TEMPLATE

Output factsheet: Strategies and action plans

Version 1

Project index number and acronym	CE614 - SUSTREE
Lead partner	BFW
Output number and title	O.T1.1 – Transnational delineation model of conservation and forest seed transfer zones in climate change
Responsible partner (PP name and number)	National Agricultural Research and Innovation Centre (NAIK ERTI) - PP4
Project website	https://www.interreg-central.eu/Content.Node/SUSTREE.html
Delivery date	19th July 2019

Summary description of the strategy/action plan (developed and/or implemented)

Climate change is likely to disrupt the balance between climate and local adaptation in tree species requiring forest managers to evaluate the suitability of non-local planting materials. We developed delineation models calibrated with data on growth performance of more than 10,000 seed sources of 7 major tree species of Europe (*Picea abies, Abies alba, Pinus sylvestris, Larix decisua, Fagus sylvatica, Quercus petraea* and *Quercus robur*) planted across a wide gradient of growing conditions. Such delineation models, also known as Universal Response Functions (URFs) predict the location of optimum seed sources or planting materials suitable for a given combination of the planting site and according to the different climate scenarios. The output from these delineation models was depicted as spatially explicit maps of best seed sources under current climate (1961-90) and two climate change scenarios (RCP 4.5 and RCP 8.5). These maps were also integrated into a decision support tool Sus-Select smartPhone App (Output OT3.2).

NUTS region(s) concerned by the strategy/action plan (relevant NUTS level)

AT11, AT12, AT13, AT21, AT22, AT31, AT32, AT33, AT34
CZ01, CZ02, CZ03, CZ04, CZ05, CZ06, CZ07
DE21, DE22, DE23, DE24, DE25, DE26, DE27
HU11, HU12, HU21, HU22, HU23, HU31, HU32, HU33
PL21, PL22, PL41, PL42, PL43PL51, PL52, PL61, Pl62, PL63, PL71, PL72, PL81, PL82, PL84, PL91, PL92
SK01, SK02, SK03, SK04

Expected impact and benefits of the strategy/action plan for the concerned territories and target groups

The delineation models are likely to inform forest and nursery managers as well as policymakers about the most suitable planting materials for reforestation of seven major tree species of Europe. Since the delineation models predict the optimum seed sources for future climate under two RCP scenarios and several timeframes (2041-60, 2061-80 and 2081-2100) it accounts for both spatial and temporal uncertainty due to climate change. This allows evaluating the risks as well as benefits of using locally available seed sources or the so-called adapted seed sources. Since the output is integrated into a smartphone app it is likely to inform more stakeholders compared to conventional means of dissemination of project outputs such as project reports and communication briefs.

Sustainability of the developed or implemented strategy/action plan and its transferability to other territories and stakeholders

The delineation models in the form of maps of suitable seed sources under current and future climate scenarios can be extended to any region of the world where data related to climate growth response are available. The system is powerful yet simple and based on algorithms that can be modified to suit the need of seed deployment of any forest tree species. In addition, the delineation models have been incorporated into a smartphone app SusSelect available on android platforms. This ensures its sustainability and periodic upgrade for utilization by a wide range of stakeholders both within and beyond the territorial boundaries of the project area i.e Central Europe.

Lessons learned from the development/implementation process of the strategy/action plan and added value of transnational cooperation

During the early stages of the development of the delineation models, it was realized that the robustness of the models depends on data from a wide range of growing conditions. Therefore SUSTREE collaborated with stakeholders both within and beyond central Europe and developed a harmonized dataset of provenance trial data which is the base of these delineation models. A data paper is under preparation aiming at free and unrestricted public use of the dataset for scientific purposes. This will ensure penetration of the developed strategy i.e the delineation models and its associated data within and beyond the territorial boundaries of Central Europe and further fortify the value of transnational cooperation.

References to relevant deliverables and web-links
If applicable, pictures or images to be provided as annex

D.T1.2.1: Workshop on forest inventory data in Central Europe
D.T1.2.2: Establishing a GIS-based database for species inventory and soil data
D.T1.2.3: Collecting soil maps for estimates of water holding capacity
D.T1.2.4: Derivation of species distribution models (SDM) for the 6 most important tree species within the CE regions
D.T1.3.1: Review and collection of existing tree species response functions
D.T1.3.2: Collection of provenance plot data for unified response function (from all EU)
D.T1.3.3: Summary and report of intraspecific response function and derivation of climate transfer limits
D.T1.4.2: Maps with delineation models for optimal seed transfer for present and 3 future climate scenarios
D.T2.2.1: Report on statistics of climate regimes with and among existing provenance delineation
D.T2.4.3: Policy brief for European policy makers

Annex 1:
Transnational delineation model of conservation and forest seed transfer zones in climate change for the 7 most important tree species of Europe

Annex 2:
Article “Disentangling the role of climate and soil on tree growth and its interaction with seed origin” written by Debojyoti Chakraborty; Robert Jandl; Stefan Kapeller and Silvio Schüler, published in 2019 in Science of the total Environement.

TRANSNATIONAL DELINEATION MODEL OF CONSERVATION AND FOREST SEED TRANSFER ZONES IN CLIMATE CHANGE

(O.T1.1)

The objective of the project is to improve integrated environmental management capacities for the protection and sustainable use of natural heritage and resources

19th July 2019

ESTABLISH A TRANSNATIONAL MODEL FOR SEED TRANSFER AND THE SUSTAINABLE UTILIZATION AND CONSERVATION OF THE GENETIC RESOURCES OF FOREST TREES IN CLIMATE CHANGE

Each year about 900 million seedlings of the major tree species are being produced and planted in the Central European regions. The utilisation of these seedlings is restricted to nationally defined eco-regions (seed/provenance zones). However, the effects of climate change are strongly changing the conditions within eco-regions and seedlings planted today may be maladapted in the future, once they become mature. As a result, there will be a lower stability and productivity of future forest stands which indirectly will affect the wood industry sector and thus the economy.

The transnational delineation models below are based on nationally available knowledge of local adaptation and climate constraints of the six main tree species of Central Europe (*Larix decidua*, *Fagus sylvatica, Picea abies, Pinus sylvestris, Quercus petraea* and *Quercus robur*). However, due to the high interest of our transnational delineation models for optimal seed transfer in climate change a supplementary species (*Abies alba*) was demanded by experts (foresters and conservation managers but also scientists working in similar fields) as the silver fir has also a very important value, especially in the alpine and sub-alpine regions.

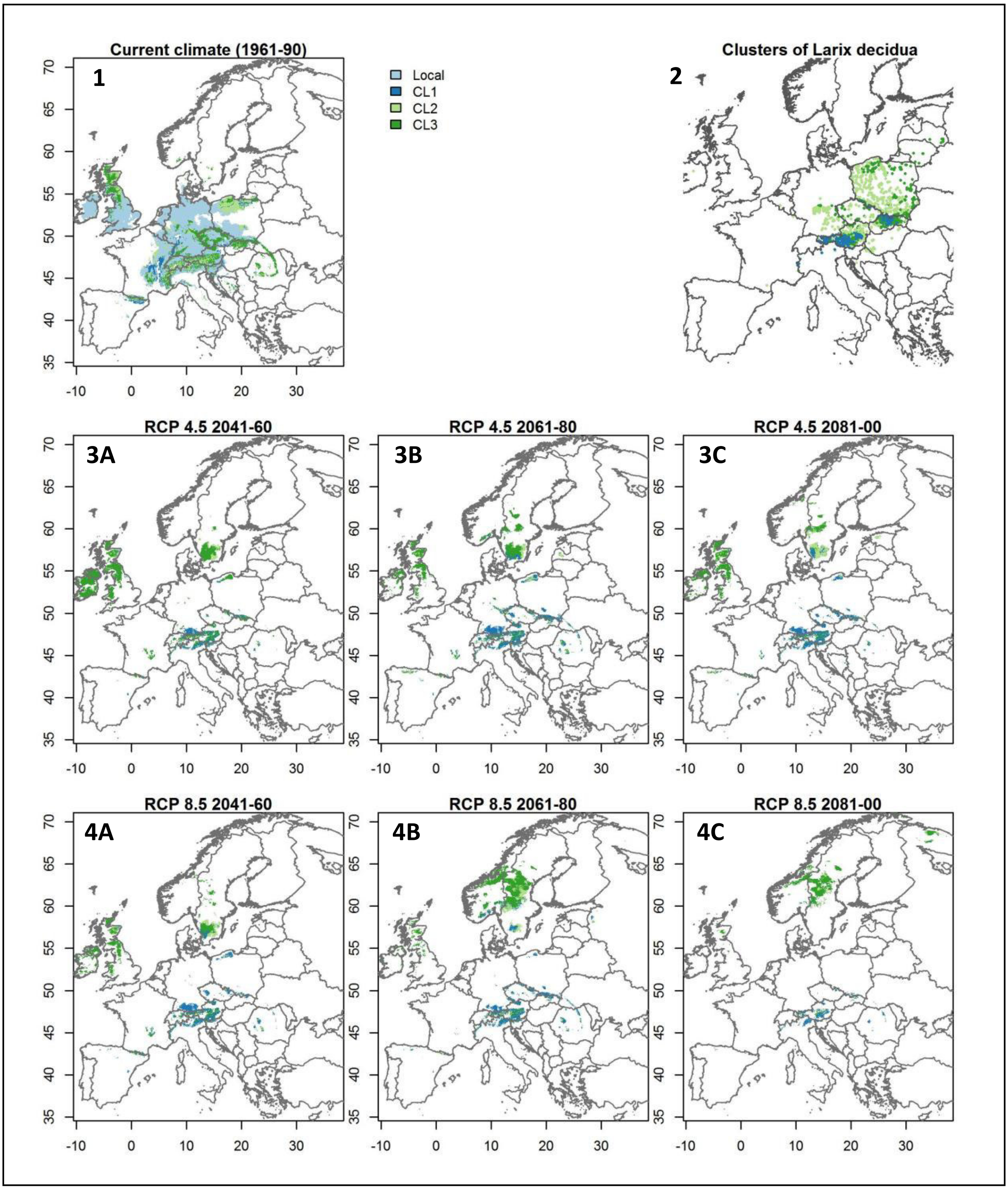
INTERPRETING THE TRANSNATIONAL MODELS FOR OPTIMAL SEED TRANSFER IN CENTRAL EUROPE

For each species, map (2) represents the geographic locations of seed sources of a species in Europe. The seed sources with similar climate have been grouped together into a cluster and have been given a unique colour code attribute. The “RCP”s stands for “Representative Concentration Pathways” which are global warming scenarios where RCP 4.5 roughly corresponds to a 2°C warming; and RCP 8.5 roughly corresponds to a warming scenario of 4-6°C.

