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Assisted tree migration can preserve the European forest carbon sink under climate change

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Climate change threatens the role of European forests as a long-term carbon sink. Assisted migration aims to increase the resilience of forest tree populations to climate change, using species-specific climatic limits and local adaptations through transferring seed provenances. We modelled assisted migration scenarios for seven main European tree species and analysed the effects of species and seed provenance selection, accounting for environmental and genetic variations, on the annual above-ground carbon sink of regrowing juvenile forests. To increase forest resilience, coniferous trees need to be replaced by deciduous species over large parts of their distribution. If local seed provenances are used, this would result in a decrease of the current carbon sink (40 TgC yr^{-1}) by 34–41% by 2061–2080. However, if seed provenances adapted to future climates are used, current sinks could be maintained or even increased to 48–60 TgC yr^{-1}.

By removing carbon dioxide from the atmosphere, forests can play a crucial role in limiting the rise in global annual temperatures to 1.5–2 °C (refs. 1,2). European forests cover ~35% of the total land surface and store ~9.8 Tg of carbon, with an average annual sequestration of 155 TgC between 2010 and 2020[3]. However, climate change-induced disturbances pose a serious threat to this carbon pool[4–6] and other forest ecosystem services. Therefore, adaptation actions are required to maintain ecosystem services and improve the resilience of forests towards further climate warming[7–10]. To use the carbon sequestration capacity of forests, tree planting and forest restoration have been suggested as nature-based solutions to mitigate global warming[11–14]. The selection of tree species, suitable forest reproductive material and the promotion of mixed forests[14,15] are expected to play important roles in forest adaptation and climate change (CC) mitigation[16,17].

Owing to the strong impact of CC on tree species distributions[18–20] and the limited migration capacity of trees[21,22], forest restoration and adaptation will need to take the site suitability of species and populations into account. Moreover, restricted gene flow, as well as the limited capacity of trees to adapt genetically to the fast pace of CC, will result in serious maladaptations (but see ref. 23), local species extinctions and a reduction of ecosystem services within the remaining forests[23–26]. Therefore, assisted migration (AM) of tree species and seed provenances have been proposed as measures to use species-specific climatic limits and local adaptations to improve the adaptive capacity

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Table 1 | Suitable cultivation areas and their variation

	Cultivation area (1,000 km²)			Change in cultivation area (%)	
	Contemporary (1991–2010)	RCP 4.5 (2061–2080)	RCP 8.5 (2061–2080)	RCP 4.5 (2061–2080)	RCP 8.5 (2061–2080)
Species	Area	Area	Area		
A. alba	173.03±11.1	5.33±0.9	1.25±0.3	−97.09±0.01	−99.29±0.01
P. abies	647.8±25.6	349.5±49.5	219.76±47.1	−45.5±0.03	−66.00±0.02
P. sylvestris	528.88±26.5	610.45±71.0	630.84±90.4	17.89±0.04	27.00±0.06
L. decidua	21.48±2.1	4.92±0.9	3.77±0.9	−76.83±0.01	−82.45±0.01
F. sylvatica	48.86±4.8	89.89±15.6	84.88±20.9	85.69±0.14	77.11±0.15
Q. petraea	72.27±11.0	8.07±1.5	14.27±3.6	−89.17±0.00	−81.00±0.01
Q. robur	77.77±8.0	501.94±65.4	615.34±89.9	493.01±0.25	601.00±0.21

The potential cultivation areas, given in 1,000 km^2, show where each of the seven species has the highest climatic suitability in contemporary climate (1991–2010) and projected CC scenarios RCP 4.5 and 8.5 for the period 2061–2080 according to the ensemble SDMs. The cultivation areas were calculated from ensemble SDMs for each species, while '±' is the standard deviation of the cultivation area due to the ten SDMs in contemporary climate and the combinations of ten SDMs and five RCMs under CC scenarios RCP 4.5 and 8.5. See Supplementary Table 1 for details.

and resilience of forests while maintaining the provision of ecosystem services[27–31]. While AM can be grouped into 'assisted gene flow' referring to the transfer of seed provenances to new locations within the present distribution range and 'assisted species migration' referring to moving seed provenances beyond the present species range, we refer to AM as a more generic term including both types[28,32]. Despite growing evidence for increasing mismatches between local adaptations and the changing climate for forest trees around the world[33,34], no comprehensive multispecies, continent-wide analysis of the needs and effects of AM exists to date, limiting our understanding of how local adaptations affect major ecosystem services such as the forest carbon sink (CS). On the European scale, such a study could motivate AM schemes for forest trees across the ranges of species and support policies on nature-based CC mitigation strategies.

