synergy Grant (ERC-SyG-2013-610028 IMBALANCE-P). Open Access funding enabled and organized by Projekt DEAL Agreement (University of Greifswald).

AUTHOR CONTRIBUTIONS

J.K. and L.M. conceived the ideas; R.W., J.K., I.B. and L.M. conducted the experiment and all co-authors assisted during the set up; J.S. and L.M. organized the data sampling with contributions from S.H.; L.M. analysed the data with contributions from R.W., J.S. and J.K.; and L.M. led the writing with contributions from all co-authors.

DATA AVAILABILITY STATEMENT

All data relevant for the analyses can be found in the Supporting Information.

ORCID

- Lena Muffler  <https://orcid.org/0000-0001-8227-7297>
- Jonas Schmeddes  <https://orcid.org/0000-0002-3425-3829>
- Robert Weigel  <https://orcid.org/0000-0001-9685-6783>
- Adrià Barbata  <https://orcid.org/0000-0002-8357-1719>
- Ilka Beil  <https://orcid.org/0000-0003-1136-1373>
- Andreas Bolte  <https://orcid.org/0000-0003-4106-0387>
- Constanze Buhk  <https://orcid.org/0000-0003-1408-0446>
- Geoffrey Klein  <https://orcid.org/0000-0001-7298-633X>
- Marcin Klisz  <https://orcid.org/0000-0001-9486-6988>
- Magnus Löf  <https://orcid.org/0000-0002-9173-2156>
- Josep Peñuelas  <https://orcid.org/0000-0002-7215-0150>
- Léonard Schneider  <https://orcid.org/0000-0001-5688-7745>
- Yann Vitasse  <https://orcid.org/0000-0002-7454-505X>
- Juergen Kreyling  <https://orcid.org/0000-0001-8489-7289>

REFERENCES

- Aitken, S. N., & Bemmels, J. B. (2016). Time to get moving: Assisted gene flow of forest trees. *Evolutionary Applications*, 9, 271–290. <https://doi.org/10.1111/eva.12293>
- Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T., & Curtis-McLane, S. (2008). Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111. <https://doi.org/10.1111/j.1752-4571.2007.00013.x>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D. D., Hogg, E. H. (T.), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., & Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259, 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderegg, W. R. L., Kane, J. M., & Anderegg, L. D. L. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3, 30–36. <https://doi.org/10.1038/nclimate1635>
- Arana, M. V., Gonzalez-Polo, M., Martinez-Meier, A., Gallo, L. A., Benech-Arnold, R. L., Sánchez, R. A., & Batlla, D. (2016). Seed dormancy responses to temperature relate to *Nothofagus* species distribution and determine temporal patterns of germination across altitudes in Patagonia. *New Phytologist*, 209, 507–520. <https://doi.org/10.1111/nph.13606>
- Ascoli, D., Maringer, J., Hackett-Pain, A., Conedera, M., Drobyshev, I., Motta, R., Cirolini, M., Kantorowicz, W., Zang, C., Schueler, S., Croisé, L., Piussi, P., Berretti, R., Palaghianu, C., Westergren, M., Lageard, J. G. A., Burkart, A., Gehrig Bichsel, R., Thomas, P. A., ... Vacchiano, G. (2017). Two centuries of mast data for European beech and Norway spruce across the European continent. *Ecology*, 98, 1473. <https://doi.org/10.1002/ecy.1785>
- Bansal, S., St Clair, J. B., Harrington, C. A., & Gould, P. J. (2015). Impact of climate change on cold hardiness of Douglas-fir (*Pseudotsuga menziesii*): Environmental and genetic considerations. *Global Change Biology*, 21, 3814–3826. <https://doi.org/10.1111/gcb.12958>
- Barbeta, A., Camarero, J. J., Sangüesa-Barreda, G., Muffler, L., & Peñuelas, J. (2019). Contrasting effects of fog frequency on the radial growth of two tree species in a Mediterranean-temperate eco-tone. *Agricultural and Forest Meteorology*, 264, 297–308. <https://doi.org/10.1016/j.agrformet.2018.10.020>
- Barna, M. (2011). Natural regeneration of *Fagus sylvatica* L.: A review. *Austrian Journal of Forest Science*, 128, 71–91.
- Bartsch, N., Lüpke, B. V., & Röhrlig, E. (2020). *Waldbau auf ökologischer Grundlage* (8th ed.). Ulmer Verlag.

- Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). ΔTraitSDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, 222, 1757–1765. <https://doi.org/10.1111/nph.15716>
- Bolte, A., Czajkowski, T., Cocozza, C., Tognetti, R., de Miguel, M., Pšidová, E., Ditmarová, L., Dinca, L., Delzon, S., Cochard, H., Ræbild, A., de Luis, M., Cvjetkovic, B., Heiri, C., & Müller, J. (2016). Desiccation and mortality dynamics in seedlings of different European beech (*Fagus sylvatica* L.) populations under extreme drought conditions. *Frontiers in Plant Science*, 7, e751. <https://doi.org/10.3389/fpls.2016.00751>
- Bolte, A., Czajkowski, T., & Kompa, T. (2007). The north-eastern distribution range of European beech – a review. *Forestry*, 80, 413–429. <https://doi.org/10.1093/forestry/cpm028>
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32. <https://doi.org/10.1023/A:1010933404324>
- Brodribb, T. J., Powers, J., Cochard, H., & Choat, B. (2020). Hanging by a thread? Forests and drought. *Science*, 368, 261–266. <https://doi.org/10.1126/science.aat7631>
- Buras, A., Rammig, A., & Zang, C. S. (2020). Quantifying impacts of the 2018 drought on European ecosystems in comparison to 2003. *Biogeosciences*, 17, 1655–1672. <https://doi.org/10.5194/bg-17-1655-2020>
- Cavin, L., & Jump, A. S. (2017). Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Global Change Biology*, 23, 362–379. <https://doi.org/10.1111/gcb.13366>
- Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R., & Medlyn, B. E. (2018). Triggers of tree mortality under drought. *Nature*, 558, 531–539. <https://doi.org/10.1038/s41586-018-0240-x>
- Choler, P., Erschbamer, B., Tribsch, A., Gielly, L., & Taberlet, P. (2004). Genetic introgression as a potential to widen a species' niche: Insights from alpine *Carex curvula*. *Proceedings of the National Academy of Sciences USA*, 101, 171–176. <https://doi.org/10.1073/pnas.22372>
- Cuervo-Alarcon, L., Arend, M., Müller, M., Sperisen, C., Finkeldey, R., & Krutovsky, K. V. (2021). A candidate gene association analysis identifies SNPs potentially involved in drought tolerance in European beech (*Fagus sylvatica* L.). *Scientific Reports*, 11, 2386. <https://doi.org/10.1038/s41598-021-81594-w>
- Donohue, K. (2009). Completing the cycle: Maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1059–1074. <https://doi.org/10.1098/rstb.2008.0291>
- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K., & Willis, C. G. (2010). Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, 41, 293–319. <https://doi.org/10.1146/annurev-ecolsys-102209-144715>
- Dulamsuren, C., Hauck, M., & Leuschner, C. (2013). Seedling emergence and establishment of *Pinus sylvestris* in the Mongolian forest-steppe ecotone. *Plant Ecology*, 214, 139–152. <https://doi.org/10.1007/s11258-012-0152-z>
- Fang, J., & Lechowicz, M. J. (2006). Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. *Journal of Biogeography*, 33, 1804–1819. <https://doi.org/10.1111/j.1365-2699.2006.01533.x>
- Faraway, J. J. (2006). Extending the linear model with R. Chapman & Hall / CRC.
- Gárate-Escamilla, H., Hampe, A., Vizcaíno-Palomar, N., Robson, T. M., & Benito Garzón, M. (2019). Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change. *Global Ecology and Biogeography*, 28, 1336–1350. <https://doi.org/10.1111/geb.12936>
- Giesecke, T., Hickler, T., Kunkel, T., Sykes, M. T., & Bradshaw, R. H. W. (2007). Towards an understanding of the Holocene distribution of *Fagus sylvatica* L. *Journal of Biogeography*, 34, 118–131. <https://doi.org/10.1111/j.1365-2699.2006.01580.x>
