Forest response to climate warming and drought in Europe

Dissertation

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“*The creation of a thousand forests is in one acorn*”.

- Ralph Waldo Emerson -

“*[…] education is liberty*”

- Wilhelm von Humboldt

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1. Summary

Global surface temperature is rising at an alarming rate. The combined forces of global warming and drought are threatening ecosystems around the world. In recent years, the Northern Hemisphere has been hit by a combination of drought and heatwave - with devastating environmental and economic consequences. These disasters, which were once considered purely rare events, have increased significantly in frequency, intensity, and duration in recent years. Forests are of great ecological and economic importance for the proper functioning of natural and human systems. Hence, forest observed susceptibility to increasing warming and droughts is of great concern. Given that the future of forests is uncertain, there is an urgent need to assess forest response to these pressing climate change issues.

This dissertation aims to expand current understanding and knowledge of forest response to climate warming and drought. To achieve this aim, this dissertation focuses on two major objectives (1) to investigate species dynamics under climate change and (2) to assess the impacts of drought on saplings and mature tree species in Europe. Through empirical research and the application of various methodological approaches, I seek to provide international leaders, forest managers, and practitioners with practical information to support their decision-making, policies, and actions.

High temperatures and altered precipitation patterns are expected to lead to shifts in climate zones and thus large-scale shifts in vegetation. As a result, species ranges are expected to shift to higher elevations or higher latitudes as their climatic optimum shifts. Yet trees that cannot cope with these changes risk being affected by climate change-induced stress. Despite extensive research, it is still unclear whether tree species can cope with global warming. An ideal model system to answer these questions is represented by mountain treelines. Mountain treelines are considered sensors of climate change, meaning that they are expected to respond quickly to climatic warming. Therefore, in **Manuscripts 1** and **2**, I contribute to the current understanding of how tree species cope with climate warming by researching tree populations from remote mountain regions.

In **Manuscript 1**, I investigated treeline dynamics based on in-situ measurements of Swiss stone pine (*Pinus cembra* L.) trees from two different protected areas in the Carpathian Mountains. Using spatial statistics, similarities and differences in the spatial structure were identified between the two *Pinus cembra* populations. In **Manuscript 2**, I assessed treeline dynamics in the Samaria National Park, on the semi-arid Mediterranean island of Crete. Using historical and recent high-resolution aerial imagery, I assessed the spatio-temporal tree dynamics over the past 70 years. In contrast to the Carpathians, where results indicated a shift of trees to higher elevations in the area protected since 1935, no shift of trees was observed in the Crete Mountains. Accordingly, the absence of climate-driven migration should raise concerns about the threats associated with future warming, drought stress, and wildfire. Therefore, conservation managers should consider options and needs to support adaptive management.

In addition to vegetation shifts, climate warming and drought periods are directly affecting the forest ecosystems of Europe. The current forests were established in the much colder climate of the 18th and 19th centuries, while the current seedlings and saplings are established in warmer conditions. Hence, germination and establishment took place under different climatic conditions. Evidence suggests that the increase in frequency and intensity of droughts will lead to abrupt changes in species composition and forest functioning. To assess species-specific responses to drought, European temperate forests are regarded as an optimal ecosystem due to their high susceptibility to drought compared to other temperate forest ecosystems. Thus, in **Manuscripts 3** and **4**, I presented a comprehensive quantification of the impact of the 2018 and 2019 summer drought on sapling species in temperate forests. The results suggested that drought damaged trees regardless of size, but saplings recovered faster than mature trees. Moreover, slow sapling recovery led to their mortality. Mortality increased from *Quercus* spp. to minor broadleaved species (e.g., pedunculate oak (*Quercus robur*) (0%), sessile oak (*Quercus petraea*) (4%), sycamore (*Acer pseudoplatanus*) (5%), European beech (*Fagus sylvatica*) (6%), silver birch (*Betula pendula*) (6%), European hornbeam (*Carpinus betulus*) (8%), field maple (*Acer campestre*) (12%), ash (*Fraxinus excelsior*) (12%), elder (*Sambucus nigra*) (16%), and rowan (*Sorbus aucuparia*) (17%)). Species-specific responses to drought are key to understanding which species are more capable of coping with climate warming and anticipated drought events. These results are essential for developing and implementing adaptive forest management strategies to mitigate the impacts of climate change.

This dissertation provides one of the first assessments of tree dynamics in the remote protected areas of the Carpathians and Crete Mountains, along with a comprehensive quantification of species-specific response to drought in Central Europe. Hence, these four studies provide conservationists, forest managers, stakeholders, and private property owners with practical information on tree dynamics and species-species response to climate warming and drought.

2. Zusammenfassung

Die globale Oberflächentemperatur der Erde steigt mit einer alarmierenden Geschwindigkeit an und globale Erwärmung und Dürre in Kombination bedrohen Ökosysteme weltweit. In den letzten Jahren wurde die nördliche Hemisphäre von Dürre und Hitzewelle heimgesucht - mit verheerenden ökologischen und wirtschaftlichen Folgen. Diese Katastrophen, die einst als seltene Ereignisse angesehen wurden, haben in den letzten Jahren in Häufigkeit, Intensität und Dauer deutlich zugenommen. Wälder sind von großer ökologischer und wirtschaftlicher Bedeutung für das reibungslose Funktionieren natürlicher und anthropogener Systeme. Daher ist die beobachtete Anfälligkeit der Wälder für die zunehmende Erwärmung und Dürren sehr besorgniserregend. Es besteht ein dringender Bedarf, die Beeinflussung der Wälder durch den Klimawandel zu untersuchen.

Diese Doktorarbeit zielt darauf ab, das aktuelle Verständnis und Wissen über die Veränderung von Wäldern als Reaktion auf Klimaerwärmung und Trockenheit zu erweitern. Um dieses Ziel zu erreichen, fokussiert sich diese Doktorarbeit auf zwei Hauptpunkte: (1) die Untersuchung von Artendynamiken unter dem Klimawandel und (2) die Bewertung der Auswirkungen von Trockenheit auf Jungbäume und ausgewachsene Bäume verschiedener Baumarten in Europa. Durch empirische Forschung und die Anwendung verschiedener methodischer Ansätze trage ich dazu bei, internationale Führungskräfte, Forstmanager und -praktiker mit konkreten Informationen zu versorgen, um ihre Entscheidungsfindung, Politik und Schutzmaßnahmen zu unterstützen.

Hohe Temperaturen und veränderte Niederschlagsmuster werden voraussichtlich zu Veränderung der Klimazonen und damit zu großräumigen Verschiebungen der Vegetationszusammensetzung führen. Daher ist zu erwarten, dass sich die Verbreitungsgebiete von Arten in höhere Lagen oder höhere Breitengrade verlagern, wenn sich ihr klimatisches Optimum räumlich verschiebt. Nicht alle Baumarten können jedoch mit diesen Veränderungen Schritt halten, und werden unter Adaptionsdruck gesetzt, was Anpassungsstress verursacht. Trotz intensiver Forschung ist immer noch unklar, wie Baumarten auf die globale Erwärmung reagieren. Baumgrenzen stellen ein ideales Modellsystem zur Beantwortung dieser Fragen dar. Baumgrenzen gelten als Sensoren für den Klimawandel, weil zu erwarten ist, dass sie relativ schnell auf ein sich erwärmendes Klima reagieren. Aus diesem Grund möchte ich in den **Manuskripten 1** und **2** einen Beitrag zum aktuellen Verständnis leisten, wie Baumarten auf die Klimaerwärmung reagieren, indem ich Untersuchungen an Baumpopulationen von entlegenen Gebirgsregionen in Europa durchführe.

In **Manuskript 1** untersuchte ich die Baumgrenzen-Dynamik anhand von in-situ-Messungen an Zirbelkiefer (*Pinus cembra* L.) in zwei verschiedenen Schutzgebieten in den Karpaten. Mit Hilfe von räumlicher Statistik wurden Ähnlichkeiten und Unterschiede in der räumlichen Struktur zwischen den beiden *Pinus cembra*-Populationen ermittelt. In **Manuskript 2** beurteilte ich die Baumgrenzen-Dynamik im Samaria-Nationalpark auf der semiariden Mittelmeerinsel von Kreta. Durch die Verwendung historischer und aktueller hochauflösender Luftbilder konnte ich die räumlich-zeitliche Baumdynamik der letzten 70 Jahre analysieren. Im Gegensatz zu den Karpaten, wo die Ergebnisse auf eine Verschiebung von Bäumen in höhere Lagen in dem seit 1935 geschützten Gebiet hindeuteten, wurde in den Bergen auf Kreta keine

Verschiebung der Baumgrenze beobachtet. Dementsprechend gibt das Ausbleiben der klimabedingten Migration Anlass zur Sorge über die Bedrohung durch zukünftige Erwärmung, Trockenstress und Waldbrände. Daher sollten Naturschutzmanager Optionen und Strategien zur Unterstützung des adaptiven Managements in Erwägung ziehen.

Neben Vegetationsverschiebungen wirken sich Klimaerwärmung und Dürreereignisse direkt auf die Waldökosysteme in Europa aus. Die derzeitigen Forsten wurden im viel kälteren Klima des 18. und 19. Jahrhunderts angelegt, während heutige Sämlinge und Setzlinge unter wärmeren Bedingungen etabliert werden. Daher fanden Keimung und Etablierung unter unterschiedlichen klimatischen Bedingungen statt. Es ist nachgewiesen, dass eine Zunahme der Häufigkeit und Intensität von Dürren zu abrupten Veränderungen der Artenzusammensetzung und der Waldfunktionen führen kann. Zur Beurteilung der artenspezifischen Reaktionen auf Trockenheit werden europäische Wälder der gemäßigten Zonen als optimales Ökosystem betrachtet, da sie im Vergleich zu anderen Ökosystemen der gemäßigten Zonen sehr empfindlich auf Trockenstress reagieren. Daher habe ich in den **Manuskripten 3** und **4** eine umfassende Quantifizierung der Auswirkungen der Sommerdürren im Jahr 2018 und 2019 auf Jungbäume in gemäßigten Wäldern vorgenommen. Die Ergebnisse zeigen, dass Dürre den Bäumen unabhängig von ihrer Größe schadet, sich Jungbäume aber schneller erholten als ältere Bäume. Gleichzeitig führte jedoch die langsame Regeneration der Jungbäume auch teilweise zu deren Absterben. Die Sterblichkeitsrate von *Quercus* spp. war am niedrigsten während kleinere Laubbaumarten die höchsten Raten aufwiesen (z.B., Stieleiche (*Quercus robur*) (0%), Traubeneiche (*Quercus petraea*) (4%), Berg-Ahorn (*Acer pseudoplatanus*) (5%), Rotbuche (*Fagus sylvatica*) (6%), Hänge-Birke (*Betula pendula*) (6%), Hainbuche (*Carpinus betulus*) (8%), Feldahorn (*Acer campestre*) (12%), Gemeine Esche (*Fraxinus excelsior*) (12%), Schwarzer Holunder (*Sambucus nigra*) (16%), and Vogelbeere (*Sorbus aucuparia*) (17%)). Artspezifische Reaktionen auf Trockenheit sind der Schlüssel zum Verständnis, welche Arten besser in der Lage sind, mit der Klimaerwärmung und den zu erwartenden Dürreereignissen umzugehen. Diese Ergebnisse sind wichtig für die Entwicklung und Umsetzung von adaptiven Waldbewirtschaftungsstrategien, um die Auswirkungen des Klimawandels zu mildern.

Diese Dissertation enthält eine der ersten Abschätzungen der Baumdynamik in den abgelegenen Schutzgebieten der Karpaten und der Gebirge auf Kreta, zusammen mit einer umfassenden Quantifizierung der artspezifischen Reaktion auf Trockenheit in Mitteleuropa. Daher bieten diese vier Studien Naturschützern, Waldmanagern, Interessensvertretern und privaten Grundbesitzern angewandte Informationen zu Baumdynamik und Reaktion von Arten auf Klimaerwärmung und Trockenheit.

3. Introduction

3.1. Motivation for the dissertation

> "*To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plants and animal life that can be put on a map*."
>
> Robert H. MacArthur (1972, p. 1)

The main objectives of science are to tackle unknown questions, synthesize and pursue new human knowledge based on true explanatory theories (Popper & Bartley 1985). Biogeography is a scientific discipline located at the interface between biology and geography (Beierkuhnlein 2007). It has a broad and interdisciplinary focus, from botany to geosciences, which promotes the integration of vast knowledge bases. Furthermore, biogeography and ecology develop a holistic background and address theoretical and methodological concepts of natural science. Among the research topics covered by these disciplines are interactions between organisms and the environment, as well as processes and mechanisms. These processes are then reflected in the spatio-temporal distribution of species across ecosystems and biomes (Beierkuhnlein 2007; Pianka 2011).

Climate change is a current global issue that has a significant impact on the spatial and temporal dynamics of tree species. High temperature and changes in precipitation patterns are expected to lead to shifts in climate zones and, consequently, to large-scale shifts in vegetation and ecosystems (Adams et al. 2009; IPCC 2019). Hence, a poleward and elevational shift in tree species has been projected (IPCC 2019). In addition, recent droughts combined with fires have affected the world's forests, causing major ecological and economic damages (Vogel et al. 2019; Kornhuber et al. 2019; Ionita & Nagavciuc 2021). As a result, forest ecosystems are severely threatened by these accelerated changes (IPCC 2018). Therefore, it is questionable how forests will respond to these changes, whether they will withstand them, or dry out. Equally important is how forests recover over time and space after extreme weather events like drought.

Europe's ecosystems are particularly threatened by global warming and drought compared to other regions at the same latitude. Climate variability and climate change in Europe are shaped by the influence of the Gulf Stream and the interaction between geographical and atmospheric aspects (the North Atlantic Oscillation (NAO) and jet stream fluctuations) (see Section 3.5 and Glossary). All these interactions are becoming increasingly uncertain as they are affected by long-term global warming trends (Peters et al. 2020). Climate warming is more pronounced at high latitudes in the Northern Hemisphere (Hoegh-Guldberg et al. 2018). Hence, European temperate forests are at greater risk than those in North America and Asia as they are located at higher latitudes. In view of all these changes, the response of forests to global warming and drought is a topical issue of great ecological and economic importance.

My personal goal is to find answers to ecological questions, such as: Are trees able to keep up with climate change? Which forests are stressed and which not? How dry is too dry to surpass the tipping point? Which species are thriving, and which are dying? Is recovery time species-specific, if so, which species recover faster? What will forests look like in the future? I address most of these research questions in this dissertation, while some may go beyond it, and offer a broader perspective on the research area.

To find an answer to some of these questions, I choose European high and low elevation forests as study regions. Mountain treelines from protected areas are ideal model systems to test how trees can cope with climate change. As treelines are sensors for climate change, they are expected to have an accelerated response to them. To test species-specific responses to drought, temperate forests were considered as an optimal ecosystem because, among European forest ecosystems, they exhibit a high vulnerability to drought (Buras et al. 2020; Schuldt et al. 2020).

In this dissertation, I emphasized the understanding of forest response to climate change by addressing research questions from two different topics, treeline research (**Manuscript 1** and **2**) and forest drought response (**Manuscript 3** and **4**). An improved understanding of forest response to climate change is a prerequisite for developing mitigation strategies and promoting advances in environmental science. Furthermore, a deeper understanding of these responses is essential for the conservation and sustainable management of future forests.

3.2. Structure of the dissertation

I start this dissertation with an introduction to the importance of forest ecosystems in sustaining ecological processes and human well-being, as well as the threats forests face. I then address general forest characteristics, such as forest cover, forest type, tree species, and their protection status in Europe. Following this, I discuss global climate change, including current and future projections and their implications for forest ecosystems. Current climate trends and their importance for ecosystem functioning need to be understood before devoting an entire chapter to forest health and the effects of extreme weather events on tree species.

The main part of the introduction begins with the effects of climate change on species dynamics (Section 3.6), starting with future projections on tree species dynamics and followed by a review on observed forest shifts that occur in Europe and their implications. In Section 3.7, I address the impact of drought on forest health. It includes a short review that highlights the current knowledge about forest response to drought, followed by drought effects on saplings and mature trees. Thereupon, I shed light on the global perspectives of forest recovery and tree mortality.

In the synopsis, I present emerging research questions in forest ecology in the face of climate change. I explain the contribution of my manuscripts to answering the previously raised questions. The synopsis concludes with considerations on future perspectives and research challenges for forest ecology.

The dissertation closes with a characterization of my contribution to each manuscript followed by the presentation of the manuscripts that comprise this dissertation. In the appendix, the manuscripts that were published during the time I was working on my dissertation are listed as well as talks and posters that I presented at national and international conferences during this period which are directly or indirectly related to this dissertation. Furthermore, the teaching and scientific reviewing activities for peer-reviewed journals are documented. To prevent confusion, the English and Latin names are given for all species referred to in the introduction when they are first mentioned, but only the Latin name is used later. For convenience, I have explained most of the concepts and terms used directly in the text, but I have included some that require a more detailed explanation in the Glossary.

Glossary: Definitions and explanations of terms and concepts used in this dissertation.

Aridity: The term aridity refers to a permanent water deficit in an area and is considered a climate type characterized by low amount of precipitation.

Drought: A temporary negative deviation from the mean precipitation combined with warming and severe heatwaves defines a drought. Summer drought is regarded as a drought during the summer months. Drought can occur across any type of climate.

Intrinsic water use efficiency (iWUE): iWUE shows the relationship between plant productivity and water consumption. It is a measure of the quantity of biomass produced per unit of water consumed by a plant (Hatfield & Dold 2019). This indicates the capacity of a tree to adapt to climate.

Jet stream**:** Strong currents that move from west to east and are driven mainly by temperature differences between low (warm) and high latitudes (cold) as well as the rotation of the Earth characterise the jet stream (Stendel et al. 2021). The currents do not flow in a straight line but meander like a river, and these meanders are called Rossby waves.

Potential natural vegetation: It is defined as the expected vegetation cover given by the climate in the absence of human activities (Chiarucci et al. 2010).

Representative Concentration Pathways (RCP): RCP are trajectories for greenhouse gas concentration in the atmosphere. The concept was used for the Fifth Assessment Report (AR5) of the International Panel on Climate Change (IPCC) in 2014. There are several RCP scenarios ranging from low to high, e.g., RCP 2.6 means a lower emission level associated with a low increase in global mean surface temperature (e.g., 1.5 ºC), while RCP 8.5 represents the scenario with the highest emissions and is consequently associated with a high temperature increase (IPCC 2019).

Resistance: Forest resistance is the ecosystem's capacity to maintain its functioning during a disturbance (Hodgson et al. 2015).

Recovery: Recovery is characterized by the capacity of the trees or ecosystem to regain their function after the disturbance impact. Recovery can be differentiated into recovery rate and recovery time. Recovery rate is the rate at which an ecosystem recovers its function, which can be relative to the pre-drought conditions or the disturbance impact. While recovery time is the duration from the end of the disturbance to the tree or ecosystem being fully recovered (Hodgson et al. 2015; Ingrisch & Bahn 2018). In the face of accelerated climate change, recovery should be regarded as the ability of an ecosystem to adapt to the new conditions, as pre-drought conditions are no longer present.

Resilience: Both components, resistance, and recovery, together represent resilience.

The North Atlantic Gulf Stream: It is also known as the Atlantic Meridional Overturning Circulation (AMOC), is part of the thermohaline circulation. The Gulf Stream originates in the Gulf of Mexico and flows northwards along the East coast of North America towards Europe, where it then splits into separate currents. Its movement is triggered by the differences in density of the water, i.e., warm and salty water (low density) flows towards the north where cools down (high density), sinks to deeper ocean layers and flows south again. Climate change is increasing precipitation in Northern Europe, and the Greenland ice sheet is melting, bringing more low-salinity, low-density freshwater into the ocean, slowing its sinking and thus weakening the flow of the Gulf Stream (Caesar et al. 2021). It influences the climate by moderating temperatures in Eastern North America and Western Europe; without it, more extreme climate events could occur.

The North Atlantic Oscillation (NAO): NAO it is an index based on the difference in atmospheric pressure at sea level between two points over time, the Subtropical (Azores) High and the Subpolar (Islandic) Low. The NAO index can be used to describe changes in the jet stream (Drouard et al. 2019). NAO has a positive (NAO+) and a negative (NAO-) phase that controls the western winds direction and strength. A (NAO+) means that the Subtropical High and Subpolar Low are stronger than the average, i.e., the westerly winds are stronger, bringing more storms and precipitation to Northern Europe, warmer than average temperatures in Central Europe and less precipitation in Southern Europe. The (NAO-) phase reflects the opposite pattern (Dahlman 2009).

Treeline ecotone**:** The treeline ecotone is an ecological boundary between the montane and alpine elevation zones. The term treeline ecotone refers to the transition from a compact forest or timberline to the few trees that are at least 2 m high, followed by open habitat. The treeline can have a diffuse form (gradual transition from close forest to single individuals), island form (groups or stripes of trees growing above the continuous forest line), abrupt form (continuous forest bordered by alpine vegetation), and krummholz form (dispersed patches of deformed or stunted trees above the forest line) (Körner 2012; Bader et al. 2021).

3.3. Forest ecosystems

> "*Humanity is cutting down its forests, apparently oblivious to the fact that we may not be able to live without them*".
>
> Isaac Asimov (1988, p. 101)

3.3.1. The importance of forest

The importance of forest ecosystems should not be underestimated. Forests cover about 31% of the global land area (FAO & UNEP 2020). They are one of the most important terrestrial ecosystems in the world, but also among the most threatened by climate change and anthropogenic activities. There are different views on whether global forest area has decreased (Keenan et al. 2015) or increased (Song et al. 2018) over time. However, forest loss has occurred primarily in the tropics, while forest in temperate regions has increased. Hence, I have highlighted here some of the most important aspects illustrating the importance of forests from the literature reviewed:

- **Biodiversity**. Forest is home to 80% of the earth's biodiversity, offering unique habitat to 80% of the amphibians, 75% of the birds, and 68% of mammal species (FAO & UNEP 2020). Large old trees are hotspots for biodiversity, facilitate connectivity, habitat recovery, influence nutrient cycles and hydrological regimes (Lindenmayer & Laurance 2017).
- **Economic value**. Forests provide several ecosystem services, such as timber, water, medicinal plants, and food, e.g., nuts, berries, and mushrooms. Since ancient times, forests have provided shelter and a source of food for many people around the world. Their timber has been used since ancestral times and is still an important resource nowadays (FAO & UNEP 2020).
- **Global carbon sequestration**. Forests absorb about 25% of the CO2 emitted by anthropogenic activities each year (Pan et al. 2011) and are the most important source of oxygen. Forests contribute significantly to terrestrial carbon sinks, and their sustainable management can help mitigate climate change (Canadell & Raupach 2008).
- **Cultural and recreational value, e.g., spiritual meaning, and historical value.** Societies have developed strong cultural and spiritual connections with forests and their large old trees, therefore they play an important role in historical art, local traditions, and modern movies (Lindenmayer & Laurance 2017; Schweiger & Svenning 2020). Large old trees are one of the most iconic biota on earth, the so-called Earth's charismatic megaflora. They are key ecosystem components with ecological, cultural, and economic value (Lindenmayer & Laurance 2017).
- **Climatic and geomorphological regulation.** Forests increase resilience to climate change, mitigate droughts, floods, soil erosion, and temperature impacts (FAO & UNEP 2020). Rain patterns are partially generated by the amount of forest cover (Meier et al. 2021). Tree diversity can mitigate the effects of climate change (Grossiord 2018; Messier et al. 2021).

3.3.2. Threats to forests

It is important to note that the aspects highlighted above are interrelated and the deterioration of one aspect triggers a chain reaction. Despite their importance and undeniable benefits for humans, forests face many threats. Out of > 60000 tree species worldwide, about 20000 are threatened and 1400 are critically endangered (FAO & UNEP 2020). Anthropocentric factors such as intensive deforestation, forest degradation, agricultural expansion, and fragmentation are already causing loss of forest cover and biodiversity. Only 40% of the global forest has high ecosystem integrity, meaning low anthropogenic modification of its structure, function, and composition (Grantham et al. 2020). These areas are mainly found in the Amazon region, Canada, and Russia. Europe has a predominantly low integrity index, only some parts from the South-East and North of Europe have areas with medium and high ecosystem integrity (Grantham et al. 2020). Intact forests support greater biodiversity, carbon sequestration, and other environmental values than degraded forests (Watson et al. 2018).

In Europe, climate change is expected to cause severe economic losses by 2100 (up to 14 to 50% of the value of forest land) (Hanewinkel et al. 2013). Important cold-adapted commercial tree species of Central Europe, such as Norway spruce (*Picea abies* Karst.) will lose large portions of their range in favour of drought-adapted species (Hanewinkel et al. 2013; Netherer et al. 2019). This will very likely result in significant ecological and economic consequences, such as changes in species composition, forest functioning and ecosystem services provided. Large old trees are vulnerable and particularly threatened by climate-related drivers, such as drought, fires, insect attack, and windstorms (McDowell & Allen 2015; Bennett et al. 2015; Lindenmayer & Laurance 2017). Given their multiple values, the mortality of large trees can lead to a cascade of events, from loss of biodiversity to ecological processes and ecosystem goods.

Eastern Europe's forests are particularly threatened by illegal logging, both in protected and unprotected areas (Kuemmerle et al. 2009; Leberger et al. 2019). Most of the remaining primary forests are in Finland and Eastern Europe (Romania, Bulgaria, and Ukraine), but they are being lost at an alarming rate (Sabatini et al. 2018). Deforestation-induced warming is a concept disputed (Pitman et al. 2009; Mahmood et al. 2014). However, Lejeune et al. (2018) showed that deforestation leads to significant local warming by increasing the intensity of hot days. Subsequently, intensive exploitation leads to the loss of tree species and thus to the loss of biodiversity and the deterioration of climatic regulation capacity. These threats are not singular, consequently, forests face an uncertain future (see Sections 3.5.1 and 3.6 for additional examples and discussions of climate change impact on forests). One key to preserving and enhancing forest functions is proper forest management through the designation and maintenance of protected areas (Hoffmann 2021).

International organizations are working to reduce the loss of forest areas and preserve their biodiversity. The United Nations Strategic Plan for Forest (UNSPF) aims to reduce the loss of forest cover and to increase the forest area by 3% worldwide by 2030 (UNSPF 2019). Similarly, the EU Biodiversity Strategy for 2030, which is part of the European Green Deal and the EU Recovery Plan, aims to stop the loss of biodiversity, support its recovery, and increase in the protected areas to at least 30% of the country's land area by 2030. This includes the restoration of forest biodiversity through sustainable forest management (European Comission 2021). Moreover, the European State Forestry Association (EUSTAFOR) expressed its agreement (e.g. afforestation) and concerns (e.g. increase in protected areas) with the objectives of the EU Biodiversity Strategy for 2030 (EUSTAFOR 2020). This means that further debates will follow until concrete action can be taken. Further strategies targeted towards forestry are still expected to be published, such as the EU Forest Strategy post-2020. Yet, the present and future effects of climate change put one of the most important resources of humans at risk. This increases the need for a deeper understanding of forest dynamics to provide international leaders and forest practitioners with reliable information to guide their decision-making, policies, and actions.

3.4. European forest cover and tree species in Europe

Forests cover about 38% of the European Union land surface (European Commission 2019). Only in the boreal (Finland, Sweden, Estonia, and Latvia) and mountainous countries (Slovenia and Austria) is forest cover above average (> 40%). Whereas most of the countries have a forest cover of around 30% (Fig. 3.4.1). Out of this, about 53% is in public ownership and 47% in private ownership (Forest Europe 2020). Forest cover has shown a great dynamic (e.g., forest loss and gain) over the years that was influenced by many natural and human-induced factors. The main causes of forest loss are timber harvesting, including illegal logging, insect outbreak, forest conversion, wildfires, and windstorms (Kuemmerle et al. 2009; Potapov et al. 2015; Munteanu et al. 2015; Senf & Seidl 2020; Hlásny et al. 2021). Nevertheless forest expansion i.e. forest gain across Europe also increased as a result of land abandonment (Munteanu et al. 2014) and as natural disturbances were reduced by fire suppression and land use, e.g. in the Alps (Bebi et al. 2017) and North-East Europe (Hansen et al. 2013).

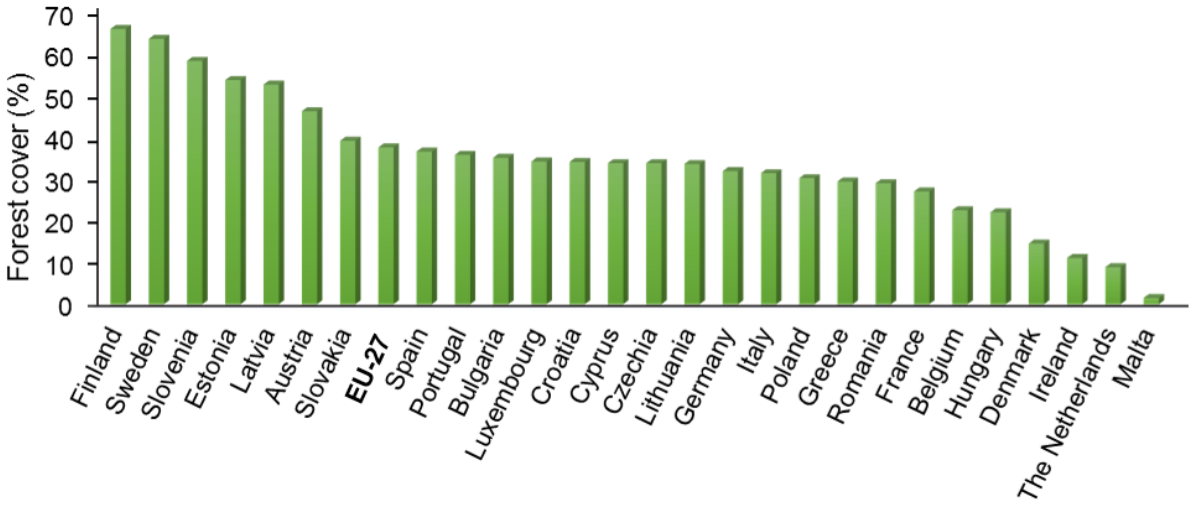

Figure 3.4.1. Forest cover for European Union (EU) countries in 2019. EU-27 represents the average forest cover (%) for the 27 countries of the European Union. Source of the data (European Commission 2019).

The diversity of European forests cannot be fully understood without linking it to the natural history of the European continent. Although in boreal and mountainous countries forest cover now exceeds 40%, most often their forests are dominated by only a few tree species, which is no coincidence. Within the Pleistocene, there were periodic fluctuations in temperature, land ice, sea level, soil, and biomass. These fluctuations correspond to glacial (cryocratic) and interglacial (protocratic, mesocratic, oligocratic, and telocratic) stages (San-Miguel-Ayanz et al. 2016). During the glacial-interglacial cycles of the Pleistocene, the range of many species was drastically reduced and some species either disappeared or managed to survive in favourable refugia. These were mainly located in Southern and South-Eastern Europe (Petit et al. 2002). These refugia (e.g. mountains ranges or islands) still have high species diversity and endemism today (EEA 2006). As a result, the European flora is considered depauperate due to the combined effects of repeated glacial cycles during the Pleistocene and natural barriers (Beierkuhnlein 2007). After the Pleistocene, the current interglacial period began, namely the Holocene epoch (11700 years ago). Holocene marked the spread of *Picea abies* into formerly glaciated areas of Scandinavia, where this species remains dominant currently.

The tree species richness of European temperate forests also reflects historical extinction events. For instance, more tree genera were lost in Europe during the harsh glacial climate of the Pleistocene than in other temperate regions of the Northern Hemisphere (Liebergesell et al. 2016). As a result, the temperate forests from East Asia harbour three times more tree species than North America and six times more than Europe (Latham & Ricklefs 1993; Liebergesell et al. 2016). Hence, in comparison with other Holarctic regions, Europe is characterized by low diversity (Ordonez & Svenning 2018). However, there are more drought- and frost-tolerant species in Europe than in North America as a result of climate filtering (Manthey & Box 2007; Liebergesell et al. 2016). Despite their lower tree diversity, deciduous temperate forests from Europe have higher functional diversity (e.g. species with different functional traits) than their counterparts from North America (Liebergesell et al. 2016). Functional diversity is very important for ecosystems as it enhances productivity and stability and improves their capacity to respond to climate change. However, this also means that this high functional diversity can easily be lost if only a few species decline.

Nowadays are around 454 native tree species in Europe (IUCN 2019) and several introduced tree species. Figure 3.4.2a visualize the range size (i.e. extent of occurrence) of the native species from Europe according to the data extracted from the Atlas of Florae Europaeae published in 2005 (Svenning & Skov 2005). Only species with a range of ≥ 10% from the European area are represented in Figure 3.4.2a. The extent of the Atlas Florae Europaeae is the same as in Figure 3.4.2b, except that it includes the island of Svalbard and does not include the Canary Islands and Cyprus. Most of the species with a range ≥ 10% of the European area (Fig. 3.4.2a) are also considered of Least Concern according to the IUCN Red List category. An exception is wych elm (*Ulmus glabra* Huds.) which has a large range size, but after the introduction of *Ophiostoma ulmi* in the 1920s and *Ophiostoma novo-ulmi* in the 1970s, known as Dutch elm disease, the number of large trees has declined dramatically (San-Miguel-Ayanz et al. 2016). The species is now classified as vulnerable at the European level (Fig. 3.4.2a). In contrast to their large range size, more data are needed for the species field elm (*Ulmus minor* Mill.), black poplar (*Populus nigra* L.), and the European white elm (*Ulmus laevis* Pall.) (Data Deficit, Fig. 3.4.2a).

The species shown in Figure 3.4.2a are some of the most common species in Europe and are part of its natural vegetation formations. It should be considered that the concept of potential natural vegetation is currently rather theoretical due to its definition (see Glossary) and ecosystem dynamics (Chiarucci et al. 2010). However, knowing the extent of potential natural vegetation can give us a better understanding of the magnitude of anthropogenic impacts on forests. According to Bohn & Neuhäusl (2003), the most extended European vegetation formations from Northern to Southern Europe that include trees as dominant characteristic are:

- Mesophytic and hygromesophytic coniferous and mixed broadleaved-coniferous forests distributed in the boreal, nemoral zones, and the mountain regions. They are dominated by Norway spruce (*Picea abies* L.), Siberian spruce (*Picea obovate* Ledeb.), Scots pine (*Pinus sylvestris* L.), Siberian pine (*Pinus sibirica* Du Tour), European larch (*Larix decidua* L.), Siberian larch (*Larix sibirica* Ledeb.), silver fir (*Abies alba* Mill.), and Siberian fir (*Abies sibirica* Ledeb.).
- Mesophytic broadleaved deciduous and mixed broadleaved/conifer forests have a wide distribution from Western to Eastern Europe. These forests include a transition from conifers to deciduous species, with European beech (*Fagus sylvatica* L.), hornbean (*Carpinus betulus* L.), common oak (*Quercus robur* L.), and sessile oak (*Quercus petraea* (Matt.) Liebl.) forest stands.
- Thermophilous mixed deciduous broadleaved forests include a variety of *Quercus* taxa, from less to more drought-tolerant, such as common oak (*Quercus robur*), sessile oak (*Quercus petraea*), Turkey oak (*Quercus cerris* L.), and pubescent oak (*Quercus. pubescens* Willd.).
- Mediterranean sclerophyllous forest and scrub comprise species of the genera *Quercus, Olea, Pistacia, Pinus,* and *Juniperus*.

Within European natural vegetation formations, tree species richness is highest in Central-Eastern and Southern Europe (Fig. 3.4.2b) (IUCN 2019). Although these regions have the highest species richness, they are also the ones where more research is needed. Several authors pointed out that South-Eastern Europe lacks data on tree species richness and tree species distribution (Svenning & Skov 2005; Mauri et al. 2017; IUCN 2019). Few tree species have a wide distribution across Europe, whereas most have an intermediate and restricted distribution (Svenning & Skov 2007). However, due to historical effects (e.g. lasting effects of large-scale events), dispersal, and climate constraints, there is a significant difference between the realized and the potential range of the tree species (Svenning & Skov 2004). Therefore, it is uncertain to what extent tree species richness and the distribution of trees will be influenced by future climate change.

Of the 454 tree species assessed so far in Europe, 168 are threatened (68 = Critically Endangered, 62 = Endangered, and 38 = Vulnerable); and there are no extinct species recorded during the Holocene (Fig. 3.4.2c). However, there is a data deficit for 57 species (13%) (IUCN 2019). This means that the proportion of the last concerned or threatened species might change slightly after the assessment of these 57 species.

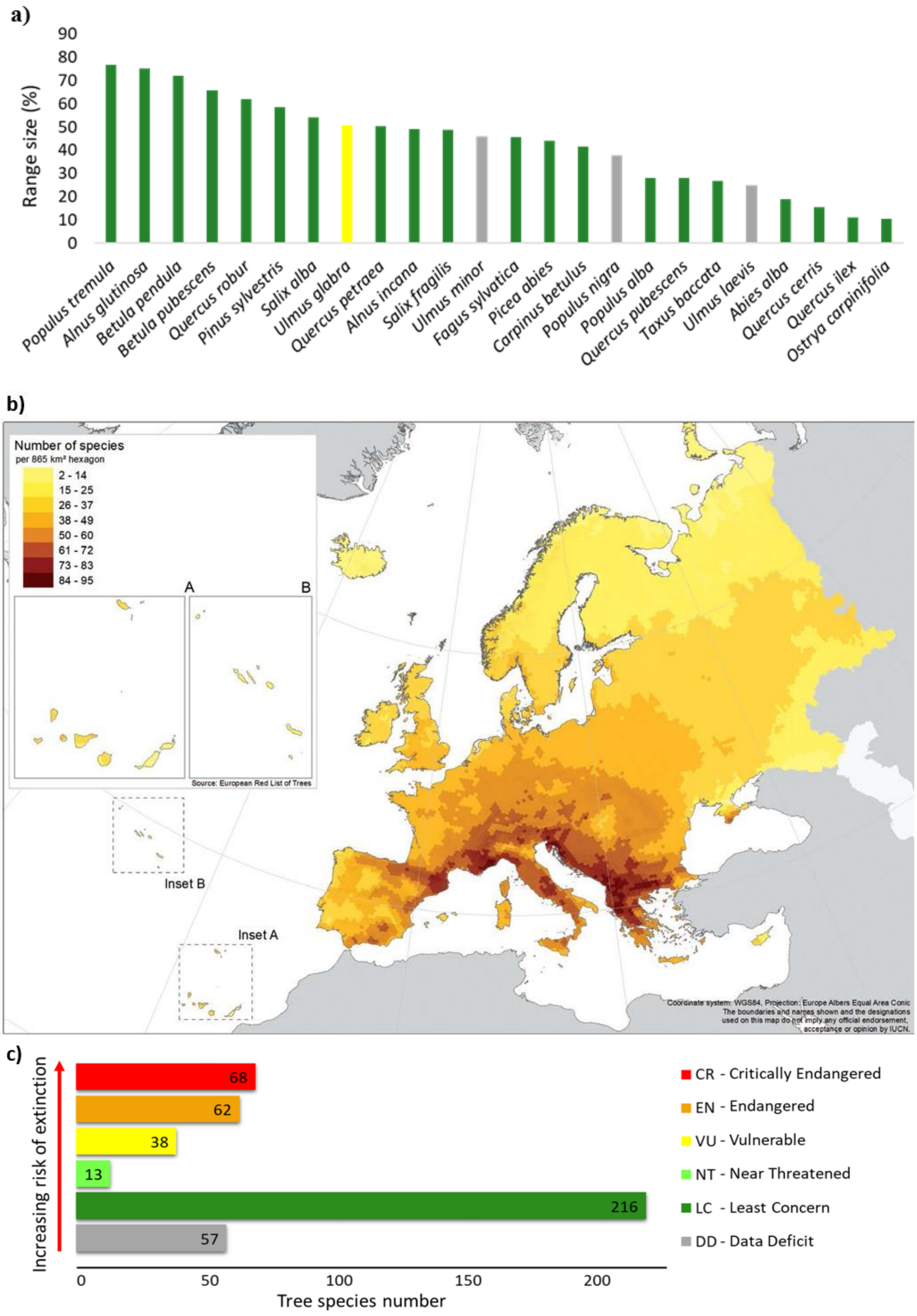

Figure 3.4.2. **a**) Tree species range size (%) for the tree species with ≥ 10% of the total area. **b**) Tree species richness across Europe. Source of the data and map (IUCN 2019). **c**) Tree species in each IUCN Red List category (n=454). In (a) the total area is represented by Europe 34° N–72 ° N and 11° W–32° E, similar in extent to (b) but including the island of Svalbard

and excluding the Canary Islands and Cyprus. The range size is computed based on the distribution of the species on the Atlas of Florae Europaeae (Svenning & Skov 2005). The colours of the bars correspond to the protection status (from c) according to the IUCN Red List category.

Most of the threatened species are found in small areas of Southern and South-Eastern Europe. For instance, the International Union for Conservation of Nature (IUCN) Red List, published in 2021, states that of the 615 conifer species assessed worldwide (Farjon 2010), 34% are threatened with extinction, of which 14 species are found in South-Eastern Europe (IUCN 2021). Similarly, the European Red List assessment showed that 42 % of the European tree species are threatened (IUCN 2019). Better monitoring, evaluation, and protection measures, including cross-border collaborations, are therefore needed to ensure the survival and successful establishment of these threatened species. Moreover, climate change is putting additional pressure on the survival and distribution of these already threatened tree species. As a result, we need to know which species can cope with these changes and for which adaptive management measures should be developed.

3.5. Climate change and forest ecosystems

> "*By felling the trees which cover the tops and sides of the mountains, men in all climates seem to bring upon future generations two calamities at once; want of fuel and a scarcity of water*."
>
> Von Humboldt & Bonpland (1819, p. 143)

3.5.1. Global climate change

Global temperature has shown a steady increase, with 0.87°C more in 2006-2015 relative to 1850-1900 (Hoegh-Guldberg et al. 2018), and is forecasted to increase further. Nevertheless, there is a significant difference between the ocean and land temperatures and between the two Hemispheres. The land temperature is higher than the ocean temperature (Rohde 2021). As a result of the distribution of the large land masses that influence atmospheric circulation and the lower albedo, the temperature in the Northern Hemisphere is higher than in the Southern Hemisphere. Furthermore, the increase in average temperature is strongest in the high latitudes of the Northern Hemisphere (Hoegh-Guldberg et al. 2018; Rohde 2021). Due to warming in recent years, the Gulf Stream (see Glossary), which is an important factor in heat distribution, has weakened, which could lead to more extreme events (Caesar et al. 2021). As global warming continues, both extreme heatwaves and precipitation are expected to increase (Lehmann et al. 2015; Hari et al. 2020).

Since the beginning of the 21st century, the Northern Hemisphere has experienced unprecedented summer droughts (see Glossary). These drought periods developed and persisted due to the combined effect of the summer North Atlantic Oscillation (NAO) and the stationary Rossby Wave-7 pattern (see Glossary), which were modulated by long-term global warming trends (Drouard et al. 2019; Peters et al. 2020). The drought periods are mainly due to lack of summer precipitation, rising temperatures and severe heat waves (Hanel et al. 2018). For instance, in the summer of 2018, the Northern Hemisphere was hit both by heat waves (in North America, North-Western Europe and the Caspian Sea region) and extreme precipitation (in Japan and South-Eastern Europe) (Kornhuber et al. 2019).

Recent summer droughts have caused human deaths, crop failures, forest fires, forest dieback, and economic loss (Gudmundsson & Seneviratne 2016; van Oldenborgh et al. 2019; Vogel et al. 2019; Büntgen et al. 2021). Moreover, these extreme weather events are predicted to increase in their frequency during the 21st century (Hoegh-Guldberg et al. 2018; IPCC 2019). Considering the climatic impact of 0.87°C, a further increase is predicted to have a strong impact on natural and managed systems. There are ongoing efforts to limit global warming to 1.5°C above the pre-industrial levels (Hoegh-Guldberg et al. 2018; Seneviratne et al. 2018). At the current rate, we would reach 1.5°C between 2030 and 2052. Nevertheless, even an increase of only 1.5°C can be associated with regional climate anomalies, such as droughts or heavy precipitation (Seneviratne et al. 2018).

3.5.2. Climate warming and drought in Europe

Geographical aspects contribute to the susceptibility of Europe to climate change. Ocean-land interactions are pronounced in Europe and are controlled by the distance to the oceans as well as heterogeneous land structures and mountain ranges. On the one hand, the climate in Europe is influenced by the energy transport of the Gulf Stream (see Glossary). Due to climate warming, the flow rate of the Gulf Stream decreased, which can impact climate variability in Europe (Caesar et al. 2021). On the other hand, the atmospheric circulation patterns are controlled by the jet stream (see Glossary), which is formed at the intersection of warm air masses with cold air masses at mid-latitude. However, as the differences between these air masses decrease due to anthropogenic warming, this could weaken the jet stream and cause a poleward shift, leading to a temporal delay in the jet stream movement (Stendel et al. 2021). One such case is the stationary Rossby Wave-7 in 2018, which caused an intense summer drought (Kornhuber et al. 2019). Therefore, both factors can potentially have an impact on climate warming and the intensity and frequency of extreme events.

In Europe, the average annual temperature raised continuously, from 6.96°C in 1979 to 8.28°C in 2013, with a mean of 7.77°C (data calculated based on the CHELSA climatological time series) (Karger et al. 2017). The European average temperature is projected to increase further with significant impact across terrestrial ecosystems (IPCC 2019). In Figure 3.5.2.1a, I show the difference between the projected average annual temperature for 2041-2060 and the average annual temperature for 1979-2013 across the European countries. The maps were created based on the CHELSA climatological data using the general circulation model (GCM) MPI-ESM-LR and the Representative Concentration Pathways (RCP) 2.6 and 8.5 (see Glossary) (Karger et al. 2017). The temperature differences are ranging between -0.5°C and 1.7°C, with North-Eastern European countries experiencing the highest temperature changes under RCP 2.6. However, if we consider the high emission scenario, RCP 8.5, all South-Eastern and Northern European countries are forecasted to experience more extreme changes in temperature (Fig. 3.5.2.1b), with a difference in temperature ranging from 0.5°C to 2.5°C.

Along with temperature rise, the precipitation regime is one of the detrimental factors affecting the forest ecosystem. Annual precipitation varied constantly across Europe, with an annual average of 740 mm between 1979 and 2013 (Karger et al. 2017). Nevertheless, the annual precipitation pattern increased since 1950 in Northern Europe while in Southern Europe decreased. Projections for precipitation are more uncertain but are predicted to increase at high latitudes in Europe under the RCP 2.6 scenario (Hoegh-Guldberg et al. 2018). In addition, regional precipitation extremes are also not excluded (Seneviratne et al. 2018). Therefore, this will lead to changes in the extension of climate classes (Beck et al. 2018). Regional climate zones shifts have already been observed at a global level (IPCC 2019).

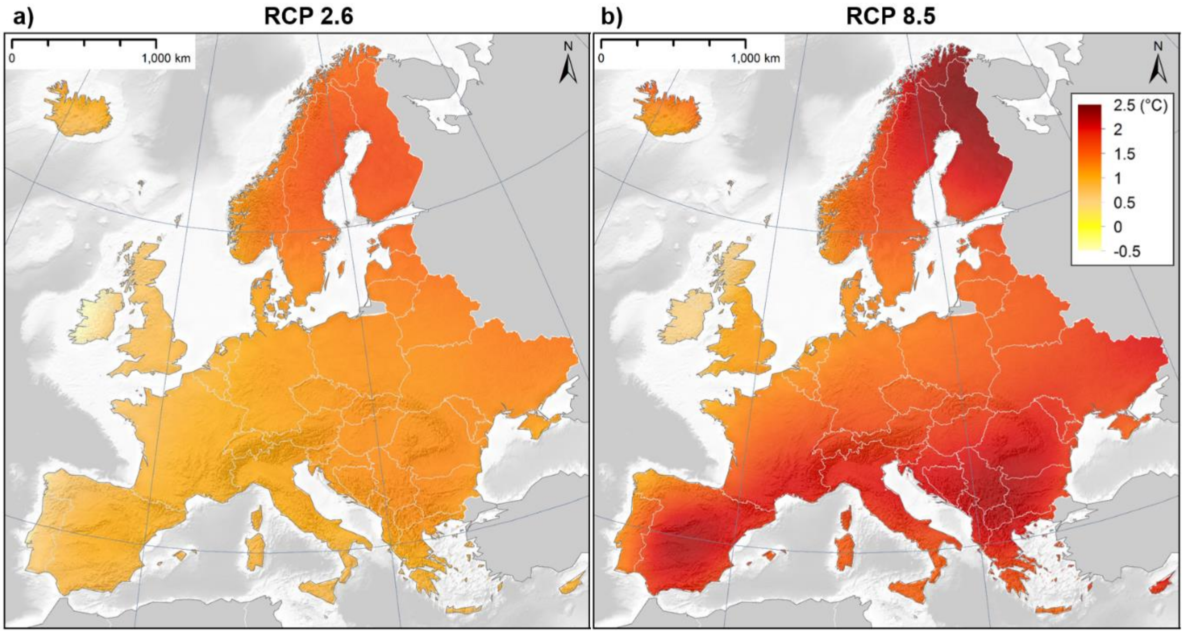

Figure 3.5.2.1. Change in average annual temperature based on mean projection for 2041-2060 relative to 1979-2013 under **a**) RCP 2.6 and **b**) RCP 8.5 emission scenarios.

In Europe, the frequency and intensity of droughts has increased over time (Hanel et al. 2018; Ionita & Nagavciuc 2021). Several summer droughts were particularly extreme, such as the drought periods of the recent years, 2003 and 2018, that affected Central Europe (Schär et al. 2004; Rebetez et al. 2006; Vogel et al. 2019), 2010 and 2015 that affected Eastern and South-Western Europe (Ionita et al. 2017), and 2019 that affected mostly Western Europe (Vautard et al. 2020). The 2018 drought mainly affected Central and North-Western Europe, while low temperatures and high precipitation were recorded in Southern and South-Eastern Europe (Spain, Greece, and Romania) (Drouard et al. 2019; Kornhuber et al. 2019). Drouard et al. (2019) showed that a positive North Atlantic Oscillation (NAO+) followed by the stationary Rossby Wave-7 pattern were mainly responsible for the seasonal anomalies of summer 2018. Drought is expected to increase in intensity, with successive drought periods such as those of 2018 and 2019 becoming more frequent (Spinoni et al. 2018; Samaniego et al. 2018). Given their increased occurrence, periods of this magnitude will therefore no longer be classified as extreme (Samaniego et al. 2018; Hari et al. 2020).

Droughts are a rising concern for terrestrial ecosystems, with subsequent impacts on forest structure and functioning (Ratcliffe et al. 2017; IPCC 2019). Several authors have emphasized that droughts have severe effects on forest ecosystems across Europe by reducing productivity (Ciais et al. 2005; Reichstein et al. 2007; Ammer 2019), affecting forest diversity (Ratcliffe et al. 2017; Ammer 2019), and increasing tree mortality (Bréda et al. 2006; Allen et al. 2010; Anderegg et al. 2013; Senf et al. 2018; Buras et al. 2020; Senf et al. 2020). Moreover, these periods of drought have resulted in a persistent soil moisture deficit, and further climate warming is projected to exceed the soil moisture deficit across Europe (Samaniego et al. 2018; Hanel et al. 2018). Which means that the vegetation will be severely affected. Nevertheless, drought events are expected to become more frequent and severe in Europe, this underlines the urgent need to understand the risk, identify and predict the declines in forest health across forest types and tree species.

In Germany, the annual temperature increased from 8.6°C in 1950 to 10.4°C in 2020 (Fig. 3.5.2.2a), whereas the precipitation varied constantly, with a mean value of 800 mm (DWD 2021a; DWD 2021b). However, a decreasing trend in precipitation can be observed after the year 2000 (Fig. 3.5.2.2b). Projections of future climatic classes for Germany show that the Köppen-Geiger Dfb climate (cold, no dry season and warm summer) will be lost to the expansion of the Cfa climate (temperate, no dry season and hot summer) (Beck et al. 2018).

Climate change and climate extremes have triggered forest disturbances, such as an increase in bark beetle reproduction rate, wind damages, and a decline in forest health across Germany. Although these disturbances are part of the ecosystem dynamics, an increase in disturbances can exceed forest resilience and alter forest recovery leading to forest degradation, or pushing the forest past the tipping point where its function and structure are irreversibly affected (Seidl et al. 2017). For instance in Germany, several studies have accounted for (1) forest productivity under climate change (Ciais et al. 2005; Albert et al. 2018); (2) edge effect (Buras et al. 2018); (3) species composition and drought tolerance (Griess et al. 2012; Mette et al. 2013; Pretzsch et al. 2013; Zang et al. 2014; Metz et al. 2016; Kunz et al. 2018; Hoffmann et al. 2018; Aldea et al. 2021; Pardos et al. 2021). Many other studies have contributed to an improved ecological understanding of forest response to climate change, but there are still open questions.

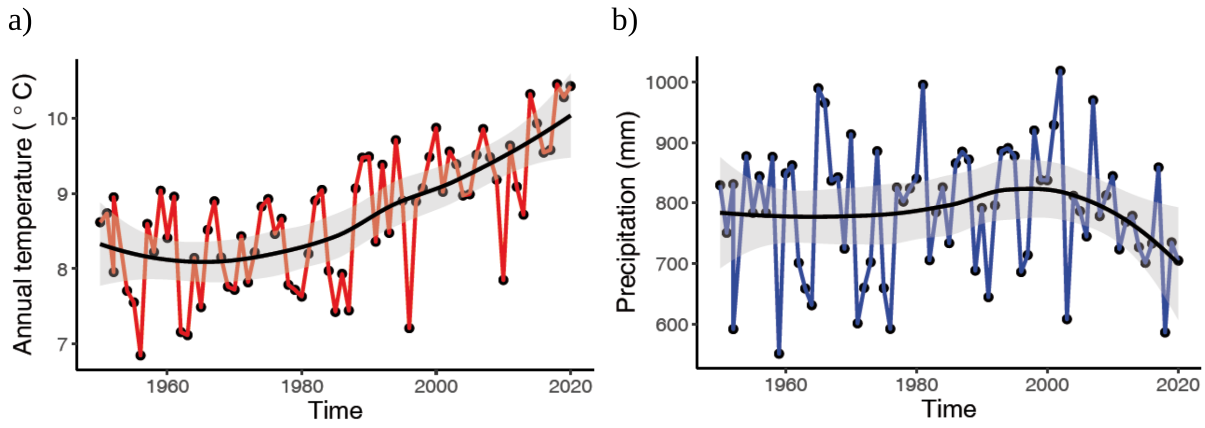

Figure 3.5.2.2. (**a**) Mean annual temperature (°C) and (**b**) average precipitation (mm) trend for Germany from 1950 to 2020. The climatic trend is given by the local weighted regression (LOESS) lines. The climatic data were extracted from the Deutscher Wetterdienst (DWD) annual raster datasets (DWD 2021a; DWD 2021b).

3.6. Forest dynamics in a changing world

> "*Natura non facit saltus*."
>
> Aristotle (384 B.C. to 322 B.C.)

Forest dynamics is a central topic in forest ecology, and its modelling remains an important area of research (Shugart 1984; Pretzsch 2009). Pretzsch (2009) defines forest dynamics as all structural changes (three-dimensional distribution of trees, often expressed as the number of trees per ha by size and age), changes in species composition, and changes caused by anthropogenic and natural disturbances. The ecology and spatial patterns of mountain treelines have been the subject of many and diverse research endeavours, and they are receiving renewed attention in the face of climate change (Holtmeier 2009; Malanson et al. 2011).

Forest structure and composition are and will be even more altered by climate change in the future. To cope with these changes, the spatial distribution of trees is expected to shift to higher elevations or higher latitudes. However, it is questionable whether trees can cope with these accelerated changes. To understand better how and if the tree species are responding to these changes, modelling and field observations needs to be used (**Manuscript 3** and **4**). Hence, in the following, I will discuss the projected tree species distribution according to future climate scenarios and the observed dynamics in Europe.

3.6.1. Projections for tree species across Europe

Forest ecologists rely on climate models to predict changes from individual trees to forest ecosystems and understand possible risks. RCP scenarios provide a good understanding of the risks posed by future climate. Many species have experienced a distribution change, altered densities or abundance, and shifts in seasonal activities and phenology as a result of climate change (IPCC 2019). However, most species and ecosystems have a limited ability to adapt, and even a 2.6°C warming poses a serious risk for many species (Hoegh-Guldberg et al. 2018).

Several models have projected a change in species richness and distribution across Europe driven by climate change. Temperate forests are projected to shift their distribution range towards boreal forests (Thuiller et al. 2006). This will cause changes in species richness and forest productivity. Moreover, these changes are species-specific, *Picea abies* habitat suitability is predicted to increase towards Northern Europe, but to decrease in Central and Southern Europe (Falk & Hempelmann 2013; Maaten et al. 2017). Whilst *Fagus sylvatica* habitat suitability is projected to increase towards higher elevation and higher latitude and decrease mainly in Southern and some parts of Central Europe (Falk & Hempelmann 2013; Maaten et al. 2017; Walentowski et al. 2017). Similar trends have been observed in *Quercus robur* and *Pinus sylvestris* (Maaten et al. 2017). However, several species are predicted to withstand a warmer and potentially drier climate, such as *Quercus petraea*, field maple (*Acer campestre L.*), chequers (*Sorbus torminalis* L.), whitebeam (*Sorbus aria* L.), *Ulmus minor*, and the large-leaved lime (*Tilia platyphyllos* Scop.) (Walentowski et al. 2017). The group of "winners" is projected to include other native species, such as *Abies alba*, ash (*Fraxinus* *excelsior* L.), and alien species, such as northern red oak (*Quercus rubra* L.), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), and black locust (*Robinia pseudoacacia* L.) (Dyderski et al. 2018).

Effects of the climate-induced shift were already observed in other species e.g., plants, mammals, and birds. Nevertheless, it is questionable whether the European native tree species will manage to keep up with climate change. It has been demonstrated that the observed shift in species is less than the expected or predicted shift by models (Chen et al. 2011). Trees have a longer lifespan and life cycles than plants, and their distribution and establishment are also limited. Although models project major changes in habitat suitability, the lifespan of a tree is most often longer than 100 years (in some species over several hundred years), whereas the climate changes are happening and predicted to happen at a much faster rate. Hence, how reliable, and close to the observations are these models?

To better assess the future distribution of tree species across Europe, we need to consider not only the climate but also the demography, dispersal, and species interactions, data which are almost always missing from models (Urban et al. 2016; Ruiz-Benito et al. 2020). Moreover, in-situ measurements should be collected to detect if the predicted shift corresponds to the observed shift and which factors might interfere (**Manuscript 1** and **2**). This information is needed to project and prevent the damaging effect of climate change on tree species. Climate-driven changes are expected to be more pronounced in areas with narrow climatic gradients, e.g., high mountains (Jentsch & Beierkuhnlein 2003). There is a particular system that is considered a sensor for climate change, the treeline ecotone. The definition and characteristics of treeline ecotones, what this "sensor of climate change" indicates, and other research questions are addressed in the next subchapter.

3.6.2. Forest dynamics at the treeline

Forest dynamics is defined by the changes that happen in forest structure and composition over time, including forest response to natural and anthropogenic disturbances (Pretzsch 2009). Changes at the treeline include tree densification and/or upward shifts in elevation. These two ecological processes are controlled by different factors, thus both should be considered in the quantitative analysis of the treeline spatial dynamics (Feuillet et al. 2020). Treeline ecotone is characterized as the transition from a close forest or forest line to the few dispersed trees that grow in groups or as single individuals and have at least 2 m in height. There are four main treeline forms: diffuse (gradual transition from close forest to single individuals), abrupt (continuous forest bordered by alpine vegetation), island (groups or stripes of trees growing above the continuous forest line), and krummholz (dispersed patches of deformed or stunted trees above the forest line) (Bader et al. 2021). Treeline elevation increases from oceanic islands, followed by continental islands, to mainland areas (continents) (Irl et al. 2016; Karger et al. 2019). The difference in treeline elevation between oceanic islands, continental islands, and mainland locations is explained by climate, isolation, and the maximum elevation of an island (Karger et al. 2019). This means that despite the climate that could allow trees to grow at a certain elevation, isolated islands have a lack of tree species adapted to the treeline. In contrast, the higher the maximum elevation of an island, the higher the treeline.

Species response to climate change generally consists either in evolutionary adaptation, or extinction. The predominant consensus is that ongoing warming simply outpaces macroevolutionary processes (Jump & Peñuelas 2005; Hof et al. 2011). Therefore, if species are unable to adapt to such drastic changes, trees can be affected. For example, damages from drought stress (Section 3.7), high evapotranspiration (Trotsiuk et al. 2021), frost damage (Chamberlain et al. 2020), insect infestations (Hlásny et al. 2021), and forest fires (Venäläinen et al. 2014) were observed and are expected to increase in Europe. Response to climate change is species-specific, with some species being winners and others being losers.

