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Climate change adaptation with non-native tree species in Central European forests: early tree survival in a multi-site field trial

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Abstract

Climate projections indicate large increases in temperature, requiring tree species to adapt or migrate faster than observed historic rates. In Central Europe, discussion in forest management has increasingly focused on how humans can assist these adaptation/migration processes, especially when important forest ecosystem services are at risk. One option is to introduce non-native tree species to help forest ecosystems adapt to climate change. We established a long-term experiment in autumn 2012 on five study sites in climatically different regions of Central Europe. The performance of five non-native tree species from warmer climates (*Abies bornmuelleriana* Mattf., *Cedrus libani* A. Rich., *Fagus orientalis* Lipsky, *Tilia tomentosa* Moench and *Tsuga heterophylla* Sarg.) was compared to that of one local species native to each site. We monitored sapling survival during the first 4 years after planting. Small differences in timing of inventory campaigns were overcome by fitting a Weibull function to survival curves and analysing time-harmonized estimates for equal biannual periods. Sapling mortality decreased over time, but early after planting, it differed between species. The native and the two non-native broadleaved species showed higher survival than the non-native coniferous species. Moreover, the site conditions of the open areas seemed to initially hamper the growth of shade-tolerant species. All species performed reasonably well during the relatively short observation period. Any differences between hazard rates almost vanished 4 years after planting, which suggests that all species tested are likely to thrive under current climate conditions. Long-term observations are, however, needed to corroborate these results.

Keywords Climate change · Assisted migration · Climate adaptation · Non-native species · Sapling survival

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Nico Frischbier and Petia Nikolova contributed equally to this work.

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Introduction

Since 1880, average worldwide temperatures have increased by almost 0.85 °C (IPCC 2014). Compared to the global average, the temperature rise in some parts of Central Europe has been significantly higher, amounting to, e.g. 1.3 °C in Germany (Kaspar and Mächel 2017), about 2.0 °C in Austria (APCC 2014) and to 1.8 °C in Switzerland (Remund et al. 2016). Forest trees react in different ways to climate change: they may be able to adapt in their current habitat or migrate, or they become extinct (Aitken et al. 2008). Current

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climate projections, however, require long-lived species to react faster than their observed rates of migration (Williams and Dumroese 2013). This has recently attracted attention to the role of the human assistance in climate adaptation and in migration processes of economically and ecologically important forest tree species.

How to best help forests adapt to their changing environment is the subject of an ongoing debate in forest science (Brang et al. 2014; Lindner et al. 2010; Trumbore et al. 2015) and among forest managers (Bolte et al. 2009; Profft and Frischbier 2009). One adaptation strategy is to speed up tree migration to new habitats through assisted species migration, which usually involves far transportation of seeds or saplings and planting at the new location (reviewed in Williams and Dumroese 2013). This also promotes a more diverse tree species composition on the target sites. To this end, economically advantageous (productive) and non-invasive (manageable) tree species are often introduced from regions already exposed to a warmer and drier climate (Brang et al. 2016; Broadmeadow et al. 2005; Isaac-Renton et al. 2014; Park et al. 2018). Such species can complement the native tree species and contribute to the continuous provision of important forest ecosystem services such as climate change mitigation (Nabuurs et al. 2017; Vor et al. 2015). The motivations for previous introductions of non-native tree species to Central Europe have been their valuable timber and high-volume production or the maintenance of functionality and ecosystem services of forests. The disadvantages of introducing them include the initial investment needed (planting), changing the habitat quality for native organisms (Didham et al. 2007), suppressing of native species (Martin et al. 2009) and increasing trees' vulnerability to pests and pathogens (Brang et al. 2016; Isaac-Renton et al. 2014; Ste-Marie et al. 2011). Most introductions of non-native tree species to Central Europe failed, either from the beginning, with low establishment rates (Bürigi and Diez 1986; Vor et al. 2015), or later with low survival rates (Brang et al. 2016; Engelmark et al. 2001). Only a few non-native species have an advantage over native species in terms of growth or timber value, e.g. the coastal variety of *Pseudotsuga menziesii* (Isaac-Renton et al. 2014; Schmid et al. 2014). However, *P. menziesii* is thought to negatively affect biodiversity, at least concerning fungal diversity and arthropod densities during winter, with possible negative consequences for birds (Schmid et al. 2014).

Only a few species that seem to tolerate warmer and drier climates have so far been subjected to rigid experimental examination, which is why new initiatives to identify and test such species have been initiated (Schölch et al. 2010; SchmieDinger et al. 2009). We report in this paper on a multi-site trial that started in 2012 focusing on five non-native species which have so far been neither frequently used nor intensively studied in Central Europe, as well as

on one additional site-specific native species to serve as a local reference (Bachmann et al. 2015; SchmieDinger et al. 2009). Almost no experimental plantations of these species exist in Central Europe, although some are described in Lembcke (1973). The particular value of our trial is the consistent multi-site approach, with sites covering a climatic gradient, where 1981–2010 the mean annual temperature ranged between 7.9 and 10.4 °C, the annual precipitation sum between 490 and 1147 mm and the annual de Martonne index (de Martonne 1926) between 26 and 61. Moreover, we used plants with identical origin (provenance) cultivated together in a controlled way.

We focus here on the survival of the previously selected non-native and site-specific native species, addressing the following questions:

1. How do the survival rates of the tested tree species differ over time?
2. Do the site and climate conditions affect the species-specific survival rates?
3. Do the native species have generally higher survival rates than non-native ones?

To this end, we monitored seedling survival during the first 4 years after planting. Weibull functions were fitted to the survival curves and time-harmonized estimates for equal biannual periods were analysed. The influence of site, species and climate conditions on plant survival was studied by multifactorial ANOVAs and general linear mixed models GLMMs.

Methods

Species selection

Four out of the five non-native species tested originate from a species selection process described in SchmieDinger et al. (2009). They identified regions in which both recent (1950–2000) and predicted (2071–2100) climatic conditions for Central Europe could be found in close proximity, assuming the IPCC emission scenario SRES-B1 (Spekat et al. 2007). In these regions, they selected species (1) with high use value that have many economic and ecological benefits and (2) without associated biotic and abiotic risks. The selection process also excluded species whose performance in Central Europe has already been well studied.

The four species then selected were Bornmuellerian fir (*Abies bornmuelleriana* Mattf., called '*A. bornmuelleriana*' henceforth), oriental beech (*Fagus orientalis* Lipsky, '*F. orientalis*'), western hemlock (*Tsuga heterophylla* (Raf.) Sarg., '*T. heterophylla*') and silver lime (*Tilia tomentosa* Moench, '*T. tomentosa*'). In addition, Lebanon cedar (*Cedrus libani*

A. Rich., '*C. libani*') was included as a species coming from a similar region to that of *A. bornmuelleriana* and *F. orientalis*.

A. bornmuelleriana is most likely a natural hybrid between Caucasian fir (*Abies nordmanniana*) and Grecian fir (*Abies cephalonica*) and has the smallest geographic distribution area among the tested species. It is found naturally in northwestern Turkey in the western Pontus Mountains, covering an altitudinal range of 800–2000 m (Schütt 1991). It tolerates low summer precipitation (Dohrenbusch 1985; Schütt 1991) and low winter temperatures and can therefore be described as drought-tolerant as well as winter- and frost-resistant. *C. libani* is naturally distributed in a limited area in the mountains of Turkey, Lebanon and Syria and is usually found at elevations of 1300–3000 m on North- and West-facing slopes on well-drained calcareous soils (Ayasligil 1997; EUFORGEN 2019; Messinger et al. 2015). Due to its high drought tolerance (Erkan and Aydin 2017), it is commonly used for afforestation outside its natural distribution range, especially on dry sites. *F. orientalis* has a relatively wide distribution range and is native to the Mediterranean and Middle Eastern areas near the Caspian Sea and the Black Sea at elevations of 200–2200 m (Kandemir and Kaya 2009; Seyer 1951). It is tolerant to shade, but its distribution is limited by late frosts (EUFORGEN 2019), regular flooding and prolonged summer droughts (Atalay 1992). *T. tomentosa* is naturally distributed in the Balkan peninsula and northwestern Turkey (Binder 2015), with an island distribution in the Nur Mountains of south-central Turkey at elevations up to 1300 m. *T. tomentosa* is very drought-tolerant, but does not tolerate average January temperatures < -5 °C (Zagwijn 1996). *T. heterophylla* occurs naturally in the humid zones of Western North America from British Columbia (Canada) to California (USA), with thus the largest distribution area of the five non-native tree species studied. *T. heterophylla* is a very shade-tolerant tree species, and its seedling can persist for decades under the canopy of other conifers (Packer 1990). In our study, *T. heterophylla* is the only species native to areas which have no land connection to Central Europe.

