



What is the potential of silver fir to thrive under warmer and drier climate?

Yann Vitasse^{1,2} · Alessandra Bottero^{1,2} · Martine Rebetez^{3,4} · Marco Conedera⁵ · Sabine Augustin⁶ · Peter Brang⁷ · Willy Tinner^{8,9}

Received: 9 January 2019 / Revised: 26 March 2019 / Accepted: 3 April 2019 / Published online: 9 April 2019
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Foresters from many countries are seeking for tree species or provenances able to cope with expected climate change. While it becomes clear that some temperate tree species will increasingly suffer from climate warming, the fate of the ecologically and economically important silver fir (*Abies alba* Mill.) remains uncertain and debated because the ecological requirements of this species, as well as its resilience to drought, are still unclear. On the one hand, paleoecological studies reveal that this species was widely distributed under much warmer climate, suggesting a high potential to cope with ongoing and future climate warming. On the other hand, species distribution models generally predict a strong decline of its climatic suitability in the future. This paper aims to clarify the potential of this species to thrive in central and western Europe under predicted climate warming by reviewing the knowledge gained from different fields. Based on insight from different fields, we argue that silver fir has a great potential to thrive under warmer conditions in western and central Europe provided sufficient rainfall, as forecasted by climate models for most regions by 2100. For instance, dendroecological studies demonstrate that silver fir is more resistant and resilient to drought compared to co-occurring species such as Norway spruce, European beech and larch. The most prominent obstacle for increasing the proportion of fir in mixed forests nowadays is ungulate browsing that often prevents its upgrowth.

Keywords Climate warming · Dendroecology · Drought · European forests · Paleoecology · *Abies alba*

Introduction

The effects of climate change-induced rapid warming and prolonged droughts are increasingly impacting forests in Europe (Stott 2016). Economically valuable tree species

have been largely favoured and planted beyond their natural (realized) ecological niche, but are now under strong pressure (Conedera et al. 2017). For example, drier and warmer climatic conditions increase the vulnerability of Norway spruce (*Picea abies* (L.) Karst.) to bark beetle outbreaks in central Europe (Jakoby et al. 2015), whereas sweet chestnut (*Castanea sativa* Mill.) in southern Europe is suffering from

Communicated by Christian Ammer.

✉ Yann Vitasse
yann.vitasse@wsl.ch

¹ Forest Dynamics, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

² SwissForestLab, Birmensdorf, Switzerland

³ Institute of Geography, University of Neuchâtel, Neuchâtel, Switzerland

⁴ Forest Dynamics, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Neuchâtel, Switzerland

⁵ Community Ecology, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Cadenazzo, Switzerland

⁶ Forest Division, Federal Office for the Environment FOEN, Bern, Switzerland

⁷ Forest Resources and Management, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

⁸ Institute of Plant Sciences, University of Bern, Bern, Switzerland

⁹ Oeschger Center for Climate Change Research, University of Bern, Bern, Switzerland

repeated summer drought (Conedera et al. 2010). Silver fir (*Abies alba* Mill.) is a key species in Europe for social, economic and ecological aspects. It is an ecologically valuable species in forests that contributes to recreation landscape and biodiversity and provides protection against gravitational hazards and erosion in mountainous regions (Mauri et al. 2016). The wood of silver fir is commercially important and often sold in lots mixed with Norway spruce. However, because of quality issues or aesthetic values (e.g., smell, falling knots, Wolf 2003), silver fir is sometimes less used by modern timber industry than other conifers such as Norway spruce, pines or European larch.

The potential of silver fir under future warmer climate in western and central Europe is unclear due to a lack of shared knowledge regarding its ecological requirements. Yet, forest managers need to know to what degree and on which sites silver fir will be able to maintain viable populations for the next 100 years and in which cases they should consider or foster alternative species. On the one hand, the current distribution of silver fir and the widely used predictions from correlative species distribution models (SDMs) suggest that silver fir will not withstand climatic conditions that will prevail in most regions of western and central Europe by the end of the century (Maiorano et al. 2013; Zimmermann et al. 2014), though most recent SDMs predict range stability of the species under global warming (Dyderski et al. 2018). On the other hand, recent paleoecological studies, as well as process-based and dynamic models accounting for biotic and abiotic disturbances, suggest that this species has a high potential to cope with the expected climate change. Silver fir may even expand in regions with predicted low summer water deficit as in the forelands of the southern Alps and most areas of central and eastern Europe (Tinner et al. 2013; Bugmann et al. 2015; Henne et al. 2015; Ruosch et al. 2016), but possibly decline in the driest and warmest areas of Europe (Bosela et al. 2018). The purpose of this review is to clarify these contradictory results and to evaluate the potential of silver fir to thrive under expected warmer and drier conditions by evaluating the evidence so far acquired from paleoecological, genetic, dendroecological and ecophysiological studies.

In the first part, we focus on the current distribution and autecology of silver fir. The second part summarizes how the growth and vitality of this species have evolved since the nineteenth century and which are the environmental drivers of the species' growth variation and mortality. Finally, the last part considers the potential of silver fir to cope with climate change, highlighting silvicultural practices that would help to foster this emblematic species in European forests.

Distribution and autecology of silver fir

Refugia and survival dynamics during glacial and interglacial cycles of the Pleistocene

The genus *Abies* Mill. is thought to have appeared at high latitudes of the Northern hemisphere at the end of the late Cretaceous around 100 million years ago during a subtropical period, evolving in different species during its southwards migration during the Eocene (Xiang et al. 2007). The genus *Abies* includes about 50 species worldwide with 9 species inhabiting the Mediterranean region in southern Europe, and the other species being concentrated in North America and East Asia. The phylogenetic branch of firs from the Mediterranean region in southern Europe separated from the North America and East Asia branch during the late Eocene (Xiang et al. 2015) or the Miocene (Semerikova and Semerikov 2014).

Among *Abies* species native to Europe, *Abies alba* Mill. is the most widespread and tallest species (Mauri et al. 2016). As for all other tree species in Europe, however, the current distribution of silver fir has been heavily shaped by the glaciations and the subsequent interglacial periods during the Quaternary, with the Alps constituting a large geographic barrier between the North and the South of Europe (Lang 1994). The Balkan peninsula, the Apennine mountains and the Iberian peninsula were the three main refugia for numerous tree species during the glacial periods of the Quaternary (Bennett et al. 1991; Terhürne-Berson et al. 2004). Palynology and genetic studies support the existence of four glacial refugia for *A. alba* during the last glacial period (reviewed, e.g., in Dobrowolska et al. 2017):

1. The Calabrian region in southern Italy (Watts 1985; Konnert and Bergmann 1995; Cheddadi et al. 2014),
2. The northern Apennines and Euganean Hills in northern Italy (Kaltenrieder et al. 2009; Samartin et al. 2016; Piotti et al. 2017; Gubler et al. 2018),
3. Northwestern Greece in the Southern Balkans massif (Konnert and Bergmann 1995; Terhürne-Berson et al. 2004; Cheddadi et al. 2014),
4. The Pyrenees, northeastern Spain and southwestern France (Konnert and Bergmann 1995; Terhürne-Berson et al. 2004; Alba-Sánchez et al. 2010; Cheddadi et al. 2014).

The postglacial recolonization of the continent by silver fir has been under intense debate over the last decades (Tinner and Lotter 2006), but recent investigations seem to confirm northern Italy and the southern Balkans as the two macrorefugia which have most effectively contributed

to its modern distribution and genetic patterns in central Europe (Muller et al. 2007; Cheddadi et al. 2014). However, we cannot exclude the presence of small refugia or even microrefugia that may have contributed to the rapid expansion of the species during the Late Glacial or early Holocene, as it was recently evidenced by the detection of a new refugium in the Euganean Hills (Kaltenrieder et al. 2009; Samartin et al. 2016; Gubler et al. 2018).

Pleistocene glacial-interglacial cycles forced tree populations to survive in very small-sized refugia. Glacial population contractions and interglacial expansions led to repeated contacts among fir species, e.g., the introgressions of *A. alba* with *A. cephalonica* in northern Greece, leading to the hybrid *Abies x borisii-regis* (Cheddadi et al. 2014). Finally, while the genus *Abies* has undergone significant morphological differentiation, this does not necessarily imply reproductive isolation (Klaehn and Winieski 1962; Linares 2011), suggesting that a geographic, rather than a genetic or physiological separation of species has occurred as the genus evolved. This is probably why all fir species originating from southern Europe are able to hybridize (Greguss et al. 1994). Interestingly, as a rare case for European conifers, but common among the subtropical to tropical conifer species of the southern and northern hemisphere, it has been hypothesized that the species *A. alba* has undergone evolutionary adaptation to strong competition with evergreen and deciduous broadleaved species by arranging its needles horizontally (instead of originally radially) to reach higher light use efficiency (Pfadenhauer and Klötzli 2015). This special subtropical needle arrangement is possibly a legacy of the warm climatic conditions of the Eocene and Miocene ca. 5–5.3 millions of years ago (Birks and Tinner 2016).