Here we demonstrate the implementation of AM in reforestation of seven major European trees by analysing a dataset of 587 range-wide provenance trials, evaluating 2,964 provenances from their entire distribution (Supplementary Table 1 and Supplementary Figs. 1–3) and combining shifts of species distributions with population transfer models. We quantify the combined effects of adapting the selection of species and seed provenances on annual above-ground CS of European forests. Although the positive effects of species mixtures on productivity are well-documented[14], our analysis is limited to single-species forests at a level of a 1 × 1 km grid cell to focus on the direct effects of seed provenance selection.

First, we selected the climatically best-suited species (species with the highest probability of occurrence) at a spatial resolution of a 1 × 1 km grid cell with multimodel ensemble species distribution models (SDMs)[35] (Supplementary Table 6) and used the underlying single-model SDMs for uncertainty analysis. Second, for each grid cell with the best-suited species, we identified the best-fitting seed provenances by modelling their annual CS. For a realistic estimation of CS, we restricted our predictions to those grid cells of the land surface, where at least 50% of the area is covered by forests[36]. Thus, our models address reforestation on previous forest sites (forest regrowth), which allows us to assume constant carbon stocks in forest soils given their high variation and uncertain response to CC and forest development[37]. To identify the best-fitting seed provenances, we developed universal response functions (URFs) for the seven tree species *Abies alba, Larix decidua, Picea abies, Pinus sylvestris, Fagus sylvatica, Quercus robur* and *Quercus petraea*. These models account for environmental and genetic trait variation in above-ground CS[38,39] and allow estimates of CS to forest regrowth until stand ages of 40 years because of (1) the mitigation potential of tree planting and reforestation needs to enfold high sequestration capacity as soon as possible to limit further global warming and (2) the limitations of the provenance dataset, which covers predominantly trials with ages up to 40 years. To use the URF for meaningful AM applications, tree species and seed source occurrences across Europe were grouped into species-specific seed provenance clusters (SPC) of climatically and geographically similar groups to correspond to range-wide local adaptation patterns (Supplementary Table 8). To quantify the effects of AM, two seed provenance sourcing scenarios were used: (1) 'local seeds' where the climate of the planting location and the historical climate of seed origin were identical and geographically proximate and (2) 'adapted seeds', where SPC producing highest CS for the climate of the planting location were selected irrespective of their climatic and geographic proximity to the planting location (Supplementary Fig. 4). These scenarios were tested for contemporary climate (1991–2010) and the period 2061–2080 under the two CC scenarios representative concentration pathways RCP 4.5 and RCP 8.5 (ref. 40). For each CC scenario, five bias-corrected regional climate models (RCMs) were applied (Supplementary Table 2) contributing to a full uncertainty analysis (Supplementary Table 9), where the variation of RCMs, the variation of SDMs and the variation of the provenance selection were used to quantify the uncertainty of future CS. The relative contributions of the sources of uncertainty[41] related to the modelling frameworks and the AM scenario were mapped to quantify the geographical distribution of the sources of uncertainties across Europe (Supplementary Table 13 and Supplementary Figs. 16–22).