The native reference species were not the same at all sites, but were selected after consultation with the respective forest administration about which species would thrive best in a future warmer and drier climate. The species chosen were: pedunculate oak (*Quercus robur* L.) in Bavaria/Germany, sessile oak (*Quercus petraea* (Matt.) Liebl.) in Thuringia/Germany and Switzerland and black pine (*Pinus nigra* Arnold var. *austriaca* Badoux) in Austria (Table 1). Both pedunculate and sessile oak are large, long-lived broad-leaved trees and among the most economically and ecologically important forest tree species that are widely distributed in Europe (Schütt and Schuck 1992). Both oak species occur on different soil and climate conditions with pedunculate oak being more tolerant to wet soils and a continental climate.

Sessile oak is also very drought-tolerant. *P. nigra* var. *austriaca* is a variety of black pine which is native to the Western Balkans and the Dalmatian coast with a northernmost occurrence in the Wienerwald (Schütt and Schuck 1992). *P. nigra* is in general light-demanding and shade-intolerant, but also resistant to wind and drought. Black pine was selected as the reference species for the Austrian site as it is one of the most economically important native conifers in southern Europe, which has also been widely used for reforestation in Central Europe.

Seeds from all non-native tree species were collected in autochthonous stands (Table 1). Seed treatment and germination were species-specific according to advice from local nurseries on *F. orientalis* in Turkey, *T. tomentosa* in Bulgaria and *C. libani* and *A. bornmuelleriana* in the state nursery of Bavaria/Southern Germany. *F. orientalis* and *T. tomentosa* were transplanted as 2-year-old seedlings to the Bavarian state nursery and grown there for two more years. The non-native species were all cultivated in the same state nursery in Southern Germany under the same environmental and soil conditions apart from *T. heterophylla*, which was cultivated in a private nursery. In contrast, the native reference species were all grown in local nurseries. While *A. bornmuelleriana* and *P. nigra* were grown in containers, the other seedlings were planted as bare-rooted seedlings (Table 1).

Study sites

Five study sites with almost identical experimental design (Table 2) were established on clear-cuts in Germany (Federal States of Bavaria and of Thuringia), Austria and Switzerland (Fig. 1). The sites were selected using a climate filter based on Worldclim data according to the procedure described in Schmiedinger et al. (2009).

Overall, the study sites represent a broad range of geological and climatic conditions typical for Central Europe and are, therefore, well suited for a trial with non-native tree species (Table 2). They are distributed throughout Central Europe along a distance of approximate 700 km North–South (OLD–MUT; the abbreviations are explained in Table 2) and nearly 1000 km West–East (MUT–BRU; Fig. 1). The sites of MUT, BRU and SCH are slightly inclined (5–10%), while the others are on level terrain (Table 2). The soils in all study sites are free of carbonate, but differ in water supply, which ranges from well-drained (GRO) to hydromorphic (SCH). The rooting depth ranges from 65 (MUT) to 115 cm (GRO). The current natural forest communities in GRO, MUT and OLD are dominated by beech, while the other two sites BRU and SCH are dominated by oaks.

Temperature and precipitation data were obtained as daily means from nearby climate stations (< 10 km), namely the Weather Service in Germany (DWD), Austria (ZAMG) and Switzerland (MeteoSwiss). In SCH, data were additionally

Table 1 Origin and type of planting stock

Tree species	Provenance	Stand of origin	Seedling characteristics before planting			Time of planting at study site (number of plots)					
			National Identification number/seed material type	Latitude/longitude (elevation, m a.s.l.)	Height (cm)	Years in nursery bed + trans-plant bed	Seedling type	Bruckneudorf (BRU)	Grossostheim Germany/Bavaria (GRO)	Muttrux Switzerland (MUT)	Oldisleben Germany/Thuringia (OLD)
<i>Abies bornmuelleriana</i>	Bolu-Adadag (Kökeç)/Turkey	225/selected seed stand	40°39'05"N/31°36'56"E (1400)	10–15	2 + 2	Container	Apr 2013 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Cedrus libani</i>	Mersin-Mersin (Arslanköy)/Turkey	233/selected seed stand	37°00'20"N/34°14'00"E (1800)	10–20	1 + 2	Bare root	n.p.	Mar 2013 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (2) Mar 2014 (1)
<i>Fagus orientalis</i>	Zonguldak-Devrek (Sarigöl)/Turkey	357/selected seed stand	41°16'25"N/32°12'30"E (870)	30–120	2 + 2	Bare root	Apr 2013 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Tilia tomentosa</i>	Ludogorie/Bulgaria	1795102120111/selected seed stand	43°43'04"N/26°05'32"E (350)	80–120	2 + 2	Bare root	Nov 2012 (2) Apr 2013 (1)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Tsuga heterophylla</i>	Clallam Bay-Tatoosh Island, West Slope Olympic Peninsula, Washington/USA	Seed zone 011-05/selected seed stand	48°23'24"N/124°53'90"W (0–150)	50–100	3 + 1	Bare root	Nov 2012 (1) Apr 2013 (2)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)	Oct 2012 (3)
<i>Pinus nigra ssp. nigra</i> (var. <i>austriaca</i>)	Baden, Lower Austria/Austria	Skie 16 (5.1)/selected seed stand	47°58'26"N/16°04'28"E (390–560)	15–20	1 + 1	Container	Apr 2013 (3)				
<i>Quercus petraea</i>	Boudry/Switzerland	PSE 1236/selected seed stand	46°96'03"N/6°81'84"E (750)	80–120	1 + 2	Bare root				Oct 2012 (3)	
	Mitteldeutsches Tief- und Hügelland/Germany	81 805/approved seed stands within the zone	Not documented	30–50	3 + 0	Bare root					Oct 2012 (3)
<i>Quercus robur</i>	Oberheingaben/Germany	81 707/approved seed stands within the zone	Not documented	15–40	1 + 0	Bare root				Oct 2012 (3)	Oct 2012 (3)

Reference tree species are shown in bold letters. Deviations from the design originally planned (three blocks per site planted in Oct 2012) are shown in italics
n.p. not planted

interpolated using inverse distance weighting. In MUT, data were interpolated using the DAYMET software (Thornton et al. 1997). The annual average temperatures for the period 1981–2010 ranged between 7.9 and 10.4 °C, with SCH representing the coldest and BRU the warmest site, and a difference of approximately 44 days in growing season length (Table 2). The annual precipitation sum varied greatly between study sites with MUT (nearly 1150 mm) being the most humid and OLD (nearly 500 mm) the driest site, with the growing season precipitation sum following a similar pattern. Based on the de Martonne index DMI (de Martonne 1926) as a measure of site aridity, OLD is the driest and MUT the wettest site in our study.

Experimental design

The trial is designed as a complete randomized block experiment with five sites, three blocks per site and six species, resulting ideally in $5 \times 3 \times 6 = 90$ plots. However, site BRU lacks *C. libani* (not planted). Each 0.1156 ha plot contains 289 (17×17) individuals of one species. The plot is subdivided into a core area with 169 (13×13) plants for later growth and yield studies, and a buffer area with 120 plants to protect the core zones from interspecific competition. The study sites were fenced and planted in fall 2012 and in spring 2013 (exception: one *C. libani* plot in SCH was planted in fall 2014) with a uniform quadratic spacing of 2.0 m.

Tending treatments to control competing vegetation were conducted annually in summer, if necessary twice. The saplings unintentionally damaged during tending were also excluded from the analyses (cumulated approximately 0–3.5% during the observation period). No treatments to reduce competition between planted saplings have been conducted so far.

Data collection and analytical approach

For this study, we monitored plant survival (alive or dead) of the planted trees at the plot level during the 4-year period after planting. Surveys were conducted at least annually. Three study sites (GRO, OLD and SCH) were usually surveyed in spring and late autumn, and two study sites (BRU, MUT) at least once a year at irregular time intervals. Overall, the number of surveys varied between species and sites from 4 to 9 (Supplementary material, Table S1), and the total observation period for a plot was 23–50 months after planting. Our analyses focused on the survival (S) and mortality (or hazard rates H) per tree species and site and are based on plot values. Plants from core and buffer areas were analysed together as no edge effects due to interspecific competition were expected during this experimental stage. Tree heights at the end of the observation period varied greatly between and within sites and species by as much as approx.

3 m. Edge effects due to adjacent old stands were avoided by clearing a buffer strip (20 m wide) around each study site.