Human influence on silver fir distribution

As for some other species such as sweet chestnut, European larch (*Larix decidua* Mill.) or walnut (*Juglans regia* L.), human activities have heavily shaped and fragmented the current distribution of silver fir. The increased fire frequency and browsing activity caused by the onset of farming produced a competitive disadvantage to silver fir with respect

to other disturbance-indifferent tree species. In fact, silver fir is one of the most palatable woody species in European mixed forests (Fig. 1). Pollen and genetic data suggest that before human-induced disturbances silver fir was abundant in lowland forests south of the Alps, and even at the Mediterranean coast competing with, e.g., subtropical *Quercus ilex* between 9000 and 7000 B.P. (Hussendörfer 1999; Tinner et al. 1999, 2013; Henne et al. 2013; Ruosch et al. 2016), reflecting a rapid recolonization of the area due to more favorable climatic conditions. Subsequently, silver fir dramatically declined between 7000 and 5000 B.P. in the warm lowlands (Tinner et al. 1999). Some authors even refer to this decline as the ‘Mid-Holocene extinction of silver fir’ (Wick and Möhl 2006). The development of farming (agriculture and grazing) along with human population increase, timber exploitation and fire disturbance have been proposed as major factors to explain the decline of silver fir during the period from 7000 and 2000 BP (Pons and Quezel 1985; Tinner et al. 1999; Conedera et al. 2017), especially from 4000 to 2000 years B.P. (Hussendörfer 1999; Colombaroli et al. 2007). Later, intensive land-use changes such as converting forests into agricultural land as well as intensive forest utilization occurred from medieval times until ~AD 1840. In addition, from the eighteenth century onwards, Norway spruce and fast growing pine (*Pinus*) species were largely planted and favoured over silver fir in central Europe to satisfy the rising need for wood supply (Bürgi and Schuler 2003). Similarly, on-site charcoal production disfavored silver fir in mixed beech-fir stands during the Middle Ages, artificially turning many forests into pure beech coppice stands as for instance on the southern slope of the Alps (Valsecchi et al. 2010). Besides, the largely employed clear-cutting silvicultural system in Europe during this period was also detrimental to silver fir (Eichenseer 1997). Although the vitality of silver fir has increased since the 1990s in many stands in central and western Europe (Büntgen et al. 2014), silver fir populations have also locally declined in other areas such as the northern Carpathians, Slovenia and Croatia, mainly due to increasing competition with European beech and ungulate browsing (Vrska et al. 2009; Ficko et al. 2011, 2016). The current expansion of its distribution toward

Fig. 1 Young fir browsed by a chamois (left), and damage caused by ungulates that have injured terminal and lateral shoots (right). Photo credit: U. Wasem



higher elevations in central and western Europe might be the result of increasing land-use abandonment (Carcaillet and Muller 2005; Chauchard et al. 2010), and of the natural spread of large predators such as the lynx or the wolf in the Alps and the Jura mountains, which have started limiting the browsing pressure by large herbivores (Schnyder et al. 2016).

Current distribution

As a result of the glacial and interglacial range contractions and expansions as well as the recent impact of human activities described above, the current distribution of silver fir is confined to central and southern Europe from 38°N latitude at the southern frontier in Calabria to 52°N latitude in eastern Poland (Fig. 2), with a higher concentration in mountain regions. From west to east, silver fir occurs

from 1°W longitude in the Pyrenees to 27°E longitude in Romania and Bulgaria (Fig. 2). Silver fir covers a wide range of elevations from below 100 m a.s.l. in Tuscany (Cortini Pedrotti 1967) and 135 m a.s.l. in Poland to elevations slightly below treeline in the Swiss Alps, around 2000 m a.s.l. (Vitasse et al. 2012). Its upper elevation limit is currently increasing mainly due to land-use change, and possibly climate warming (Chauchard et al. 2010). Silver fir is often mixed with European beech at lower elevations or latitudes, whereas it is frequently found with Norway spruce, Scots pine (*Pinus sylvestris* L.), and exceptionally with Swiss stone pine (*Pinus cembra* L.) at higher elevations or latitudes. Within this large distribution range, silver fir becomes less abundant in the drier areas at low elevations as in the Hungarian plains (Fig. 2) and is rare in the most continental valleys of the Alps (Vitasse et al. 2018a).

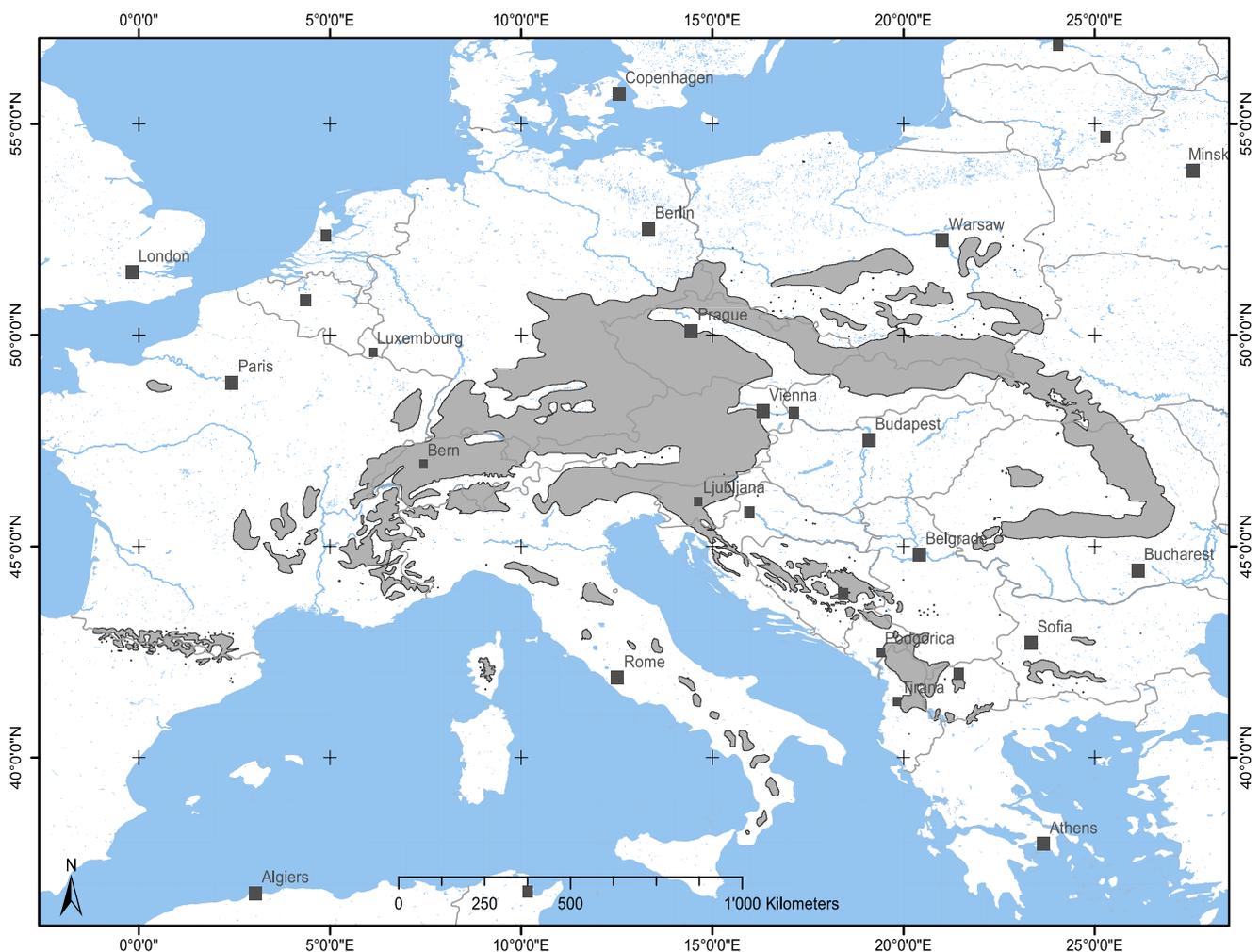


Fig. 2 Current distribution of silver fir. Adapted from EUFORGEN (2003)

Autecology of silver fir based on its current distribution

Generally, silver fir thrives in a large range of temperature conditions (annual temperature from ~7 to 13 °C or summer temperature from 14 to 19 °C), and is mostly found in areas where annual precipitation exceeds 800–1000 mm (Aussenac 2002; Gomez 2012; Tinner et al. 2013). It can withstand low temperatures in winter, around –30 °C (Savill et al. 2016), whereas it is considered sensitive to late frost in spring (Ellenberg 2009), which reduces seedling survival (Aussenac 2002). Fir is sensitive to low air humidity (Guicherd 1994; Rohner and Thürig 2015; Etzold and Zweifel 2018) and prefers oceanic rather than continental climates. A powerful taproot allows the species at its adult stage to cope with dry conditions by accessing deepwater reserves. Juvenile trees are more sensitive to drought, especially air dryness (Aussenac 2002, see next paragraph), and therefore better develop under a canopy that buffers temperature variations and increases air humidity.

Fir can grow in an array of soil types, from acidic to neutral pH, and from poor to rich nutrient availability, but prefers humid and deep soils that do not dry out easily (Mauri et al. 2016; Savill et al. 2016). Where these conditions are lacking (on soils having poor water retention and/or on south facing slopes with high solar radiation) silver fir becomes sensitive to drought (Cailleret and Davi 2011; Gomez 2012). The species is also sensitive to atmospheric pollution, in particular to sulfur dioxide, which has caused its decline in many parts of Europe during the period 1950–1990 (Elling et al. 2009, 2012) when unprecedented concentrations of SO₂ in the air were reached (Hoesly et al. 2018).