Large changes in forest composition required under climate change

All SDMs and climate model combinations indicate that CC is projected to cause drastic shifts in the climatic suitability of tree species, calculated as the species with the highest probability of occurrence in each forested grid cell of Europe (Table 1 and Supplementary Table 10). The suitability of conifers such as *P. abies, A. alba* and *L. decidua*, which have dominant shares in Central and Northern European forests as a result of their wide cultivation in past centuries[42], declines drastically resulting in major shifts in species distributions (Table 1 and Supplementary Table 10), as reported previously[16,19]. Under future climate, the relative share of broadleaved species such as *F. sylvatica* and *Q. robur* is expected to exceed the share of conifers (Table 1 and Supplementary Fig. 8) but all species will experience declines in suitable habitats, especially in south and southeastern Europe[35]. Although the uncertainty in suitable cultivation areas due to different SDMs, RCMs and their combination varies between species and increases from an average of 4% under contemporary climate to 25% under RCP 8.5 (Table 1, Supplementary Table 10 and Supplementary Figs. 5 and 6), the rankings of species in suitable cultivation areas remain largely constant (Supplementary Fig. 8).

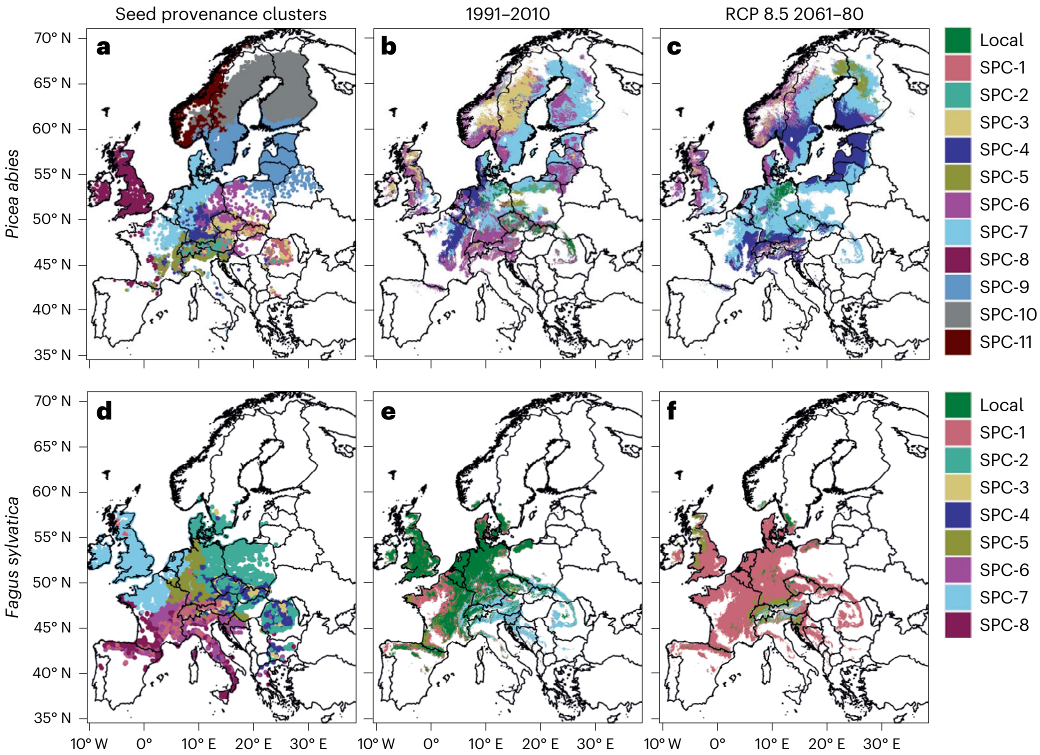

Fig. 1 | Seed provenance clusters of *P. abies* and *F. sylvatica* and their application for assisted migration. **a**–**f**, Geographic locations (**a**,**d**) of the SPC and distribution maps of *P. abies* (**b**,**c**) and *F. sylvatica* (**e**,**f**), where the SPC that are predicted to yield the highest annual CS for each 1 × 1 km grid cell are marked in the respective SPC colour. Green colours mark areas where local seed sources are the most productive seed provenances. SPC selections are shown for contemporary climate (1991–2010) and future climate under the RCP 8.5 scenario in the period 2061–2080. Best-suited SPC in the RCP 8.5 scenario was identified by URFs predicted for the mean climate of the five RCMs (Supplementary Table 2). See Supplementary Fig. 11 for other species. For better visualization, the maps present every 1 × 1 km grid cell of the contemporary distribution of the species, while the CSs reported in the study are restricted only to forested grid cells of Europe.