The impacts of climate change will be reflected in species composition. On the one hand, the advancing treeline ecotone may impose species displacement, reduction of alpine grassland, and fragmentation of the alpine habitat (Greenwood & Jump 2014). Impacts to biodiversity are expected, such as reduction in diversity and loss of species. More widespread species, e.g., herbaceous species and trees, from lower elevations are expected to move to higher elevations, resulting in higher competition and displacement of specialized species with lower niche tolerance. On the other hand, a lag in treeline response may have positive effects on alpine communities because they have time to shift before being displaced by the advancing treeline (Greenwood & Jump 2014). Negative aspects, however, may be associated with greater stress factors, such as drought stress on stationary trees and herbaceous species (Mamet et al. 2019). In addition, tree growth and productivity are expected to increase with the growing season (Juntunen et al. 2002) as long as there are no limitations due to evaporative demand, soil water content (Trotsiuk et al. 2021), or other factors. This raises questions about the ability of current species to cope with ongoing climate warming.

Is treeline advance able to keep pace with climate change?

To answer this question in detail, I conducted a literature review at the European level. The data were compiled from review publications (Harsch et al. 2009; Lu et al. 2021; Hansson et al. 2021) and other publications on treeline dynamics in Europe published between 2019 and 2020 but not included in the above reviews. The search was conducted on Web of Science using the search term (treeline* shift*), where (*) is indicated to find plural and inflected forms of words. I recorded general information about the treeline (e.g., study sites, coordinates, elevational shift rate (m/y), the study period, main methods, species, treeline form, and elevation). If some information was not reported and could not be found in other publications by the same author, I have indicated this in the list with NA (no data). Studies with multiple sites analysed were included separately if the required information was provided for each site. To minimize bias from reports of treeline advance, which were expected to be published more frequently than reports of no advance, the search criterion included studies that had appropriate methods for detecting changes in treeline (Harsch et al. 2009). A total of 274 sites from 86 published studies were included. Some studies used remote sensing, maps, historical images combined with field measurements (28%), while most used only field measurements, such as dendrochronology (72%). A list with all the data and publications can be found in Appendix 8.1. at the end of the dissertation.

In the 274 European treeline sites, the most frequent tree families are Pinaceae (51%), followed by Betulaceae (38.7%) and mixed tree or other species (10.3%). The most common species that form or are part of the treeline are *Picea abies* (common in many regions in Europe), *Larix decidua*, bog pine (*Pinus mugo* Turra), *Pinus cembra*, green alder (*Alnus viridis* A. Gray), rowan (*Sorbus aucuparia* L.) (the Alps and the Carpathians), *Pinus sylvestris*, Arctic downy birch (*Betula pubescens* var. *pumila* (L.) Govaerts) (Scandinavian Mountains), *Larix sibirica*, Siberian spruce (*Picea obovata* Ledeb.), *Pinus sibirica*, *Alnus alnobetula* subsp. *fruticosa* (Rupr.) Raus (Ural Mountains), Mountain pine (*Pinus uncinata* Ramond ex DC.), Canary Island pine (*Pinus canariensis* C.Sm.), black pine (*Pinus nigra* J.F.Arnold), Turkish pine (*Pinus brutia* Ten.), Mediterranean cypress (*Cupressus sempervirens* L.) (common in particular mountain regions or islands of Southern Europe).

In contrast to the general focus on the Alps, the Pyrenees, the Scandes, and the Ural Mountains, the South-Eastern mountain of Europe, which are one of the objects of study in this dissertation, were less researched and the studies had a lower duration than in Central and Northern Europe (Fig. 3.6.2.1ab). Hence, in **Manuscripts 1** and **2,** the treeline dynamics in the Carpathian Mountains (Romania) and the White Mountains (Crete, Greece) is assessed. The species that constitute the treeline in these two areas are *Pinus cembra* in the Carpathians and *Cupressus sempervirens*, *Pinus brutia* in the White Mountains. For better localization, these two studies were highlighted in Figure 3.6.2.2.

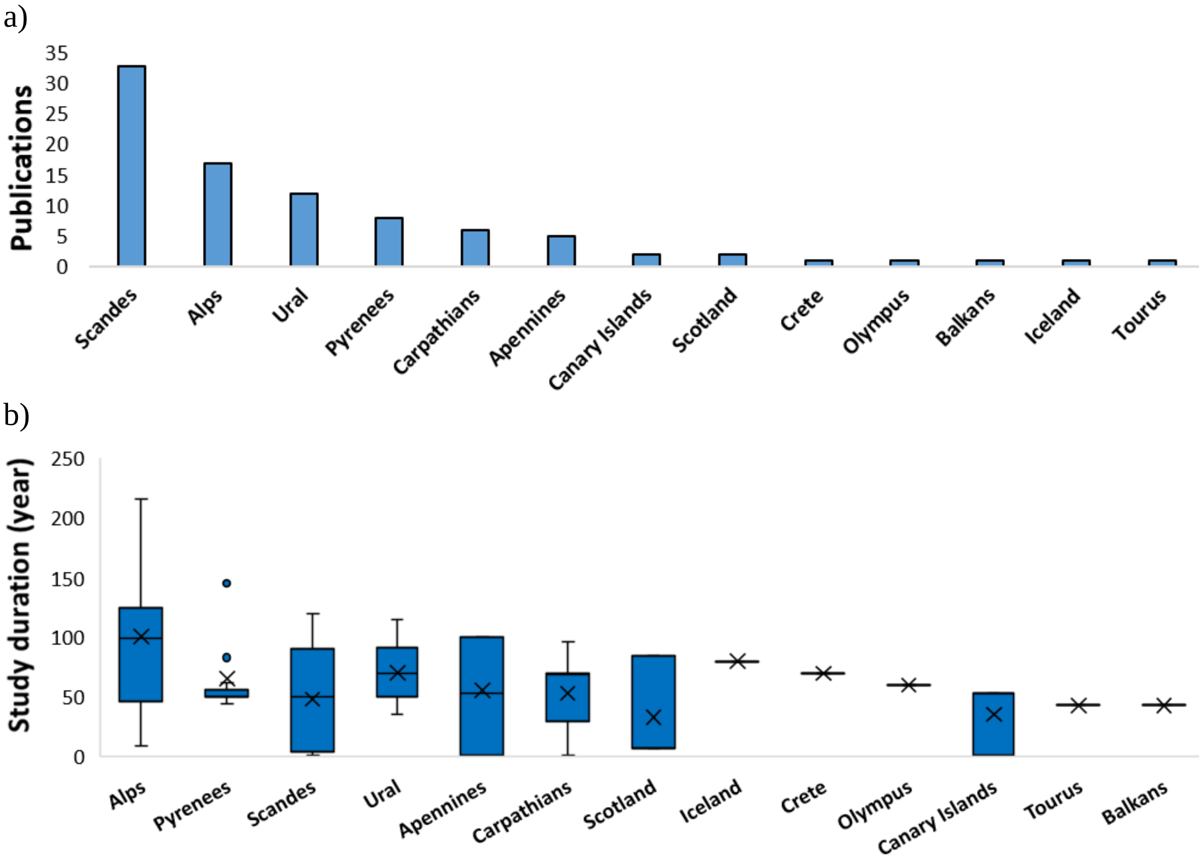

Figure 3.6.2.1. (**a**) The number of publications (n=86) and (**b**) their duration (years) per study region. The median is represented as an x symbol.

The location and shift of the treeline for continental Europe are shown in Figure 3.6.2.2. Treelines ascended in 62% of sites, remained stable in 33.2%, and descended in 4.7% of the 274 European sites (Fig. 3.6.2.2). The altitudinal shift of the treeline in Europe is 0.91 m/year (altitudinal shift calculated for the 215 sites for which the advance and retreat shift was specified, while stationary treelines received a value of 0). The treeline shift increases from South-Western to North-Eastern Europe, with the Pyrenees (0.19 m/year) < the Alps (0.30 m/year) < the Urals (0.72 m/year) < the Scandes Mountains (1.16 m/year) (Fig. 3.6.2.3). Another study showed that out of 143 sites assessed in the Northern Hemisphere, 88.8% of treelines ascended, 10.5% remained stable and 0.7% descended (Lu et al. 2021). Although a similar pattern is observed, a higher percentage of sites in Europe have a stationary treeline. In the face of global warming, this raises concerns about the ability of trees to follow the treeline altitudinal optimum. The elevational rate of treeline shift (0.35 m/year) calculated for the Northern Hemisphere during 1901-2018 is half what would be expected from climate alone (Lu et al. 2021).

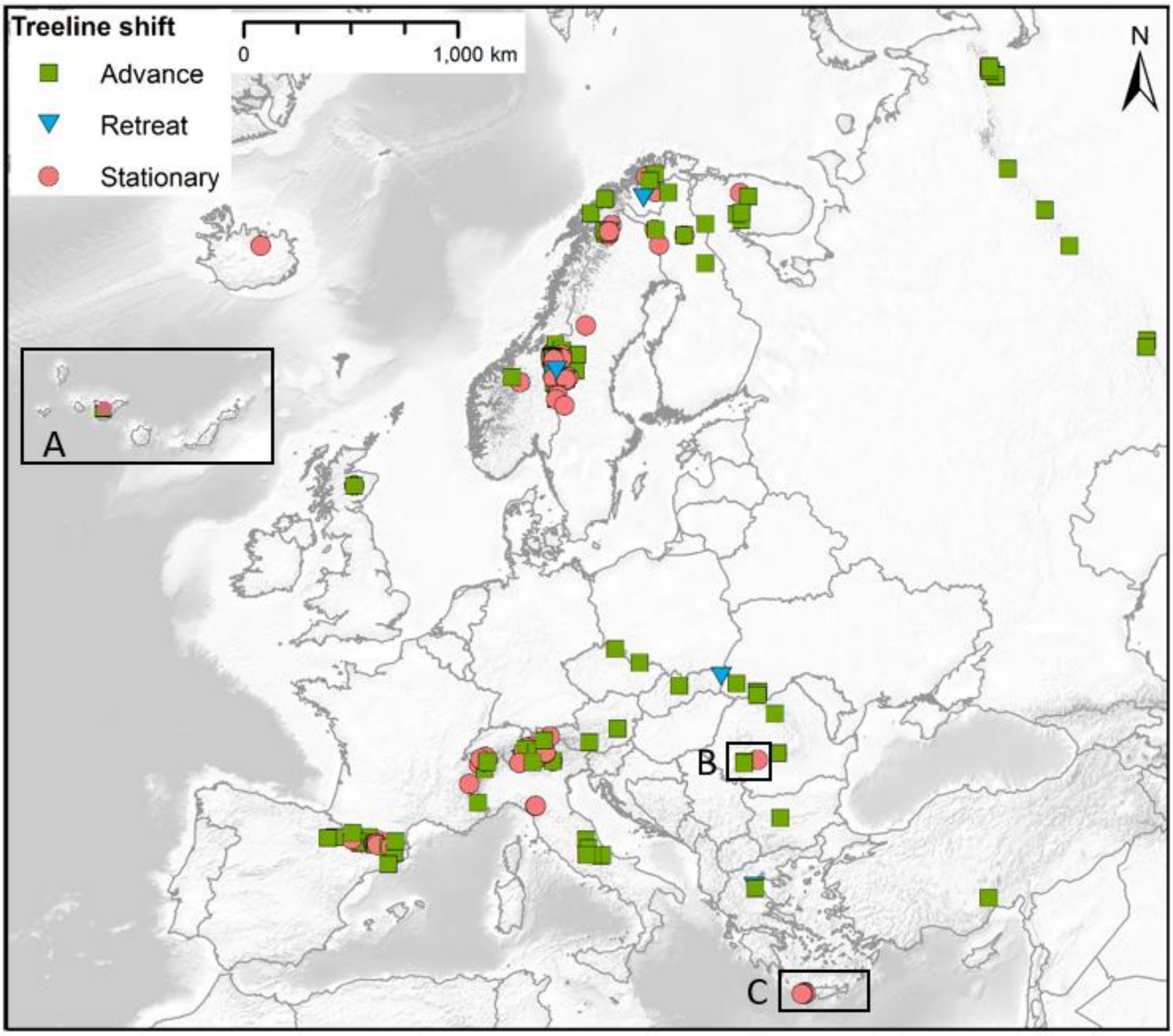

Figure 3.6.2.2. Location of the 274 treeline sites (86 studies) in continental Europe. Green square, red dots, and blue triangle are sites showing advancing, stationary and retreating treelines, respectively. The altitudinal (n=259) and latitudinal (n=15) treeline shift is included. Inset A shows the Canary Islands. The marked areas correspond to the study sites included in this dissertation (**Manuscript 1** (B) and **2** (C))

For the European Alps, the potential timberline was estimated at a mean elevation of 1880 m (1976–2000) and projected between 2120 and 2820 m by the end of the 21st century (based on RCP 2.6 and RCP 8.5, respectively) (Rubel et al. 2017). However, based on the current maximum treeline elevation observed at sites in the Alps in Figure 3.6.2.3, the mean value is 2236 m (1500 m min., 2640 m max.) (Appendix 1). Moreover, there are local patterns whose underlying factors are often unclear, e.g., treeline shift rates are higher in the subarctic than in the temperate zone (Lu et al. 2021) and spatially close areas can show contrasting patterns (Fig. 3.6.2.2).

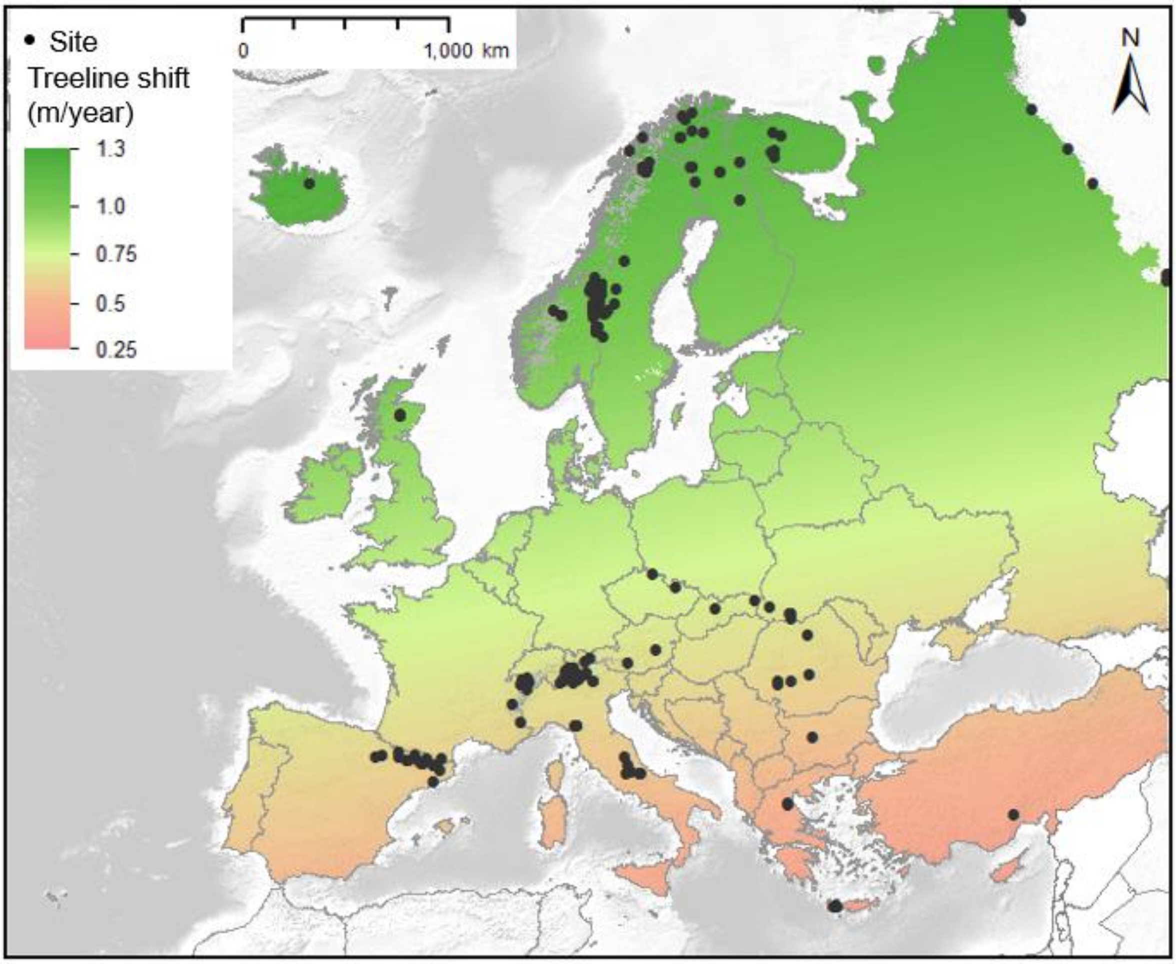

Figure 3.6.2.3. Altitudinal treeline shift (m/year). The gradient pattern is calculated using the linear regression trend interpolation (polynomial order = 1). Sites for which elevation shift was reported were used for the interpolation (n=215).

In the Alps, climate warming-induced an upward shift in plant species' optimum elevation of 6.2 to 7.1 m/y (Vitasse et al. 2021). However, studies have shown that in the Alps, not all species shift upwards, but some shifted downwards (Lenoir et al. 2010; Vitasse et al. 2021). This pattern was analysed for animals and plants and it was shown that terrestrial insects are the only ones keeping up with climate change, whereas most plants and trees are too slow to keep up with these changes (Vitasse et al. 2021). In the French mountains, seedlings' establishment was on average 29 m higher than adult trees, as their optimum was on average 69 m higher (Lenoir et al. 2009). A similar pattern was observed in one of the study areas from

Manuscript 1, where established *Pinus cembra* saplings were found 88 m higher than adult trees. Therefore, even if the population dynamic at the treeline is responding to climate change, the processes taking place between warming and other environmental factors and their impact on saplings' establishment are not yet clearly understood (Lett & Dorrepaal 2018). To summarize, the general rate of treeline advance is slower than climate warming and this has several driving factors that will be further discussed.

What causes the advance of the treeline?

Studies investigating drivers for treeline advances found regional and local differences. In subarctic regions of the Northern Hemisphere, autumn precipitation was the primary driver, while in temperate regions, both temperature and autumn precipitation accelerated the treeline shift (Rees et al. 2020; Lu et al. 2021). Hence, on a large scale, precipitation appears to be a more important driver than temperature, but on a local scale, multiple factors are at play. Although climate change is expected to shift the treeline altitudinal optimum, inducing an increase in tree growth (Camarero et al. 2021), microclimatic, geomorphological, and pedological factors combined with current and past land use appear to account for more of the vegetation variability than climate change (Hagedorn et al. 2014; McIntire et al. 2016; Cudlín et al. 2017). The availability of shelter sites (wind protection, low radiation, high snow cover) favours saplings' establishment. Furthermore, human land use prevents the rapid expansion of tree species both in lowland areas and at the treeline. In several regions of the Alps, the Pyrenees and the Scandinavian Mountains, land abandonment or reduced grazing pressure favoured recolonization of tree species and the advancement of treelines (Camarero & Gutiérrez 2004; Gehrig-Fasel et al. 2007; Treml & Chuman 2015; Vitali et al. 2019).

In addition to microclimatic and land-use factors, there are species-specific seed production rates and dispersal strategies. Trees cannot migrate by themselves, they depend on the dispersal of their seeds, successful germination, and survival, which is a slow process. Seedling survival and germination showed mixed responses to climate warming, whereas seedling growth increased with warming (Lett & Dorrepaal 2018). Moreover, seed production and viability showed to be sensitive to soil moisture and growing season in the tundra ecosystems, therefore this might affect treeline advance (Brown et al. 2019). In the Pyrenees, a significant decrease in seed production and dispersal along an elevational gradient was observed for *Pinus uncinata* (wind-dispersed seeds) (Anadon-Rosell et al. 2020). Likewise, in the Alps, natural recruitment of *Pinus cembra* (animal-dispersed seeds) was shown to be limited by dispersal rather than soil moisture and temperature (Neuschulz et al. 2018). Therefore, seed production and poor dispersal ability could slow the upward advance of the treeline.

Consequently, there is considerable variability in the response of treelines to climate change and geomorphologic factors, with some treelines advancing, others remaining stable or even receding and lagging behind climate change. This variability will have profound effects on ecosystem structure and function (Greenwood & Jump 2014). However, currently, there are still significant uncertainties and insufficient data to accurately predict the direction and magnitude of these effects. To understand when and where these changes in structure and function will occur, further studies and data at high spatial and temporal resolution are needed.

3.7. Impact of climate extremes on forest

> "*Tree death is so commonplace that the casual observer might logically assume it to be well understood by biologist. […] But overall the patterns and causes of tree death typically are complex, and we are beginning to appreciate the complexities*."
>
> Jerry F. Franklin (1987, p. 1)

After concentrating on future climate change projections and observed climate change shifts on the treelines, I will further focus on the impacts of climate extremes on forest health. In addition to the global increase in mean annual temperature and local variations in precipitation, climate change also includes potential local climate extremes (Section 3.5). Extreme impacts have manifold consequences for nature and society. For example, prolonged periods of precipitation deficit, as well as high evapotranspiration from the soil, can lead to drought (IPCC 2012). Drought periods are affecting forest structure, composition and cause tree mortality (Allen et al. 2015). Consequently, for a better understanding of the impacts of climate change on forests, both climate-induced shifts and the response of forests to drought should be assessed.

The main aim of this chapter is to assess the response of temperate forests to drought. Hence, two of the case studies in this dissertation were conducted in temperate forests of Central Europe (**Manuscript 3** and **4**); therefore, my primary focus in this chapter will be on European forests. I will describe progress in forest ecology related to drought by conducting a literature survey. I then explain the importance of understanding sapling and mature tree responses to drought in a heterogeneous ecosystem. In the end, I direct the attention to forest recovery and mortality patterns and the key drivers that either promote recovery or push trees over the "tipping point".

3.7.1. Current knowledge about forest response to drought

In this subchapter, I will illustrate the current knowledge about forest drought. I will start by outlining the research development on forest drought that took place in the last 70 years by conducting a literature survey. Further, I emphasize the impact of the drought at the global and European level.

Forest dynamics are in a process of change, i.e., the entire forest system is in a process of reorganization due to anthropogenic drivers that induce an increase in CO2 and temperature, and intensifying short-term disturbances, such as drought, wildfire, insect outbreaks, land-use changes (McDowell et al. 2020). Therefore, hotter droughts are linked to the emerging climate warming of the Anthropocene. Droughts also occurred in the past but their intensity increased at an alarming rate in recent years, e.g., the intensity of the European summer droughts since 2015 is unprecedented (Büntgen et al. 2021). The frequency and intensity of droughts are therefore threatening forest ecosystems on a large scale.

The survey on forest drought response included only peer-reviewed journals (including articles, reviews, and letters). For this literature survey, I searched through all publications listed in the Web of Science that addressed *forest drought* in the title, abstract, or keywords using the search string TOPIC: (*forest drought**) OR TOPIC: ("*forest drought*"), where (*) is given to find plural and inflected forms of words. These terms appeared primarily in forestry and ecological journals, but it should be noted that they could also appear in other related journals. While this search is simplified and may include publications that relate to forest drought in a different context, a general trend can be identified. The literature survey was conducted on 16.04.2021. The study period covers 70 years (1950 – 2020), with a total number of 12781 publications found.

The systematic survey reveals that the first paper on forest drought dates back to 1961, and the second one in 1979. Therefore, forest drought was not a continuous topic in science before the 1980s. Since the 1980s, forest drought has been an ongoing topic in science, but it was not until after 2000 that the number of scientific publications on forest drought started to increase rapidly (Fig. 3.7.1.1). This pattern reflects the increasing importance of the topic to the scientific community and society.

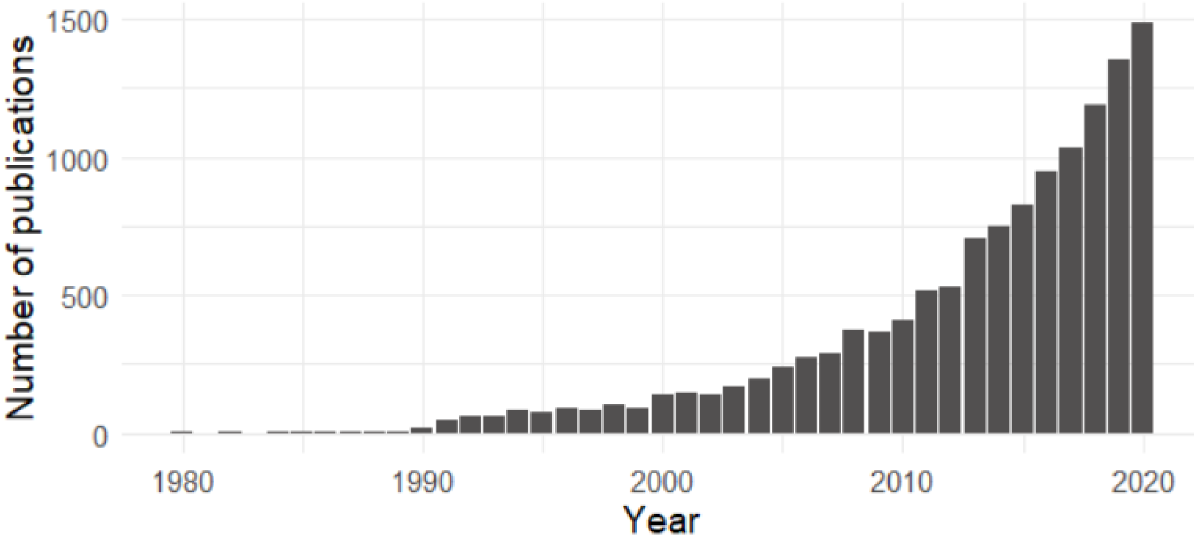

Figure 3.7.1.1. The number of publications (article, review, and letters) per year addressing forest drought in the title, abstract, or keywords (n=12781). The literature survey was conducted in the Web of Science Core Collection, applying the search string TOPIC: (forest drought*) OR TOPIC: ("forest drought") for the period 1950 to 2020. Only two related papers were found before 1980, one in 1961 and the other in 1979, years that were not plotted here for better visualization.

The increasing importance of forest drought in science is related to the extreme anthropogenic changes that have devastating ecological and economic consequences worldwide. Temperature and heat exacerbate drought stress and tree mortality (Williams et al. 2013). These heat-related impacts led to local and global disasters, such as major crop failures, extreme wildfires, as in the Siberian forest, Amazon rainforest, Australian forests, and California, resulting in deaths and billions of dollars lost (Vogel et al. 2019). At the European level, forests experienced intense drought stress, local wildfires (in Finland, Norway, Latvia, Greece, Portugal, and the United Kingdom), increasing insect infestations, and tree mortality (Vogel et al. 2019; Buras et al. 2020; Schuldt et al. 2020; Hlásny et al. 2021). Forests from less drought-adapted regions of Central Europe also underwent severe drought stress, with subsequent tree mortality (**Manuscript 3** and **4**). Given the increasing intensity and frequency of droughts, it is it is unclear what the future of forests will look like. To find an answer, it is important to understand the effects of drought on current sapling and tree species and their recovery. Therefore, I will discuss below the response of saplings and mature trees to drought, the importance of tree recovery in maintaining forest functions, and the factors that trigger tree mortality. All of these relate to **Manuscripts 3** and **4** from this dissertation.

3.7.2. Drought effects on saplings and mature trees

In this section, I first discuss the process of natural regeneration and establishment as a basis for understanding why an important part of my dissertation focuses on the response of saplings to drought. I refer here to natural regeneration as the process by which forests become established naturally, i.e., by trees growing from seeds that fall and germinate naturally. Further, I will outline the main differences in the effects of drought on saplings and mature trees.

In Europe, broadleaved species are one of the main natural vegetation types. For instance, the natural distribution of *Fagus sylvatica* ranges from Southern Europe (Northern Spain, Southern Italy, and Greece) to the Baltic countries (Southern Sweden and Norway). In contrast, coniferous species are mostly native to high-altitude mountainous regions or sandy dry areas. Yet, coniferous species were widely planted in Europe from the end of the 18th century for their rapid growth and timber value. They grew successfully outside their natural range for many years. Thus, although *Fagus sylvatica* could dominate the forests in Germany as potential natural vegetation, in fact about 53% of the forest area consists of coniferous species such as *Picea abies* and *Pinus sylvestris,* 31% are deciduous forests (*Fagus sylvatica*, *Quercus robur,* and *Quercus petraea*), and 13% are mixed forests (BMEL 2012; Holzwarth et al. 2020). However, climate change is reshaping the fate of these coniferous forests. Both conifer species are less stable in face of climate extremes being in the last years severely affected, *Picea abies* by bark beetle infestation and *Pinus sylvestris* by drought-induced mortality. The increasing benefits of more diverse forests have shifted attention towards a conversion from coniferous to mixed and deciduous forests (Pretzsch 2019; Messier et al. 2021). As a matter of fact, the process of adaptation by increasing biodiversity is rather slow. Even aged and monospecific stands of conifers are still prevalent in Central Europe and will take time for a change.

Nevertheless, there are processes of natural dispersal and establishment that indicate changes in community assemblages. Currently, we are witnessing an ecological succession in which native deciduous trees are reclaiming their habitat by establishing naturally under coniferous plantations. This was already observed during the field research I conducted for this dissertation in Germany, where establishment of *Abies alba* and *Pinus sylvestris* was low (present in up to 5 plots out of 214 plots). I observed the same pattern during field trips in the Romanian forests where *Quercus petraea* and *Fagus sylvatica* established under *Pinus sylvestris* plantations. As well, under *Pinus nigra* and *Pinus sylvestris* plantations, broadleaved species such as *Fagus sylvatica*, *Carpinus betulus*, *Fraxinus excelsior*, manna ash (*Fraxinus ornus* L.), and many other minor broadleaved species are successfully regenerating (Hereş et al. 2021). Another case was observed in Spain at the Southern edge of *Pinus sylvestris* distribution, where higher regeneration of *Quercus* spp. seedlings was observed under *Pinus* *sylvestris* trees (Vilà-Cabrera et al. 2013). This means that native deciduous tree species are reclaiming their habitat and even gaining new areas.

Forest microclimates regulate biotic responses to climate change. As a result, seedlings, and saplings inside the forest benefit from milder climatic conditions compared to open habitats. Large trees can buffer the exposure of saplings to direct solar radiation and wind, reduce temperature and humidity variation (De Frenne et al. 2019). However, their equilibrating effect cannot ensure sapling survival during extreme weather conditions, such as periods of drought. It is therefore unclear how saplings respond to drought, what the recovery and mortality patterns are. Therefore, in **Manuscripts 3** and **4**, I focus on sapling response to drought, recovery, and subsequent mortality. The survival of saplings during drought is important because they are the forest of tomorrow.

As trees develop, their physiological and structural complexity increases. Besides the microclimatic conditions to which saplings and mature trees are exposed, both have various physiological traits that help them cope with drought stress. For instance, photosynthetic capacity increases with ontogeny, but under dry conditions, it decreases more in seedlings than in mature trees, while saplings have an intermediate value (Cavender-Bares & Bazzaz 2000). Root mass increases with tree size, but so does the canopy evaporation (Poorter et al. 2012). Under drought, intrinsic water use efficiency (iWUE) decreases in all age classes, but only mature trees can increase iWUE in response to drought (Cavender-Bares & Bazzaz 2000). The crowns of mature trees are directly exposed to solar radiation and have higher evaporative demand (Bennett et al. 2015). Not only are mature trees more sensitive to drought, but they also tend to have higher insect infestations, as bark beetles prefer large trees to small ones (Bennett et al. 2015; Stovall et al. 2019; Schuldt et al. 2020). Therefore, both saplings and mature trees have specific traits that can help them or make them more susceptible to drought.

It is evident that, apart from the size of the tree, the species identity also matters if climate sensors are addressed (**Manuscript 3** and **4)**. *Quercus* spp. are among the most drought tolerant species. Drought impact seems to be similar on both small and large trees, but their recovery is size dependent, i.e., small *Quercus* spp. recover better after drought than large *Quercus* spp. (Zang et al. 2012). *Fagus sylvatica*, the most common and naturally dominating deciduous tree species in Central Europe, is generally considered to be sensitive to temperature and drought (Geßler et al. 2007). Consequently, some researchers expect the species to be strongly affected by climate change (Zang et al. 2014; Knutzen et al. 2017), while others assume it to be less affected due to its high plasticity and adaptability (Bréda et al. 2006; Schuldt et al. 2016). However, under recent drought conditions, large *Fagus sylvatica* trees were affected in both the rear-edge and central distributions (i.e., the low- and mid-latitude populations), but recovered within the next 1-3 years (Dorado-Liñán et al. 2019; Schuldt et al. 2020; Rohner et al. 2021). As well, *Fagus sylvatica* regeneration is limited by dry and hot conditions, hence its high plasticity might not be sufficient to support regeneration in the future as the climate warms (Muffler et al. 2021).

Pinus sylvestris is regarded as more of a drought-avoidant species, but has been shown to be susceptible to drought-induced mortality at the forest edge under recent drought conditions (2015 and 2018) (Buras et al. 2018; Schuldt et al. 2020). *Picea abies* is very susceptible to drought and particularly vulnerable to bark beetle (*Ips typographus*) infestation. Whereas *Abies alba* is considered less susceptible to drought and pests than *Picea abies* (de Groot & Ogris 2019). These bark beetle outbreaks are triggered by the ongoing rise in temperature and local summer drought (Seidl, Müller, et al. 2016). In **Manuscript 4**, I showed that both saplings and mature trees were severely affected by the 2018 summer drought, however, the drought impact is species-specific. In addition, I demonstrated that mature trees show long-lasting drought damage compared to sapling species, therefore, their recovery trajectories differ. The importance of forest recovery and the key drivers are addressed in the next section.

3.7.3. Forest recovery after drought impact

Forest capacity to withstand disturbance impacts and regain its functioning afterward is a key concept in ecology. The terminology used to characterize the state of an ecological system before, during, and after a disturbance has long been disputed and continues to evolve (Holling 1973; Grimm & Wissel 1997; Lloret et al. 2011; Hodgson et al. 2015; Ingrisch & Bahn 2018; Gessler et al. 2020). In the 1970s, the concept of resilience was introduced into ecology by Holling (1973), and meanwhile the concepts of resistance and recovery (see Glossary) have also been introduced to better characterise a system in the face of a disturbance and afterwards. The concepts of resistance, recovery, and resilience are cross-disciplinary, incorporating insights from physics, engineering, ecology, and epistemology (Holling 1973; Ingrisch & Bahn 2018; Dornelles et al. 2020). Their semantics-based distinctions are important for unambiguous measurements. Currently, different equations are depending on the considered semantics of the resistance, recovery, and resilience indices used to calculate them (Ingrisch & Bahn 2018). In forest ecology, the definitions and equations developed by Lloret et al. (2011) have, in recent years, been used extensively to quantify the state of forest ecosystems before, during, and after a drought period.

Carpenter et al. (2001) suggested that resilience is spatiotemporally dependent. This means that the resilience of the system depends on the time and scale at which the measurements are taken. As the climate warms and the frequency of droughts increases, the definition of an extreme weather event becomes variable, signifying that what was considered an extreme drought in the past may be considered a common event in the future. Here, I will refer to resistance, recovery, and resilience as defined in the Glossary. However, it is important to note that in the context of climate change, forest recovery should be seen as an adaptation to future conditions, as pre-drought conditions are unlikely to reoccur. This can be explained by the fact that climate change is occurring faster than the forest natural adaptation process.

Resilience can therefore be achieved through resistance or recovery (Hodgson et al. 2015; Seidl, Spies, et al. 2016). A system can be more resilient because it recovers at a high rate, therefore having a short recovery time, or because it is more resistant during the disturbance event (Hodgson et al. 2015). Resistance to and recovery from disturbances (e.g., drought) can jointly or separately drive resilience (Hodgson et al. 2015; Ingrisch & Bahn 2018). Consequently, we need to consider which of the two processes predominantly drive resilience. This can be helpful because forest managers can decide whether they want a forest that is resistant to disturbance, one that recovers quickly, or one that can avoid tipping points (Hodgson et al. 2015).

Generally, forest ecosystems show low resistance to drought damage, e.g., evergreen gymnosperms from Mediterranean forests (Gazol et al. 2018), *Picea abies*, and alien species from Central Europe (Pretzsch et al. 2013; Hoffmann et al. 2018; Kohler et al. 2019). Resistance seems to be influenced by forest stand composition, but this cannot be generalized because it depends on species identity, stand characteristics, and especially water supply (Pardos et al. 2021). Contrasting results were found when comparing *Fagus sylvatica* from mixed and pure stands. For instance, *Fagus sylvatica* was more resistant in *Fagus*-*Quercus* mixed stands than in pure stands (Pretzsch et al. 2013), but less resistant in *Fagus*-*Picea* mixed stands than in pure stands (Rukh et al. 2020).

Forest ecosystems were shown to be already strongly impacted by drought, wherefore their resistance (system functioning) was already degraded. This is exemplified by the consecutive droughts of 2018 and 2019 during which both saplings and mature trees in Central Europe were severely affected, leading to increased defoliation and mortality (Brun et al. 2020; Scharnweber et al. 2020; Hari et al. 2020). The capacity to recover their functioning is therefore a very important aspect.

However, the recovery trajectories of tree species following drought are poorly understood. Therefore, in **Manuscripts 3** and **4**, I address forest recovery following drought. I compare recovery trajectories among tree species to better understand species-specific responses and estimate the time needed for each species to reach a stable state. Thereby, I consider both the recovery rate and the recovery time. To achieve a better understanding of recovery patterns, I will further identify and explain the key drivers and limitations of forest recovery based on the current literature (Table 3.7.3.1).

Table 3.7.3.1 Main drivers of change in forest recovery following drought ("+" short recovery time, "-" long recovery time and "+ -" mixed effects)

Effect	Drivers of tree recovery	References
+	Precipitation	(Gallé et al. 2007; Gallé & Feller 2007; Anderson-Teixeira et al. 2013; Schwalm et al. 2017)
+	CO2 concentration	(Anderson-Teixeira et al. 2013; Schwalm et al. 2017)
+ -	Species-specific recovery	(Cavin et al. 2013; Anderegg, Schwalm, et al. 2015; Schwalm et al. 2017; Gazol et al. 2018; Hoffmann et al. 2018; Forner et al. 2018; DeSoto et al. 2020), **Manuscript 3** and **4**
+ -	Biodiversity	(Pretzsch et al. 2013; Grossiord et al. 2014; Metz et al. 2016; Schwalm et al. 2017), **Manuscript 3** and **4**
-	Warmer or extreme temperature	(Schwalm et al. 2017)
-	Gross primary productivity (GPP)	(Schwalm et al. 2017)

Effect	Drivers of tree recovery	References
-	Slope	(Lloret et al. 2004; Gazol et al. 2017)
-	Soil moisture	(Gazol et al. 2017; Gazol et al. 2018)
-	Defoliation	(Galiano et al. 2011) and **Manuscript 4**

- **High post-drought precipitation.** The amount of precipitation after the drought enhances the rate of recovery and as a result, also shortens the recovery time (Anderson-Teixeira et al. 2013; Schwalm et al. 2017). Moreover, the recovery time is shorter in wet areas (mean annual precipitation > 1000 mm) than in arid areas (mean annual precipitation < 500 mm) (Anderegg, Schwalm, et al. 2015). For instance, *Fagus sylvatica* and *Quercus pubescens* saplings showed complete recovery of photosynthetic activity after rewatering (Gallé et al. 2007; Gallé & Feller 2007).
- **CO2 fertilization.** Although precipitation and temperature are the main factors influencing recovery, CO2 fertilisation proved to be an additional significant factor, reducing recovery time by 4 months (Schwalm et al. 2017). High CO2 enhances photosynthesis, consequently, young trees might increase the leaf and root biomass (Anderson-Teixeira et al. 2013).
- **Species-specific recovery.** A global study by Anderegg et al. (2015) has underlined that there are differences in recovery between Pinaceae (gymnosperms) and Fagaceae (angiosperms). For example, Pinaceae species show higher drought legacy effects, i.e. they grow slower after a drought and therefore recover slower than Fagaceae or Cuppresaceae (Anderegg, Schwalm, et al. 2015). However, DeSoto et al. (2020), found no difference in recovery between gymnosperms and angiosperms. Considering the contradictory results, further studies need to be conducted to highlight the main drivers. Locally, *Fagus sylvatica* showed higher drought damage but a slower recovery rate than *Quercus petraea* in stands from Western (Cavin et al. 2013) and Central Europe (**Manuscript 3** and **4**). In the Mediterranean region, Portuguese oak (*Quercus faginea* Lam.) recovered more slowly than *Pinus nigra* due to its poor water use efficiency (Forner et al. 2018).
- **Biodiversity.** In grassland communities, species diversity promotes rapid recovery from drought (Isbell et al. 2015), but this theory has not been proven in forest ecosystems. Consequently, there are contradictory views on the role of biodiversity in promoting recovery, with some studies showing no effect, negative effects, or positive effects (Grossiord et al. 2014; Schwalm et al. 2017). Therefore, more evidence is needed to arrive at a general conclusion.
- **Temperature extremes (cold and warm).** Warm post-drought temperature repress recovery, meaning that as temperature rises, the recovery time also increases (Schwalm et al. 2017).
- **High gross primary productivity (GPP).** GPP is correlated with long recovery time (Schwalm et al. 2017).
- **Slope.** Topographic complexity can result in patchy vegetation because of nutrient and water accumulation in certain areas. Steep slopes correspond with high erosion and low

water retention. Therefore, these areas may be more affected by drought during dry periods, resulting in slow tree recovery (Lloret et al. 2004).

- **Soil moisture.** Recovery time decreases with soil moisture. Sites with more xeric soils showed fast recovery (Gazol et al. 2018).
- **Defoliation.** During drought, trees may shed their leaves to reduce evapotranspiration, but this leads to depletion of carbon reserves. Hence, their recovery is prolonged due to defoliation (Galiano et al. 2011).

This brief assessment suggests that forest recovery process is likely to be altered by climate warming and drought. Research on forest recovery is ongoing as there are many unanswered questions. To improve our understanding of tree response to drought stress and recovery, we need to expand the temporal scale, i.e., we should consider conditions before, during, and after drought. These can determine whether or not a tree can recover. Severe or repeated droughts can affect the dynamics of forest recovery, leading to changes in forest structure and function (Anderson-Teixeira et al. 2013). Recovery should be seen not only as the capacity of the trees to regain their functioning, but also to adapt to the new conditions. Forest ecosystems are very important for humans as they can regulate the climate, e.g., forestation is estimated to increase summer precipitation by $7.6 \pm 6.7\%$ (Meier et al. 2021) and store several gigatons of carbon (Bastin et al. 2019).

3.7.4. Tree mortality

Tree mortality is a natural process. However, an accelerated and widespread spatio-temporal pattern of tree mortality has been reported, which cannot be explained by natural population dynamics (Allen et al. 2010). Drought- and heat-induced tree mortality has been observed in all biomes around the world, including even tropical rainforests (Allen et al. 2010; Hartmann, Moura, et al. 2018). Hartmann et al. (2018) updated a map of drought and heat-induced tree mortality across the globe that revealed substantial mortality events in North America and Europe.

Tree mortality causes a cascade of ecological consequences, including loss of biodiversity, nutrient cycling, fires, loss of carbon and ecosystem services (water supply, timber, and land value). Across Central Europe, species of high economic value such as *Picea abies*, *Pinus sylvestris*, and *Fagus sylvatica* have been severely damaged by the 2018 drought (Brun et al. 2020; Schuldt et al. 2020). Important functional contributions of trees to climate regulation and carbon sequestration are severely affected due to tree mortality (Section 3.3.1). Most trees do not die during drought but within a few months or years following the drought (depending on drought damage, environmental conditions, species-specific resistance, and recovery). Therefore, drought triggers mortality, but it is a spiral of events that leads to either recovery or mortality (Franklin et al. 1987; Schwalm et al. 2017).

Climate-induced physiological stress is expected to increase tree mortality. In addition, other stressors such as insect infestation, pathogens, and wildfires are expected to enhance tree mortality (Anderegg, Hicke, et al. 2015; McDowell & Allen 2015; IPCC 2019). Both high and low latitude forests are threatened by such extreme events (Lindner et al. 2010; Mokria et al. 2015; IPCC 2019).

Precipitation patterns are one of the major factors affecting the terrestrial ecosystem and especially the forest ecosystem by influencing tree mortality. Trees can tolerate high temperatures if water is available (Kirschbaum 2000). Of concern is a decrease in precipitation with increasing temperature. High temperatures lead to an increase in the vapor pressure deficit, i.e., the dry and hot air increases evapotranspiration from the stomata of the leaf and causes it to dry out. The vapor pressure deficit is projected to continue to increase, therefore drought stress in forests will also increase at an unprecedented rate by 2050 (Williams et al. 2013).

In Central Europe, the growth of *Fagus sylvatica* is mainly driven by the amount of precipitation during the growing season. The growth of *Pinus sylvestris*, by contrast, is correlated with the average temperature of March, but this is merely a proxy for the role of available energy for photosynthesis (Scharnweber et al. 2011; Harvey et al. 2020). Nevertheless, temperature and solar radiation are not directly linked, as a warmer climate is also associated with higher humidity and cloudiness.

European annual mean temperature has risen continuously since 1979 and is expected to rise further, while precipitation patterns tend to vary locally (decreasing in Southern Europe and increasing in Northern Europe, while no consistent pattern can be seen in Central Europe, see Section 3.5.2). In addition, the frequency and intensity of droughts are expected to increase (Section 3.5). As a result, temperature warming is expected to exceed soil moisture throughout Europe (Samaniego et al. 2018). In Germany, temperatures have risen steadily over the last 40 years, while precipitation has decreased over the last 10 years (Section 3.5). These patterns, combined with severe summer droughts and insect infestation, have resulted in a local increase in tree mortality (Schuldt et al. 2020).

Crown defoliation is an indicator of tree vitality and health. Tree vitality indicators have a rapid response to drought (Rohner et al. 2021) and subsequent recovery (**Manuscript 3** and **4)**. As the frequency and intensity of droughts is increasing, tree vitality is decreasing, and the defoliation trend is accelerating. Carnicer et al. (2011) showed that a decline in crown condition correlates with tree mortality. This pattern is not singular, e.g., Sousa-Silva et al. (2018) showed increasing defoliation trends for *Quercus petraea*, *Quercus robur*, and *Fagus sylvatica* in Belgium between 1990 and 2015. In Germany, the 2018 summer drought led to a sharp decline in the vitality of saplings, which subsequently resulted in species-specific mortality (**Manuscript 4)**. For example, among 15 common sapling species, *Sorbus aucuparia* saplings had the highest mortality, *F. sylvatica* intermediate mortality, and *Quercus* spp. saplings had the lowest mortality (**Manuscript 4)**. As drought periods become more frequent and intense, forest managers need to know which species are at risk and which can withstand the drought-related threats. Thus, understanding species-specific tree mortality is critical for long-term forest management.

4. Synopsis

4.1. Synthesis of the manuscripts

In the following, I provide a summary of the manuscripts included in this dissertation and explain how they address unanswered questions in forest ecology. In addition, I present the main findings and indicate how they can inform conservationists, forest managers, and stimulate new debates in the scientific community. Each of the manuscripts included addresses one of the most pressing issues posed by climate warming and drought on forest ecosystems, i.e., climate-induced tree shifts and drought-related impacts on forest health.

By outlining the key findings of each manuscript, I aim at providing an overview of how forests will function under projected climate warming and extreme weather conditions. To achieve this aim, I specifically address (1) the ability of trees to cope with climate change by analysing spatial tree dynamics at the treeline and (2) the capacity of trees to withstand and recover from drought. In Table 4.1.1, I briefly explain the aim and methods used in each manuscript and how the results contribute to the advancement of knowledge in forest ecology.

Furthermore, in Section 8.1 of the Appendix, I have included the database created for the review conducted in Section 3.5.2, followed by a list of publications and manuscripts not included in this dissertation (Section 8.2). In Section 8.3, I list the other activities that I did while I was writing this dissertation, such as the talks and posters presented at national and international conferences, teaching activities, participation in summer schools and my activities as a scientific reviewer for peer-reviewed journals.

Table 4.1.1. A summary of the manuscripts that are part of this dissertation, including their aim, data used, methodology, key findings, and how the results advance the scientific foundation of forest ecology.

	Aim	Data	Method	Key findings	Scientific advances in forest ecology
1	Spatial dynamics of isolated populations of *Pinus cembra* in protected areas in the Carpathians	In-situ survey	Spatial statistics - point pattern analysis	- Saplings are established at higher elevation than mature trees in a long-term protected area	- Establishment of isolated populations is possible through individual conservation strategies
2	Treeline shift under climate change in the Mediterranean region	High-resolution aerial imagery	Georeferencing, tree mapping, multivariate statistics	- Trees do not always track climate change - Aridity might limit tree establishment at the treeline in the Mediterranean region	- Be aware of the potential temporal lag in treeline upper shift despite climate change - Be informed about the need to develop management strategies that can prevent the threats associated with climate warming, such as insect outbreaks and forest fires
3	Impact of drought on saplings and their recovery in temperate forests	In-situ survey	Univariate, multivariate statistics, recovery index	- The impact of drought on 10 common deciduous species - Species-specific recovery trajectory after the 2018 summer drought	- Data and understanding of deciduous tree species response to drought - Have knowledge of species-specific recovery
4	Drought impact on mature trees and saplings in Central European forests	In-situ survey and remote sensing data	Remote sensing analysis, multiple linear regression	- Mature trees undergo longer-lasting drought impact compared to saplings - Sapling recovery from drought and subsequent mortality is species-specific	- Be informed of the differences between the drought response of saplings and mature trees - Build knowledge of the main deciduous tree species that can thrive under more frequent and intense drought periods.

Manuscript 1 presents the spatial dynamics of two isolated populations of *Pinus cembra* in the Carpathian Mountains. Climate change is impacting the dynamics of tree populations in Europe; hence it is questionable whether trees can keep up with these changes (Section 3.6.2). Treelines are considered sensors of climate change, therefore climate-induced upward shifts can be easily detected and quantified by in-situ measurements. *Pinus cembra* is a keystone species endemic to European forests. In the Alps and the Carpathians, *Pinus cembra* forms the treeline together with few other species, such as *Picea abies*, *Larix decidua*, and *Pinus mugo*. Compared to the Alps, the Carpathians have only isolated populations, some with few *Pinus cembra* trees left, which makes them more vulnerable to climate changes. The studied isolated populations are within to two protected areas with different protection status. One population is in a Natura 2000 protected area (established in 2007) and the other in a national park (Category II, IUCN, established in 1935). Here, I argue that a long-term protection status combined with stricter protection would better promote *Pinus cembra* establishment and as a result it would enhance the elevational shift. Using spatial pattern analysis, I detected specific structural patterns. The spatial distribution of the trees indicated an upward shift in the long-term protected area (the national park), whereas in the newly established area (Natura 2000) the dynamic cannot be translated into an expansion. This work is the first to provide an assessment of the spatial dynamics of *Pinus cembra* between two protected areas in the Southern Carpathians. Thus, these findings extend the knowledge about the structural dynamics of isolated populations from Eastern European protected areas. Moreover, these results highlight the need for individual conservation strategies that can better promote the establishment and survival of tree species, especially in areas where few individuals survive. The Carpathian Mountains are home to most of the remaining primary forests of Europe, but they are being lost at an alarming rate (Sabatini et al. 2018). This region undergo greater forest loss inside protected areas than outside (Kuemmerle et al. 2009; Leberger et al. 2019). Therefore, stronger conservation measures are needed for the maintenance of these fragile mountain ecosystems, which are the source of many of our ecosystem services.

Manuscript 2 aims at identifying spatio-temporal variability in tree density and treeline position. Despite significant research on treeline response to climate change, a clear trend is not yet evident. Moreover, there are regional deviations in treeline dynamics that are less well known, especially in remote areas where in situ measurements are often limited. Therefore, historical high-resolution images from 1945 and new imagery from 2008 and 2015 were used to detect treeline changes in a remote area of Greece. The study sites are in a protected area (Category II, IUCN), namely the Samaria National Park from the Mediterranean island of Crete. The research was conducted at four sites with different aspect and treeline elevation. Despite rising temperature over the years and irrespective of treeline elevation and aspect, I found no treeline shift. The temporal lag in treeline response could be explained by the increasing aridity (see Glossary) over time (an average decrease in precipitation of 170 mm) and by a combination of topographic and microclimatic factors that play an important role at high elevations. These findings indicate that trees are too slow to track temperature changes, which could induce risks as the optimal elevation changes rapidly (Section 3.6.2). This is the first study in the South-Eastern Mediterranean region to analyse treeline changes over 70 years on high-resolution images. Progressive warming combined with a decrease in precipitation in South-Eastern

Europe results in an intensification of climatic aridity (Cheval et al. 2017). Hence, the decrease in precipitation is a major factor limiting the establishment of trees in the Mediterranean region (Peñuelas & Sardans 2021). Furthermore, these results should be linked to the review conducted at the European level in Section 3.6.2, where I show that treelines ascended in 62% of sites, remained stable in 33.2%, and even declined in 4.7% of the sites. In addition, Southern Europe has a lower shift of the treeline compared to Northern Europe. The lack of climate-induced migration should raise concerns about the threats associated with future warming, drought, insect outbreaks, and forest fires. Thus, the results offer new insights that could trigger further discussion among ecologists and biogeographers.

Manuscript 3 approaches another relevant research topic in forest ecology given the accelerated climate warming and drought intensity. The threats posed by climate change to the world's forests make it important to identify whether species can cope with recent temperature increases and changing rainfall patterns. For this purpose, both climate-mediated migration (**Manuscript 1, 2,** and Section 3.6.2) and forest response to unforeseen climatic events (Section 3.7) should be assessed. Due to these rapid changes, coniferous species that have been extensively planted outside their natural range in Europe in the past appear to be at risk of abrupt decline due to climate-related drivers. Therefore, recently more attention has been paid to deciduous tree species, as they are the main natural vegetation of temperate forests and potentially of future forests in large parts of Europe. Nonetheless, Europe has experienced several droughts in recent decades, with the 2018 drought being one of the most extreme, thus deciduous tree species fate under such conditions is still uncertain. Consequently, **Manuscript 3** focuses on the effects of the 2018 drought on broadleaf saplings from temperate forests in Central Europe. These results showed that *Carpinus betulus*, *Sorbus aucuparia*, *Frangula alnus*, and *Sambucus nigra* were the most affected species, while *Fagus sylvatica* and *Betula pendula* were the least affected. Interestingly, all species had a fast recovery one year later. Sites with high species diversity were found to be more affected by drought as competition for resources increased. Thus, these results show which tree species withstand drought better and which recover faster after a period of drought. These findings are a contribution to one of the most pressing problems in forestry, i.e., the response of forests to climate warming and drought, which is of great importance for biodiversity, climate regulation, ecosystem processes and humans. This manuscript provides the first assessment of the sapling response to the 2018 and 2019 droughts in temperate forests of Central Europe.

Manuscript 4 expands **Manuscript 3** by addressing the impact of drought on both saplings and mature trees and their recovery. Moreover, sapling survival and mortality were assessed. For this analysis, the same sites as in **Manuscript 3** were used and in addition, the mature tree health was calculated based on remote sensing data at 10 x 10 m resolution. Using this approach, I was able to show that mature trees are more affected by drought and consequently recover slower than saplings. Moreover, I found that saplings with slower recovery are more prone to mortality than those that recover faster after the drought. Comparisons of the 15 most common species showed which species are more affected by drought, which recover faster, and which have the highest mortality after drought. For example, the percentage of mortality varied among species such as *Quercus robur* (0%), *Quercus petraea* (4%), *Acer pseudoplatanus* (5%), *Fagus sylvatica* (6%), *Betula pendula* (6%), *Carpinus betulus* (8%), *Acer campestre* (12%), *Fraxinus* *excelsior* (12%), *Sambucus nigra* L. (16%), and *Sorbus aucuparia* (17%). Since drought impacts, post-drought recovery, and mortality rates are known for the most common tree species, this is valuable information for stakeholders, forest managers, and private forest owners to make decisions about which tree species to plant in the future (Section 3.7.3 and 3.7.4). These findings can be transferred to other temperate forest regions, as they cover both major and minor deciduous tree species of European forests.

4.2. Selected emerging research challenges for forest ecology under climate change

4.2.1. Mountain treelines – prospect and research needs

Over the years, the mountain treeline has been the subject of multiple studies and continues to be an important area of research (Körner 2012). However, describing treelines characteristics usually was very loosely and ambiguous which lead to various definitions of the treeline ecotone and not comparable studies. Therefore, a global framework should be followed (Bader et al. 2021). Improved recognition of tree patterns should enable a better quantitative assessment and comparable research. To understand the tree dynamics at the treeline (including growth, reproduction, establishment, and survival), as well as the relationships between tree species and environmental factors, more research is needed at the local and landscape scale (Lu et al. 2021). Studies of tree regeneration at the treeline and driving factors are necessary but rare. Also, climatic effects (summer and winter conditions) on seedlings' establishment and survival need to be closer evaluated before driving general conclusions (Holtmeier & Broll 2007; Hagedorn et al. 2014).

The sensitivity of trees and their response to extreme events should be considered in future studies, as warming increases evaporative demand, which can enable forest fires to advance at higher elevation (Holtmeier & Broll 2007; Trotsiuk et al. 2021; Alizadeh et al. 2021; Hlásny et al. 2021). The capacity of trees to cope with climate change could lag and tree mortality might increase at high elevation. This will likely cause a major change in species communities and their interactions at the treeline. In addition, long-term and more systematic monitoring are needed to understand and disentangle species-specific responses to climatic and anthropogenic factors (Vitasse et al. 2021). Consequently, an improved representation of interactions and processes at the treeline should be incorporated into process-based and empirical models to provide more reliable projections of future forest dynamics at the treeline.

Furthermore, there is a particular need for studies in remote or inaccessible areas. Dynamic distribution models (DDMs), joint species distribution models (JSDMs), remote sensing, and deep learning techniques combined with field data can rapidly help fill knowledge gaps in remote areas. The data used in **Manuscript 2** can be analysed using deep learning techniques. The methods are rather new in ecology, but of real benefit, as we can analyse larger and remote areas more quickly. Deep learning tools, such as Convolutional Neural Networks (CNN), allow us to extract a variety of individual tree characteristics from remote sensing (Kattenborn et al. 2021).

4.2.2. Future perspectives on drought-induced impacts on forest

Significant progress has been made in identifying the response of tree species to drought (Section 3.7.1 and 3.7.2), but there are still unanswered and new questions. Extreme climate events are occurring with greater intensity globally, threatening forest ecosystems and increasing uncertainty about the fate of future forests (McDowell et al. 2020). Due to these climate extremes combined with an increase in disturbances, nonlinear or abrupt responses of forest ecosystems are expected (Ratajczak et al. 2018), e.g., altered dynamics, forest functioning and/or increased tree mortality. These translate into uncertainties about the capacity of the forest ecosystem to cope with such changes. However, investigating and reducing these uncertainties is difficult because there are no historical analogues. Knowledge gaps might result from limited datasets available, which are often time-consuming or costly to collect, the lack of theoretical and structural frameworks suitable, and a limited spatio-temporal frame (Ruiz-Benito et al. 2020; Maréchaux et al. 2021). Therefore, after revising the current state of research (Section 3.6) and the research needs highlighted in current publications, I have identified several key priorities for future research on forest response to drought. The key priorities are divided into needs for monitoring and data recording and needs for progress in modelling:

Data collection:

- **Standardized monitoring of forest health, and tree mortality** (Trumbore et al. 2015; Hartmann, Schuldt, et al. 2018). Internationally standardized monitoring is critical for comparable research.
- **More data on tree mortality**. In terms of areas surveyed, data are not yet available for large areas from Eastern Europe, Asia, Mexico, South America, and Africa (Hartmann, Moura, et al. 2018). The data gap prevents us from assessing and predicting tree mortality in response to projected climate change.
- **Data at species level and data on intraspecific as well as interspecific interactions.** Research is mainly conducted on common species in response to drought, thus there is still a lack of data for less common species that can be more stress-tolerant than common species (Kunz et al. 2018). Moreover, often intra- and interspecific interactions are either neglected or generally less understood within and across ecosystems (Grossiord 2018).
- **Open data and open-source software - the key to transparency and reproducibility.** Climate change and biodiversity loss is a global problem, and we should collaborate to find solutions. Therefore, with high-quality and big data, researchers can improve our understanding and generate new insights.