Silver fir is very shade tolerant (Ellenberg 2009) and unlike Scots pine, and to a lesser extent Norway spruce, it is favoured by a dense canopy during its recruitment phase as shade limits the competition of other species (de Andrés et al. 2014; Mauri et al. 2016; Savill et al. 2016). However, fir seedlings are very susceptible to browsing by large herbivores, which can jeopardize or heavily reduce the regeneration success of the species, in particular under deep shade where its capacity for compensatory growth is limited (Ammer 1996; Motta 1996; Kupferschmid et al. 2013). Regarding insects, it is occasionally attacked, in particular during extended drought, by the fir engraver beetle (*Pityokteines curvidens*), which leads to yellowing, reddening and finally the death of older or weakened trees (Maksymov 1950). Another insect affecting young trees is the silver fir adelges (*Dreyfusia nordmanniana*), an aphid that can cause important damage to young trees (Ravn et al. 2013). As for other tree species, damage by insect pests is expected to increase in the future as these insects develop faster under warmer conditions. Silver fir is also sensitive to the white mistletoe, which has been shown to significantly reduce its

growth (Noetzli et al. 2003; Durand-Gillmann et al. 2014). Finally, the species does not display any adaptive traits to fire disturbance (thick bark, resprouting capacity, serotinous cones) and is thus particularly disadvantaged in case of intense and repeated fires (Tinner et al. 2000; Caudullo and Tinner 2016).

Sensitivity of the species to mean and extreme climatic events

Insight from dendroecological studies

Dendroecological studies allow to improve our understanding of the relationship between tree growth and climatic factors, as well as resistance (capacity to avoid growth reduction during extreme events or disturbances) and resilience (ability to regain pre-disturbance growth levels) of species to extreme climatic events, such as the exceptional drought that occurred in summer 2003 in Europe. Numerous dendroecological studies have been conducted on silver fir attempting to identify the main environmental drivers of growth variation. Silver fir growth rates have overall substantially increased in many European regions during the period 1880–1950, likely promoted by warmer climate with similar levels of summer precipitation, as well as fertilization by nitrogen deposition and human-induced CO₂ increase (Büntgen et al. 2014).

During the 1970s and the early 1980s, a marked growth decline and dieback was synchronously detected in many forests for several tree species in Europe, especially silver fir. Silver fir growth decline was observed in the central Pyrenees (Chéret et al. 1987), in the Vosges mountains (Becker et al. 1989), in Bavaria (Elling et al. 2009), in the Black Forest in southwest Germany (Elling et al. 2009; Vitali et al. 2017), in Croatia (Čavlović et al. 2015), in the Swiss Jura mountains (Bloesch 1983) and in eastern Europe such as in Romania and Slovakia (Gazol et al. 2015; Bosela et al. 2016, 2018), also visible in the examples of the average annual fir growth shown for three stations in southeastern Germany, Poland and Slovenia in Fig. 3 (panels d, e and f, respectively). This growth decline and mortality were attributed to increased air pollution during the 1970s, in particular due to the strong increase in sulfur dioxide emissions (SO₂), which reached a maximum air concentration in the early 1980s in Europe (Hoesly et al. 2018), causing substantial damage to conifer needles (Schütt and Cowling 1985; Kandler and Innes 1995; Elling et al. 2009; Čavlović et al. 2015). Sulfur dioxide in the air forms, together with NH₃, ammonium sulfate, which then deposits on soil and trees, causing damage to the needles. Furthermore, sulfur deposition leads to soil acidification that reduces soil pH, and, below a pH of < 4.5, mobilizes Al, which is toxic for tree fine roots

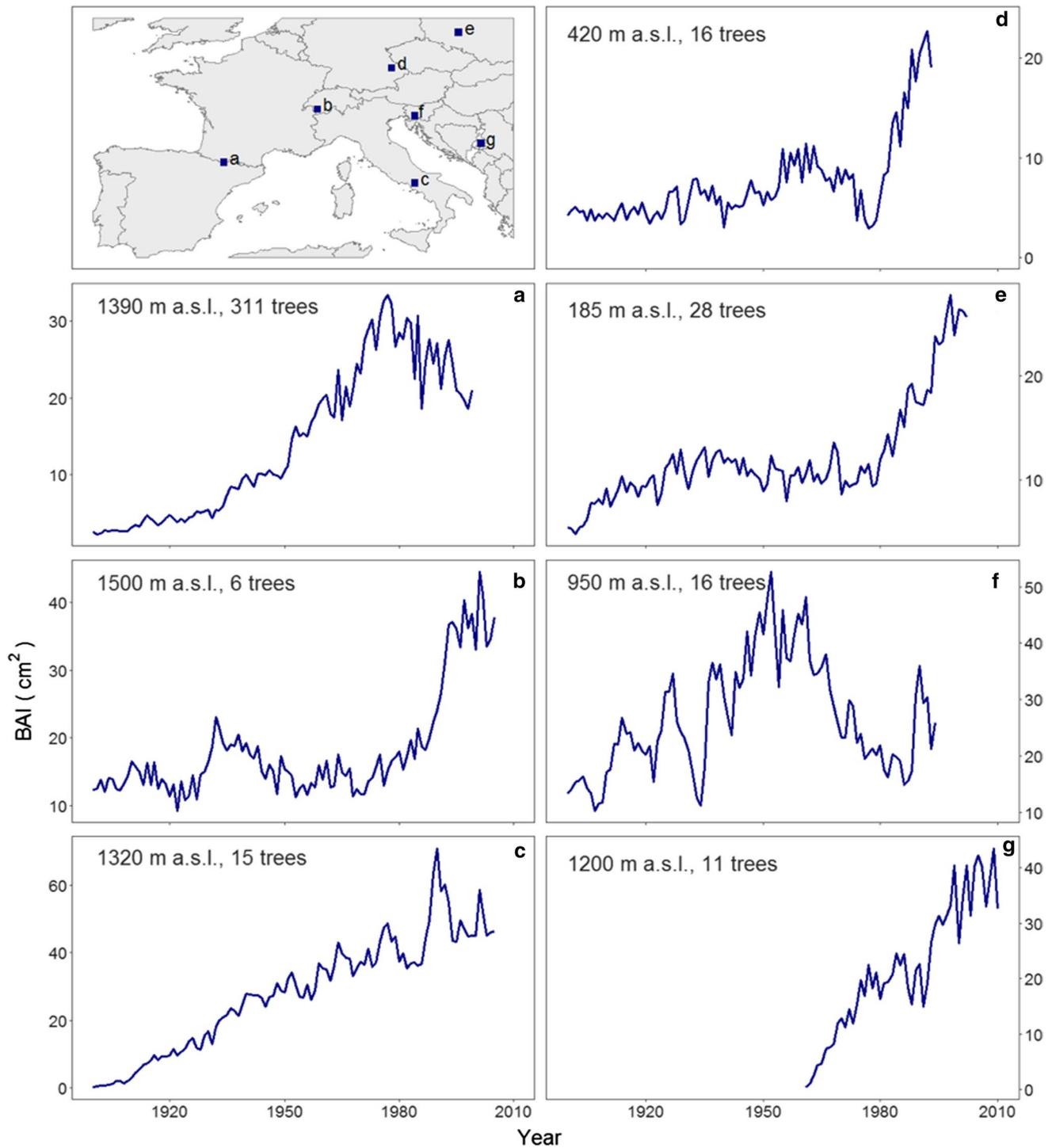


Fig. 3 Examples of average annual fir growth (expressed as basal area increments, BAI, $\text{cm}^2 \text{year}^{-1}$) in the Pyrenees (a, data from Camarero et al. 2011), Switzerland (b, data from ITRDB, Büntgen SWIT309), central Italy (c, data from Lombardi et al. 2008), Germany (d, data from ITRDB, Wilson GERM060), Poland (e, data from ITRDB, Szymura POLA021), Slovenia (f, data from ITRDB, Levanic SLOV002)

and Bosnia and Herzegovina (g, data from Ducić et al. 2014). Elevation (in m a.s.l.) and sample size are reported in each panel. Note that different sampling designs used in dendroclimatological studies can bias population growth rate estimates (Nehrbass-Ahles et al. 2014) but these examples are used here to show the general growth pattern observed in Europe since 1900

(Van Breemen et al. 1982; Gruber 1994). The lower vitality of silver fir during the 1970s due to high concentrations of sulfur dioxide in the air has largely affected the analyses on its growth responses to other stressors occurring during the same period (e.g., the severe drought 1976, Uhl et al. 2013), hence overestimating the effects of such stressors.

Finally, since the 1980s contrasting growth responses have been observed for silver fir across Europe (Gazol et al. 2015; Bosela et al. 2018). On the one hand, silver fir has grown exceptionally fast since the mid-1980s in central and northern Europe, but also in central and northern Italy, and this trend has been even enhanced since 2000 (Büntgen et al. 2014; Bosela et al. 2018, also visible in the few examples displayed in Fig. 3). This growth improvement was presumably the consequence of the decline of atmospheric SO₂, air warming with constant precipitation and/or the further increase in nitrogen deposition (acting as fertilizer) observed in most parts of western and central Europe (Elling et al. 2009; Büntgen et al. 2014). However, for the latter factor, the results of the National Forest Inventory in Switzerland show that high nitrogen depositions can lead to reduced fir growth (Rohner et al. 2018), which was also observed in intensive monitoring plots (Etzold and Zweifel 2018). Nevertheless, radial growth has been reported to decline since the 1980s toward its southwestern distribution limit such as in the Spanish Pyrenees (Camarero et al. 2011; Linares and Camarero 2012; Camarero et al. 2015; Gazol et al. 2015, see example shown in Fig. 3b) or in southeastern France (Cailleret et al. 2014). In Spain, the recent growth decline of silver fir and dieback observed locally is the likely consequence of the cumulative effect of very dry years that have followed the exceptionally warm and dry summer of 2003 (Macias et al. 2006; Peguero-Pina et al. 2007; Camarero et al. 2011; Linares and Camarero 2012; Büntgen et al. 2014; Gazol et al. 2015; Davi and Cailleret 2017; Latreille et al. 2017). However, the different growth patterns observed in the Spanish Pyrenees could also be related to the different lineage of this population and its possible lower genetic diversity caused by genetic drift.