The scenarios for AM (Supplementary Fig. 4) of the seven main tree species focused on optimizing the CS potential of the regenerated forests. On the basis of extensive range-wide provenance trials, our models indicate that the CS for most of the tree species can be optimized if non-local SPC suitable for projected CC scenarios are being planted (Fig. 1 and Supplementary Figs. 9 and 11).

Local seed provenances offer optimal CS in regenerated forests only on restricted parts of their range (Supplementary Table 11). In contemporary climate, local seed provenances provide higher CS compared to adapted seed provenances only in 3–4% of the total suitable area of *P. abies* and *P. sylvestris*, 15–18% in *L. decidua* and *A. alba*, 8–16% in the two oak species (8–17%) but 50% in case of *F. sylvatica* (Supplementary Table 11). Under the strong CC scenario RCP 8.5, the suitable area for deployment of local seed provenances decreased to 2–19% of the respective species distribution. The strongest decline in suitable areas for local material was observed in *F. sylvatica* (5% of the area) and *Q. petraea* (8%) (Supplementary Table 11). The suitable area for deploying local seeds remained largely constant for *L. decidua*, *P. sylvestris* and *A. alba* and slightly increased from 8% to 15% for *Q. robur* (Supplementary Table 11). Under contemporary climate, the uncertainty in the share of suitable area for local and adapted seed sources is small ranging from 0.1% to 1.2% of the total area for local material and from 0.6% to 2.1% for adapted material (Supplementary Table 11). For future climate scenarios, uncertainty increased to between 0.5% and 4.0% for local seed sources and 3.4% and 30.9% of the total area for adapted seed sources. The poor performance of many local seed sources regarding CS even under contemporary climate might be explained by the incomplete expansion of many European tree species after the last glaciation[21] and by adaptation lags of many tree populations observed particularly within marginal populations[23,33,43–46]. Previously, such adaptation lags were mainly found for growth and productivity[45] but more recently also for phenological or physiological traits[23,44,46].

Following AM, the best seed provenances of *A. alba* originate from the cold and dry regions of the Carpathians, whereas for *L. decidua*, the best seed provenances originate from lower elevations of mountain regions of eastern central Europe and the Polish lowlands, where the native range consists of small scattered populations[47]. For *P. abies* (Fig. 1) and *P. sylvestris* (Supplementary Fig. 11), conifers with a large geographic range, a variety of SPC from the Carpathians, central and atlantic Europe are suitable each for a specific region. For the deciduous species *F. sylvatica* (Fig. 1) and *Q. petraea*, SPC from the alpine and atlantic regions performed best over a large part of the future distribution, while for *Q. robur*, SPC from central and partly southeastern Europe outperformed others (Supplementary Fig. 11). Irrespective of variations in their recommended cultivation area due to underlying SDM–RCM–URF combinations, the relative ranking of productive SPC remains largely constant with a few SPC being most suitable across large parts of the future distribution areas (Supplementary Figs. 9 and 11).

Assisted migration can maintain European forest carbon sequestration

Tree species change and seed provenance selections have strong effects on the annual CS of forest regrowth (Table 3). If local seed provenances are selected, the change from predominantly coniferous species to deciduous trees is expected to decrease the overall CS of the reforestations[48] from 39.76 ± 1.14 TgC yr^{-1} to 23.46 ± 0.98 TgC yr^{-1} under RCP 4.5 and 21.67 ± 2.54 TgC yr^{-1} under RCP 8.5 scenarios in the period 2061–2080 (Fig. 2 and Table 2).