Modelling approaches:

- **Scaling from local level/in-situ data to forest systems** (Hartmann, Moura, et al. 2018). By using new technologies, such as ground-based monitoring combined with remote sensing, we can gain a better understanding of processes on a larger scale.

- **Identify drivers and thresholds** of forest drought decline. Thresholds are needed to better understand forest response to drought and to predict mortality patterns in different ecosystems (Allen et al. 2015).
- **More accurate projections of future forest resilience to drought.** Models capable of accounting for accelerated climate change and a better understanding of forest resilience to drought are needed (Trumbore et al. 2015; Albrich et al. 2020). Such models are more difficult because of the large temporal and spatial scale, but they are necessary to identify resilience mechanisms across forest ecosystems. In addition, it is equally important to establish whether or not future climate change will overcome forest resilience, where, and when. This requires reliable spatial and temporal projections.
- **Realistic projections of drought-induced tree mortality across spatial scales** (Hartmann, Moura, et al. 2018). Better predictions of forest damage and drought-induced mortality are of major importance because they allow us to know where and when specific locations will be affected. Modelling approaches are essential as they allow us to identify vulnerable populations and develop appropriate mitigation measures in a timely manner (Jump et al. 2010).

To provide reliable support to conservationists, forest managers, stakeholders, and private owners, and to minimize the loss of biodiversity and ecosystem services, researchers need more data to build accurate models and improve overall understanding. In addition, many forest processes are not yet fully understood and need further research (Section 3.6.2). This can also be enhanced through increased communication between forest practitioners, scientists, and citizens. Citizen science can bring the public closer to science, and their engagement can be mutually beneficial. On the one hand, citizens can get involved in various projects, which helps spread awareness of pressing issues, improve conservation efforts, and support public education (McKinley et al. 2017). On the other hand, citizens can collect in-situ data, participate in scientific projects, and be active contributors, which is beneficial to the scientific community (Fritz et al. 2017). I am also convinced that the power of change lies in every human being and that education increases mindfulness, i.e., people's behaviour towards nature. Working together, we can tackle challenges and overcome barriers.

5. Declaration of my contributions to each manuscript

Manuscript 1

Title: **Differences in the spatial structure of two *Pinus cembra* L. populations in the Carpathian Mountains**

Authors: **Beloiu, M**., & Beierkuhnlein, C.

Journal and status: published in ***Forests***, impact factor 2.63, 10, 4, 326, (2019)

Personal contribution: idea and concept: 70%, field work: 100%, data analysis and figures: 90%, writing: 85 %, corresponding author

Manuscript 2

Title: **No treeline shift despite climate change over the last 70 years**

Authors: **Beloiu, M.**, Poursanidis, D., Tsakirakis, A., Chrysoulakis, N., Hoffmann, S., Lymberakis, P., Barnias, A, Kienle, D. & Beierkuhnlein, C.

Journal and status: published in ***Forest Ecosystems***, impact factor 3.64, 9: 100002, (2022)

Personal contribution: idea and concept: 20%, data acquisition (0%), data analysis and figures: 90%, writing: 70 %, corresponding author

Manuscript 3

Title: **High recovery of saplings after severe drought in temperate deciduous forests**

Authors: **Beloiu, M.**, Stahlmann, R. & Beierkuhnlein, C.

Journal and status: published in ***Forests***, impact factor 2.63, 11, 4, 546, (2020)

Personal contribution: idea and concept: 40%, field work: 65%, data analysis and figures: 90%, writing: 90 %, corresponding author

Manuscript 4

Title: **Mature trees suffer longer-lasting drought impact and recover more slowly than saplings in Central European forests**

Authors: **Beloiu, M.**, Stahlmann, R. & Beierkuhnlein, C.

Journal and status: published in ***Forest Ecology and Management***, impact factor 3.55, 509: 120075, (2022)

Personal contribution: idea and concept: 60%, field work: 90%, data analysis and figures: 90%, writing: 95 %, corresponding author

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7. Manuscripts

7.1. Manuscript 1 - Differences in the spatial structure of two *Pinus cembra* L. populations in the Carpathian Mountains

Title: Differences in the spatial structure of two *Pinus cembra* L. populations in the Carpathian Mountains

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Abstract: *Pinus cembra* L. is a key species of high elevation forest ecosystems in Europe. However, in most mountain ranges, its importance has declined considerably. Remnant populations are often isolated and their dynamics and functioning are not well understood. Here, we apply novel approaches in pattern analysis to two *P. cembra* populations in the Carpathian Mountains in order to identify commonalities and divergences in their spatial structure and dynamics. Four study sites (1.2 ha each) were investigated within the treeline ecotone in two protected areas that differ in terms of protection status. Based on height and diameter, the individuals were classified into three size-classes: sapling, intermediate and adult trees. Spatial distribution and interactions between tree sizes were analyzed using point pattern analysis. The overall structure of all trees was aggregated at a small distance and regular at a greater distance in the population from the Natura 2000 site ($p = 0.002$), while in the National Park population it was a random pattern. However, the general patterns do not apply to tree size classes and the relationship among them. In the Natura 2000 site, there was no correlation, all the trees were mixed, regardless of their size. In the National Park, the sapling and intermediate were strongly clustered ($p = 0.001$), but the adult trees were spatially separated from all juveniles, forming patches at a lower elevation. In both areas, spatial patterns indicate the dynamics of the *P. cembra* population. Whereas in the National Park population, there is evidence of an upward shift, which cannot be confirmed in Natura 2000, where size classes are completely mixed and the dynamic does not translate into an expansion of the population area. The spatial differences between the two populations indicate that conservation strategies need to be developed more individually to support the regeneration of these isolated populations.

Keywords: forest management; treeline dynamics; mark correlation; point pattern analysis; national park; natura 2000

1. Introduction

Spatial patterns are essential for understanding the structure, dynamics, and functioning of plant communities [1,2]. As contrasted with stochastic distributions, these scale-dependent patterns are controlled by processes such as seed dispersal, biotic interactions, and nutrient or water availability, each of which in turn is scale-dependent [2–4]. Moreover, facilitation and competition are important drivers of the spatial structure of the species [5,6]. In harsh conditions, high density of young and mature tree species can increase the growth and survivorship [5,7]. Establishment and survival of seedlings have been explained by several theories, such as dispersal limitation and Janzen–Connell hypothesis. Janzen–Connell hypothesis asserts that seed predators, herbivores, intraspecific competition, and pathogens affect the establishment and survival of seedlings near the parent trees [8,9]. Therefore, the hypothesis predicts a higher survival of seedlings at a greater distance from the conspecific trees. This hypothesis has been developed for tropical forests, but has been applied and also confirmed in temperate forests [10,11]. Processes that influence the spatial structure and forest dynamics can be provided by analyzing spatial patterns and tree relationships [12]. Point pattern analysis effectively detects the spatial structure and relationships established between trees by using the size structure and distribution of the age or height of tree populations [13].

Pinus cembra L. is a tree species endemic to the European region, and a component of the subalpine forests [14]. The species is abundant in the central Alps, but only small and isolated populations exist in the Carpathian Mountains [14,15]. Among these, the populations from the Tatra and Retezat Mountains are the largest, with over one thousand individuals, and greater genetic diversity than those in the Alps [16–19]. However, most of the Carpathian populations have a very low number of individuals, under 150 [16,19], which makes them more prone to inbreeding depression and low genetic variation [17,18]. Generally, marginal populations tend to exhibit lower density than central populations [20,21], resulting in increased sensitivity towards environmental and anthropogenic impacts. These aspects highlight their importance in ecology and conservation [17]. Studying the current spatial patterns and the structural dynamics of isolated or marginal populations may help us to understand the processes that influence their expansion or retraction [12]. In the Romanian Carpathians, *P. cembra* grows at an elevation between 1350 m and 2200 m a.s.l., and has *Picea abies* Karst. as its main competitor [16]. A single bird species, *Nucifraga caryocatactes* L., is the only vector for seed dispersal for *P. cembra*. The *N. caryocatactes* occurrence is abundant in the Romanian Carpathians [22]. Biotic factors, such as seed deposition, seed predation, overstorey, and understorey vegetation, are considered to be more important for the species' natural establishment and regeneration than abiotic factors [23]. *P. cembra* has a restrictive habitat in Romania and is part of the protected habitat types of the Natura 2000 network [24]. However, the species is threatened by human activities (such as livestock grazing and tourism) that have fragmented its natural habitat, reducing its regeneration [15].

In the harsh climate of the treeline ecotone, forest dynamics and structure have been strongly altered by human land use [25]. The treeline ecotone is a transition zone between the closed forest and the upper limit of the isolated individuals [26,27]. The treeline ecotone range (Table S1) varies mainly due to thermal limitations, anthropogenic influences, and mechanical causes [26]. In the Romanian Carpathians, *P. cembra* occurs always inside protected areas [19] and may fall sometimes under areas with different status of protection. Protected areas contribute to habitat maintenance by controlling deforestation and pastoralism [28,29]. Human pressure varies significantly with protection status [29]. Between 1880 and 2000 deforestation close to the treeline ecotone was more intense in the Carpathians compared to the Swiss Alps [30,31]. In recent years human influence has decreased in both areas [25,32]. In Romania, the coverage of protected areas increased from 4.1% in 1989 to 24% in 2017 of the total country area [22]. In addition to the well-known IUCN protected area categories, the Natura 2000 network was created at the European Union level. Its aim is to facilitate the protection of threatened species and natural habitats not through strict protection but rather through a sustainable approach to promote traditional practices [22]. Unlike national parks (IUCN category II), the lack of funding for the European Natura 2000 network leads to social and economic tensions rather than actual conservation and development [22]. National parks often have core zones with more restrictive management than the Natura 2000 network.

To capture also possible differences induced by the protection status, two populations of *P. cembra* were sampled in two areas: a Natura 2000 site, established in 2007, which does not benefit from strict protection; and a National Park (IUCN category II), which has been under protection since 1935. The Natura 2000 site was influenced by past anthropogenic disturbances and presents a higher grazing intensity than the Retezat National Park [33]. So far, *P. cembra* populations were mainly analyzed by dendrochronology, to reconstruct the past climate [34,35]. In addition, responses to present and future climate change were assessed [14]. Although the spatial structure has been analyzed in the Alps [25,36], little is known about the spatial distribution of individuals and spatial patterns of the tree sizes in the Carpathian Mountains.

The purpose of this paper is to study the spatial structure and dynamics of two isolated populations of *P. cembra* in the protected areas of the Carpathian Mountains. Our specific objectives are to: (1) characterize the spatial structure of *P. cembra* populations, (2) evaluate and compare the spatial relationship within and between the two populations, and (3) assess their tree size hierarchy. The achievement of these objectives will provide insights into processes that enhance the dynamics and functioning of isolated populations and can be made inferences about their future distribution at the treeline ecotone.

2. Methods

2.1 Study Area

The study sites are located in the treeline ecotone, in two subdivisions of the Southern Carpathians, Romania (Figure 1). One of the study sites is located in the Retezat National Park (IUCN category II). In addition, this protection status overlaps with other categories of protected areas, including a scientific reserve (IUCN category Ia). The second study site is located in the Parâng Mountains, with the site having been included in the Natura 2000 network since 2007, under the Habitats Directive, as a site of community importance (SCI). The elevation of the treeline ecotone depends on the study sites. In the site from the Retezat National Park, the treeline ecotone has a range between ~1730 and 2058 m a.s.l., whereas in the Natura 2000 site only between ~1670 and 1820 m a.s.l. (Table S1). The tree population has a small and isolated distribution (Figure 1). There is clear evidence of historic and present-day mixed land-use near the site, a high density of roads passing through the site, and at the treeline ecotone old stumps and remains of *Pinus mugo* Turra, *Picea abies* and *P. cembra* have been observed. The intensity of grazing is higher in the Natura 2000 site than in the Retezat National Park, with a 0.42 sheepfold/km2 compared to 0.19 sheepfold/km2 [33].

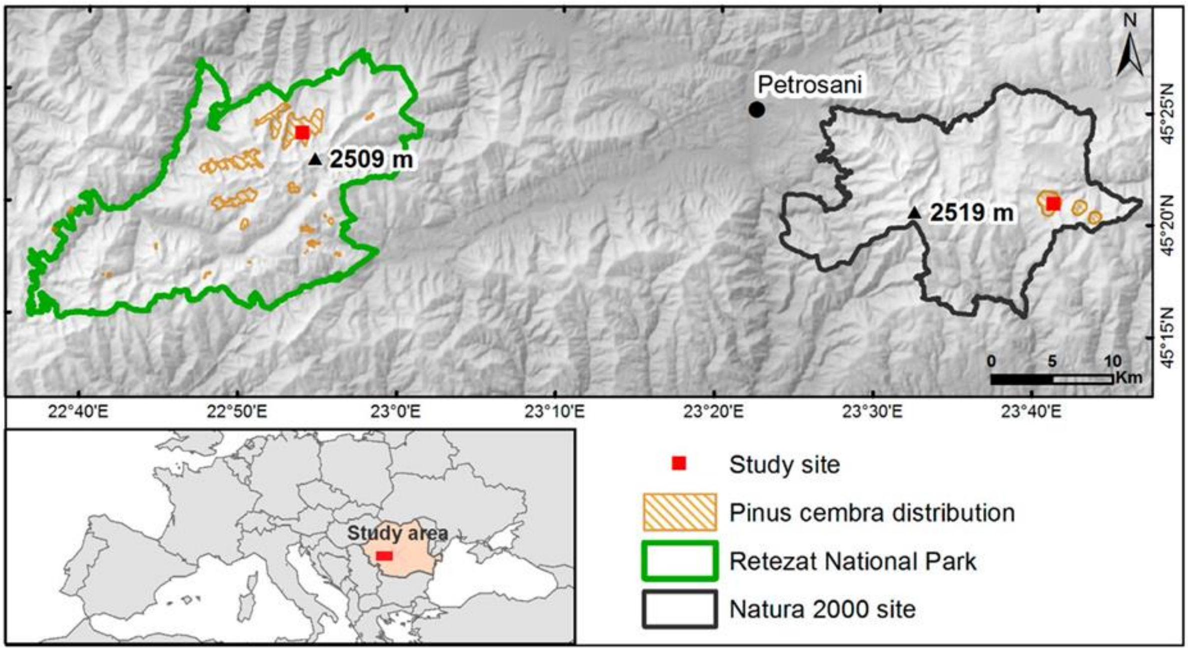


Figure 1. Study sites in the Southern Carpathians, Romania.

Both massifs have a glacial morphology with a maximum elevation of 2509 m a.s.l. (Peleaga peak) in the Retezat Mountains, and 2519 m a.s.l. (Parângul Mare peak) in the Parâng Mountains. The soils are orthic podzols with a crystalline schist bedrock. The mean annual temperature is −0.5 °C at 2190 m a.s.l. (1959–2009) in the Retezat Mountains and below −1 °C above 2200 m a.s.l. in the Parâng Mountains; the mean annual precipitation is almost similar across both sites: 1100–1400 mm in the Retezat Mountains, and 1000–1200 mm in the Parâng Mountains [37,38].

Four large rectangular plots (200 × 60 m, 1.2-ha) were established in the treeline ecotone

(Figure 2). All plots were aligned from low to high elevations (Table S1). Two plots were established in the Rea Valley—Retezat National Park. One plot was situated at an elevation of 1754 m a.s.l. (Figure 2a), on a 8%–38% northeast slope, with 55% *Pinus mugo*, 40% *P. cembra* and 5% herbaceous plants. The other plot was situated at 1886 m a.s.l., on a 38%–76% northeast slope (Figure 2b), with 40% *P. mugo*, 25% *P. cembra*, 20% rock outcrops and 15% *Vaccinium–Rhododendron* shrubs and herbaceous plants. The other two plots were established in the Dengheru Valley—Parâng Mountains. One plot was situated at an elevation of 1719 m a.s.l. (Figure 2c), with the understory dominated by 60% *Vaccinium–Rhododendron* shrubs and herbaceous plants, 20% *P. cembra* and 20% *Picea abies*. The other plot was situated at 1726 m a.s.l. (Figure 2d), with 70% *Vaccinium–Rhododendron* shrubs and herbaceous plants, 20% *P. cembra* and 10% *Picea abies*. Both plots had a northwest slope with a variation between 14% and 38%. Tree distributions contain areas of lower density that can be caused by habitat heterogeneity, such as edaphic conditions.

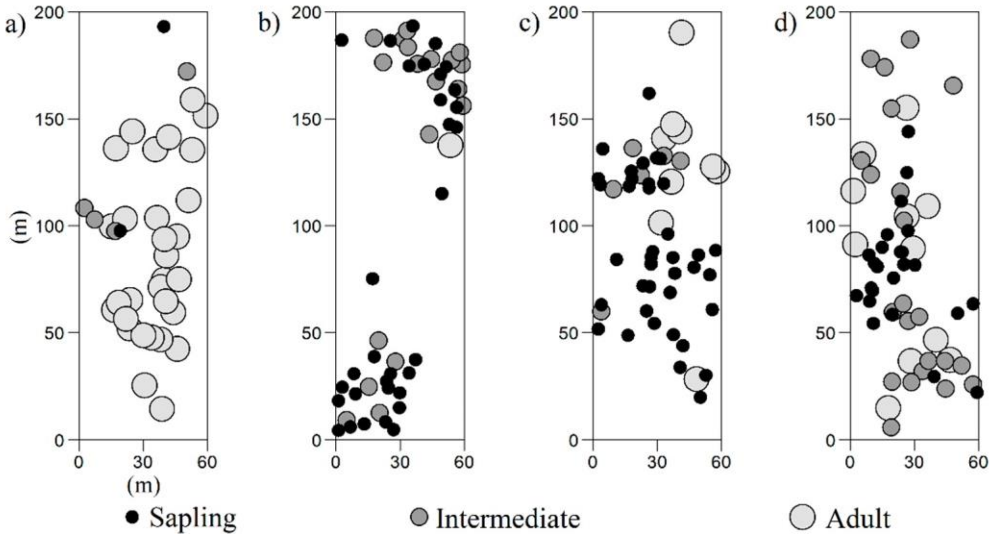


Figure 2. Spatial distribution of *Pinus cembra* L. within the plots from the Retezat National Park (**a**,**b**); and from the Natura 2000 site (**c**,**d**). The quantitative marks indicate the tree sizes: sapling (10–130 cm height), intermediate (1–15 cm diameter breast height), adult (>15 cm diameter breast height).

In both study sites, *P. cembra* occurs in association with *Picea abies* at a lower elevation, forming a mixed forest, and at higher elevation occurs with *Pinus mugo*, *Sorbus aucuparia L.*, and *Alnus viridis* DC. The height of all *P. cembra* individuals taller than 10 cm was measured in all plots. The diameter was measured at 1.3 m height for all individuals ≥1.3 m. Where multiple stems were growing from the same base, only the largest was measured. The locations of trees were mapped using a global positioning system (GPS) device with an accuracy of 1 to 3.5 m (Garmin GPSMAP 62). In total, 112 individuals were mapped and measured in the Natura 2000 site, and 88 individuals in the Retezat National Park. The trees were categorized into three classes: sapling, intermediate and adults (Table 1). The data was collected during two field surveys, one in 2016 and the other in 2017.

Table 1. Recorded individuals and diameter at breast height for three size classes of *Pinus cembra* L. in the Carpathian Mountains. Diameter at breast height (DBH).

Plots	Natura 2000 Site	Retezat National Park
# sapling (10–130 cm height)	64	33
# intermediate (1–15 cm DBH)	28	24
# adult (>15 cm DBH)	20	31
DBH Intermediate (cm) (mean, min-max)	5.4 (1.9–14.3)	6.1 (0.6–14.9)
DBH Adult (cm) (mean, min-max)	44.2 (15.2–111.4)	32.6 (16.5–55.4)

2.2 Spatial Patterns Analysis

To assess whether all the trees in each site had a clumped (grouped together), random or regular spatial distribution a point pattern analysis was used. The univariate inhomogeneous pair correlation function (*ginhom(r)*) can be applied for heterogeneous plots and is defined as:

$$ginhom(r) = Kinhom^{J}(r)/(2 \times pi \times r), \tag{1}$$

where $Kinhom^{J}(r)$ is the derivative of the inhomogeneous K function and r is the distance. This function accounts for spatial heterogeneity [39,40].

The inhomogeneous g(r) with the heterogeneous Poisson null model (HP) was applied to account for second-order effect [41]. Large-scale aggregation is attributed to environmental heterogeneity (soil, nutrients, elevation, slope) and small-scale clustering (<20 m) is attributed to plant–plant interactions [42]. Values above the totally random distribution curve (HP—the 95% confidence interval) indicates a clumped distribution, within the HP indicates a random distribution and below the HP a regular distribution. The univariate inhomogeneous pair-correlation function *ginhom(r)* was used with 1000 Monte Carlo simulations and 95% confidence interval to analyze and compare the distribution patterns (regular, clustered or random) of tree individuals. The bandwidth was determined for each dataset by using the cross-validated bandwidth selection function [43]. The Epanechnikov kernel and Ripley's isotropic edge correction were applied to the data [43]. The function g(r) accounts for point density at a specific distance, while the related inhomogeneous K(r) is a cumulative distribution function that calculates the average number of points in a given radius *r* [41]. From an ecological point of view, K(r) makes the interpretation of the results more difficult but has the advantage of better testing of the goodness-of-fit [44]. Therefore, we used both inhomogeneous g(r) for detecting fine-scale patterns and K(r) for the confirmation of the null model.

2.3 Modelling the Spatial Relationship between Tree Sizes

Analysis of bivariate pattern revealed the interaction structure between two types of points (e.g., sapling vs. adult). If the points had extra information attached to them (called quantitative marks: the attribute of the point, such as tree height or diameter) then a bivariate analysis can be carried out [37,39]. Bivariate cross-k multitype analysis (*Kij(r)*) can be defined by analogy to Ripley’s K-function:

$$k_{ji}(r) = \lambda_j^{-1} E \tag{2}$$

The function estimates the expected (E) density (λ) of points of type j (e.g., “sapling”) within a given distance r of a point of type i (e.g., “adult”) [43,45,46]. The cross-k analysis was used to assess the intra-size spatial relationship between different tree size classes. Type j points are positively correlated, random or negatively correlated, with type i points when the observed cross-k curve is above, within or below the 95% confidence interval [13]. Ecologically, a positive correlation means attraction between tree size classes (such as between sapling and intermediate individuals), the random pattern signifies spatial independence, therefore there is no relationship and a negative correlation means segregation or repulsion between tree size classes. The cross-k function was used under complete spatial randomness (CSR) with a 1000 Monte Carlo simulations, a bandwidth of 9 m and an isotropic edge correction [13,43]. In addition, we also used the cross-type pair correlation function to confirm the spatial patterns detected by the cross-k function.

2.4 Spatial Correlation and Autocorrelation

In order to evaluate the spatial correlation of the given marks of *P. cembra*, mark correlation function *kmm(r)* for multitype point processes was used:

$$k_{mm}(r) = P_{0u}[(M(0), M(u)]/P[M = M'], \tag{3}$$

where P_{0u} denotes the conditional probability given that there are points at the location 0 and u separated by a distance r; $M(0)$ and $M(u)$ are the marks attached of those two points and P is the probability of drawing independently random marks from the marginal distribution of marks that are equal to each other ($M = M'$) [43]. The function helps to test if the quantitative marks of individuals are spatially aggregated or segregated. If marks (S—sapling, I—intermediate, and A—adult) assigned to points are independent, then the function is equal to one for all distances. If *kmm(r)* > 1 it means that points located apart at distance r tend to have larger marks indicating a positive correlation. A *kmm(r)* < 1 indicates negative correlation and points tend to have smaller marks [47]. From an ecological point of view, the values of the function can be associated with interaction effects such as independence, attraction or mutual stimulation, inhibition or mutual suppression of the trees [48].

The mark correlation function can detect only the multitude of sizes at a given distance r but mark variogram $\gamma(r)$ can show if individuals have the same or different size at a certain distance from one another, therefore, both analyses were necessary to assess the local size hierarchy of the trees. The function calculates the squared difference between the marks of the pairs of points, within a certain distance r where x and $x + r$ are the points at location x and $x + r$; E is the expectation [47,49]:

$$\gamma(r) = \frac{1}{2}E(m(x) - m(x + r))^2;\ r > 0 \tag{4}$$

Values of $\gamma(r) < 1$ signify a positive autocorrelation, suggesting a similar size of the neighbors, and individuals with similar marks tend to be found together. Values of $\gamma(r) > 1$ suggest a negative autocorrelation, which entails a strong difference in the marks, with trees of different sizes more likely to be close to each other [50]. Within the resulting graphs, along the line representing the observed values, the troughs show groups of tall trees, while the crests show groups of small trees [47,51,52]. In bivariate analysis (*kmm(r)*) the data are highly correlated, spatially independent or negatively correlated when above, within or below the 95% confidence interval, while the reverse is true for mark variogram ($\gamma(r)$).

The markcorr and markvario functions were used under complete spatial randomness (CSR) with a 1000 Monte Carlo simulation of the null model. Moreover, the bandwidth (h = 9.5 m) was calculated and the isotropic edge correction was applied to the data [13,43]. The *p*-value corresponds to the Loosmore and Ford goodness-of-fit test (GoF) for spatial point patterns. The GoF test was computed for each analysis in order to evaluate the suitability of the models [53]. For the design of the plots ArcGIS 10.5 software (ESRI, Redlands, CA, USA) was used, and the statistical analysis was carried out using the open source software R version 3.5.1 (R Core Team) [39] with the ‘spatstat’ package [43].

3. Results

3.1 General Spatial Distribution Pattern

The spatial distribution of all *P. cembra* individuals showed a significant aggregation pattern in the Natura 2000 site and a random pattern in the Retezat National Park. In the Natura 2000, the trees were clustered at a small distance, up to 5 m, random between 5 and 30 m and regular at a greater distance (30–40 m). Although the pattern varied from clustered to regular, it was significant ($p = 0.002$, Figure 3a). The significant pattern was also confirmed by the inhomogeneous K(r) function. In the Retezat National Park, although the trees appeared aggregated in the plots, due to habitat heterogeneity, the analysis showed a random pattern that was in a continuous decline to a regular pattern at a greater distance (30–40 m) (Figure 3b). The random patterns indicated an independent spatial location of the trees. Most of the observed values fell within the confidence interval, indicating a random distribution ($p = 0.291$). These results were confirmed also by “Ripley’s K function”, as inhomogeneous K(r) values showed a decreasing pattern from random to regular but significant ($p = 0.009$).

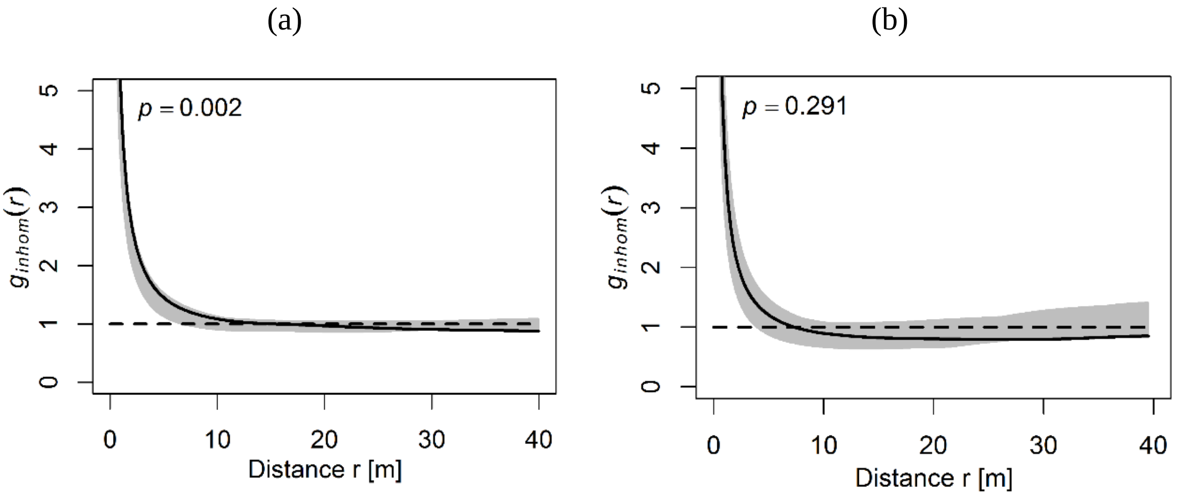
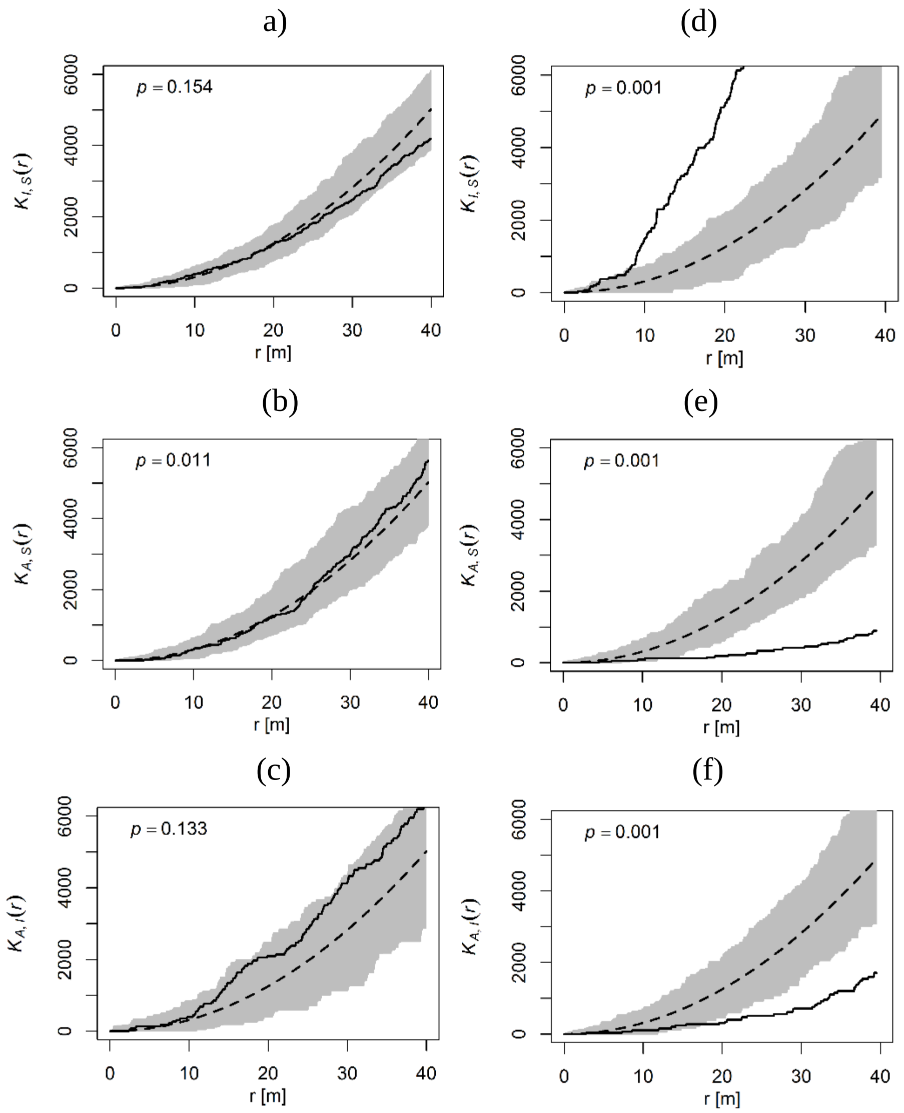


Figure 3. Spatial pattern (pair correlation g(r)) of all *P. cembra* L. individuals from the Natura 2000 site (**a**) and the Retezat National Park (**b**). The solid line shows observed g(r) values, the dashed line denotes the totally random distribution curve (HP) and the gray area represents the 95% confidence interval.

3.2 Spatial Distribution of the Tree Size Classes

The spatial distribution of tree size classes showed different patterns between the protected areas. In the Natura 2000 site was not a significant pattern between the tree size classes ($p > 0.05$), although there were variations depending on the spatial structure of the species (Figure 4a–c). The cross-type pair correlation function confirmed the random pattern ($p > 0.05$).

In the Retezat National Park, only one class presented a positive correlation, the other two had a negative correlation. Although the saplings displayed strong aggregation around the intermediate trees ($p = 0.001$, Figure 4d), especially at a distance greater than 3 m, they showed a significant negative correlation toward the adults at distances greater than 10 m ($p = 0.001$, Figure 4e). The cross-type pair correlation function confirmed the significance of spatial patterns ($p < 0.001$) and presented a similar scale of clustering and segregation. The intermediate trees displayed also a strong negative correlation with respect to adult trees ($p = 0.001$, Figure 4f), but the values of the cross-type pair correlation presented some variations. The observed values were outside the confidence interval only between 20–30 m, but the overall result was not significant ($p > 0.05$). This indicates that the pattern was not very strong and the intermediate trees were segregated at a distance of 20–30 m from the adult trees.



Natura 2000 site Retezat National Park

Figure 4. The spatial relationship (cross-k function Kij (r)) between individuals belonging to different tree size classes. The solid line shows observed Kij (r) values, the dashed line denotes the complete spatial randomness (CSR) and the gray area represents the 95% confidence interval. (a,d): Intermediate–Sapling, (b,e): Adult–Sapling, (c,f): Adult–Intermediate.

3.3 Size Hierarchies

The distribution of the heights and diameters, kmm(r) values, showed different pattern within each protected area. In the Natura 2000 site, both intermediate to sapling and adult to sapling classes displayed a positive correlation, indicating the dominance of trees with larger marks at distances between 10 and 20 meter (p = 0.001, p = 003, Figure 5a,b). The adult to intermediate class showed a random distribution (p = 0.868, Figure 5c). In the Retezat National Park, the adult to sapling and adult to intermediate classes displayed a positive significant correlation (p = 0.001, Figure 5e,f). The pattern was significant at a distance greater than 5 m, indicating an attraction or mutual stimulation effect. Intermediate to sapling size classes displayed a random distribution at all distances (p = 0.889, Figure 5d).

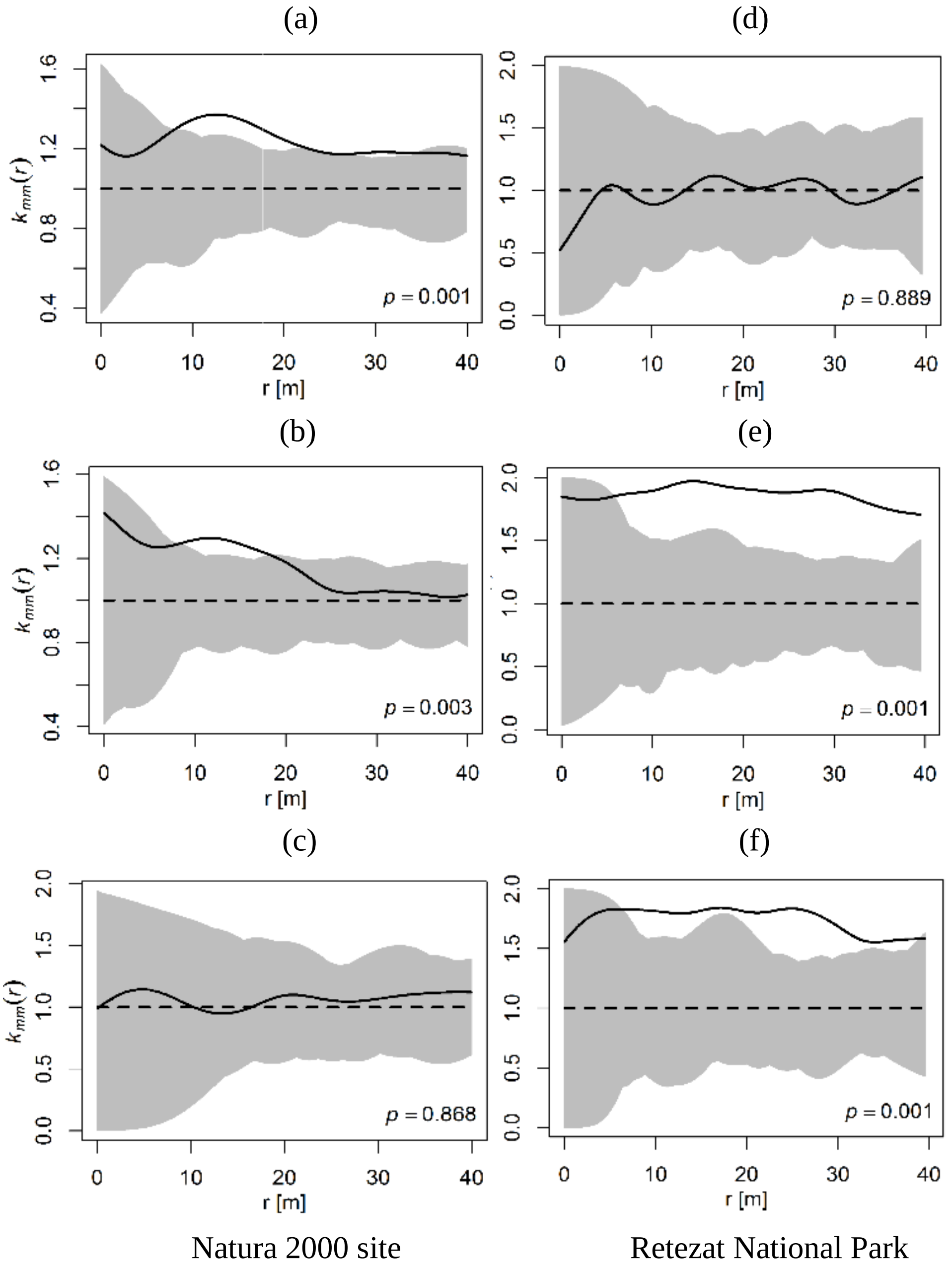


Figure 5. Multitude of size classes at distance r (mark correlation kmm(r)). The solid line shows observed kmm(r) values, the dashed line denotes the CSR and the gray area represents the confidence envelope. (a,d): Intermediate–Sapling, (b,e): Adult–Sapling, (c,f): Adult–Intermediate.

The analysis of the spatial autocorrelation, i.e., mark variogram, showed the distribution and similarity of tree marks, supporting the previous analysis. In the Natura 2000 site, between the intermediate and sapling class was a positive autocorrelation (*p* = 0.001, Figure 6a). Therefore, at a distance of 10 to 20 m, trees of similar size were more likely to be found together than trees of different sizes. Although the generated line was almost in the confidence interval, the adult to sapling class showed a positive correlation (*p* = 0.003, Figure 6b). The adult to intermediate class displayed a random pattern (*p* = 0.855, Figure 6c). In the Retezat National Park, the intermediate to sapling class presented a random distribution (p = 0.904, Figure 6d). The adult to sapling and the adult to intermediate classes displayed a stronger autocorrelation, starting with a distance of 5 m (p = 0.001, Figure 6e,f). In all figures corresponding to mark correlation and mark variogram functions, the troughs and crests of the observed values denoted the oscillations between groups of different sizes. These oscillations showed how different group sizes alternated along the distance r, even if they were not always significantly different. Also, large Kmm (r) values can indicate that patches of large trees were located at a greater distance between them.

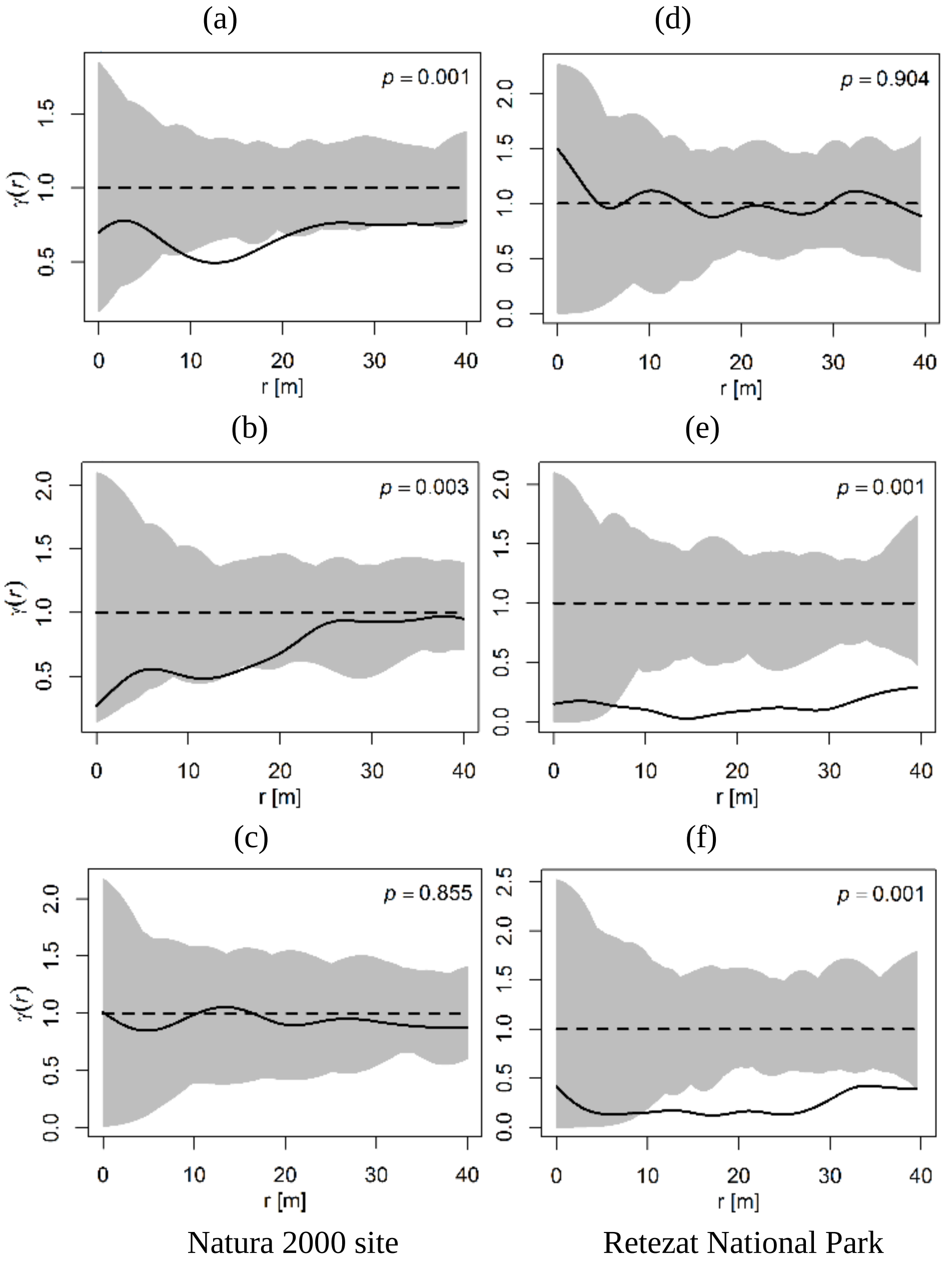


Figure 6. Spatial autocorrelation (mark variogram γ(r)) of *Pinus cembra* size classes. The solid line shows observed γ(r) values, the dashed line denotes the CSR and the gray area represents the confidence envelope. (a,d): Intermediate–Sapling, (b,e): Adult–Sapling, (c,f): Adult–Intermediate.

4. Discussion

The main objective of the study was to assess the spatial structure and dynamics of isolated populations of *P. cembra* L. at the treeline ecotone in the Carpathian Mountains. Univariate point pattern analysis was performed to identify the general patterns at the treeline and bivariate point pattern analysis to assess the relationships established between tree size classes and to detect tree size hierarchy. The significant differences detected between and within the protected areas are evidence of population dynamics.

4.1 Spatial Patterns at the Treeline

Despite the heterogeneity of the sites, the spatial patterns of all *P. cembra* individuals showed different population dynamics. In the Natura 2000 site, the species presented aggregation at a small scale and regularity at a greater scale, whereas in the Retezat National Park was a random to a regular pattern. The observed patterns might have several possible explanations.

Firstly, the clustered pattern might be caused by the selective seed distribution by *N. caryocatactes*. The bird can cache several thousands of seeds each year. Although the range of activity of *N. caryocatactes* varies, it can easily cover 700 m in elevation [27], which explains the wide range of *P. cembra* (~1730–2058 m a.s.l.) above the timberline (forest line) in the Retezat National Park. *N. caryocatactes* prefers convex topography, with less snow cover, such as small ridges, slopes, and especially rocky outcrops, where makes groups of caches at short distance between them [27,36,54].

Secondly, biotic interactions are another important factor in the establishment of *P. cembra*. Species establishment is higher above the timberline when there is less seed predation [23]. However, above 2160 m, the mortality increases due to lower temperature limitation [55]. Thicker snow cover and late snowmelt influence the development of snow fungi which are a major factor of sapling mortality [54], leading to the establishment of the species only in certain patches. Recent studies have shown that climatic warming correlated with water limitation can lead to range contraction of *Picea engelmannii* [56].

Thirdly, large-scale heterogeneity can influence the spatial dynamics of trees [40]. Therefore, using the inhomogeneous functions, we excluded the large-scale variation in habitat, quantifying only the direct plant-plant interaction on the spatial patterns. The regular patterns indicate that trees tend to be at a certain distance apart. Regular patterns are specific to larger trees since competition leads to regularity during the time. However, both sites showed random patterns, often between 10 and 30 m, suggesting that the trees are distributed randomly and that there is no competition or segregation between them. These results are partly in agreement with a previous study conducted in the Stelvio National Park, the Alps, where at the treeline was a clustered pattern, but at the timberline was an aggregated to a regular pattern [25].

4.2 Spatial Structure and Facilitation

The spatial relationship between individuals of different tree sizes can be a consequence of the different protection status of the study sites, which can imply deviations in the spatial structure. Areas with a low level of protection status (such as Natura 2000) and past disturbances, showed spatial patterns that were random. In undisturbed environments, the spatial structure of the species presented cases of strong aggregation but also segregation depending on the main environmental variables. However, in the following paragraphs, we make several assumptions for the existing patterns.

Human disturbance affects the forest structure and tree species can react differently, for instance, regeneration and tree-ring growth decrease or increase depending on the ability of the species to adapt to the disturbance [57,58]. It was shown that after disturbances, the regeneration density decreases with distance from the remnant trees [57]. However, the Natura 2000 site has been protected since 2007 and may not show any visible signs of a regeneration pattern. *P. cembra* recruitment increased in the Alps after grazing and human disturbances decreased [58]. In addition, in areas disturbed by grazing, the advance of the treeline is curtailed [59,60]. Therefore, a high density of trees at the timberline is expected, but not at the treeline, which can explain the random pattern among tree classes and the low *P. cembra* range from the Natura 2000 site. Shade-tolerant species, such as *Tsuga heterophylla* Sarg. had high intraspecific competition in young and old stands [6]. However, random patterns do not support competition between *P. cembra* size classes. A recent study showed that due to climatic warming, *Pinus flexilis* E.James established above the treeline even in soils that are a core habitat for *Pinus longaeva* D.K.Bailey [61]. Our study does not include information about neighboring species, therefore, even if there is no intraspecific competition, further research is needed to verify interspecific competition.

The clustered pattern between intermediate and sapling class from the Retezat National Park population indicates attraction and facilitation relationship among individuals. Facilitation and competition can shape the structure and dynamics of the species and their balance changes over different life stages of the species [5,6]. Saplings were strongly segregated from the adult trees in the Retezat National Park, but independent in the Natura 2000. Although it has been shown that *N. caryocatactes* hides the seeds near tree trunks [62], the results suggest that the saplings recruitment is higher at a greater distance from the adult trees in the Retezat National Park.

Growth and establishment of this species are strongly linked to temperature [58,59,63]. In the Retezat National Park, the majority of the intermediate trees and sapling individuals were found on the plot located at the upper elevation (1886 m a.s.l.). The results have shown that saplings were strongly aggregated around the intermediate trees, indicating that they grow together at a similar elevation. Moreover, the segregation pattern of adult from the sapling and intermediate individuals confirm that is a different spatial distribution between the adult and the juvenile trees. In the last 60 years, many tree species, including *P. cembra* advanced in elevation, colonizing the treeline ecotone, as a result of recent warming [64]. Long-term protection status conferred by the Retezat National Park can be translated into a natural establishment of *P. cembra* at a higher elevation. Since neither seed distribution nor human disturbance limited the distribution of the species, it can shift to a higher elevation. Along the Romanian Carpathian range, Rodna National Park (IUCN category II) benefits from a long conservation history, such as the Retezat National Park, hence, *P. cembra* is well-represented there. Whereas in areas with a low level of protection status and influenced by past disturbances, such as Natura 2000 sites or natural parks (IUCN category V), the species is mostly underrepresented [16,19]. In undisturbed areas of the Alps, recruitment and growth of *P. cembra* started at the treeline around 1850. This increase was attributed to higher summer temperatures [58]. The general upward shift of the treeline due to a higher temperature is accepted and supported by several studies [59,64,65]. Therefore, the spatial segregation of adults from the sapling and intermediate individuals is not strictly related to the lack of facilitation, but rather to the recent increase in temperature. Our findings reveal that sapling recruitment is not directly enhanced by the presence of larger trees nearby, being in agreement with the Janzen–Connell hypothesis. This seems to be a pattern available for both areas, but further research is needed to provide possible explanations for this.

4.3 Local Size Hierarchies

The positive spatial correlations, as well as autocorrelations between the intermediate to sapling size classes and adult to sapling size classes from the Natura 2000 population, indicate that similar-sized trees formed patches, whereas adult and intermediate trees were mixed. In the National Park, although the adult to sapling size classes and adult to intermediate size classes formed groups of the same size, the sapling to intermediate trees were mixed together. Beside the patchy structure, the positive spatial correlations indicate an attraction and mutual stimulation between trees with similar size [46,66]. Trees in patches tend to be larger than those outside a patch [50,52]. On the one hand, these patterns could have been produced because of variations in microsite conditions such as nutrient and light availability. On the other hand, might be the effect of a self-thinning process [67]. Due to the limitations induced by the accuracy of the data, inhibition at a lower scale can be obscured, but larger-scale patterns can be clearly detected [68].

Such positive autocorrelations are usually characteristic of a natural forest, where trees are distributed in a clumped or random manner [52]. Therefore, even the protection status offered by the Natura 2000 network can be beneficial for the species in the long term, since low aggregation was already detected. Another study showed a spatial aggregation of *P. cembra* in the Alps after a long period of time without human disturbances [28]. Similar results have been observed also at the initial stage of a subalpine *Abies* forest [52].

5. Conclusions

The study evaluated the spatial structure and dynamics of two *Pinus cembra* populations at the treeline ecotone in the Carpathian Mountains. There is strong evidence of variation within *P. cembra's* spatial structure when comparing the two sites. Firstly, there was a variation of tree spatial structure among protected areas. The spatial distribution of all trees showed clustered patterns at a small distance and regular patterns at greater distances in the Natura 2000 site, whereas in the Retezat National Park showed a random pattern. Secondly, there were also different relationships between the tree size classes within each study site. The spatial patterns within the Natura 2000 population were mainly random, with few positive autocorrelations, but in the Retezat National Park population, adult trees formed their own groups, spatially separated from the sapling and intermediate trees. In addition, sapling and intermediate trees were highly aggregated, forming groups at higher elevations in the Retezat National Park, indicating an upward shift.

These results contribute to a new background in the debate regarding the treeline dynamics and the mechanisms that are controlling it. This study demonstrates that there are several similarities and dissimilarities in the spatial structure depending on the past and present forest management, anthropogenic disturbances and natural regeneration of *P. cembra*. Considering spatial patterns of two isolated populations of *P. cembra* at the treeline ecotone, we captured the differences and similarities of their dynamics and functioning. There are numerous arguments that support our findings, but further research is needed in order to generalize them. The quantitative description of *P. cembra*'s spatial patterns provides forest managers with specific information to enhance the regeneration to maintain the genetic diversity of these isolated tree populations. Further research is needed to reveal the relationships between *P. cembra* individuals and heterospecific neighboring trees.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/4/326/s1, Table S1: Plots design. The treeline ecotone range and the elevation of the plots. Pinus cembra L. size classes: sapling, intermediate, adult.

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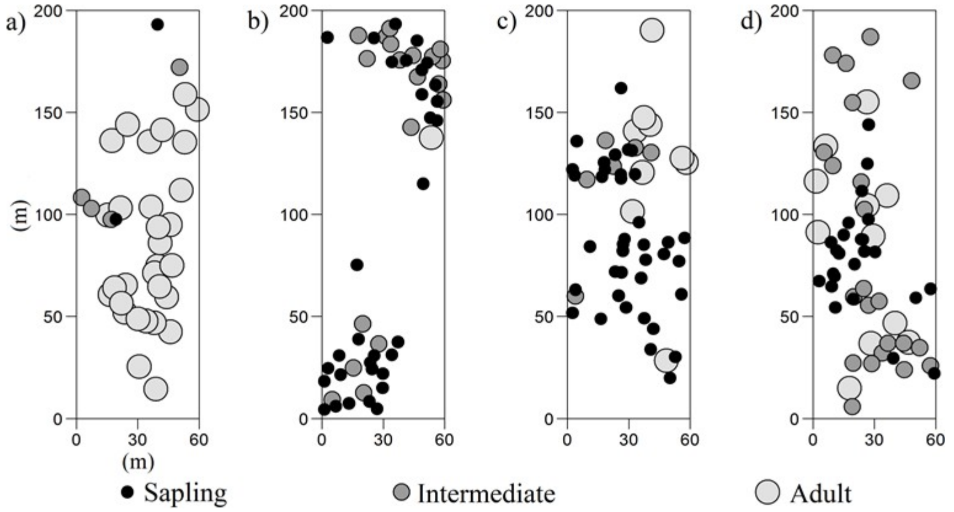
Supplementary Information

S1. Plots design.

The treeline ecotone range and the elevation of the plots.

Pinus cembra L. size classes: sapling, intermediate, adult.

Elevation m a.s.l.	**Retezat National Park**	**Natura 2000 site**
Forest line	1730 (± 20) m	1670 (± 20) m
Treeline	1920 (± 10) m	1770 (± 10) m
Tree species line	2058 m	1820 m



Plot minimum elevation	a)	1736 m	b)	1860 m	c)	1697 m	d)	1712 m
Plot maximum elevation		1772 m		1921 m		1737 m		1740 m
Plot middle elevation		1754 m		1886 m		1719 m		1726 m

7.2. Manuscript 2 - No treeline shift despite climate change over the last 70 years

Title: No treeline shift despite climate change over the last 70 years

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Abstract

Background

The recent rise in temperature and shifting precipitation regimes threaten ecosystems around the globe to different degrees. Treelines are expected to respond to climate warming by shifting to higher elevations, but it is unclear whether they can track temperature changes. Here, we integrated high-resolution aerial imagery with local climatic and topographic characteristics to study the treeline dynamic from 1945 to 2015 on the semi-arid Mediterranean island of Crete, Greece.

Results

During the study period, the mean annual temperature at the treeline increased by 0.81°C, while the average precipitation decreased by 170 mm. The treeline is characterized by a diffuse form, with trees growing on steep limestone slopes (> 50°) and shallow soils. Moreover, the treeline elevation decreases with increasing distance from the coast and with aspect (south > north). Yet, we found no shift in the treeline over the past 70 years, despite an increase in temperature in all four study sites. However, the treeline elevation correlated strongly with topographic exposure to wind ($R^2 = 0.74$, $p < 0.001$). Therefore, the temporal lag in treeline response to warming could be explained by a combination of topographic and microclimatic factors, such as the absence of a shelter effect and a decrease in moisture.

Conclusion

Although there was no treeline shift over the last 70 years, climate change has already started shifting the treeline altitudinal optimum. Consequently, the lack of climate-mediated migration at the treeline should raise concerns about the threats posed by warming, such as drought damages, and wildfire, especially in the Mediterranean region. Therefore, conservation management should discuss options and needs to support adaptive management.

Keywords: aerial imagery, protected area, continental island, Mediterranean region, high mountains, temperature, precipitation, climate change, forest dynamics

Background

Over the past century, mean annual temperatures have risen globally (Seneviratne et al. 2014), with pronounced warming trends and rapid biodiversity changes occurring at high elevations and latitudes (Ohmura 2012; Garcia et al. 2014; Lamprecht et al. 2018; Ripple et al. 2020; Vitasse et al. 2021). The Mediterranean region of Europe is particularly sensitive to global warming as it is located in a transition zone between the semi-arid regime of north Africa and the temperate humid regime of central Europe (Giorgi & Lionello 2008). The European Mediterranean biome is a hotspot of endemic species (Myers et al. 2000) and is home to more tree species than central-northern Europe (Svenning & Skov 2005). Particularly mountain regions and islands in this hotspot are of great importance for biodiversity as endemism increases with elevation and geographical isolation (Steinbauer et al. 2013; Steinbauer et al. 2016). Climate change is expected to shift the species elevational optimum (Vitasse et al. 2021), yet it is not clear if trees can track these changes (Hof et al. 2011). Studies showed that the observed tree species shift, is smaller than the expected or predicted shift (Chen et al. 2011; Zhu et al. 2012; Vitasse et al. 2021). Unlike animals, trees cannot migrate by themselves. They have a long lifespan, and their dispersal and establishment at the treeline is rather limited (Dullinger et al. 2004; Neuschulz et al. 2018), therefore it is unclear whether trees can track recent temperature changes. If trees do not adapt to these changes, consequential damage from drought, wildfires, high evapotranspiration and low soil water can be expected (Venäläinen et al. 2014; Coulthard et al. 2017; Trotsiuk et al. 2021).

Despite the large numbers of studies on treeline dynamics, continental islands are underrepresented in treeline studies; instead, most studies focus on mainland areas (Bogaert et al. 2011; Mathisen et al. 2014; Suwal et al. 2016; Zindros et al. 2020). A fundamental difference between treelines on islands and the continents is the higher degree of ecological isolation resulting in a high proportion of endemism and less ecological niche occupancy toward the summits of islands (Steinbauer et al. 2016). On the one hand, given their legacy of isolation, edaphic and geological conditions, continental Mediterranean islands are expected to host less adapted tree species compared to mainland areas (Irl et al. 2016). On the other hand, these conditions qualify for strict protection which is also expected to facilitate the expansion of forest cover (Leberger et al. 2019). The subalpine and alpine zone of the Mediterranean and the continental island of Crete are centers of endemism and thus of substantial importance for the Mediterranean biodiversity hotspot (Myers et al. 2000; Vogiatzakis et al. 2003; Kazakis et al. 2007; Spanos et al. 2008; Vogiatzakis et al. 2016). However, an upward shift of treelines can also lead to the reduction of habitats for endemic alpine species (Kidane et al. 2019). Therefore, such processes and possible dynamics need to be monitored precisely.

The treeline elevations worldwide increase from oceanic islands followed by continental (shelf) islands, to continents (mainland areas) (Irl et al. 2016; Karger et al. 2019). The latitudinal gradient of treeline elevation demonstrates the dependence of treeline elevations on climate. As the establishment of trees beyond the alpine and polar treelines is mainly caused by temperature-driven growing conditions (Körner 2012), climate warming is expected to shift treelines to higher elevations and latitudes, particularly in the Northern Hemisphere (Gatti et al. 2019; Lu et al. 2021). In addition to climate, the effects of local site conditions, such as the shelter effect should also be considered (Holtmeier & Broll 2007; McIntire et al. 2016).

The upper treeline that is separating the montane and the alpine elevation zone ("alpine treeline") is a fundamental ecological and conspicuous physiognomic boundary along the elevation gradient in high mountains. The treeline ecotone can range from rather abrupt forest margins to island, and to diffuse transition zones including in some cases a zone with characteristic shrub life forms ("krummholz") (Körner & Paulsen 2004; Holtmeier 2009; Harsch & Bader 2011). Causes and processes resulting in a sharp transition between forest and open ecosystems are multifold and still under debate (Jobbágy & Jackson 2000; Holtmeier 2009; Körner 2012; Irl et al. 2016). Temperature is among the most important and global drivers of treelines on the mainlands (Körner 2012) and plays also on islands a prominent role (Irl et al. 2016; Karger et al. 2019). In many cases, the treeline ecotone has not a clear boundary but it is characterized by a gradual decrease in tree height and density as elevation increases (Harsch & Bader 2011). Obviously, the advantage of "*being a tree*" comes at the treeline to an end. The minimum growth temperature is currently the most prominent explanation of global treeline patterns (Körner 2012): sapling survival and regeneration are limited since they are atmospherically coupled and touch higher boundaries of air masses under colder conditions. Moreover, disturbance regimes (Jentsch & Beierkuhnlein 2003) and topographical characteristics can influence the local conditions, leading to local treeline dynamic patterns (Salzer et al. 2014; Vitali et al. 2018). In addition, microhabitats e.g. rocky outcrops with consequences on isolation and snow cover are modifying zonal conditions for a given elevation (Batllori et al. 2009; Scherrer & Körner 2010; McIntire et al. 2016; Cudlín et al. 2017). Different treeline structure is a result of the combined effect of topography and human influence, however, there is no doubt about the essential influence of long-term climatic conditions on the height of the tree line. Therefore, treelines are seen as a sensor for climatic changes (Suwal et al. 2016; Gatti et al. 2019).