Not surprisingly, the climatic effect over the growth of silver fir varies within its distribution area. Typically, at lower elevations in the central part of its range, growth is positively related to precipitation, such as in the Black Forest in southwestern Germany (van der Maaten-Theunissen et al. 2012; Vitali et al. 2018), in the Vosges and Jura Mountains in eastern France and northwestern Switzerland (Rolland et al. 1999), in southeastern France (Latreille et al. 2017) or in central Italy (Mazza et al. 2014), whereas at mid- and high elevations, it responds positively to increased winter, spring and early summer temperature, but is not significantly affected by variation in precipitation (van der Maaten-Theunissen et al. 2012; Vitali et al. 2018). Although summer droughts reduce silver fir growth, the impact is less

pronounced than for other co-existing tree species. For example, the often co-occurring Norway spruce displays a higher sensitivity to summer droughts, regardless of elevation, in southwestern Germany (van der Maaten-Theunissen et al. 2012; Vitali et al. 2017) or in the French Alps (Desplaque et al. 1998). Similarly, long-term monitoring of tree growth and tree-ring analyses conducted in Switzerland, in southern Germany and southern France show that silver fir is more resistant to drought than Norway spruce, larch and European beech (Zingg and Bürgi 2008; Cailleret and Davi 2011; Rothe et al. 2011; Zang et al. 2014), and as resistant as Douglas fir (*Pseudotsuga menziesii*; Vitali et al. 2017).

Three elements could explain the relatively high resistance of silver fir to drought. First, silver fir's primary growth cessation occurs early in the season, usually in early July, while the strongest droughts generally occur in July and August (Aussenac 2002). Second, fir often grows on deep soils and its pivotal root system allows it to access water in deeper layers, in contrast to Norway spruce, and to a lesser extent European beech (Stokes et al. 2007). Third, this species controls its transpiration efficiently via the rapid closure of its stomata in response to vapour-pressure deficit (VPD) increase (Guicherd 1994; Aussenac 2002; Nourtier et al. 2014), even in deep and wetter soil (Nourtier et al. 2014). This rapid stomatal closure under dry air, starting when VPD exceeds ca. 0.3 kPa (Guicherd 1994), is referred to as 'avoidance strategy' of drought for minimizing the risk of xylem embolism (Jones and Sutherland 1991). Thus, silver fir can potentially endure severe short occasional droughts, but needs in the long term a relatively high air humidity for photosynthesis, growth and nonstructural carbohydrate reserves to compete with the other species. It is probably for this reason that this species is particularly found on north-exposed slopes and deep soils (Henne et al. 2013) with high atmospheric humidity, especially at the southern margin of its distribution.

Growth responses to climate: insights from warming experiments, transplant experiments and provenance trials

In contrast to other dominant tree species in Europe, such as Norway spruce or European beech, only a few studies have dealt with the sensitivity of silver fir to drought and warmer temperatures. Experimental measurements of the photosynthetic capacity of silver fir seedlings exposed to various temperatures (from 10 to 40 °C) in climate chambers during 24 h showed a rather high tolerance to heat stress with irreversible injuries to the photosystem occurring only above 47 °C for seedlings acclimatized to 10 °C (Robakowski et al. 2002), with a photosynthetic optimum around 20 °C (only 15 °C for Norway spruce, Gomez 2012). By contrast, numerous provenance trials have been conducted during the second

half of the twentieth century to select provenances with high performance in terms of growth and stem quality, but also to detect provenances with high drought tolerance. Overall, most provenance trials highlighted little genetic differentiation among provenances for adaptive traits such as frost resistance (Larsen 1986), growth (Larsen 1986; Commarmot 1997; Bourdenet 1998; Vitasse et al. 2009; Kerr et al. 2015; Frank et al. 2017b), or drought resilience (Sindelar and Beran 2008; George et al. 2015), despite the very contrasting local climate conditions the investigated populations originate from (Herzog and Rotach 1990). Generally, provenances from the highest elevations are more resistant to frost and develop more slowly than those from lower altitudes (Larsen 1986; Vitasse et al. 2009). However, genetic differentiation in silver fir is generally lower than in other species such as Norway spruce or European beech (Vitasse et al. 2009; Frank et al. 2017b), which reduces the risk that silver fir will suffer from maladaptation under warmer climate (Frank et al. 2017a).

The recolonization trajectories of silver fir populations during the last glacial-interglacial cycles seem to have produced two genetically distinct lineages in central Europe with different sensitivities to climatic variations (Bosela et al. 2016). For instance, a study based on tree-ring width series and genetic samples from 78 populations along the Carpathian Arc has shown that the Balkan lineage has higher genetic diversity and is more sensitive to drought at the beginning of the growing season than the western lineage originating from northern Italy, which is more sensitive to summer drought (Bosela et al. 2016). Finally, successful silver fir plantations located at the warm edge of its distribution exist, demonstrating the high plasticity of this species. For example, the ~200-year-old fir plantation in Varramista, Tuscany, located only 30 m above sea level, as well as other lowland stands in Tuscany, show successful natural fir regeneration and relatively low to no dieback (Cortini Pedrotti 1967; Birks and Tinner 2016; Tinner et al. 2016) (Fig. 4) where moisture availability is sufficiently high (e.g., deep soils at slope bottom, northern slopes).

Potential ability of silver fir to face climate warming in Europe

Divergences between model predictions and paleoecological studies

Most species distribution models (SDMs) based on correlative approaches between current species occurrence and related climatic conditions predict dramatic losses of climatic suitable areas for silver fir in Europe by the end of the century, irrespective of the climate scenario considered (Badeau et al. 2007; Zimmermann et al. 2016). By contrast,



Fig. 4 Plain lowland *A. alba* forest at Varramista, Tuscany, close to the Mediterranean Sea. Species co-occurring in the forest with *A. alba* are *Quercus ilex*, *Fraxinus ornus*, *Ilex aquifolium*, *Hedera helix*, *Vitis sylvestris*, *Castanea sativa*, *Quercus petraea*, *Ficus carica*, *Acer campestre*, *Corylus avellana*, *Ruscus aculeatus*. Mean temperatures at the site are ca. 24 °C in July, 7 °C for January, and 15.5 °C for the whole year. Annual mean precipitation in the area reaches ca. 850 mm with a pronounced summer drought in July and August (ca. 25 mm mean precipitation each). However, the trees may have access to ground water on this site. Source of climatic data: Cortini Pedrotti (1967); vegetation survey and picture: W. Tinner (20 May 2014)

paleoecology and genetic studies suggest that before strong human influence (i.e., about 5000 years ago), silver fir occurred abundantly under significantly warmer climates than today, likely exceeding the current temperature at the warm edge of its distribution by 5–9 °C (reviewed in Tinner et al. 2013). These studies therefore suggest that silver fir has high potential to face climate warming, which is also supported by recent dynamic vegetation model results (Ruosch et al. 2016), provided browsing pressure and fire disturbance remain (naturally) low (Keller et al. 2002; Henne et al. 2011, 2013; Ruosch et al. 2016). SDMs are based on correlations between today's species occurrences and climatic parameters. This makes them unable to capture rare and past occurrences, as in the case of fir at the warm margins of its climatic niche. Consequently, SDMs may fail to attribute climate suitability to extant silver fir forests in southern Europe (Maiorano et al. 2013; Tinner et al. 2013). Even when paleoecological data were included at the European scale to refine the models, SDM results still suggested dramatic losses of future climate suitability of silver fir in about 40% of its current range by 2100 based on scenario B1 (Maiorano et al. 2013). This failure might be caused by the rarity of pollen records and modern occurrences from the warmest areas of the Mediterranean, resulting in a modest overall spatial resolution and coverage that impedes SDM to deliver reliable local assessments. In contrast, SDMs that used highly resolved spatial data were able to accurately simulate the extant range of *Abies alba* including the southernmost populations (Tinner et al. 2013), and do not predict

a dramatic decrease of suitable climate of this species under moderate climate change scenarios (Dyderski et al. 2018). For instance, by using occurrence data from the Global Biodiversity Information Facility and EUFORGEN in addition to occurrence data provided from national forest inventories (typically used in SDMs), Dyderski et al. (2018) showed also the lowest proportion of threatened area (12.8%) for silver fir in the future under a moderate climatic scenario compared to the other 11 European forest tree species studied. Similarly, recent dendroecological studies suggest that growth of silver fir will likely be enhanced in future decades in the Black Forest in southwestern Germany, even under the most extreme climatic scenario (RCP8.5) because the species could benefit from warmer winters and springs compensating for drier summers (Vitali et al. 2018).