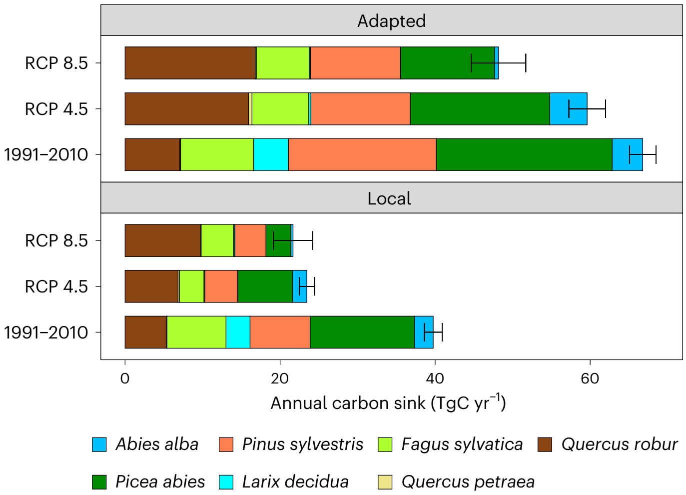

Fig. 2 | Effects of assisted migration on the annual CS of European forests. Total annual above-ground CS (TgC yr^{-1}) for the seven tree species under the two seed source scenarios 'adapted' and 'local' seed provenances. Local are those seed provenances that are geographically proximate to the planting locations and where the climate of the planting location and the historical climate of seed origin are identical. Adapted seeds are those SPC producing the highest annual CS for the climate of the planting location irrespective of their climatic similarity and geographic proximity to the planting location. CS from local and adapted seed sources in RCP 4.5 and 8.5 scenarios were identified by URFs predicted for the mean climate of five RCMs (Supplementary Table 2). The error bars represent the standard deviation of the annual CS (TgC yr^{-1}) of the sum of the seven species and are calculated from the different combinations of SDMs, URFs and RCMs.

Table 2 | Effect of seed origin on annual CS of European forests

AM scenario	Species	Contemporary 1991–2010	RCP 4.5 2061–2080	RCP 8.5 2061–2080
Adapted seed sources	*A. alba*	3.94±0.23	4.83±0.89	0.52±0.18
	P. abies	22.69±0.8	17.98±2.37	12.12±2.93
	P. sylvestris	19.09±0.85	12.83±1.42	11.63±1.83
	L. decidua	4.48±0.38	0.28±0.05	0.15±0.04
	F. sylvatica	9.42±1	7.32±1.26	6.83±1.67
	Q. petraea	0.1±0.01	0.44±0.09	0.13±0.04
	Q. robur	7.06±0.78	15.93±2.26	16.79±1.9
	Annual CS (TgC yr^{-1})	66.78±1.72	59.61±2.36	48.18±3.52
	Annual CO_2 removal ($TgCO_2$ yr^{-1})	244.85±6.3	218.57±8.65	176.64±9.52
Local seed sources	*A. alba*	2.42±0.16	1.85±0.3	0.29±0.1
	P. abies	13.46±0.52	7.07±0.89	3.21±1.88
	P. sylvestris	7.75±0.4	4.25±0.55	4.02±0.79
	L. decidua	3.1±0.27	0.11±0.02	0.15±0.02
	F. sylvatica	7.62±0.73	3.17±0.53	4.19±1.02
	Q. petraea	0.04±0	0.16±0.03	0.06±0.02
	Q. robur	5.36±0.54	6.84±0.95	9.75±1.4
	Annual CS (TgC yr^{-1})	39.76±1.14	23.46±0.98	21.67±2.54
	Annual CO_2 removal ($TgCO_2$ yr^{-1})	145.79±4.15	86.03±3.6	79.46±9.33

Annual CS (TgC yr^{-1}) and CO_2 removal ($TgCO_2$yr^{-1})±s.d. when best-suited species are planted with local or adapted seed provenances. Annual CS from local and adapted seed sources in RCP 4.5 and 8.5 scenarios were identified by URFs predicted for the mean climate of five RCMs (Supplementary Table 2). Standard deviations of the annual CS and CO_2 removal were estimated from the combination of SDMs, URFs and RCMs.

If instead, the most productive SPC according to AM for the respective climate is planted, reforestations could contribute to an increase of annual CS to 66.78 ± 1.72 TgC yr^{-1} under contemporary climate and 59.61 ± 2.36 TgC yr^{-1} under the RCP 4.5 scenario during 2061–2080. Moreover, even under the pessimistic CC scenario RCP 8.5, AM would allow increasing the annual CS slightly to 48.18 ± 3.52 TgC yr^{-1} during 2061–2080 (Fig. 2 and Table 3). Despite variations in CS due to various combinations of SDMs, URFs and RCMs (Supplementary Tables 12 and 13) all models indicate a higher annual CS of adapted seed sources compared to local seed sources and the relative contribution of the seven species on annual CS remained constant (Fig. 2, Table 2 and Supplementary Table 12).