Earth observation and precise geospatial information are key for understanding current patterns of important ecosystem boundaries, which is the precondition to monitor and analyze future changes. Aerial imagery, multispectral satellite data, and airborne-based lidar measurements allow us to identify individual trees and can be utilized to investigate tree growth in inaccessible and remote areas over time, improving the ability to study and understand their dynamics (Chen et al. 2015; Bolton et al. 2018; Hoffmann, Schmitt, et al. 2018). However, these are usually limited in their spatial and temporal coverage, e.g. Landsat MSS data availability begins from the 1970s but spatially too coarse (60 m) to accurately identify trees. Historical aerial imagery from 1945 provides a unique and powerful data source on the land cover that enables long-time studies. Nevertheless, historical aerial imageries at high resolution (1.83–2.74 m) are still rarely used in forest cover changes (Nita et al. 2018; Rendenieks et al. 2020). Nonetheless, they are especially useful when trying to understand past conditions from periods before satellite imagery was available.

In this study, we used both historical imagery from 1945 and new imagery (2008 and 2015) to identify treeline shifts in remote, inaccessible, and protected areas of the steep mountains of Crete over a period of 70-year of anthropogenic climate change. We combined high-resolution aerial imagery with local climatic and topographic characteristics to investigate the temporal dynamics of realized treeline elevation. The study area is established in the White Mountains of the renowned Samaria National Park on Crete, a Mediterranean and continental island of Greece (Fig. 1). We specifically address the following questions: 1) Did the realized treeline change over time? 2) To which degree is the recent continental island treeline influenced by distance to the coast and wind exposure? 3) Is there an asymmetric position of treelines related to aspect? To answer these questions, we mapped the realized treeline elevation over time by using aerial images from 1945, 2008, and 2015; all images were ortho-rectified and capable of change detection at a fine scale. We then compared the realized treeline elevation between the years on four study locations with distinct topography.

Methods

Study area. The current area of the Samaria National Park (58,454 ha) is a multi-designated protected area. In 1962 Samaria was declared a National Park. Since then, it was additionally designated as a Man and Biosphere Reserve by UNESCO, and a Diploma of Protected Areas by the Council of Europe. It also includes two sites that belong to EU's Natura 2000 protected area network and is also an Important Bird Area of Greece, alongside other numerous national designations. The National Park's area ranges in elevation from sea level up to over 2,400 m a.s.l. (highest peak is at 2,454 m a.s.l.) with over 50 of its peaks exceeding the 2,000 m a.s.l. range. It is dissected by nine main gorges, with a predominant north to south direction, the longest of which is the Gorge of Samaria, with a length of 13 km. The protected areas of Samaria host a unique diversity of priority species in the European context (Hoffmann, Beierkuhnlein, et al. 2018). Until the mid-1950’s the area included uncontrolled pastoral pressure, logging, seasonal fires for the establishment of pasture lands, and small-scale agricultural activities. The main activities today (anthropogenic pressures) are tourism and semi-extensive, free-range pastoralism, however, grazing is limited within the Samaria National Park (Spanos et al. 2008). The abandonment of these lands led to the natural reforestation of old pastoral and agricultural plots with pines and cypresses (*Pinus brutia*, *Cupressus sempervirens*) (Papanastasis 2004). In contrast to the broadleaved evergreens of the area (e.g., *Quercus coccifera*, *Pistacia lentiscus*), these species are resistant to grazing pressures and thus form the main forest communities. Of the two conifer species present, cypresses are the ones that form the timberline (Spanos et al. 2008). Some of the other prominent species of the alpine areas of the Lefka Ori mountains in the limits of Samaria National Park are the shrubs *Berberis cretica* (up to 1 m height), *Prunus prostrata* (~30 cm height), and *Satureja spinosa* (~12 cm height). The Samaria National Park and its location in Crete and Greece, along with the regions selected for this study, can be seen in Fig. 1.

In total, four study sites were selected, in the N, W, S, and E areas of the Samaria National Park, and all entirely within its borders. A few potential study areas had to be excluded from the comparative survey due to the poor quality of some historical aerial photos from 1945. Reasons for this exclusion were strong shading due to extreme inclinations or artifacts due to damage to the initial aerial photo slides. Mediterranean mountain ecosystems have been exposed to millennia of human pressures and land-use changes resulting in soil erosion and degradation (Shakesby 2011; Riva et al. 2017). The investigation includes a variety of anthropogenic pressures, with currently low human pressure areas in northern, western, and southern study sites (N, S, and W) and more pronounced human influences on the eastern study site (E). Tree location was mapped over a 5 km transect along the treeline, with a mean distance between study sites of >6 km. The selected study sites are shown in Fig. 1.

The studied treeline elevations ranged from 1,270 to 1,884 m a.s.l. with the lowest treeline elevation on the northern (N) site and the highest treeline elevations on the southern (S) sites (Table 1.). The northern study site (N) is the most remote concerning road infrastructure and human activities, both historically and presently, with a treeline ranging from 1,250 and 1,550 m a.s.l.. The southern study site (S) is characterized by very steep topography and is distant to human activities and pressures, both historically and presently. Dense canopy closure appears on areas below the treeline, signifying forest-line thickening and the treeline appears relatively spread in the 1,500–1,900 m a.s.l. range. In contrast, the eastern study site (E) is the region closest to roads and human settlements, on both study periods, with partial canopy closure on some areas below the treeline, which appears predominantly in the 1,200–1,550 m a.s.l. range. The western study site (W) is close to the Samaria Gorge (the core of the Samaria National Park). At the W site, the treeline is more concentrated in the 1,450-1,850 m a.s.l. range.

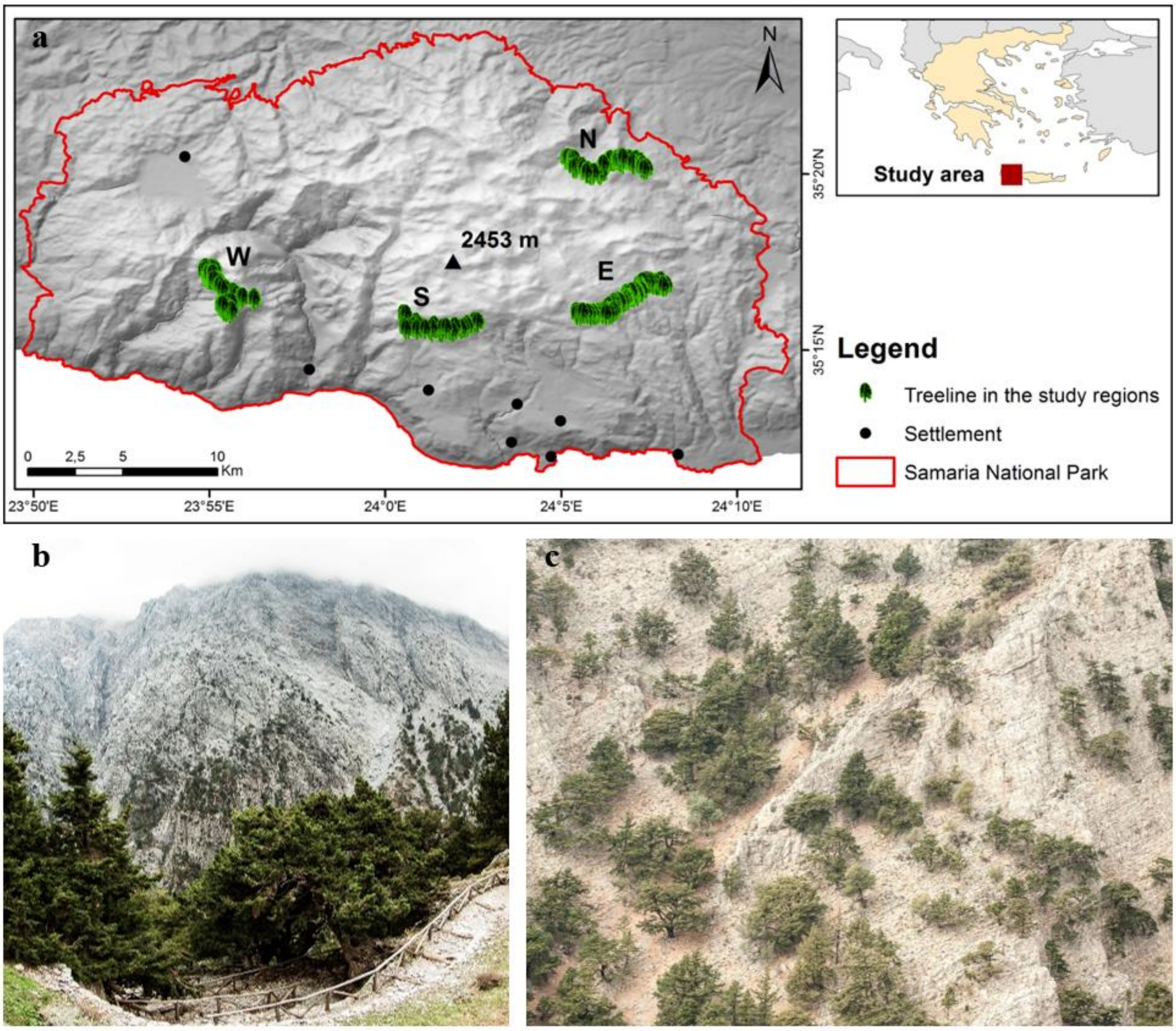

Figure 1. (**a**) Treeline in the four study sites (N= north, E= east, W= west, S= south) of the Samaria National Park in Greece. (**b**) View of the treeline from the southern slopes of the Samaria Gorge. (**c**) Tree growing on steep slopes of the Lefka Ori mountains (White Mountains).

Climate data. We used monthly data provided by the National Oceanic and Atmospheric Administration (NOAA) for the Souda meteorological station (148 m, at a distance of 10 km from the study area), Crete, Greece (NOAA/NCDC 2019). The mean annual temperature (°C) and the average precipitation (mm) were calculated between 1979 and 2020. Climate station data for a longer period and a higher elevation were not available for the study region. However, to account for the climatic conditions at the treeline, we extracted the mean annual temperature (°C) and the average precipitation (mm) from the CHELSA (Climatologies at high resolution for the earth's land surface areas) timeseries dataset (1979 - 2013). The Chelsa dataset has a resolution of ~1 km (Karger et al. 2017; Karger et al. 2018). This dataset has the advantage of capturing the climate trend from the treeline. Moreover, the precipitation algorithm includes wind fields, valley exposition, and boundary layer height (Karger et al. 2017). Local weighted regression (LOESS) lines were used to represent temperature and precipitation trends over the years. The De Martonne aridity index (IDM) was calculated based on the annual temperature and precipitation (1979-2013) from the treeline using the following formula:

De Martonne aridity index = Precipitation / (Temperature+10)

We used this index to determine if climatic conditions at the treeline have changed, as high values indicate more humid conditions and low values indicate drier conditions.

Aerial images. The availability of the aerial imagery for three reference years (1945, 2008, and 2015) from the archive of the National Cadastre & Mapping Agency S.A. (Ktimatologio 2016) allows the use of greyscale (8bit) and color (24bit) orthorectified and co-registered imagery with Root Mean Square Error (RMSE) of RMSEx ≤ 1,00 m, RMSEy ≤ 1,00 m, RMSExy ≤ 1,41 m and an RMSE of ≤ 2,44 m, for CE 95%. The images from 1945 have a resolution of 2 m, while those from 2008 and 2015 have a spatial resolution of 1 m and 25 cm. The historical aerial images (1945) have been further co-registered with the imagery of 2008 and 2015 to eliminate slight shifts in flight lines. Characteristic landscape features, e.g., rock formations, were used, and, for each image, 5 to 6 such reference ground control points were selected, resulting in an RMSE < 4 m for (CE 95%). In each region, the tree individuals found at the highest elevation and having a size of 2 m, were selected manually, using visual interpretation of the ortho-rectified aerial images by expert forest scientists, using QGIS Desktop Software v.2.18.20. We thus measure treeline elevation by the elevation of individual trees that form the treeline. These treeline measurements were grouped according to their study periods (1945, 2008, and 2015). We mapped over 550 individual trees (Table 1). We considered only those trees with a crown diameter greater than 1.5 m or those with typical crown shading.

Table 1. Tree number for each study site (N= north, S= south, E= east, W= west) per year (1945, 2008, 2015). The individual trees were mapped on the aerial images and their elevation was calculated based on the Digital Elevation Model (DEM).

Study site	**Tree number**			**Treeline elevation (m a.s.l.)**
	1945	**2008**	**2015**	**(mean, min-max)**
N	120	119	120	1384 (1270 – 1581)
S	70	73	72	1639 (1524 – 1884)
E	177	177	177	1544 (1455 – 1666)
W	192	200	202	1585 (1438 – 1763)
Total	**559**	**569**	**571**	

Topographical characteristics and data analysis. A series of variables and indices were calculated based on the Digital Elevation Model (DEM) at 5 m pixel size (Ktimatologio 2016), such as elevation, slope, aspect, wind exposition index, topographic wetness index, and the topographic profile using ArcMap 10.7.1 and SAGA GIS 6.3.0 software. Wind direction and velocity next to the ground are influenced by the land surface (Böhner & Antonić 2009).

Therefore, we used the wind exposition index as a proxy. Wind exposition index values > 1 indicate areas exposed to wind and < 1 indicate wind shadowed areas. The topographic wetness index is used as a proxy for soil moisture (Kopecký et al. 2021). The distance to the coast was calculated based on the location of each tree and the coastline using the tool “Near”, method geodesic in ArcMap 10.7.1.

A Shapiro-Wilk test was employed to check the normality of the data and a Levene test to check the homogeneity of variance, both requirements for a valid analysis of variance (ANOVA) test. In case these assumptions were not met, a non-parametric Kruskal-Wallis test was conducted. ANOVA and Kruskal-Wallis tests were applied to compare treeline elevation values across years, aspect, slope, topographic wetness index, distance to the coast across study sites, and wind exposition index across the aspect. If the Kruskal-Wallis test was significant, the difference between groups was tested using Dunn's Kruskal-Wallis multiple comparisons test. A linear regression model with the square root transformation of the explanatory variable was applied to assess the relationship between the treeline elevation and wind exposition index, based on the four study sites (N, S, E, and W). All statistical analyses were conducted with the software R 3.6.3 (R Core Team 2020) and the additional packages pgirmess, FSA, ggpubr, and ggplot2 v3.2.2.

Results

The graphical representation of the treeline for the eastern (E) study area is shown in Fig. 2a. Whereas, in Fig. 2bc. a section from the E treeline is shown on the aerial images from 1945 and 2015 representing the tree location. We found no significant treeline shifts between the study years (1945, 2008, and 2015) (Fig. 2d, $p = 0.05$) and within the study sites (Fig. 2e, $p > 0.05$). However, the treeline elevation was significantly different between N, E, W, and S study sites (Fig. 3a, $p < 0.001$). The northern study site is placed at 15 km from the sea, whereas the southern study site is only at a 4 km distance from the coastline. The slope was significantly lower on the E and higher on N, S, and W study sites ($p < 0.05$), whereas both S and N study sites, did not present significant differences in terms of slope ($p > 0.05$) (data not shown here). The topographic wetness index was not statistically significant for none of the study sites ($p > 0.05$) (data not shown here). The distance to the coast decreased from N to S and every study group was significantly different (Fig. 3b, $p < 0.001$). The topographic profile represents the relief of Crete in a cross-section (30 km) from the south to the north coast of the island. On this profile, the treeline elevation from the S and N study site is indicated (Fig. 3c). Moreover, the treeline has a diffuse form in each study site, e.g. tree density decreases with increasing elevation.

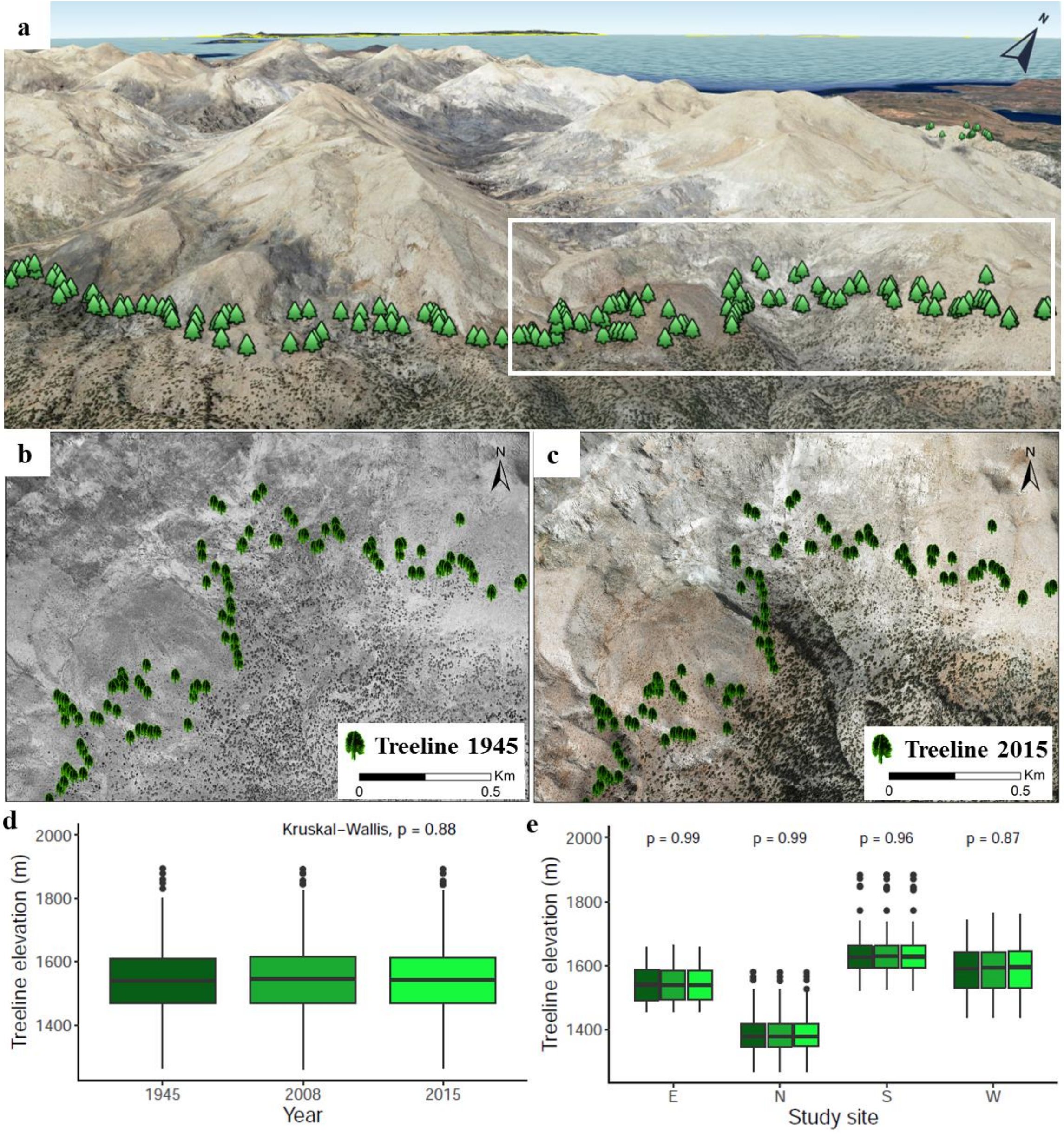

Figure 2. Treeline elevation across years and study sites. **(a)** Graphical representation of the treeline in the eastern (E) study site. The graphical imagery was obtained from Google Earth Pro© version 7.3.3.7786 (https://www.google.com/earth/). (**b**) Treeline mapped on the aerial image for 1945 and (**c**) 2015 that corresponds to the highlighted square (white) from (**a**). Boxplot comparing treeline elevation across (**d**) study years, 1945 (n = 559), 2008 (n = 569), and 2015 (n=571) and (**e**) study sites. Boxplot components: medians (black lines), interquartile range (whiskers), and outliers (black dots) are shown.

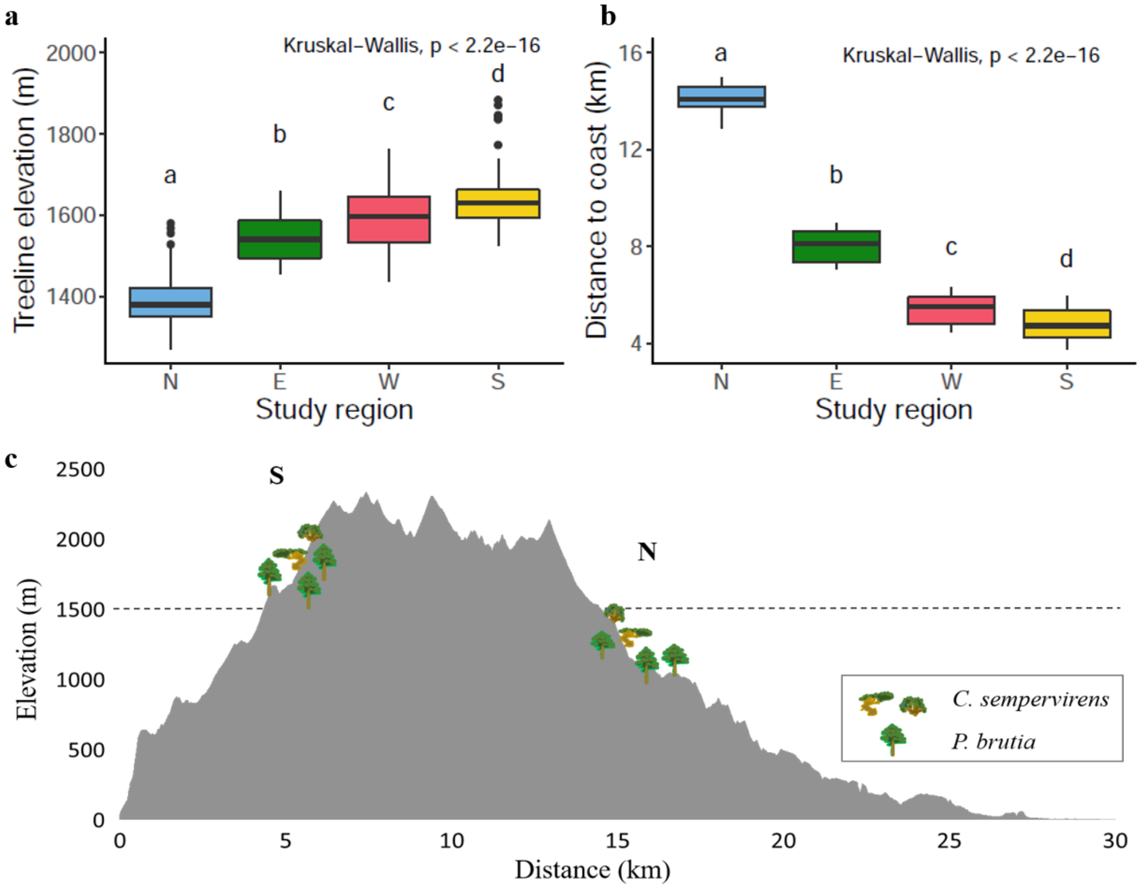

Figure 3. Treeline elevation (m a.s.l.) across (**a**) study sites and (**b**) distance to coast (km) for the four study sites (N= north, E= east, W= west, S= south). N=120, E=177, W=202, S= 72, n=571. Boxplot components as defined in Fig. 3. The letters above boxplots indicate significant differences between boxplots as calculated by Dunn's Kruskal-Wallis multiple comparisons test. (**c**) Topographic profile from the south to the north coast of the island of Crete, crossing through the S and N study sites. The treeline elevation in the S and N study site is indicated by the green symbols as a representation of the tree species (*Pinus brutia* and *Cupressus sempervirens*). The topographic profile is based on the Digital Elevation Model (DEM) at 5 m resolution.

The mean annual temperature in the investigated area increased by 1°C (Fig. 4a) and the average precipitation varied over the years with a mean of 630 mm between 1979 and 2020 for the Souda meteorological station (Fig. 4b). This covers the period of a substantial repercussion of global climate to emissions anthropogenic greenhouse gases. However, there was a relatively stable annual mean temperature between 1979 and 1995, but it increased steadily from 1995 to 2020. Such a delayed response in warming could be related to the marine environment of the island. In addition, temperature and precipitation at the treeline followed the same pattern as near the coast (Fig. 4cd). However, the average precipitation decreased slightly over time.

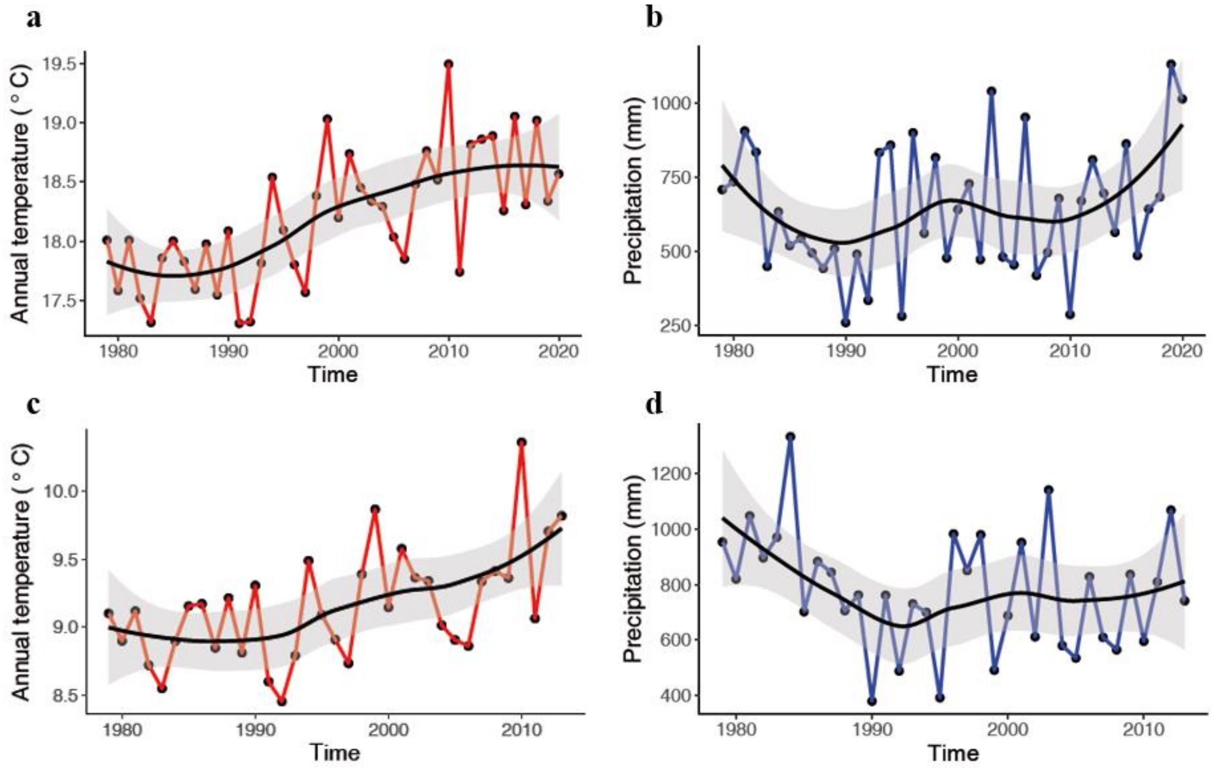

Figure 4. (**a**) Mean annual temperature (°C) and (**b**) average precipitation (mm) trend between 1979 and 2020 for the Souda meteorological station, Crete, Greece. (**c**) Mean annual temperature (°C) and (**d**) average precipitation (mm) trend for the treeline based on the CHELSA timeseries (1979 - 2013). The climatic trend is represented using local weighted regression (LOESS) lines.

Temperature increased in each study area from 1979 to 2013, while average precipitation decreased. The mean temperature decreases from N (10.08°C) to S (8.10°C). Thus, there is a 2 °C difference in mean temperature between these sites (Fig. 5a). The increase in temperature was significant for all sites ($R^2 = 0.82$, $p < 0.001$). The temperature increase between 1979-2013 was 0.81°C for the E site, 0.75°C for the N site, 0.76°C for the S site, and 0.7°C for the W study site. Precipitation decreased across all sites, with an average of 170 mm between 1979 and 2013. The decrease in precipitation was significant at the N and E sites, while the W and S sites showed the same pattern but was not significant (Fig. 5b). Moreover, treeline elevation correlates strongly with the wind exposition index (Fig. 5c, $R^2 = 0.74$, $p < 0.001$). In Figure 5d, the De Martone Drought Index shows a shift at the treeline from very humid to humid climate over the years. All study sites were statistically significant ($p < 0.001$). Therefore, the trees grow on steep slopes (with a mean angle of E=39°, N=48°, S=52°, W=60°) with high topographic wind exposure. The W, followed by the S and N study areas were the steepest ($p < 0.001$, an angle betwen 30° to 70°, data not shown). On SW facing slope the wind exposition index is significantly higher than on N, NE, S, and SE facing slopes (Fig. 6a, $p < 0.001$). Individual trees are located at a higher elevation on the S, SE, and SW facing slopes (Fig. 6b, $p < 0.001$). In addition, slopes facing S, SW, W, N, NE, and NW have higher slopes than the one facing E and SE ($p < 0.001$, data not shown).

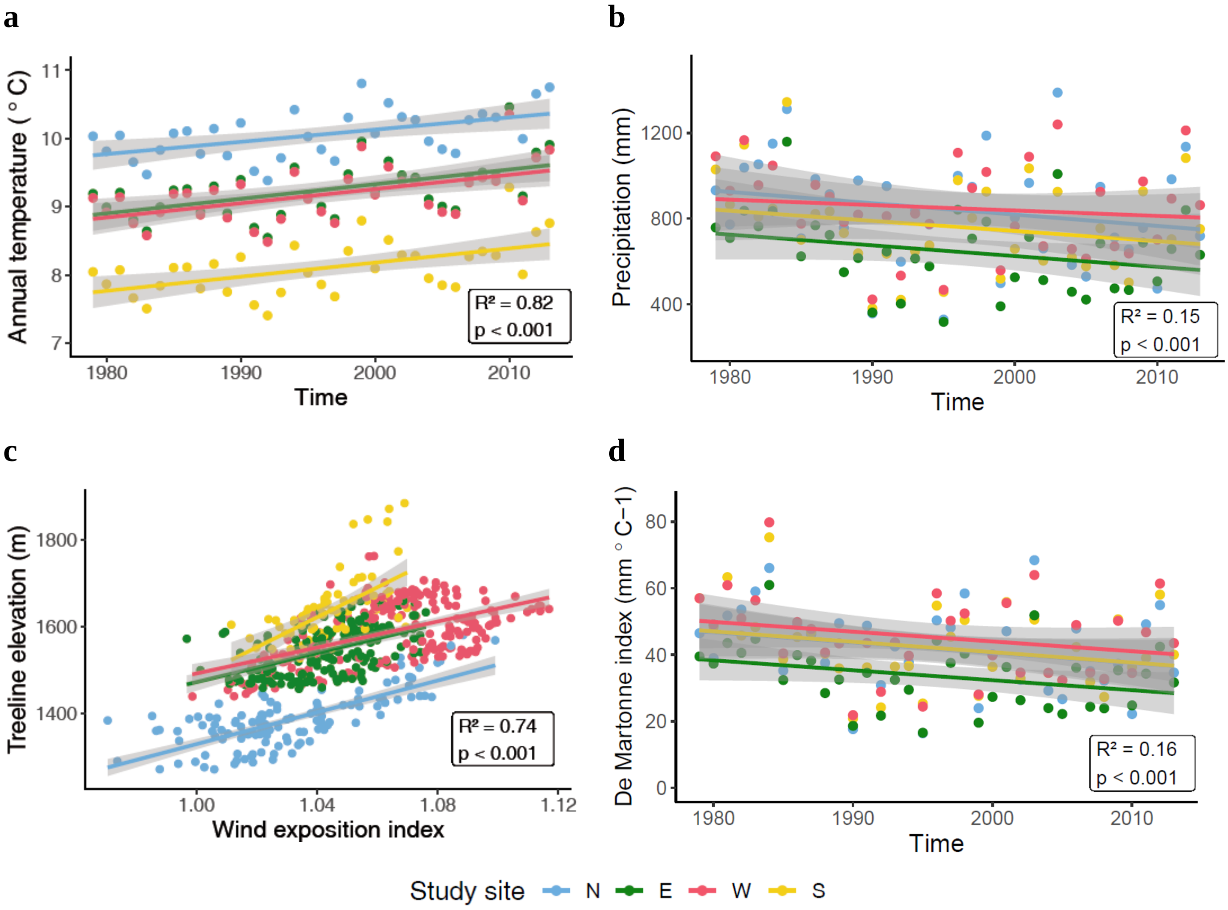

Figure 5. (**a**) Annual temperature and (**b**) average precipitation (mm) for each study site from 1979 to 2013. (**c**) Wind exposition index versus treeline elevation for the four study sites (N= north, E= east, W= west, S= south). Wind exposition index values > 1 indicate areas exposed to wind and < 1 indicate wind shadowed areas. (**d**) De Martonne aridity index (IDM). IDM values between 10 and 20 indicate semi-arid, 20-24 mediterranean, 24-28 semi-humid, 28-35 humid, 35-55 very humid, and >55 extremely humid climate.

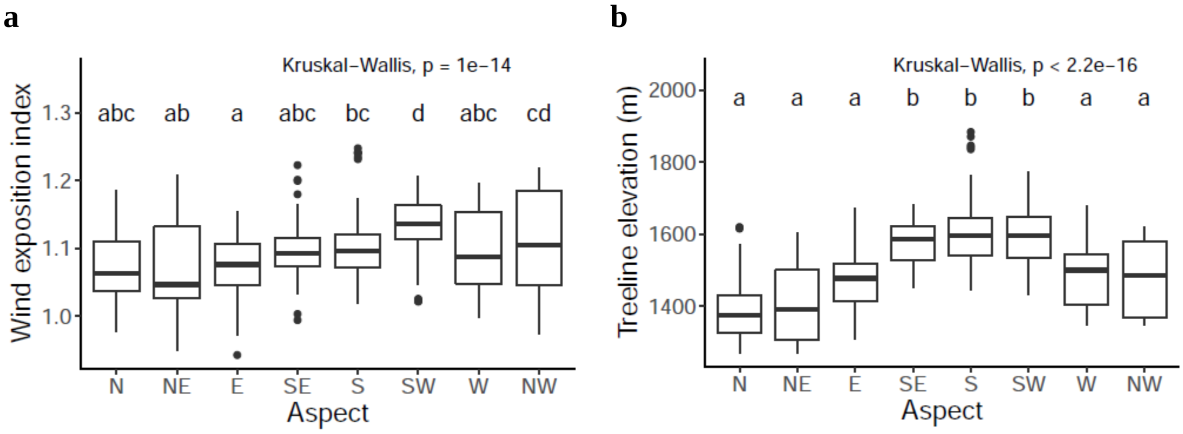

Figure 6. (**a**) Wind exposition index across aspect. Wind exposition index values > 1 indicate areas exposed to wind and < 1 indicate wind shadowed areas. (**b**) Treeline elevation across aspect. Boxplot components as defined in Fig. 3. Letters above boxplots are defined as in Fig. 3.

Discussion

Our results show that the treeline has remaned stable despite a significant increase in temperature over the past 70 years. These results could have several explanations, which are discussed further. Temperature increased by 0.81 °C, while precipitation decreased by 170 mm at treeline sites, indicating a warming and drying trend that exacerbates moisture stress by accelerating evapotranspiration. Although temperature and precipitation can accelerate treeline shifts, an increase in temperature and a decrease in precipitation at the treeline showed to be a bottleneck factor. Tree establishment is limited by precipitation, especially in semi-arid areas with low water storage capacity (e.g., limestone), as it increases evapotranspiration, which exacerbates moisture stress (Peñuelas & Sardans 2021). Recently, several studies have shown that despite an increase in temperature, precipitation and thus soil moisture limit establishment at the treeline (Moyes et al. 2015; Rees et al. 2020; Sigdel et al. 2021). The climate in the Samaria National Park, Crete, is predicted to continue to change in the future (Hoffmann et al. 2019; Hoffmann & Beierkuhnlein 2020). As a result, the area will continue to warm and become drier, which will affect tree establishment at the treeline. Already in the summer of 2021, heat waves with temperatures above 46 °C and forest fires were recorded in the Mediterranean region, especially in Greece (Copernicus Land Monitoring Service 2021).

Islands are generally less affected by global warming because the marine environment buffers temperature increases, i.e., the surface temperature difference between land and the nearby ocean results in constant ocean breeze and precipitation that can buffer the effects of climate change on coastal regions (Sutton et al. 2007). However, continental islands such as the island of Crete are likely more affected by warming than oceanic islands due to shorter distances to the mainland (Harter et al. 2015). We also found distance to the coast to be a potential factor for treeline elevation on the island of Crete. The distance to the coast affects local temperatures, i.e. cooling in summer and warming in winter. The distance from the coast is higher on the N study site (15 km) and lower on the S study site (4 km), with N > E > W > S. This might explain why in the S study site, the treeline elevation is at a higher elevation than in the N study site, which is further away from the sea and thus exposed to more extreme and growth-limiting temperatures.

Establishment of trees at higher elevations may be limited by microclimatic factors, such as lack of shelter from neighboring trees that can increase wind exposure (McIntire et al. 2016). At the study sites, trees grow mainly in areas with high topographic wind exposure (Fig 5c), therefore this might already limit their further expansion. The wind exposition index showed that the treeline from the S, E, and W study sites is more exposed to wind (values > 1, Fig. 5c) and thus cool and humid air masses, which could explain a higher treeline elevation. The island of Crete is also exposed to a series of winds throughout the year, such as Khamsin (south winds), Etesian (north winds), and Föhn. Khamsin winds are coming from Libya and are associated with the extreme dust episodes from the Sahara. This contributes to the formation of Föhn winds (hot and dry) on the leeward side (north Crete) (Nastos et al. 2017) which leads to low humidity in northern Crete (Prezerakos 1994). The north winds, Etesian, come from the Aegean Sea and are dry and cool in summer. Therefore, the mountain peaks are characterized by very arid, hot, and dry conditions in summer, whereas in winter, they are covered by snow. That conforms to the aridity index indicating that the western part of the island experienced a humid climate from 1951 to 1990, while the east side had a sub-humid dry climate (Nastos et al. 2013).

Topographic, geomorphologic and pedological factors, such as steep slopes with shallow soils, limit germination, establishment, and survival at the treeline (Holtmeier & Broll 2012; Cudlín et al. 2017). The limestone slopes on which the trees grow have an angle of mainly >50°, which prevents the formation of thick soil layers. Treelines tend to be lower on oceanic volcanic islands than on continental islands and the mainland because oceanic islands are more remote and isolated, have lower mountain mass effect, and more severe drought conditions in their alpine zone due to trade winds (Leuschner 1996; Irl et al. 2016). This is even more pronounced in the study area because the geologic substrate is represented byhighly karstified limestone, which has limited ability to store water. This constraint could be responsible for the temporal lag in treeline change recorded in this study area. Therefore, topographical effects might considerably shape the Crete treeline ecotones and drive their dynamics.

The treelines of the four study sites have different elevations, with N < E < W < S (Fig. 3a). In the N study site, the treeline occurs at the lowest elevation (mean of 1,384 m a.s.l.), while in S it is at the highest elevation (mean of 1,639 m a.s.l.). The difference in the elevation of the treeline between the study sites can be the result of topographical effects. In the study region, treeline elevation was significantly higher on S, SE, and SW facing slopes (Fig. 6a). The steeper relief, especially in the W, S and N study sites, is barely accessible and therefore unsuitable for extensive grazing. Furthermore, differences between N and S slopes are mainly attributed to temperature since S slopes are presumed to have a higher temperature in the northern hemisphere. On the contrary, in the study area is a lower temperature at the S sites. This could be explained by the low distance to the coast and the climate buffering effect of the sea. Despite temperature differences between the N and S aspects, mixed responses have been reported, e.g. Paulsen & Körner (2001) showed no difference in treeline elevation in the Swiss Alps, while Vitali et al. (2018) found a faster expansion of *Pinus nigra* on the southern slope than on the northern slope in the Apennines.

Traits of treeline-forming species could also be key to understand treeline dynamics. *Pinus brutia* and *Cupressus sempervirens* are remnants of the natural population and both grow up to high elevation on Crete, being part of the treeline. *P. brutia* cones are serotinous and seeds production decreases with increasing elevation (Boydak 2004). Seed production and dispersal appeared to be a limiting factor also in other mountain systems, as they decreases with elevation (Neuschulz et al. 2018; Anadon-Rosell et al. 2020). Compared to *P. brutia*, *C. sempervirens* is less flammable and can have both serotinous and non-serotinous cones (Lev-Yadun 1995). Both species are thus well adapted to the temperate Mediterranean climate with hot and dry summers and fire (Boydak 2004; Baldi et al. 2011). We could, however, not analyze the role of drought and fire in forming this treeline as there is no appropriate data on changes in the drought and fire regime on Crete over such a long period. Forest fires in Crete mainly occur in scrub and pasture areas with little vegetation, mainly in phrygana and maquis. Based on this and local ecological knowledge, forest fires do not have a major impact on the shape of the treeline.

Human land use is another well-known driver of treeline dynamics (Gehrig-Fasel et al. 2007). Grazing limits the regeneration of both *P. brutia* and *C. sempervirens* (Brofas et al.

2006). Although overgrazing with goats was a common practice in ancient times on Crete, it decreased over time and nowadays, local pastoral activities are concentrated in mid-elevation areas with sufficient vegetation for food. In the Samaria Nationl Park grazing is restricted both in the core zone (25% grassland area) and in the peripheral area (51% grassland area) (Spanos et al. 2008). Furthermore, some parts have been abandoned after the declaration of the National Park in 1962. This difference in land use has resulted in significant changes in forest area and density of *P. brutia* in Crete. For instance, forest area and density of *P. brutia* increased in the protected area of Samaria National Park as a result of land abandonment, but decreased in the unprotected area of Mount Ida (2,456 m) due to the increase in the number of sheep and goats over the past 50 years (Papanastasis 2004). Thus, the effect of soil trampling from grazing activities is also reduced in our study areas. This offered the tree species the opportunity to establish through natural regeneration.

Compared to unprotected areas, highly protected areas experience reduced human pressure and less forest loss which promotes natural regeneration (Beloiu & Beierkuhnlein 2019; Leberger et al. 2019). However, despite the protection status since 1962, past and present grazing activities might still limit seedling establishment and development at the treeline. In another protected area of Greece, the Olympus Mountains, both an upward shift and a retreat of the treeline were observed, which could not be explained by climate alone (Zindros et al. 2020). However, a major difference between our study region and Olympus Mountain is the topography and the sufficient soils that can promote sapling establishment. While the study areas from the Lefka Orimountains are dominated by exposed limestone and steep slopes instead of a developed layer of soil (Fig. 1). Steep slopes and absence of suitable substrate can be major limiting factors in treeline advance (Macias-Fauria & Johnson 2013; Cudlín et al. 2017).

The treeline on the continental island of Crete has a diffuse form and tree density decreases with increasing elevation. Diffuse treelines are more sensitive to changes in temperature and are more likely to exhibit earlier upward shifts than krummholz, island treelines, and abrupt treelines (Harsch & Bader 2011). Consequently, our results were unexpected and thus stimulate the fundamental debate on treeline dynamics as a result of recent climatic changes highlighted in the introduction. In the global context, the Mediterranean treeline generally occurs at exceptionally high temperatures and very low elevations, e.g. on Mount Olympus, Greece, at 2,320 m a.s.l. and 8˚C; on Mount Helmos, Greece, at 2,100 m and 11,1˚C; on the Maiella massif, Apennines,Italy, at 1,820 m a.s.l. and 10.5 ˚C (Körner 2012). However, the treeline on Crete is formed at a significantly lower elevation (between 1,270 and 1,884 m a.s.l.), with a mean elevation of 1,536 m a.s.l. in Samaria National Park. The elevation of the Crete treeline shows significant stability between 1945 and 2015 even though it occurs at much lower elevation than most other Mediterranean treelines. Thus, the observed treeline elevations on Crete is below the globally modelled potential treeline. Its temporal stability thereby suggests a temporal lag in treeline response due to relatively stable climate conditions until 1990 and topographical drivers that keep the treeline elevation low.

In the Northern Hemisphere, 66% of the treeline showed an increase, 34% showed no shift (Hansson et al. 2021), and other studies even showed a retreat of about 1% (Harsch et al.

2009; Lu et al. 2021). Hence, the general trend is that the treeline is advancing at 0.35 m/year, but even that is too slow to keep pace with climate warming (Rees et al. 2020; Lu et al. 2021). We showed that treeline elevation remained stable regardless of temperature increase and precipitation variation. Therefore, tree species growing at the treeline in Crete do not track contemporary climate change. Similar to these results, many studies from Central and Northern Europe found a stable or even declining trend in treeline elevation (Harsch et al. 2009; Hansson et al. 2021). Moreover, several ecological models and field observations showed no climate effects on ecosystem composition and species shift in the Mediterranean basin (Camarero & Gutiérrez 2004; Gritti et al. 2006) and at high latitudes (Zhu et al. 2012). Nevertheless, we also found that the treeline ecotone was enriched with a few tree individuals over the years. Consequently, temperature increases alone cannot promote treeline advancement if precipitation decreases (Moyes et al. 2015; Sigdel et al. 2018; Rees et al. 2020; Lu et al. 2021).

Conclusions

Our results have revealed that, based on high-resolution aerial images, there was no shift in the treeline elevation between 1945 and 2015 on the continental island of Crete. Therefore, tree species growing at the treeline are unable to keep up with rising temperatures. The absence of treeline shift is mainly due to a combination of climatic and topographic factors, such as decreasing precipitation with increasing temperature, and the lack of a shelters effect due to high topographic wind exposure. The temporal lag in treeline shift could impose risks as the optimum elevation changes. Aerial imageries proved particularly suitable on inaccessible steep terrain where in-situ monitoring is limited or impossible, a distinct advantage in mountainous areas. Our findings demonstrate the benefits of using historical high-resolution remote sensing images in stimulating the controversial debate about treeline dynamics under climate change. The continental island of Crete is home to particularly many endemic species and thus very important for biodiversity conservation.

Data availability: Datasets analyzed in the current study are available online on https://zenodo.org/record/4404269#.X-zbEtgzaUk.

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Author Contributions

D.P. and C.B. conceived the idea, D.P. and M.B. led the writing process. M.B. processed the climate data, mapped the treeline on the aerial images, did the statistical analysis, and prepared the figures. P.L., A.B., and A.T. analyzed the aerial images. S.H. contributed to the writing. C.B., S.H., D. K., and N.C. provided feedback on the manuscript. N.C. and C.B. supervised the research activity. All authors revised and approved the final version of the manuscript.

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7.3. Manuscript 3 - High recovery of saplings after severe drought in temperate deciduous forests

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Abstract: Drought episodes are predicted to increase their intensity and frequency globally, which will have a particular impact on forest vitality, productivity, and species distribution. However, the impact of tree species interaction on forest vulnerability to drought is not yet clear. This study aims to assess how deciduous saplings react to drought and whether tree species diversity can buffer the impact of drought stress on tree saplings. Based on field measurements of crown defoliation and species diversity, vulnerability, drought recovery, and species interaction were analyzed. Fieldwork was carried out in Central Eastern Germany in 2018 during the vegetation season and repeated in 2019. Ten random saplings were measured in each of the 218 plots (15 × 15 m) with 2051 saplings in total out of 41 tree species. We found that 65% of the saplings experienced defoliation during the drought of 2018, of which up to 13% showed complete defoliation. At the species level, *Fagus sylvatica* L. and *Betula pendula* Roth. saplings were less affected (<55%), whereas *Carpinus betulus* L., *Sorbus aucuparia* L., and *Frangula alnus* Mill. saplings were the most affected (≥85%). One year later, in 2019, *C. betulus* and *S. aucuparia* had a faster recovery rate than *F. sylvatica*, *B. pendula*, *Quercus* spp., and *Crataegus* spp. ($p < 0.001$). Furthermore, we showed that forest stands with high sapling species diversity had a reduced vitality under drought stress ($p < 0.001$), indicating a higher competition for resources. The study provides evidence that *F. sylvatica* saplings can withstand and survive to persistent drought. Species-specific responses to drought are essential to be considered for implementing adaptive forest management strategies to mitigate the impact of climate change.

Keywords: precipitation; broadleaf forests; tree vitality; drought stress; European beech saplings; climate change

1. Introduction

Globally, warming results in an increasing frequency, intensity, and duration of heat waves and droughts [1]. More intense, frequent, and longer heat waves and drought periods are expected for this century [2,3]. Central Europe is characterized by a seasonal temperate climate with warm summers. Projections for future climatic classes for Central Europe expect that the Köppen–Geiger Cfb climate (temperate, without dry season, and warm summer) will be partly maintained, but the Cfa climate (temperate, without dry season, and hot summer) will extend at the loss of Dfb climate (cold, without dry season, and warm summer) in eastern Central Europe [4]. This implies that summer drought (precipitation in the driest month in summer <40 mm month^{-1} and precipitation in the driest month in summer < precipitation in the wettest month in winter/3) is not expected in the long-term average conditions. However, in recent years, occasional summer heat waves with severe periods of drought were observed in Central Europe in 2003 [5–8] and recently in 2018/19 [9,10]. Equally extreme drought was recorded in Eastern Europe in 2010 [11]. At the end of the 20th century, European summer temperatures had already exceeded the reconstructed temperatures for the last 500 years [12]. The ecological impact of repeated strong periods of drought and heat will even be accelerated [13], particularly in ecosystems that are not adapted to extreme conditions such as the temperate forest [14]. Given that current mature trees have established during a much cooler climate of the 19th century, it is questionable whether the mature forests stands are already adjusted to the current thermal and hydric regime. Frequency and severity of drought and heat stress increase tree mortality globally [15]. Therefore, trends in climate-related physiological stress of mature and sapling trees need to be addressed.

Temperate deciduous forests represent the predominant natural zonal ecosystems with European beech (*Fagus sylvatica* L.) as a dominating species in major plant communities [16]. European temperate deciduous forest ecosystems are characterized by a very low diversity in tree species compared to other Holarctic regions of the temperate biome (NE America, E Asia). As a consequence of the strong impact of Pleistocene climatic fluctuations in this high latitude combined with dispersal barriers (mountain ridges, Mediterranean Sea), the European tree flora is considered to be depauperate [17]. Therefore, it is crucial to understand the warming and drought impacts on key species such as *F. sylvatica*. Species-specific negative growth responses to warming were detected for Central European trees with a particular impact on *F. sylvatica* [18,19]. Less abundant tree European deciduous species were found to be more drought-tolerant than *F. sylvatica* [20,21]. However, Metz et al. [22] found that drought susceptibility of *F. sylvatica* is modified by the tree species composition. Obviously, there is an influence of tree species diversity and composition on the responses of tree species to drought [23], but also an effect of drought on the competitive behavior of tree species [24].

Natural regeneration through seed dispersal, germination, and the establishment of cohorts of juvenile trees is the main process for the sustainable development of forests, enhancing local biodiversity and increasing resilience to extreme climatic events [25]. Juvenile trees are protected by the mature tree canopy from heat-related stress as they are not directly exposed to the atmosphere. However, in contrast to mature trees, juveniles only exhibit shallow root systems that do not reach deep into the ground, thus the tolerance of trees to environmental stress is predicted to increase with ontogeny [26]. The root system deepens with age, but water uptake and transpiration rates depend on species and site characteristics [27]. Tree ability to survive, grow, reproduce, and increase longevity under stressful conditions is given by their vitality, which can be used as a stress indicator [28]. An exponential increase in mortality with canopy defoliation has been shown in Europe [29,30]. However, the impact of species diversity on sapling susceptibility to drought and their interaction with mature trees is unclear.

Tree species distribution ranges are reflected in the species' response to climatic extremes, which can be assessed through common garden experiments (e.g., Muffler et al. [31]). Whilst in Central European deciduous forests, climatic turning points shifting the interspecific competition between species have been modeled [32], however, model projections cannot cover the role of climatic singularities. As a consequence, common garden experiments and models need to be supported by observational studies when such events take place. This study aims to investigate the direct impact of extraordinary summer drought on natural regeneration of deciduous tree saplings in a large area of Central Europe and their potential recovery in the following year. Therefore, the following questions were addressed: (1) How do deciduous saplings react to severe drought? (2) Does tree species diversity buffer the impact of drought stress on tree saplings? To answer these questions, we surveyed the changes in tree vitality brought by the drought of 2018 in a large number of tree sapling species. We focused on the 10 most abundant species that are important for forest productivity, ecological stability, and biodiversity. We also analyzed the effect of species diversity on tree sapling vitality. We hypothesized finding species-specific responses reflecting the ecological niches and distribution ranges of contributing tree species.

2. Materials and Methods

2.1. Study Area

The study area is located in central-eastern Germany (Northern Bavaria) (Figure 1) and is dominated by deciduous, mixed, and coniferous forests. The petrography of the bedrock is very diverse (dominated by limestone, followed by schist and slate) and as a consequence, soils differ considerably with cambisol, podzol, rendzina, histosol, and luvisol as the main soil types (Supplementary Materials 2, Table S1).

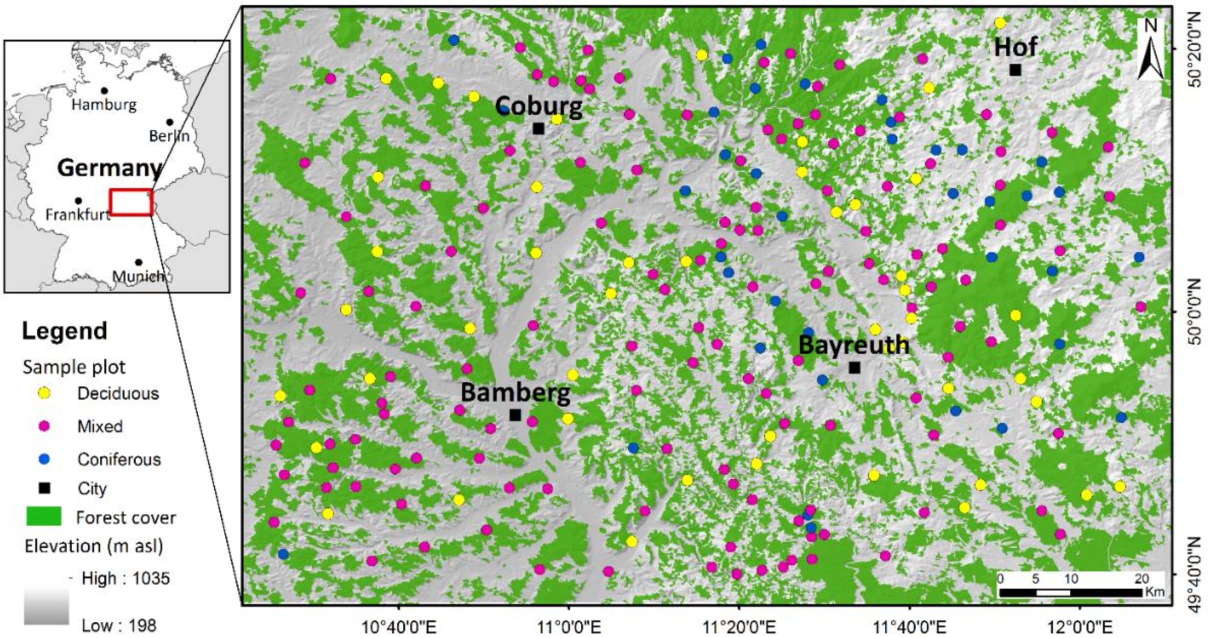


Figure 1. Location of the 218 plots in the three forest types. Forest cover based on digital landscape model (DLM) 1:250,000 (DLM250), © GeoBasis-DE/BKG 2020.

2.2. Environmental Data

Climatic data (temperature, precipitation, and evapotranspiration) were extracted from the raster dataset (1 × 1 km) provided by the German Meteorological Service. Soil type was extracted from the raster dataset (1 × 1 km) of the European Soil Databases (ESDB) version v2.0 [33,34]. Available water capacity (AWC) was extracted from the raster dataset "Topsoil physical properties for Europe (based on Land Use and Coverage Area frame Survey [LUCAS] topsoil data)" [35]. The European digital elevation model (EU-DEM) version 1.1 (25 m) [36] was used. The forest layer was extracted from the digital landscape model 1:250,000 (DLM250) [37].

During the period 1970–2019, the average annual precipitation ranged from 570 to 1344 mm, with a mean of 957 mm (Supplementary Materials 1, Figure S1a), and the average annual temperature ranged from 4.8 to 9.4 °C, with a mean of 7.1 °C for the study area (Supplementary Materials 1, Figure S1b) [38,39]. The average precipitation in the study sites during the summer months of 2018 was 50% less than in the period December 1999–November 2017 (Figure 2). The average precipitation from 2018 (595 mm) was less than the average precipitation of 2003 (611 mm) (Supplementary Materials 1, Figure S1c). Moreover, in 2018, the annual potential evapotranspiration (749 mm) exceeded the average precipitation (595 mm) (data not shown). Between 2000 and 2019, the average precipitation decreased with 91 mm, while the mean annual temperature increased with 0.5 °C (Supplementary Materials 1, Figures S1c,d). In 2019, the average precipitation was 736 mm and the mean annual temperature was 9.5 °C (Supplementary Materials 1, Figures S1c,d). The Standardized Precipitation Evapotranspiration Index (SPEI) for the period 2000–2019 indicated a more severe drought in 2018 than in 2003 and 2019. In 2019, it was a normal to moderate drought (Supplementary Materials 3, S1a–e).

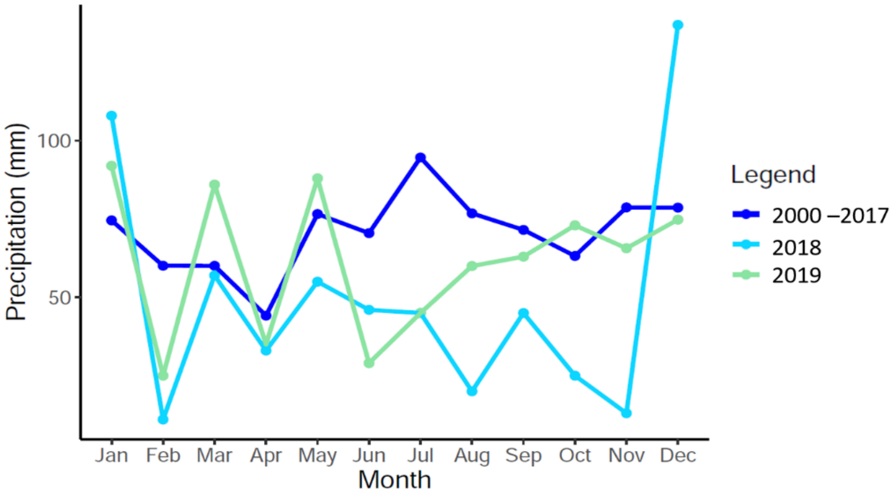


Figure 2. Monthly average precipitation from January to December for the period 2000–2017, 2018, and 2019 at the study site. The precipitation data were extracted from the raster dataset (1 × 1 km) of the German Meteorological Service

2.3. Field Measurements

Fieldwork was carried out during August and September in 2018 and repeated in 2019. The 218 plots (15 × 15 m) were established in 2018 based on a random selection of locations within the forest surface of the entire investigation area. To reduce spatial autocorrelation through sampling, the plots were positioned at a minimum distance of 1 km. From these random points, the nearest naturally established group of sapling deciduous trees in the understory was detected. Among these plots, 47 were located in stands with deciduous trees in the canopy, 133 in mixed forest, and 38 in stands dominated by mature conifers (Supplementary Materials 2, Table S1). The basal area (BA) for the respective forest stand was measured using the Bitterlich stick [40]. The mean BA for the forest stands ranged from 3 to 41 m^2 ha^{-1}, with a mean value of 22.4 m^2 ha^{-1}. The percentage of mature and sapling canopy cover was assessed separately for each plot in 2019. Species richness and abundance were recorded per plot. Elevation and Global Positioning System (GPS) coordinates were recorded for each plot.

For each plot, 10 deciduous tree saplings ≥ 1.3 m of height and with a diameter at breast height (DBH) below 10 cm were measured. All 10 saplings were selected randomly and marked for future comparison. Only in a few cases, less than 10 saplings could be sampled at a given plot. In 2019, five plots (50 saplings) out of 218 plots could no longer be considered because they were affected by human intervention and 48 saplings out of 21 plots could not be identified because the labels were missing. In total, 2149 saplings were recorded in 2018 and 2051 in 2019. However, only the 2051 saplings were used for further analysis. All saplings were attributed to a tree species.