To homogenize the response between sites and to be able to obtain survival estimates any time, we calculated survival rates S using Eq. 1:

$$S_t = \frac{i_t}{i_0} \tag{1}$$

where i_0 is the total number of plants of one tree species in a plot at planting time ($t=0$) and i_t the number of plants still alive at survey time t since planting.

Hazard rates H indicate the way in which mortality has developed over time. They were calculated for the periods between two surveys t_x and t_{x+1} and then normed for yearly or half-yearly rates (Eq. 2):

$$H_{x,x+1} = (S_x - S_{x+1}) / (t_{x+1} - t_x) \quad [\text{year}^{-1} \text{ or } 6 \text{ months}^{-1}] \tag{2}$$

The following separate analyses were then conducted:

1. Plant survival $S(4)$ for the entire observation period
 To harmonize the variation in planting times and observation periods, we did not compare observed survival rates S_t , but the parameters of statistical model fits and predictions at defined time steps after planting. We therefore applied a survival function $S(t)$ according to Staupendahl (2011, Eq. 3) to each plot:

$$S(t) = \exp\left(-\left(\frac{t}{\beta}\right)^\alpha\right) \tag{3}$$
 where t (in years, given in two decimals) is the time since planting and β (> 0) indicates the time at which the mortality of the Weibull-Distribution used is 63.2% ($S_\beta = 0.368$). The hazard rate coefficient α (> 0) of the Weibull-Distribution according to Staupendahl (2011) characterizes the relative age-related risk, where values < 1 indicate ‘elevated risk at young age’, values of 1 ‘age-indifferent risk’ and values > 1 ‘elevated risk at high age’. The model coefficients α and β should therefore be interpreted together. Equation 3 has shown its usefulness in several mortality studies (Staupendahl and Möhring 2011; von Gadow et al. 2014; Neuner et al. 2015). Predicted values for the fourth year (48 months) after planting $S(4)$ were used to analyse the species and site dependency of plant survival rates.
2. Plant hazard rate for the initial (H_{ini}) and later (H_{lat}) phase

Plant hazard rates H were separately analysed for the initial phase (H_{ini} : the 1st and 2nd growing seasons after planting combined) and a later phase (H_{lat} : usually the 3rd and 4th growing seasons after planting combined). The reason for separately analysing H_{ini} and H_{lat} was that

Table 2 Site and climatic characteristics of the study sites

Site (abbreviation)	Bruckneudorf Austria (BRU)	Grossostheim Ger- many/Bavaria (GRO)	Muttrux Switzerland (MUT)	Oldisleben Germany/ Thuringia (OLD)	Schmellenhof Ger- many/Bavaria (SCH)
Geographical position (°)	47°58'18"N 16°41'20"E	49°95'32"N 9°05'58"E	46°52'44"N 6°44'21"E	51°29'05"N 11°19'99"E	49°82'46"N 11°56'87"E
Elevation (m a.s.l.)	330	127	658	195	495
Aspect	South–East	No	South–East	No	North–East
Slope (%)	0–10	0	10	0	5
Geology	Loess over pliocene gravel, schist and gneiss	Aeolian sand and aeolian sand over alluvial terrace gravel	Moraine	Loess over sandstone	Heavy clay over sand- stone
Soil type ^a	Dystric cambisol	Arenic dystric cam- bisol	Cambisol (carbonate- free)	Cambisol (carbonate- free), partially podzols	Haplic stagnosol
Rooting depth (cm)	100	115	65	80	70
Natural plant associa- tion	<i>Carici pilosae-carpini- netum</i>	<i>Asperulo fagetum/ luzulo fagetum</i>	<i>Galio-odorati fagetum typicum</i>	<i>Luzulo fagetum/galio carpinetum</i>	<i>Stellario carpine- tum caricetosum brizoides</i>
Climate (1981–2010)					
Meteorological stations used	Bruckneudorf	Schaafheim-Schlier- bach	interpolated ^b	Artern	interpolated ^b
Mean annual temper- ature (°C)	10.4	10.0	8.8	9.3	7.9
Mean min/max annual temperature (°C)	6.5/15.0	5.5/14.6	5.0/13.3	5.2/13.7	3.5/12.8
Mean growing season ^c tempera- ture (°C)	18.2	16.2	15.5	16.2	14.6
Mean duration of growing season ^d (days year ⁻¹)	199	187	170	180	155
Annual precipitation sum (mm)	758	650	1147	490	812
Growing season pre- cipitation sum (mm)	413	289	498	264	383
Annual de Martonne index ^e	37.2	32.5	61.0	25.5	45.4
Growing season de Martonne index	14.6	11.0	19.6	10.1	15.6
Range of the annual extreme minimum temperature (°C)	– 14.9 to – 12.3	– 17.7 to – 15.0	– 14.9 to – 12.3	– 17.7 to – 15.0	– 17.7 to – 15.0
Plant hardiness zone ^f	7b	7a	8a	7a	7a

^aSoil classification is according to FAO (2015)

^bDaily means of temperature and precipitation were interpolated on the basis of MeteoSwiss (for MUT) and DWD (for SCH) data recorded at the meteorological stations closest to the sites

^cThe growing season is defined as May 1 through September 30 (Otto 1994)

^dThe mean duration of the annual growing season is calculated as the number of days per year with mean temperatures ≥ 10 °C

^eThe de Martonne index was calculated as $DMI = \frac{P}{T+10}$, with P =precipitation sum (mm) and T =mean temperature (°C) for the corresponding period (year or growing season) (de Martonne 1926)

^fPlant hardiness zone is according to USDA plant hardiness zone map (2012)

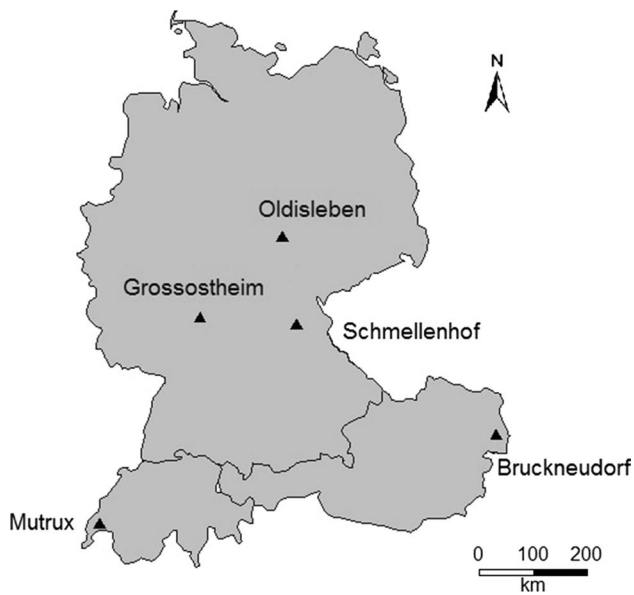


Fig. 1 Location of the five study sites in Austria (Bruckneudorf BRU), Germany (Grossostheim GRO, Oldisleben OLD, Schmellenhof SCH) and Switzerland (Mutrux MUT)

we assumed the first two growing seasons to be influenced by planting stress (Grossnickle 2005). The duration of the initial phase was approximately 24 months, beginning with the day of planting for each plot and ending always in October after the second growing season. The later phase for each plot started after two growing seasons and ended at the time of the last inventory in 2016. These rules allowed the different planting and inventory times to be taken into account (cf. Table 1).

3. Comparison of the plant hazard rate of the non-native and native species (H_{rel})

We compared H_{lat} of native and non-native tree species (3rd and 4th year after planting) and calculated the species-specific H_{rel} as the difference between the average annual mortality of the non-native species in each plot and the site-specific average annual mortality of the native species in the three blocks. This approach should eliminate any study site effects. The native species was used as reference, assuming that it indicates a site-specific survival standard.

4. Seasonal plant hazard rate H_{season}

We used the regular survival inventories in the spring and autumn of 2015–2016 on the three study sites (GRO, OLD, SCH) where such regular assessments were available to obtain the half-year resolution (for methodological details, see Ameztegui and Coll 2013). The summer period was defined as the time between data acquisition in spring (March–June) and autumn (October–November). Winter was defined as the time between the autumn

data acquisition and the spring data acquisition. Only the data assessed after the end of the second growing season were used to exclude the initial phase which was assumed to be influenced by planting stress.

Statistical analyses

Equation 3 was parameterized by applying nonlinear regression analysis using sequential quadratic optimization with condition bounds (Morales et al. 2011). The adjusted coefficient of determination $adjR^2$ was used to describe the goodness of fit.