Under contemporary climate, the CS of the modelled forest stands would account for about 26% of the observed annual CS (155 TgC yr^{-1}) of European forests[3] if planted with local seed materials and for about 43% if adapted seed sources are used (Table 2). Given that the seven species encompass around two-thirds of the European forest area[3] and that our models encompass forest regrowth until the age of 40 years, these model predictions cover the approximate magnitude of observed CSs realistically.

In contemporary climate, a substantial portion of this CS in regrowing forests is attributable to conifers, irrespective of the seed provenances being planted (Fig. 2 and Table 2). Under CC (scenario RCP 8.5), the contribution of conifers to the CS, especially of *P. abies* and *P. sylvestris*, declines from 75 to 50% if adapted seed sources are planted and from 40 to 15% if local seed sources are used. This is due to their decreasing suitable area, whereas the contribution of broadleaved species to CS increases (Fig. 2 and Table 2). Although the suitable areas for conifers decline in CC, AM contributes more to higher CS of conifers as compared to broadleaved species (Table 3).

In general, all species gained in annual CS when adapted seed provenances were planted but the benefits of AM were more evident under CC (Table 3) despite increasing uncertainties (Table 3). For regrowing conifers, AM results in a gain of 150–200% (RCP 4.5) annual CS as compared to local seed provenances, while for broadleaved species a gain of 130–172% can be expected (Table 3). The higher gains in conifers are in contrast to the lower genetic differentiation among populations as compared to broadleaved trees[49]. This might be explained either by the lesser coverage of the broadleaved species' niches by the provenances and trial sites within our dataset (Supplementary Figs. 2 and 3) or by the broader climatic niche of the conifer species resulting in stronger selection and more local adaptations to manifold regional climates or by higher phenotypic plasticity[46,50–52]. The observed CS differences between local and adapted SPC are not restricted to a certain geographic region and adapted SPC outperforms local provenances within all bioclimatic regions of Europe (Supplementary Fig. 12). However, the gains of adapted SPC are more pronounced in central and northern Europe such as in alpine, boreal and atlantic than in the Pannonian and Mediterranean regions mainly because the seven selected species will have only low suitability in southern Europe in CC. Also, the spatial analysis of components of uncertainty did not reveal notable geographical variation. The components contributed by the AM scenario, explained in total 91% of the variance observed in CS (Supplementary Table 13 and Supplementary Figs. 16–18). However, uncertainties due to modelling framework, that is the choice of RCMs and the SDM algorithms were more pronounced in northern and northeastern Europe than elsewhere (Supplementary Table 13 and Supplementary Figs. 19–22).

Our empirical data are based on provenance trials mostly established with seed lots from natural unimproved forests. Tree breeding

Table 3 | Relative gains in annual CS by assisted migration

	Contemporary	RCP4.5	RCP8.5
Species	**1991–2010**	**2061–2080**	**2061–2080**
A. alba	62.6±5.2	160.27±14	75.01±19.9
P. abies	68.53±6.1	154.27±15.1	70.27±10.2
P. sylvestris	146.41±8.0	202.06±23.3	146.15±21.3
L. decidua	44.23±3.0	150.00±11.3	0.10±18
F. sylvatica	23.55±2.8	130.77±15.2	63.16±22
Q. petraea	150.00±1.1	172.73±6.1	100.01±17.6
Q. robur	31.77±3.9	132.78±11.3	72.31±22.1

The gain in annual CS (%) by changing seed procurement from local to adapted seed provenances. CS from local and adapted seed sources in RCP4.5 and 8.5 scenarios were identified by the URFs predicted for the mean climate of five RCMs (Supplementary Table 2). Standard deviations of relative gains (%) were estimated by the combination of the various SDMs, URFs and RCMs.

programmes, where productivity gains of 10–25% are typically achieved within a breeding generation[53] allow for a further increase of annual CS if AM is considered[54,55]. Scientific studies across disciplines such as genecological experiments[56], provenance trials[57–59], dendroclimatic analysis[60] and genome studies[43,61], although limited in their geographic scale, have indicated that adapted seed provenances are required to avoid maladaptation and mitigate consequences of CC. Our recommendation for AM based on range-wide empirical data confirms this overarching scientific agreement across disciplines regarding CS.