To assess the vitality and drought damage, a simple classification was applied with the following vitality classes: (1) Undamaged/all leaves are undamaged by drought and do not show color changes**;** (2) partly damaged/individual leaves and branches of the sapling trees are damaged but the entire plant has still a major part of undamaged leaves; and (3) completely damaged/all leaves and branches of the plant show drought damage. Crown defoliation can serve as a stress indicator and correlates with tree growth [28].

2.4. Data Analysis

Changes in sapling vitality between 2018 and in 2019 and changes in the three vitality classes were assessed using Fisher's exact test for count data and the pairwise comparison. The McNemar test, followed by a symmetry test for paired data from the "rcompanion" package [41], was used to determine whether the proportion of damaged saplings increased after the 2018 drought. Sapling recovery index was estimated as the ratio between the performance in terms of vitality after (2019) and during the drought of 2018, where values <1 indicate a decrease in performance (vitality) after the event [42]. The species recovery was assessed using the non-parametric Kruskal–Wallis test. Resilience and resistance index could not be calculated because vitality data were not available before the 2018 drought.

Tree species biodiversity was characterized by the Shannon diversity index. The diversity index was calculated for (1) all tree species from the plot; (2) all sapling species; and (3) all mature tree species. The Shannon diversity index was calculated based on species richness and species abundance, using the diversity function from the vegan package [43]. The vitality mode per plot was calculated and two groups were formed, the undamaged (vitality 1) and damaged group (vitality 2 and 3). The two classes (undamaged and damaged) were created because the sample size of completely damaged saplings (vitality 3) was too small in 2019 to meet the test criteria. The non-parametric Kruskal–Wallis test was used to check if there was a difference in terms of species diversity between the undamaged and damaged groups.

The influence of environmental variables (i.e., soil type, elevation) as well as forest stand characteristics (i.e., tree cover, BA) on tree vitality was tested using analysis of variance (ANOVA) and the non-parametric Kruskal–Wallis test. Normality of the data was checked with the Shapiro–Wilk test ($p > 0.05$) and homogeneity of variance was checked with the Levene test ($p > 0.05$). Statistical comparison for multiple groups was evaluated using the Tukey Honestly Significant Difference (HSD) test following ANOVA and Dunn's test after a significant Kruskal–Wallis test. The comparison between multiple vitality classes based on the soil type was evaluated by the Fisher test. The McNemar test was used to assess if the number of damaged saplings increased after the 2018 drought. The SPEI drought index was calculated based on the climatic data provided by the German Meteorological Service (monthly precipitation and temperature) and using the SPEI package for the time scale 1, 2, 6, and 12 months. The potential evapotranspiration was calculated according to the Thornthwaite equation [44]. All statistical analyses were conducted with the software R 3.6.0 [45] and the additional packages FSA, RVAideMemoire, rgdal, raster v3.0-7, and ggplot2 v3.2.1.

3. Results

3.1. Saplings Response to Drought Stress and Their Recovery

In 2018, out of 2051 saplings measured, 35% were undamaged (vitality 1), 52% were partly damaged (vitality 2), and 13% were completely damaged (vitality 3). Whereas, in 2019, there was a significant difference between vitality groups in the order undamaged (72%) > partly damaged (22%) > completely damaged (6%) (McNemar test, $p < 0.001$) (Figure 3a and Supplementary Materials 1, Table S1). A significant shift in tree vitality was found between the two study periods. The forward shift patterns showed that saplings that were partly and completely damaged (vitality 2 and 3) in 2018 had significantly shifted toward the undamaged state (vitality 1) in 2019 (Fisher's exact test, $p < 0.001$) (Figure 3b). This indicates a high recovery of the saplings damaged by the drought of 2018. However, there was also a backward shift, a lower percentage of saplings that were undamaged in 2018 were completely damaged in 2019 (Figure 3a). Out of 2051 saplings remeasured in 2019, 125 saplings recorded complete damage, with the aboveground compartment entirely defoliated.

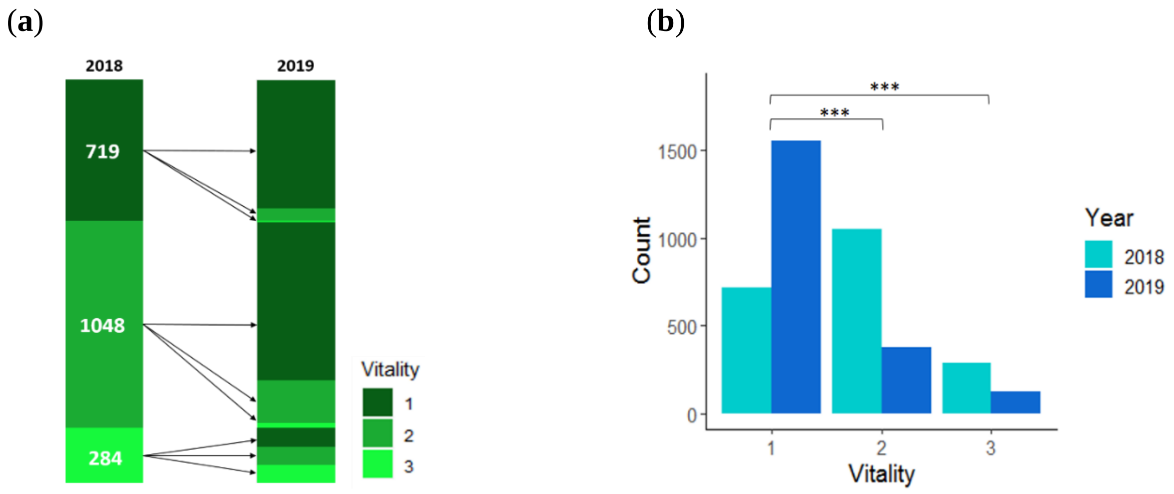
Out of 41 tree sapling species measured, the 10 most abundant tree species found in more than 20 plots in 2018 and 2019 were *Fagus sylvatica*, rowan (*Sorbus aucuparia* L.), European hornbeam (*Carpinus betulus* L.), silver birch (*Betula pendula* Roth.), oak (*Quercus* spp.), sycamore (*Acer pseudoplatanus* L.), common hazel (*Corylus avellana* L.), alder buckthorn (*Frangula alnus* Mill.), elder (*Sambucus nigra* L.), and hawthorn (*Crataegus* spp.) (Table 1). We identified three species of *Quercus*, sessile oak *(Q. petraea* (Matt.) Liebl.) as the most abundant, followed by pedunculated oak (*Q. robur* L.) and red oak (*Q. rubra* L.). *Quercus* spp. were regarded together due to the occurrence of hybridization between *Q. petraea* and *Q. robur*.

Table 1. Ten most abundant tree saplings measured in 2018 and 2019 (1777 individuals) for their diameter at breast height (DBH) and vitality (1 = undamaged, 2 = partly damaged, 3 = completely damaged).

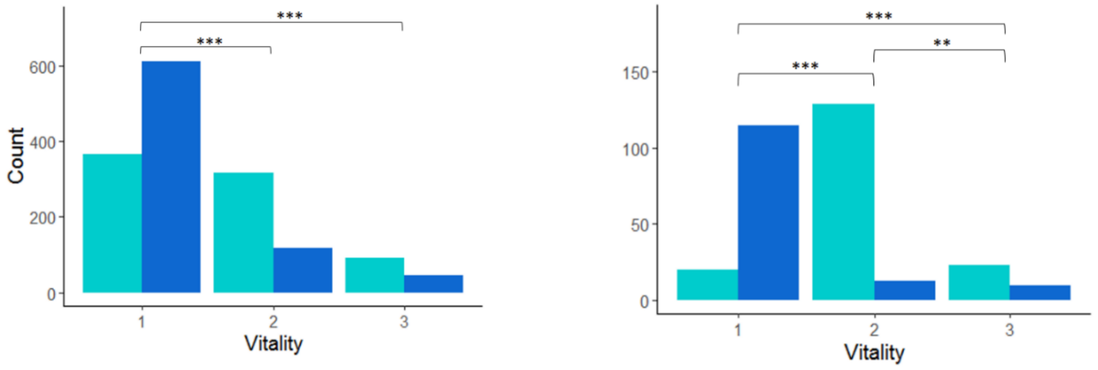
Species	**No./Plot**	**DBH (mm) (mean, min–max)**	**Vitality 2018**			**Vitality 2019**		
			1	**2**	**3**	**1**	**2**	**3**
Fagus sylvatica	772/141	21 (1–94)	365	317	90	611	117	44
Sorbus aucuparia	221/78	20 (2–70)	24	127	70	157	44	20
Carpinus betulus	172/48	20 (2–82)	20	129	23	139	24	9
Betula pendula	145/41	18 (2–63)	66	68	11	115	25	5
Quercus spp.	113/44	25 (2–79)	36	72	5	65	44	4
Acer pseudoplatanus	103/48	19 (1–57)	36	54	13	88	8	7
Corylus avellana	99/53	16 (1–54)	36	54	9	77	17	5
Frangula alnus	52/22	17 (1–44)	8	35	9	39	8	5
Sambucus nigra	52/20	16 (3–63)	16	19	17	24	22	6
Crataegus spp.	48/27	23 (1–70)	18	28	2	31	15	2

At species level, there were significant differences in vitality between the species. Of the 10 abundant species, *F. sylvatica* and *B. pendula* recorded the least damage. The most affected species were *S. aucuparia, C. betulus, F. alnus*, and *S. nigra*, with the proportion of completely damaged saplings exceeding that of undamaged saplings. Sapling vitality classes recorded a significant shift in their structure ($p < 0.001$) between 2018 and 2019 for all 10 abundant species (Figures 3c–g, and Supplementary Materials 1, Figure S2). *F. sylvatica* showed a dominant proportion of undamaged saplings in 2018, but in the following year, there was a strong backward shift in vitality classes ($p < 0.001$) (Figure 3c).

The recovery rate of *C. betulus* and *S. aucuparia* was significantly higher than that of *Quercus* spp., *F. sylvatica*, *B. pendula,* and *Crataegus* spp. (Figure 4). *A. pseudoplatanus, C. avellana*, and *F. alnus* also recorded a high rate of recovery after the drought of 2018, whereas *S. nigra* had a slower rate of recovery, but this was not significant (Figure 4). None of the species analyzed showed a significant decrease in performance in 2019 (recovery index < 1), therefore they either maintained the same vitality or recovered.



(**c**) *Fagus sylvatica* (*n* = 772) (**d**) *Carpinus betulus* (*n* = 172)



(**e**) *Quercus* spp. (*n* = 113) (**f**) *Betula pendula* (*n* = 145) (**g**) *Sorbus aucuparia* (*n* = 221)

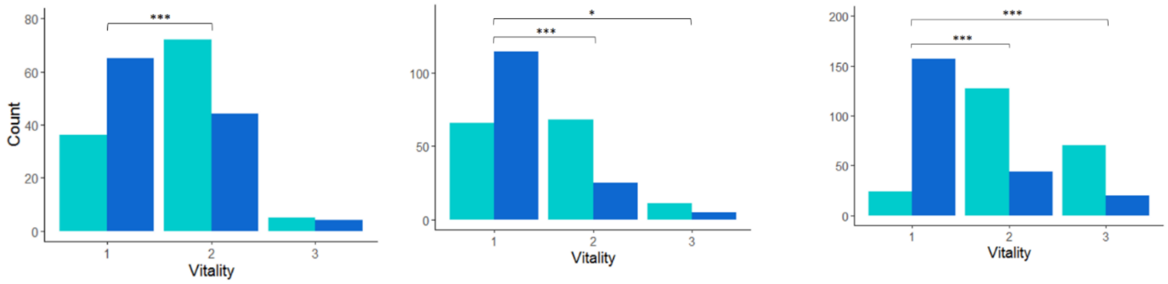


Figure 3. Vitality classes of all saplings (*n* = 2051). (**a**) Assessment of sapling vitality and their survival after the drought of 2018. The barplot on the left (2018) shows the fraction of saplings belonging to each category of vitality measured in 2018. The barplot on the right (2019) shows the fraction of saplings that have retained the same vitality, increased, or decreased their vitality. (**b**) Differences in sapling vitality classes between 2018 and 2019 for all saplings. (**c**–**g**) Vitality of *Fagus sylvatica*, *Carpinus betulus*, *Quercus* spp., *Betula pendula*, and *Sorbus aucuparia* in 2018 and one year later (2019). Vitality 1 = undamaged, 2 = partly damaged, 3 = completely damaged saplings. Stars show the statistically significant difference between vitality groups based on Fisher's exact test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

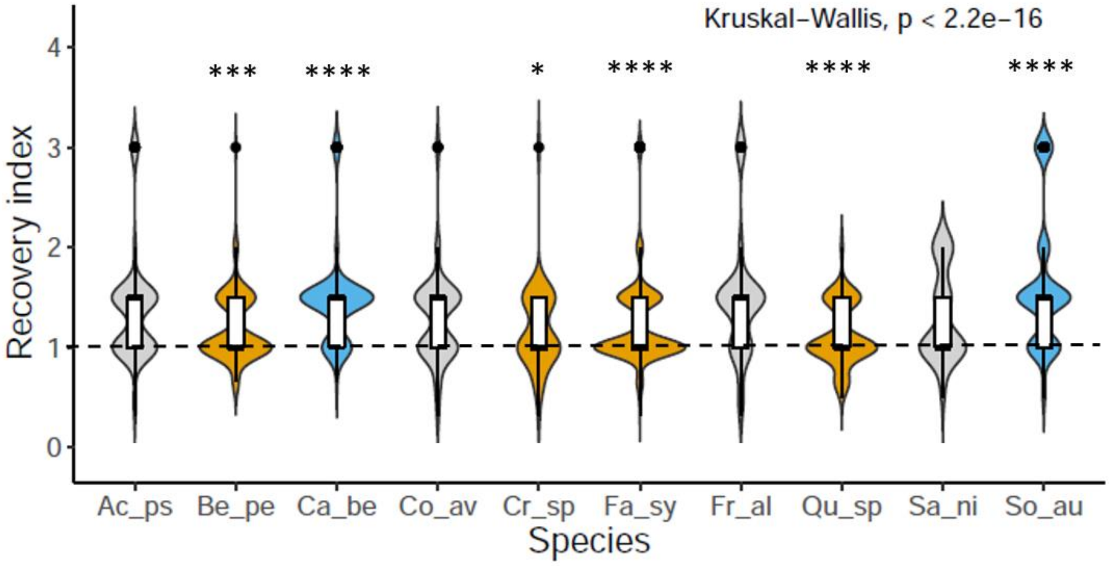


Figure 4. Sapling recovery index and species significance. Values < 1 indicate decline in performance, > 1 indicate increase in performance after the event and 1 indicates same state as during the event (colors: blue > 1, orange = 1, grey = not significant). Ac_ps—*Acer pseudoplatanus*; Be_pe—*Betula pendula*; Ca_be—*Carpinus betulus*; Co_av—*Corylus avellana;* Cr_sp—*Crataegus* spp.; Fa_sy—*Fagus sylvatica*; Fr_al—*Frangula alnus*; Qu_sp—*Quercus* spp.; Sa_ni—*Sambucus nigra*; and So_au—*Sorbus aucuparia*. Stars show the statistical significance between species (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$).

3.2. Species Diversity and Stand Characteristics

Species richness was between one and 10 tree species per plot, with a mean of five species per plot. Shannon diversity index for all tree species varied between 0.13 and 2.19, with a mean of 1.19. In 2018, forest stands with high tree diversity (mature and sapling trees) showed a reduced vitality than sites with low tree species diversity ($p < 0.001$) (Figure 5a). Additionally, sites with higher sapling diversity showed increased vulnerability to drought (Kruskal–Wallis test, $p < 0.001$), whereas mature tree species diversity had a neutral effect (Kruskal–Wallis test, $p > 0.05$). One year later, in 2019, species diversity did not differ between the undamaged and damaged plots ($p > 0.05$) (Figure 5b). Furthermore, sapling and mature tree diversity showed no significant difference in 2019 (Kruskal–Wallis test, $p > 0.05$) (data not shown). Plots with saplings undamaged had a higher canopy cover ($p < 0.05$) (Figure 5c). Saplings growing under mature trees with high canopy cover exhibited a lower vitality ($p < 0.001$) (Figure 5d).

Saplings with higher DBH experienced higher damage during the drought in 2018 and also one year later (Figures 6a,b). All 10 most abundant species showed a decrease in vitality with DBH, however, only for *Crataegus* spp. and *S. nigra* was the decrease significant in 2019 (Kruskal–Wallis test, $p < 0.01$) (data not shown). Moreover, the forest stand with a higher BA had more damaged saplings, but this relationship was not significant (Kruskal–Wallis test, $p > 0.05$). The relationship between AWC and sapling vitality per plot was assessed for 2018 and 2019, however, there were no significant differences between the groups ($p > 0.05$) (Supplementary Materials 1, Figure S3).

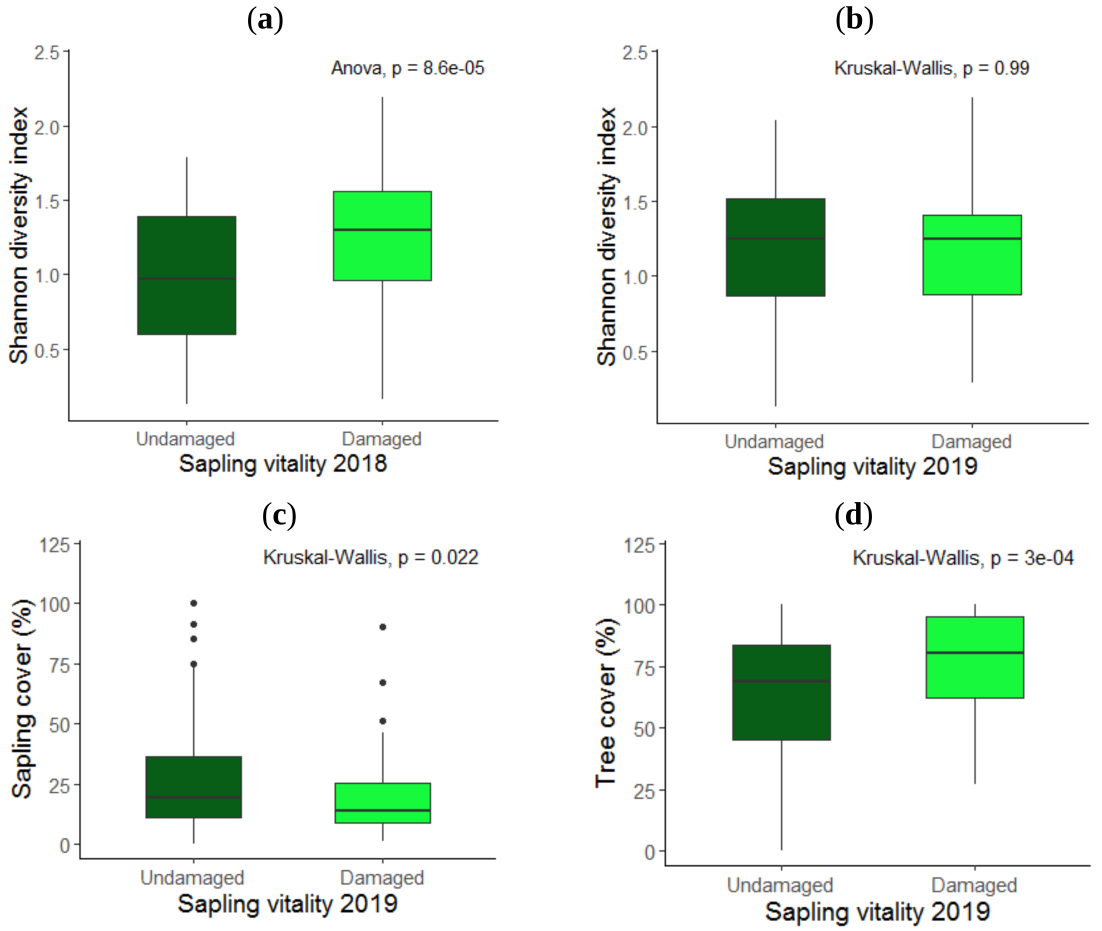


Figure 5. Shannon diversity index for all tree species and sapling vitality per plot in 2018 (**a**) and 2019 (**b**). (**c**) Sapling vitality and sapling cover (%); (**d**) Sapling vitality and mature tree cover (%). (**a**) The 53 plots undamaged and 160 damaged in 2018; (**b**–**d**) The 159 plots with saplings undamaged and 54 plots with saplings damaged in 2019.

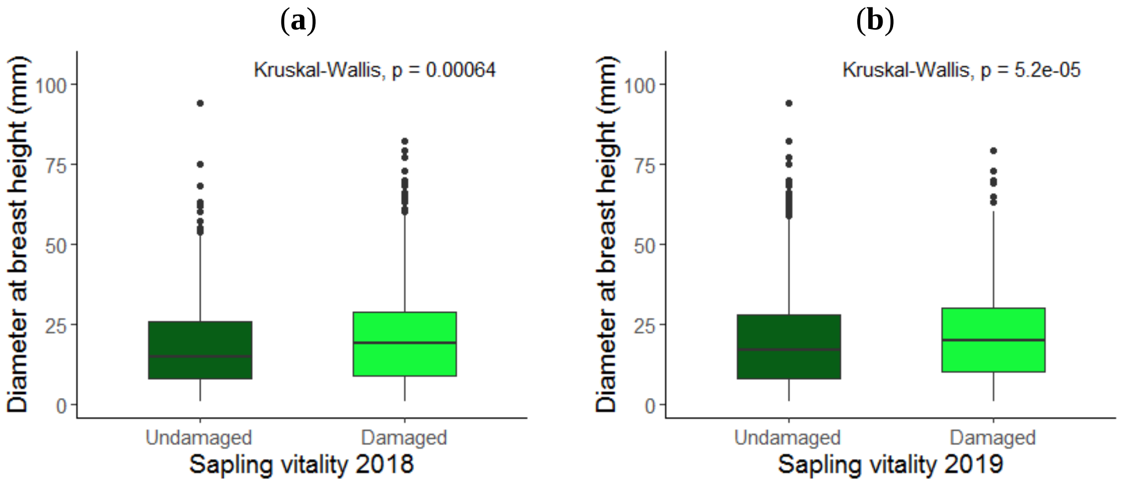


Figure 6. Sapling vitality and diameter at breast height (DBH) for all saplings (*n* = 2051). (**a**) Sapling vitality in 2018, 718 undamaged, and 1333 damaged saplings; (**b**) Sapling vitality in 2019, 1480 undamaged, and 571 damaged saplings.

Of the 10 most abundant species, *F. sylvatica, S. aucuparia, C. betulus, B. pendula, Quercus* spp., *C. avellana, F. alnus,* and *Crataegus* spp. dominated mainly on cambisol and podzol soils, while *A. pseudoplatanus* and *S. nigra* were mostly found on podzol and rendzina soils (Supplementary Materials 2, Table S2). Tree saplings were affected by drought in large proportions in all soil types. However, saplings growing in luvisol were, in 2018, significantly more damaged than those on cambisol, podzol, and rendzina (Fisher's test, $p < 0.05$) (Supplementary Materials 2, Tables S3a,b). The number of damaged saplings in 2019 was higher than the number of undamaged saplings in 2018 in luvisol and this proportion was statistically different than in cambisol and podzol (Fisher's exact test, $p < 0.05$, Supplementary Materials 2, Table S3b). In 2019, in each type of soil, the saplings recovered in high proportions. The number of saplings damaged during the drought of 2018 was statistically higher than the number of saplings damaged after the drought in 2019 (McNemar test $p < 0.001$) in all soil types (Supplementary Materials 2, Table S4).

4. Discussion

Our study yielded four major findings: (1) across all saplings, the summer drought of 2018 led to an increase in defoliation (decrease in vitality) of all investigated species, with *F. sylvatica* and *C. betulus* saplings less affected, whereas *C. betulus, S. aucuparia,* and *F. alnus* were the species most affected by drought; (2) the recovery rate was dependent on species, *C. betulus* and *S. aucuparia* recovered faster than *Quercus* spp., *F. sylvatica*, *B. pendula*, and *Crataegus* spp.; (3) forest stands with high species diversity were more exposed to drought stress than stands with low species diversity; and (4) saplings with higher DBH were more affected by drought stress than saplings with lower DBH.

4.1. Drought Response and Species Recovery

During the drought of 2018, 65% of the tree saplings (n = 2051) from the study area experienced a significant decrease in vitality. Sustained drought stress leads to a reduction in the canopy (i.e., decrease leaf growth, loss of older foliage), photosynthetic activity, and storage reserve [14,46]. In the study area, more than 85% of the saplings of *S. aucuparia, C. betulus, F. alnus,* and *S. nigra* experienced high defoliation rates. Such severe defoliation is associated with an increase in the nutrient cycle and a change in the biogeochemical cycles of the forest due to leaf fall [30]. However, the drought period of 2018 was not characterized by unprecedented high-temperature values in the study area, but rather a significantly lower amount of precipitation, especially during the summer months, compared to the average values of previous years (Figure 2 and SPEI drought index Supplementary Materials 3, S1). Additionally, during the 2003 drought, a decline in European forest productivity was not caused by high temperatures, but rather by water limitations [47]. Low soil moisture reduces decomposition and mineralization, which leads to a shortage of nutrients [48]. Therefore, tree growth was found to be reduced during drought, but enhanced after the drought [49] when the nutrients were again accessible to the tree species.

The repeated survey in summer 2019 allowed us to detect a shift in tree vitality. Partially damaged saplings shifted mainly to undamaged saplings, indicating a high recovery rate after one year (Figure 3a). In 2018, only 35% of the saplings were undamaged, compared to 72% one year later. A similar study in the Mediterranean forests also identified a fast canopy recovery after significant drought dieback, regardless of age [50]. Although a high percentage of saplings recovered in 2019, 22% of the saplings were still partially damaged and 6% recorded complete defoliation. The SPEI drought index indicated a severe drought in 2018, but only a normal to moderate drought in 2019. However, the average precipitation was lower in 2019 (736 mm) compared to the average between 2000 and 2017 (957 mm). This partial recovery of the canopy can result from chronic stress, branch decline, and poor bud development, which in turn can increase susceptibility to further stress [14]. For example, crown defoliation increased during the drought events between 1987–2006 for both coniferous and deciduous species in Spain, with partial recovery after the events [30]. Moreover, Dobbertin and Brang [29] showed that the rate of mortality increased exponentially with crown defoliation in deciduous and coniferous forests in Switzerland. The vulnerability of already damaged saplings may increase under repeated drought stress, probably resulting in a complete dieback.

Tree recovery depends on the tree species strategies to cope with drought stress enhanced by the site conditions. Water limitation is considered the main factor for tree survival [51]. Species exhibit morphological and physiological traits that allow them to cope with drought stress to some extent. During severe drought events, defoliation of the canopy determines a decrease in photosynthetic capacity, which leads to depletion of the carbon reserves, followed either by a longer recovery phase of the surviving trees or their death [52]. Accordingly, all 10 abundant species recovered in high proportions, with S. *aucuparia* and *C. betulus* having a faster recovery rate than *F. sylvatica*, *Quercus* spp., *B. pendula*, and *Crataegus* spp. (Figure 4). The resistance and resilience of these species could not be assessed with the current dataset, therefore, further studies should be done.

The extensive defoliation of *S. aucuparia* under the drought of 2018 indicates a catastrophic failure of the hydraulic system. *S. aucuparia* is a species that is adapted to a short growing season, tolerates cold, frost, shade, high temperatures, and has a high ability to grow in different soil conditions, but does not tolerate drought [53]. Although it is currently a widespread species in Europe, a shift to upper elevation and latitude has been shown [54] and under future climate scenarios, it is predicted that it will lose more climate space than it gains, especially from Southern and Eastern Europe [55,56]. In the study area, a high proportion of *S. aucuparia* saplings are growing in cambisol and podzol. The species is highly dependent on the site characteristics, however, it is categorized as having a medium-deep root system (100 cm) [57]. Despite their high vulnerability to drought, *S. aucuparia* saplings had faster recovery than *Quercus* spp. and *F. sylvatica* (Figure 4). Similar to our results, in an experimental setup, *Sorbus torminalis* seedlings also showed a faster recovery rate compared to *Quercus* spp. and *F. sylvatica* [20]. In contrast, mature trees of *S. torminalis* and *Q. petraea* had a lower recovery than *F. sylvatica* [21]. This indicates that seedlings and saplings respond similarly to drought stress, but this may not be consistent with the performance of mature trees.

Among the species examined, saplings of *F. sylvatica* were less susceptible to drought stress and had a significant post-drought recovery (Figure 4). *F. sylvatica* is limited by temperature, drought, and humidity availability, however, it is predicted that its range will shrink in the south, be stable in central, and expand in northern Europe [58]. Under moderate drought stress, *F. sylvatica* fine-root production and length increases, being able to foster water uptake, however, under severe soil drought it decreases leading to root mortality [59]. Moreover, experimental setups showed that the photosynthetic performance of *F. sylvatica* and *Q. pubescens* saplings was severely impaired during a severe drought but recovered completely after re-wetting [60,61]. This suggests that the aboveground and belowground compartments are both severely affected by drought stress. In the study area, out of 772 *F. sylvatica* saplings, only 90 experienced complete defoliation during the drought of 2018 and 44 one year later. Compared to common garden experiments in which saplings were exposed to short term drought stress (e.g., four weeks) [60,61], the saplings from the study area were exposed to prolonged drought stress with low average spring and summer precipitation. Therefore, these results underline the ability of *F. sylvatica* saplings to cope with prolonged drought stress and recover.

Although mature trees of *Quercus* spp. have deeper roots and are considered to have a higher drought tolerance than *F. sylvatica* [49,62,63], our results showed that *Quercus* spp. saplings were even more vulnerable to drought than those of *F. sylvatica*. However, both species had a similar recovery rate (*F. sylvatica* 1.22 and *Quercus* spp. 1.12). In contrast, Kunz et al. [21] reported a higher recovery for *F. sylvatica* compared to *Q. petraea* mature trees. *Q. petraea* were the most common saplings in our study area. Both species have moderate drought resistance, with a less sensitive and deeper root system, they can access deeper water sources, however, a high density of *Quercus* shallow fine roots is found on the upper horizon, where the risk of drought is higher [62]. *Quercus* species have different preferences regarding soil conditions [64]; in the study area, they were found mostly in podzol, followed by cambisol and luvisol. Despite the drought resistance of *Quercus* spp., when mixed with *F. sylvatica*, the latter is competitively superior [62]. Additionally, in southern Europe, although canopy defoliation has increased in recent years, consistent with tree mortality, *F. sylvatica* has a lower mortality rate compared to *Pinus* spp. and *Quercus* spp. [30].

Tree saplings of *B. pendula* and *F. sylvatica* were found mainly in cambisol and podzol and experienced similar rates of defoliation. However, both species can tolerate different soil conditions. *B. pendula* is not drought tolerant but has a deep rooting system [65]. Therefore, the high shade tolerance of *F. sylvatica* saplings [66], together with the ability to deepen and intensify the root system under drought conditions, seems to lead to an efficient strategy, comparable to that of *B. pendula*. *S. nigra* had rather a low recovery compared to *A. pseudoplatanus*, but neither was significant. *S. nigra* can grow under poor soil conditions, but it is not drought tolerant [67]. In contrast, *A. pseudoplatanus* is a medium shade-tolerant [66] and moderately drought-sensitive species, which prefers locations with moderate to high soil moisture and nutrient-rich content [68]. Although most saplings of these two species were found in cambisol and rendzina soils, they were partly damaged during the 2018 drought but recovered in high proportions in 2019. Seedlings of other European *Acer* species (*A. campestre* and *A. platanoides*) showed a higher drought recovery compared to *F. sylvatica* and *Q. petraea* [20], whereas mature trees of *Q. petraea* showed a lower recovery than *Acer* and *F. sylvatica* species after drought [21]. Therefore, seedlings and sapling of *Acer* species may recover better from drought stress than mature trees.

C. betulus and *F. alnus* were found mainly in cambisol and podzol, but can also grow in a range of soils and are shade-tolerant species. Both species recorded a high level of defoliation, which may be explained by their preference for moist soils [69–71]. Nevertheless, saplings of *C. betulus* had a high rate of recovery. *C. betulus*, along with *A. campestre, S. torminalis,* and *S. aria*, are predicted to be among the best species adapted to a warmer and possibly drier climate in Central Europe in the future [72]. In conclusion, we found very species-specific responses to drought in deciduous saplings that have been mainly established through natural regeneration in the forest understory.

4.2. Species Diversity

Forest stands with high sapling species diversity showed more signs of reduced vitality. The Shannon diversity index for the total tree species decreased with the increase in sapling vitality in 2018. This can mean that forest stands that are more susceptible to drought (e.g., on shallow soils or with limited nutrient availability) have higher species diversity. It is less likely that the diversity of species and intraspecific competition would be the reason for this phenomenon because there is an incidence that diversity can mediate drought stress [23]. One year later, in 2019, no such effect was found any more due to the recovery of many saplings, which indicates a high resilience of the sapling community. The importance of species diversity in buffering forest drought vulnerability in European forests has been addressed in recent studies [49,73–76], however, unanimous consent has not yet been reached [23]. Grossiord [23] has shown that most studies have been done at the mature stage of development, therefore an assessment at the sapling level has been missing up to now. Species interaction is predicted to mitigate drought impact on trees by better partitioning resources among neighboring species or by facilitation as a result of tree species interaction (i.e., -intra/interspecific interaction in aboveground and belowground tree compartments) [23]. Positive effects of species interaction have been shown in several studies in temperate forests [22,49,73], indicating that mixed forest stands are more appropriate to mitigate the effects of global warming. However, such positive effects are expected in the long term and do not exclude short-term individual and species-specific responses to extreme events that are more likely to occur in highly diverse communities.

At the mature level, we identified a neutral effect of tree diversity on sapling vitality, where such an effect is considered to be determined by environmental conditions [77], whereas sapling diversity correlated negatively with vitality. Forest stands with a high diversity of saplings exhibited a low tree vitality. A negative relationship between species diversity and tree vitality was also found in other ecosystems [23]. It is discussed whether functional redundancy (i.e., functional niches overlap) may lead to stressful conditions during drought events with scarce water availability [73]. Enhanced transpiration is promoting competition for nutrients and water [14,76,78].

In species-rich stands, *F. sylvatica* is found to exhibit strong underground competitiveness, pushing the other species' root system toward the surface including those of *Q. petraea* [79]. In species-rich stands, soil water extraction is high at the beginning of the drought, but decreases considerably under severe drought stress since the soil already has low water content; whereas in *F. sylvatica* dominant stands, soil water extraction was low at the beginning of the drought and increased during the drought [80]. Therefore, it can be emphasized that soil water resources from species-rich forests can be depleted faster than in the stands dominated purely by *F. sylvatica*. However, there are specific conditions in different ecosystems. A negative relation between species diversity and tree vitality has been shown in temperate, boreal, steppe, dry, and humid Mediterranean climates [75].

We showed that among the investigated groups of saplings in the understory, those saplings with a higher diameter at breast height (DBH) underwent more intense defoliation compared to those with lower DBH. This finding partly contradicts the assumption that resistance to environmental stress generally increases with ontogeny [26]. Since larger saplings need more resources to ensure their survival under mature tree canopies than smaller saplings [46], this can explain their higher defoliation under drought stress. Tree diameter may play an important role in the resistance, recovery, and resilience of the trees to drought. However, there is no general agreement whether smaller or larger trees are more vulnerable to drought because this depends on the site conditions and the duration of the drought.

As expected, the cover of saplings decreased with their vitality in 2019 (Figure 5c). Therefore, their photosynthetic tissue was not yet fully recovered. However, we should consider that sapling recovery is species-dependent. Our results also show that saplings growing under mature trees with a large canopy cover exhibit a lower vitality (Figure 5c). These results indicate that the relationship between mature trees and saplings is not only characterized by facilitation, but can promote higher susceptibility to drought stress and affect the sapling's recovery. Partly similar to our results, it was shown that the crown dieback of saplings and mature trees of *F. sylvatica* can decrease with the soil water storage, plant height, species diversity, and light availability [81]. In our case, soil available water capacity (AWC) did not show a significant relationship with sapling vitality. However, saplings growing in luvisol were more susceptible to drought damage.

Extreme drought episodes are predicted to re-emerge in Bavaria with a higher intensity and frequency. The historic climate, warm temperate, and fully humid (Cfb) climate is predicted to change to a warmer/wetter climate in the wintertime and warmer/drier climate during spring and summer [82]. Winter precipitation is more likely to cause run-off and floods than to increase plant water availability [82]. This will have a great impact on plant growth [7]. Therefore, for efficient mitigation of climate change impacts on broadleaved tree species, it is critical to understand and include the effect of drought on saplings in the development of future forest management strategies.

5. Conclusions

In the understory of Central European forest ecosystems, tree sapling defoliation intensity and the recovery rate were affected by drought in a species-dependent way. This can affect the trajectories of natural regeneration in forest development. It needs to be understood how extreme drought influences juvenile trees in the understory, which cannot be monitored by remote sensing. Although more than 50% of the tree saplings experienced defoliation during the drought in 2018, the recovery rate was high in 2019. We identified that *F. sylvatica* and *B. pendula* saplings were capable of withstanding and surviving the extreme drought better than other species, whereas *C. betulus* and *S. aucuparia* recovered faster than *F. sylvatica*, *Quercus* spp., *Crataegus* spp., and *B. pendula* species. Moreover, forest stands with high sapling species diversity appear to have a reduced vitality under drought conditions. Until now, it cannot be disentangled whether this is an effect of interspecific competition or higher species richness on naturally resource-limited stands. Sapling vitality was also related to the canopy cover and the soil type, however, further work needs to be focused on the interaction of saplings and mature tree species under drought stress. These findings can help to design adapted long-term strategies for forest management in the face of an increasing likelihood of extreme climatic conditions.

Supplementary Materials: Supplementary Materials 1. Climatic variables and vitality of tree saplings per species. Supplementary Materials 2. Vitality of the tree saplings corresponding to the soil type. Supplementary Materials 3: Standardized Precipitation Evapotranspiration Index (SPEI) for the study area.

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Supplementary information

Surprising recovery of saplings to severe drought in temperate deciduous forests

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Supplement 1: Climatic variables and vitality of tree saplings per species.

Files in this Data Supplement:

Figure S1 a-d

Table S1

Figure S2

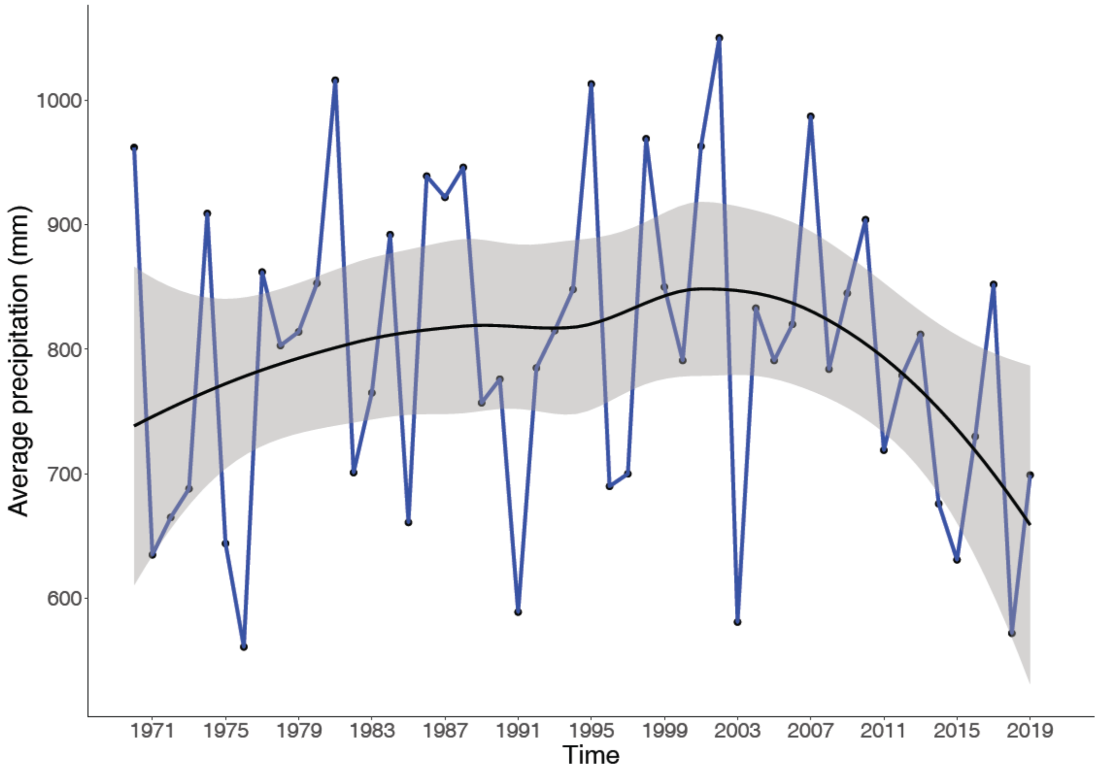


Figure S1a. Local weighted regression (LOESS) lines of average precipitation (mm) between 1970 and 2019 for the study area. Climatic data extracted from the raster data set (1 x 1 km) of the German Meteorological Service.

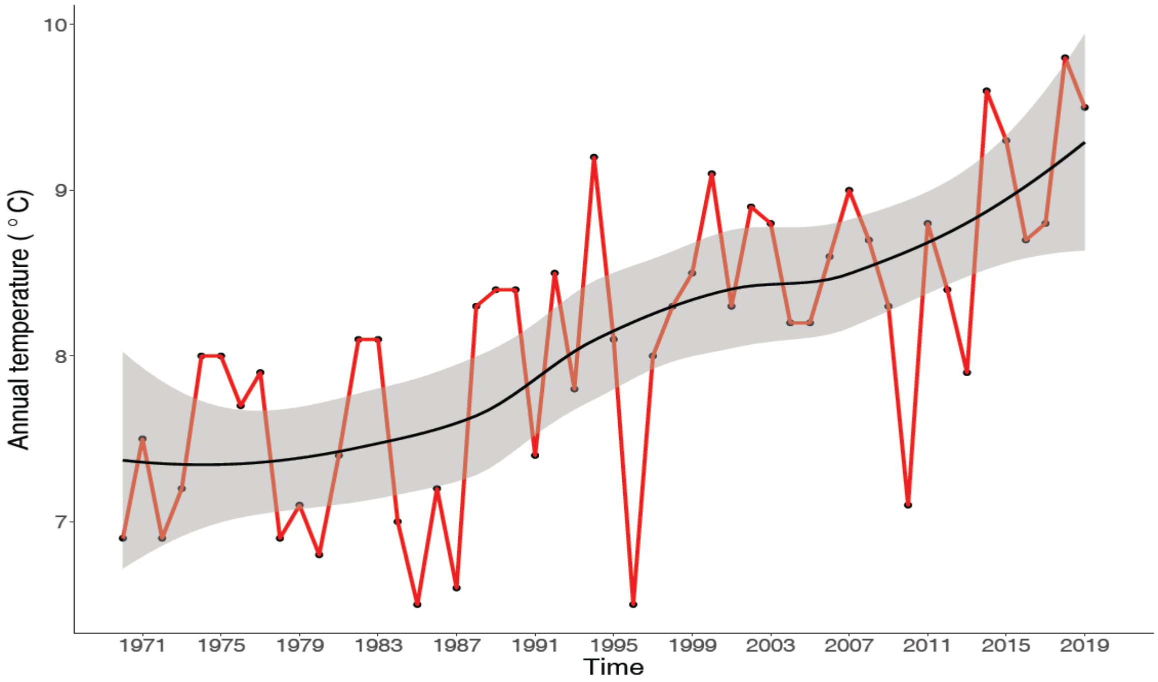


Figure S1b. Local weighted regression (LOESS) lines of mean annual temperature (°C) between 1970 and 2019 for the study area. Climatic data extracted from the raster data set (1 x 1 km) of the German Meteorological Service.

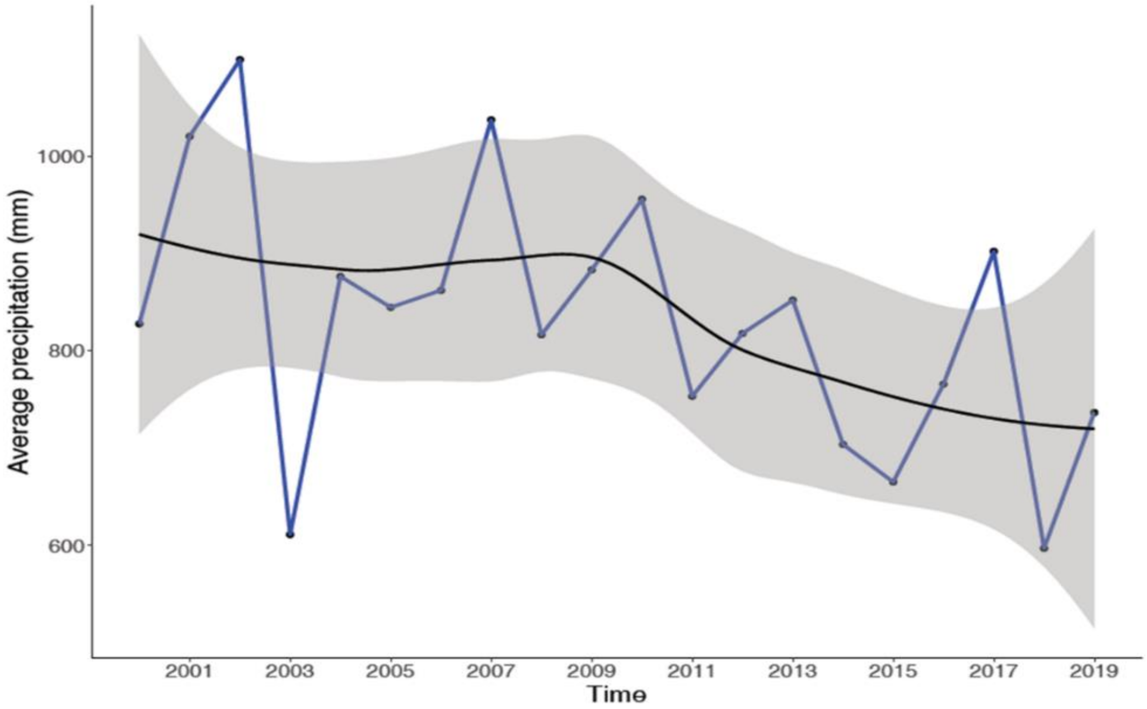


Figure S1c. Local weighted regression (LOESS) lines of average precipitation (mm) between 2000 and 2019 for the study area. Climatic data extracted from the raster data set (1 x 1 km) of the German Meteorological Service.

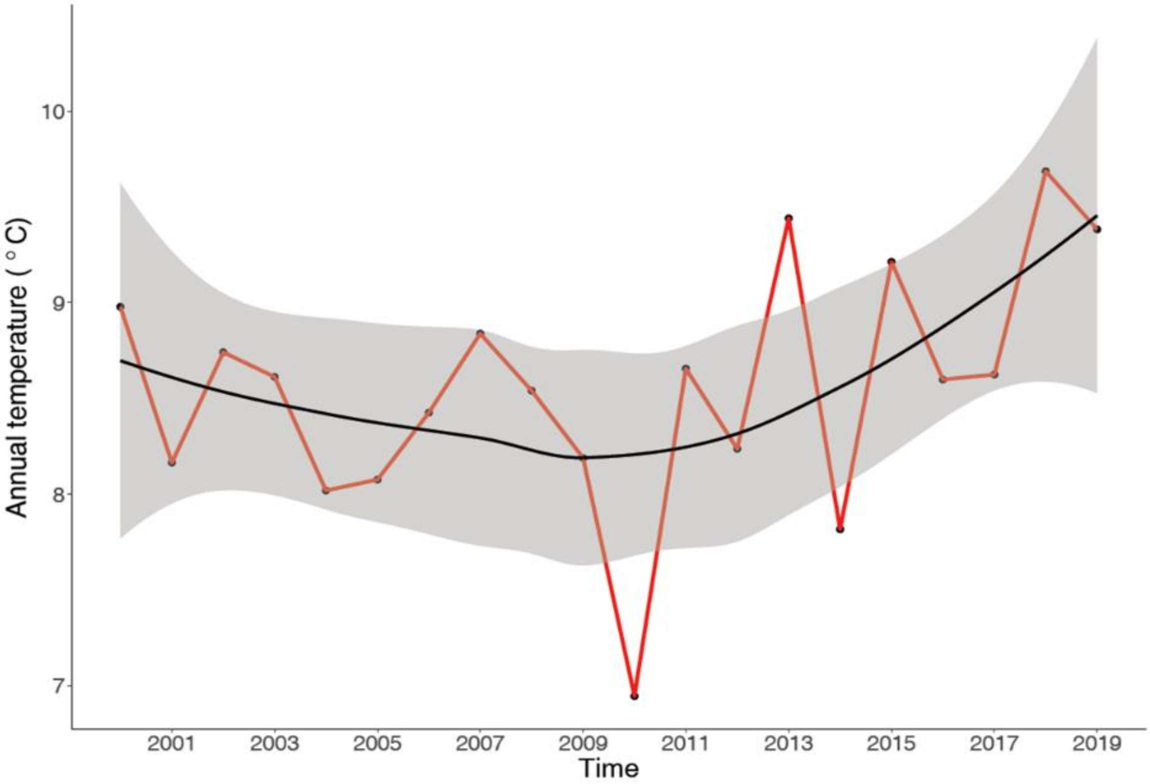
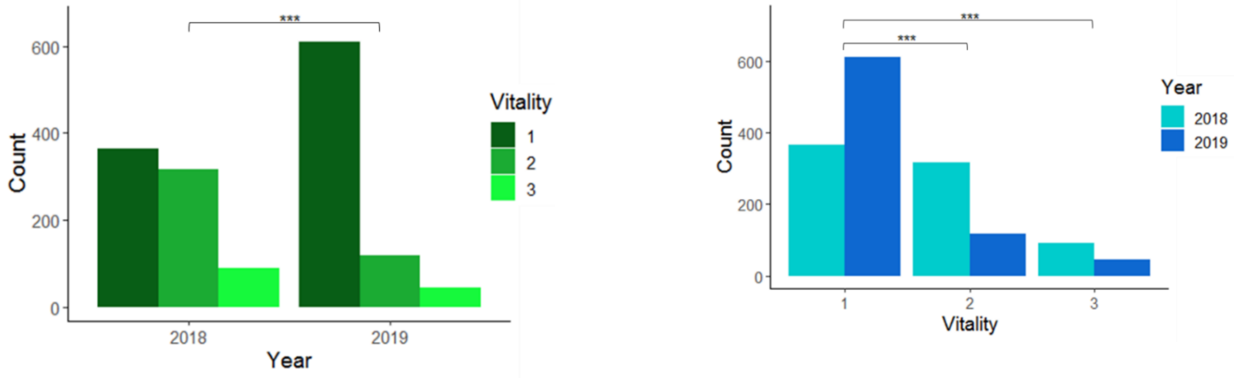


Figure S1d. Local weighted regression (LOESS) lines of mean annual temperature (°C) between 2000 and 2019 for the study area. Climatic data extracted from the raster data set (1 x 1 km) of the German Meteorological Service.

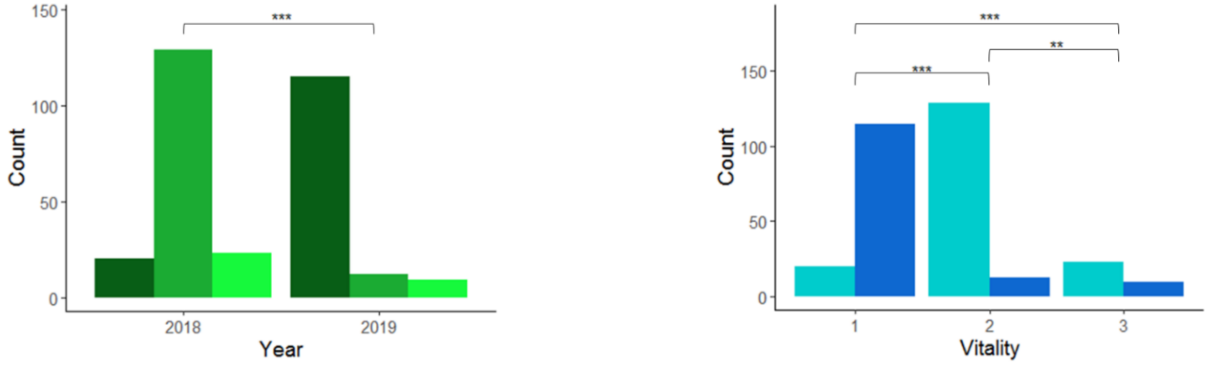
Table S1. Contingency table for sapling vitality during the drought of 2018 and one year later. Vitality 1 = undamaged, 2 = damaged, 3 = completely damaged sapling.

Vitality	**2019**			
2018	**1**	**2**	**3**	**Sum**
1	**632**	79	7	718
2	756	**270**	23	1049
3	92	97	**95**	284
Sum	1480	446	125	2051

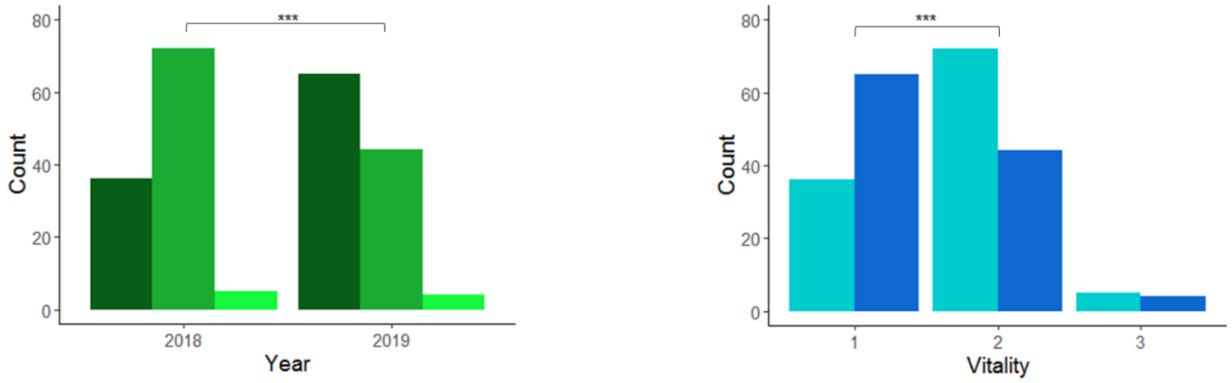
McNemar's Chi-Squared test for count data was applied to the data from Table 1. McNemar's test indicated a significant difference between the vitality classes (chi-squared = 667.51, p-value < 2.2e-16). Pairwise comparison showed that the number of undamaged saplings in 2019 is higher than that of damaged saplings and completely damaged saplings (1/1: 2/2 p-value < 0.001, 1/1 : 3/3 p-value < 0.001). Also, the number of damaged saplings was significantly greater than that of the completely damaged saplings (2/2: 2/3 p-value < 0.001).