Univariate multifactorial ANOVAs were provided to test the effects of the main factors, *study site* and *tree species*, and of the random factor, *block*, on the response variables $S(4)$, H_{ini} , H_{lat} , H_{rel} and H_{season} . The interaction *study site* \times *tree species* was also included to test whether species effects are site-dependent. For H_{season} , the categorical variable *season* (winter, summer) was additionally included. Tests for normality (Shapiro–Wilk) and variance homogeneity (Levene) were conducted for model residuals. As a measure of the effect size, the partial Eta-square (*partial* η^2) was used (Cohen 1973), combined with a partial level of significance.

To test the potential influence of weather during the later observation period 2015–2016 on H_{lat} , we applied GLMM using the site-specific continuous variable DMI, which combines annual average temperature and precipitation sum. *Tree species* and its interaction with DMI were also included in the statistical models, while *block* served as a nested random effect in DMI instead of *study site*. For that purpose, we utilized the *MASS* package (Venables and Ripley 2002) in the R-environment (R Core Team 2014). Our model was fitted by the *glmmPQL*-function. Due to the log-normal-shaped distribution of our dependent variable, we selected Gaussian (*link* = ‘log’) as our family argument.

For multiple comparisons, subsequent LSD (least significant difference) post hoc tests with Bonferroni correction (Bärlocher 1999) were performed (*LSD.test* function of the *agricolae* package in R), and the least-square means of the interaction estimates were pairwise compared by the *lsmeans* function with Bonferroni correction (*lsmeans* package in R). All computations were performed using SPSS (IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY, IBM Corp.) and R software (version 3.4.4, R Core Team 2014).

Results

Survival of the tree species during the 4-year observation period after planting

In total, we calculated 87 survival functions from 661 plot surveys, including the survey just after planting. Fits of the data to the survival function according to Eq. 3 were good for almost all plots, with $\text{adj}R^2 \geq 0.8$ in all but three cases (minimum: $\text{adj}R^2 = 0.321$, Supplementary material, Table S2). These exceptions occurred on plots located at the OLD site, where hazard was very low for two plots with *F. orientalis* and one plot with the native species *Q. robur*.

The predicted 4-year survival rates $S(4)$ differed significantly between tree species (ANOVA, $p \leq 0.001$; with the strongest effect with a *partial* η^2 of 0.772) and study sites ($p \leq 0.001$; *partial* $\eta^2 = 0.37$), and both factors strongly interacted with each other ($p \leq 0.001$; *partial* $\eta^2 = 0.703$) (Table 3). The random variable *block*, which was included in all models, was not significant ($p = 0.371$; *partial* $\eta^2 = 0.035$).

Across all sites, the native species had the highest survival rates $S(4)$ (average 0.771), followed by *T. tomentosa* (average 0.688), *A. bornmuelleriana* (average 0.302) and *C. libani* (average 0.240) had the lowest rates (comparisons of the post hoc LSD-Bonferroni test are shown in Table 4), with the rates of the other species somewhere in-between. Averaged over all species, $S(4)$ was significantly higher (0.652) in OLD than in all other sites (range 0.423–0.498). The post hoc tests of the interaction term yielded a maximum $S(4)$ for the native species in OLD and a minimum $S(4)$ for *C. libani* in MUT, so that the species–site combinations could be split into groups with low, average and high plant survival. However, the survival rates in the low and high plant survival groups differed significantly in only some species (Supplementary material, Table S3). For 13 of the combinations, the plant survival was low (range of $S(4) = 0.106$ – 0.335). *T. tomentosa* and *A. bornmuelleriana* in SCH had an average $S(4)$ of approximately 0.5, whereas for 14 of the combinations plant survival (> 0.570) was predicted to be high because native species occurred in this group. Thus, none of the study sites was characterized by only high plant survival.

As a general rule, losses in the first year after planting tended to be higher than later. Afterwards, three types of survival pattern emerged (Fig. 2): (1) comparatively low survival during the second year, followed by low losses, with both patterns being consistent across the sites (*A. bornmuelleriana* and *C. libani*), (2) prevailing constant losses across the whole study period, but with the extent of the losses varying greatly among the study sites (*F. orientalis*, *T. heterophylla*) and (3) relatively high survival during the first year

($S > 0.6$) followed by low losses, with both patterns being consistent across the sites (*T. tomentosa*, native species). These survival patterns are in line with the parameters of the survival function, α as an expression of age-related risk and β of time of 0.63 mortality (Eq. 3), which also divides the species into three groups (Fig. 3). *A. bornmuelleriana* and *C. libani* had relatively high early mortality (α clearly < 1), and the mortality rates quickly reached 0.632 ($\beta < 27$ years; Fig. 3 and Supplementary material, Table S2). In contrast, the native species and *T. tomentosa* had moderate hazard rates ($\alpha < 2.2$), combined with moderate-to-high plant survival ($2 < \beta < 60,000$). The highest ranges of α and β were found in the third group, which consisted of *F. orientalis* and *T. heterophylla*. For some plots of these tree species, very high hazard rates for older trees were projected ($\alpha = 8.9$, for *T. heterophylla*; Supplementary material, Table S2), while *F. orientalis* was even projected to survive for unrealistically long periods ($H_{104,200\text{years}} = 0.632$; Supplementary material, Table S2).

Table 3 ANOVAs outcome for survival rates 4 years after planting $S(4)$, initial hazard rate (H_{ini}), later hazard rate (H_{lat}) and plant hazard rate of the non-native species compared to the rates of the native species (H_{rel})

Variable	<i>df</i>	MS	<i>F</i> value	Partial η^2
<i>S(4)</i>				
Species	5	0.679	37.859***	0.772
Site	4	0.129	7.176***	0.370
Site \times species	19	0.126	6.992***	0.703
Block	2	0.018	1.010 ns	0.035
H_{ini}				
Species	5	0.178	39.546***	0.779
Site	4	0.034	7.507***	0.349
Site \times species	19	0.025	5.479***	0.650
Block	2	0.002	0.363 ns	0.013
H_{lat}				
Species	5	0.005	3.474**	0.237
Site	4	0.010	7.284***	0.342
Site \times species	19	0.004	2.747**	0.482
Block	2	0.004	2.551 ns	0.084
H_{rel}				
Species	4	0.004	2.430 ns	0.174
Site	4	0.007	4.471**	0.280
Site \times species	15	0.005	2.750**	0.473
Block	2	0.005	2.848 ns	0.110

Main factors are *species* and *site* as well as their interaction term, while *block* was included as a random factor

df degrees of freedom, *MS* mean square

F value with significance levels *** $p \leq 0.001$; ** $p < 0.01$; * $p < 0.05$, ns $p > 0.05$, and partial η^2 as a measure of the effect size

Table 4 Predicted parameters per tree species and study sites: $S(4)$ = plant survival S for the entire observation period of 4 years; H_{ini} = plant hazard rate for the initial phase (1st and 2nd growing seasons after planting); H_{lat} = plant hazard rate for the later phase (3rd and 4th growing seasons after planting); H_{rel} = plant hazard rate of the non-native compared to the native species

Factors studied (number of plots)	Parameters			
	$S(4)$	H_{ini}	H_{lat}	H_{rel}
Tree species				
Native tree species (15)	0.771 ± 0.185 ^a	0.090 ± 0.082 ^a	0.011 ± 0.013 ^a	
<i>Abies bornmuelleriana</i> Mattf. (15)	0.302 ± 0.164 ^{cd}	0.310 ± 0.077 ^{bc}	0.011 ± 0.009 ^a	0.000 ± 0.006 ^a
<i>Cedrus libani</i> A. Rich (12)	0.240 ± 0.174 ^d	0.359 ± 0.092 ^c	0.018 ± 0.013 ^a	0.008 ± 0.011 ^a
<i>Fagus orientalis</i> Lipsky (15)	0.606 ± 0.299 ^b	0.150 ± 0.131 ^a	0.052 ± 0.090 ^a	0.009 ± 0.080 ^a
<i>Tilia tomentosa</i> Moench (15)	0.688 ± 0.158 ^{ab}	0.104 ± 0.078 ^a	0.044 ± 0.038 ^a	0.009 ± 0.073 ^a
<i>Tsuga heterophylla</i> Sarg. (15)	0.405 ± 0.300 ^c	0.248 ± 0.137 ^b	0.048 ± 0.068 ^a	0.016 ± 0.037 ^a
Study sites				
BRU (15)	0.487 ± 0.339 ^b	0.204 ± 0.165 ^{ab}	0.074 ± 0.105 ^b	0.053 ± 0.104 ^a
GRO (18)	0.498 ± 0.316 ^b	0.211 ± 0.158 ^b	0.034 ± 0.029 ^a	0.024 ± 0.029 ^{ab}
MUT (18)	0.491 ± 0.256 ^b	0.214 ± 0.109 ^b	0.003 ± 0.004 ^a	0.003 ± 0.004 ^b
OLD (18)	0.652 ± 0.313 ^a	0.140 ± 0.151 ^a	0.024 ± 0.029 ^a	0.020 ± 0.028 ^{ab}
SCH (18)	0.423 ± 0.208 ^b	0.255 ± 0.112 ^b	0.027 ± 0.016 ^a	0.006 ± 0.015 ^b