Limitations and conflicts

Our analysis may be subject to potential limitations, which encompass deficiencies in the available data and constraints associated with the models. Although our transfer models are built upon one of the largest continental tree provenance datasets, we were only able to model the provenance transfer of seven main tree species common to central and northern Europe, which dominate, however, within two-thirds of Europe's forests[62]. This is because past provenance experiments with a valid representation of full distribution areas are limited to few stand-forming and commercially important species[63]. Data for rare and scattered distributed trees are rarely available and this limits the extension of our predictions to mixed forest types. Another uncertainty could be the inclusion of data from non-autochthonous seed sources because forests in Europe have been managed for centuries and seed provenances mainly of conifers have been transferred historically[64,65]. Thus, our data may include a certain amount of non-autochthonous seed sources, where the known seed origin might be different from the original local adaptation. However, a high number of non-autochthonous seed sources in the dataset is expected to weaken the relationship between climate and provenance origin and would result in a possible underestimation of AM effects. Also, we limit the uncertainty of imperfect empirical data by grouping provenances into large-scale SPC. Our analysis also leaves out Mediterranean forests, where similar adaptation lags due to growth decline were reported[33,66,67].

The applied transfer models focus on productivity and carbon sequestration for expected future long-term mean climate; therefore, they may not account for extreme climate events or biotic/abiotic disturbances, which pose a serious risk for the future provision of ecosystem services[4,5,9,68,69]. Moreover, productivity and CS might not be the only traits for which tree populations developed local adaptations. It can be expected that trade-offs exist between productivity and other traits, such as tolerance to frost[69], drought or insect outbreaks, which are not explicitly considered here and may reduce the resilience of forests with transferred populations. Therefore, provenance trials need to be further exploited for developing several trait models for AM as a basis for potential implementation. This would complement increasing evidence for local adaptations and future maladaptation in traits related to phenology and drought tolerance[23,25,70], which suggests that seed sources from more southern and drier sites are more drought tolerant and may be used also in core areas of species distributions[25,71,72]. Also, drought recovery and resilience were recently found to be positively correlated to growth and competitive ability in provenance trials established at the warm and dry distribution edges of the species[73,74], suggesting that selecting trees for higher carbon stocks under future conditions might also improve drought performance.

Since the main focus of our analysis was to demonstrate the role of AM on CS, simplified assumptions of selecting the single species with the highest climatic suitability in each 1 × 1 km forested grid cell were made. Although it is widely considered that mixed forests may increase productivity and CS through higher yields and can reduce drought sensitivity and mortality[15,16], this simplification was required because mixed forests across Europe are composed of different species combinations with species-specific mixture–productivity relationships[75,76] and range-wide models to quantify mixture effects are not available yet[77].

To quantify the uncertainty of model choice and the source of climate data, best-suited species and provenances were identified for five RCMs, different SDMs and the subsequent URFs. Although the uncertainty of the various model predictions increased from the current climate to the most extreme CC scenario, the cultivation areas for the best-suited tree species and SPC as well as their relative contribution to annual CS remained stable irrespective of the model combination. Our transfer models are applied only within the changing climatic niche of the target species as modelled by state-of-the-art SDMs[35]. While this allows us to model the forest CS within the climatic space of the past species distribution and avoids predictions beyond the climate conditions of our trial observations (Supplementary Fig. 2 and 3), it does predict changes in tree species and provenances across large geographic distances. Such drastic changes in the forest might have genetic[78], ecological[79,80], social[81,82] and economic[16] consequences, which need to be weighed against the outcomes of inaction[83]. Given the overwhelming evidence from distribution models[19,35,84] and increasing forest disturbances[6,68], changing forest species compositions and species distributions are the most widely accepted measure to adapt forests to CC[7,8,10]. However, the limited migration capacities of many species to reach suitable areas[22,85] and the increasing population maladaptation[23,86] will ultimately limit natural species reshuffling and endanger forest ecosystem services[85] if increasingly mismatching local adaptations are ignored. Therefore, inaction in species and provenance selection may increase the vulnerability of current tree populations to CC[10,83,87,88] and endanger valuable genetic resources[89,90].