The crucial role of water availability

Ecophysiological and dendroecological studies suggest that silver fir is rather tolerant to warm temperatures (often qualified as a thermophilous or warm-temperate species), and can cope to a certain extent with severe summer drought, being similarly resistant as Douglas fir, but more than Norway spruce or European beech (Zang et al. 2014; Vitali et al. 2017). The analysis of climate data from its current distribution and bioclimatic models allow to estimate that silver fir requires rainfall greater than 600–700 mm per year and greater than 90–120 mm during the three warmest summer months (Tinner et al. 2013). These climatic conditions are currently present in most parts of its fragmented distribution and beyond (Panagos et al. 2015). We surmise that silver fir can thrive under such low limits of precipitation provided that the soil can store sufficient water, air humidity is sufficient, or that deep water can be accessed by the taproots (Aussenac 2002; Henne et al. 2013; Tinner et al. 2013). Thus, with sufficient precipitation or air humidity during the growing season, and limited fire and browsing disturbance, silver fir may thrive in most parts of central and western Europe. This may apply even in southern Europe in lowlands near the Mediterranean coast, as revealed by the existence of mixed cryptic *Abies alba*–*Quercus ilex* stands that regenerate spontaneously in central and southern Italy on suitable soils (Cortini Pedrotti 1967; Tinner et al. 2013; Birks and Tinner 2016). However, these conditions may no longer be present in the lowlands of the Mediterranean region in the future (Ruosch et al. 2016), where summer precipitation is predicted to significantly decrease by 2100, such as in Spain, southern France and Italy (IPCC 2013).

Promoting silver fir in European forests

Silvicultural practices and wildlife management will strongly influence the future occurrence of silver fir in European

forests. As a pronounced late-successional species, silver fir is particularly sensitive to silvicultural practices. In stands with fir presence, practices which cause abrupt environmental changes such as clear-cutting negatively affect silver fir (Eichenseer 1997) as it was the case in the past in regions such as the Carpathians (Vrska et al. 2009). In contrast, silver fir regeneration profits from long regeneration periods and slow removal of shelter trees. Uneven-aged silvicultural systems providing low light conditions such as the single-tree or the group selection system allow the regeneration of silver fir to outcompete other species, which is not the case under elevated light intensity (Grassi et al. 2004). Moreover, even with the most appropriate silvicultural system, fir recruitment often fails if browsing pressure is not sufficiently limited by wildlife management (Ficko et al. 2016) or appropriate protective measures, such as individual protections or fences.

Promoting silver fir in future European forests means introducing it in stands where it is currently absent. This can be best achieved by underplanting silver fir seedlings in adult stands of other species, at any time in uneven-aged stands, or one to two decades before the final cut in regular (mono-layered) stands, to allow the seedlings of silver fir to benefit from a competitive advantage over the regeneration of other species. In most cases, such underplanting will require protective measures against browsing (Kupferschmid et al. 2013).

Genetic pool and other fir species

Beyond silvicultural interventions, sustainable management requires some thoughts to promote the genetic diversity of the species (guarantor of a high potential for adaptation) and to consider the use of other Mediterranean fir species. As previously mentioned, silver fir seems to have a less diversified genetic variation between populations than other forest species such as Norway spruce. This low genetic variability among populations may somewhat paradoxically be beneficial as it allows for a more generalist behavior in the face of climatic hazards, reducing the risk of ‘maladaptation’ under future climate (Frank et al. 2017a). Such an interpretation is supported by new paleogenetic results from warm areas where the species went locally extinct as a consequence of excessive anthropogenic disturbance (Schmid et al. 2017). Nevertheless, although the genetic diversity among populations seems low, genetic diversity within populations is high, even in marginal populations (Brousseau et al. 2016), which is an asset for the species to adapt to climate warming. This high genetic diversity can also be promoted using silvicultural practices that foster pollination over long distances, for example by reducing the stem density of reproducing trees (see synthesis of the different methods in Lefèvre et al. 2014).

Besides, silver fir resistance to weather extremes has probably been underestimated within extant populations. Some marginal populations are currently growing in sites with a much warmer and drier climate than the climatic limits commonly found in the literature. For example, populations growing in central and southern Italy, at only 30 m of elevation, are accompanied by an array of typically Mediterranean species (Tinner et al. 2016). It is, however, not advisable to rely only on such marginal populations as seed sources since they are isolated and therefore possibly prone to genetic erosion (Belletti et al. 2017). More investigations should be conducted on these marginal populations to assess whether they have genetically evolved to better tolerate summer drought and could therefore potentially be used as seed source.

Other Mediterranean fir species could also be considered as alternatives to Norway spruce or European beech in a warmer-than-today Europe, such as *A. cephalonica* or *A. borisii-regis*, which share physical properties of wood and similar ecological requirements to those of silver fir, but with a higher resistance to prolonged droughts. Provenance tests using these species were conducted in southern France at various altitudes and showed a high potential for both species to grow in drier climates and to cope with long periods of summer drought (Fady 1993). This strong resilience to drought can be explained by their early spring phenology and short growing season, with both species ending their annual growth only within 30–45 days after the emergence of new needles, well before the occurrence of summer droughts (Fady 1993). However, the precocious phenology may put these two species at greater risk of frost, a risk that remains high in and north of the Alps despite climate warming (Vitasse et al. 2018b) and to which silver fir seems more adapted. Further investigations are needed to assess the potential of other fir species to thrive in the central and southern part of silver fir distribution.

Conclusions

The debate concerning the future suitability of silver fir to thrive under warmer and drier climates is still open and based on contradictory positions that derive from studies using markedly different approaches. However, this synthesis unambiguously shows that it is possible to reconcile these positions. Despite recent progresses in SDM simulations that now predict range stability or moderate change of silver fir under strongly warming climates (Dyderski et al. 2018), the heavy impact of humans in restricting the current distribution of the species suggests caution when interpreting the outcomes of SDMs. Therefore, it is not surprising that paleoecological and process-based modeling studies challenge SDM-inferred predictions that claim strong declines of the

species in central Europe. Dendroecological studies support the paleoecological evidence, demonstrating that silver fir is more resistant and resilient to drought than Norway spruce, European beech, or larch, and similar to Douglas fir in this respect, especially since sulfur dioxide concentrations have decreased. Given the growing scientific evidence for the species' ability to cope with climate change, it seems reasonable to preserve and foster this emblematic species in European forests, particularly in mountainous areas where it plays a vital role for prevention against erosion and avalanches.

A concern is that silver fir may suffer more in the future from insect attacks such as the fir engraver beetle (*Pityokteines curvidens*), which is favored by rising temperatures and summer droughts. Rising temperature is expected to accelerate the development cycle of this beetle, while increasing summer drought may weaken fir trees, but this is also true for other host/pest pairs such as Norway spruce and the spruce bark beetle (*Ips typographus*). A cautious forest management, aimed at gradually increasing the presence of silver fir in mixed forests, is therefore justified. Such a procedure would mimic the natural conditions before the advent of agriculture, when *Abies alba* was growing in species rich and climatically resilient mixed forests in Mediterranean and temperate Europe.

Acknowledgements This review was funded by the research program 'Forest and Climate Change' of the Federal Office for the Environment and the Swiss Federal Research Institute WSL, and was also supported by the SwissForestLab. This paper was initially published in French in *Schweizerische Zeitschrift für Forstwesen* (Vitasse et al. 2018a) and was adapted with the agreement of this journal to upscale the results to an international readership across Europe.

Data accessibility The sources of the data used in Fig. 3 are cited in the caption legend of the figure.

Author contributions PB and SA conceived the idea. YV led the writing with input from all the other authors. AB collected the data shown in Fig. 3 and drew Fig. 3.

References

- Alba-Sánchez F, López-Sáez JA, Pando BBd, Linares JC, Nieto-Lugilde D, López-Merino L (2010) Past and present potential distribution of the Iberian *Abies* species: a phytogeographic approach using fossil pollen data and species distribution models. *Divers Distrib* 16(2):214–228
- Ammer C (1996) Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *For Ecol Manag* 88(1–2):43–53
- Aussenac G (2002) Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. *Ann For Sci* 59(8):823–832
- Badeau V, Dupouey J-L, Cluzeau C, Drappier J (2007) Aires potentielles de répartition des essences forestières d'ici 2100. *RDV techniques ONF (hors-série n°3):62–66*