Data are shown as mean ± standard deviation across plots. Different letters indicate significant differences in the parameters for the tree species and study sites (post hoc LSD-Bonferroni test, $p < 0.05$). Differences between means sharing a letter are not statistically significant

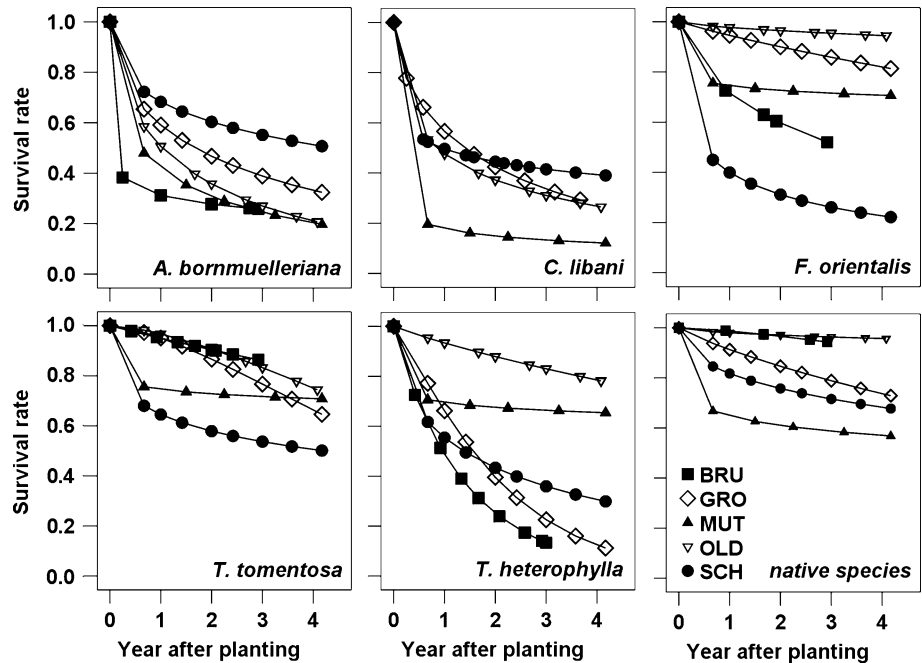
Hazard for the tree species during the initial and the late phases

Tree species had the strongest effect on H_{ini} ($p \leq 0.001$; partial $\eta^2 = 0.779$; Table 3), followed by study site ($p \leq 0.001$; partial $\eta^2 = 0.349$). Both factors interacted significantly ($p \leq 0.001$, partial $\eta^2 = 0.650$), but the random factor *block* did not influence H_{ini} ($p = 0.697$, partial $\eta^2 = 3$).

The initial annual hazard rate (H_{ini}) ranged greatly between 0 (*F. orientalis* in OLD) and 0.538 year⁻¹ (*C.*

libani in SCH) and was often predicted to be very high (> 0.4), particularly for *C. libani*, *A. bornmuelleriana* and *T. heterophylla* (Fig. 4). Averaged over all study sites, H_{ini} was the lowest for the native tree species, plus *T. tomentosa* and *F. orientalis* (0.090–0.150 year⁻¹; Table 4), and highest for *C. libani* (0.359 year⁻¹). The lowest average H_{ini} of 0.140 year⁻¹ was predicted in OLD, followed by BRU (0.204 year⁻¹), while the highest average initial hazard rate was in SCH (0.255 year⁻¹; Table 4). Similarly to $S(4)$, the trees grouped into species–site

Fig. 2 Predictions of survival rate S based on site- and species-specific survival functions (Eq. 3, derived from three blocks per site) over real inventory time (symbols) within the total observation period of 23–50 months after planting. Note: the native species on the study sites vary (see Table 1)



combinations (Supplementary material, Table S4). In the group with a high initial plant hazard (range of $H_{ini} = 0.282\text{--}0.386 \text{ year}^{-1}$), mostly conifer species were represented, while broadleaved species were concentrated in the group with a low initial plant hazard (range of $H_{ini} = 0.017\text{--}0.14 \text{ year}^{-1}$). However, *T. heterophylla* and *F. orientalis* were present in both groups, while native species had low initial plant hazard in most plots.

Surviving plants were in general able to overcome the initial planting stress (Fig. 4). In comparison with H_{ini} , later hazard H_{lat} (3rd and 4th year) markedly decreased to low values, ranging between 0.003 year^{-1} in MUT and 0.074 year^{-1} in BRU (Table 4). The standardized H_{lat} did not only strongly decrease over time, but the effect size of the factor species also decreased markedly ($p = 0.008$; partial $\eta^2 = 0.237$; Table 3). In contrast, the effect of the study site remained at a similar level during the later phase ($p \leq 0.001$; partial $\eta^2 = 0.342$), and the random variable *block* remained insignificant ($p = 0.087$, partial $\eta^2 = 0.084$).

During the later phase, the average plant hazard ranged from 0.011 year^{-1} (native species, *A. bornmuelleriana*) to 0.052 year^{-1} (*F. orientalis*) (Table 4). However, H_{lat} did not significantly differ between species (post hoc LSD-Bonferroni test). Regarding sites, only in BRU did H_{lat} remain high (0.074 year^{-1} ; Table 4).

Three to 4 years after planting, the plant hazard rates had mostly become similar among the different sites and species, with H_{lat} remaining high only for *F. orientalis* in BRU (0.197 year^{-1} ; Supplementary material, Table S5). For the three combinations, *T. heterophylla* in BRU, *T. tomentosa* in OLD and *T. tomentosa*

in GRO, H_{lat} was around 0.100 year^{-1} , but for *T. tomentosa* and the native species in MUT, no late hazard was evident ($H_{lat} = 0 \text{ year}^{-1}$). Only in MUT, all species had $H_{lat} < 0.010 \text{ year}^{-1}$.

No clear patterns arose when relating H_{lat} to the site-specific climate variables in 2015 and 2016. The values averaged over 2 years ranged from 9.1 to $11.3 \text{ }^\circ\text{C}$ for temperature, from 438 to $1068 \text{ mm year}^{-1}$ for precipitation sum and from 21.6 to 54.9 for the DMI (Supplementary material, Table S6). In comparison with the climate during the period 1981–2010 at the study sites, the years 2015 and 2016 were clearly warmer ($+0.7$ to $+1.2 \text{ }^\circ\text{C}$) and drier (-52 to $-186 \text{ mm year}^{-1}$) and, thus, more arid (DMI decreased by 3.9 and 11.6). No significant effects of DMI ($p = 0.159$), tree species ($p = 0.614$) and their interaction ($p = 0.832$) on hazard rates in the late phase (H_{lat}), however, were detected in the GLMM (data not shown).

Hazard of the non-native tree species compared to that of the native species during the late phase

In the 3rd and 4th years after planting, the non-native tree species showed similar hazard rates to the native ones, excluding *F. orientalis* and *T. heterophylla* in BRU as well as *T. tomentosa* in GRO and OLD, which had still high $H_{rel} > 0.05 \text{ year}^{-1}$ (Fig. 5). Interestingly, although both *A. bornmuelleriana* and *C. libani* had initially high hazard rates (cf. H_{ini} ; Fig. 4), after the second growing season their hazard rates were as low as those typical for the corresponding native species (H_{rel} ranged around 0.000 year^{-1} ; Fig. 5). Nevertheless, the post hoc tests

Fig. 3 Parameter estimates for α and β per species and block (according to Eq. 3)