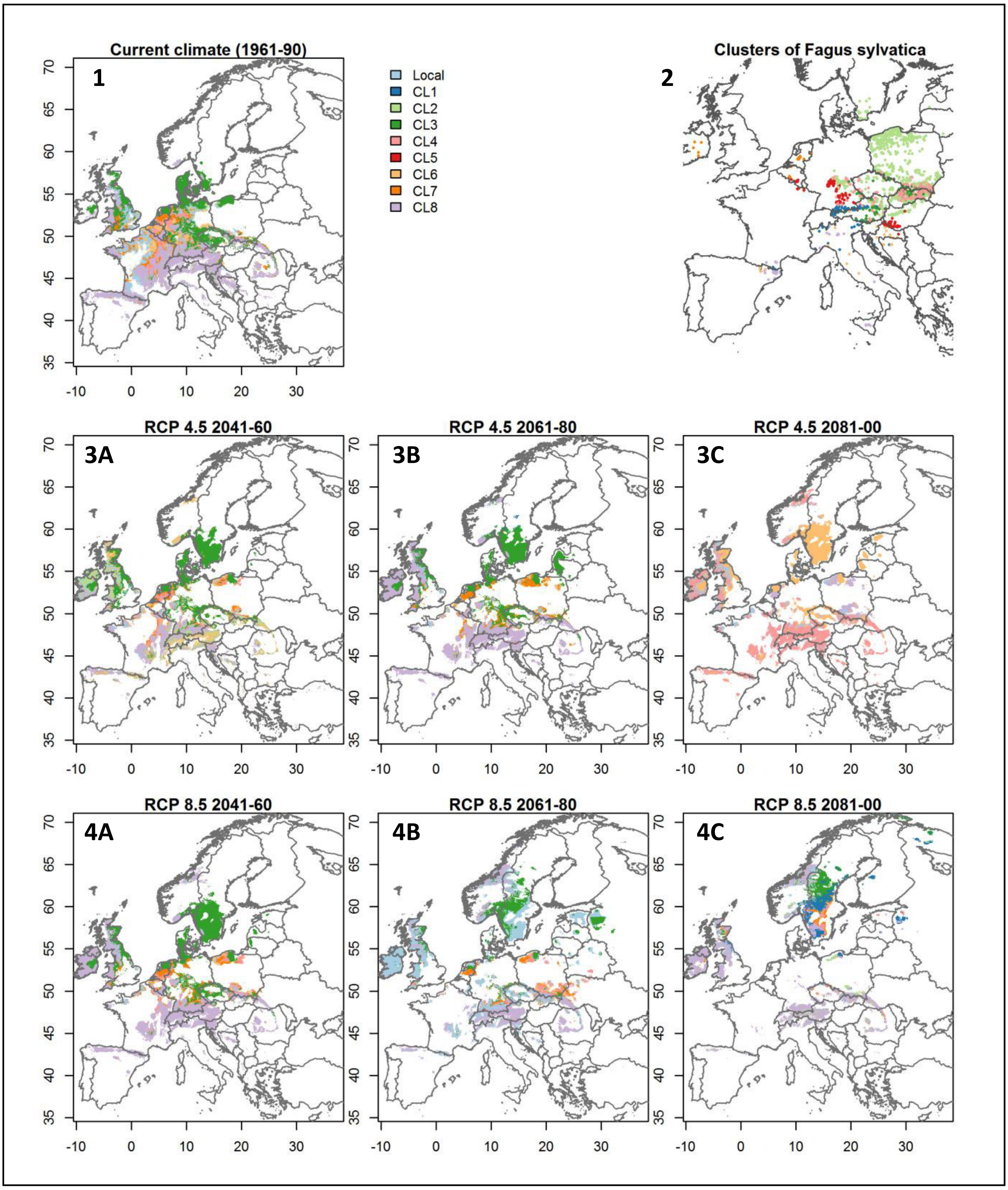
Maps 1, 3A, 3B, 3C and 4A, 4B, 4C within each model depicts the locations in Europe, when planted with a seed source cluster (from map 2) will have best performance in terms of tree height.

The maps of best seed source performances are given for (1) current climate i.e. 1961-1990 and three future time frames 3A, 3B, 3C and 4A, 4B, 4C which denotes the following years 2041-2060; 2061-2080; and 2081-2100.

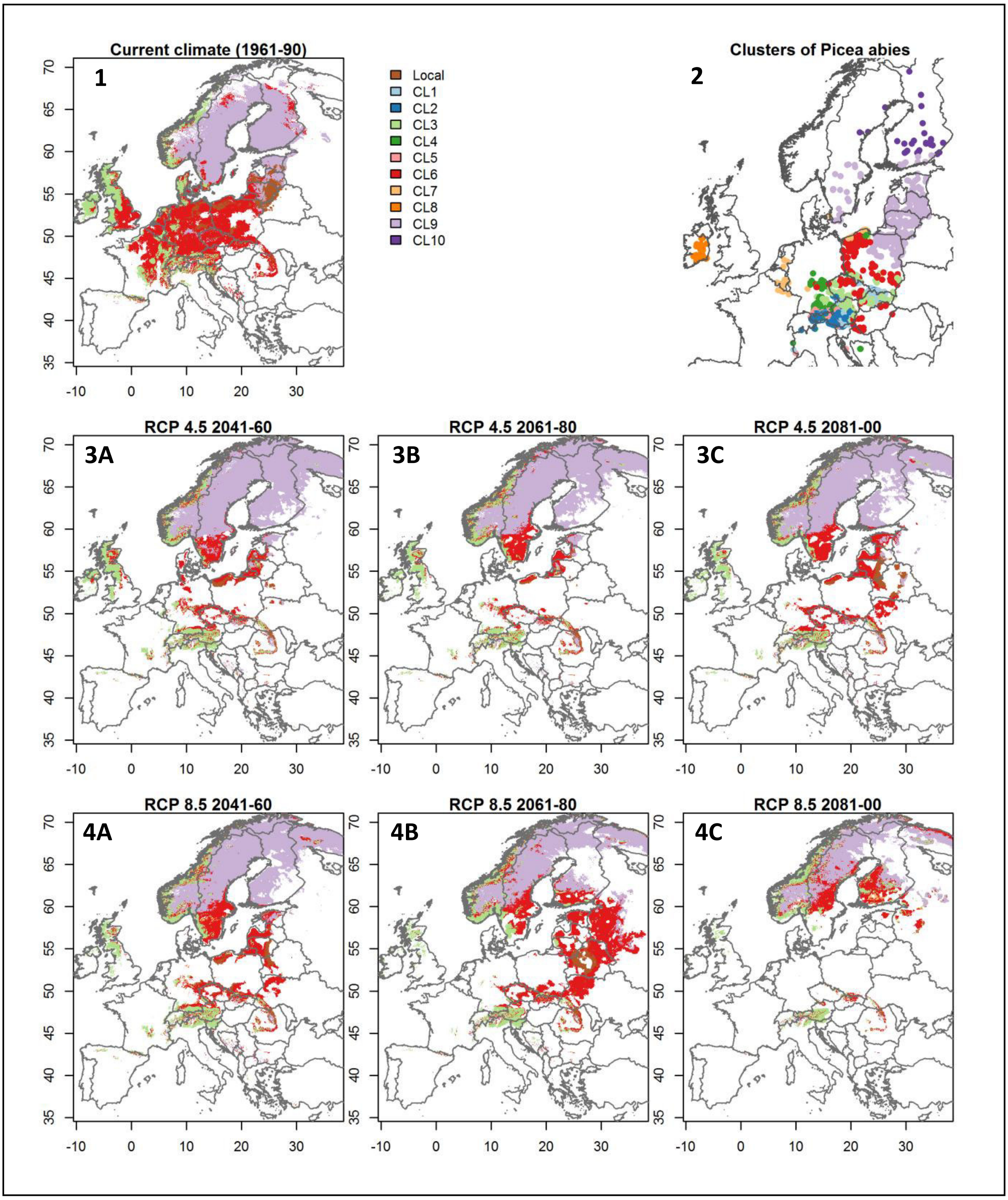
Larix deciduas (European larch)



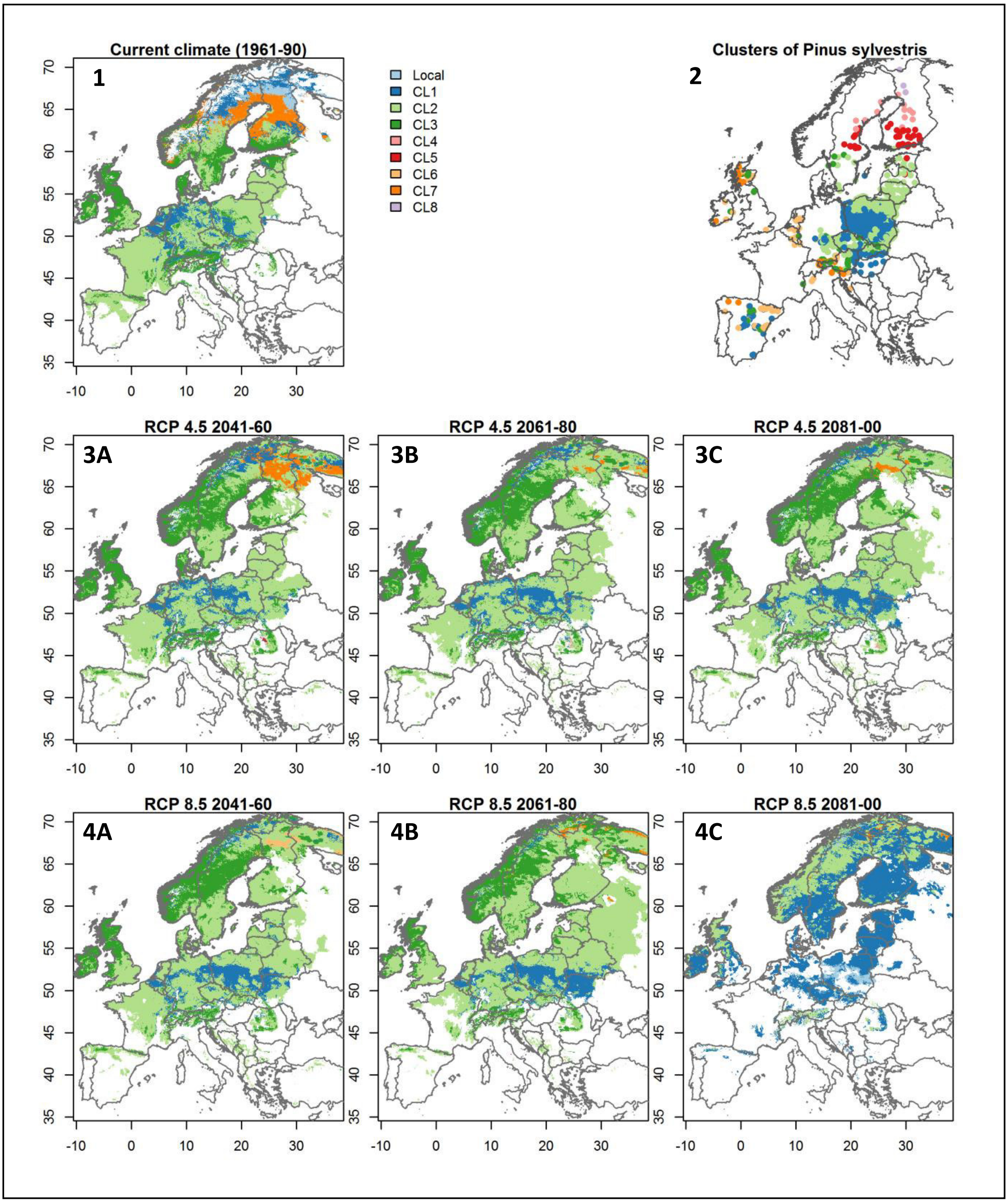
Fagus sylvatica (European beech)