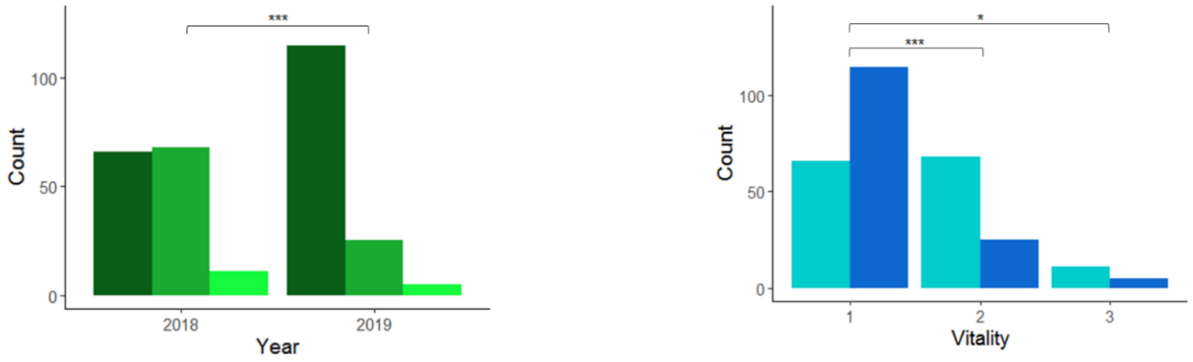
Fagus sylvatica N=772



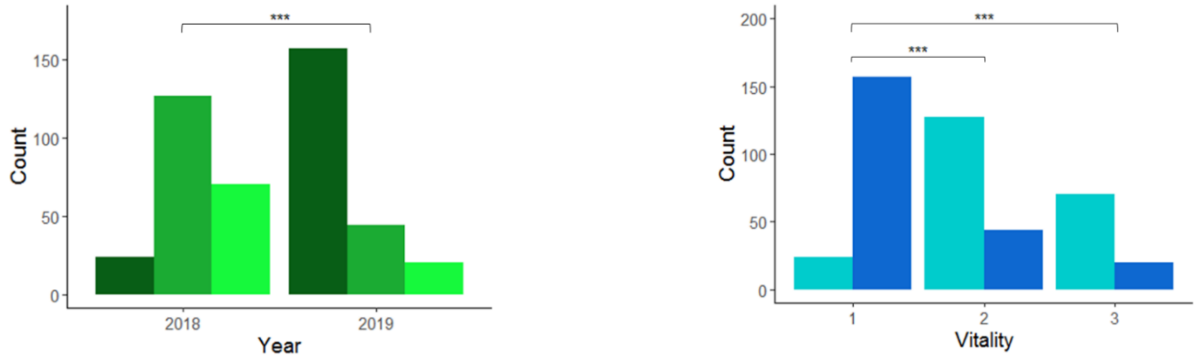
Carpinus betulus, N=172



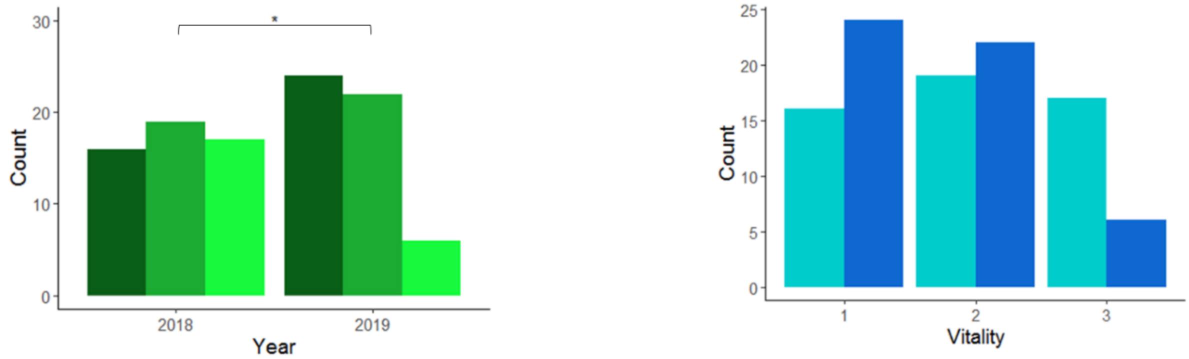
Quercus spp., N=113



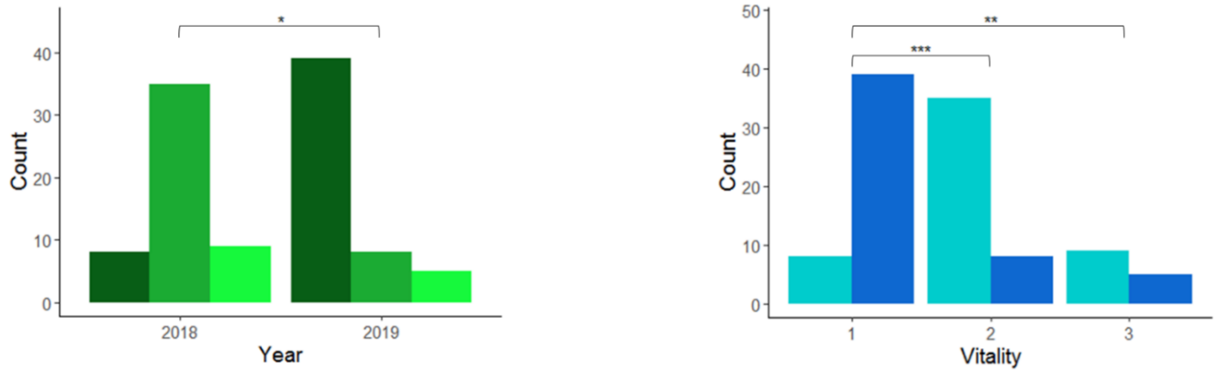
Betula pendula, N=145



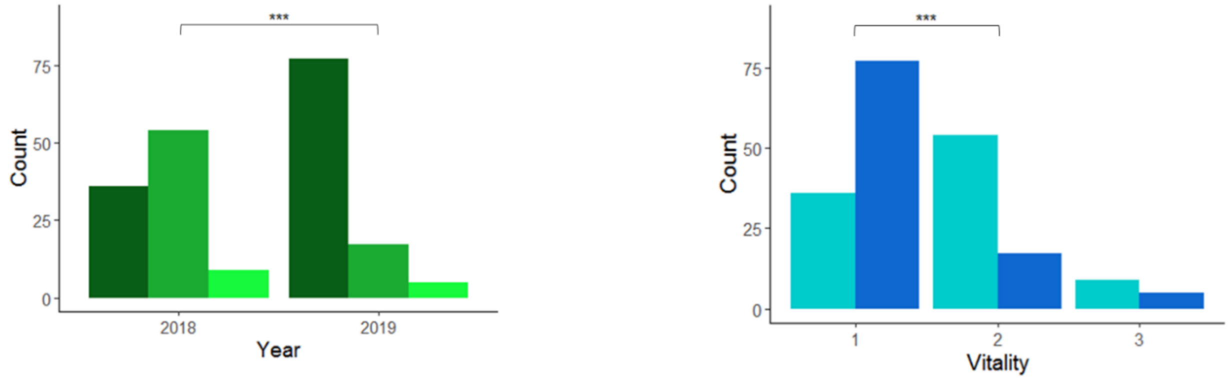
Sorbus aucuparia, N=221



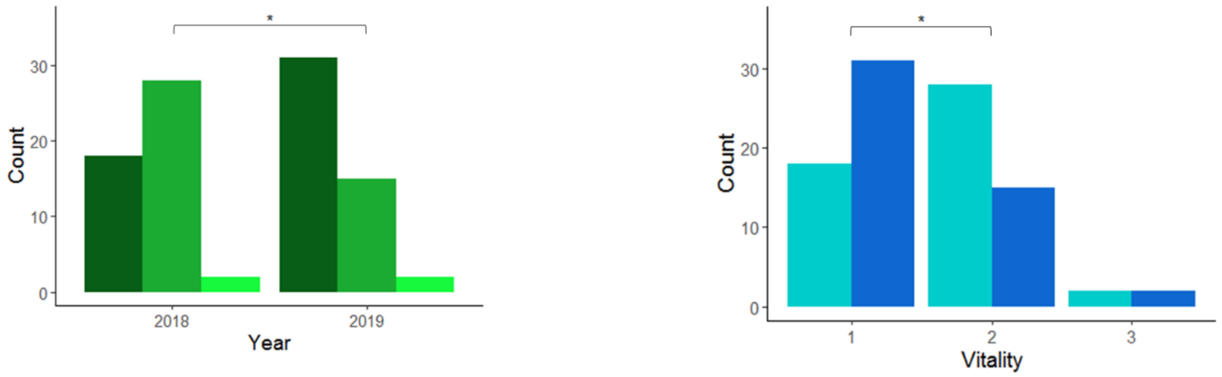
Sambucus nigra, N=52



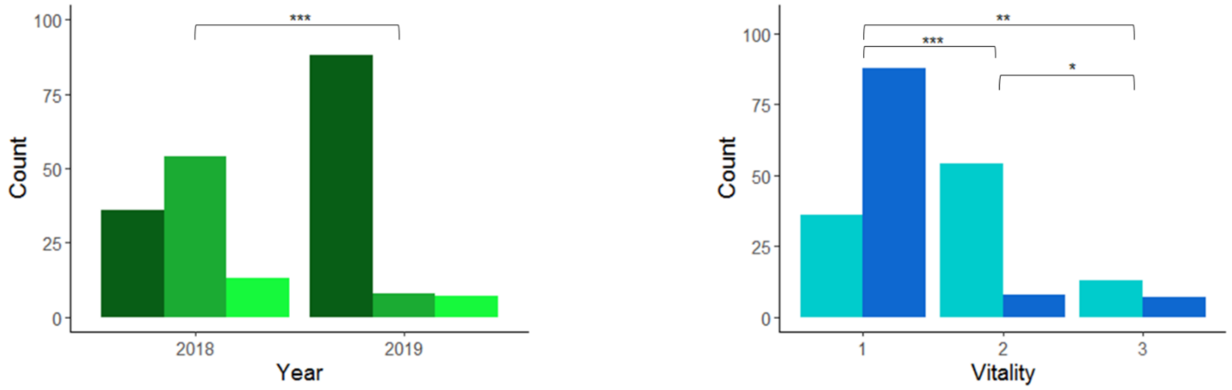
Frangula alnus, N=52



Corylus avellana, N=99



Crataegus spp., N= 48



Acer pseudoplatanus, N= 103

Figure S2. Vitality of most abundant species (*Fagus sylvatica* (n=772), *Carpinus betulus* (n=172), *Quercus* spp. (n=113), *Betula pendula* (n=145), *Sorbus aucuparia* (n=221), *Sambucus nigra* (n= 52), *Frangula alnus* (n=52), *Corylus avellana* (n=99), *Crataegus* spp. (n=48), and *Acer pseudoplatanus* (n = 103)). The left graphs show the difference in terms of vitality between the two years (2018 and 2019) and the right graphs show the difference between the vitality classes (1, 2, and 3). Vitality 1 = undamaged, 2 = partly damaged, 3 = completely damaged sapling.

Supplement 2: Vitality of the tree saplings corresponding to the soil type.

Files in this Data Supplement:

Table S1, S2, and S3

Table S1. Number of the tree species found on each soil type.

Species	Cambisol	Luvisol	Podzol	Rendzina
Fagus sylvatica	444	21	230	77
Sorbus aucuparia	140	17	59	5
Carpinus betulus	97	14	49	12
Betula pendula	102	0	42	1
Quercus spp.	35	12	65	1
Acer pseudoplatanus	55	13	15	25
Corylus avellana	51	1	212	26
Frangula alnus	19	1	26	6
Sambucus nigra	31	0	8	13
Crataegus spp.	17	0	20	11

Table S2. Pairwise comparisons using Fisher's exact test for count data to test the hypothesis of no difference in undamaged/damaged saplings between soil types (cambisol, luvisol, podzol, and rendzina).

a) Sapling classification (undamaged/damaged) corresponding to the soil types. Fisher's Exact Test for Count Data, p-value = 0.007

Soil	Undamaged 2018	Damaged 2018	Undamaged 2019	Damaged 2019
Cambisol	382	705	802	285
Luvisol	**18**	**80**	65	**33**
Podzol	227	390	449	168
Rendzina	91	158	164	85

b) Comparison of soil types between undamaged and damaged saplings (2018 and 2019).

	Cambisol: Luvisol	**Cambisol: Podzol**	**Cambisol: Rendzina**	**Luvisol: Podzol**	**Luvisol: Rendzina**	**Podzol: Rendzina**
Undamaged 2018: Damaged 2018	**0.01**	0.71	0.86	**0.01**	**0.01**	1.00
Undamaged 2018: Undamaged 2019	0.16	0.77	0.52	0.15	0.11	0.77
Undamaged 2018: Damaged 2019	**0.03**	1.00	0.38	**0.03**	0.16	0.38
Damaged 2018: Undamaged 2019	0.16	1.00	0.69	0.16	0.42	0.68
Damaged 2018: Damaged 2019	1.00	0.77	0.16	1.00	0.55	0.38
Undamaged 2019: Damaged 2019	0.29	0.81	0.09	0.38	1.00	0.16

c) Comparison between undamaged and damaged saplings (2018 and 2019) base on soil types.

	Comparison	**p.Fisher**	**p.adj.Fisher**
1	**Undamaged 2018 : Damaged 2018**	**0.002**	**0.01**
2	Undamaged 2018 : Undamaged 2019	0.10	0.16
3	**Undamaged 2018 : Damaged 2019**	**0.01**	**0.03**
4	Damaged 2018 : Undamaged 2019	0.22	0.26
5	Damaged 2018 : Damaged 2019	0.31	0.31
6	Undamaged 2019 : Damaged 2019	0.04	0.08

Table S3. Contingency table for undamaged and damaged sapling during the drought of 2018 and after it (2019) for the following soil types: a) cambisol, b) luvisol, c) podzol, and d) rendzina. McNemar's Chi-Squared test for count data was applied to each soil type

a)

Cambisol	**2019**		
2018	**Undamaged**	**Damaged**	**Sum**
Undamaged	345	**37**	382
Damaged	**457**	248	705
Sum	802	285	1087

McNemar's chi-squared = 355.39, p-value < 2.2e-16

b)

Luvisol	**2019**		
2018	**Undamaged**	**Damaged**	**Sum**
Undamaged	17	**1**	18
Damaged	**48**	32	80
Sum	65	33	98

McNemar's chi-squared = 43.184, p-value = 4.983e-11

c)

Podzol	**2019**		
2018	**Undamaged**	**Damaged**	**Sum**
Undamaged	195	**32**	227
Damaged	**254**	136	390
Sum	449	168	617

McNemar's chi-squared = 170.77, p-value < 2.2e-16

d)

Rendzina	**2019**		
2018	Undamaged	Damaged	Sum
Undamaged	75	**16**	91
Damaged	**89**	69	158
Sum	164	85	249

McNemar's chi-squared = 49.371, p-value = 2.118e-12

7.4. Manuscript 4 - Drought impacts in forest canopy and deciduous tree saplings in Central European forests

Title: Drought impacts in forest canopy and deciduous tree saplings in Central European forests

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Abstract

Forests worldwide are increasingly exposed to extreme weather events. Drought deteriorates the health, structure, and functioning of forests, which can lead to reduced diversity, decreased productivity, and increased tree mortality. Therefore, it is an urgent need to assess the impact of drought on tree species. Due to differences in tree physiology, saplings and mature trees are likely to respond specifically to drought conditions. In contrast to mature trees, little is known about the response of saplings to drought. Here, we combine in-situ field measurements for saplings of deciduous tree species with remote sensing for forest canopy to assess drought damage, recovery, and sapling mortality patterns during a centennial drought (2018, 2019) and beyond (2020). We measured 2051 saplings out of 214 plots in Central Germany. Forest canopy health was assessed using 10 x 10 m resolution satellite observations for the same locations. We (1) demonstrate that forest canopy exhibits long-lasting drought-induced effects, (2) show that saplings have a remarkable capacity to recover from drought and survive a subsequent drought, (3) demonstrate that reduced sapling recovery leads to their mortality, (4) reveal that drought damage on saplings increases from pioneer to non-pioneer species, and mortality is ranking from *Sorbus aucuparia* > *Sambucus nigra* > *Fraxinus excelsior, Acer campestre, Frangula alnus* > *Ulmus glabra* > *Carpinus betulus* > *Betula pendula, Fagus sylvatica* > *Acer pseudoplatanus* > *Quercus petraea* > *Corylus avellana, Crataegus spp.,* > *Prunus avium, Quercus robur*; and (5) link drought response to site conditions, indicating that species diversity and winter precipitation as relevant indicators of tree health. If periods of drought become more frequent, as expected, this could negatively impact mid-term forest recovery, alter long-term tree species assemblages and reduce biodiversity and functional resilience of forest ecosystems. We suggest that models of forest response to drought should differentiate between the forest canopy and understory and also consider species-specific responses as we found a broad spectrum of responses within the same plant functional type of deciduous tree species in terms of drought damage and recovery.

Keywords

summer drought 2018; temperate forests; climate change; Sentinel-2; forest health; tree recovery; sapling mortality

1. Introduction

Despite the long life cycles of trees, forests are one of the ecosystems most threatened by short but intense climate extremes (Allen et al. 2015). The capacity of forests to maintain their contribution to carbon sequestration is uncertain if turnover increases due to climate warming (Büntgen et al. 2019). Global climate change is expected to cause a progressive increase in hot temperature extremes and more intense and severe droughts (Seneviratne et al. 2014; IPCC 2019). The Central European drought of 2018 (Vogel et al. 2019) was followed by a second dry and extremely hot year in 2019 (Vautard et al. 2020). In addition, the 2018 drought was significantly stronger compared to the 2003 drought and had major impacts on less drought-adapted ecosystems in Central and Northern Europe (Buras et al. 2020; Schuldt et al. 2020). Such climate extremes are predicted to threaten and reduce plant diversity (Thuiller et al. 2005), cause changes in plant communities (Komatsu et al. 2019), affect forest diversity and productivity (Ratcliffe et al. 2017; Ammer 2019), and increase tree mortality (Anderegg et al. 2013; Senf et al. 2018; Buras et al. 2020; Senf et al. 2020), amongst others. The 2003 drought caused a decline in forest productivity and carbon storage across Europe (Ciais et al. 2005; Reichstein et al. 2007). This highlights the urgent need to identify, understand, and predict declines in forest performance and health across species and ecosystems (Trumbore et al. 2015).

Droughts trigger forest physiological responses that can vary at inter-and intraspecific levels depending on regional and local factors (Kunz et al. 2018; Bose, Gessler, et al. 2020; Gazol et al. 2020; Hereş et al. 2021). Drought can induce anomalies in foliage color, reduce foliage density (Sousa-Silva et al. 2018; Bigler & Vitasse 2021), and cause crown dieback (Lloret et al. 2004). Prolonged or successive droughts in forests can lead to long-lasting chronic effects on the stem and crown structure of trees (Carnicer et al. 2011) and predispose them to insect attack (Anderegg, Hicke, et al. 2015; Stephenson et al. 2019). The 2018 drought caused premature discoloration and defoliation of leaves in temperate forests in Central Europe (Schuldt et al. 2020; Rohner et al. 2021).

Recovery is a key ecological process that influences forest stability, structure, and function in the face of extreme events (Anderson-Teixeira et al. 2013; Hodgson et al. 2015;

Donohue et al. 2016). Tree recovery is defined as the capacity of a system to return to a stable state and function after a disturbance (Ingrisch & Bahn 2018; Gessler et al. 2020). The effects of drought stress episodes on forests can be assessed by analyzing their drought response and recovery time (Lloret et al. 2011; Schwalm et al. 2017). Understanding which species are most affected and how they recover from extreme droughts has implications for the design of adaptive management strategies, the development of decision support systems for forest management, and for understanding processes that enhance the adaptability of forests to new conditions (Messier et al. 2015). Drought damage and recovery are species-specific and depend on stand composition in both saplings (Beloiu et al. 2020) and mature trees (Pretzsch et al. 2013; Anderegg, Schwalm, et al. 2015; Pretzsch et al. 2020). The canopy of large trees can buffer the exposure of saplings to direct atmospheric conditions, such as solar radiation, lower leaf temperature, and evaporation (Bennett et al. 2015; Frenne et al. 2021). However, the patterns of sapling recovery and their relationship to survival and mortality are not yet clear.

Various methods have been used to quantify the forest response to drought, ranging from seedling experiments (Buhk et al. 2016; Rötzer et al. 2017; Müller et al. 2020) to field measurements (Mette et al. 2013; Pretzsch et al. 2013) and satellite observations (Karnieli et al. 2010; Gazol et al. 2018). Field measurements are the gold standard for assessing forest changes, while the satellite data from the Copernicus Sentinel-2 mission provide high-resolution (10 x 10 m) images (Drusch et al. 2012) that can capture vegetation conditions over a large area. Combining in situ and remote sensing observations allows us to better capture the response of tree species to drought and their recovery. Tree vitality (e.g. leaf discoloration and crown defoliation) and the Normalized Difference Vegetation Index (NDVI) are proxies for forest health and tree growth and are effective approaches for drought assessment (Karnieli et al. 2010; Brun et al. 2020; Gazol et al. 2020; Rohner et al. 2021). Moreover, increased crown defoliation is regularly associated with increased tree mortality (Carnicer et al. 2011).

Here we present a spatial and temporal analysis of drought-induced changes in both saplings of deciduous tree species and forest canopy (i.e. the canopy of the mature trees above the saplings). We focus mainly on deciduous tree species, as they are the naturally predominant trees and forests in the temperate biome of Central Europe. In late summer 2018, 2019, and 2020 we conducted a field study to assess sapling response to drought, sapling recovery, and mortality. Forest canopy response to drought was assessed using NDVI data for the same sites and time. In addition, we explain tree health by biotic and abiotic drivers such as biodiversity, climatic and edaphic variables. Specifically, we aim to address the following questions: (1) How severe is the impact of the drought and what is the recovery time for the forest canopy and saplings? (2) Which sapling species are more susceptible to drought? (3) How do recovery patterns of the sapling canopy influence sapling mortality? We comprehensively analyzed (a) the drought damage in saplings and forest canopy, (b) drought response in the 15 most common sapling species, (c) sapling recovery and mortality patterns, and (d) the environmental drivers (biotic and abiotic).

2. Methods

2.1. Study area

The study area is in Central Europe, in northern Bavaria (~11.000 km²), Germany (Fig. 1). The elevation varies between 200 m to 1035 m asl. (EEA 2016). The study area is covered by coniferous, deciduous, and mixed forests. The main tree species are beech (*Fagus sylvatica* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), pedunculate oak (*Quercus robur* L.), common hornbeam (*Carpinus betulus* L.), silver birch (*Betula pendula* Roth.), Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.), followed by minor broadleaved species, like mountain-ash (*Sorbus aucuparia* L.), sycamore maple (*Acer pseudoplatanus* L.), common hazel (*Corylus avellana* L.), alder buckthorn (*Frangula alnus* Mill.), black elder (*Sambucus nigra* L.), and hawthorn (*Crataegus* spp.).

The climate of the study area is oceanic, with continental influences. The average precipitation is 957 mm and the mean annual temperature is 7.1 ⁰ C for the period 1970-2020 (DWD 2021b; DWD 2021a). Over time, there was a drop in precipitation and an increase in temperature. The most severe drought was recorded in 1971-1974, 2003, and 2018. However, 2018 was the driest year (595 mm) since 1970 for the study area. The geology has a high complexity, with cambisol, podzol, rendzina, and luvisol as the main soil types.

2.2. Sapling vitality and the recovery index

Sapling vitality assessments were carried out during the summer term (August and September) from 2018 to 2020. Across the study area, 218 plots (10 × 10 m) were established in 2018 based on a random selection of locations within the forest area. The same plots were surveyed again in 2019, but out of 218 plots, 4 were damaged and were excluded from the measurements. In 2020, 174 plots were resurveyed. To reduce spatial autocorrelation, the plots were located at a mean distance of 6,9 km (min = 0.8 km, max = 10 km) (Figure 1). From these random locations, the nearest naturally established group of broadleaved saplings was detected. A Trimble Geo 7X satellite navigation device with an external antenna and SAPOS®-HEPS (High-precision real-time positioning service) was used to acquire the position of the center of each plot. An accuracy of better than 50 cm was always achieved.

Broadleaved saplings from natural regeneration were considered for the measurements as they represent the natural vegetation of the study area (Bohn & Neuhäusl 2003). Hence, 10 random broadleaved saplings ($\geq$ 1.3 m height, $\leq$ 10 cm diameter at breast height), irrespective of species, were selected and tagged in each plot. The tagged saplings were measured in 2018 and re-measured in 2019 and 2020. Only in a few cases, there were less than 10 saplings per plot sampled. In 2018, 2149 saplings of 41 species were assessed, while in 2019, 2051 saplings and in 2020, a total of 1709 saplings. In 2019 and 2020 few saplings were broken, cut, or presented deer browsing damage, and therefore were not considered for the analysis (Table 1).

The measurements done for the saplings, such as the diameter at breast height (dbh), sapling cover, vitality, and mortality are listed in the Supplementary materials, Table 1. The vitality was assessed each year, for each sapling tagged and was calculated based on crown condition (Eichhorn, et al. 2016). The three categories of vitality are 1 - undamaged (the leaves showed minor or no sign of early discoloration), 2 - partly damaged (individual leaves and branches showed early discoloration and premature leaf senescence), 3 - strongly damaged (all leaves and branches of the plant showed premature leaf-shedding and dry branches).

As tree death occurs over time, we monitored tree mortality for both saplings and mature trees in 2020. Despite the damage to the tree canopy, there were no dead trees on the plots. We classified saplings as dead (leafless trees with dry stems) only in the third year (2020) in which no recovery was observed. All tree species from the plot were determined during in-situ measurements. Forest type (deciduous, coniferous, and mixed forests) was defined based on the most dominant tree species in the forest where the plot was located.

2.3. Environmental data and remote sensing data

A table with all the variables that were used to explain saplings and forest canopy response to drought, their source, and resolution can be found in Supplementary materials, Table 2. Monthly precipitation, temperature, soil moisture, and evapotranspiration were extracted from the raster dataset (1 x 1 km) provided by the German Meteorological Service (DWD). Precipitation and temperature values were calculated for the growing season, April-August, and for the dormant season, October - March (a period in which trees cease their active growth, and deciduous species shed their leaves until new leaves are coming in spring and the growth begins). Moreover, the De Martonne aridity index was calculated for the growing season:

$$\text{De Martonne aridity index} = \text{Precipitation} / (\text{Temperature}+10)$$

Where precipitation is the sum between April and August, and temperature is the mean for the same months. The higher the De Martonne index values, the more water is available for tree growth (Supplementary materials Table 3) (Baltas 2007; Bhuyan et al. 2017). We used the index to describe the extreme drought conditions for summer 2018.

The soil samples were taken at 20 cm depth, except when the soil was too shallow, it was measured at 10 cm deep. Each sample consisted of a mixture of five subsamples (4 in the corners of the plot and one in the middle). Soil pH was measured in the laboratory. The depth of the organic layer and the soil horizons (A and B) were measured using tape and a soil gouge auger. Based on the European digital elevation model (EU-DEM) version 1.1 (25 m) the slope and elevation were extracted for each plot. The canopy height was extracted from the global forest height map (Potapov et al. 2021). The forest cover is extracted from the digital landscape model (DLM) 1:250,000 (BKG 2019).

To determine the effects of drought on mature trees and their recovery within the same plots, forest canopy NDVI was used as a proxy. For this, Sentinel-2 satellite images (Drusch et al. 2012), were downloaded from the U.S. Geological Survey (USGS) Earth Resources Observation website (https://www.usgs.gov/). We used images at a resolution of 10 m x 10 m and with a cloud cover of less than 10 % from 2015, 2018, 2019 (August), and 2020 (September). The acquisition of the image was intended to match the main period of the fieldwork, only in 2020 no image from August was available, therefore September was considered. 2016 and 2017 were not considered for the analysis because the clouds cover was too high from June to September. The Sentinel-2 Level 1C (L1C) was used. The atmospheric correction of L1C was done using the Sen2Cor processor in Sentinel Application Platform (SNAP) and was followed by cloud masking. The NDVI was calculated following the formula:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{Red}) / (\mathrm{NIR} + \mathrm{Red})$$

Where NIR is the reflection in the near-infrared spectrum and RED is the reflection in the red range of the spectrum. NDVI values range from -1 to +1, with -1 usually corresponding to water bodies, values close to 0 correspond to barren land, urban areas, and values close to +1 correspond to dense vegetation. The NDVI value was extracted based on the coordinates for the center of each plot and using bilinear interpolation.

2.4. Statistical analysis

Differences in sapling vitality between the study years were examined for the most common species with Fisher's test. We assessed the distribution of the data using the Shapiro-Wilk test (e.g., for each group or variable used) to determine whether the data were normally or non-normally distributed and to decide on the method required. After assessing the distribution of the data, the non-parametric test, Kruskal-Wallis, and the Dunn post-hoc test from the FSA package were used for comparisons between groups (e.g. to determine which species recover more quickly).

The recovery index was calculated as suggested by Lloret et al. (2011), where recovery is estimated as the ratio of performance after and during the disturbance. In our case, we used the categorical values of vitality as a proxy for sapling performance and based on these values we calculate the patterns of sapling recovery. To calculate the recovery index for saplings, vitality values were first reversed and then the difference between post-drought vitality and vitality during the drought period was calculated. Recovery index values range from -2 to +2, with values < 0 indicating a decline in vitality, > 0 indicating an increase in vitality after the event, and 0 indicating the same state as during the event i.e., the reference value. The most common sapling species were selected based on ≥ 20 individuals over ≥ 10 plots, resulting in 15 species (Table 1). These species were classified into pioneer sapling species and late-successional sapling species. As defined by Brzeziecki and Kienast (1994), pioneer species (i.e., early successional species) have developed different life-history strategies than non-pioneer species (i.e., late-successional species). Hence, the pioneer species are *Acer campestre, Acer pseudoplatanus*, *Betula pendula*, *Corylus avellana*, *Crataegus* spp., *Frangula alnus*, *Fraxinus excelsior*, *Prunus avium*, *Sambucus nigra*, *Sorbus aucuparia* and the *n*on-pioneer species are *Fagus sylvatica, Quercus petraea, Quercus robur, Carpinus betulus, Ulmus glabra.*

Forest canopy health for each plot was assessed based on the NDVI values, where the recovery index is the difference between post-drought NDVI and NDVI during the drought period. In this case, 0 is considered the reference value. Given the difference in measurements (continuous and categorical values), the evaluation of the forest canopy and understory was done separately. The R package "raster" was used to process the NDVI raster files.

We used multiple linear regressions to investigate the strength and the shape of the relationship between drought damage and environmental drivers (e.g. climatic, edaphic, topographic, and biotic). The environmental drivers used, their source, and resolution are shown in Table 2 from the Supplementary materials, and the model results are shown in Table 3. Multiple linear regressions make several key assumptions, such as a linear relationship, multivariate normality, no multicollinearity, and hemoschedascity. Thus, only uncorrelated variables were used (<0.7), as indicated in Table 2 from the Supplemental materials. The distribution of residues was checked for each model and the residuals were plotted versus the fitted values to check for homoscedasticity. We also assessed potential multicollinearity between explanatory variables using the variance inflation factor (VIF). The VIF was calculated using the VIF() function from the "regclass" package. A VIF of 1 indicates no multicollinearity, while a VIF greater than 5 indicates high multicollinearity. We computed a cluster analysis of incident points using the Optimized hot spot analysis tool to determine if the study sites (plots) formed statistically significant spatial clusters. The analysis (p-value > 0.05, at 95% confidence level) indicated that the plots are not clustered. This reflects that the plots are randomly distributed and on average 6.9 km apart. The mean vitality of the 10 saplings was calculated for each plot. This mean vitality was used as the response variable in multiple linear regression models. To better illustrate the spatial impact of drought on saplings from 2018, an inverse distance weighted (IDW) interpolation was calculated. This interpolation allows spatial patterns of sapling vitality (i.e., from areas with undamaged saplings to areas with strongly damaged saplings) to be identified that would otherwise be difficult to detect. All the statistical analyses were conducted in R (R Core Team 2020). The "ggpubr" and "ggplot2 v3.2.1" packages were used to visualize the results.

3. Results

3.1 Drought responses of saplings and forest canopy

In 2018, mean precipitation for the growing season (April-August) was less than half of the normal amount (450-500 mm) in the study area. De Martonne aridity index indicated a summer with arid to semi-arid climatic conditions for the temperate region of Central Germany (Supplementary materials, Fig. S1, Table 3). During the 2018 drought, the saplings in the central-western part of the study area were more affected than those in the eastern part of the study area (Fig. 1).

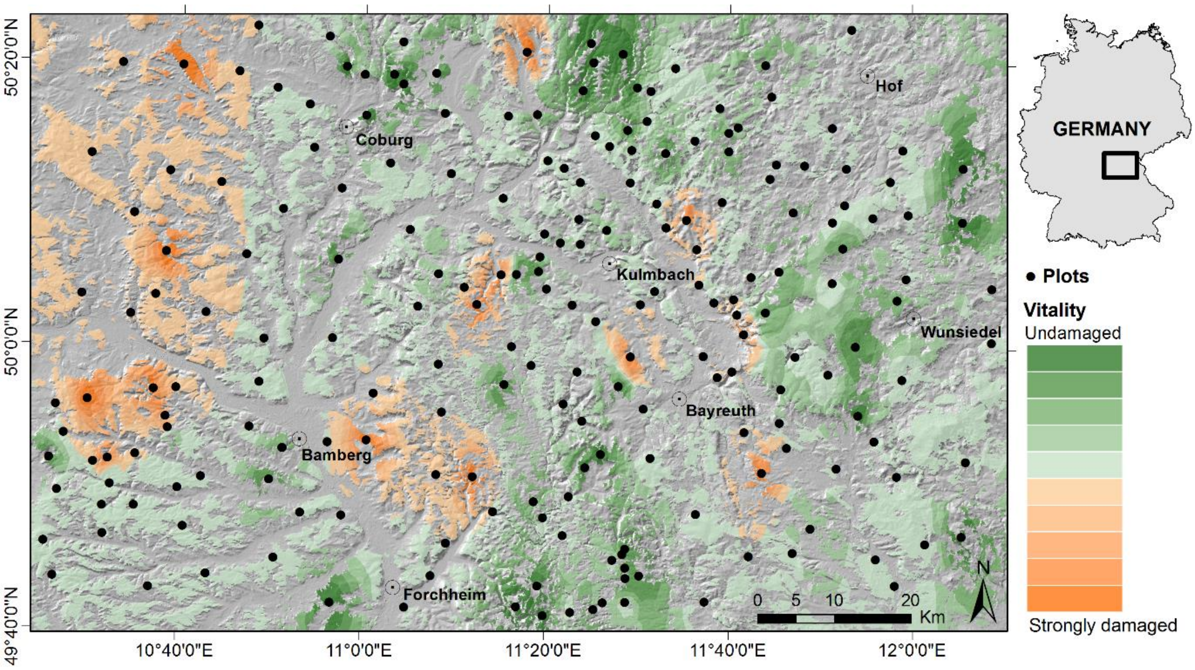

Figure 1. Spatial patterns of sapling vitality within the forest area in 2018. N = 214 plots. The vitality values range from 1 = undamaged saplings (green) to 3 = strongly damaged saplings (orange). The map was created using the inverse distance weighted (IDW) interpolation method.

In Fig. 2a we present the conceptual results of drought impact and recovery on forest canopy (i.e. mature trees) and understory (i.e. saplings). The forest canopy showed significantly lower NDVI values (unhealthy trees) during drought (2018 and 2019) than before (2015) and after (2020) the drought (Fig. 2ab). Whereas saplings showed low vitality in 2018 (51 % partly damaged and 14 % strongly damaged), but high vitality in 2019 and 2020 (75% and 68% undamaged, respectively) (Fig. 2c). Figures 2d and 2e show the legacy of the drought. The forest canopy recovered two years after the 2018 drought, while saplings recovered one year after the drought. Therefore, we demonstrate that forest canopy exhibits long-lasting drought damage. Saplings from the same plots experienced intense damage in 2018, but recovered one year later. Furthermore, after three years of monitoring, we can prove that induced drought damage leads to sapling death in temperate forests. 8 % of the saplings measured in 2018 died by 2020 due to drought-induced mortality, while 18% were partly damaged (Fig. 2c). Mature trees in the plots exhibited severe browning, dry branches, and partial canopy dieback, but none of them died during the monitoring years.

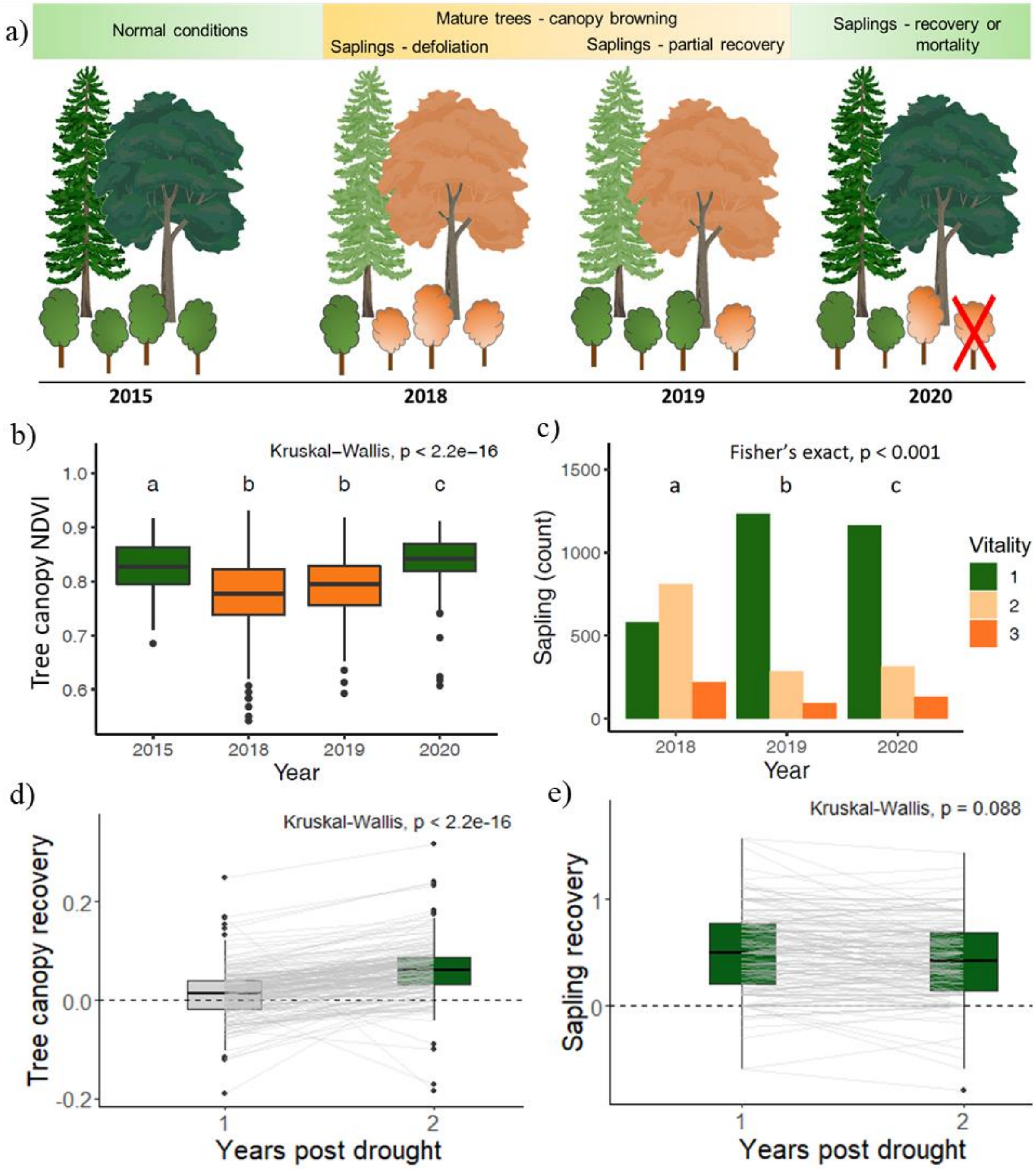

Figure 2. **a)** Ilustration of forest health before, during, and after the drought. **b)** Changes in forest canopy health across years and **c)** differences in saplings vitality between the study years (2018, 2019, 2020, n = 1606). The legacy effects of the 2018 drought on **d)** forest canopy and **e)** saplings. Values < 0 indicate a decline in recovery, > 0 an increase in recovery after the event, and 0 the same state as during the event i.e., the reference value. Vitality 1 = undamaged, 2 = partly damaged, 3 = strongly damaged saplings, in 2020, 3 = completely dry saplings. The tree image source is www.freepikcompany.com. Boxplot components: median (black lines), interquartile range (whiskers), and outliers (black dots) are shown. Letters in the figures indicate significant differences between groups. Differences between boxplots were determined using Dunn's Kruskal-Wallis multiple comparisons test and differences between vitality groups were calculated using Fisher's exact test.

3.2 Drought-response of 15 sapling species

Pioneer species were more affected by drought than non-pioneer deciduous species. The drought damage ranking for the most common species is *S. aucuparia* > *P. avium* > *C. betulus* > *F. alnus* > *Q. robur* > *U. glabra* > *S. nigra* > *C. avellana* > *Crataegus spp.* > *A. pseudoplatanus* > *F. excelsior* > *Q. petraea* > *B. pendula* > *F. sylvatica* > *A. campestre* (based on mean values between vitality 2 and 3). Remarkably, the sapling species maintained a similar proportion of vitality in 2020 as in 2019 (Table 1). Although *Q. robur* saplings were more affected by drought than *Q. petraea* in 2018, they recovered by 2020.

All species exhibited high vitality following the 2018 drought, with species-specific differences. Most species recovered after the 2018 drought and maintained their vitality in the next years, e.g. *F. sylvatica* and *B. pendula* (Supplementary materials, Fig. S2ab). While other species, such as *S. aucuparia, C. betulus,* and *A. pseudoplatanus* recovered fast but showed a slight decrease in vitality in 2020 (Table 1). There are two cases where sapling vitality increased rapidly one year after the 2018 drought but decreased significantly in 2020, such as *C. betulus* and *S. aucuparia* (Supplementary materials, Fig. S1cd). For example, the pioneer species, *S. aucuparia*, recovered very fast in 2019, but in 2020 the leaves were brown, and many trees were completely dry. Hence, several pioneer species had high mortality, such as *S. aucuparia, S. nigra, A. campestre, F. alnus* and *F. excelsior*. Species with no or the lowest mortality were *Q. robur, P. avium, C. avellana, Crataegus* spp., and *A. pseudoplatanus*. This can be noticed in Table 1 and the Supplementary materials, Fig. S2d, where the changes in the vitality between the years 2019 and 2020 were significant.

Table 1. Number and vitality of tree species expressed as a percentage for the most common species in 2018, 2019, and 2020. The three categories of vitality are 1 - undamaged, 2 - partly damaged, 3 - strongly damaged. In 2020, category 3 was replaced by dead saplings. Then NA values (no data) correspond to saplings broken, cut, or damaged by deer browsing and therefore no data were collected. The maximum percentage of saplings per vitality class (1, 2, or 3) is highlighted in bold.

	No.	Vitality 2018 %			Vitality 2019 %				Vitality 2020 %			
Tree species		1	2	3	1	2	3	NA(%)	1	2	Dead	NA(%)
Acer campestre	26	**58**	27	15	**65**	27	8	0	**69**	12	12	8
Acer pseudoplatanus	88	35	**53**	11	**86**	7	6	1	**74**	15	5	7
Betula pendula	99	40	**53**	7	**75**	20	5	0	**78**	12	6	4
Carpinus betulus	137	15	**71**	15	**83**	10	7	0	**66**	21	8	5
Corylus avellana	90	34	**58**	8	**79**	12	4	4	**76**	18	2	4
Crataegus spp.	43	35	**60**	5	**63**	33	5	0	**67**	26	2	5
Fagus sylvatica	643	**50**	40	10	**80**	13	4	3	**76**	11	6	7
Frangula alnus	52	15	**67**	**17**	**73**	13	10	4	**71**	12	12	6
Fraxinus excelsior	25	36	**56**	8	**44**	**44**	12	0	**48**	32	12	8
Prunus avium	32	13	**59**	**28**	**63**	38	0	0	**59**	28	0	13
Quercus petraea	52	38	**56**	6	**67**	27	6	0	**67**	17	4	12

Quercus robur	23	17	**83**	0	**65**	35	0	0	**83**	17	0	0
Sambucus nigra	45	29	**40**	**31**	**47**	44	9	0	**58**	24	16	2
Sorbus aucuparia	176	10	**53**	**37**	**68**	17	13	2	35	**42**	17	6
Ulmus glabra	48	23	**69**	8	**75**	17	8	0	**67**	21	10	2
All species	**1709**	36	**51**	14	**75**	17	6	2	**68**	18	**8**	6

3.3 Recovery patterns to drought for understory and forest canopy

3.3.1 Recovery of saplings after the drought is species-specific

Rapid sapling recovery was identified one year after the 2018 drought. All sapling species showed an increase in vitality (Fig. 2a, values > 0) or maintained their vitality (values = 0). However, there are significant differences in recovery between species. *S. aucuparia* had the fastest recovery than all other species, followed by *C. betulus* which had a higher recovery than *F. sylvatica*, *F. excelsior*, *B. pendula, Q. petraea*, *A. campestre*, and *Crataegus* spp. (Fig. 3a). Other species, such as *A. campestre*, *B. pendula, C. avelana*, *Crataegus* spp., *F. sylvatica*, *F. alnus, F. excelsior, Q. petraea*, and *S. nigra* had a similar recovery. Based on the difference between the reference value of the recovery index (0 = meaning the species have the same vitality as during the event), all species, except *A. campestre* and *F. excelsior* showed a significantly higher recovery than the reference value. *S. aucuparia, P. avium, C. betulus, F. alnus, and A. pseudoplatanus,* are the top five species with the highest significant difference from the reference value, meaning the highest recovery (Supplementary materials Fig. S3a).

The difference in recovery from 2018 to 2020 between species is less significant than the one from 2018 to 2019 (Fig 3ab, and Supplementary materials Fig. S3ab). *C. betulus* was more affected by drought than *F. sylvatica,* but also had a higher recovery (Fig 3b). From 2019 to 2020 only *S. aucuparia* shows a significant decrease in vitality. The other species show similar vitality as in 2019 (Fig 2c). Although most of the species showed no difference in recovery (from 2019 to 2020, Fig 2c), there is a significant difference from the reference value for all species, both positive and negative (Supplementary materials Fig. S3c).

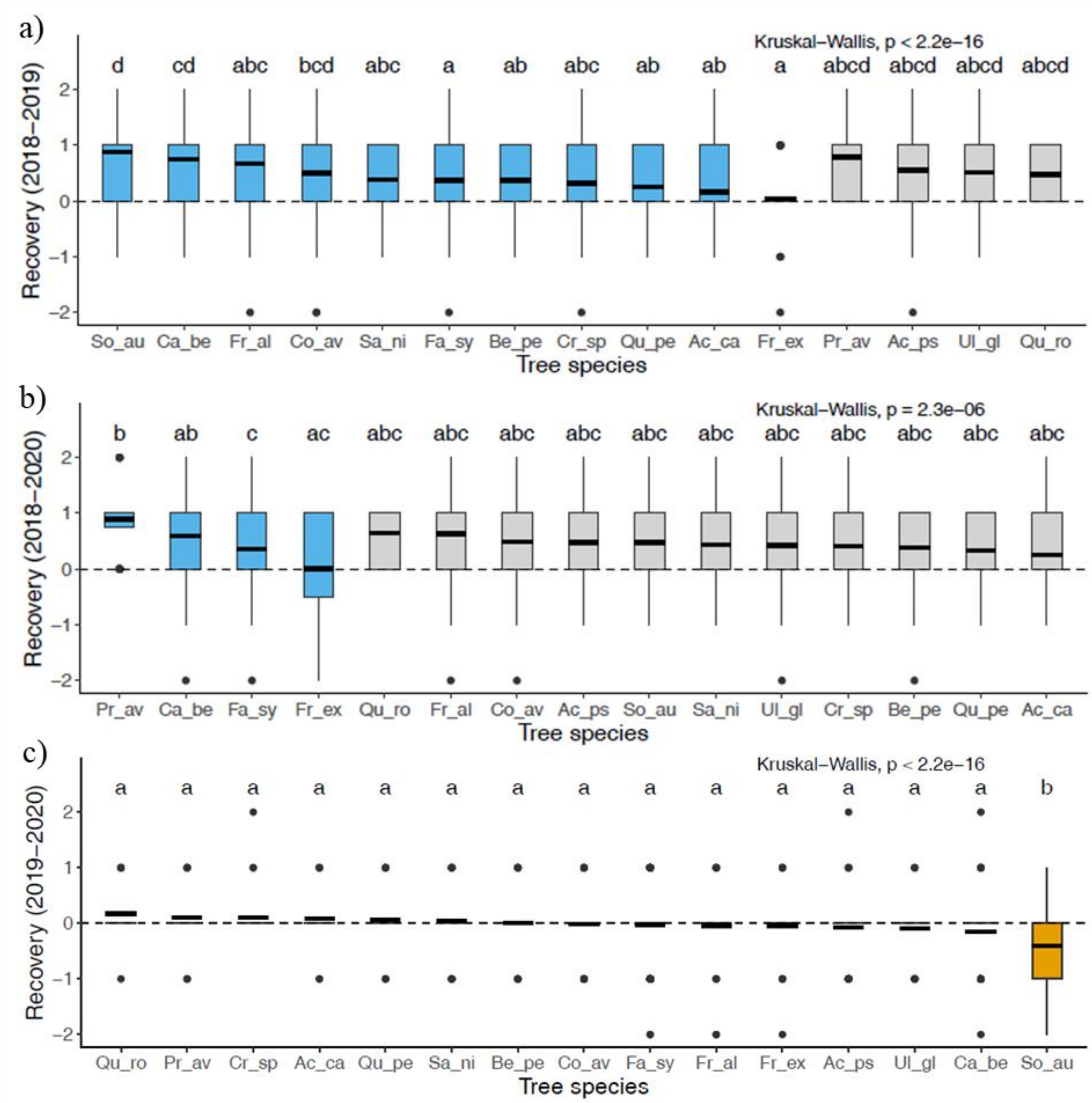

Figure 3. Sapling recovery index and pairwise comparison tests between species. **a)** Species recovery between 2018 and 2019, **b)** 2018 and 2020, and **c)** 2019 and 2020. Values < 0 indicate a decline in vitality, > 0 an increase in vitality after the event and 0 the same state as during the event (colors: blue > 0 significant, orange < 0 significant, grey = not significant). Species are sorted from highest to lowest recovery, according to their significance. Ac_ca - *Acer campestre* (n=24); Ac_ps - *Acer pseudoplatanus* (n=83); Be_pe - *Betula pendula* (n=95); Ca_be - *Carpinus betulus* (n=120); Co_av - *Corylus avellana* (n=86); Cr_sp - *Crataegus* spp. (n=41); Fa_sy - *Fagus sylvatica* (n=597); Fr_al - *Frangula alnus* (n=49); Fr_ex – *Fraxinus excelsior* (n=23); Pr_av - *Prunus avium* (n=28); Qu_pe - *Quercus petraea* (n=46); Qu_ro - *Quercus robur* (n=23); Sa_ni - *Sambucus nigra* (n=44); and So_au - *Sorbus aucuparia* (n=165); Ul_gl - *Ulmus glabra* (n=47). Boxplot components: mean (black lines), interquartile range (whiskers), and outliers (black dots) are shown. The letters above boxplots indicate significant differences between boxplots as calculated by Dunn's Kruskal-Wallis multiple comparisons test.

3.3.2 High recovery after drought in coniferous forests

Forest canopy showed significantly different NDVI values between forest types under normal conditions (i.e. in 2015 and 2020, coniferous < mixed < deciduous, Supplementary materials, Fig. S4a). During the 2018 severe drought, tree canopy vitality decreased in all forest types, with coniferous forests generally having lower values than mixed and deciduous forests ($p < 0.001$, Supplementary materials, Fig. S4ab). Nevertheless, mixed forests emerged as the most resistant of the three forest types to the 2018 drought (i.e., they had the smallest decrease in NDVI between 2015 and 2018). Despite the slow recovery of coniferous forests in 2019, forest types retain similar vitality values as in 2018. In terms of canopy recovery, coniferous forests had a higher recovery than mixed forests, while deciduous forests had intermediate values (Supplementary materials, Fig. S5ab). This means that the canopy of coniferous forests was more affected by drought than that of deciduous forests.

3.4 Saplings mortality risk is associated with reduced recovery to drought

Our results show that the main difference between surviving and now dead saplings is that surviving saplings recovered better from drought. Whereas reduced recovery (low capacity to reach pre-drought vitality rates) results in sapling mortality (Fig. 5). This pattern is observed after one year from the drought in Supplementary materials, Fig. S6 but is accentuated two years after the drought (Fig. 5). In the long term, reduced recovery is associated with sapling mortality.

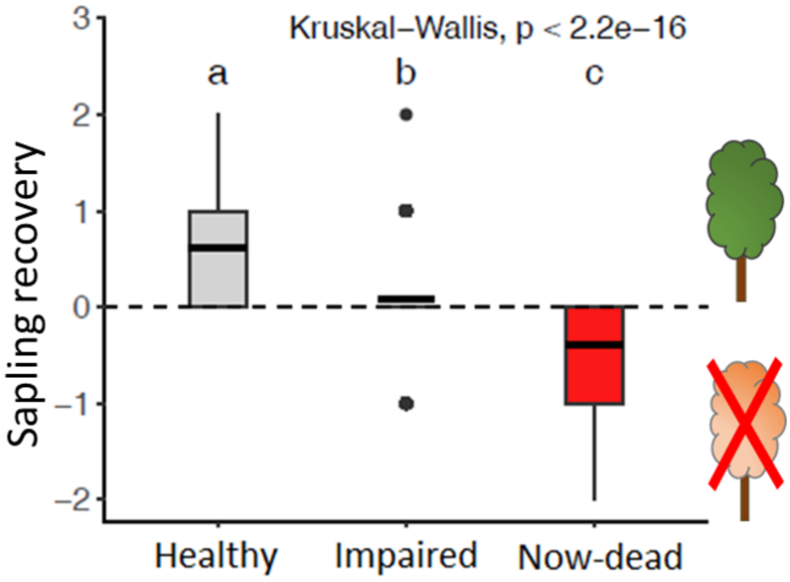

Figure 5. Differences in recovery between surviving (healthy = vitality 1, impaired = vitality 2) and now dead saplings. The recovery index was computed based on the vitality differences between 2020 and 2018. Values < 0 indicate a decline in vitality, > 0 indicate an increase in vitality after the event, and 0 indicates the same state as during the event.

3.5 Biotic and abiotic drivers

Sapling vitality increased with soil depth and sapling cover and decreased with sapling diversity (Table 2, M1). Precipitation, temperature, elevation, soil type, pH, and slope values were not significantly correlated with the sapling vitality (data not shown). In 2018, canopy vitality was not significantly correlated with temperature or precipitation during either the growing or dormant seasons but was instead influenced by forest type and canopy height (Table 2, M2, and Supplementary materials, Table 4 and S7a). Furthermore, tree canopy vitality did not correlate with either the De Martonne drought index or soil moisture (data not shown). However, in 2019, the tree canopy vitality was better explained by the mean temperature and precipitation for the dormant season i.e. canopy NDVI decreased with higher winter temperature and increased with winter precipitation (Table 2, M3, and Supplementary materials, T4 and S7a), than by the mean temperature of the growing season (data not shown). In 2020, the canopy vitality was not significantly correlated with temperature but increased with tree diversity (Supplementary materials, Table 4). Generally, in 2015, 2019, and 2020 canopy vitality was positively correlated with tree diversity, while in 2018 was not significant ($p < 0.05$, Table 2 and Supplementary materials, Table 4).

Table 2. Multiple linear regression model to explain the drivers of mean sapling defoliation (M1) per plot and forest canopy vitality (M2 and M3). Temperature values are calculated for the dormant season 10.2017 - 03.2018, and 10.2018 - 03.2019. Exp.var. = explanatory variable, Resp.var. = response variable, Est. = estimates, SE = standard error. The explanatory variables are introduced in the methods. A stepwise-backward variable selection procedure based on AIC was performed.

	M1 Resp.var. - Mean sapling vitality (defoliation) in 2018		
Exp.var.	Est.	SE	*p*
Soil depth (cm)	-0.004	0.001	0.026
Sapling cover (%)	-0.005	0.001	< 0.001
Sapling diversity	0.199	0.057	< 0.001
Adjusted R-squared			**0.14**
***p* - value**			**< 0.001**

	M2 Resp.var. - NDVI 2018			**M3** Resp.var. - NDVI 2019		
Exp.var.	Est.	SE	*p*	Est.	SE	*p*
Temperature 10-03	-0.010	0.006	0.133	-0.132	0.020	< 0.001
Coniferous	0.688	0.025	< 0.001	0.902	0.028	< 0.001
Mixed	0.054	0.011	< 0.001	0.027	0.010	0.006
Deciduous	0.082	0.015	< 0.001	0.070	0.011	< 0.001
Tree diversity	0.009	0.011	0.398	0.020	0.008	0.024
Canopy height (m)	0.002	0.0007	< 0.001	0.001	0.000	0.037
Adjusted R-squared			**0.147**			**0.288**
***p* - value**			**< 0.001**			**< 0.001**

4. Discussion

4.1 Drought impact on saplings

Given that extreme heat waves and droughts have been shown to increase over the last years (IPCC 2021), there is a clear need to identify the tree species that are most vulnerable to these changes and to understand why some species are more sensitive to extreme conditions than others. Hence, previous studies have explored the effects of drought on mature trees at local and continental scale (Senf et al. 2019; Hereş et al. 2021; Bose et al. 2021). However, to our knowledge, our study provides the first empirical evidence of drought impact on a large number of broadleaf saplings and their subsequent recovery and mortality patterns in Central Europe. Our data come from temperate forests, but the study includes a large number of deciduous tree species (41) that are representative for European forests and of great economic and ecological importance. Conifer plantations replaced large areas of the naturally predominant deciduous forest ecosystems of Central Europe in the 20th century. These managed forests were focused on rapidly growing, economically important, and native conifers such as *P. abies* or *P. sylvestris*. In recent years, such forests suffer strongly from bark beetle outbreaks and other pests (Schuldt et al. 2020). For this reason, we focused on the natural regeneration of the species pool of deciduous broadleaf trees in the understory.

Based on a sampling of 1709 broadleaf saplings through deciduous, coniferous, and mixed forests in Central Europe over three years, we identified patterns of drought sensitivity and remarkably fast recovery (one year after the drought, Fig. 2e). We found that most pioneer broadleaved tree species were the most affected by drought, whereas the non-pioneer species such as *Q. petraea,* and *F. sylvatica* were the least affected by drought. *Sorbus aucuparia* and *C. betulus* showed the strongest signals of recovery. Contrary to our findings on saplings, another study showed that mature trees of *S. torminalis* and *A. campestre* have a higher drought resistance than *F. sylvatica*, but the latter has a higher recovery (Kunz et al. 2018). Nevertheless, non-pioneer species such as *Q. robur* and *Q. petraea*, as well as the pioneer species *B. pendula*, which are characterized by a deeper root system, are among the most drought-resistant species in our study area. This suggests their capacity for coping with uncertain climatic conditions and their increased role in the future forests.

Generally, trees do not die directly during the drought but continue to thrive for months or even years after the drought before they die. We found that the pioneer species, *S. aucuparia*, had the most severe drought damage in 2018, and recovered greatly in 2019, but was insufficient to prevent its high mortality in 2020. On the one hand, this species is not drought tolerant and not well adapted to habitats with water stress (Raspé et al. 2000). On the other hand, this attempt to invest quickly in recovering the drought-damaged plant vascular tissue may not be the best strategy, as it can lead to reduced investment in pest protection (Anderegg, Hicke, et al. 2015; Trugman et al. 2018; Gessler et al. 2020). We have not quantified the pest infestation; therefore, this should be addressed in future research. Nevertheless, species with fast recovery can be rather more susceptible to future droughts in the long term (Gessler et al. 2020).

Trees with crowns in or above the canopy are more exposed to high solar radiation and higher evaporation than understory trees (Bennett et al. 2015). This suggests that sapling transpiration is relatively buffered by larger trees. Our results show that sapling vitality during the drought of 2018 increased with soil depth and sapling cover but decreased with saplings diversity.

We also show that high recovery in saplings is strongly correlated with survival, while a reduced or a decline in recovery leads to mortality (Fig. 5). Most pioneer species that had reduced recovery after the drought, showed high mortality, such as *S. nigra*, *F. excelsior*, *F. alnus*, and *A. campestre.* A review study reveals that seedlings that previously underwent mild water stress showed increased resistance to future water shortages (Kozlowski & Pallardy 2002), which indicates an acclimation. The same pattern was observed in experiments on *P. sylvestris* seedlings (Seidel & Menzel 2016; Bose, Moser, et al. 2020), plant, and shrub species (Backhaus et al. 2014). However, our data showed that the reduced recovery after the intense drought of 2018 leads to sapling mortality, therefore the water scarcity proved to be beyond the survival limit for these species. Similar to saplings, a high rate of defoliation coupled with reduced recovery lead to tree mortality, indicating long-lasting chronic effects of drought on tree stem and crown structure (Dobbertin & Brang 2001; Carnicer et al. 2011). Hence, early and severe defoliation, in the long run, is more a sign of weakness than a defensive strategy.

Mitigation of climate extremes requires pro-active nature-based solutions (Beierkuhnlein 2021) and to enhance forest resilience, lessons learned from community forestry must be leveraged (Devisscher et al. 2021). New incentives and interventions are needed to manage forests as complex adaptative systems (i.e. increase the adaptive capacity of forest in the face of future uncertainties) (Messier et al. 2015). Thus, the remarkable capacity of saplings to recover rapidly from drought and survive a second dry summer suggests considerable potential for forest management based on natural regeneration and recruitment. Natural regeneration and recruitment can support the implementation of continuous cover forestry across Europe. Tree response to drought has important implications for future forest productivity, carbon cycling, and the future provision of goods and services that we benefit from as a society today. In addition, data on crown defoliation improve tree mortality models and thus can help us better predict future tree mortality (Dobbertin & Brang 2001). Therefore, it is necessary to incorporate these findings on forest canopy and understory response to drought into the development of new strategies that can decrease the effect of climate extremes on forests.

4.2 Drought legacy in forest canopy

Forest canopy showed long-lasting drought-induced effects on crown structure (Fig. 2d), i.e., reduced or incomplete recovery persisted for 2 years in the forest canopy. This is in line with observations showing that the recovery time of plant vascular tissue increases with the tree size (Trugman et al. 2018). Moreover, reduced growth and incomplete recovery can persist for 1 to 4 years depending on site conditions (Anderegg, Schwalm, et al. 2015).

The combined droughts of 2018 and 2019 are reflected in the reduced forest canopy vitality (i.e. low NDVI values). Such repetitive droughts can alter the recovery time and push the forest beyond the “tipping point”- associated with tree mortality - and lead to a deterioration of the forest ecosystem (Anderson-Teixeira et al. 2013; Schwalm et al. 2017). We showed that the NDVI in 2015 is slightly lower that in 2020, most likely due to the 2015 drought period and heatwave from Central Europe that had a lower intensity than in 2018. Nevertheless, the study region was not strongly impacted by this event (Laaha et al. 2017) as it was affected by the 2018 drought (Fig. 2ab).

A significant NDVI pattern was observed in different forest types during the drought period, with NDVI values for coniferous < mixed < deciduous forests. In contrast to deciduous trees, some coniferous trees exhibit drought-triggered bark beetle outbreaks, leading to infestation and mortality, especially in *P. abies* (Netherer et al. 2019; Schuldt et al. 2020). We observed recent dieback of *P. abies* and *P. sylvestris* stands in the study area, but such cases did not occur in our plots. Although drought could trigger further pathogen infestation in coniferous, we show that under favorable conditions (in 2020) coniferous on our sites have recovered. An even faster recovery was observed in *F. sylvatica* (Rohner et al. 2021).

Although diversity is expected to increase the resistance of ecosystems to climate extremes (Isbell et al. 2015), the role of tree diversity in mitigating drought effects is not yet clear in forestry. There is evidence for negative, neutral, and positive effects (Grossiord 2018; Sousa-Silva et al. 2018). Our results based on forest canopy NDVI suggest that under intense drought (2018), diversity had a neutral effect, but under milder drought, such as in 2019, had a positive effect, meaning that tree health increase with tree diversity. New studies showed that species resistance to drought is dependent on stand composition, tree age, and water supply (Pretzsch et al. 2020; Pardos et al. 2021). Nevertheless, we showed that in 2015, 2019, and 2020, forest health increased with tree diversity.

Even though the De Martonne aridity index revealed that the study region was exposed to arid conditions during the summer of 2018, the climatic and edaphic variables showed no correlation with NDVI. This might be explained by the high temperature and low precipitation over the entire area and the low resolution of the climatic variables that could not capture the local conditions. Nevertheless, in 2019, the dormant season climate proved to be a better predictor of tree health than the growing season climate, and this is in line with findings on plant species (Kreyling et al. 2019; Evers et al. 2021). Consequently, winter precipitation rather than summer precipitation explained a higher increase in tree canopy vitality in 2019. This is consistent with a recent study showing that deciduous trees such as *F. sylvatica* and *Q. robur* rely mainly on winter precipitation, while *P. abies* relies on more variable seasonal water sources (Allen et al. 2019). The study area experienced a combined increase in temperature and severe water stress in 2018 and 2019, which coupled with biotic agents (e.g., bark beetles) produced high mortality in *P. abies* and *P. sylvestris* (personal field observations). Similar trends in drought-induced mortality have been observed in Central Europe (Brun et al. 2020; Buras et al. 2020) and globally (Allen et al. 2010).