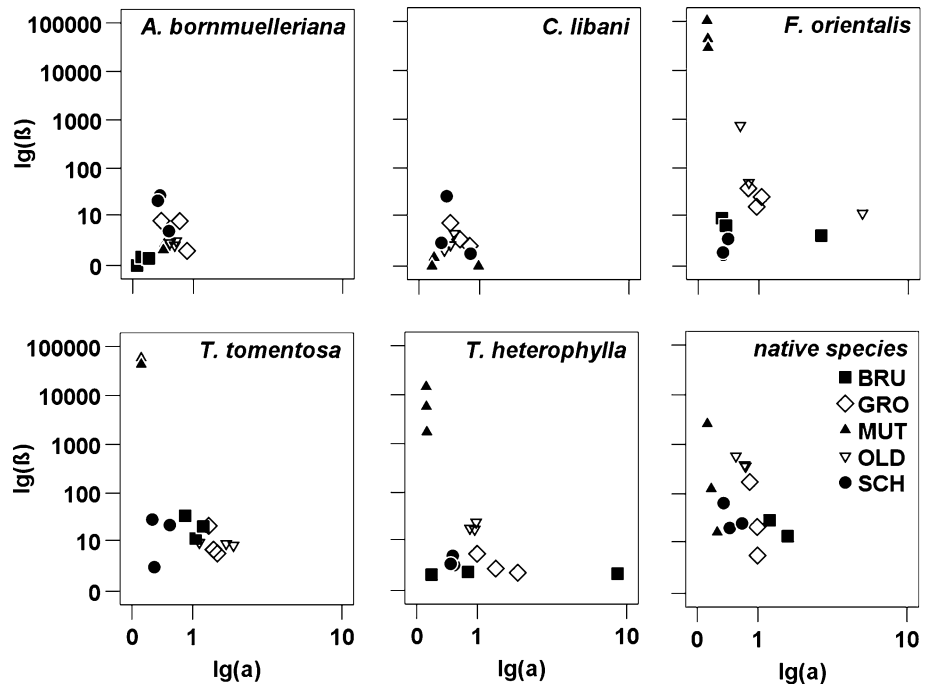
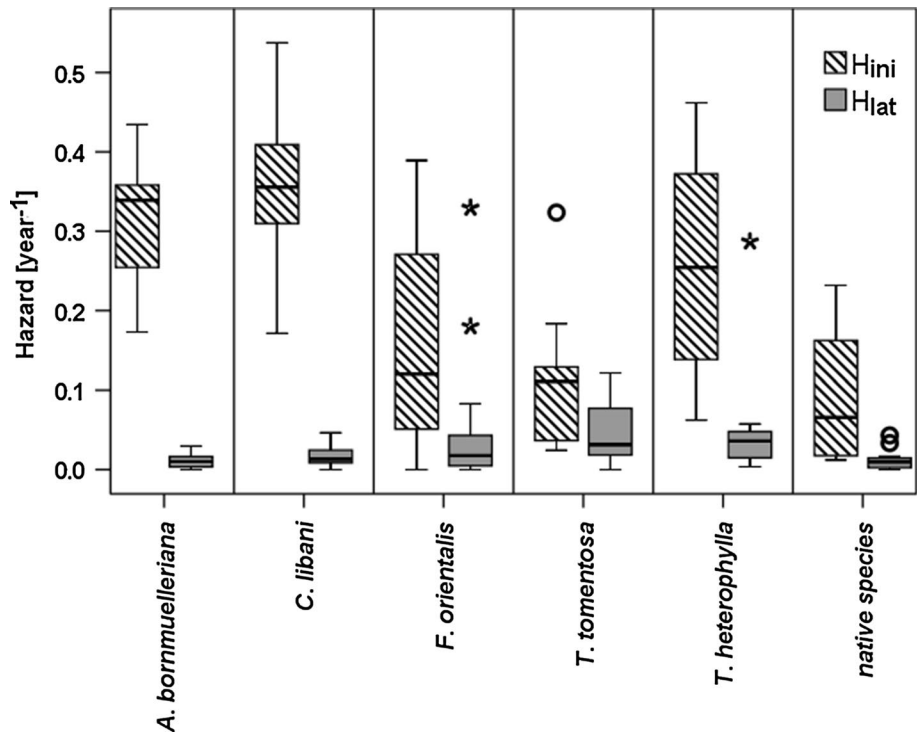


Fig. 4 Species-specific standardized annual hazard rates during the first 2 years after planting (H_{ini} ; striped box plots) and during the following 2 years (H_{lat} ; grey box plots) (○ outliers, * extreme values)



revealed no significant differences in H_{rel} among the species, but the differences among the study sites were significant ($p \leq 0.05$; partial $\eta^2 = 0.280$; Table 3). The highest H_{rel} was detected in BRU (0.053 year^{-1} ; Table 4), and the lowest in MUT and SCH ($0.003\text{--}0.006 \text{ year}^{-1}$), with GRO and OLD somewhere in-between (0.020 and 0.024 year^{-1}).

The highest H_{rel} was found for *F. orientalis* in BRU (0.176 year^{-1} ; Supplementary material, Table S7), followed by *T. heterophylla* on the same site and by *T. tomentosa* in GRO and OLD (H_{rel} ranging between 0.032 and 0.091 year^{-1}). The predicted plant hazard rates of all other combinations were statistically similarly low in comparison with the corresponding native tree species.

Seasonal hazard during the late phase

In the later phase after plant establishment, we did not find any significant seasonal differences in hazard rates when comparing winter and summer mortality (H_{season} ; Fig. 6). This was the case for all three study sites included in this analysis (GRO, OLD, SCH), as well as for all species. The factor *season observed* was not significant (ANOVA, $p = 0.334$; data not shown). Moreover, the relative survival rates of the non-native tree species did not differ seasonally from those of the locally adapted native species (results not shown).

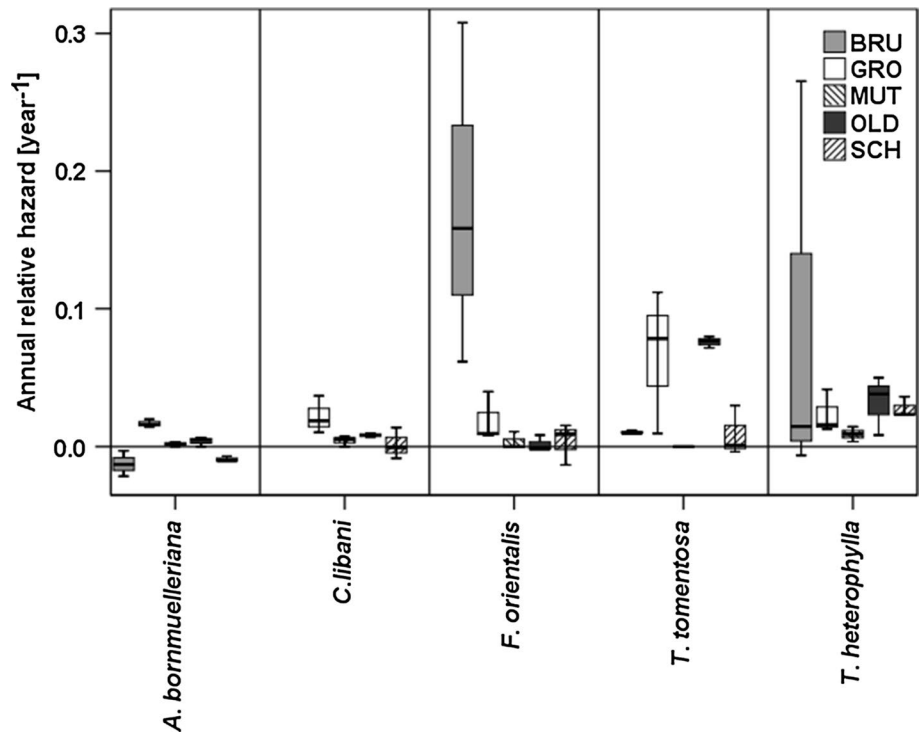
Discussion

Differences in survival rates between tree species

The survival rates of the six tree species differed early after planting, but much less later (Table 3, Fig. 4). The early survival of the native species (mostly *Quercus* spec., in BRU *P. nigra*) and the two broadleaved species *F. orientalis* and *T. tomentosa* was significantly higher than that of the other species, and lowest for the three non-native conifers. This was also the pattern for the entire period of 50 months. The low survival rate of the three non-native conifers does not seem to be attributable to one single factor. We discuss here potential key factors, i.e. the quality of plant material and plant handling, the initial plant size, the fine-root mycorrhization and the sprouting ability, that could influence the observed species-specific survival rates.