- Becker MG, Landmann G, Levy G (1989) Silver fir decline in the Vosges mountains (France): role of climate and silviculture. *Water Air Soil Pollut* 48:77–86
- Belletti P, Ferrazzini D, Ducci F, De Rogatis A, Mucciarelli M (2017) Genetic diversity of Italian populations of *Abies alba*. *Dendrobiology* 77:147–159
- Bennett K, Tzedakis P, Willis K (1991) Quaternary refugia of north European trees. *J Biogeogr* 18:103–115
- Birks HJB, Tinner W (2016) Past forests of Europe. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) European atlas of forest tree species. Publication Office of the European Union, Luxembourg, pp 36–39
- Bloesch U (1983) Beitrag zum Problem des Weisstannensterbens: Untersuchungen über die langfristige Entwicklung der absterbenden Weisstannen auf repräsentativen Standorten inner- und ausserhalb des Optimalbereiches der Weisstanne auf Grund der Zwangsnutzungsstatistiken im Kanton Neuenburg, sowie Abklärung der Kausalzusammenhänge, insbesondere mit klimatischen Hypothesen. Professur für Waldbau. – ETH Zürich, p 74
- Bosela M, Popa I, Gömöry D, Longauer R, Tobin B, Kyncl J, Kyncl T, Nechita C, Petráš R, Sidor CG, Šebeň V, Büntgen U (2016) Effects of post-glacial phylogeny and genetic diversity on the growth variability and climate sensitivity of European silver fir. *J Ecol* 104(3):716–724
- Bosela M, Lukac M, Castagneri D, Sedmák R, Biber P, Carrer M, Konôpka B, Nola P, Nagel TA, Popa I, Roibu CC, Svoboda M, Trotsiuk V, Büntgen U (2018) Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Sci Total Environ* 615:1460–1469
- Bosela M, Lukac M, Castagneri D, Sedmák R, Biber P, Carrer M, Konôpka B, Nola P, Nagel TA, Popa I, Roibu CC, Svoboda M, Trotsiuk V, Büntgen U (2018) Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Sci Total Environ* 615(Supplement C):1460–1469
- Bourdenet P (1998) Essais d'adaptation et peuplements de référence de sapins méditerranéens mis en place par l'Office National des Forêts. *Forêt méditerranéenne* 19(2):183–188
- Brousseau L, Postolache D, Lascoux M, Drouzas AD, Källman T, Leonarduzzi C, Liepelt S, Piotti A, Popescu F, Roschanski AM (2016) Local adaptation in European firs assessed through extensive sampling across altitudinal gradients in southern Europe. *PLoS ONE* 11(7):e0158216
- Bugmann H, Brang P, Elkin C, Henne PD, Jakoby O, Lévesque M, Lischke H, Psomas A, Rigling A, Wermelinger B (2015). Climate change impacts on tree species, forest properties, and ecosystem services. In: OCCR, FOEN, MeteoSwiss, C2SM, Agroscope, ProClim (eds) CH2014-impacts, toward quantitative scenarios of climate change impacts in Switzerland
- Büntgen U, Tegel W, Kaplan JO, Schaub M, Hagedorn F, Bürgi M, Brázdil R, Helle G, Carrer M, Heussner K-U, Hofmann J, Kontic R, Kyncl T, Kyncl J, Camarero JJ, Tinner W, Esper J, Liebhold A (2014) Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Front Ecol Environ* 12(2):100–106
- Bürgi M, Schuler A (2003) Driving forces of forest management—an analysis of regeneration practices in the forests of the Swiss Central Plateau during the 19th and 20th century. *For Ecol Manag* 176(1):173–183
- Cailleret M, Davi H (2011) Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient. *Trees Struct Funct* 25(2):265–276
- Cailleret M, Nourtier M, Amm A, Durand-Gillmann M, Davi H (2014) Drought-induced decline and mortality of silver fir differ among three sites in Southern France. *Ann For Sci* 71(6):643–657
- Camarero JJ, Bigler C, Linares JC, Gil-Pelegrín E (2011) Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *For Ecol Manag* 262(5):759–769
- Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM (2015) To die or not to die: early warnings of tree dieback in response to a severe drought. *J Ecol* 103(1):44–57
- Carcaillet C, Muller SD (2005) Holocene tree-limit and distribution of *Abies alba* in the inner French Alps: anthropogenic or climatic changes? *Boreas* 34(4):468–476
- Caudullo G, Tinner W (2016) *Abies*–Circum-Mediterranean firs in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, De Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) European atlas of forest tree species. Publication Office of the European Union, Luxembourg, pp 50–51
- Čavlović J, Bončina A, Božić M, Goršič E, Simončič T, Teslak K (2015) Depression and growth recovery of silver fir in uneven-aged Dinaric forests in Croatia from 1901 to 2001. *Forestry* cpv026
- Chauchard S, Beilhe F, Denis N, Carcaillet C (2010) An increase in the upper tree-limit of silver fir (*Abies alba* Mill.) in the Alps since the mid-20th century: a land-use change phenomenon. *For Ecol Manag* 259(8):1406–1415
- Cheddadi R, Birks HJB, Tarroso P, Liepelt S, Gömöry D, Dullinger S, Meier ES, Hülber K, Maiorano L, Laborde H (2014) Revisiting tree-migration rates: *Abies alba* (Mill.), a case study. *Veg Hist Archaeobot* 23(2):113–122
- Chéret V, Dagnac J, Fromard F (1987) Le dépérissement du sapin dans les Pyrénées luchonnaises. *Revue forestière française* 39(1):12–24
- Colombaroli D, Marchetto A, Tinner W (2007) Long-term interactions between Mediterranean climate, vegetation and fire regime at Lago di Massaciucoli (Tuscany, Italy). *J Ecol* 95(4):755–770
- Commarmot B (1997) Anbauversuch mit kalabrischen Tannen in verschiedenen Höhenlagen—erste Ergebnisse. *Schweiz Z Forstwiss* 148:353–365
- Conedera M, Barthold F, Torriani D, Pezzatti G (2010) Drought sensitivity of *Castanea sativa*: case study of summer 2003 in the Southern Alps. *Acta Hort* 866:297–302
- Conedera M, Colombaroli D, Tinner W, Krebs P, Whitlock C (2017) Insights about past forest dynamics as a tool for present and future forest management in Switzerland. *For Ecol Manag* 388:100–112
- Cortini Pedrotti C (1967) *L'abetina di Varramista* (Pisa). *Flora fanerogamica e briologica e caratteristiche geobotaniche*. *Webbia* 22(1):39–65
- Davi H, Cailleret M (2017) Assessing drought-driven mortality trees with physiological process-based models. *Agric For Meteorol* 232:279–290
- de Andrés EG, Camarero JJ, Martínez I, Coll L (2014) Uncoupled spatiotemporal patterns of seed dispersal and regeneration in Pyrenean silver fir populations. *For Ecol Manag* 319:18–28
- Desplanque C, Rolland C, Michalet R (1998) Dendroclimatologie comparée du sapin et de l'épicéa dans les zones internes des vallées alpines nord-occidentales (France et Italie). *Ecologie* 29(1–2):351–355
- Dobrowolska D, Bončina A, Klumpp R (2017) Ecology and silviculture of silver fir (*Abies alba* Mill.): a review. *J For Res* 22(6):326–335
- Ducić V, Ivanović R, Mihajlović J, Gnjato R, Trbić G, Čurčić NB (2014) Dendroindication of drought in Rogatica region (Eastern Bosnia). *Arch Biol Sci* 67(1):201–211
- Durand-Gillmann M, Cailleret M, Boivin T, Nageleisen L-M, Davi H (2014) Individual vulnerability factors of silver fir (*Abies alba* Mill.) to parasitism by two contrasting biotic agents: mistletoe (*Viscum album* L. ssp. *abietis*) and bark beetles (*Coleoptera: Curculionidae: Scolytinae*) during a decline process. *Ann For Sci* 71(6):659–673