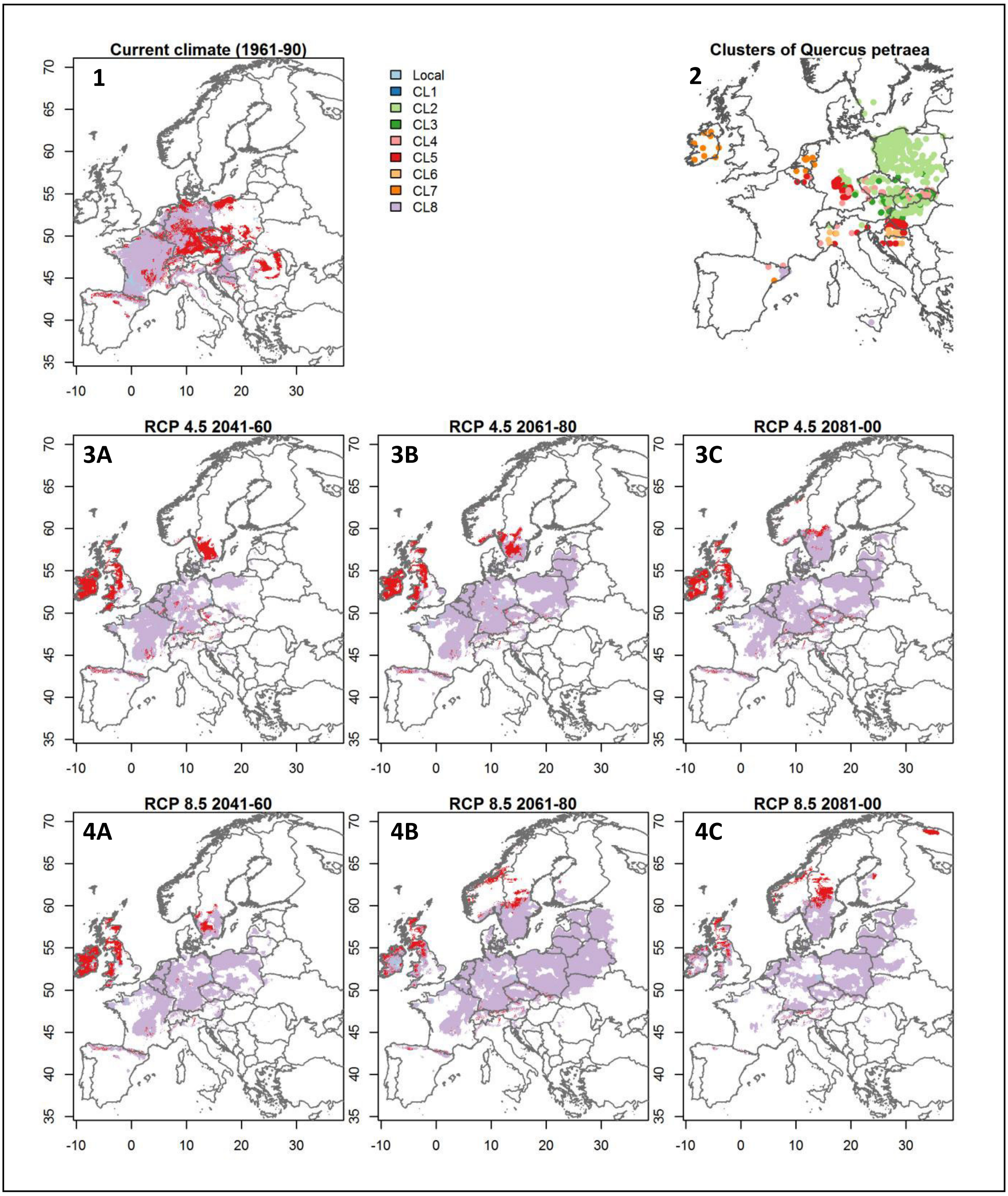
Picea abies (Norway spruce)



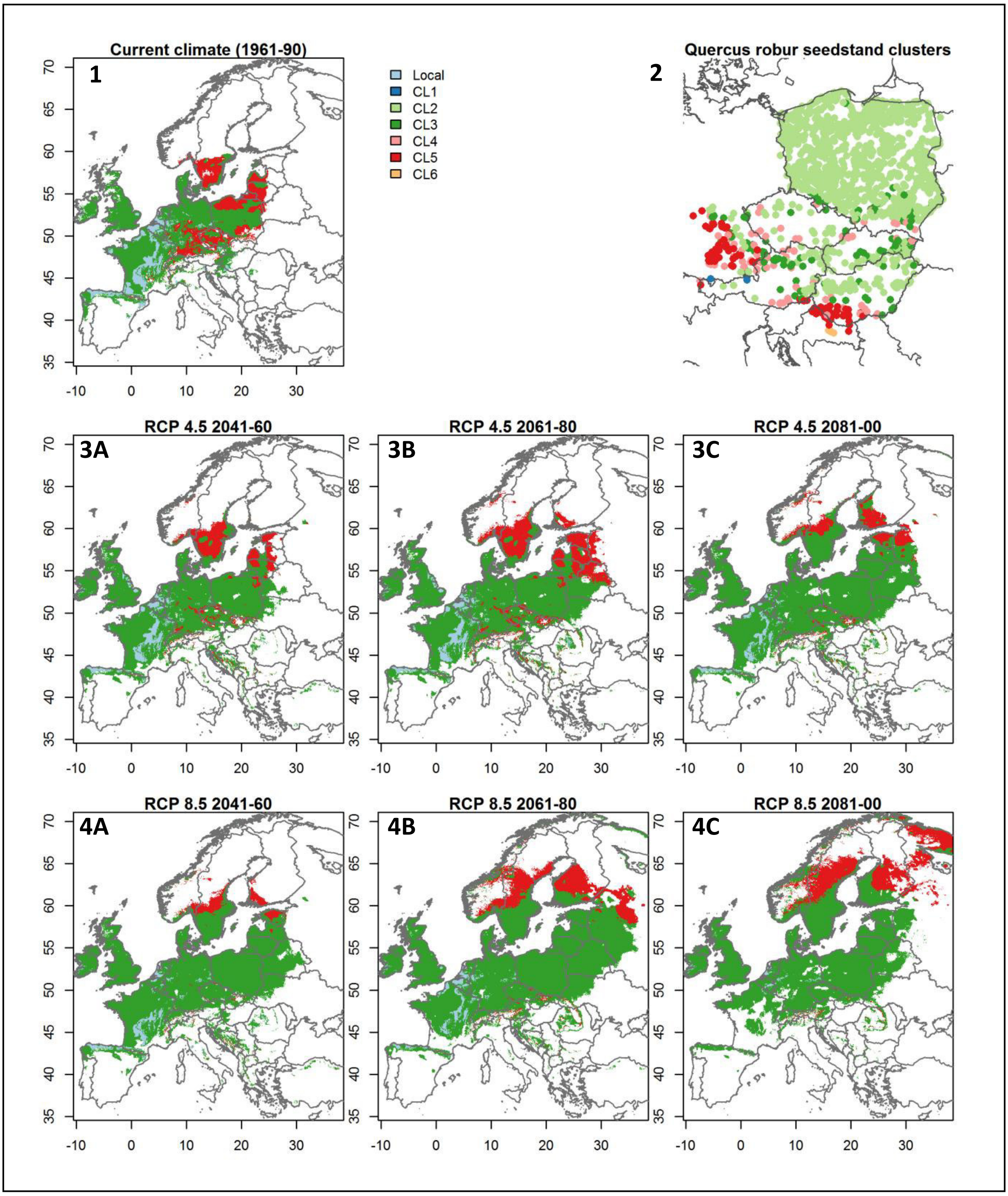
Pinus sylvestris (Scots pine)



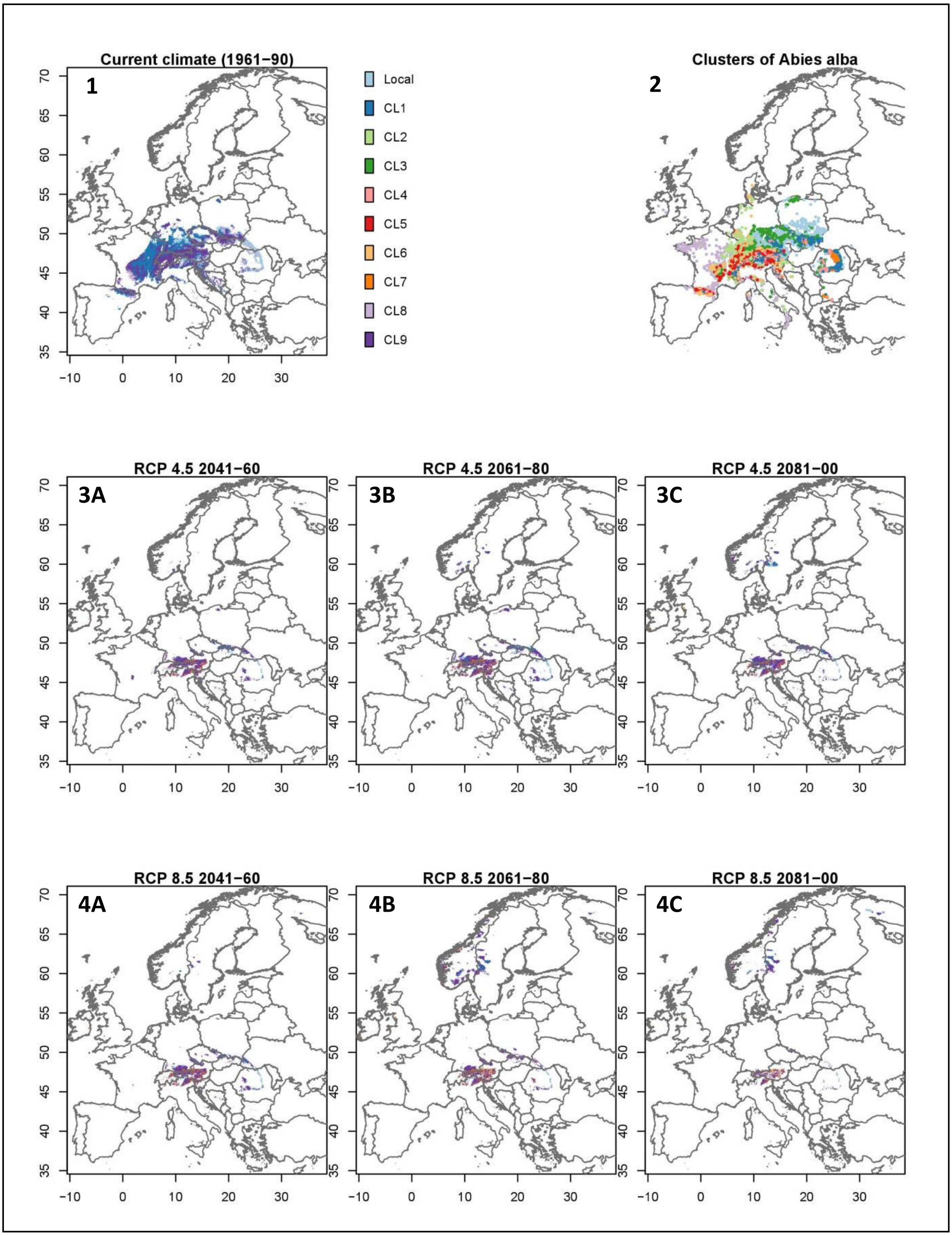
Quercus Petraea (Sessile oak)