Bareroot saplings have often been reported to have higher mortality than container saplings (e.g. Grossnickle and El-Kassaby 2016). The survival rates of bareroot saplings after 13 years in two *C. libani* afforestations in Turkey amounted to 81% and 94% (Erkan and Aydin 2017). The rates were, respectively, 10% and 3% higher if container saplings were used. Oner et al. (2015) report survival rates of 84–89% for *C. libani* after the first year in Turkey, in a climate with 400–600 mm precipitation and 10–11 °C mean annual temperature. Bareroot saplings usually have less root–soil contact, which may have

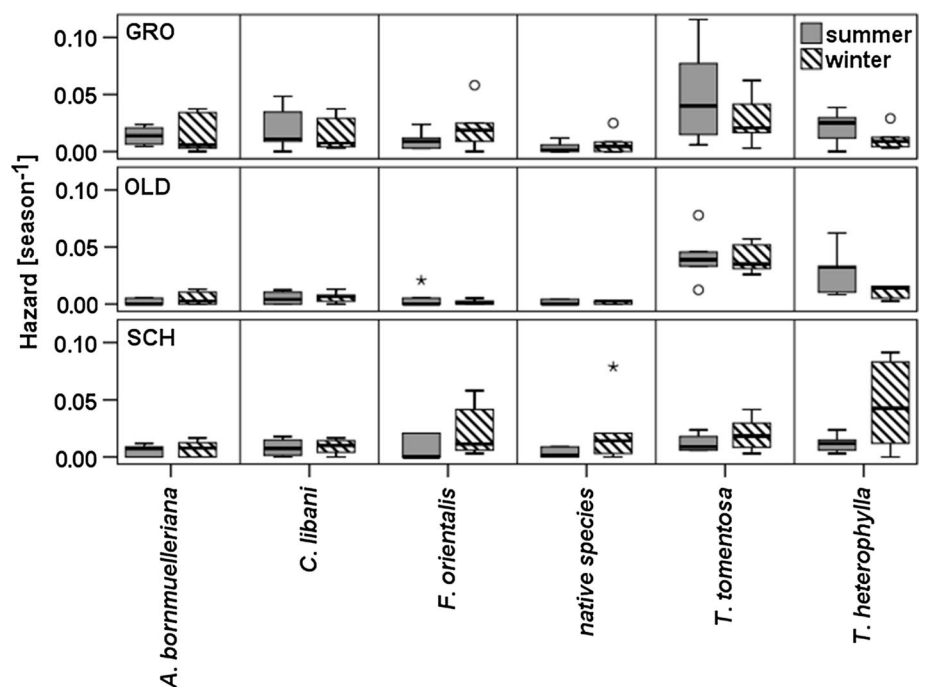
Fig. 5 Annual hazard rates of the five non-native tree species calculated as a difference to the hazard rate of the corresponding native tree species, within the 3rd and 4th year after planting together in the five different study sites



disadvantages compared to containerized plants (Erkan and Aydin 2017), especially under stressful conditions after planting such as drought. *C. libani* seems to be sensitive in this regard, as container plants have often been preferred in forest restoration within its natural distribution range, e.g. on semiarid and arid sites (Çalışkan

and Boydakt 2017). In our trial, bareroot saplings from replacement plantings in autumn 2014 on the site OLD had 14% mortality after 2 years, and container saplings replanted in autumn 2015 in MUT showed only 2% mortality after 1 year (unpublished data). This clearly shows that survival rates in both container and bareroot *C. libani* can also be high in a Central European climate. We therefore

Fig. 6 Hazard rates H_{season} standardized for the two winter seasons 2014/2015 and 2015/2016 (striped box plots) and the two summer seasons 2015 and 2016 (grey box plots) for the three sites with data enabling this comparison (○ outliers, * extreme values)



believe that during plant lifting and handling in our trial some of the roots dried out. In the technical notes, we made to describe the establishment of the sites, some desiccation was observed, but our lack of experience with *C. libani* meant we were unable at that time to anticipate the consequences of our observation for the initial high mortality.

Problems with the plant material are also likely to explain why *A. bornmuelleriana* suffered such high early mortality despite the use of container saplings, which usually survive better than bareroot seedlings (Grossnickle and El-Kassaby 2016). *A. bornmuelleriana* saplings had the smallest initial size (10–15 cm) of all non-native species (Table 1). For successful sapling development, Stimm et al. (2014) recommend initial heights of 30–50 cm, or even 50–80 cm if there is competition. Clearly, the *A. bornmuelleriana* saplings in our trial were planted when they were small, which probably has influenced their physiological performance during the first 2 years. A conceptual physiological model presented by Villar-Salvador et al. (2012) shows the complex influence of sapling size on plant survival: increases in sapling size, especially in the new root mass, result in greater sapling vigour and survival. Small-sized saplings usually have lower growth capacity initially as a result of problems in N remobilization, carbohydrate storage or plant hydraulics (Burdett 1990; Villar-Salvador et al. 2012). However, individual plant growth is out the focus of this study. Therefore, a next step will be to analyse the relationship between plant size and survival, and to clarify how species-specific this relationship is.

One explanation of the high early mortality of *C. libani* and *A. bornmuelleriana* saplings is the poor mycorrhiza colonization of their roots. While no mycorrhizal fungi were found on *C. libani* roots before planting and after 2.5 years on the MUT site (Nikolova et al. 2016, p. 32), the two species identified on *A. bornmuelleriana* saplings disappeared over time. *T. heterophylla* has a vesicular–arbuscular mycorrhiza and was not analysed. All other species showed an increase in mycorrhizal diversity, in particular the broadleaved *F. orientalis*, *T. tomentosa* and *Q. petraea*, which was the local native species at the MUT site. Although these findings are based only on investigations in MUT, they are in line with Bucharova (2017) and Bucharova et al. (2019), who stress potential difficulties in the local adaptation of species from very different regions due to an initial lack of biotic interactions. In our study, such an initial mismatch in plant–soil–microbial interactions might have boosted the early sapling mortality of *C. libani* and *A. bornmuelleriana*.

Among the coniferous species, *T. heterophylla* showed the highest variation in the initial hazard and survival (Figs. 2, 4) between the sites as well as in the warmest site BRU, which is South-East exposed (Table 2). In a trial established at

mid-elevation on southern Vancouver Island (Arnott 1981), the mean survival rates of *T. heterophylla* in the fifth year after planting were lower in bareroot (around 60%) than in container (around 90%) saplings. The lowest survival rates of bareroot saplings were detected in South-exposure (40%), only half of the survival in North-exposure (80%). Thus, one possible explanation for the striking variability in *T. heterophylla* survival may be that the young plants are susceptible to desiccation. In addition, there is observational evidence that biotic factors, such as infection with *Heterobasidion* spec., *Botrytis cinerea* Pers. and *Armillaria mellea* (Vahl) P. Kumm, have affected *T. heterophylla* sapling survival on some sites, especially in OLD, if they grow in patches with high relative humidity and relatively low temperatures during May (Heydeck, LFE Brandenburg, pers. comm.).

The comparatively high survival rate of broadleaved species could also be related to their ability to sprout. During the initial phase, top-dying was observed in saplings of all broadleaved species (e.g. for MUT see Nikolova et al. 2016, p. 29). This may partly be related to the root–shoot ratio being unbalanced after lifting the relatively large plants (Table 1). In conifer saplings, top-dying was more often the first sign of subsequent death than in broadleaved saplings, which are able to resprout and regenerate much more easily than coniferous trees through their epicormic shoots (sprouts). In 2017, in a separate study in OLD (Frischbier et al. unpubl.), the broadleaved species exhibited resprouting much more often than the conifers (*T. tomentosa*), or a second or even a third annual flush (*Q. petraea* and *F. orientalis*), as well as reiteration from irregular buds (in this order: *T. tomentosa*, *Q. petraea* and *F. orientalis*, but also *T. heterophylla*).

The survival of 35–59% in *F. orientalis* after two growing seasons is similar to the survival rate of planted saplings reported by Tabari et al. (2005) in open conditions (55%) in Iran in a humid climate with cold winters and dry summers. At the end of the first growing season, however, the survival rate of *F. orientalis* saplings was about 75% under closed and semi-closed stands, but decreased significantly to 18% and 32% under open or moderately open stands (Tabari 2008). These findings are in line with the known high-shade tolerance of *Fagus* sp., including *F. orientalis* saplings growing in naturally regenerating forests, where the survival rate of *F. orientalis* saplings was found to be the highest in dense stands or in small gaps (Peltier et al. 1997; Topaçoğlu and Genç 2018). Not only sunburn, but also late frost may damage *Fagus* saplings, with *F. orientalis* being more robust than *F. sylvatica* (Tabari et al. 2007). In our trial, *F. orientalis* had to establish in the open with no shade or frost protection, which may have led to the relatively high initial hazard rate on the warmest site (i.e., BRU), and the coldest site (i.e., SCH) (Fig. 2, Table 2).