- Dyderski MK, Paž S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? *Glob Change Biol* 24(3):1150–1163
- Eichenseer F (1997) Entwicklung der Tannenanteile in Ostbayern im 19. und 20. Jahrhundert. *Forst und Holz* 52(17):498–501
- Ellenberg HH (2009) *Vegetation ecology of central Europe*. Cambridge University Press, Cambridge
- Elling W, Dittmar C, Pfaffelmoser K, Rötzer T (2009) Dendroecological assessment of the complex causes of decline and recovery of the growth of silver fir (*Abies alba* Mill.) in Southern Germany. *For Ecol Manag* 257(4):1175–1187
- Elling W, Heber U, Polle A, Beese F (2012) Schädigung von Waldökosystemen: Auswirkungen anthropogener Umweltveränderungen und Schutzmaßnahmen. Spektrum Akademischer Verlag, Heidelberg
- Etzold S, Zweifel R (2018) TreeNet – Daten und Analysen der ersten fünf Messjahre. Mit Beiträgen von: Haeni, M.; Burri, S.; Braun, S.; Walthert, L.; Dawes, M.; Buchmann, N.; Haeler, E.; Köchli, R.; Schaub, M.; Eugster, W. *WSL Berichte* 72. 69 S
- EUFORGEN (2003) Distribution map of silver fir (*Abies alba*). First published in 2003, updated on 25 November 2011
- Fady B (1993) Caractéristiques écologiques et sylvicoles des sapins de Grèce dans leur aire naturelle et en plantation dans le sud de la France. Perspectives pour le reboisement en région méditerranéenne. *Revue forestière française* 45(2):119–133
- Ficko A, Poljanec A, Boncina A (2011) Do changes in spatial distribution, structure and abundance of silver fir (*Abies alba* Mill.) indicate its decline? *For Ecol Manag* 261(4):844–854
- Ficko A, Roessiger J, Bončina A (2016) Can the use of continuous cover forestry alone maintain silver fir (*Abies alba* Mill.) in central European mountain forests? *Forestry* 89(4):412–421
- Frank A, Howe GT, Sperisen C, Brang P, Clair JBS, Schmatz DR, Heiri C (2017a) Risk of genetic maladaptation due to climate change in three major European tree species. *Glob Chang Biol* 23(12):5358–5371
- Frank A, Sperisen C, Howe GT, Brang P, Walthert L, St Clair JB, Heiri C (2017b) Distinct genecological patterns in seedlings of Norway spruce and silver fir from a mountainous landscape. *Ecology* 98(1):211–227
- Gazol A, Camarero JJ, Gutiérrez E, Popa I, Andreu-Hayles L, Motta R, Nola P, Ribas M, Sangüesa-Barreda G, Urbinati C (2015) Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J Biogeogr* 42(6):1150–1162
- George J-P, Schueler S, Karanitsch-Ackerl S, Mayer K, Klumpp RT, Grabner M (2015) Inter- and intra-specific variation in drought sensitivity in *Abies spec.* and its relation to wood density and growth traits. *Agric For Meteorol* 214:430–443
- Gomez, N (2012) Quel avenir pour le sapin et l'Épicéa? Synthèse bibliographique sur l'autécologie et la vulnérabilité comparée du sapin et de l'Épicéa dans le cadre des changements climatiques. Rendez-vous techniques (hors série no. 6):3–8
- Grassi G, Minotta G, Tonon G, Bagnaresi U (2004) Dynamics of Norway spruce and silver fir natural regeneration in a mixed stand under uneven-aged management. *Can J For Res* 34(1):141–149
- Greguss L, Longauer R, Krajnáková J (1994) Progress in the breeding program of specific hybridization of first (a review). In: Eder W (ed) *Ergebnisse des 7. IUFRO-Tannensymposiums der WP S1.01-08 "Ökologie und Waldbau der Tanne"*, pp 144–153
- Gruber F (1994) Morphology of coniferous trees: possible effects of soil acidification on the morphology of Norway spruce and silver fir. In: Godbold D, Hättermann A (eds) *Effects of acid rain on forest processes*. Wiley-Liss, Wilmington, pp 265–324
- Gubler M, Henne PD, Schworer C, Boltshauser-Kaltenrieder P, Lotter AF, Bronnimann S, Tinner W (2018) Microclimatic gradients provide evidence for a glacial refugium for temperate trees in a sheltered hilly landscape of Northern Italy. *J Biogeogr* 45(11):2564–2575
- Guicherd P (1994) Water relations of European silver fir (*Abies alba* Mill.) in 2 natural stands in the French Alps subject to contrasting climatic conditions. *Ann Sci For* 51(6):599–611
- Henne PD, Elkin CM, Reineking B, Bugmann H, Tinner W (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *J Biogeogr* 38(5):933–949
- Henne PD, Elkin C, Colombaroli D, Samartin S, Bugmann H, Heiri O, Tinner W (2013) Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landsc Ecol* 28(5):819–833
- Henne PD, Elkin C, Franke J, Colombaroli D, Calò C, La Mantia T, Pasta S, Conedera M, Dermody O, Tinner W (2015) Reviving extinct Mediterranean forest communities may improve ecosystem potential in a warmer future. *Front Ecol Environ* 13(7):356–362
- Herzog M, Rotach P (1990) Trockenresistenz und Immissionshärte der Weisstanne (*Abies alba* Mill.): Frühstuntersuchungen mit vier Provenienzen. *Schweizerische Zeitschrift für Forstwesen* 141(12):989–1010
- Hoesly RM, Smith SJ, Feng L, Klimont Z, Janssens-Maenhout G, Pitkanen T, Seibert JJ, Vu L, Andres RJ, Bolt RM (2018) Historical (1750–2014) anthropogenic emissions of reactive gases and aerosols from the Community Emissions Data System (CEDS). *Geosci Model Dev* 11(1):369
- Hussendörfer E (1999) Genetic variation of silver fir (*Abies alba* Mill.) populations in Switzerland. *For Genet* 6(2):101–113
- IPCC (2013) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press
- Jakoby O, Wermelinger B, Stadelmann G, Lischke H (2015) Borkenkäfer im Klimawandel Modellierung des künftigen Befallsrisikos durch den Buchdrucker (*Ips typographus*)
- Jones H, Sutherland R (1991) Stomatal control of xylem embolism. *Plant Cell Environ* 14(6):607–612
- Kaltenrieder P, Belis CA, Hofstetter S, Ammann B, Ravazzi C, Tinner W (2009) Environmental and climatic conditions at a potential Glacial refugial site of tree species near the Southern Alpine glaciers New insights from multiproxy sedimentary studies at Lago della Costa (Euganean Hills, Northeastern Italy). *Quat Sci Rev* 28(25–26):2647–2662
- Kandler O, Innes JL (1995) Air pollution and forest decline in Central Europe. *Environ Pollut* 90(2):171–180
- Keller F, Lischke H, Mathis T, Möhl A, Wick L, Ammann B, Kienast F (2002) Effects of climate, fire, and humans on forest dynamics: forest simulations compared to the palaeological record. *Ecol Model* 152(2):109–127
- Kerr G, Stokes V, Peace A, Jinks R (2015) Effects of provenance on the survival, growth and stem form of European silver fir (*Abies alba* Mill.) in Britain. *Eur J For Res* 134(2):349–363
- Klaehn F, Winieski J (1962) Interspecific hybridization in the genus *Abies*. *Silvae Genet* 11(5/6):130–142
- Konnert M, Bergmann F (1995) The geographical distribution of genetic variation of silver fir (*Abies alba*, Pinaceae) in relation to its migration history. *Plant Syst Evol* 196(1):19–30
- Kupferschmid AD, Zimmermann S, Bugmann H (2013) Browsing regime and growth response of naturally regenerated *Abies alba* saplings along light gradients. *For Ecol Manag* 310:393–404
- Lang G (1994) *Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse*. Fischer, Jena

- Larsen JB (1986) Die geographische Variation der Weißtanne (*Abies alba* Mill.) Wachstumsentwicklung und Frostresistenz. Forstwiss Centbl 105(1):396–406
- Latreille A, Davi H, Huard F, Pichot C (2017) Variability of the climate-radial growth relationship among *Abies alba* trees and populations along altitudinal gradients. For Ecol Manag 396:150–159
- Lefèvre F, Boivin T, Bontemps A, Courbet F, Davi H, Durand-Gillmann M, Fady B, Gauzere J, Gidoïn C, Karam M-J, Lalagüe H, Oddou-Muratorio S, Pichot C (2014) Considering evolutionary processes in adaptive forestry. Ann For Sci 71(7):723–739
- Linares JC (2011) Biogeography and evolution of *Abies* (Pinaceae) in the Mediterranean basin: the roles of long-term climatic change and glacial refugia. J Biogeogr 38(4):619–630
- Linares JC, Camarero JJ (2012) Growth patterns and sensitivity to climate predict silver fir decline in the Spanish Pyrenees. Eur J For Res 131(4):1001–1012
- Lombardi F, Cherubini P, Lasserre B, Tognetti R, Marchetti M (2008) Tree rings used to assess time since death of deadwood of different decay classes in beech and silver fir forests in the central Apennines (Molise, Italy). Can J For Res 38:821–833
- Macias M, Andreu L, Bosch O, Camarero JJ, Gutiérrez E (2006) Increasing aridity is enhancing silver fir (*Abies alba* Mill.) water stress in its south-western distribution limit. Clim Change 79(3–4):289–313
- Maiorano L, Cheddadi R, Zimmermann NE, Pellissier L, Petitpierre B, Pottier J, Laborde H, Hurdu BI, Pearman PB, Psomas A, Singarayer JS, Broennimann O, Vittoz P, Dubuis A, Edwards ME, Binnery HA, Guisan A (2013) Building the niche through time: using 13,000 years of data to predict the effects of climate change on three tree species in Europe. Glob Ecol Biogeogr 22(3):302–317
- Maksymov JK (1950) Untersuchungen über den krummzahnigen Weißtannenborckenkäfer *Ips curvidens* Germ. während seiner Massenvermehrung 1947–49 in der Schweiz. ETH Zurich
- Mauri A, de Rigo D, Caudullo G (2016). *Abies alba* in Europe: distribution, habitat, usage and threats. In: European atlas of forest tree species. Publication Office of the European Union, pp 48–49
- Mazza G, Gallucci V, Manetti MC, Urbinati C (2014) Climate–growth relationships of silver fir (*Abies alba* Mill.) in marginal populations of Central Italy. Dendrochronologia 32(3):181–190
- Motta R (1996) Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the western Italian Alps. For Ecol Manag 88:93–98
- Muller SD, Nakagawa T, De Beaulieu J-L, Court-Picon M, Carcaillet C, Miramont C, Roiron P, Bouterin C, Ali AA, Bruneton H (2007) Post-glacial migration of silver fir (*Abies alba* Mill.) in the south-western Alps. J Biogeogr 34(5):876–899
- Nehrbass-Ahles C, Babst F, Klesse S, Nötzli M, Bouriaud O, Neukom R, Dobbertin M, Frank D (2014) The influence of sampling design on tree-ring-based quantification of forest growth. Glob Change Biol 20(9):2867–2885
- Noetzli KP, Müller B, Sieber TN (2003) Impact of population dynamics of white mistletoe (*Viscum album* ssp. *abietis*) on European silver fir (*Abies alba*). Ann For Sci 60(8):773–779
- Nourtier M, Chanzy A, Cailleret M, Yingge X, Huc R, Davi H (2014) Transpiration of silver fir (*Abies alba* Mill.) during and after drought in relation to soil properties in a Mediterranean mountain area. Ann For Sci 71(6):683–695
- Panagos P, Ballabio C, Borrelli P, Meusburger K, Klik A, Rousseva S, Tadić MP, Michaelides S, Hrabalíková M, Olsen P (2015) Rainfall erosivity in Europe. Sci Total Environ 511:801–814
- Peguero-Pina JJ, Camarero JJ, Abadía A, Martín E, González-Cascón R, Morales F, Gil-Pelegrín E (2007) Physiological performance of silver-fir (*Abies alba* Mill.) populations under contrasting climates near the south-western distribution limit of the species. Flora Morphol Distrib Funct Ecol Plants 202(3):226–236
- Pfadenhauer JS, Klötzli FA (2015) Vegetation der Erde: Grundlagen, Ökologie, Verbreitung. Springer, Berlin
- Piotti A, Leonarduzzi C, Postolache D, Bagnoli F, Spanu I, Brousseau L, Urbinati C, Leonardi S, Vendramin GG (2017) Unexpected scenarios from Mediterranean refugial areas: disentangling complex demographic dynamics along the Apennine distribution of silver fir. J Biogeogr 44(7):1547–1558
- Pons A, Quezel P (1985) history of the flora and vegetation and past and present human disturbance in the Mediterranean region. In: Gomez-Campo C (ed) Plant conservation in the Mediterranean area. Geobotany 7. W. Junk, pp 25–43
- Ravn HP, Havill N, Akbulut S, Footitt R, Serin M, Erdem M, Mutun S, Kenis M (2013) *Dreyfusia nordmanniana* in Northern and Central Europe: potential for biological control and comments on its taxonomy. J Appl Entomol 137(6):401–417
- Robakowski P, Montpied P, Dreyer E (2002) Temperature response of photosynthesis of silver fir (*Abies alba* Mill.) seedlings. Ann For Sci 59(2):163–170
- Rohner B, Thürig E (2015) Entwicklung klimasensitiver Wachstumsfunktionen für das Szenariomodell «Massimo». Schweizerische Zeitschrift für Forstwesen 166(6):389–398
- Rohner B, Waldner P, Lischke H, Ferretti M, Thürig E (2018) Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects. Eur J For Res 137(1):29–44
- Rolland C, Michalet R, Desplanque C, Petetin A, Aime S (1999) Ecological requirements of *Abies alba* in the French Alps derived from dendro-ecological analysis. J Veg Sci 10(3):297–306
- Rothe A, Dittmar C, Zang C (2011) Tanne–vom Sorgenkind zum Hoffnungsträger. LWF Wissen 66:59–63
- Ruosch M, Spahni R, Joos F, Henne PD, Knaap WO, Tinner W (2016) Past and future evolution of *Abies alba* forests in Europe—comparison of a dynamic vegetation model with palaeo data and observations. Glob Change Biol 22(2):727–740
- Samartin S, Heiri O, Kaltenrieder P, Kühl N, Tinner W (2016) Reconstruction of full glacial environments and summer temperatures from Lago della Costa, a refugial site in Northern Italy. Quat Sci Rev 143:107–119
- Savill P, Wilson SM, Mason B, Jinks R (2016) Silver firs (*Abies* spp) of Europe and the Near East: species, silviculture, and utilisation potential. Q J For 110:16–27
- Schmid S, Genevest R, Gobet E, Suchan T, Sperisen C, Tinner W, Alvarez N (2017) HyRAD-X, a versatile method combining exome capture and RAD sequencing to extract genomic information from ancient DNA. Methods Ecol Evol 8(10):1374–1388
- Schnyder J, Ehrbar R, Reimoser F, Robin K (2016) Huftierbestände und Verbissintensitäten nach der Luchswiederansiedlung im Kanton St. Gallen. Schweizerische Zeitschrift für Forstwesen 167(1):13–20
- Schütt P, Cowling EB (1985) Waldsterben, a general decline of forests in central Europe: symptoms, development and possible causes. Plant Dis 69(7):548–558
- Semerikova SA, Semerikov VL (2014) Molecular phylogenetic analysis of the genus *Abies* (Pinaceae) based on the nucleotide sequence of chloroplast DNA. Russ J Genet 50(1):7–19
- Sindelar J, Beran F (2008) Comparison of some exotic species of *Abies* genus with chosen silver fir provenances on the plots of town Pisek. Commun Inst For Bohem 24:99–114
- Stokes A, Ghani MA, Salin F, Danjon F, Jeannin H, Berthier S, Kokutse AD, Frochot H (2007) Root morphology and strain distribution during tree failure on mountain slopes. In: Stokes A, Spanos I, Norris JE, Cammeraat E (eds) Eco-and ground bio-engineering: the use of vegetation to improve slope stability: proceedings of the first international conference on eco-engineering, 13–17 September 2004. Springer Netherlands, pp 165–173