Quercus robur (English oak)



Abies alba (Silver fir)



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Disentangling the role of climate and soil on tree growth and its interaction with seed origin

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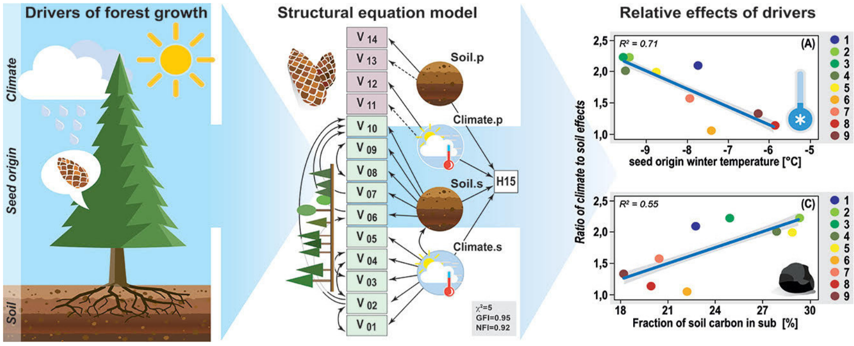
HIGHLIGHTS

- We disentangle the relative roles of climate and soil of planting locations and provenance origins on juvenile tree growth.
- Climate and soil of the planting location are dominant drivers of growth wheras provenance origin play minor role.
- The relative effects of climate and soil vary among different provenance groups
- Climatic constraints are dominant, if materials from colder origin and higher altitude are planted.
- Soil and climate conditions are equally important if provenances originating from warm sites planted.

GRAPHICAL ABSTRACT



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ABSTRACT

When considering options for adapting forests under climate change, climate is treated as the dominant driver of forest growth, while soil properties are often ignored mainly due to shortage of accurate data. The effects of climate and soil on forest growth may vary due to local adaptation to both climate and soil, and these local adaptations might need to be considered when transferring seed provenances under climate change.

Data from 29 provenance trials of Norway spruce (*Picea abies* (L.) Karst.) across a wide gradient of planting conditions in Austria was used to develop Structural Equation Models (SEMs) to quantified the role of climatic and soil drivers and their interactions on juvenile growth performance and to test if provenance origin affects the relative importance of these drivers.

Climate and soil of the planting site location were found to have similar direct effects on juvenile tree growth, however, climate was found to be more important because of additional indirect effects via interactions with soil parameters. Notably, the relative effects of climate and soil vary among different provenance groups. Climate constraints are dominant for seed sources originating from colder and/or high altitude locations, while test site climate and soil are equally important contributors of growth for provenances originating from warmer origin and lower elevation sites. Together with the better growth performance of the latter provenance group their plasticity allows them to utilize a wide range of soil conditions.

1. Introduction

Understanding the major drivers of forest growth is of utmost importance to predict forest development, the provision of ecosystem

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0048-9697/

services and in particular forest carbon storage under global warming (Pan et al., 2011; Pretzsch et al., 2014; Reyer et al., 2017). A complex interaction of biotic and abiotic factors drives forest growth by influencing photosynthesis, gross and net primary production or plant and soil respiration (de Vries et al., 2017). While the climatic drivers on forest growth such as solar radiation, temperature, precipitation, and extreme climatic events have been exhaustively investigated (Kardol et al., 2010; Toledo et al., 2011; Barsoum et al., 2015; Hlásny et al., 2017), scarcity of high resolution data on chemical and physical soil properties prevent their widespread use in forest growth studies.

The relationship of individual chemical and physical soil parameters to forest growth were often reported to be weak and inconsistent across soil gradients and tree species (Jandl and Herzberger, 2001; Mina et al., 2017) and its overall effects on forest growth and carbon sequestration are under debate (e.g Fernández-Martínez et al., 2014; Du, 2015; Kutsch and Kolari, 2015). Moreover, the majority of contemporary studies assume that the relative role of different drivers of forest growth remains constant across the species' distribution range (but see: Me Chave et al., 2001; Baker et al., 2003). However, tree species occur under a wide range of environmental conditions within their natural ranges exhibiting manifold local adaptations (Aitken et al., 2008; Ishizuka and Goto, 2012; Kreyling et al., 2014). Local adaptations and intraspecific variation in forest growth should be considered because the choice of planting material is the only aspect of afforestation that can be influenced by management, whereas climate and soil are relatively inert to management intervention. Models which describe the intraspecific variation of functional traits commonly include climatic drivers of planting location and seed origin (Rehfeldt et al., 2002; Wang et al., 2010; Chakraborty et al., 2015), while cumulative non-climatic indices are interpreted from model residuals (O'Neill et al., 2007). Studies simultaneously considering the effects of climate, soil and seed origin are scarce (Toledo et al., 2011; Manrique-Alba et al., 2017).

Norway spruce (*Picea abies* [L.] Karst.), the most widespread conifer in Central Europe, occurs from approximately 300 m up to 2000 m above sea level, encompassing a wide range of climate and soil conditions. In climate change, the future of Norway spruce is under pressure due to the species' high sensitivity to drought spells (Lévesque et al., 2013; Van Der Maaten-Theunissen et al., 2013; Montwé et al., 2014) and increasing bark beetle populations (Seidl et al., 2008; Pureswaran et al., 2018). Previous studies on the intraspecific variation of the species and the phenotypic response to climate (Kapeller et al., 2012) showed that populations from warm and drought-prone areas are appropriate candidates for extended silvicultural utilization under future climate conditions. However, the success of such assisted seed transfer will also depend on the phenotypic response to soil conditions.

In the present study, we aim at disentangling the roles of climate conditions and soil characteristics of both planting location and seed origin on growth performance of juvenile Norway spruce in the Eastern Alps. We identify and compare the relative contributions of major climate and soil variables on juvenile tree growth. Furthermore, we investigate the effect of seed origin on the relative role of climate and soil variables on growth and discuss our findings in the light of assisted migration.

2. Materials and methods

2.1. Provenance trials

The study utilizes data from the 29 Austrian provenance trials (hereinafter referred to as trial sites) established in 1978 which includes 360 Austrian provenances and 60 provenances from Germany, Poland, Czech Republic, Slovakia, Slovenia and Bulgaria (Fig. 1). Seed material commercially harvested during 1971 were pre-cultivated in climatic chambers and the young seedlings transplanted to nursery beds. The planting design was a randomized block design at 29 individual sites across Austria (Nather and Holzer, 1979). The number of tested provenances on each planting site ranged from 20 to 53 (29 on average). Each provenance was planted in three randomized blocks (repetitions) with 50 individuals of provenances in each block with a spacing of 1.5 × 1.5 m. Complete measurement of all 29 trials was done in 1988 when the trials reached an age of 10 years.

2.2. Soil data

Soil characteristics of all 29 trials sites were quantified by representative field observations and chemical analysis. The investigations included 39 soil physical and chemical properties measured at three layers: the litter layer, 0–10 cm, and 10–20 cm of the mineral soil (Table S1 in Supporting Information). These soil properties include pH, the total content of carbon and nitrogen, the exchangeable cations (sodium, potassium, calcium, magnesium, manganese, iron, aluminum) and the cation exchange capacity etc. (Fleck et al., 2016). The potential and effective soil water holding capacity were estimated based on soil texture and rock content according to Gartner et al. (2018).

The geographic origin (latitude, longitude, and altitude) of the planted 420 seed provenances, i.e. the locations where the seeds were harvested was less precise and did not allow the characterization of the soil conditions as accurately as the trials sites. Therefore, the soil properties of the provenance origin were obtained from the European Soil Database 2.0 (European Commission and the European Soil Bureau Network, 2004). This allowed us to retrieve information on available soil water capacity (AWC), the percentage of carbon in soil, the fraction of clay, silt and sand and soil pH (Table S1).

Although the trials were originally established in sites where the soil is not the major limiting factor, the soil properties of the trials are rather heterogeneous (Fig. S1 in supporting information), for example, total nitrogen content varied from 2 to 20 mg/g of soil, and pH ranged from 3 to 8 (Fig. S1). The distribution of these soil variables (Fig. S1) can be seen as a good representation of forests soils in Austria (Englisch et al., 1992).

2.3. Climate data

Climate data for the trial sites and for the geographic origin of the provenances were provided by the Austrian meteorological service, the Central Institute for Meteorology and Geodynamics (ZAMG). These data include monthly time series from 1971 to 2008 for precipitation sums, precipitation minimum, and maximum, temperature means, minimum and maximum, the length of vegetation period and growing degree days (Table S1). For each location of the provenance origin and trial site, climate data from the nearest 15 stations have been selected, weighted according to horizontal distance and processed in a linear regression against altitude. Finally, climate data for trial sites were averaged for the period 1978 to 1988, which corresponds to period from trial establishment until our measurements. Climate data for the provenance origin were averaged across the total 38-years climate record as this data should rather represent the long-term adaptation to the respective site climate.

Overall, the trial sites and provenance origins in this study span across a wide geographic and climatic gradient covering almost the whole climatic range of current Norway spruce habitats in Central Europe (Fig. 1A) with mean annual temperature ranging from 2.6 to 9.2 °C and annual precipitation from 535 to 2392 mm (Fig. 1). Furthermore, the trials and the provenances also represent a wide altitudinal gradient with trials from 280 to 1700 m asl and provenances from 160 to 1650 m asl (Fig. 1).