- Gómez, J. M. (2004). Bigger is not always better: Conflicting selective pressures on seed size in *Quercus ilex*. *Evolution*, 58, 71–80. <https://doi.org/10.1554/02-617>
- Hampe, A., & Petit, R. J. (2005). Conserving biodiversity under climate change: The rear edge matters. *Ecology Letters*, 8, 461–467. <https://doi.org/10.1111/j.1461-0248.2005.00739.x>
- Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 dataset. *International Journal of Climatology*, 34, 623–642. <https://doi.org/10.1002/joc.3711>
- Jackson, S. T., Betancourt, J. L., Booth, R. K., & Gray, S. T. (2009). Ecology and the ratchet of events: Climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences USA*, 106, 19685–19692. <https://doi.org/10.1073/pnas.0901644106>
- Jump, A. S., Hunt, J. M., Martínez-Izquierdo, J. A., & Peñuelas, J. (2006). Natural selection and climate change: Temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology*, 15, 3469–3480. <https://doi.org/10.1111/j.1365-294X.2006.03027.x>
- Jump, A. S., Hunt, J. M., & Peñuelas, J. (2006). Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, 12, 2163–2174. <https://doi.org/10.1111/j.1365-2486.2006.01250.x>
- Jump, A. S., & Peñuelas, J. (2005). Running to stand still: Adaptation and the response of plants to rapid climate change. *Ecology Letters*, 8, 1010–1020. <https://doi.org/10.1111/j.1461-0248.2005.00796.x>
- Kawecki, T. J. (2008). Adaptation to marginal habitats. *Annual Review of Ecology, Evolution, and Systematics*, 39, 321–342. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095622>
- Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7, 1225–1241. <https://doi.org/10.1111/j.1461-0248.2004.00684.x>
- Kelly, M. (2019). Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20180176. <https://doi.org/10.1098/rstb.2018.0176>
- Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M. T., & de Winter, W. (2010). Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change - range, abundance, genetic diversity and adaptive response. *Forest Ecology and Management*, 259, 2213–2222. <https://doi.org/10.1016/j.foreco.2009.12.023>
- Kramer, K., Ducousoo, A., Gömöry, D., Hansen, J. K., Ionita, L., Liesebach, M., Lorentz, A., Schüler, S., Sulikowska, M., de Vries, S., & von Wühlisch, G. (2017). Chilling and forcing requirements for foliage bud burst of European beech (*Fagus sylvatica* L.) differ between provenances and are phenotypically plastic. *Agricultural and Forest Meteorology*, 234–235, 172–181. <https://doi.org/10.1016/j.agrformet.2016.12.002>
- Kreyling, J., Puechmaille, S. J., Malyshev, A. V., & Valladares, F. (2019). Phenotypic plasticity closely linked to climate at origin and resulting in increased mortality under warming and frost stress in a common grass. *Ecology and Evolution*, 9, 1344–1352. <https://doi.org/10.1002/ece3.4848>
- Kovats, R. S., Valentini, R., Bouwer, L. M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., & Soussana, J.-F. (2014). 2014: Europe. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebti, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects* (pp. 1267–1326). Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge, UK and New York, NY: Cambridge University Press.
- Larcher, W. (2005). Climatic constraints drive the evolution of low temperature resistance in woody plants. *Journal of Agricultural Meteorology*, 61, 189–202. <https://doi.org/10.2480/agrmet.61.189>

- Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1763–1768. <https://doi.org/10.1126/science.1157704>
- Leuschner, C., & Ellenberg, H. (2017). *Vegetation ecology of Central Europe* (Revised and extended version of the 6th German edition). Springer.
- Leuschner, C., Meier, I. C., & Hertel, D. (2006). On the niche breadth of *Fagus sylvatica*: Soil nutrient status in 50 Central European beech stands on a broad range of bedrock types. *Annals of Forest Science*, 63, 355–368. <https://doi.org/10.1051/forest:2006016>
- Magri, D., Vendramin, G. G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latałowa, M., Litt, T., Paule, L., Roure, J. M., Tantau, I., Van Der Knaap, W. O., Petit, R. J., & De Beaulieu, J.-L. (2006). A new scenario for the Quaternary history of European beech populations: Palaeobotanical evidence and genetic consequences. *New Phytologist*, 171, 199–221. <https://doi.org/10.1111/j.1469-8137.2006.01740.x>
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>
- Meier, I. C., & Leuschner, C. (2008). Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiology*, 28(2), 297–309. <https://doi.org/10.1093/treephys/28.2.297>
- Mordecai, E. A. (2012). Soil moisture and fungi affect seed survival in California grassland annual plants. *PLoS ONE*, 7, e39083. <https://doi.org/10.1371/journal.pone.0039083.t001>
- Muffler, L., Weigel, R., Hacket-Pain, A. J., Klisz, M., Maaten, E., Wilmking, M., Kreyling, J., & Maaten-Theunissen, M. (2020). Lowest drought sensitivity and decreasing growth synchrony towards the dry distribution margin of European beech. *Journal of Biogeography*, 47, 1910–1921. <https://doi.org/10.1111/jbi.13884>
- Övergaard, R., Gemmel, P., & Karlsson, M. (2007). Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry*, 80, 555–565. <https://doi.org/10.1093/forestry/cpm020>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Paul, J. R., Sheth, S. N., & Angert, A. L. (2011). Quantifying the impact of gene flow on phenotype-environment mismatch: A demonstration with the scarlet monkeyflower *Mimulus cardinalis*. *The American Naturalist*, 178(Suppl 1), S62–S79. <https://doi.org/10.1086/661781>
- Peñuelas, J., Ogaya, R., Boada, M., & Jump, S. A. (2007). Migration, invasion and decline: Changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography*, 30, 829–837. <https://doi.org/10.1111/j.2007.0906-7590.05247.x>
- Petit, R. J., & Hampe, A. (2006). Some evolutionary consequences of being a tree. *Annual Review of Ecology, Evolution, and Systematics*, 37, 187–214. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110215>
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ruehr, N. K., Gast, A., Weber, C., Daub, B., & Arneth, A. (2016). Water availability as dominant control of heat stress responses in two contrasting tree species. *Tree Physiology*, 36, 164–178. <https://doi.org/10.1093/treephys/tpv102>
- Rumpf, S. B., Hülber, K., Klonner, G., Moser, D., Schütz, M., Wessely, J., Willner, W., Zimmermann, N. E., & Dullinger, S. (2018). Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences USA*, 115, 1848–1853. <https://doi.org/10.1073/pnas.1713936115>
- Sáenz-Romero, C., Lamy, J.-B., Ducouso, A., Musch, B., Ehrenmann, F., Delzon, S., Cavers, S., Chatupka, W., Dağdaş, S., Hansen, J. K., Lee, S. J., Liesebach, M., Rau, H.-M., Psomas, A., Schneek, V., Steiner, W., & Zimmermann, N. E., & Kremer, A. (2017). Adaptive and plastic responses of *Quercus petraea* populations to climate across Europe. *Global Change Biology*, 23, 2831–2847. <https://doi.org/10.1111/gcb.13576>
- Saltre, F., Duputie, A., Gaucherel, C., & Chuine, I. (2015). How climate, migration ability and habitat fragmentation affect the projected future distribution of European beech. *Global Change Biology*, 21, 897–910. <https://doi.org/10.1111/gcb.12771>
- Savolainen, O., Pyhäjärvi, T., & Knürr, T. (2007). Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, 38, 595–619. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095646>
- Schafer, M., & Kotanen, P. M. (2003). The influence of soil moisture on losses of buried seeds to fungi. *Acta Oecologica*, 24, 255–263. <https://doi.org/10.1016/j.actao.2003.09.001>
- Scherrer, D., Vitasse, Y., Guisan, A., Wohlgemuth, T., & Lischke, H. (2020). Competition and demography rather than dispersal limitation slow down upward shifts of trees' upper elevation limits in the Alps. *Journal of Ecology*, 108(6), 2416–2430. <https://doi.org/10.1111/1365-2745.13451>
- Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T. E. E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D. B., Rammig, A., ... Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic and Applied Ecology*, 45, 86–103. <https://doi.org/10.1016/j.baae.2020.04.003>
- Skomarkova, M. V., Vaganov, E. A., Mund, M., Knöhl, A., Linke, P., Boerner, A., & Schulze, E.-D. (2006). Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. *Trees*, 20, 571–586. <https://doi.org/10.1007/s00468-006-0072-4>
- Stojnić, S., Suchocka, M., Benito-Garzón, M., Torres-Ruiz, J. M., Cochard, H., Bolte, A., Cocozza, C., Cvjetković, B., de Luis, M., Martinez-Vilalta, J., Raebild, A., Tognetti, R., & Delzon, S. (2018). Variation in xylem vulnerability to embolism in European beech from geographically marginal populations. *Tree Physiology*, 38, 173–185. <https://doi.org/10.1093/treephys/tpx128>
- Suszka, B., Müller, C., & Bonnet-Masimbert, M. (1996). *Seeds of forest broadleaves: From harvest to sowing*. Inst. National de la Recherche Agronomique.
- Sykes, M. T., Prentice, I. C., & Cramer, W. (1996). A bioclimatic model for the potential distributions of North European tree species under present and future climates. *Journal of Biogeography*, 23, 203–233.
- Tachiki, Y., & Iwasa, Y. (2010). Both seedling banks and specialist seed predators promote the evolution of synchronized and intermittent reproduction (masting) in trees. *Journal of Ecology*, 98, 1398–1408. <https://doi.org/10.1111/j.1365-2745.2010.01729.x>
- Thiel, D., Kreyling, J., Backhaus, S., Beierkuhnlein, C., Buhk, C., Egen, K., Huber, G., Konnert, M., Nagy, L., & Jentsch, A. (2014). Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research*, 133, 247–260. <https://doi.org/10.1007/s10342-013-0750-x>
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>

- Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences USA*, 102, 8245–8250. <https://doi.org/10.1073/pnas.0409902102>
- Urbíeta, I. R., Pérez-Ramos, I. M., Zavala, M. A., Marañón, T., & Kobe, R. K. (2008). Soil water content and emergence time control seedling establishment in three co-occurring Mediterranean oak species. *Canadian Journal of Forest Research*, 38, 2382–2393. <https://doi.org/10.1139/X08-089>
- Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., & Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, 17, 1351–1364. <https://doi.org/10.1111/ele.12348>
- van der Maaten, E., Hamann, A., van der Maaten-Theunissen, M., Bergsma, A., Hengeveld, G., van Lammeren, R., Mohren, F., Nabuurs, G.-J., Terhürne, R., & Sterck, F. (2017). Species distribution models predict temporal but not spatial variation in forest growth. *Ecology and Evolution*, 7, 2585–2594. <https://doi.org/10.1002/ece3.2696>
- Varsamis, G., Merou, T., Takos, I., Malesios, C., Manolis, A., & Papageorgiou, A. C. (2020). Seed adaptive traits of *Fagus sylvatica* populations in northeastern Greece. *Forest Science*, 66, 403–415. <https://doi.org/10.1093/forsci/fxaa003>
- Vilà-Cabrera, A., Premoli, A. C., & Jump, A. S. (2019). Refining predictions of population decline at species' rear edges. *Global Change Biology*, 25, 1549–1560. <https://doi.org/10.1111/gcb.14597>
- Vitasse, Y., Bresson, C. C., Kremer, A., Michalet, R., & Delzon, S. (2010). Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology*, 24, 1211–1218. <https://doi.org/10.1111/j.1365-2435.2010.01748.x>
- Vornam, B., Decarli, N., & Gailing, O. (2004). Spatial distribution of genetic variation in a natural beech stand (*Fagus sylvatica* L.) based on microsatellite markers. *Conservation Genetics*, 5, 561–570. <https://doi.org/10.1023/B:COGE.00000041025.82917.ac>
- Wagner, M., & Mitschunas, N. (2008). Fungal effects on seed bank persistence and potential applications in weed biocontrol: A review. *Basic and Applied Ecology*, 9, 191–203. <https://doi.org/10.1016/j.baae.2007.02.003>
- Wang, F., Israel, D., Ramírez-Valiente, J.-A., Sánchez-Gómez, D., Aranda, I., Aphalo, P. J., & Robson, T. M. (2021). Seedlings from marginal and core populations of European beech (*Fagus sylvatica* L.) respond differently to imposed drought and shade. *Trees*, 35, 53–67. <https://doi.org/10.1007/s00468-020-02011-9>
- Williams, M. I., & Dumroese, R. K. (2013). Preparing for climate change: Forestry and assisted migration. *Journal of Forestry*, 111, 287–297. <https://doi.org/10.5849/jof.13-016>
- Yuan, W., Zheng, Y. I., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A. K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J. E. M. S., Qin, Z., Quine, T., ... Yang, S. (2019). Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Science Advances*, 5, eaax1396. <https://doi.org/10.1126/sciadv.aax1396>
- Zas, R., Cendán, C., & Sampredo, L. (2013). Mediation of seed provisioning in the transmission of environmental maternal effects in Maritime pine (*Pinus pinaster* Aiton). *Heredity*, 111, 248–255. <https://doi.org/10.1038/hdy.2013.44>
- Kovats, R. S., Valentini, R., Bouwer, L. M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., & Soussana, J.-F. (2014). 2014: Europe. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebti, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects* (pp. 1267–1326). Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change. Cambridge, UK and New York, NY: Cambridge University Press.

BIOSKETCH

Lena Muffler is interested in global change and the impact of extreme weather events (winter cold, late frost and drought) on forest ecosystems. In her PhD studies she focused on the in situ responses of European beech (i.e. local adaptation and phenotypic plasticity) to environmental changes by applying a combination of various methods such as ecological experiments, dendroecology and statistical modelling. She and the co-authors collaborate on questions on the response of tree species to climate change.

SUPPORTING INFORMATION

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

How to cite this article: Muffler L, Schmeddes J, Weigel R, et al. High plasticity in germination and establishment success in the dominant forest tree *Fagus sylvatica* across Europe. *Global Ecol Biogeogr*. 2021;30:1583–1596. <https://doi.org/10.1111/geb.13320>