5. Conclusion

Overall, our findings underline that compound droughts have long-lasting effects on forest canopy and recovery was only possible after the periods of drought (i.e., after the 2018 and

2019 droughts). Further exposure to climatic extremes might lead to long-term alteration of forests and increased mortality. Despite being severely affected by drought, deciduous saplings showed a remarkable capacity to recover quickly from drought and survive a subsequent dry summer. Under drought conditions, most pioneer sapling species and one of the non-pioneer species, *C. betulus*, were severely affected, some of which had the highest mortality rates. In contrast, most non-pioneer species, such as *Q. petraea*, *Q. robur*, and *F. sylvatica* and the pioneer species *B. pendula* and *A. pseudoplatanus* showed notable resilience, recovery and low mortality rates. Accordingly, they are expected to be best adapted to the warmer and possibly drier climate of future temperate forests compared to other broadleaf species. Moreover, these findings reveal the critical role of recovery after a drought period, i.e. reduced recovery leads to sapling mortality.

Tree planting is seen as a major climate change mitigation strategy (Bastin et al. 2019). Our results thus provide valuable information on which species can better withstand the impacts of drought, which can help foresters make decisions that take into account the risks of future drought events on tree survival. The remarkable capacity of deciduous saplings to recover after drought suggest considerable potential for forest management based on natural regeneration and recruitment. Thus, any efforts to increase the resilience of the European forests in the face of climate warming and drought should consider the response of saplings to drought.

CRediT author statement

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Conflicts of Interest

The authors declare no conflicts of interest.

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Supplementary data

The data used are included in the Supplementary material.

Appendix A. Supplementary material

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Supplementary materials

Table 1. Sapling measurements done in the field.

Measurements	Year of measurement
Diameter at breast height (dbh)	The dbh of each tagged sapling was measure with a caliper in 2018.
Vitality	The vitality was assessed for each sapling tagged each year 2018, 2019, 2020. In 2019 and 2020, the vitality of the saplings was fully assessed by the first author, while in 2018 the main author and the last author did the measurements. This was needed due to the extended area and the timely need of the vitality assessment. However, this assessment was done after a session of training. The measurements took place during the vegetation period, specifically, in August and September.
Sapling cover	-Was visually estimated at the plot level for each species. This measurement was done entirely by the first author.
Sapling mortality	Sapling vitality was observed in 2018, 2019 and 2020. As tree death occurs over time, sapling mortality was assessed in 2020 for the tagged saplings.

Table 2. Environmental variables that were used for the analysis.

Category	**Variables**	**Resolution**	**Field**	**Source**
Climate data	- Monthly precipitation - Monthly temperature - Monthly soil moisture	1 km		(DWD 2021a; DWD 2021b)
Topography	Digital elevation model (DEM) Aspect and slope (calculated based on DEM)	25 m		(EU-DEM 2020)
Edaphic	Soil pH		x	
	Soil depth		x	
	Soil type	1:1 000 000		(Hollis J.M. et al. 2006)
Vegetation	Sapling cover (%)		x	
	Sapling diversity		x	
	Tree cover (%)		x	
	Tree species diversity		x	
	Sapling vitality		x	(Eichhorn, et al. 2016)
	Tree canopy height	30 m		(Potapov et al. 2021)

Table 3. De Martonne index aridity classification with the corresponding precipitation amounts, adapted after (Baltas 2007).

De Martonne aridity index

Aridity classification	**Values**	**Precipitation (mm)**
Arid	<10	<200
Semi-arid	10 - 20	200 - 400
Mediterranean	20 - 24	400 - 500
Semi-humid	24 - 28	500 - 600
Humid	28 - 35	600 - 700
Very humid	35 - 55	700 - 800
Extremely humid	>55	>800

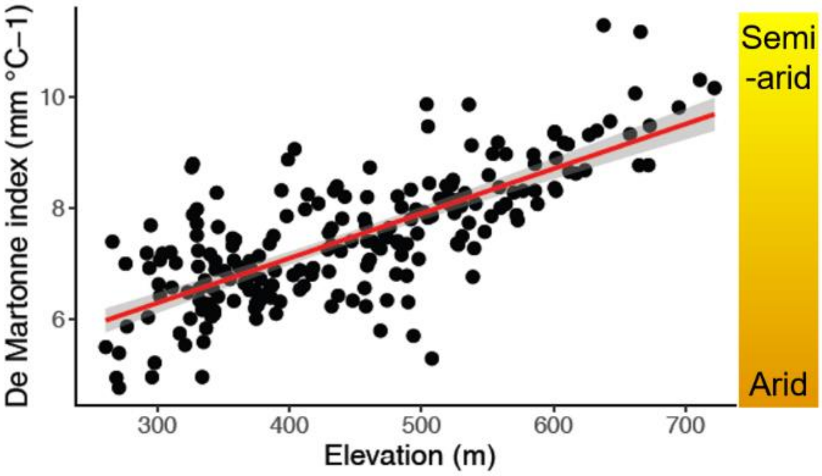
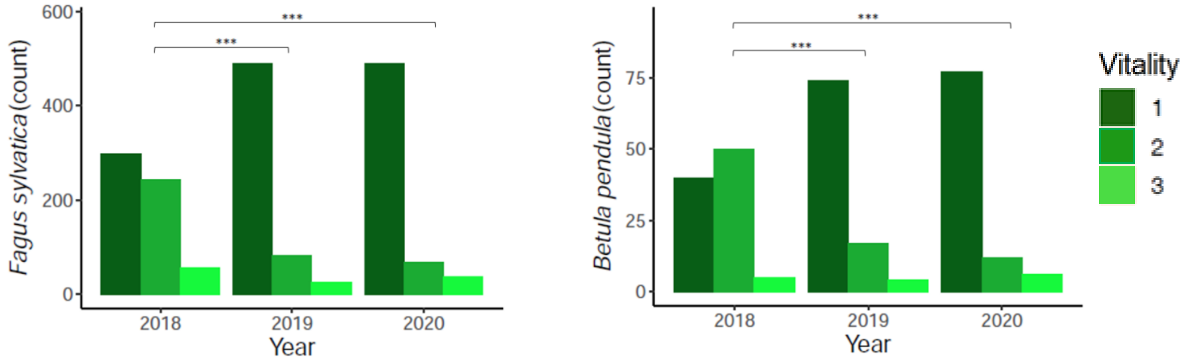
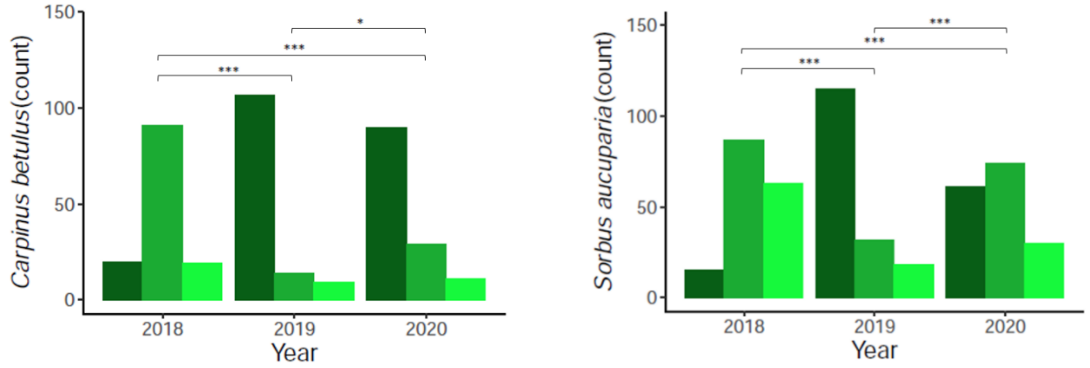


Figure S1. De Martonne aridity index for the growing season (April-August 2018) across elevation.



a) n=597

b) n=95



c) n=130

d) n=165

Figure S2. Differences in saplings vitality classes between 2018, 2019 and 2020. (a–d) Vitality of *Fagus sylvatica*, *Betula pendula*, *Carpinus betulus*, and *Sorbus aucuparia*. Vitality 1 = undamaged, 2 = partly damaged, 3 = completely damaged saplings, in 2020, 3= completely dry saplings. Stars show the statistically significant difference between vitality groups based on Fisher's exact test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

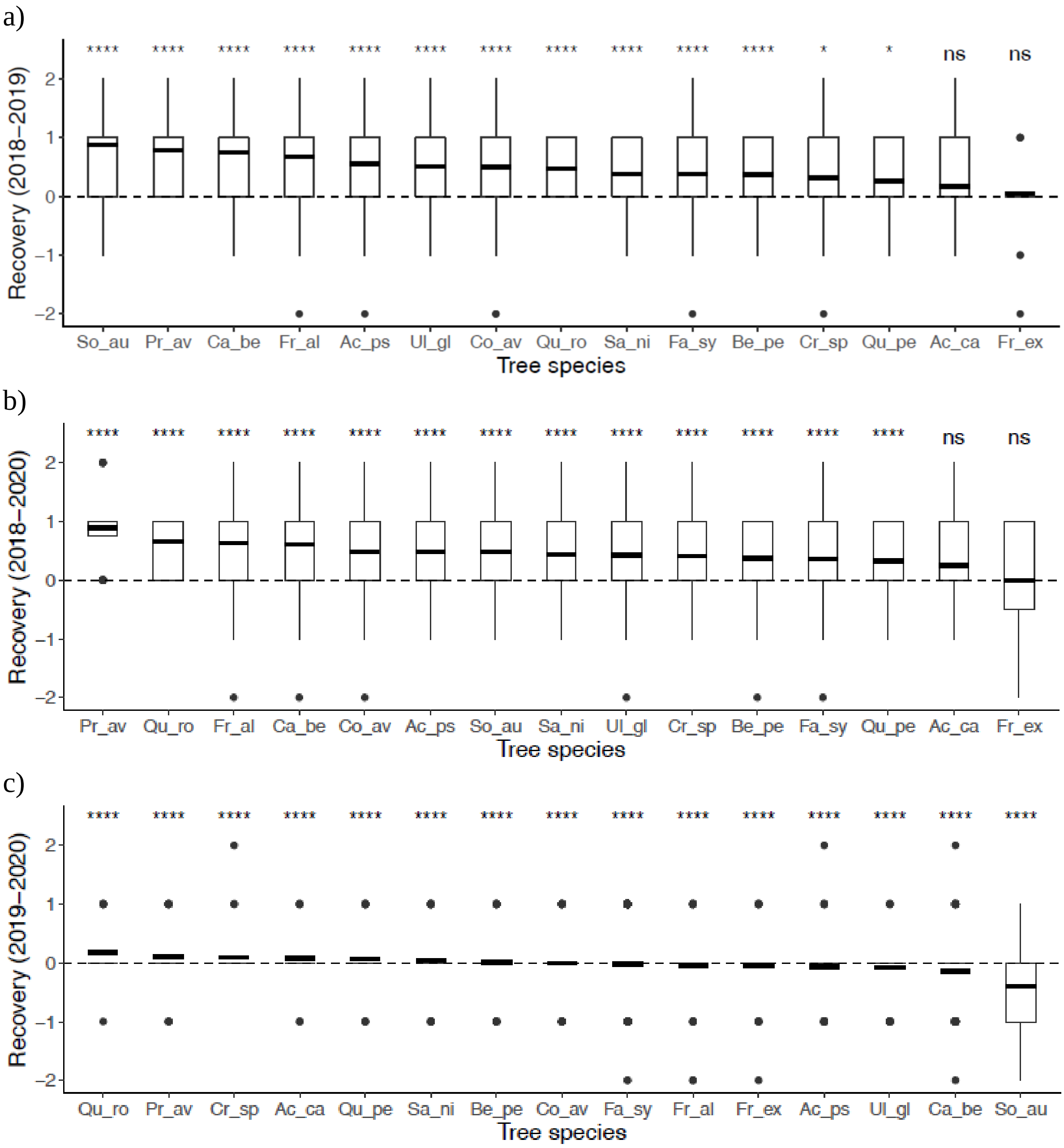


Figure S3. Sapling recovery index and tree species difference from the reference value, zero, within each group. a) Relationship between Recovery index and tree species at one year after the drought (2018 - 2019) and b) at two years after the drought (2018 - 2020), c) between the second and third year after the drought (2019 - 2020). Values < 0 indicate decline in performance, > 0 indicate increase in performance after the event and 0 indicates same state as during the event. Ac_ca - *Acer campestre* (n=24); Ac_ps - *Acer pseudoplatanus* (n=83); Be_pe - *Betula pendula* (n=95); Ca_be - *Carpinus betulus* (n=120); Co_av - *Corylus avellana* (n=86); Cr_sp - *Crataegus* spp. (n=41); Fa_sy - *Fagus sylvatica* (n=597); Fr_al - *Frangula alnus* (n=49); Fr_ex – *Fraxinus excelsior* (n=23); Pr_av - *Prunus avium* (n=28); Qu_pe - *Quercus petraea* (n=46); Qu_ro - *Quercus robur* (n=23); Sa_ni - *Sambucus nigra* (n=44); and So_au - *Sorbus aucuparia* (n=165); Ul_gl - *Ulmus glabra* (n=47). Stars show the statistical significance between the reference value of 1 (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, **** $p < 0.0001$, ns = not significant).

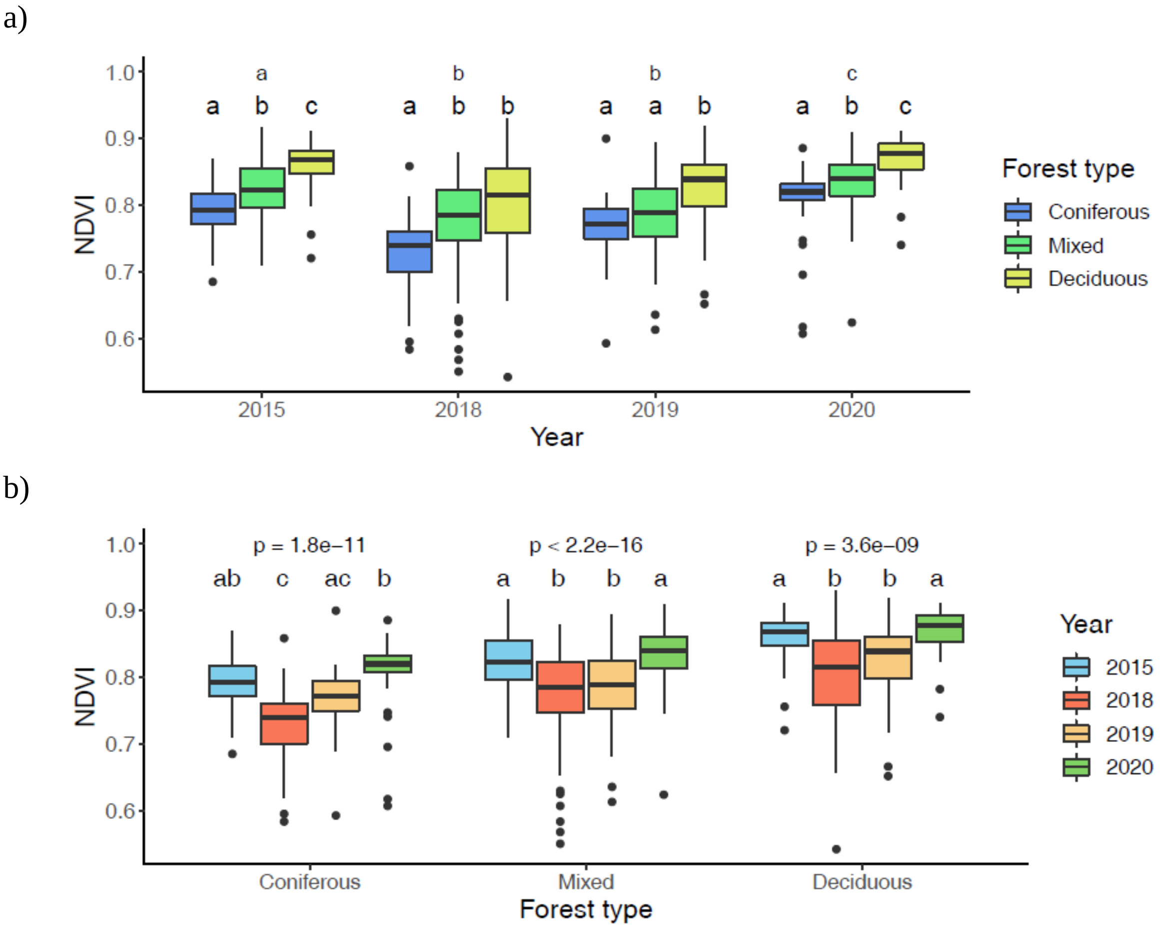


Figure S4. Normalized difference vegetation index (NDVI) across **a)** study years and **b)** forest types. Canopy NDVI values were extracted from Sentinel 2 images at 10 m resolution for the study plots (n=214) and different years (2015, 2018, 2019, and 2020). Mixed forests = 131, deciduous = 46, and coniferous = 37 plots. Boxplot components: median (black lines), interquartile range (whiskers), and outliers (black dots) are shown. Different letters above boxplots indicate significant differences between boxplots as calculated by Dunn's Kruskal-Wallis multiple comparisons test.

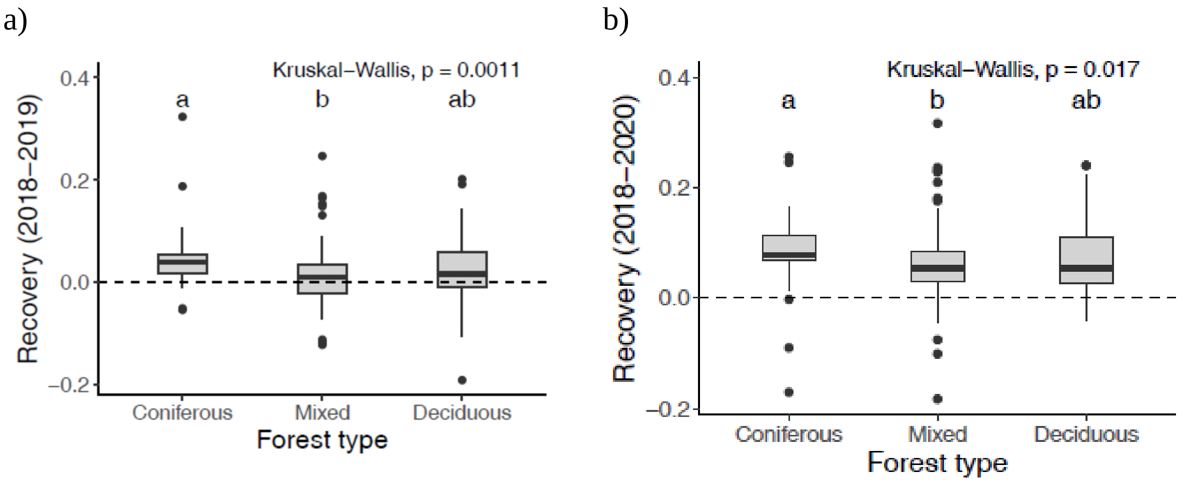


Figure S5. Differences in canopy recovery between forest types. Recovery index was computed based on the canopy NDVI values from **a)** 2018 and 2019, and **b)** 2018 and 2020. Values < 0 indicate a decline in vitality, > 0 indicate an increase in vitality after the event, and 0 indicates the same state as during the event. Boxplot components and significance as defined in Fig. 2.

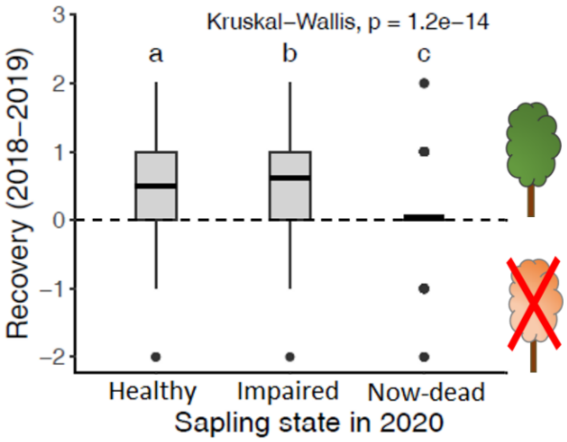
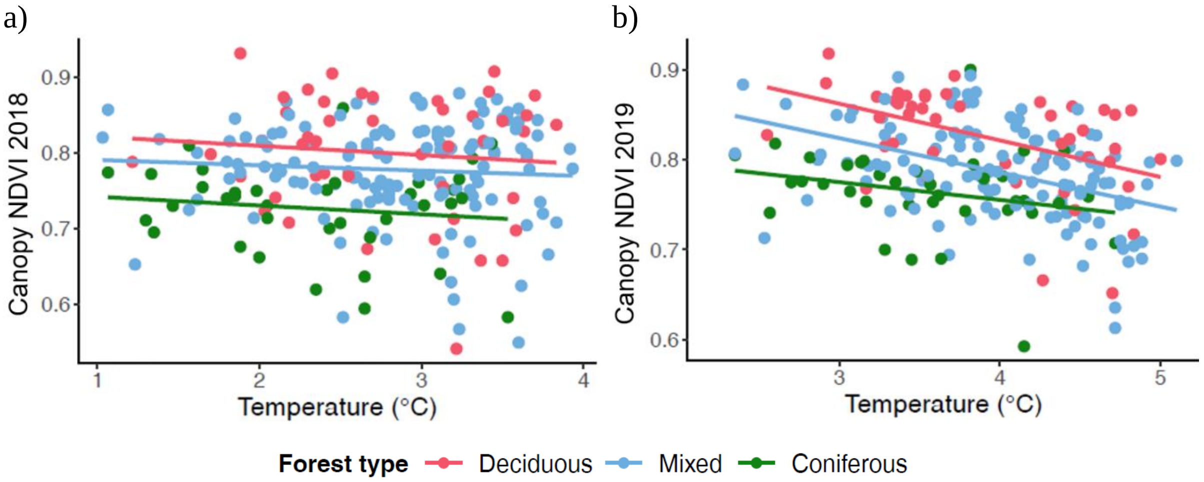


Figure S6. Differences in recovery between surviving (healthy and impaired) and now dead saplings. The recovery index was computed based on the vitality differences between 2019 and 2018. Values < 0 indicate a decline in vitality, > 0 indicate an increase in vitality after the event, and 0 indicates the same state as during the event. On the x-axis is given the tree sapling status in 2020 (healthy = vitality 1, impaired = vitality 2, and now-dead = vitality 3).

Table 4. Multiple linear regression model to explain the canopy NDVI as a function of precipitation, temperature, and forest type (coniferous, mixed and deciduous). The explanatory variables are introduced in the methods section. Since precipitation and temperature are highly correlated, we created a separate model for each of these two variables. Resp.var. = response variable , 10-03.17/18 = 10.2017 – 03.2018, 10-03.18/19 = 10.2018 – 03.2019.

Model	**Resp. var.**	**Explanatory variable**	**Estimate**	**Standard error**	**Trend**	**p-value**
M1	NDVI 2018	log(Precipitation 10-03.17/18)	0.013	0.025	+	0.595
		Coniferous	0.579	0.162	+	< 0.001
		Mixed	0.050	0.014	+	< 0.001
		Deciduous	0.079	0.015	+	< 0.001
		Tree Shannon diversity	0.009	0.011	-	0.427
		Canopy height (m)	0.002	0.0007	+	< 0.001
		Adjusted R-squared = 0.139				**< 0.001**
M2	NDVI 2019	log(Precipitation 10-03.18/19)	0.102	0.016	**+**	**< 0.001**
		Coniferous	0.119	0.102	+	0.242
		Mixed	0.022	0.010	**+**	0.028
		Deciduous	0.072	0.011	**+**	< 0.001
		Tree Shannon diversity	0.018	0.008	+	0.036
		Canopy height (m)	0.001	0.0005	+	0.017
		Adjusted R-squared = 0.256				**< 0.001**
M3	NDVI 2018	Temperature 10-03.17/18	-0.010	0.006	-	0.133
		Coniferous	0.688	0.025	+	< 0.001
		Mixed	0.054	0.011	+	< 0.001
		Deciduous	0.082	0.015	+	< 0.001
		Tree Shannon diversity	0.009	0.011	-	0.398
		Canopy height (m)	0.002	0.0007	+	< 0.001
		Adjusted R-squared = 0.147				**< 0.001**
M4	NDVI 2019	Temperature 10-03.18/19	-0.132	0.020	**-**	**< 0.001**
		Coniferous	0.902	0.028	+	< 0.001
		Mixed	0.027	0.010	+	0.008
		Deciduous	0.070	0.011	+	< 0.001
		Tree Shannon diversity	0.020	0.008	+	0.020
		Canopy height (m)	0.001	0.000	+	0.042
		Adjusted R-squared = 0.275				**< 0.001**
M5	NDVI 2020	Temperature 10-03.19/20	-0.003	0.004	-	0.501
		Coniferous	0.793	0.023	+	< 0.001
		Mixed	0.019	0.009	+	0.031
		Deciduous	0.060	0.010	+	< 0.001
		Tree Shannon diversity	0.020	0.007	+	0.007
		Canopy height (m)	0.001	0.0004	+	0.032
		Adjusted R-squared = 0.195				**< 0.001**



S7. **a)** Relationship between normalized vegetation index (NDVI), temperature, and forest type, for 2018 (temperature $p > 0.05$, forest type $p < 0.001$) and **b)** 2019 ($p < 0.001$, R squared = 0.26). Mean temperature for the dormant season, October – March for 2017 - 2018 and 2018-2019. The relationship is calculated with a multiple linear model. The extended model with coefficients is in Table 2.

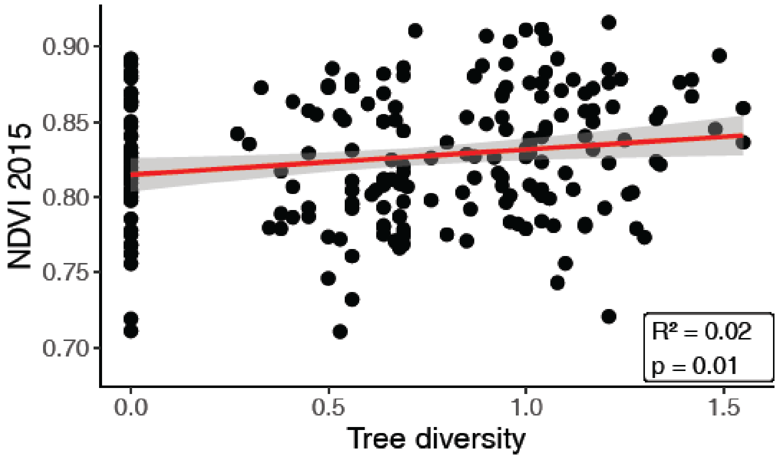


Figure S8. Relationship between canopy NDVI in 2015 and Shannon tree diversity, with 95% confidence intervals.

Data

Table 5. Sapling vitality data. The three categories of vitality are 1 - undamaged, 2 - partly damaged, 3 - strongly damaged. In 2020, category 3 was means dead saplings. Sample = tree id, DBH = diameter at breast height (mm), Vitality_2018 = sapling vitality in 2018.

Plot	**Sample**	**Species**	**DBH (mm)**	**Vitality_2018**	**Vitality_2019**	**Vitality_2020**
1_10	1	*Sorbus aucuparia*	9	1	1	2
1_10	10	*Sambucus nigra*	33	1	2	1
1_10	2	*Betula pendula*	11	2	1	1
1_10	3	*Acer pseudoplatanus*	23	1	1	1
1_10	4	*Sorbus aucuparia*	11	2	1	1
1_10	5	*Quercus petraea*	54	1	1	1
1_10	6	*Robinia pseudoacacia*	29	1	2	1
1_10	7	*Quercus petraea*	25	1	1	1
1_10	8	*Frangula alnus*	22	2	1	1
1_10	9	*Quercus petraea*	9	1	1	1
1_11	1	*Acer pseudoplatanus*	3	1	1	2
1_11	10	*Prunus avium*	9	2	1	2
1_11	2	*Sorbus aucuparia*	48	2	1	2
1_11	3	*Corylus avellana*	13	1	1	1
1_11	4	*Corylus avellana*	27	1	1	1
1_11	5	*Corylus avellana*	11	1	1	1
1_11	6	*Sorbus aucuparia*	4	2	1	2
1_11	7	*Corylus avellana*	6	1	1	1
1_11	8	*Corylus avellana*	32	1	1	1
1_11	9	*Corylus avellana*	3	1	1	1
1_12	1	*Sambucus nigra*	6	1	1	1
1_12	10	*Sambucus nigra*	18	1	1	1
1_12	2	*Sambucus nigra*	7	1	1	1
1_12	3	*Sambucus nigra*	3	1	1	1
1_12	4	*Sambucus nigra*	7	1	1	1
1_12	5	*Sambucus nigra*	9	1	1	1
1_12	6	*Sambucus nigra*	6	1	1	1
1_12	7	*Sambucus nigra*	8	1	1	1
1_12	8	*Sambucus nigra*	6	1	1	1
1_12	9	*Sambucus nigra*	5	1	1	1
1_14	1	*Quercus petraea*	34	2	1	2

1_14	10	*Betula pendula*	20	3	3	3
1_14	2	*Crataegus spec.*	11	1	1	1
1_14	3	*Fagus sylvatica*	20	3	2	1
1_14	4	*Fagus sylvatica*	1	3	3	3
1_14	5	*Carpinus betulus*	8	2	2	1
1_14	6	*Fagus sylvatica*	5	3	2	1
1_14	7	*Fagus sylvatica*	1	3	2	3
1_14	8	*Fagus sylvatica*	1	3	2	2
1_14	9	*Betula pendula*	16	3	3	3
1_15	1	*Sorbus aucuparia*	12	2	1	1
1_15	10	*Frangula alnus*	6	2	1	1
1_15	2	*Betula pendula*	63	1	1	1
1_15	3	*Sorbus aucuparia*	5	2	1	1
1_15	4	*Sorbus aucuparia*	5	2	1	1
1_15	5	*Sorbus aucuparia*	10	2	1	1
1_15	6	*Fagus sylvatica*	41	1	1	1
1_15	7	*Quercus petraea*	27	1	1	1
1_15	8	*Sorbus aucuparia*	6	2	1	1
1_15	9	*Sorbus aucuparia*	3	2	1	1
1_17	1	*Fagus sylvatica*	37	1	1	1
1_17	10	*Fagus sylvatica*	14	1	1	1
1_17	2	*Fagus sylvatica*	11	1	1	1
1_17	3	*Fagus sylvatica*	14	1	1	1
1_17	4	*Fagus sylvatica*	48	1	1	1
1_17	5	*Fagus sylvatica*	28	1	1	1
1_17	6	*Fagus sylvatica*	41	1	1	1
1_17	7	*Fagus sylvatica*	4	1	1	1
1_17	8	*Fagus sylvatica*	5	1	1	1
1_17	9	*Fagus sylvatica*	26	1	1	1
1_18	1	*Fagus sylvatica*	21	1	1	1
1_18	10	*Fagus sylvatica*	24	1	1	1
1_18	2	*Fagus sylvatica*	8	1	1	1
1_18	3	*Fagus sylvatica*	9	1	1	1
1_18	4	*Fagus sylvatica*	27	1	1	1
1_18	5	*Fagus sylvatica*	13	1	2	1
1_18	6	*Fagus sylvatica*	23	1	1	1
1_18	7	*Fagus sylvatica*	21	1	1	1
1_18	8	*Fagus sylvatica*	21	1	1	1

1_18	9	*Fagus sylvatica*	18	1	1	1
1_2	1	*Acer pseudoplatanus*	19	2		1
1_2	10	*Sorbus aucuparia*	30	3	3	3
1_2	2	*Acer pseudoplatanus*	28	2	2	1
1_2	3	*Acer pseudoplatanus*	27	2	1	1
1_2	4	*Fagus sylvatica*	7	2	2	2
1_2	5	*Tilia cordata*	33	2	1	2
1_2	6	*Quercus petraea*	34	1	2	1
1_2	7	*Sorbus aucuparia*	7	3	1	1
1_2	8	*Frangula alnus*	15	3	3	3
1_2	9	*Sorbus aucuparia*	28	2		
1_20	1	*Corylus avellana*	5	2	1	1
1_20	10	*Acer pseudoplatanus*	18	2	1	
1_20	2	*Corylus avellana*	7	2	1	
1_20	3	*Sorbus aucuparia*	6	1	1	
1_20	4	*Acer pseudoplatanus*	9	2	1	1
1_20	5	*Carpinus betulus*	5	2	1	1
1_20	6	*Acer pseudoplatanus*	5	1	1	1
1_20	7	*Populus tremula*	3	1	1	1
1_20	8	*Prunus avium*	3	1	1	
1_20	9	*Carpinus betulus*	6	2	1	1
1_21	1	*Corylus avellana*	4	2	1	2
1_21	10	*Corylus avellana*	26	2	1	1
1_21	2	*Fagus sylvatica*	24	1	1	1
1_21	3	*Crataegus spec.*	12	1	3	1
1_21	4	*Fagus sylvatica*	6	1	1	2
1_21	5	*Fagus sylvatica*	16	1	1	1
1_21	6	*Acer pseudoplatanus*	22	1	1	1
1_21	7	*Fagus sylvatica*	39	1	1	1
1_21	8	*Fagus sylvatica*	9	1	1	1
1_21	9	*Corylus avellana*	13	1	2	1
1_22	1	*Acer pseudoplatanus*	2	3	1	1
1_22	10	*Acer pseudoplatanus*	4	2	1	
1_22	2	*Acer pseudoplatanus*	4	1	1	1
1_22	3	*Sambucus nigra*	5	2	1	2
1_22	4	*Lonicera xylosteum*	4	1	1	1
1_22	5	*Acer campestre*	8	1	1	1
1_22	6	*Acer pseudoplatanus*	8	3	1	1

1_22	7	*Fraxinus excelsior*	6	2	2	3
1_22	8	*Fraxinus excelsior*	8	1	1	1
1_22	9	*Corylus avellana*	15	3	1	1
1_23	1	*Salix caprea*	14	1	1	1
1_23	10	*Betula pendula*	6	2	1	1
1_23	2	*Salix caprea*	13	2	1	1
1_23	3	*Fagus sylvatica*	8	1	1	1
1_23	4	*Betula pendula*	19	2	1	2
1_23	5	*Fagus sylvatica*	6	1	1	1
1_23	6	*Betula pendula*	2	2	1	1
1_23	7	*Betula pendula*	4	2	2	
1_23	8	*Salix caprea*	20	2	1	1
1_23	9	*Betula pendula*	7	1	2	3
1_24	1	*Sorbus aucuparia*	49	2	1	2
1_24	10	*Aesculus hippocastanum*	4	2	1	2
1_24	2	*Sorbus aucuparia*	28	2	1	2
1_24	3	*Sorbus aucuparia*	40	3	1	2
1_24	4	*Aesculus hippocastanum*	25	2	1	2
1_24	5	*Cornus sanguinea*	5	1	1	1
1_24	6	*Cornus sanguinea*	10	1	1	1
1_24	7	*Cornus sanguinea*	7	1	1	1
1_24	8	*Cornus sanguinea*	45	1	1	1
1_24	9	*Sorbus aucuparia*	12	3	1	2
1_25	1	*Pyrus pyraster*	27	1	1	1
1_25	10	*Crataegus spec.*	9	1	1	1
1_25	2	*Quercus robur*	36	2	1	1
1_25	3	*Quercus robur*	45	2	1	1
1_25	4	*Corylus avellana*	3	1	3	3
1_25	5	*Quercus robur*	43	2	2	1
1_25	6	*Sorbus aucuparia*	3	3	2	3
1_25	7	*Quercus robur*	44	1	1	1
1_25	8	*Sorbus aucuparia*	2	2	2	3
1_25	9	*Crataegus spec.*	12	1	1	1
1_27	1	*Fagus sylvatica*	41	2	2	3
1_27	10	*Fagus sylvatica*	28	3	1	1
1_27	2	*Fagus sylvatica*	22	2	1	1
1_27	3	*Fagus sylvatica*	30	3	1	1
1_27	4	*Fagus sylvatica*	8	3	2	2

1_27	5	*Fagus sylvatica*	30	3	1	2
1_27	6	*Fagus sylvatica*	20	3	2	1
1_27	7	*Fagus sylvatica*	43	2	2	1
1_27	8	*Fagus sylvatica*	27	3	2	3
1_27	9	*Fagus sylvatica*	29	3	3	2
1_28	1	*Fagus sylvatica*	12	2	1	1
1_28	10	*Fagus sylvatica*	21	2	1	1
1_28	2	*Fagus sylvatica*	9	2	1	1
1_28	3	*Fagus sylvatica*	9	2	1	1
1_28	4	*Fagus sylvatica*	6	2	1	1
1_28	5	*Fagus sylvatica*	7	1	1	1
1_28	6	*Fagus sylvatica*	5	3	1	3
1_28	7	*Fagus sylvatica*	10	3	1	1
1_28	8	*Fagus sylvatica*	6	2	1	1
1_28	9	*Fagus sylvatica*	6	1	1	1
1_29	1	*Prunus avium*	26	3	1	1
1_29	10	*Pyrus pyraster*	19	2	1	1
1_29	2	*Prunus avium*	22	3	1	1
1_29	3	*Prunus avium*	44	3	2	2
1_29	4	*Prunus avium*	10	3	1	2
1_29	5	*Quercus petraea*	25	2	2	
1_29	6	*Quercus petraea*	69	2	2	1
1_29	7	*Malus sylvestris*	11	2	1	2
1_29	8	*Prunus avium*	44	3	1	2
1_29	9	*Prunus avium*	28	3	1	1
1_30	1	*Fagus sylvatica*	11	1	1	1
1_30	10	*Fagus sylvatica*	5	1	1	1
1_30	2	*Fagus sylvatica*	4	2	2	3
1_30	3	*Fagus sylvatica*	6	1	1	1
1_30	4	*Fagus sylvatica*	6	1	1	1
1_30	5	*Fagus sylvatica*	4	1	1	1
1_30	6	*Fagus sylvatica*	49	1	1	1
1_30	7	*Fagus sylvatica*	26	2	1	1
1_30	8	*Fagus sylvatica*	1	1	1	1
1_30	9	*Fagus sylvatica*	4	1	1	1
1_31	1	*Fagus sylvatica*	5	2	1	1
1_31	10	*Fagus sylvatica*	8	2	1	1
1_31	2	*Fagus sylvatica*	7	2	1	1

1_31	3	*Fagus sylvatica*	9	2	1	1
1_31	4	*Fagus sylvatica*	21	1	1	1
1_31	5	*Fagus sylvatica*	4	2	1	1
1_31	6	*Fagus sylvatica*	15	2	1	1
1_31	7	*Fagus sylvatica*	3	2	1	1
1_31	8	*Fagus sylvatica*	5	3	3	
1_31	9	*Fagus sylvatica*	39	2	2	2
1_32	1	*Fagus sylvatica*	6	2	1	1
1_32	10	*Fagus sylvatica*	19	2	1	1
1_32	2	*Fagus sylvatica*	6	1	1	1
1_32	3	*Fagus sylvatica*	17	2	1	1
1_32	4	*Fagus sylvatica*	9	2	1	1
1_32	5	*Fagus sylvatica*	8	2	1	1
1_32	6	*Fagus sylvatica*	37	2	1	1
1_32	7	*Fagus sylvatica*	3	1	1	1
1_32	8	*Fagus sylvatica*	21	2	1	1
1_32	9	*Fagus sylvatica*	8	2	1	1
1_33	1	*Crataegus spec.*	19	2	1	1
1_33	10	*Carpinus betulus*	23	3	3	3
1_33	2	*Carpinus betulus*	10	2	2	2
1_33	3	*Crataegus spec.*	18	2	1	1
1_33	4	*Carpinus betulus*	9	1	2	3
1_33	5	*Carpinus betulus*	7	2	1	
1_33	6	*Ligustrum vulgare*	1	1	1	1
1_33	7	*Ligustrum vulgare*	2	2	1	1
1_33	8	*Crataegus spec.*	8	2	1	1
1_33	9	*Crataegus spec.*	7	2	1	1
1_34	1	*Carpinus betulus*	19	2	1	1
1_34	10	*Carpinus betulus*	4	2	1	
1_34	2	*Carpinus betulus*	20	2	1	2
1_34	3	*Carpinus betulus*	4	2	1	2
1_34	4	*Fagus sylvatica*	4	1	1	
1_34	5	*Carpinus betulus*	11	2	1	2
1_34	6	*Carpinus betulus*	18	2	1	2
1_34	7	*Corylus avellana*	22	1	1	1
1_34	8	*Carpinus betulus*	9	2	1	2
1_34	9	*Corylus avellana*	29	2	1	1
1_35	1	*Fagus sylvatica*	24	1	3	3

1_35	10	*Fagus sylvatica*	11	1	1	1
1_35	2	*Fagus sylvatica*	17	1	2	1
1_35	3	*Fagus sylvatica*	8	2	2	2
1_35	4	*Fagus sylvatica*	32	1	1	1
1_35	5	*Fagus sylvatica*	20	1	2	1
1_35	6	*Fagus sylvatica*	17	1	1	2
1_35	7	*Fagus sylvatica*	9	2	2	1
1_35	8	*Fagus sylvatica*	17	2	3	3
1_35	9	*Fagus sylvatica*	25	1	2	1
1_36	1	*Acer pseudoplatanus*	18	2	1	1
1_36	10	*Carpinus betulus*	17	3	3	3
1_36	2	*Acer pseudoplatanus*	6	2	1	1
1_36	3	*Fagus sylvatica*	6	2	1	1
1_36	4	*Carpinus betulus*	28	3	2	3
1_36	5	*Tilia cordata*	29	2	1	1
1_36	6	*Fagus sylvatica*	8	2	2	2
1_36	7	*Fagus sylvatica*	29	2	1	1
1_36	8	*Carpinus betulus*	20	3	3	3
1_36	9	*Fagus sylvatica*	6	2	1	1
1_37	1	*Fagus sylvatica*	7	3	1	
1_37	10	*Prunus avium*	12	3	2	2
1_37	2	*Fagus sylvatica*	6	3	1	
1_37	3	*Acer pseudoplatanus*	10	1	1	1
1_37	4	*Prunus avium*	27	3	2	1
1_37	5	*Prunus avium*	9	3	2	2
1_37	6	*Fagus sylvatica*	21	2	1	1
1_37	7	*Fagus sylvatica*	46	3	2	1
1_37	8	*Acer pseudoplatanus*	3	1	1	1
1_37	9	*Fagus sylvatica*	5	3	2	2
1_38	1	*Carpinus betulus*	2	2	1	1
1_38	10	*Carpinus betulus*	22	3	3	3
1_38	2	*Crataegus spec.*	6	1	1	
1_38	3	*Corylus avellana*	4	2	3	
1_38	4	*Fagus sylvatica*	29	2	1	1
1_38	5	*Carpinus betulus*	20	2	2	1
1_38	6	*Corylus avellana*	13	2	2	2
1_38	7	*Carpinus betulus*	20	2	1	1
1_38	8	*Carpinus betulus*	20	2	1	1

1_38	9	*Carpinus betulus*	39	2	2	1
1_39	1	*Carpinus betulus*	6	2	1	1
1_39	10	*Fagus sylvatica*	7	1	1	1
1_39	2	*Fagus sylvatica*	24	1	1	2
1_39	3	*Fagus sylvatica*	4	1	1	2
1_39	4	*Fagus sylvatica*	2	3	3	3
1_39	5	*Fagus sylvatica*	6	2	1	2
1_39	6	*Fagus sylvatica*	13	2	1	1
1_39	7	*Carpinus betulus*	5	2	1	1
1_39	8	*Tilia cordata*	29	2	1	2
1_39	9	*Fagus sylvatica*	20	1	1	1
1_4	1	*Sorbus aucuparia*	19	3	1	2
1_4	10	*Betula pendula*	9	1	1	1
1_4	2	*Sorbus aucuparia*	21	2	1	2
1_4	3	*Quercus petraea*	26	2	2	2
1_4	4	*Sorbus aucuparia*	19	2	3	3
1_4	5	*Quercus petraea*	22	1	1	1
1_4	6	*Quercus petraea*	31	3	2	2
1_4	7	*Quercus petraea*	48	2	3	3
1_4	8	*Acer pseudoplatanus*	32	2	1	1
1_4	9	*Sorbus aucuparia*	11	2	1	2
1_40	1	*Fagus sylvatica*	7	2	2	2
1_40	10	*Fagus sylvatica*	23	2	1	1
1_40	2	*Fagus sylvatica*	18	3	1	2
1_40	3	*Fagus sylvatica*	19	2	2	1
1_40	4	*Tilia cordata*	20	3	2	2
1_40	5	*Fagus sylvatica*	5	3	2	2
1_40	6	*Fagus sylvatica*	6	3	1	1
1_40	7	*Fagus sylvatica*	15	3	2	1
1_40	8	*Fagus sylvatica*	5	3	2	1
1_40	9	*Fagus sylvatica*	7	2	1	1
1_41	1	*Cornus sanguinea*	6	2	1	1
1_41	10	*Carpinus betulus*	8	2	1	2
1_41	2	*Crataegus spec.*	19	2	1	1
1_41	3	*Prunus avium*	7	2	1	1
1_41	4	*Prunus avium*	48	2	2	1
1_41	5	*Crataegus spec.*	4	2	1	1
1_41	6	*Ligustrum vulgare*	6	1	1	1

1_41	7	*Prunus avium*	11	2	2	2
1_41	8	*Prunus avium*	21	2	2	1
1_41	9	*Prunus avium*	26	2	1	1
1_42	1	*Fagus sylvatica*	29	2	1	
1_42	10	*Fagus sylvatica*	5	1	1	1
1_42	2	*Fagus sylvatica*	5	2	1	1
1_42	3	*Fagus sylvatica*	18	3	2	
1_42	4	*Fagus sylvatica*	24	2	1	1
1_42	5	*Acer campestre*	2	1	1	
1_42	6	*Fagus sylvatica*	28	1	1	
1_42	7	*Fagus sylvatica*	29	2	1	1
1_42	8	*Fagus sylvatica*	10	3	1	
1_42	9	*Fagus sylvatica*	22	2	1	
1_43	1	*Carpinus betulus*	37	3	1	2
1_43	10	*Carpinus betulus*	37	2	1	3
1_43	2	*Sorbus torminalis*	10	2	1	1
1_43	3	*Fagus sylvatica*	4	3	2	3
1_43	4	*Carpinus betulus*	7	3	1	2
1_43	5	*Carpinus betulus*	39	2	1	2
1_43	6	*Carpinus betulus*	6	3	3	1
1_43	7	*Carpinus betulus*	11	3	3	3
1_43	8	*Fagus sylvatica*	10	3	3	3
1_43	9	*Fagus sylvatica*	4	3	3	3
1_44	1	*Fagus sylvatica*	5	1	1	1
1_44	10	*Fagus sylvatica*	19	1	1	1
1_44	2	*Fagus sylvatica*	10	1	1	1
1_44	3	*Fagus sylvatica*	16	1	1	1
1_44	4	*Fagus sylvatica*	20	1	1	1
1_44	5	*Fagus sylvatica*	11	1	1	1
1_44	6	*Fagus sylvatica*	7	1	1	1
1_44	7	*Fagus sylvatica*	5	1	1	1
1_44	8	*Fagus sylvatica*	12	1	1	1
1_44	9	*Fagus sylvatica*	9	2	1	1
1_45	10	*Frangula alnus*	14	2	1	1
1_45	2	*Frangula alnus*	12	3	2	
1_45	4	*Sorbus aucuparia*	4	3	1	2
1_45	5	*Sorbus aucuparia*	31	3	1	2
1_45	6	*Frangula alnus*	15	3	1	1

1_45	7	*Frangula alnus*	5	2	1	2
1_45	8	*Sorbus aucuparia*	4	3	1	2
1_45	9	*Quercus robur*	10	2	1	2
1_46	1	*Ulmus glabra*	28	2	2	1
1_46	10	*Ulmus glabra*	9	2	3	3
1_46	2	*Ulmus glabra*	9	2	2	2
1_46	3	*Ulmus glabra*	21	2	1	1
1_46	4	*Ulmus glabra*	37	2	2	1
1_46	5	*Ulmus glabra*	16	2	2	1
1_46	6	*Ulmus glabra*	12	2	3	3
1_46	7	*Ulmus glabra*	18	2	1	1
1_46	8	*Ulmus glabra*	10	2	1	1
1_46	9	*Ulmus glabra*	19	2	1	1
1_48	1	*Acer campestre*	10	1	1	1
1_48	10	*Juglans regia*	21	2	1	1
1_48	2	*Acer campestre*	7	3	1	1
1_48	3	*Acer campestre*	21	2	1	1
1_48	4	*Prunus spinosa*	5	1	1	3
1_48	5	*Acer campestre*	23	1	1	2
1_48	6	*Acer campestre*	8	2	1	1
1_48	7	*Acer campestre*	34	1	1	1
1_48	8	*Acer campestre*	24	1	1	1
1_48	9	*Prunus spinosa*	18	1	1	1
1_49	1	*Cornus sanguinea*	17	1	1	1
1_49	10	*Cornus sanguinea*	6	1	1	1
1_49	2	*Frangula alnus*	29	2	2	1
1_49	3	*Cornus sanguinea*	26	2	1	1
1_49	4	*Sorbus aucuparia*	6	2	1	3
1_49	5	*Cornus sanguinea*	9	1	1	1
1_49	6	*Cornus sanguinea*	3	1	1	1
1_49	7	*Sorbus aucuparia*	10	2	1	1
1_49	8	*Corylus avellana*	13	2	1	1
1_49	9	*Cornus sanguinea*	10	1	1	1
1_50	1	*Quercus robur*	38	2	1	1
1_50	10	*Betula pendula*	25	2	2	1
1_50	2	*Betula pendula*	17	2	2	1
1_50	3	*Sorbus aucuparia*	39	3	1	2
1_50	4	*Sorbus aucuparia*	31	3	1	1

1_50	5	*Betula pendula*	38	2	1	1
1_50	6	*Quercus robur*	14	2	2	1
1_50	7	*Quercus robur*	12	2	1	1
1_50	8	*Betula pendula*	10	2	2	1
1_50	9	*Sorbus aucuparia*	24	3	2	2
1_51	1	*Fagus sylvatica*	20	2	1	2
1_51	10	*Fagus sylvatica*	34	2	1	1
1_51	2	*Fagus sylvatica*	24	2	2	2
1_51	3	*Fagus sylvatica*	10	3	2	2
1_51	4	*Fagus sylvatica*	41	2	1	1
1_51	5	*Fagus sylvatica*	24	2	2	1
1_51	6	*Fagus sylvatica*	23	2	2	1
1_51	7	*Fagus sylvatica*	11	3	3	3
1_51	8	*Quercus robur*	23	2	2	2
1_51	9	*Fagus sylvatica*	8	3	2	3
1_52	1	*Betula pendula*	18	2	1	1
1_52	10	*Betula pendula*	2	2	1	1
1_52	2	*Quercus robur*	16	2	2	1
1_52	3	*Quercus robur*	45	1	1	1
1_52	4	*Betula pendula*	47	1	1	1
1_52	5	*Quercus robur*	4	2	1	1
1_52	6	*Betula pendula*	32	2	1	1
1_52	7	*Betula pendula*	32	2	2	1
1_52	8	*Betula pendula*	2	2	1	1
1_52	9	*Quercus robur*	2	2	2	2
1_53	1	*Pyrus pyraster*	17	1	1	
1_53	10	*Sorbus aucuparia*	22	2	1	2
1_53	2	*Sorbus aucuparia*	10	3	3	
1_53	3	*Fagus sylvatica*	23	3	1	
1_53	4	*Cornus sanguinea*	12	2	1	
1_53	5	*Corylus avellana*	13	2	1	
1_53	6	*Fagus sylvatica*	33	2	1	1
1_53	7	*Cornus sanguinea*	47	2	3	3
1_53	8	*Fagus sylvatica*	33	2	1	1
1_53	9	*Cornus sanguinea*	30	2	2	3
1_54	1	*Frangula alnus*	44	2	1	3
1_54	10	*Frangula alnus*	2	2	1	1
1_54	2	*Sorbus aucuparia*	17	2	1	2

1_54	3	*Sorbus aucuparia*	50	2	1	2
1_54	4	*Fagus sylvatica*	46	1	1	1
1_54	5	*Frangula alnus*	4	2	1	1
1_54	6	*Sorbus aucuparia*	70	2	1	2
1_54	7	*Fagus sylvatica*	75	1	1	1
1_54	8	*Sorbus aucuparia*	47	2	1	2
1_54	9	*Quercus petraea*	55	2	1	2
1_55	1	*Sorbus aucuparia*	22	3	1	1
1_55	10	*Malus sylvestris*	9	2	2	2
1_55	2	*Tilia cordata*	15	1	1	1
1_55	3	*Prunus avium*	23	2	2	2
1_55	4	*Sorbus aucuparia*	5	3	1	1
1_55	5	*Sorbus aucuparia*	15	2	3	3
1_55	6	*Ulmus glabra*	9	2	2	2
1_55	7	*Corylus avellana*	14	3	1	1
1_55	8	*Sorbus aucuparia*	6	3	3	3
1_55	9	*Malus sylvestris*	7	1	1	2
1_56	1	*Acer pseudoplatanus*	11	1	1	1
1_56	10	*Fraxinus excelsior*	10	2	1	1
1_56	2	*Sorbus aucuparia*	18	2	1	1
1_56	3	*Sambucus nigra*	12	2	2	2
1_56	4	*Sorbus aucuparia*	41	2	1	1
1_56	5	*Betula pendula*	24	2	1	1
1_56	6	*Sorbus aucuparia*	21	3	2	1
1_56	7	*Sorbus aucuparia*	23	2	1	1
1_56	8	*Tilia cordata*	2	2	1	1
1_56	9	*Sorbus aucuparia*	14	2	1	2
1_57	1	*Carpinus betulus*	9	2	1	1
1_57	10	*Carpinus betulus*	26	1	1	1
1_57	2	*Carpinus betulus*	7	2	1	1
1_57	3	*Sorbus aucuparia*	13	3	3	3
1_57	4	*Carpinus betulus*	5	2	1	1
1_57	5	*Prunus avium*	5	2	1	
1_57	6	*Carpinus betulus*	8	2	1	1
1_57	7	*Crataegus spec.*	12	1	1	1
1_57	8	*Quercus petraea*	2	1	1	1
1_57	9	*Sorbus aucuparia*	27	2	1	1
1_58	1	*Quercus petraea*	26	2	1	1

1_58	10	*Salix caprea*	22	2	2	3
1_58	2	*Sorbus aucuparia*	44	2	2	2
1_58	3	*Alnus glutinosa*	43	2	2	2
1_58	4	*Quercus petraea*	19	1	1	1
1_58	5	*Frangula alnus*	6	2	3	3
1_58	6	*Quercus petraea*	33	2	1	2
1_58	7	*Frangula alnus*	33	2	1	1
1_58	8	*Quercus petraea*	25	2	2	1
1_58	9	*Betula pendula*	51	2	1	1
1_59	1	*Acer pseudoplatanus*	26	3	2	1
1_59	10	*Tilia cordata*	40	2	1	1
1_59	2	*Fagus sylvatica*	19	3	2	2
1_59	3	*Acer pseudoplatanus*	42	3	2	1
1_59	4	*Fagus sylvatica*	6	3	1	1
1_59	5	*Sorbus aucuparia*	15	3	2	2
1_59	6	*Fagus sylvatica*	13	2	1	1
1_59	7	*Acer platanoides*	2	2	1	1
1_59	8	*Acer pseudoplatanus*	2	2	3	3
1_59	9	*Acer pseudoplatanus*	1	3	3	3
1_6	1	*Fagus sylvatica*	12	1	1	1
1_6	10	*Fagus sylvatica*	26	1	1	1
1_6	2	*Fagus sylvatica*	10	1	1	1
1_6	3	*Fagus sylvatica*	15	1	1	1
1_6	4	*Fagus sylvatica*	20	1	1	1
1_6	5	*Fagus sylvatica*	15	1	1	1
1_6	6	*Fagus sylvatica*	17	1	1	1
1_6	7	*Fagus sylvatica*	19	1	1	1
1_6	8	*Fagus sylvatica*	14	1	1	1
1_6	9	*Fagus sylvatica*	23	1	1	1
1_60	1	*Fagus sylvatica*	37	1	1	1
1_60	10	*Fagus sylvatica*	26	2	1	1
1_60	2	*Fagus sylvatica*	30	1	1	1
1_60	3	*Fagus sylvatica*	33	1	1	1
1_60	4	*Corylus avellana*	10	3	1	1
1_60	5	*Fagus sylvatica*	35	1	1	1
1_60	6	*Fagus sylvatica*	29	1	1	1
1_60	7	*Fagus sylvatica*	11	1	1	1
1_60	8	*Fagus sylvatica*	13	1	1	1

1_60	9	*Fagus sylvatica*	22	1	1	1
1_61	1	*Fagus sylvatica*	13	3	2	1
1_61	10	*Acer campestre*	8	3	2	3
1_61	2	*Fagus sylvatica*	13	2	2	1
1_61	3	*Fagus sylvatica*	6	3	3	3
1_61	4	*Acer campestre*	15	3	3	3
1_61	5	*Carpinus betulus*	26	3	3	3
1_61	6	*Carpinus betulus*	19	3	2	2
1_61	7	*Carpinus betulus*	15	3	3	3
1_61	8	*Fagus sylvatica*	43	3	2	3
1_61	9	*Fagus sylvatica*	31	3	2	2
1_63	1	*Fagus sylvatica*	17	2	1	2
1_63	10	*Sorbus aucuparia*	32	2	1	1
1_63	2	*Sambucus nigra*	3	2	1	1
1_63	3	*Fagus sylvatica*	19	1	1	1
1_63	4	*Prunus avium*	9	2	2	1
1_63	5	*Fagus sylvatica*	40	2	1	1
1_63	6	*Crataegus spec.*	11	1	1	1
1_63	7	*Tilia cordata*	17	2	1	1
1_63	8	*Corylus avellana*	9	2	1	1
1_63	9	*Fagus sylvatica*	8	3	3	3
1_65	1	*Fagus sylvatica*	3	2	2	1
1_65	10	*Fagus sylvatica*	2	1	1	1
1_65	2	*Fagus sylvatica*	6	1	1	1
1_65	3	*Fagus sylvatica*	2	3	3	3
1_65	4	*Fagus sylvatica*	17	1	1	1
1_65	5	*Fagus sylvatica*	10	1	1	1
1_65	6	*Fagus sylvatica*	21	1	1	1
1_65	7	*Fagus sylvatica*	14	1	1	1
1_65	8	*Fagus sylvatica*	10	1	1	1
1_65	9	*Fagus sylvatica*	9	1	1	1
1_66	1	*Corylus avellana*	24	2	1	1
1_66	10	*Amelanchier x lamarckii*	24	2	3	2
1_66	2	*Quercus petraea*	25	1	1	1
1_66	3	*Frangula alnus*	26	1	3	3
1_66	4	*Sorbus aucuparia*	44	2	1	1
1_66	5	*Cotoneaster integerrimus*	13	1	2	1
1_66	6	*Acer pseudoplatanus*	26	2	1	1

1_66	7	*Quercus petraea*	6	1	1	1
1_66	8	*Frangula alnus*	12	2	3	2
1_66	9	*Quercus petraea*	26	1	1	1
1_67	1	*Carpinus betulus*	27	2	1	1
1_67	10	*Carpinus betulus*	20	2	1	1
1_67	2	*Fraxinus excelsior*	11	1	1	2
1_67	3	*Carpinus betulus*	22	2	1	1
1_67	4	*Tilia cordata*	18	3	2	
1_67	5	*Tilia cordata*	35	2	2	2
1_67	6	*Carpinus betulus*	15	2	1	
1_67	7	*Carpinus betulus*	13	2	1	2
1_67	8	*Fraxinus excelsior*	2.7	2	1	1
1_67	9	*Corylus avellana*	23	2	1	1
1_69	1	*Fagus sylvatica*	6	1	1	1
1_69	10	*Fagus sylvatica*	10	1	1	1
1_69	2	*Fagus sylvatica*	42	2	1	1
1_69	3	*Fagus sylvatica*	48	2	1	1
1_69	4	*Corylus avellana*	7	2	1	1
1_69	5	*Fagus sylvatica*	32	2	1	1
1_69	6	*Fagus sylvatica*	52	1	1	1
1_69	7	*Fagus sylvatica*	14	1	1	1
1_69	8	*Fagus sylvatica*	19	2	1	1
1_69	9	*Fagus sylvatica*	13	1	1	1
1_7	1	*Betula pendula*	2	2	1	1
1_7	10	*Fagus sylvatica*	4	1		1
1_7	2	*Betula pendula*	6	3	3	3
1_7	3	*Fagus sylvatica*	4	1	1	1
1_7	4	*Sorbus aucuparia*	6	3	1	2
1_7	5	*Betula pendula*	4	3	3	3
1_7	6	*Frangula alnus*	4	3	1	1
1_7	7	*Sorbus aucuparia*	4	3	1	2
1_7	8	*Fagus sylvatica*	4	1	1	1
1_7	9	*Sorbus aucuparia*	6	3	1	2
1_70	1	*Fagus sylvatica*	10	1	1	1
1_70	10	*Fagus sylvatica*	26	1	1	1
1_70	2	*Fagus sylvatica*	9	1	1	1
1_70	3	*Fagus sylvatica*	20	1	1	1
1_70	4	*Fagus sylvatica*	19	1	1	1