2.4. Statistical analysis

The effects of climate and soil of trial sites and provenance origin on forest growth were analyzed in two steps. First, the most influential climate and soil drivers were selected from the list of potential indicators

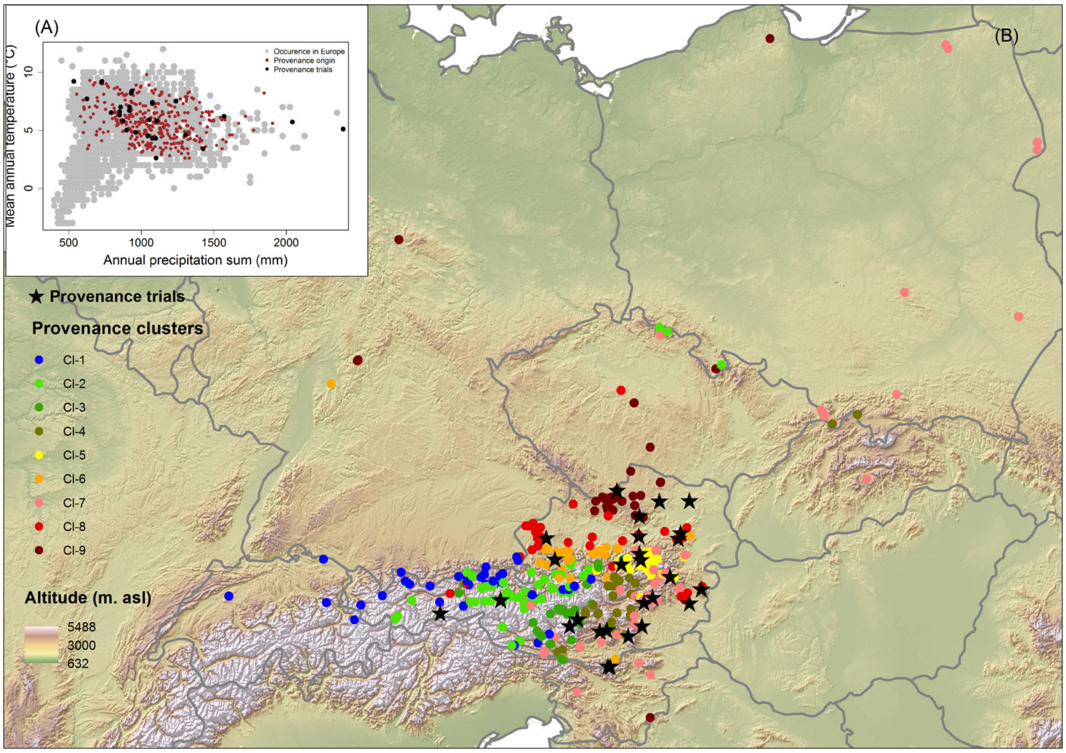

Fig. 1. (A) The provenance trials, provenance origin and natural distribution of Norway spruce in Europe within a bioclimatic parameter space depicted by mean annual temperature (°C) and annual precipitation sum (mm). (B) Geographic locations of the provenance trials (black stars) of Norway spruce in Austria and their provenance origin in central Europe. The provenances were clustered into 9 groups based on climatic and geographic similarities according to Kapeller et al. (2012). The provenance clusters are shown in coloured circles and trial locations in black stars.

described in Table S1 with an unsupervised machine learning algorithm Random Forest (Breiman, 2001). Second, using the resulting set of selected drivers as manifest variables, structural equation modeling (SEM) (Grace, 2008) was applied to infer the simultaneous influences of climatic and soil of trial sites and provenance origin on mean height of Norway spruce at age 15 (H15) henceforth referred to as *juvenile tree height*. Juvenile tree height of individual provenance and provenance cluster at each trial site was used as the indicator of growth performance since no management was done until the age of 15.

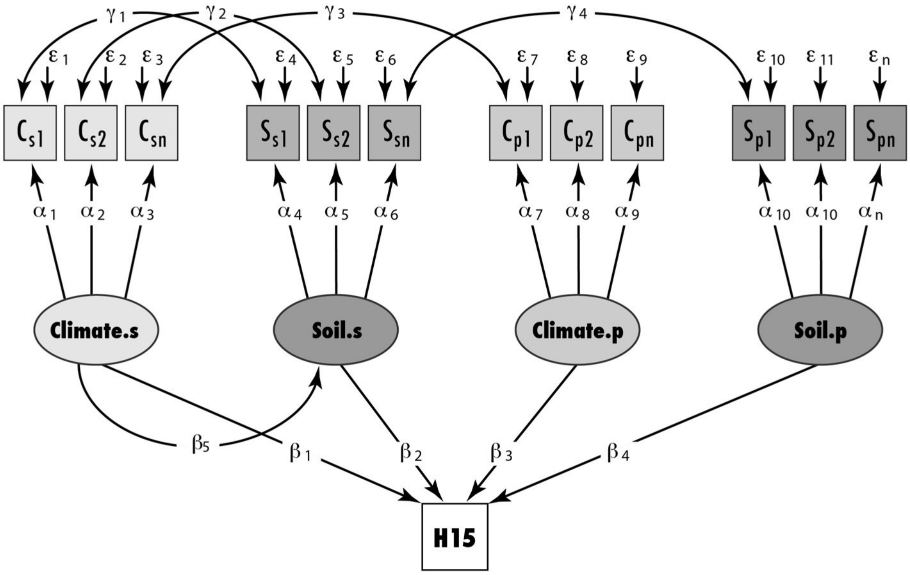

Fig. 2. The generic design of an apriori structural equation model (SEM) analyzed to understand the relative influence of climate and soil variables for both trial sites and provenance origin on height growth performance (mean height at age 15; H15) of juvenile Norway spruce. Ellipses indicate latent variables, boxes represent manifest variables such as climatic and soil variables. Suffix ".s" represent trial site and ".p" represents provenance origin. Note that only three indicators variables are shown for each latent variables Climate.s, Soil.s, Climate.p, Soil.p to represent the full set {1, 2, …, n} of drivers selected from the potential list of drivers (Table S1) by means of recursive feature elimination process. Single headed arrows denote a direct influence in the model, double headed arrows represent interactions between variables. ε denotes error terms, α indicates standardized coefficient of manifest variables, β represents standardized coefficient of latent variables, C_{s1}–C_{sn} indicators of climate of trial sites, S_{s1}–S_{sn} indicators of soil of trial sites, C_{p1}–C_{pn} indicators of climate of provenance origin, S_{p1}–S_{pn} indicators of soil of trial sites, γ denotes standardized coefficients of interactions. Direct effect of a variable, for example, C_{s1} is $(\alpha_1 * \beta_1)$. Indirect effects of a variable for example, climate.s is $(\beta_5 * \beta_2)$. Total efect of a driver is a sum of direct and indirect effects for example: Total effect of climate is $\beta_1 + \beta_5 * \beta_2$.

From the list of 85 potential manifest variables (Table S1), the most important ones were selected with the recursive feature elimination approach (RFE) implemented with the Random forest algorithm (Breiman, 2001). Within the RFE approach variables were eliminated iteratively, starting from the full set of potential predictors (Table S1), retaining only those variables that reduce the mean square error over random permutations of the same variable. This subset of manifest variables was subsequently used as drivers within the SEM framework.

Contrasting to traditional multivariate approaches, SEMs have the ability to go beyond the consideration of independent single parameter processes, allowing the examination of simultaneous influences and to incorporate latent variables, i.e. variables that cannot be measured directly but can be expressed by one or more observable manifest variables. For an a priori *SEM*, we incorporated four major drivers of juvenile tree height: climate (1) and soil (2) of the trial locations as well as climate (3) and soil (4) of the seed origin as latent variables (Fig. 2). These four variables were defined by a number of manifest variables (Table S1).

In order to test if the juvenile tree height performance of populations with specific local adaptations is rather controlled by climate or soil parameters, we developed individual SEMs for each of the nine provenance clusters. These nine provenance clusters were built on basis of similarities in climate and geographic origin of the Austrian provenances using principal component analysis and *k-means* clustering following Kapeller et al. (2012) and thus resemble homogenous groups for which we expect common environmental selection. For defining the clusters climate data of provenance origin with respect to the 20 climatic variables (Table S1) were used. These provenance clusters are Cluster 1: North and Central Alps: low and middle elevations; Cluster 2: North and Central Alps: high elevations; Cluster 3: Southeastern Alps incl. Karawanks; Cluster 4: Eastern intermediate Alps; Cluster 5: the Northeastern border of the Alps; Cluster 6: the Northwestern border of the Alps; Cluster 7: Southeastern fringe of the Alps; Cluster 8: Northern alpine foreland; Cluster 9: Bohemian massif. In a second step, provenances from outside Austria were assigned to these nine groups using the same principal components as in Kapeller et al. (2012). The clusters vary in climate from 2 to 7.3 °C mean annual temperature and 730–1380 mm annual rainfall representing a wide the range of growing conditions of Norway spruce in Austria (see Table S2 in supporting information and Kapeller et al., 2012).

Using the mean juvenile tree height of each of these nine provenance clusters as dependent variables and the climate and soil of the trial sites as latent variables, nine individual SEMs, one for each provenance clusters were developed.

To determine the predictive strength and magnitude of each explanatory variable (manifest and latent variables) within the various SEMs, we used the standardized path coefficients of the SEMs, which are analogous to regression weights. A series of goodness-of-fit tests were done to evaluate the parameterization of our SEMs. This included relative Chi-squared (χ^2/df) value where values 2–8 represents good fit (Hooper et al., 2005). Since our data was not always adjusted to a multinormal distribution, other goodness-of-fit tests, such as the goodness-of-fit index (GFI) and Bentler-Bonett normed-fit index (NFI) were performed (Shipley, 2000; Iriondo et al., 2003). GFI and NFI range between 0 and 1, with values >0.90 indicating a good fit (Hooper et al., 2005).

All statistical analyses and figures were developed with the R environment for statistical computing and visualization (R Core Team, 2016).

3. Results

3.1. Climatic and non-climatic drivers of growth performance

Out of the 85 climates and soil variables (Table S1), 7 climate and 7 soil variables of both trial sites and provenance origin were selected as drivers in the SEM. The a priori *SEM* model which includes climate and soil of trial sites and seed origin as latent variables explains around 65% of the observed variation in juvenile height growth and fits the data well with GFI and NFI > 0.90 (Table 1, Fig. 3). Climate and soil of trial sites are the most dominant driver of juvenile tree height growth (Table 1, Fig. 3) and have significantly stronger total effect sizes (climate effects, $\beta_1 + \beta_5 * \beta_2 = 0.755$ and soil effects, $\beta_2 = -0.43$) compared to climate and soil of provenance origin ($\beta_3 = 0.06$ and $\beta_4 = -0.001$). Within the climatic range of our study, growth is positively influenced by temperature and negatively by precipitation (Fig. 3). The dominant climatic drivers of the trial sites for height growth in descending order of its effects sizes (Table 1) are mean temperature of warmest quarter (MTWQ.s), heat-moisture index of the warmest quarter (WrHMI.s), temperature seasonality (Ts.s), annual precipitation sum (MAP.s) and mean precipitation of the warmest quarter (MPWQ). Major soil drivers of trial sites were percentage of fine particles in the soil (Fpar.s), real field capacity of the soil (FCap.s), soil pH in layer 0–10 cm (pH.s), soil nitrogen at 0–10 cm depth (N.s) and cation exchange capacity at 0–10 cm (CEC.s). The magnitude of the effects varied between the soil variables with Fpar.s having the highest effect size and CEC.s having the lowest effect size (Fig. 3, Table 1).