The initial hazard of *T. tomentosa* was low (median = 0.11 year⁻¹) during the first 2 years after planting (Fig. 4), and similar to that of the native species (median = 0.06 year⁻¹; Fig. 4) and *F. orientalis* (median = 0.12 year⁻¹; Fig. 4). To our knowledge, only a few studies have investigated the survival rates of *T. tomentosa* saplings. In the first year after germination, *T. tomentosa* had the highest survival rate (99.95%) and developed the largest leaf area, root and stem biomass among all tested *Tilia* species (i.e., *T. cordata* and *T. platyphyllos*) in the seedbed (Panchev and Ivanova 2017). Another example is an experimental plantation in northern Bulgaria, in which the survival rate of *T. tomentosa* aged 20 years was 95% (average hazard 0.0025 year⁻¹) if the planting density was low (spacing 3.6 × 1.8 m; cf. 42% in *Cedrus atlantica*) and 72% (0.014 year⁻¹) if the planting density was high (spacing 2.0 × 1.2 m; Kalmukov 2012).

General evolution of survival rates

In our experiment, sapling mortality decreased markedly over time. First-year mortality was higher than later mortality in most species on most sites. This phenomenon has often been observed in experimental plantations (Binder 1992; Don et al. 2007), in practical forestry (Grossnickle 2005) and is usually ascribed to planting stress. However, H_{ini} was generally higher in most non-native coniferous species (Table S4), whereas H_{lat} was generally higher in *T. heterophylla* and the non-native broadleaved species (Table S5). The survival rate of the native reference species was, on average, high over the whole study period. The reasons for this general pattern may include a combination of plant-specific adaptations such as: (1) increased plant size and thus photosynthetic and growth/storage capacity in the later phase of the initially small-sized coniferous saplings (Grossnickle and MacDonald 2018; Villar-Salvador et al. 2012), (2) continued adjustment of the root-shoot ratio in initially large-sized broadleaved seedlings (Grossnickle 2005; Stimm et al. 2014) and (3) faster adaptation to biotic site conditions in the reference tree species originating from shorter geographic distances (Bucharova et al. 2019).

Thus, individual plant morphological and physiological attributes defining seedling quality seem to be the most important in shaping plant performance at the time of establishment. The losses that occur later are usually unrelated to planting stress or seedling quality but due to other factors (Burschel and Huss 1987), for example competing ground vegetation and climatic extremes (Ameztegui and Coll 2013; Davis et al. 1999). The tending treatments conducted to control competing vegetation are likely to have

increased the plant survival of all species at all sites. In the short observation period of only 50 months, potentially lethal climatic extremes such as severe summer droughts or strong late frosts did not occur (for the period of H_{lat} see Supplementary material, Table S6), and thus not influence survival. The observed general evolution of survival rates indicates that the initial differences between the hazard rates of the tree species with geographically nearby origins (i.e., the native species) and those transplanted from geographically more distant regions (i.e., the non-native species) almost vanished 4 years after planting (Table 4).

Do site conditions affect species-specific survival rates?

Overall, we did not find any effects of site conditions on species-specific survival. While the initial mortality was the lowest in the driest site OLD, the plant hazard rate for the later phase was the lowest in the wettest site MUT (Table 4). The initial adaptation of the non-native species to their new habitat seemed thus best on the OLD experimental site, which has the smallest climatic distance to the area of origin of the seed sources. Similarly, testing early establishment of four *Quercus* species, Martín-Alcón et al. (2016) found lower summer mortality in the provenances which came from drier sites, possibly due to their more conservative water-use behaviour. The highest late mortality, but also the highest survival rate of the native relative to the non-native species, were recorded in BRU (Table 4). The high H_{lat} in BRU was mainly in the tree species that initially had large-sized seedlings, namely *F. orientalis*, *T. heterophylla* and *T. tomentosa* (Table S5), which supports our view that some of them still had not adjusted their root–shoot ratio to the warmer conditions typical for that site. These non-native tree species might have suffered an internal water disbalance due to the high evaporative demand. In addition, seedlings of *F. orientalis* and *T. heterophylla* are very shade-tolerant. They may have been particularly stressed by being directly exposed to full-light conditions on this warm site.

The differences in H_{lat} could not be explained by site-specific climatic variability within the observation period 2015–2016, which is not surprising since the survival rate varied greatly between species and sites. Our statistical examination revealed within-site differences played no role here. In addition, some species were planted in autumn and others in spring (e.g. in BRU, GRO, SCH; Table 1). Planting in spring might have reduced the initial plant survival if the summer after planting was dry. Our analysis of H_{season} on the GRO, OLD and SCH sites revealed, however, no seasonal extremes, which suggests that the effects of either winter frosts or summer droughts played little role. Late frosts affected *A. bornmuelleriana* saplings on all study sites, but

mostly on lateral shoots which flush earlier than the terminal leader.

Relative hazard rate of the non-native species

The relative hazard rate suggests that the non-native and the local native tree species tested have, in general, adapted similarly well to the new environment (Table 4), with the exception of *F. orientalis* in BRU, *T. tomentosa* in GRO and OLD and *T. heterophylla* in all study sites (Fig. 5). The survival of these shade-tolerant tree species generally improved with time, but H_{lat} still remained high relative to the native species three to 4 years after planting. One explanation for the continuing seedling mortality of these shade-tolerant tree species might be the complete lack of a forest overstory, which can play an essential role during the establishment phase as it protects seedlings from direct exposure to light and thus reduces their evaporative demand (Martín-Alcón et al. 2016). In support of this, Tabari et al. (2005) reported higher survival rates of *F. orientalis* seedlings from northern Iran in small gaps (50 m²) than in larger gaps (600 m²) with more light intensity. At the same time, reference species are light-demanding in all sites, which could give them advantages over the non-native ones when growing in open areas, particularly during the establishment phase. Interestingly, the two species with the lowest early survival, *A. bornmuelleriana* and *C. libani*, later performed just as well as the local native species (Fig. 5). This indicates that the survivors of the initial phase might have developed deeper roots during the late study period, which may have improved their nutrient status and late field performance (Grossnickle and El-Kassaby 2016). Where the native species survived consistently better on a certain site only, as in the case of the GRO site (Fig. 5), a factor particular to that site probably gave the native species an advantage. In the case of GRO, we suspect that the native *Q. robur* was the only species able to access the deeper soil layers with its tap roots, which still have plenty of water available during dry periods.

Limitations of the approach

Despite our trial's systematic, ensuring consistency in planting and measurement campaigns was a challenge. While we were able to measure a set of common variables using consistent inventory methods, we only partly achieved the same run-time, timing and frequency of the campaigns. For the analysis of sapling survival, this heterogeneity was overcome by fitting a Weibull function to survival curves according to Staupendahl (2011), and analysing time-harmonized estimated values for equal periods within the run-time. The Staupendahl function, which was developed for long-term stand-level mortality, also proved useful for the short time period of 50 months in our trial, and problems arose only

where early mortality was almost nil, as it was for *F. orientalis* and the native species in OLD. However, the interpretation of the parameters of the Staupendahl function is only straightforward if α is an expression of an age-related risk, which was high in the first 2 years for *A. bornmuelleriana* and *C. libani*, moderate both at an early and later stage for *T. tomentosa* and the native species, or variable (*F. orientalis* and *T. heterophylla*). The projection of the survival times from the Staupendahl function was, however, unrealistically long for some species, e.g. *F. orientalis* and *T. heterophylla* in MUT (see Supplementary material, Table S2). This is not surprising since it is difficult to predict life expectancy reliably on the basis of early survival data.

Our results are restricted to an observation period of 50 months, during which no potentially lethal climatic extremes, such as severe summer droughts or strong late frosts, occurred. This period is too short to draw conclusions about the long-term survival of the species studied since the order of their survival rates can change over decades and during longer time periods (Ameztegui and Coll 2013, Binder 1992, Barbeito et al. 2012). To obtain robust conclusions, the suitability of non-native tree species in a changing climate needs to be followed for at least several decades so that the likelihood that the plants will be exposed to climate extremes and pathogens is high. More extensive geographic coverage than in our multi-site trial would also increase the chances of detecting such effects. Including several provenances per species and using different types of plant material and planting methods would also improve the findings, but resource limitations made this impossible in our trial.

Conclusions and outlook

The strength of a multi-site trial lies in its potential for generalization since reaction patterns can be observed in different environments. Plant performance in the establishment phase provided important experimental data and gave first indications of how likely the local adaptation of foreign tree species to the new environment will be successful. In our multi-site trial, all species performed reasonably well during the relatively short observation period of 50 months, although the initial mortality of the non-native conifers *Abies bornmuelleriana* and *Cedrus libani* was high. Moreover, the site conditions of the open areas seemed to initially hamper the growth of shade-tolerant species.

In future analyses of our trial, we intend to address tree growth as well as plant health (i.e., biotic interactions) in order to obtain a more complete picture of the performance of the five exotic species in comparison with the local native reference species. In spite of the short survey period, the experimental data from our study are an important

contribution to the current debate on assisted migration (Bucharova 2017).

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Compliance with ethical standards

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

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