- Stott P (2016) How climate change affects extreme weather events. *Science* 352(6293):1517–1518
- Terhürne-Berson R, Litt T, Cheddadi R (2004) The spread of *Abies* throughout Europe since the last glacial period: combined macrofossil and pollen data. *Veg Hist Archaeobot* 13(4):257–268
- Tinner W, Lotter AF (2006) Holocene expansions of *Fagus sylvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? *Quat Sci Rev* 25(5):526–549
- Tinner W, Hubschmid PH, Wehrli M, Amman B, Conedera M (1999) Long-term forest fire ecology and dynamics in southern Switzerland. *J Ecol* 87(2):273–289
- Tinner W, Conedera M, Gobet E, Hubschmid P, Wehrli M, Ammann B (2000) A palaeoecological attempt to classify fire sensitivity of trees in the southern Alps. *The Holocene* 10(5):565–574
- Tinner W, Colombaroli D, Heiri O, Henne PD, Steinacher M, Untenecker J, Vescovi E, Allen JR, Carraro G, Conedera M (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecol Monogr* 83(4):419–439
- Tinner W, Conedera M, Bugmann H, Colombaroli D, Gobet E, Vescovi E, Heiri O, Joos F, Luterbacher J, La Mantia T (2016) Europäische Wälder unter wärmeren Klimabedingungen: neue Erkenntnisse aus Paläoökologie und dynamischer Vegetationsmodellierung. *AFZ-Der Wald* 71(18):45–49
- Uhl E, Ammer C, Spellmann H, Schölch M, Pretzsch H (2013) Wachstumstrend und Stressresilienz von Tanne und Fichte im Vergleich. *Allg Forstund Jagdzeitung* 184(11–12):278–292
- Valsecchi V, Carraro G, Conedera M, Tinner W (2010) Late-Holocene vegetation and land-use dynamics in the Southern Alps (Switzerland) as a basis for nature protection and forest management. *The Holocene* 20(4):483–495
- Van Breemen N, Burrough P, Velthorst Ev, Van Dobben H, de Wit T, Ridder Td, Reijnders H (1982) Soil acidification from atmospheric ammonium sulphate in forest canopy throughfall. *Nature* 299(5883):548–550
- van der Maaten-Theunissen M, Kahle H-P, van der Maaten E (2012) Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. *Ann For Sci* 70(2):185–193
- Vitali V, Buntgen U, Bauhus J (2017) Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in southwestern Germany. *Glob Change Biol* 23(12):5108–5119
- Vitali V, Buntgen U, Bauhus J (2018) Seasonality matters—the effects of past and projected seasonal climate change on the growth of native and exotic conifer species in Central Europe. *Dendrochronologia* 48:1–9
- Vitasse Y, Delzon S, Bresson CC, Michalet R, Kremer A (2009) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can J For Res* 39(7):1259–1269
- Vitasse Y, Hoch G, Randin CF, Lenz A, Kollas C, Körner C (2012) Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. *J Biogeogr* 39(8):1439–1449
- Vitasse Y, Rebetez M, Augustin S, Brang P (2018a) Quel avenir pour le sapin blanc en Suisse sous les effets des changements climatiques? *Schweizerische Zeitschrift für Forstwesen* 169(3):131–142
- Vitasse Y, Schneider L, Rixen C, Christen D, Rebetez M (2018b) Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. *Agric For Meteorol* 248:60–69
- Vrska T, Adam D, Hort L, Kolar T, Janik D (2009) European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians: a developmental cycle or a linear trend induced by man? *For Ecol Manag* 258:347–356
- Watts WA (1985) A long pollen record from Laghi di Monticchio, southern Italy: a preliminary account. *J Geol Soc* 142(3):491–499
- Wick L, Möhl A (2006) The mid-Holocene extinction of silver fir (*Abies alba*) in the Southern Alps: a consequence of forest fires? *Palaeobotanical records and forest simulations. Veg Hist Archaeobot* 15(4):435
- Xiang X, Cao M, Zhou Z (2007) Fossil history and modern distribution of the genus *Abies* (Pinaceae). *Front For China* 2(4):355–365
- Xiang Q-P, Wei R, Shao Y-Z, Yang Z-Y, Wang X-Q, Zhang X-C (2015) Phylogenetic relationships, possible ancient hybridization, and biogeographic history of *Abies* (Pinaceae) based on data from nuclear, plastid, and mitochondrial genomes. *Mol Phylogenet Evol* 82(Part A):1–14
- Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. *Glob Change Biol* 20(12):3767–3779
- Zimmermann NE, Normand S, Psomas A (2014) PorTree Final Report: A project funded by the BAFU-WSL program on “Forests and Climate Change” in Switzerland. ETH Zurich. https://www.wsl.ch/lud/portree/_docs/FinalReport_PorTree_vers20160106.pdf
- Zimmermann NE, Schmatz D, Gallien L, Körner C, Huber B, Frehner M, Küchler M, Psomas A (2016) Répartition des espèces forestières et adéquation des stations. In: Pluess AR, Augustin S, Brang P (eds) *Forêts et changements climatiques—Éléments pour des stratégies d’adaptation*. Office fédéral de l’environnement OFEV, Berne; Institut fédéral de recherche WSL, Birmensdorf. Haupt, pp 205–228
- Zingg A, Bürgi A (2008) Trockenperioden seit 1900 und Waldwachstum: eine Analyse langfristiger Datenreihen! Drought periods since 1900 and growth of forest stands: an analysis of long-term data series. *Schweizerische Zeitschrift für Forstwesen* 159(10):352–361

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.