The effects of the trial sites soil on juvenile height growth were also strongly influenced by the climate of trial sites via indirect effects (Fig. 3, Table 1). For example, MTWQ negatively effects soil nitrogen at 0–10 cm depth (N.s), which in turn effects soil pH at depth 0–10 cm (pH.s) negatively. Soil pH of trial sites (pH.s) is effected indirectly by both soil variables such as soil nitrogen (N.s), cation exchange capacity at 0–10 cm soil depth (CEC.s) and climate variable such as MTWQ.s.

The relevance of climate variables of provenance origin is dominated by the minimum temperature of the coldest month (MCMT.p) and the precipitation of the warmest quarter (MPWQ.p) whereas the soil of provenance origin was mainly characterized by available soil water capacity (AWC.p) and percentage of coarse fragments in the soil (Cfrag.p). Anyhow, the climatic effects of provenance origin were comparably low and the soil effects of provenance origin on H15 were almost negligible (Fig. 3, Table 1).

3.2. How provenance origin influences the relative role of climate and soil on forest growth

The applied nine individual SEMs explained between 53 and 82% of the variation in height growth (Table 2) where R^2 of clusters from colder origins (1–3) tended to be higher than those from warmer origins. The total climate effects ($\beta_c = 0.34$ to 0.78) of the provenance clusters were consistently stronger than the soil effects ($\beta_2 = -0.42$ to -0.17) (Table 2). On average, height growth performance of Clusters 7 (Southeastern fringe of the Alps) and 9 (Bohemian massif) is slightly better compared to other such as Cluster3 (Southeastern Alps including the Karawanks) across the range of planting sites in Austria (Fig. S1 in supporting information).

The relative influence of climate and soil of trial sites on height growth vary among the provenance cluster (Fig. 4). If seeds originate from regions with low coldest month temperature (MCMT ~ −9 °C) and high precipitation in the summer (Fig. 4), the climate of planting location is the dominant driver of tree growth as shown by high ratio of total effect of climate (β_c) to soil (β_2). With increasing coldest month temperature and decreasing precipitation of the warmest quarter (Fig. 4) the soil effects increases and becomes equal to climate influence (ratio of climate to soil effects close to 1). Relative effects of climate and soil of planting location on height growth also depend on the soil properties of the seed origin. Climatic effects on growth performance are dominant if seeds originating from soils with higher carbon content are being planted (Fig. 4). Available water capacity of the seed origin does not seem to influence the relative influence of climate and soil of planting location on height growth (Fig. 4).

Variation also exists in effect sizes of individual trial site climate and soil variables on height growth depending on the climate of seed origin

Table 1
Major drivers of juvenile tree height performance of Norway Spruce. Sufffix ".s" refers to trial site and ".p" refers to provenance origin. Direct effect of a manifest variable is calculated as a multiplicative combination of α and β in Fig. 1. Indirect effects are calcuated as multiplicative combination of and α, β and γ (Fig. 1). Total effect of a driver is a sum of direct and indirect effect.

Variable type	Acronym	Manifest variables	Direct effect	Indirect effect	Total effect
Manifest	MTWQ.s	Mean temperature of warmest quarter (°C)	0.411	0.518	0.929
Manifest	WrHMI.s	Heat moisture Index of Warmest Quarter	0.346	0.278	0.624
Manifest	Ts.s	Temperature seasonality (st.deviation)	0.335	0.268	0.603
Manifest	Fpar.s	Fine particle percentage (%)	0.319	0.000	0.319
Manifest	FCap.s	Real field capacity of soil	0.294	0.000	0.294
Manifest	MTCM.p	Minimum temperature of coldest month (°C)	0.055	0.000	0.055
Manifest	Cfrag.p	Coarse fragments in soil (%)	−0.002	0.000	−0.002
Manifest	AWC.p	Available water capacity	−0.002	0.000	−0.002
Manifest	MPWQ.p	Precipitation of warmest quarter	−0.052	0.000	−0.052
Manifest	pH.s	Soil pH in layer (0–10 cm)	−0.164	0.000	−0.164
Manifest	N.s	Soil nitrogen content of layer (0–10 cm)	−0.324	0.090	−0.234
Manifest	CEC.s	Cation exchange capacity of layer (0–10 cm)	−0.337	−0.108	−0.445
Manifest	MAP.s	Annual precipitation sum (mm)	−0.279	−0.221	−0.500
Manifest	MPWQ.s	Precipitation of warmest quarter (mm)	−0.279	−0.225	−0.504
Latent	Climate.s	Climate of trial site	0.420	0.335	0.755
Latent	Soil.s	Soil of trial site	−0.430	0.000	−0.430
Latent	Climate.p	Climate of provenance origin	0.060	0.000	0.060
Latent	Soil.p	Soil of provenance origin	−0.003	0.000	−0.003
		Total R^2			0.648

(Fig. S5 in supporting information). For example effect of summer drought or the heat-moisture index of the warmest quarter (WrHMI.s) on height growth is more important if provenances originating from colder and wet locations are planted. Effect sizes of soil pH of trial sites on height growth increase with minimum temperature of coldest month and decrease with precipitation of warmest quarter of seed origin. Influence of cation exchange capacity also increases with an increase in minimum coldest month temperature and decreases with increase in warmest quarter precipitation of seed origin.

4. Discussion

In this study, we analyzed the influence and interactions of various climatic and non-climatic drivers of growth performance of Norway spruce in Austria. Our study demonstrates that climate and soil of the trial sites have a similar direct effect on juvenile tree growth, though climate also acts indirectly and provides the highest overall contribution to forest growth (Fig. 3, Table 1). Environmental variables (soil and climate) of provenance origin also commonly referred to as seed origin were found to be negligible in the overall model, but if provenances were stratified by their origin, significant differences in the partitioning of the soil and climate effects of trial sites were found, providing evidence for a provenance-region specific ability to utilize the available soil fertility (Table 2).

4.1. Multiple factors and their interactions drive forest growth

The most important climate variables of trial sites were those which characterized temperature and drought stress during growing periods

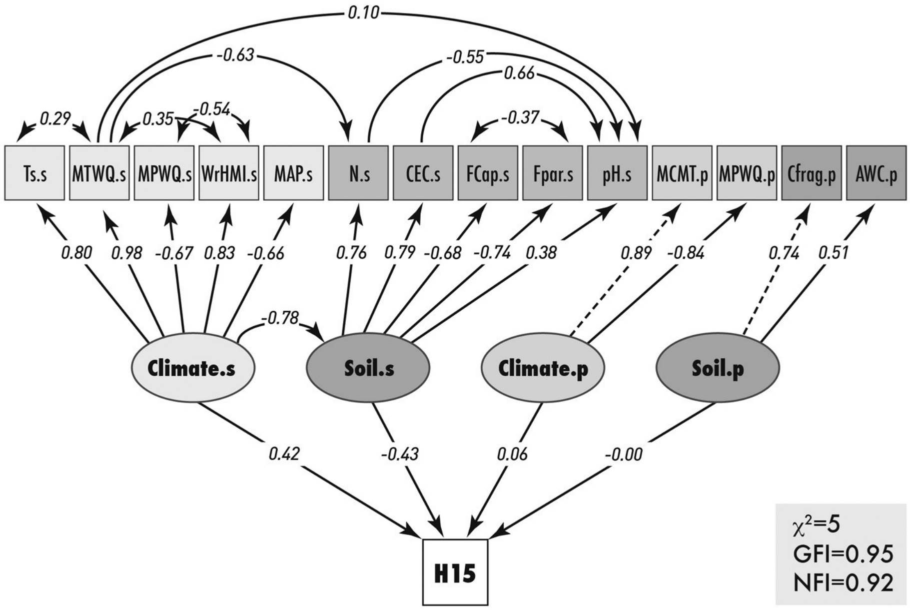

Fig. 3. Relative influences of climate, soil and genetics. Ellipses indicate latent variables, boxes represent drivers and manifest variables such as climatic and soil variables. Suffix ".s" represent trial sites and ".p" represents provenance origin. Here Latent variables: Climate.s = Climate of trial site, Soil.s = Soil of trial site, Climate.p = Climate of provenance origin, Soil.p = Soil of provenance origin. Arrows represent influences with standardized coefficient. Single headed arrows denote a direct influence in the model, double headed arrows represent interactions between variables. Solid and dashed lines depict significant and non-significant paths respectively. χ^2 is the relative chi-squared (χ^2/df) where values 2–8 represents good fit (Hooper et al., 2005). GFI represents the goodness-of-fit index and (NFI) represents the Bentler-Bonett normed-fit. GFI and NFI range between 0 and 1, with values >0.90 indicating a good fit (Hooper et al., 2005).

Table 2
The influence of climate ($\beta_c = \beta_1 + \beta_5 * \beta_2$) and soil ($\beta_2$) of trial site on height growth performance of juvenile Norway Spruce depending on the planted seed source or provenance cluster. The ratio of β_c and soil β_2 represents the relative influence of climate and soil on height growth performance. R^2 refers to total variation in height growth performance explained by each of the 9 SEMs for individual provenance clusters.[a]

Cluster	Climate $\beta_c = (\beta_1 + \beta_5 * \beta_2)$	Soil β_2	Climate to soil ratio[a] $\frac{\beta_c}{\beta_2}$	R^2
1	0.777	−0.370	−2.10	0.725
2	0.648	−0.291	−2.23	0.815
3	0.648	−0.291	−2.23	0.815
4	0.342	−0.169	−2.02	0.528
5	0.685	−0.343	−2.00	0.698
6	0.444	−0.419	−1.06	0.682
7	0.551	−0.349	−1.58	0.748
8	0.463	−0.403	−1.15	0.684
9	0.456	−0.340	−1.34	0.584

[a] Absolute value of the climate to soil ratio was used to examine the effects of climate of provenance origin on the relative influence of planting location climate and soil on juvenile tree height in Fig. 4.

such as MTWQ.s, MPWQ.s, and WrHMI.s; temperature seasonality (TSS.s) and annual precipitation (MAP.s).

Juvenile tree height increases with increasing temperature of trial sites. (Fig. S3 in supporting information). However, an increase in precipitation both in the summer (MPWQ.s) and throughout the year do not translate into taller trees (Fig. S3). Also, drought conditions, which can approximately be estimated by WrHMI.s, do not affect growth performance negatively (Fig. S3D) as also found by Kapeller et al. (2012). This is in contrast to other dendroecological studies (e.g. Zang et al., 2014) or genetic analysis (Trujillo-Moya et al., 2018) which showed that extreme drought events result into strong growth reductions mainly in diameter growth. Our study spans across a wide range of climate and altitudinal gradient (Kapeller et al., 2012). Along with this altitudinal gradient, the sensitivity of growth to temperatures in higher elevations is stronger than the sensitivity of growth to precipitation in lower elevations. Another explanation could be that the analyzed trees have not experienced droughts of extreme magnitude during their growing period from 1978 to 1988, which was still a decade of relatively stable temperate climate.