Conclusion

Reforestation and restoration needs in European forests[6] require decisions on the selection of tree species and seed provenances. Despite evidence of large-scale species shifts and increasing genetic maladaptation in forest trees, there has been little effort to incorporate this knowledge into ongoing tree plantation initiatives, forest restoration programmes and national and transnational regulations. Preventing maladaptation of current forests can provide a major boost to nature-based solutions for CC mitigation such as forest restoration while ensuring resilience and preserving the forest CS[12,60,91]. Our results provide evidence for strong effects of seed provenance selection on the CS under future climate and demonstrate that improving forest resilience by planting species for future climate needs to be combined with adequate provenance selection to preserve the annual CS of European forests. Changing species composition alone will result in decreasing CS and the risk of failing the European Union target for climate neutrality[92]. This evidence calls for further research and transnational cooperation to develop and implement AM and to quantify possible trade-offs between productivity and other traits to avoid unknown risks of AM implementation.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-024-02080-5.

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Data availability

The provenance trials dataset is available via Figshare at https://figshare.com/s/98e405d56bb789b08cb0 (ref. 93). The ECLIPS 2.0 dataset is available via Zenodo at https://doi.org/10.5281/zenodo.3952159 (ref. 94).

Code availability

R codes developed for and used in this study are available upon request.

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Author contributions

D.C. conceived the idea of the paper, formulated research questions, developed and carried out analysis and wrote the paper. A.C. supported analysis in the revised paper. D.B., G.B., E.C., A.H., AD., M.I., R.L., G.M., K.P., E.P., R.S., T.M.S., T.S., A.S., S. Stojnic and K.V. provided provenance trial data. M.B.G., A.K. and L.N. provided provenance trial data and edited the paper. A.B. provided computing resources and edited the paper. R.B., J.C., J.G., J.P.G., M.K., J.K. and J.S. contributed to running URF models. M.L. contributed to running URF models and edited the paper. A.S. carried out paper revisions. S. Schueler conceived the idea of the paper and analysis, obtained research funding, contributed trial data and wrote the paper.

Competing interests

The authors declare no competing interests.

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Study description	Collection of published and unpublished tree provenance data and modelling
Research sample	NA
Sampling strategy	NA
Data collection	Collecting all available provenance data from the seven species available from the author team and publications
Timing and spatial scale	Analysed provenance trial data include datasets from the 20 and the 21 century, Europe, partly Asia
Data exclusions	Incomplete dataset and data from implausible coordinates
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No	Yes	
☒	☐	Demonstrate how to render a vaccine ineffective
☒	☐	Confer resistance to therapeutically useful antibiotics or antiviral agents
☒	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☒	☐	Increase transmissibility of a pathogen
☒	☐	Alter the host range of a pathogen
☒	☐	Enable evasion of diagnostic/detection modalities
☒	☐	Enable the weaponization of a biological agent or toxin
☒	☐	Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	
Novel plant genotypes	
Authentication	

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	
Files in database submission	
Genome browser session (e.g. UCSC)	

Methodology

Replicates	
Sequencing depth	
Antibodies	
Peak calling parameters	
Data quality	

Software

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation

Instrument

Software

Cell population abundance

Gating strategy

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type

Design specifications

Behavioral performance measures

Imaging type(s)

Field strength

Sequence & imaging parameters

Area of acquisition

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software

Normalization

Normalization template

Noise and artifact removal

Volume censoring

Statistical modeling & inference

Model type and settings

Effect(s) tested

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference (See Eklund et al. 2016)	
Correction	

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	
Graph analysis	
Multivariate modeling and predictive analysis	