The soil variables used in the SEMs describe the general soil nutrient pool and availability via CEC.s, N_2.s, and pH.s; and parameters describing the water holding capacities such as FCap.s and Fpar.s. A steady growth is maintained with an increase in N_2.s and CEC.s until a certain concentration (for example 4–5 mg N_2 per gram soil; or in case of CEC 150 mol/kg soil). Beyond, this, a further increase in soil fertility levels off at nitrogen-rich sites. In our study, sites with high soil nitrogen content and cation exchange capacity were located at higher altitudes (Fig. S4 in supporting information). Therefore the apparent reduction in growth at higher soil nitrogen and soil fertility (Fig. S3F) may also result from the poor rate of nitrogen mineralization at higher altitudes causing a decline in the amount of organic nitrogen available for the plant (Garten and Hanson, 2006; Schindlbacher et al., 2010). Another cause may be that sites with critically low levels of soil nutrients (N_2 and CEC) were not sampled in our study.

Overall, the soil properties at the trial sites represent above-average conditions within the range of Austrian forest soils. This is expected because experimental trials are often established at sites where soil properties do not critically limit tree growth. The soil conditions of the trials as well as provenance origin also cover a wide range of conditions (Fig. S1). Majority of the provenance trials have high nutritional status and are acidic, with some calcareous soils with high rock content and consequently lower field capacity (Fig. S1).

We found that the climate of trial sites had stronger influences compared to the soil (Fig. 3, Table 1). This finding was expected, however, not explicitly reported and discussed in recent studies. For example, Toledo et al. (2011) found climate variables to be a predominantly

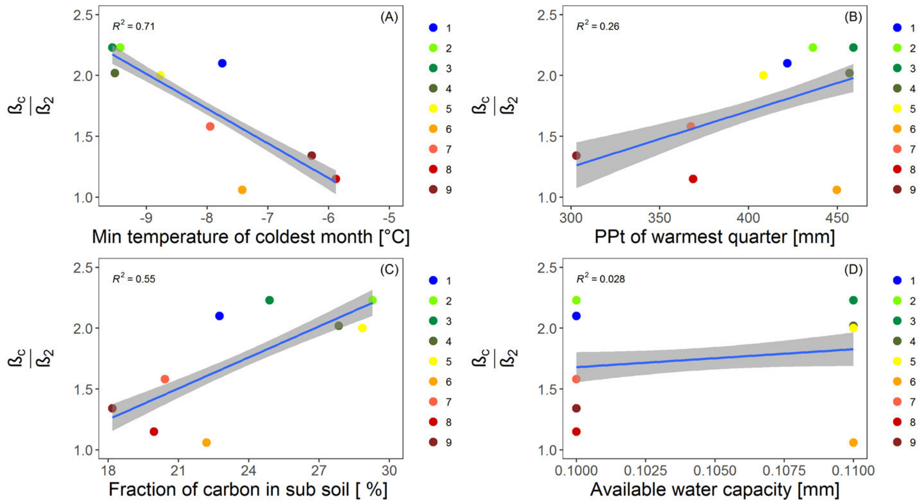

Fig. 4. Absolute value of the ratio between total effects of (β_c) and soil (β_2) of trial sites (see Table 2 for details) as a response to climate and soil of provenance origin; A) minimum temperature of coldest month, (B) precipitation of warmest quarter of provenance origin, (C) fraction of carbon in sub soil and (D) Available soil water capacity. Here climate and soil variables of provenance origin represents mean value of climate and soil variables of each provenance clusters. The colors represent provenance clusters. The climate to soil ratio close to 1 means equal effects size of climate and soil of planting location whereas ratio above 1 represents a dominance of climate variables over soil variables and vice versa. The gray band represents 95% confidence interval. * represents significant correlations (Pearson's correlation coefficient); ranging from 0.26 to 0.71 and $p < 0.00$ in A, B and C, whereas the correlation depicted in D is insignificant.

stronger predictor of forest growth in comparison with soil variables which was disputed by Ferry et al. (2012). The effects of soil vs. climate variables was recently also discussed for tree species distributions: here, tree species occurrences were suggested to be more strongly driven by soil variables if the climatic heterogeneity is low (Diekmann et al., 2015) and were found to be even predominant on regional scales covering restricted parts of species distributions (Walthert and Meier, 2017). Such interactions between climate and soil were also found in our study, suggesting that soil and climate influence forest growth interdependently. For example effects of soil nitrogen is regulated indirectly by summer temperature whereby warmer sites are likely to have higher nitrogen related limitation compared to cooler sites (Fig. 3, Table 1). Effects of soil cation exchange capacity (CEC.s), an indicator of soil fertility is also regulated by both soil and climate factors such as summer temperature and soil nitrogen. Sites with warmer summers and lower nitrogen limitation usually have higher soil fertility, which leads to higher growth performance compared to colder sites with lower nitrogen content.

We found that soil variables from a depth of 0–10 cm were more influential for the growth of Norway spruce compared to soil variables at litter layer and inorganic layer at 10–20 cm depth. This is probably because the trees were still quite young and the majority of the fine root biomass is located within the upper 20 cm of the soil profile in a wide range of growing conditions in Austria (Berger and Hager, 2000). Moreover, the soil properties of 0–10 and 10–20 cm are closely correlated.

4.2. Seed origin modifies the relative drivers of growth

The dominance of the environmental factors (climate and soil) of trial sites over that of provenance or seed origin as found in our study was also reported in several forest tree species (Ghalambor et al., 2007; Wang et al., 2010; Rehfeldt et al., 2014; Chakraborty et al., 2015). In part, this may result from the lower quality of environmental data of the seed origin compared to the trial sites. The exact locations of the provenance origin were less precise and mainly described by the given forest district and altitude. Therefore, we could estimate the soil conditions only from soil maps at a lower spatial resolution. Also, climate data depict only the trial mean over a 38 year period which should represent long-term adaptation to the respective site climate, though we know that temperature and day-length during seed embryogenesis might result into epigenetic modifications and phenotypic variation (Skrøppa et al., 2007; Bräutigam et al., 2013). Also, it may be possible that some of the provenances used in our study are not autochthonous and thus create additional variation.

Despite differences in data quality of the historic trials evaluated here, the selection of seed sources is the only decision which is to be made by forest and restoration managers, whereas soil and climate of the plantation site are fixed management constraints. If provenances originate from cold and moist environments (typical of higher elevation areas), their growth performance is mainly controlled by climatic factors (Fig. 4). The growth of the productive provenances (Kapeller et al., 2012) originating from lower elevation, warm and dry regions (Fig. 4), is strongly regulated by the respective soil conditions, indicating a higher plasticity to cope with differences in physical and chemical soil characteristics. Higher plasticity of spruce populations from lower elevations was already reported for phenotypic traits, for example, crown types (Gruber, 1990). It might be explained by the stronger climatic selection pressures on juvenile spruce in cold and moist environments as compared to warm and dry provenance origins (Kapeller et al., 2017). Generally, provenances originating from currently warm and dry parts of the Norway spruce distribution such as the southeastern fringe of the Alps and Bohemian massif were found to be the most productive ones under climate change in Central Europe (Gömöry et al., 2010; Ge et al., 2011; Kapeller et al., 2012; Schueler et al., 2013). These provenances seem to be able to maintain optimal tree growth in a variety of forest soils and might thus provide only limited risk if planted in assisted gene flow and migration scenarios. In particular, provenances might be slightly moved up to higher elevations to support an increase in tree productivity (Kapeller et al., 2012). Less plastic seed sources originating from higher elevations only have limited applications in seed transfers, but at the same time, our study shows that they should be able to react to higher temperature with better growth within their native environment. We did find an interaction between the environmental variables of seed origin and planting site neither for the soil nor climate variables (Fig. 3). This suggests that the provenances with the best growth performance today will also be the most productive ones under other climate and soil conditions. Low and insignificant interactions between seed source and plantation site climate are a common observation in coniferous trees (Wang et al., 2010; Chakraborty et al., 2015) and indicate, that phenotypic growth variation among population is not evenly distributed across their ranges, (Kapeller et al., 2017) but certain regions and populations provide substantially higher growth potential.

5. Conclusions

The productivity of tree species with a wide natural distribution such as the Norway spruce is influenced by a complex interaction of climatic and non-climatic factors. These interactions are further modified depending on the material being planted. We found that climate and soil factors are equally important for driving growth performance of juvenile Norway spruce across when direct effects were considered. However, climatic influences assumed greater importance when additional indirect effects via interactions with soil parameters were taken into account. In addition, the relative dominance of climate and soil factors depends on the origin of the planting materials. By incorporating the climate and soil of seed origins into an assessment framework such as the one used in this study, the genetic factors are also indirectly incorporated. The insignificance of the soil of provenance origin found in this study does not necessarily mean that soil factors of the seed sources are not important for forest growth. It shows that gridded soil data, as available and used in this study may not accurately represent the micro level variations in site conditions in Austria. Therefore we recommend that information on soil conditions of seed origin should also be reported in provenance trials and for ongoing seed legislation in order to improve the data quality of future experiments.

Data accessibility

Data files used for the analyses in this study are available at the Dryad Digital Repository: doi: https://doi.org/10.5061/dryad.877ts.

Competing interests

None.

CRediT authorship contribution statement

Debojyoti Chakraborty: Conceptualization, Formal analysis, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Robert Jandl:** Conceptualization, Data curation. **Stefan Kapeller:** Data curation. **Silvio Schueler:** Conceptualization, Funding acquisition, Validation, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.11.093.

References

Aitken, S.N., Yeaman, S., Holliday, J.A., et al., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x.

Baker, T., Swaine, M., Burslem, D., 2003. Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspect. Plant Ecol. Evol. Syst. 6, 21–36. https://doi.org/10.1078/1433-8319-00040.

Barsoum, N., Eaton, E.L., Levanič, T., et al., 2015. Climatic drivers of oak growth over the past one hundred years in mixed and monoculture stands in southern England and northern France. Eur. J. For. Res. 134, 33–51. https://doi.org/10.1007/s10342-014-0831-5.

Berger, T.W., Hager, H., 2000. Physical top soil properties in pure stands of Norway spruce (*Picea abies*) and mixed species stands in Austria. For. Ecol. Manag. 136, 159–172. https://doi.org/10.1016/S0378-1127(99)00286-8.

Bräutigam, K., Vining, K.J., Lafon-Placette, C., et al., 2013. Epigenetic regulation of adaptive responses of forest tree species to the environment. Ecol. Evol. 3, 399–415. https://doi.org/10.1002/ece3.461.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Chakraborty, D., Wang, T., Andre, K., et al., 2015. Selecting populations for non-analogous climate conditions using universal response functions: the case of Douglas-fir in Central Europe. PLoS One 10, e0136357. https://doi.org/10.1371/journal.pone.0136357.

Diekmann, M., Michaelis, J., Pannek, A., 2015. Know your limits — the need for better data on species responses to soil variables. Basic Appl. Ecol. 16, 563–572.

Du, E., 2015. Uncertain effects of nutrient availability on global forest carbon balance. Nat. Clim. Chang. 5, 958–959.

Englisch, M., Karrer, G., Mutsch, F., 1992. Methodische Grundlagen. Mitt. Forst. Bundesversuch. 168/14 (5), 22.

European Commission and the European Soil Bureau Network, 2004. The European Soil Database Distribution Version 2.0. CD-ROM doi: citeulike-article-id:14258119.

Fernández-Martínez, M., Vicca, S., Janssens, I.A., et al., 2014. Nutrient availability as the key regulator of global forest carbon balance. Nat. Clim. Chang. 4, 471–476. https://doi.org/10.1038/nclimate2177.

Ferry, B., Bontemps, J.-D., Blanc, L., Baraloto, C., 2012. Is climate a stronger driver of tree growth than disturbance? A comment on Toledo et al. (2011). J. Ecol. 100, 1065–1068. https://doi.org/10.1111/j.1365-2745.2011.01895.x.

Fleck, S., Cools, N., De Vos, B., et al., 2016. The level II aggregated forest soil condition database links soil physicochemical and hydraulic properties with long-term observations of forest condition in Europe. Ann. For. Sci. 73, 945–957. https://doi.org/10.1007/s13595-016-0571-4.

Garten, C.T., Hanson, P.J., 2006. Measured forest soil C stocks and estimated turnover times along an elevation gradient. Geoderma 136, 342–352. https://doi.org/10.1016/j.geoderma.2006.03.049.

Gartner, K., Herzberger, E., Reiter, R., Englisch, M., Leitgeb, E., 2018. Kennwerte zum Wasser- und Lufthaushalt österreichischer Böden. Mitt. Österreich. Bodenk. Gesellsch. 85, 39–56.

Ge, Z.M., Kellomäki, S., Peltola, H., et al., 2011. Impacts of changing climate on the productivity of Norway spruce dominant stands with a mixture of Scots pine and birch in relation to water availability in southern and northern Finland. Tree Physiol. 31, 323–338. https://doi.org/10.1093/treephys/tpr001.

Ghalambor, C.K., McKay, J.K., Carroll, S.P., Reznick, D.N., 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct. Ecol. 21, 394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x.

Gömöry, D., Foffová, E., Kmet, J., et al., 2010. Norway spruce (*Picea abies* [L.] Karst.) Provenance variation in autumn cold hardiness: adaptation or acclimation? Acta Biol. Cracov. Ser. Bot. 52, 42–49. https://doi.org/10.2478/v10182-010-0022-8.

Grace, J.B., 2008. Structural Equation Modeling and Natural Systems. 361. Cambridge Univ Press. https://doi.org/10.1086/586991.

Gruber, F., 1990. Verzweigungssystem, Benadelung Und Nadelfall der Fichte (*Picea abies*) (Branching System, Needle Fall and Needle Density of Norway Spruce (*Picea abies*)). Birkhäuser Basel.

Hlásny, T., Trombik, J., Bošeľa, M., et al., 2017. Climatic drivers of forest productivity in Central Europe. Agric. For. Meteorol. 234–235, 258–273. https://doi.org/10.1016/j.agrformet.2016.12.024.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35. https://doi.org/10.1890/04-0922.

Iriondo, J.M., Albert, M.J., Escudero, A., 2003. Structural equation modelling: an alternative for assessing causal relationships in threatened plant populations. Biol. Conserv. 113, 367–377. https://doi.org/10.1016/S0006-3207(03)00129-0.

Ishizuka, W., Goto, S., 2012. Modeling intraspecific adaptation of *Abies sachalinensis* to local altitude and responses to global warming, based on a 36-year reciprocal transplant experiment. Evol. Appl. 5, 229–244. https://doi.org/10.1111/j.1752-4571.2011.00216.x.

Jandl, R., Herzberger, E., 2001. Is soil chemistry an indicator of tree nutrition and stand productivity? Bodenkultur 52, 155–163.

Kapeller, S., Lexer, M.J., Geburek, T., et al., 2012. Intraspecific variation in climate response of Norway spruce in the eastern Alpine range: selecting appropriate provenances for future climate. For. Ecol. Manag. 271, 46–57. https://doi.org/10.1016/j.foreco.2012.01.039.

Kapeller, S., Dieckmann, U., Schueler, S., 2017. Varying selection differential throughout the climatic range of Norway spruce in Central Europe. Evol. Appl. 10, 25–38. https://doi.org/10.1111/eva.12413.

Kardol, P., Todd, D.E., Hanson, P.J., Mulholland, P.J., 2010. Long-term successional forest dynamics: species and community responses to climatic variability. J. Veg. Sci. 21, 627–642. https://doi.org/10.1111/j.1654-1103.2010.01171.x.

Kreyling, J., Buhk, C., Backhaus, S., et al., 2014. Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. Ecol. Evol. 4, 594–605. https://doi.org/10.1002/ece3.971.

Kutsch, W.L., Kolari, P., 2015. Data quality and the role of nutrients in forest carbon-use efficiency. Nat. Clim. Chang. 5, 959–960.

Lévesque, M., Saurer, M., Siegwolf, R., et al., 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. Glob. Chang. Biol. 19, 3184–3199. https://doi.org/10.1111/gcb.12268.

Manrique-Alba, À., Ruiz-Yanetti, S., Moutahir, H., et al., 2017. Soil moisture and its role in growth-climate relationships across an aridity gradient in semiarid *Pinus halepensis* forests. Sci. Total Environ. 574, 982–990. https://doi.org/10.1016/j.scitotenv.2016.09.123.

Me Chave, J.R., Ra, B.R., Dubois, M.-A., 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. J. Trop. Ecol. 17, 79–96. https://doi.org/10.1017/S0266467401001055.

Mina, M., Huber, M.O., Forrester, D.I., et al., 2017. Multiple factors modulate tree growth complementarity in Central European mixed forests. J. Ecol. 106/3, 1106–1119.

Montwé, D., Spiecker, H., Hamann, A., 2014. An experimentally controlled extreme drought in a Norway spruce forest reveals fast hydraulic response and subsequent recovery of growth rates. Trees Struct. Funct. 28, 891–900. https://doi.org/10.1007/s00468-014-1002-5.

Nather, J., Holzer, K., 1979. Über die Bedeutung und die Anlage von Kontrollflächen zur Prüfung von anerkanntem Fichtenpflanzgut. Forst. Bundesversuch. Wien 181.

O'Neill, G.A., Nigh, G., Wang, T., Ott, P.K., 2007. Growth response functions improved by accounting for nonclimatic site effects. Can. J. For. Res. 37, 2724–2730. https://doi.org/10.1139/X07-100.

Pan, Y., Birdsey, R.A., Fang, J., et al., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993. https://doi.org/10.1126/science.1201609.

Pretzsch, H., Biber, P., Schütze, G., et al., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. Nat. Commun. https://doi.org/10.1038/ncomms5967.

Pureswaran, D.S., Roques, A., Battisti, A., 2018. Forest insects and climate change. Curr. For. Rep., 1–16 https://doi.org/10.1007/s40725-018-0075-6.

R Core Team, 2016. R Core Team R. R A Lang. Environ. Stat. Comput. R Found. Stat. Comput, Vienna, Austria http://www.R-project.org.

Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., et al., 2002. Intraspecific responses to climate in *Pinus sylvestris*. Glob. Chang. Biol. 8, 912–929. https://doi.org/10.1046/j.1365-2486.2002.00516.x.

Rehfeldt, G.E., Jaquish, B.C., López-Upton, J., et al., 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. For. Ecol. Manag. 324, 147–157. https://doi.org/10.1016/j.foreco.2014.02.040.

Reyer, C.P.O., Bathgate, S., Blennow, K., et al., 2017. Are forest disturbances amplifying or canceling out climate change-induced productivity changes in European forests? Environ. Res. Lett. https://doi.org/10.1088/1748-9326/aa5ef1.

Schindlbacher, A., De Gonzalo, C., Díaz-Pinés, E., et al., 2010. Temperature sensitivity of forest soil organic matter decomposition along two elevation gradients. Temp. J. Geophys. Res. 115, 10. https://doi.org/10.1029/2009JG001191.

Schueler, S., Kapeller, S., Konrad, H., et al., 2013. Adaptive genetic diversity of trees for forest conservation in a future climate: a case study on Norway spruce in Austria. Biodivers. Conserv. 22, 1151–1166. https://doi.org/10.1007/s10531-012-0313-3.

Seidl, R., Rammer, W., Jäger, D., Lexer, M.J., 2008. Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. For. Ecol. Manag. 256, 209–220. https://doi.org/10.1016/j.foreco.2008.04.002.

Shipley, B., 2000. Cause and Correlation in Biology. A User's Guide to Path Analysis, Structural Equations and Causal Inference. 20. https://doi.org/10.1017/CBO9780511605949.

Skrøppa, T., Kohmann, K., Johnsen, Ø., et al., 2007. Field performance and early test results of offspring from two Norway spruce seed orchards containing clones transferred to warmer climates. Can. J. For. Res. 37, 515–522. https://doi.org/10.1139/X06-253.

Toledo, M., Poorter, L., Peña-Claros, M., et al., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J. Ecol. 99, 254–264. https://doi.org/10.1111/j.1365-2745.2010.01741.x.

Trujillo-Moya, C., George, J.-P., Fluch, S., et al., 2018. Drought sensitivity of Norway spruce at the species' warmest fringe: quantitative and molecular analysis reveals high genetic variation among and within provenances. G3 (Bethesda) 8, 1225–1245. https://doi.org/10.1534/g3.117.300524.

Van Der Maaten-Theunissen, M., Kahle, H.P., Van Der Maaten, E., 2013. Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. Ann. For. Sci. 70, 185–193. https://doi.org/10.1007/s13595-012-0241-0.

de Vries, W., Posch, M., Simpson, D., Reinds, G.J., 2017. Modelling long-term impacts of changes in climate, nitrogen deposition and ozone exposure on carbon sequestration of European forest ecosystems. Sci. Total Environ. 605–606, 1097–1116. https://doi.org/10.1016/j.scitotenv.2017.06.132.

Walthert, L., Meier, E.S., 2017. Tree species distribution in temperate forests is more influenced by soil than by climate. Ecol. Evol. 7, 9473–9484. https://doi.org/10.1002/ece3.3436.

Wang, T., O'Neill, G.A., Aitken, S.N., 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. Ecol. Appl. 20, 153–163. https://doi.org/10.1890/08-2257.1.

Zang, C., Hartl-Meier, C., Dittmar, C., et al., 2014. Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Glob. Chang. Biol. 20, 3767–3779. https://doi.org/10.1111/gcb.12637.