1_70	5	*Fagus sylvatica*	26	1	1	1
1_70	6	*Fagus sylvatica*	47	1	1	1
1_70	7	*Fagus sylvatica*	9	1	1	1
1_70	8	*Frangula alnus*	10	2	1	1
1_70	9	*Fagus sylvatica*	54	1	1	1
1_71	1	*Fagus sylvatica*	15	2	1	
1_71	10	*Fagus sylvatica*	20	2	1	1
1_71	2	*Fagus sylvatica*	22	1	1	1
1_71	3	*Fagus sylvatica*	17	1	1	
1_71	4	*Acer pseudoplatanus*	26	2	1	1
1_71	5	*Corylus avellana*	28	2	1	1
1_71	6	*Fagus sylvatica*	21	2	1	1
1_71	7	*Fagus sylvatica*	15	2	1	1
1_71	8	*Fagus sylvatica*	20	2	1	
1_71	9	*Fagus sylvatica*	19	2	1	1
1_72	1	*Ulmus glabra*	7	2	1	1
1_72	10	*Corylus avellana*	32	2	1	1
1_72	2	*Fagus sylvatica*	28	2	1	2
1_72	3	*Sorbus aucuparia*	24	3	1	2
1_72	4	*Sorbus aucuparia*	23	3	1	2
1_72	5	*Acer pseudoplatanus*	6	2	1	1
1_72	6	*Acer pseudoplatanus*	33	2	1	1
1_72	7	*Sorbus aucuparia*	14	3	1	2
1_72	8	*Acer pseudoplatanus*	9	2	1	1
1_72	9	*Ulmus glabra*	8	2	1	1
1_73	1	*Fagus sylvatica*	28	2	1	1
1_73	10	*Fagus sylvatica*	42	2	1	1
1_73	2	*Fagus sylvatica*	49	2	1	1
1_73	3	*Fagus sylvatica*	41	2	1	1
1_73	4	*Fagus sylvatica*	17	2	1	1
1_73	5	*Fagus sylvatica*	12	2	1	1
1_73	6	*Fagus sylvatica*	50	2	1	1
1_73	7	*Fagus sylvatica*	23	2	1	1
1_73	8	*Fagus sylvatica*	33	2	1	1
1_73	9	*Fagus sylvatica*	29	2	1	1
1_8	1	*Ulmus glabra*	16	1	1	1
1_8	10	*Ulmus glabra*	14	2	1	1
1_8	2	*Ulmus glabra*	15	1	1	1

1_8	3	*Ulmus glabra*	9	1	1	1
1_8	4	*Ulmus glabra*	21	1	1	1
1_8	5	*Ulmus glabra*	11	1	1	1
1_8	6	*Ulmus glabra*	16	1	1	1
1_8	7	*Fagus sylvatica*	24	2	1	1
1_8	8	*Ulmus glabra*	4	1	2	3
1_8	9	*Fagus sylvatica*	12	1	1	1
1_9	1	*Fagus sylvatica*	17	1	1	2
1_9	10	*Fagus sylvatica*	6	1	1	1
1_9	2	*Corylus avellana*	26	1	1	1
1_9	3	*Fagus sylvatica*	9	1	1	2
1_9	4	*Fagus sylvatica*	4	1	1	2
1_9	5	*Fagus sylvatica*	22	1	1	1
1_9	6	*Fagus sylvatica*	8	1	1	1
1_9	7	*Fagus sylvatica*	13	1	1	2
1_9	8	*Fagus sylvatica*	34	1	1	1
1_9	9	*Fagus sylvatica*	29	1	1	1
2_10	1	*Carpinus betulus*	34	2	1	1
2_10	10	*Carpinus betulus*	25	2	1	1
2_10	2	*Carpinus betulus*	41	2	1	1
2_10	3	*Sorbus aucuparia*	35	2	1	1
2_10	4	*Sorbus aucuparia*	16	2	2	2
2_10	5	*Carpinus betulus*	27	2	1	1
2_10	6	*Acer pseudoplatanus*	21	2	1	1
2_10	7	*Acer pseudoplatanus*	35	2	3	3
2_10	8	*Euonymus europaeus*	17	1	1	1
2_10	9	*Sorbus aucuparia*	33	2	1	2
2_11	1	*Populus tremula*	46	2	1	1
2_11	10	*Sorbus aucuparia*	28	2	1	2
2_11	2	*Sorbus aucuparia*	11	3	3	3
2_11	3	*Sorbus aucuparia*	30	3	1	3
2_11	4	*Frangula alnus*	18	2		
2_11	5	*Populus tremula*	32	2	1	1
2_11	6	*Sorbus aucuparia*	22	2	1	2
2_11	7	*Sorbus aucuparia*	9	3	1	2
2_11	8	*Betula pendula*	13	2	1	2
2_11	9	*Sorbus aucuparia*	7	2	1	2
2_12	1	*Tilia cordata*	42	2	1	1

2_12	10	*Tilia cordata*	69	2	1	1
2_12	2	*Sorbus aucuparia*	57	2	2	3
2_12	3	*Tilia cordata*	45	1	1	1
2_12	4	*Sorbus aucuparia*	63	3	2	2
2_12	5	*Sorbus aucuparia*	43	3	3	3
2_12	6	*Tilia cordata*	30	3	1	1
2_12	7	*Sorbus aucuparia*	20	3	1	2
2_12	8	*Tilia cordata*	66	2	1	1
2_12	9	*Tilia cordata*	60	2	1	1
2_15	1	*Sorbus aucuparia*	27	2	1	1
2_15	10	*Acer pseudoplatanus*	40	2	2	2
2_15	2	*Sorbus aucuparia*	20	3	3	3
2_15	3	*Prunus avium*	22	2	1	1
2_15	4	*Carpinus betulus*	33	2	1	1
2_15	5	*Acer pseudoplatanus*	34	2	1	1
2_15	6	*Fraxinus excelsior*	36	1	1	1
2_15	7	*Acer pseudoplatanus*	32	3	1	1
2_15	8	*Prunus avium*	32	2	1	
2_15	9	*Sorbus aucuparia*	25	2	1	1
2_17	1	*Fraxinus excelsior*	23	1	1	1
2_17	10	*Sorbus aucuparia*	40	3	2	2
2_17	2	*Fagus sylvatica*	16	2	1	1
2_17	3	*Sorbus aucuparia*	10	3	2	1
2_17	4	*Ulmus glabra*	37	1	1	1
2_17	5	*Ulmus glabra*	33	1	1	1
2_17	6	*Acer pseudoplatanus*	15	2	1	1
2_17	7	*Acer pseudoplatanus*	37	2	1	1
2_17	8	*Acer pseudoplatanus*	30	2	1	1
2_17	9	*Acer pseudoplatanus*	10	3	1	1
2_6	1	*Sorbus aucuparia*	63	2	2	2
2_6	10	*Sambucus nigra*	55	3	2	1
2_6	2	*Sorbus aucuparia*	36	2	1	1
2_6	3	*Sorbus aucuparia*	20	2	1	1
2_6	4	*Acer pseudoplatanus*	22	1	1	1
2_6	5	*Acer pseudoplatanus*	23	2	1	2
2_6	6	*Acer pseudoplatanus*	16	2	1	1
2_6	7	*Sorbus aucuparia*	30	1	1	2
2_6	8	*Acer pseudoplatanus*	26	1	1	1

2_6	9	*Sambucus nigra*	10	3	2	1
2_8	1	*Betula pendula*	52	2	1	1
2_8	10	*Frangula alnus*	20	1	1	1
2_8	2	*Betula pendula*	24	2	2	2
2_8	3	*Acer pseudoplatanus*	13	2	1	2
2_8	4	*Acer pseudoplatanus*	30	2	1	1
2_8	5	*Acer pseudoplatanus*	25	3	3	3
2_8	6	*Acer pseudoplatanus*	27	2	1	2
2_8	7	*Acer pseudoplatanus*	28	2	1	
2_8	8	*Frangula alnus*	20	2	1	1
2_8	9	*Betula pendula*	15	1	1	1
2_9	1	*Sorbus aucuparia*	21	1	1	1
2_9	10	*Sorbus aucuparia*	24	2	1	2
2_9	2	*Sorbus aucuparia*	10	2	1	1
2_9	3	*Sorbus aucuparia*	26	1	1	2
2_9	4	*Sorbus aucuparia*	7	2	1	1
2_9	5	*Sorbus aucuparia*	30	2	1	1
2_9	6	*Sorbus aucuparia*	18	2	1	1
2_9	7	*Sorbus aucuparia*	29	1	1	1
2_9	8	*Sorbus aucuparia*	24	2	1	1
2_9	9	*Sorbus aucuparia*	31	2	1	1
3_100	1	*Acer platanoides*	8	2	1	1
3_100	10	*Prunus padus*	21	2	1	1
3_100	2	*Carpinus betulus*	19	1	1	1
3_100	3	*Fagus sylvatica*	10	2	2	1
3_100	4	*Fagus sylvatica*	42	2	2	3
3_100	5	*Acer platanoides*	3	1	1	1
3_100	6	*Fagus sylvatica*	34	2	1	1
3_100	7	*Acer platanoides*	18	1	1	1
3_100	8	*Fagus sylvatica*	22	1	1	1
3_100	9	*Corylus avellana*	15	3	3	2
3_101	1	*Carpinus betulus*	42	1	1	1
3_101	10	*Fagus sylvatica*	29	2	1	1
3_101	2	*Carpinus betulus*	21	2	1	1
3_101	3	*Carpinus betulus*	30	1	1	1
3_101	4	*Fagus sylvatica*	28	3	3	3
3_101	5	*Fagus sylvatica*	30	2	1	1
3_101	6	*Fagus sylvatica*	25	1	1	1

3_101	7	*Fagus sylvatica*	38	2	1	2
3_101	8	*Fagus sylvatica*	34	1	1	1
3_101	9	*Fagus sylvatica*	28	2	1	1
3_102	1	*Sorbus aucuparia*	3	1	1	
3_102	10	*Carpinus betulus*	27	2	1	1
3_102	2	*Fagus sylvatica*	8	3	1	
3_102	3	*Carpinus betulus*	25	2	1	2
3_102	4	*Carpinus betulus*	22	2	1	2
3_102	5	*Betula pendula*	18	3	2	
3_102	6	*Carpinus betulus*	27	2	1	2
3_102	7	*Carpinus betulus*	55	3	1	2
3_102	8	*Fagus sylvatica*	10	3	2	2
3_102	9	*Betula pendula*	22	3	3	
3_104	1	*Betula pendula*	28	1	1	1
3_104	10	*Betula pendula*	21	1	1	1
3_104	2	*Betula pendula*	10	1	1	1
3_104	3	*Betula pendula*	28	2	1	1
3_104	4	*Betula pendula*	4	2	1	1
3_104	5	*Betula pendula*	31	1	1	1
3_104	6	*Betula pendula*	18	2	1	1
3_104	7	*Betula pendula*	5	2	1	1
3_104	8	*Betula pendula*	20	1	1	1
3_104	9	*Betula pendula*	9	2	2	2
3_108	1	*Fagus sylvatica*	11	2	1	1
3_108	10	*Quercus petraea*	10	1	2	2
3_108	2	*Fagus sylvatica*	24	2	1	1
3_108	3	*Fagus sylvatica*	68	2	1	1
3_108	4	*Fagus sylvatica*	14	1	1	1
3_108	5	*Fagus sylvatica*	9	1	1	1
3_108	6	*Quercus petraea*	64	2	1	1
3_108	7	*Fagus sylvatica*	13	1	1	1
3_108	8	*Fagus sylvatica*	69	2	1	1
3_108	9	*Fagus sylvatica*	23	1	1	1
3_109	1	*Carpinus betulus*	10	2	1	2
3_109	10	*Acer campestre*	6	2	1	1
3_109	2	*Carpinus betulus*	82	2	1	2
3_109	3	*Acer platanoides*	4	1	1	1
3_109	4	*Carpinus betulus*	3	2	1	1

3_109	5	*Carpinus betulus*	5	2	1	
3_109	6	*Carpinus betulus*	2	2	1	1
3_109	7	*Acer campestre*	6	2	1	1
3_109	8	*Fraxinus excelsior*	31	2	2	1
3_109	9	*Fraxinus excelsior*	52	2	2	2
3_11	1	*Corylus avellana*	1	2	1	1
3_11	10	*Carpinus betulus*	8	2	1	1
3_11	2	*Corylus avellana*	7	2	1	1
3_11	3	*Corylus avellana*	3	2	1	1
3_11	4	*Corylus avellana*	6	2	1	1
3_11	5	*Corylus avellana*	3	2	1	1
3_11	6	*Corylus avellana*	5	1	1	1
3_11	7	*Corylus avellana*	8	2	1	1
3_11	8	*Corylus avellana*	6	2	1	1
3_11	9	*Corylus avellana*	8	2	1	1
3_110	1	*Fagus sylvatica*	52	2	1	1
3_110	10	*Carpinus betulus*	31	2	1	1
3_110	2	*Fagus sylvatica*	54	2	1	1
3_110	3	*Carpinus betulus*	53	2	1	1
3_110	4	*Fagus sylvatica*	40	2	1	1
3_110	5	*Fagus sylvatica*	36	2	1	1
3_110	6	*Fagus sylvatica*	70	2	1	1
3_110	7	*Fagus sylvatica*	39	2	1	1
3_110	8	*Fagus sylvatica*	53	2	1	1
3_110	9	*Sorbus aucuparia*	26	2	1	1
3_111	1	*Carpinus betulus*	14	2	1	1
3_111	10	*Carpinus betulus*	47	1	1	1
3_111	2	*Carpinus betulus*	12	1	1	1
3_111	3	*Fagus sylvatica*	12	2	2	3
3_111	4	*Carpinus betulus*	6	2	1	1
3_111	5	*Quercus petraea*	79	3	3	3
3_111	6	*Carpinus betulus*	12	1	1	1
3_111	7	*Carpinus betulus*	30	2	1	1
3_111	8	*Carpinus betulus*	49	2	1	1
3_111	9	*Fagus sylvatica*	11	2	1	1
3_112	1	*Carpinus betulus*	41	2	1	1
3_112	10	*Fagus sylvatica*	61	2	1	1
3_112	2	*Carpinus betulus*	14	1	1	1

3_112	3	*Fagus sylvatica*	5	1	1	1
3_112	4	*Carpinus betulus*	6	2	1	1
3_112	5	*Carpinus betulus*	8	1	1	1
3_112	6	*Carpinus betulus*	21	2	1	1
3_112	7	*Carpinus betulus*	6	1	1	1
3_112	8	*Carpinus betulus*	6	1	1	1
3_112	9	*Carpinus betulus*	18	2	1	1
3_113	1	*Carpinus betulus*	39	2	1	2
3_113	10	*Fagus sylvatica*	44	3	3	3
3_113	2	*Quercus petraea*	27	2	1	1
3_113	3	*Quercus petraea*	14	2	1	1
3_113	4	*Fagus sylvatica*	40	2	2	2
3_113	5	*Fagus sylvatica*	43	2	1	2
3_113	6	*Fagus sylvatica*	28	3	2	2
3_113	7	*Fagus sylvatica*	40	2	2	2
3_113	8	*Fagus sylvatica*	73	3	2	3
3_113	9	*Fagus sylvatica*	29	3	3	3
3_114	1	*Fagus sylvatica*	17	2	1	1
3_114	10	*Fagus sylvatica*	52	2	1	1
3_114	2	*Carpinus betulus*	20	1	1	1
3_114	3	*Carpinus betulus*	22	2	1	1
3_114	4	*Fagus sylvatica*	34	2	1	1
3_114	5	*Fagus sylvatica*	54	2	1	1
3_114	6	*Fagus sylvatica*	64	2	1	1
3_114	7	*Fagus sylvatica*	39	2	1	1
3_114	8	*Carpinus betulus*	13	2	1	1
3_114	9	*Fagus sylvatica*	10	2	1	1
3_115	1	*Fagus sylvatica*	18	2	1	1
3_115	10	*Fagus sylvatica*	7	2	1	1
3_115	2	*Fagus sylvatica*	59	2	1	1
3_115	3	*Fagus sylvatica*	8	2	1	1
3_115	4	*Fagus sylvatica*	9	2	1	1
3_115	5	*Fagus sylvatica*	52	2	1	1
3_115	6	*Fagus sylvatica*	23	1	1	1
3_115	7	*Fagus sylvatica*	7	2	1	1
3_115	8	*Fagus sylvatica*	4	2	1	1
3_115	9	*Quercus petraea*	18	2	1	1
3_116	1	*Fagus sylvatica*	34	2	2	

3_116	10	*Fagus sylvatica*	28	1	1	1
3_116	2	*Fagus sylvatica*	41	2	1	1
3_116	3	*Fagus sylvatica*	23	1	1	1
3_116	4	*Fagus sylvatica*	16	1	1	1
3_116	5	*Fagus sylvatica*	55	1	1	1
3_116	6	*Fagus sylvatica*	31	1	1	1
3_116	7	*Fagus sylvatica*	41	1	1	1
3_116	8	*Fagus sylvatica*	31	2	1	1
3_116	9	*Fagus sylvatica*	33	2	1	1
3_119	1	*Fagus sylvatica*	20	2	1	1
3_119	10	*Fagus sylvatica*	14	2	1	1
3_119	2	*Fagus sylvatica*	17	1	1	1
3_119	3	*Fagus sylvatica*	30	2	1	1
3_119	4	*Fagus sylvatica*	4	1	1	1
3_119	5	*Fagus sylvatica*	6	1	1	1
3_119	6	*Fagus sylvatica*	42	2	1	1
3_119	7	*Fagus sylvatica*	19	1	1	1
3_119	8	*Fagus sylvatica*	24	2	1	1
3_119	9	*Fagus sylvatica*	14	1	1	1
3_12	1	*Fagus sylvatica*	12	1	1	1
3_12	10	*Fagus sylvatica*	13	1	1	1
3_12	2	*Crataegus spec.*	17	1	2	2
3_12	3	*Carpinus betulus*	45	2	2	1
3_12	4	*Ulmus glabra*	25	2	1	1
3_12	5	*Acer pseudoplatanus*	25	1	1	1
3_12	6	*Fagus sylvatica*	18	1	1	1
3_12	7	*Fagus sylvatica*	17	1	1	1
3_12	8	*Fagus sylvatica*	9	2	1	1
3_12	9	*Fagus sylvatica*	12	1	1	1
3_120	1	*Fagus sylvatica*	3	2	1	1
3_120	10	*Carpinus betulus*	5	2	1	1
3_120	2	*Carpinus betulus*	28	1	1	1
3_120	3	*Carpinus betulus*	8	1	1	1
3_120	4	*Carpinus betulus*	17	2	1	1
3_120	5	*Fagus sylvatica*	21	2	1	1
3_120	6	*Carpinus betulus*	5	2	1	2
3_120	7	*Carpinus betulus*	8	2	1	1
3_120	8	*Carpinus betulus*	47	2	1	1

3_120	9	*Carpinus betulus*	21	2	1	1
3_122	1	*Quercus petraea*	2	1	2	2
3_122	10	*Fagus sylvatica*	4	2	1	1
3_122	2	*Fagus sylvatica*	27	2	1	1
3_122	3	*Fagus sylvatica*	2	3	1	1
3_122	4	*Fagus sylvatica*	3	2	1	1
3_122	5	*Fagus sylvatica*	7	2	1	1
3_122	6	*Fagus sylvatica*	46	1	1	1
3_122	7	*Quercus petraea*	6	1	2	1
3_122	8	*Fagus sylvatica*	29	2	1	1
3_122	9	*Fagus sylvatica*	5	1	1	1
3_123	1	*Fagus sylvatica*	37	2	1	
3_123	10	*Sorbus aucuparia*	20	3	1	2
3_123	2	*Fagus sylvatica*	6	2	1	1
3_123	3	*Fagus sylvatica*	42	2	1	1
3_123	4	*Fagus sylvatica*	4	2	1	
3_123	5	*Fagus sylvatica*	51	2	1	1
3_123	6	*Fagus sylvatica*	46	2	1	1
3_123	7	*Fagus sylvatica*	7	2	1	3
3_123	8	*Fagus sylvatica*	37	1	1	1
3_123	9	*Fagus sylvatica*	14	2	1	
3_131	1	*Fagus sylvatica*	20	1	1	1
3_131	10	*Fagus sylvatica*	7	2	1	1
3_131	2	*Fagus sylvatica*	7	1	1	1
3_131	3	*Fagus sylvatica*	23	1	1	1
3_131	4	*Fagus sylvatica*	41	2	1	1
3_131	5	*Fagus sylvatica*	19	1	1	1
3_131	6	*Fagus sylvatica*	28	2	1	1
3_131	7	*Fagus sylvatica*	14	1	1	1
3_131	8	*Fagus sylvatica*	26	1	1	1
3_131	9	*Fagus sylvatica*	15	1	1	1
3_132	1	*Fagus sylvatica*	7	3	3	3
3_132	10	*Fagus sylvatica*	16	3	1	2
3_132	2	*Quercus petraea*	24	2	2	2
3_132	3	*Fagus sylvatica*	4	1	1	1
3_132	4	*Fagus sylvatica*	17	3	1	1
3_132	5	*Fagus sylvatica*	7	3	1	1
3_132	6	*Fagus sylvatica*	3	2	1	2

3_132	7	*Fagus sylvatica*	32	3	1	1
3_132	8	*Quercus petraea*	40	2	1	1
3_132	9	*Fagus sylvatica*	8	2	1	1
3_139	1	*Fagus sylvatica*	22	1	1	1
3_139	10	*Fagus sylvatica*	61	2	1	1
3_139	2	*Fagus sylvatica*	13	1	1	1
3_139	3	*Fagus sylvatica*	27	1	1	1
3_139	4	*Acer platanoides*	19	1	1	1
3_139	5	*Acer pseudoplatanus*	3	2	1	1
3_139	6	*Fagus sylvatica*	20	2	1	1
3_139	7	*Lonicera xylosteum*	1	1	1	2
3_139	8	*Fagus sylvatica*	26	2	1	1
3_139	9	*Corylus avellana*	19	2	1	1
3_14	1	*Sambucus nigra*	17	3	2	1
3_14	10	*Sambucus nigra*	10	2	2	2
3_14	2	*Sambucus nigra*	13	3	2	2
3_14	3	*Ulmus glabra*	3	1	1	1
3_14	4	*Sambucus nigra*	5	3	2	2
3_14	5	*Sambucus nigra*	35	3	2	2
3_14	6	*Sambucus nigra*	5	3	2	2
3_14	7	*Acer pseudoplatanus*	1	2	1	2
3_14	8	*Ulmus glabra*	1	1	1	1
3_14	9	*Crataegus spec.*	47	2	1	1
3_15	1	*Fagus sylvatica*	24	2		3
3_15	10	*Fagus sylvatica*	37	2		2
3_15	2	*Fagus sylvatica*	2	2		
3_15	3	*Fagus sylvatica*	33	2		1
3_15	4	*Fagus sylvatica*	46	2		1
3_15	5	*Fagus sylvatica*	25	2		1
3_15	6	*Fagus sylvatica*	26	2		1
3_15	7	*Fagus sylvatica*	52	2		3
3_15	8	*Fagus sylvatica*	36	2		1
3_15	9	*Fagus sylvatica*	55	1		1
3_16	1	*Fagus sylvatica*	10	2	3	3
3_16	10	*Fagus sylvatica*	16	3	3	3
3_16	2	*Fagus sylvatica*	38	1	1	1
3_16	3	*Carpinus betulus*	15	3	1	2
3_16	4	*Tilia cordata*	35	3	1	1

3_16	5	*Fagus sylvatica*	17	2	1	2
3_16	6	*Fagus sylvatica*	27	2	1	1
3_16	7	*Fagus sylvatica*	24	3	3	3
3_16	8	*Fagus sylvatica*	19	3	3	3
3_16	9	*Fagus sylvatica*	24	3	3	2
3_17	1	*Fagus sylvatica*	5	1	1	1
3_17	10	*Fagus sylvatica*	6	1	1	1
3_17	2	*Sambucus nigra*	7	3	3	3
3_17	3	*Sambucus nigra*	63	3	3	3
3_17	4	*Sambucus nigra*	55	3	3	3
3_17	5	*Corylus avellana*	19	2	1	1
3_17	6	*Sambucus nigra*	29	2	2	3
3_17	7	*Sambucus nigra*	4	2	1	1
3_17	8	*Fagus sylvatica*	8	1	1	1
3_17	9	*Corylus avellana*	15	1	1	1
3_18	1	*Tilia cordata*	13	3	2	2
3_18	10	*Corylus avellana*	15	3	2	2
3_18	2	*Tilia cordata*	34	3	2	2
3_18	3	*Tilia cordata*	17	3	2	2
3_18	4	*Tilia cordata*	12	3	3	3
3_18	5	*Fagus sylvatica*	45	2	2	1
3_18	6	*Tilia cordata*	5	3	3	3
3_18	7	*Sorbus torminalis*	10	2	2	1
3_18	8	*Fagus sylvatica*	9	3	2	2
3_18	9	*Corylus avellana*	31	2	1	1
3_19	1	*Frangula alnus*	9	3	1	3
3_19	10	*Fagus sylvatica*	29	1	1	1
3_19	2	*Acer platanoides*	2	1	1	3
3_19	3	*Sorbus aucuparia*	4	2	1	3
3_19	4	*Prunus avium*	39	2	2	2
3_19	5	*Fagus sylvatica*	10	1	1	1
3_19	6	*Corylus avellana*	10	1	1	1
3_19	7	*Fagus sylvatica*	19	1	1	1
3_19	8	*Fagus sylvatica*	12	1	1	1
3_19	9	*Sorbus aucuparia*	4	3	1	2
3_2	1	*Fagus sylvatica*	39	2	3	3
3_2	2	*Fagus sylvatica*	33	1	2	2
3_2	3	*Fagus sylvatica*	46	1	1	2

3_2	4	*Fagus sylvatica*	33	1	1	1
3_2	5	*Fagus sylvatica*	44	1	2	2
3_20	1	*Crataegus spec.*	11	2	1	1
3_20	10	*Crataegus spec.*	10	1	1	1
3_20	2	*Acer campestre*	28	3	3	3
3_20	3	*Crataegus spec.*	70	2	2	1
3_20	4	*Acer campestre*	39	1	2	2
3_20	5	*Crataegus spec.*	21	2	2	2
3_20	6	*Crataegus spec.*	11	2	2	2
3_20	7	*Crataegus spec.*	12	1	1	1
3_20	8	*Acer campestre*	57	1	2	2
3_20	9	*Crataegus spec.*	53	2	2	2
3_22	1	*Carpinus betulus*	19	3	3	3
3_22	10	*Carpinus betulus*	13	3	1	2
3_22	2	*Ulmus glabra*	20	2	1	2
3_22	3	*Ulmus glabra*	10	3	3	3
3_22	4	*Acer platanoides*	38	2	2	1
3_22	5	*Acer pseudoplatanus*	14	3	1	
3_22	6	*Ulmus glabra*	22	2	2	2
3_22	7	*Ulmus glabra*	35	2	1	1
3_22	8	*Ulmus glabra*	10	3	3	3
3_22	9	*Carpinus betulus*	35	2	1	2
3_23	1	*Fagus sylvatica*	28	1	1	1
3_23	10	*Sorbus aucuparia*	33	2	1	1
3_23	2	*Fagus sylvatica*	2	1	1	1
3_23	3	*Fagus sylvatica*	8	1	1	1
3_23	4	*Fagus sylvatica*	31	1	1	1
3_23	5	*Fagus sylvatica*	12	1	1	1
3_23	6	*Fagus sylvatica*	8	1	2	1
3_23	7	*Fagus sylvatica*	6	1	1	1
3_23	8	*Fagus sylvatica*	24	1	1	1
3_23	9	*Fagus sylvatica*	25	1	1	1
3_25	1	*Fagus sylvatica*	12	1	1	1
3_25	10	*Quercus petraea*	4	2	1	1
3_25	2	*Sorbus aucuparia*	17	2	1	2
3_25	3	*Fagus sylvatica*	31	2	1	1
3_25	4	*Sorbus aucuparia*	12	3	1	1
3_25	5	*Fagus sylvatica*	13	2	1	1

3_25	6	*Populus tremula*	3	3	1	2
3_25	7	*Sorbus aucuparia*	4	3	1	2
3_25	8	*Corylus avellana*	22	2	1	1
3_25	9	*Fagus sylvatica*	3	2	1	1
3_26	1	*Sorbus aucuparia*	5	3	3	3
3_26	10	*Sorbus aucuparia*	4	2	3	
3_26	2	*Sorbus aucuparia*	6	2	3	
3_26	3	*Acer pseudoplatanus*	29	1	1	1
3_26	4	*Quercus petraea*	2	3	3	
3_26	5	*Acer pseudoplatanus*	22	1	1	1
3_26	6	*Sorbus aucuparia*	3	2	1	2
3_26	7	*Sorbus aucuparia*	10	2	1	1
3_26	8	*Corylus avellana*	19	1	1	1
3_26	9	*Corylus avellana*	12	1	1	1
3_27	1	*Acer pseudoplatanus*	14	2	1	2
3_27	10	*Frangula alnus*	5	2	1	1
3_27	2	*Acer pseudoplatanus*	11	2	1	2
3_27	3	*Betula pendula*	2	2	1	1
3_27	4	*Corylus avellana*	18	1	1	1
3_27	5	*Corylus avellana*	13	2	1	1
3_27	6	*Sorbus aucuparia*	24	2	1	1
3_27	7	*Acer pseudoplatanus*	22	1	1	2
3_27	8	*Fagus sylvatica*	42	2	1	2
3_27	9	*Corylus avellana*	34	1	1	1
3_28	1	*Fagus sylvatica*	35	2	1	1
3_28	10	*Fagus sylvatica*	18	2		
3_28	2	*Fagus sylvatica*	13	2	1	1
3_28	3	*Fagus sylvatica*	23	1	1	1
3_28	4	*Fagus sylvatica*	15	1	1	1
3_28	5	*Fagus sylvatica*	11	1	1	2
3_28	6	*Fagus sylvatica*	25	2	1	1
3_28	7	*Sorbus aucuparia*	6	2	1	1
3_28	8	*Sorbus aucuparia*	4	3	1	2
3_28	9	*Fagus sylvatica*	47	2	1	2
3_29	1	*Sorbus aucuparia*	5	3	1	2
3_29	10	*Sorbus aucuparia*	6	2	1	2
3_29	2	*Sorbus aucuparia*	28	3	1	1
3_29	3	*Fagus sylvatica*	3	1	1	1

3_29	4	*Sorbus aucuparia*	20	3	2	3
3_29	5	*Betula pendula*	33	2	2	2
3_29	6	*Fagus sylvatica*	4	2	1	2
3_29	7	*Sorbus aucuparia*	14	3	3	3
3_29	8	*Carpinus betulus*	6	2	1	2
3_29	9	*Fagus sylvatica*	13	1	1	1
3_3	4	*Fagus sylvatica*	45	1	1	1
3_3	5	*Fagus sylvatica*	44	1	1	1
3_3	7	*Fagus sylvatica*	33	1	1	1
3_30	1	*Fagus sylvatica*	31	1	1	1
3_30	10	*Fagus sylvatica*	27	1	2	1
3_30	2	*Fagus sylvatica*	33	2	2	2
3_30	3	*Fagus sylvatica*	25	1	1	1
3_30	4	*Fagus sylvatica*	20	1	1	2
3_30	5	*Fagus sylvatica*	25	1	2	2
3_30	6	*Fagus sylvatica*	53	1	1	1
3_30	7	*Fagus sylvatica*	52	2	1	1
3_30	8	*Fagus sylvatica*	29	1	1	1
3_30	9	*Fagus sylvatica*	42	1	2	1
3_31	1	*Crataegus spec.*	17	2	2	2
3_31	10	*Crataegus spec.*	39	2	2	2
3_31	2	*Crataegus spec.*	24	2	2	2
3_31	3	*Crataegus spec.*	41	1	2	2
3_31	4	*Crataegus spec.*	31	1	2	
3_31	5	*Crataegus spec.*	20	2	2	2
3_31	6	*Crataegus spec.*	19	1	1	1
3_31	7	*Sambucus nigra*	29	2	2	1
3_31	8	*Sambucus nigra*	32	3	2	
3_31	9	*Crataegus spec.*	32	3	3	3
3_32	1	*Crataegus spec.*	9	2	1	1
3_32	10	*Populus tremula*	13	2	1	1
3_32	2	*Quercus robur*	5	1	1	1
3_32	3	*Sorbus aucuparia*	27	2	1	1
3_32	4	*Quercus robur*	16	2	1	1
3_32	5	*Frangula alnus*	8	2	1	1
3_32	6	*Quercus robur*	16	2	1	1
3_32	7	*Frangula alnus*	16	3	1	1
3_32	8	*Frangula alnus*	25	2	1	2

3_32	9	*Quercus robur*	2	2	1	1
3_33	1	*Sorbus aucuparia*	4	3	3	3
3_33	10	*Sorbus aucuparia*	13	3	3	3
3_33	2	*Sorbus aucuparia*	26	3	3	3
3_33	3	*Crataegus spec.*	18	2	2	2
3_33	4	*Sorbus aucuparia*	21	3	3	3
3_33	5	*Corylus avellana*	12	2	2	2
3_33	6	*Quercus petraea*	29	2	1	1
3_33	7	*Sorbus aucuparia*	19	2	1	1
3_33	8	*Sorbus aucuparia*	17	3	2	3
3_33	9	*Quercus petraea*	23	2	2	2
3_34	1	*Sorbus aucuparia*	6	2	1	2
3_34	10	*Sorbus aucuparia*	4	2	2	3
3_34	2	*Corylus avellana*	46	2		1
3_34	3	*Sorbus aucuparia*	15	3		3
3_34	4	*Corylus avellana*	36	2	1	1
3_34	5	*Crataegus spec.*	11	2	1	1
3_34	6	*Sorbus aucuparia*	11	3		2
3_34	7	*Sorbus aucuparia*	17	2	2	2
3_34	8	*Corylus avellana*	6	2	1	1
3_34	9	*Sorbus aucuparia*	22	3	2	3
3_37	1	*Acer platanoides*	13	2	2	
3_37	10	*Corylus avellana*	6	1	1	1
3_37	2	*Ulmus glabra*	26	2	1	1
3_37	3	*Fagus sylvatica*	12	2	1	1
3_37	4	*Ulmus glabra*	21	2	1	1
3_37	5	*Fagus sylvatica*	6	2	2	1
3_37	6	*Acer pseudoplatanus*	11	1	1	1
3_37	7	*Fagus sylvatica*	10	2	2	1
3_37	8	*Acer campestre*	25	2	1	1
3_37	9	*Fagus sylvatica*	8	2	2	1
3_38	1	*Fagus sylvatica*	12	2	1	2
3_38	10	*Fagus sylvatica*	28	1	1	1
3_38	2	*Fagus sylvatica*	10	1	2	1
3_38	3	*Fagus sylvatica*	10	2	1	1
3_38	4	*Fagus sylvatica*	15	2	1	1
3_38	5	*Fagus sylvatica*	40	2	1	1
3_38	6	*Carpinus betulus*	15	2	1	1

3_38	7	*Fagus sylvatica*	21	2	2	1
3_38	8	*Fagus sylvatica*	11	2	1	1
3_38	9	*Corylus avellana*	9	2	1	1
3_39	1	*Fagus sylvatica*	22	2	1	1
3_39	10	*Acer campestre*	8	2	2	1
3_39	2	*Corylus avellana*	17	1	2	1
3_39	3	*Carpinus betulus*	9	3	1	1
3_39	4	*Acer platanoides*	22	1	1	2
3_39	5	*Pyrus pyraster*	27	1	2	1
3_39	6	*Carpinus betulus*	7	2	2	2
3_39	7	*Corylus avellana*	6	3	2	2
3_39	8	*Corylus avellana*	16	2	2	1
3_39	9	*Ulmus glabra*	13	3	2	2
3_4	2	*Betula pendula*	53	3	2	2
3_4	3	*Fagus sylvatica*	39	1	1	1
3_4	4	*Fagus sylvatica*	38	1	1	1
3_4	5	*Acer pseudoplatanus*	30	2	1	1
3_4	7	*Corylus avellana*	15	1	1	1
3_41	1	*Fagus sylvatica*	13	2	1	
3_41	10	*Fagus sylvatica*	40	1	1	
3_41	2	*Fagus sylvatica*	36	1	1	
3_41	3	*Fagus sylvatica*	38	1	1	1
3_41	4	*Fagus sylvatica*	11	1	1	
3_41	5	*Fagus sylvatica*	33	1	1	
3_41	6	*Fagus sylvatica*	11	1	1	
3_41	7	*Fagus sylvatica*	39	2	1	1
3_41	8	*Fagus sylvatica*	11	1	1	1
3_41	9	*Fagus sylvatica*	26	1	1	1
3_43	1	*Alnus glutinosa*	23	2	1	1
3_43	10	*Betula pendula*	21	2	1	1
3_43	2	*Alnus glutinosa*	17	2	2	2
3_43	3	*Alnus glutinosa*	42	2	2	2
3_43	4	*Alnus glutinosa*	28	2	2	3
3_43	5	*Fagus sylvatica*	11	2	1	2
3_43	6	*Alnus glutinosa*	13	3	2	2
3_43	7	*Alnus glutinosa*	18	2	2	2
3_43	8	*Alnus glutinosa*	8	2	1	1
3_43	9	*Alnus glutinosa*	8	2	1	1

3_44	1	*Sambucus nigra*	5	2	1	2
3_44	10	*Fagus sylvatica*	14	1	1	1
3_44	2	*Fagus sylvatica*	18	1	1	1
3_44	3	*Fagus sylvatica*	63	2		
3_44	4	*Corylus avellana*	8	2	1	1
3_44	5	*Fagus sylvatica*	57	2	1	1
3_44	6	*Carpinus betulus*	4	1	1	1
3_44	7	*Corylus avellana*	11	2	1	2
3_44	8	*Sambucus nigra*	4	1	1	1
3_44	9	*Acer campestre*	3	1	2	1
3_45	1	*Fagus sylvatica*	10	1	1	1
3_45	10	*Fagus sylvatica*	4	1		
3_45	2	*Fagus sylvatica*	9	1	1	1
3_45	3	*Fagus sylvatica*	2	2		
3_45	4	*Fagus sylvatica*	9	1		
3_45	5	*Fagus sylvatica*	11	1	1	1
3_45	6	*Fagus sylvatica*	4	2	1	1
3_45	7	*Fagus sylvatica*	2	1	1	1
3_45	8	*Fagus sylvatica*	7	1		
3_45	9	*Fagus sylvatica*	6	1	1	1
3_46	1	*Sorbus aucuparia*	4	3	3	3
3_46	10	*Corylus avellana*	15	2	1	
3_46	2	*Corylus avellana*	16	2	1	1
3_46	3	*Corylus avellana*	21	2		1
3_46	4	*Sorbus aucuparia*	8	3	2	2
3_46	5	*Fagus sylvatica*	19	2	1	1
3_46	6	*Fagus sylvatica*	21	1	1	1
3_46	7	*Corylus avellana*	30	2	2	1
3_46	8	*Sorbus aucuparia*	16	3	3	3
3_46	9	*Fagus sylvatica*	21	2		
3_47	1	*Fagus sylvatica*	6	1		1
3_47	10	*Fagus sylvatica*	2	1	1	1
3_47	2	*Fagus sylvatica*	8	1	1	1
3_47	3	*Acer pseudoplatanus*	5	2	1	1
3_47	4	*Viburnum lantana*	5	2	3	1
3_47	5	*Fagus sylvatica*	5	1	1	1
3_47	6	*Fagus sylvatica*	5	1	1	1
3_47	7	*Fagus sylvatica*	13	2	1	1

3_47	8	*Acer pseudoplatanus*	4	2	1	1
3_47	9	*Fagus sylvatica*	22	1	1	1
3_48	1	*Acer pseudoplatanus*	6	1	3	1
3_48	10	*Acer pseudoplatanus*	8	1	1	1
3_48	2	*Acer pseudoplatanus*	6	1	1	1
3_48	3	*Fagus sylvatica*	23	1	1	1
3_48	4	*Acer pseudoplatanus*	5	1	1	1
3_48	5	*Corylus avellana*	8	1	3	2
3_48	6	*Fagus sylvatica*	18	1	1	1
3_48	7	*Sambucus nigra*	19	2	1	1
3_48	8	*Corylus avellana*	10	1	1	1
3_48	9	*Acer pseudoplatanus*	8	1	1	1
3_49	1	*Corylus avellana*	11	1	1	1
3_49	10	*Juglans regia*	4	1	1	1
3_49	2	*Acer pseudoplatanus*	3	2	1	1
3_49	3	*Acer campestre*	2	1	1	1
3_49	4	*Cornus mas*	4	1	1	1
3_49	5	*Corylus avellana*	7	1	1	1
3_49	6	*Corylus avellana*	10	1	1	1
3_49	7	*Fagus sylvatica*	2	1	1	1
3_49	8	*Cornus mas*	3	1	1	1
3_49	9	*Corylus avellana*	3	1	1	1
3_5	1	*Crataegus spec.*	1	2	1	1
3_5	10	*Frangula alnus*	24	1	1	1
3_5	2	*Fagus sylvatica*	1	1	1	1
3_5	3	*Frangula alnus*	1	2	1	1
3_5	4	*Frangula alnus*	39	1	1	1
3_5	5	*Frangula alnus*	2	2		
3_5	6	*Fagus sylvatica*	49	1	1	1
3_5	7	*Frangula alnus*	15	2	2	1
3_5	8	*Frangula alnus*	32	1	2	1
3_5	9	*Frangula alnus*	28	1	1	1
3_50	1	*Fagus sylvatica*	13	2	1	1
3_50	10	*Fagus sylvatica*	5	2	1	1
3_50	2	*Betula pendula*	4	2	1	1
3_50	3	*Betula pendula*	17	2	1	1
3_50	4	*Fagus sylvatica*	5	1	1	1
3_50	5	*Fagus sylvatica*	10	1	1	1

3_50	6	*Betula pendula*	10	2	1	1
3_50	7	*Fagus sylvatica*	8	2	1	1
3_50	8	*Fagus sylvatica*	14	1	1	1
3_50	9	*Betula pendula*	5	2	1	1
3_53	1	*Fagus sylvatica*	22	1	1	1
3_53	10	*Fagus sylvatica*	32	2	2	1
3_53	2	*Fagus sylvatica*	29	2	2	1
3_53	3	*Crataegus spec.*	16	1	1	1
3_53	4	*Fagus sylvatica*	36	1	1	1
3_53	5	*Acer pseudoplatanus*	26	2	2	1
3_53	6	*Corylus avellana*	14	1	1	1
3_53	7	*Corylus avellana*	15	2	2	1
3_53	8	*Fagus sylvatica*	27	1	1	1
3_53	9	*Corylus avellana*	9	2	2	1
3_54	1	*Fagus sylvatica*	15	3	3	3
3_54	10	*Fagus sylvatica*	9	1	1	1
3_54	2	*Fagus sylvatica*	7	1	1	1
3_54	3	*Fagus sylvatica*	50	1	1	1
3_54	4	*Fagus sylvatica*	7	2	1	1
3_54	5	*Fagus sylvatica*	39	2	1	1
3_54	6	*Fagus sylvatica*	32	2	1	1
3_54	7	*Fagus sylvatica*	38	1	1	1
3_54	8	*Fagus sylvatica*	16	2	1	1
3_54	9	*Fagus sylvatica*	40	1	1	1
3_55	10	*Carpinus betulus*	31	1	1	1
3_55	2	*Acer campestre*	23	1	2	1
3_55	3	*Acer campestre*	18	2	2	1
3_55	4	*Acer campestre*	19	1	1	1
3_55	6	*Crataegus spec.*	52	3	1	1
3_55	7	*Crataegus spec.*	32	2	1	1
3_55	8	*Crataegus spec.*	27	2	1	1
3_55	9	*Carpinus betulus*	16	2	1	1
3_56	1	*Prunus avium*	12	1	1	1
3_56	10	*Carpinus betulus*	8	2	1	1
3_56	2	*Carpinus betulus*	10	2	1	1
3_56	3	*Carpinus betulus*	26	2	1	1
3_56	4	*Prunus avium*	12	1	1	1
3_56	5	*Prunus avium*	6	2	1	1

3_56	6	*Carpinus betulus*	7	2	1	1
3_56	7	*Carpinus betulus*	11	2	1	1
3_56	8	*Carpinus betulus*	19	2	2	2
3_56	9	*Carpinus betulus*	9	2	1	1
3_57	1	*Quercus rubra*	20	1	1	1
3_57	10	*Fagus sylvatica*	19	1	1	1
3_57	2	*Fagus sylvatica*	34	2	2	1
3_57	3	*Quercus rubra*	17	1	1	1
3_57	4	*Quercus rubra*	18	1	1	1
3_57	5	*Fagus sylvatica*	39	2	1	1
3_57	6	*Quercus rubra*	30	1	1	1
3_57	7	*Tilia cordata*	17	1	1	2
3_57	8	*Tilia cordata*	45	3	1	2
3_57	9	*Betula pendula*	3	1	1	1
3_58	1	*Frangula alnus*	24	2	1	1
3_58	10	*Frangula alnus*	4	3	1	1
3_58	2	*Frangula alnus*	13	2	1	1
3_58	3	*Crataegus spec.*	47	2	1	1
3_58	4	*Sorbus aucuparia*	6	3	1	1
3_58	5	*Frangula alnus*	20	2	1	1
3_58	6	*Frangula alnus*	36	2	1	1
3_58	7	*Frangula alnus*	15	3	2	1
3_58	8	*Frangula alnus*	11	2	1	1
3_58	9	*Frangula alnus*	9	2	1	1
3_59	1	*Betula pendula*	4	2	1	1
3_59	10	*Betula pendula*	5	2	1	1
3_59	2	*Prunus avium*	19	2	1	1
3_59	3	*Fagus sylvatica*	4	2	1	1
3_59	4	*Crataegus spec.*	23	2	1	1
3_59	5	*Betula pendula*	6	2	1	1
3_59	6	*Sorbus aucuparia*	6	3	1	1
3_59	7	*Quercus robur*	22	2	1	1
3_59	8	*Quercus robur*	2	2	1	1
3_59	9	*Betula pendula*	35	2	1	1
3_6	1	*Fagus sylvatica*	29	1	1	1
3_6	10	*Fagus sylvatica*	36	1	1	1
3_6	2	*Fagus sylvatica*	22	1	1	1
3_6	3	*Fagus sylvatica*	65	2	2	2

3_6	4	*Fagus sylvatica*	35	1	1	1
3_6	5	*Fagus sylvatica*	44	1	1	1
3_6	7	*Fagus sylvatica*	48	2	2	1
3_60	1	*Prunus spinosa*	8	2	1	1
3_60	10	*Fraxinus excelsior*	55	1	2	2
3_60	2	*Acer pseudoplatanus*	18	3	1	2
3_60	3	*Cornus sanguinea*	18	2	1	1
3_60	4	*Cornus sanguinea*	22	2	1	1
3_60	5	*Fraxinus excelsior*	19	1	2	1
3_60	6	*Cornus sanguinea*	15	2	1	1
3_60	7	*Acer pseudoplatanus*	19	2	2	2
3_60	8	*Cornus sanguinea*	33	2	1	1
3_60	9	*Prunus spinosa*	12	1	1	1
3_62	1	*Acer pseudoplatanus*	12	1	1	1
3_62	10	*Acer platanoides*	12	1	1	1
3_62	2	*Sorbus aucuparia*	6	2	2	2
3_62	3	*Sambucus nigra*	14	2	2	2
3_62	4	*Acer platanoides*	3	1	1	1
3_62	5	*Fagus sylvatica*	50	2	1	1
3_62	6	*Fagus sylvatica*	22	2	2	1
3_62	7	*Sambucus nigra*	9	2	1	1
3_62	8	*Acer platanoides*	21	2	1	1
3_62	9	*Acer platanoides*	13	1	1	1
3_63	1	*Betula pendula*	29	2	2	1
3_63	10	*Fagus sylvatica*	2	1	1	1
3_63	2	*Fagus sylvatica*	10	1	1	1
3_63	3	*Fagus sylvatica*	6	1	1	1
3_63	4	*Fagus sylvatica*	12	1	1	1
3_63	5	*Fagus sylvatica*	18	1	1	1
3_63	6	*Sorbus aucuparia*	34	2	1	1
3_63	7	*Sambucus nigra*	3	2	2	1
3_63	8	*Fagus sylvatica*	11	1	1	1
3_63	9	*Betula pendula*	19	2	2	1
3_64	1	*Fagus sylvatica*	18	1	1	1
3_64	10	*Prunus padus*	32	3	3	3
3_64	2	*Carpinus betulus*	9	2	1	1
3_64	3	*Carpinus betulus*	7	2	2	1
3_64	4	*Tilia cordata*	34	2	1	1

3_64	5	*Carpinus betulus*	7	3	2	1
3_64	6	*Fagus sylvatica*	28	1	1	1
3_64	7	*Fagus sylvatica*	28	1	1	1
3_64	8	*Corylus avellana*	27	1	1	1
3_64	9	*Corylus avellana*	6	1	1	1
3_65	1	*Fagus sylvatica*	8	1	1	
3_65	10	*Fagus sylvatica*	11	1	1	
3_65	2	*Fagus sylvatica*	7	1	1	
3_65	3	*Sorbus aucuparia*	7	1	1	2
3_65	4	*Fagus sylvatica*	7	1	1	
3_65	5	*Sorbus aucuparia*	14	1	1	1
3_65	6	*Fagus sylvatica*	25	1	1	1
3_65	7	*Sorbus aucuparia*	9	1	1	
3_65	8	*Fagus sylvatica*	16	2	1	
3_65	9	*Fagus sylvatica*	6	1	1	2
3_66	1	*Sorbus aucuparia*	39	2	2	2
3_66	10	*Fagus sylvatica*	13	2	1	
3_66	2	*Sorbus aucuparia*	25	3	3	3
3_66	3	*Sorbus aucuparia*	32	2	1	1
3_66	4	*Sorbus aucuparia*	25	2	2	1
3_66	5	*Fagus sylvatica*	15	2	2	1
3_66	6	*Fagus sylvatica*	17	1	1	1
3_66	7	*Fagus sylvatica*	24	1	1	
3_66	8	*Fagus sylvatica*	6	1	2	1
3_66	9	*Fagus sylvatica*	33	2	1	1
3_67	1	*Betula pendula*	32	1	1	1
3_67	10	*Sambucus nigra*	38	2	1	1
3_67	2	*Sambucus nigra*	10	2	1	1
3_67	3	*Sambucus nigra*	9	2	1	1
3_67	4	*Sambucus nigra*	7	2	1	1
3_67	5	*Betula pendula*	4	1	1	1
3_67	6	*Betula pendula*	17	1	1	1
3_67	7	*Betula pendula*	34	1	1	1
3_67	8	*Betula pendula*	7	1	1	1
3_67	9	*Sorbus aucuparia*	11	1	1	1
3_68	1	*Betula pendula*	8	1	1	1
3_68	10	*Sorbus aucuparia*	14	1	1	1
3_68	2	*Betula pendula*	11	1	1	1

3_68	3	*Betula pendula*	12	1	1	1
3_68	4	*Betula pendula*	29	1	1	1
3_68	5	*Betula pendula*	9	1	1	1
3_68	6	*Betula pendula*	26	1	1	1
3_68	7	*Betula pendula*	17	1	1	1
3_68	8	*Betula pendula*	5	1	1	1
3_68	9	*Betula pendula*	46	2	1	1
3_69	1	*Sorbus aucuparia*	9	1	1	1
3_69	10	*Sorbus aucuparia*	11	3	1	2
3_69	2	*Sorbus aucuparia*	4	3	2	2
3_69	3	*Sorbus aucuparia*	11	2	1	
3_69	4	*Sorbus aucuparia*	18	2	1	2
3_69	5	*Sorbus aucuparia*	15	2	1	2
3_69	6	*Sorbus aucuparia*	11	2		
3_69	7	*Sorbus aucuparia*	12	2	2	1
3_69	8	*Sorbus aucuparia*	4	2	1	
3_69	9	*Sorbus aucuparia*	22	1	1	2
3_7	1	*Betula pendula*	3	1	1	1
3_7	10	*Fagus sylvatica*	7	2	1	1
3_7	2	*Betula pendula*	4	2	1	2
3_7	3	*Betula pendula*	20	2	1	1
3_7	4	*Fagus sylvatica*	9	1	1	1
3_7	5	*Betula pendula*	14	1	1	1
3_7	6	*Fagus sylvatica*	9	1	1	1
3_7	7	*Fagus sylvatica*	15	1	1	1
3_7	8	*Fagus sylvatica*	8	1	1	1
3_7	9	*Fagus sylvatica*	9	2	1	1
3_70	1	*Frangula alnus*	15	1	1	1
3_70	10	*Frangula alnus*	16	2	1	1
3_70	2	*Sorbus aucuparia*	13	3	2	2
3_70	3	*Frangula alnus*	28	2	2	2
3_70	4	*Sorbus aucuparia*	7	2	1	2
3_70	5	*Frangula alnus*	24	2	2	1
3_70	6	*Frangula alnus*	11	2	1	1
3_70	7	*Sorbus aucuparia*	10	2	1	1
3_70	8	*Frangula alnus*	8	1	1	2
3_70	9	*Frangula alnus*	22	2	1	1
3_8	1	*Corylus avellana*	45	2	1	2

3_8	10	*Corylus avellana*	21	2	1	2
3_8	2	*Fraxinus excelsior*	37	2	2	2
3_8	3	*Acer pseudoplatanus*	8	1	1	1
3_8	4	*Corylus avellana*	20	2	1	2
3_8	5	*Fraxinus excelsior*	26	2	1	3
3_8	6	*Corylus avellana*	26	2	1	1
3_8	7	*Corylus avellana*	21	3	2	2
3_8	8	*Corylus avellana*	3	2	1	2
3_8	9	*Corylus avellana*	16	2	1	2
3_82	1	*Sorbus aucuparia*	19	2	1	1
3_82	10	*Sorbus aucuparia*	17	1	1	1
3_82	2	*Fagus sylvatica*	37	1	1	1
3_82	3	*Sorbus aucuparia*	19	2	1	1
3_82	4	*Fagus sylvatica*	4	1	1	1
3_82	5	*Fagus sylvatica*	11	2	1	1
3_82	6	*Fagus sylvatica*	20	1	1	1
3_82	7	*Quercus petraea*	18	2	1	1
3_82	8	*Corylus avellana*	8	1	1	1
3_82	9	*Sorbus aucuparia*	6	1	1	1
3_83	1	*Fagus sylvatica*	52	2	2	2
3_83	10	*Fagus sylvatica*	6	2	2	2
3_83	2	*Fagus sylvatica*	4	1	1	2
3_83	3	*Fagus sylvatica*	11	1	1	2
3_83	4	*Fagus sylvatica*	4	1	1	1
3_83	5	*Fagus sylvatica*	4	1	1	2
3_83	6	*Fagus sylvatica*	6	1	1	1
3_83	7	*Fagus sylvatica*	46	1	1	2
3_83	8	*Fagus sylvatica*	9	1	1	2
3_83	9	*Fagus sylvatica*	10	1	1	2
3_84	1	*Fagus sylvatica*	18	3	3	3
3_84	10	*Fagus sylvatica*	6	1	1	1
3_84	2	*Fagus sylvatica*	18	1	1	1
3_84	3	*Fagus sylvatica*	38	2	1	1
3_84	4	*Fagus sylvatica*	12	1	1	1
3_84	5	*Fagus sylvatica*	20	1	1	1
3_84	6	*Fagus sylvatica*	39	1	1	1
3_84	7	*Fagus sylvatica*	36	1	1	1
3_84	8	*Fagus sylvatica*	27	1	1	1

3_84	9	*Fagus sylvatica*	21	1	1	1
3_86	1	*Betula pendula*	22	1	1	1
3_86	10	*Betula pendula*	21	1	1	1
3_86	2	*Betula pendula*	23	2	1	1
3_86	3	*Betula pendula*	5	1	1	1
3_86	4	*Betula pendula*	7	1	1	1
3_86	5	*Betula pendula*	8	2	1	1
3_86	6	*Betula pendula*	15	1	1	1
3_86	7	*Betula pendula*	8	2	1	1
3_86	8	*Betula pendula*	18	2	1	1
3_86	9	*Betula pendula*	21	1	1	1
3_87	1	*Sorbus aucuparia*	21	2	1	2
3_87	10	*Betula pendula*	62	1	1	1
3_87	2	*Sorbus aucuparia*	24	2	1	2
3_87	3	*Betula pendula*	13	1	1	1
3_87	4	*Betula pendula*	33	1	2	1
3_87	5	*Sorbus aucuparia*	41	2	1	1
3_87	6	*Betula pendula*	23	1	1	1
3_87	7	*Betula pendula*	6	1	1	1
3_87	8	*Sorbus aucuparia*	29	2	1	2
3_87	9	*Betula pendula*	44	1	1	2
3_88	1	*Acer platanoides*	16	1	1	1
3_88	10	*Fraxinus excelsior*	37	1	3	3
3_88	2	*Acer pseudoplatanus*	24	2	1	1
3_88	3	*Acer platanoides*	32	1	1	1
3_88	4	*Betula pendula*	25	2	1	1
3_88	5	*Acer platanoides*	34	1	1	1
3_88	6	*Fraxinus excelsior*	30	2	2	1
3_88	7	*Acer platanoides*	35	1	1	1
3_88	8	*Quercus petraea*	10	2	2	
3_88	9	*Acer pseudoplatanus*	13	2	1	
3_89	1	*Acer pseudoplatanus*	22	1	1	2
3_89	10	*Fagus sylvatica*	68	1	1	
3_89	2	*Sorbus aucuparia*	34	3	2	3
3_89	3	*Sorbus aucuparia*	10	3	1	2
3_89	4	*Acer pseudoplatanus*	36	2	1	1
3_89	5	*Sorbus aucuparia*	22	2	2	2
3_89	6	*Sorbus aucuparia*	17	3	3	

3_89	7	*Sorbus aucuparia*	28	3	3	3
3_89	8	*Acer pseudoplatanus*	39	1	1	1
3_89	9	*Acer pseudoplatanus*	28	2	1	1
3_9	1	*Tilia cordata*	13	2	1	1
3_9	10	*Sambucus nigra*	31	3	2	2
3_9	2	*Sambucus nigra*	18	3	2	3
3_9	3	*Tilia cordata*	7	2	1	
3_9	4	*Sambucus nigra*	22	3	2	3
3_9	5	*Corylus avellana*	3	1		2
3_9	6	*Tilia cordata*	33	2	1	1
3_9	7	*Tilia cordata*	14	2	1	1
3_9	8	*Tilia cordata*	42	2	1	2
3_9	9	*Ulmus glabra*	19	2	1	2
3_90	1	*Fagus sylvatica*	42	1	1	1
3_90	10	*Fagus sylvatica*	30	1	1	1
3_90	2	*Fagus sylvatica*	8	1	1	1
3_90	3	*Betula pendula*	10	1	1	1
3_90	4	*Fagus sylvatica*	5	1	1	1
3_90	5	*Fagus sylvatica*	39	1	1	1
3_90	6	*Fagus sylvatica*	36	1	1	1
3_90	7	*Fagus sylvatica*	28	1	1	1
3_90	8	*Fagus sylvatica*	37	1	1	1
3_90	9	*Fagus sylvatica*	42	1	1	1
3_91	1	*Fagus sylvatica*	18	2	2	2
3_91	10	*Fagus sylvatica*	22	1	1	
3_91	2	*Fagus sylvatica*	18	2	2	2
3_91	3	*Fagus sylvatica*	22	3	3	3
3_91	4	*Fagus sylvatica*	17	2	2	2
3_91	5	*Fagus sylvatica*	9	1	1	
3_91	6	*Fagus sylvatica*	17	2	1	
3_91	7	*Fagus sylvatica*	32	2	1	1
3_91	8	*Fagus sylvatica*	23	2	2	1
3_91	9	*Fagus sylvatica*	26	3	3	3
3_92	1	*Prunus avium*	17	2	2	1
3_92	10	*Fraxinus excelsior*	29	3	3	
3_92	2	*Fraxinus excelsior*	25	2	2	2
3_92	3	*Prunus avium*	26	1	1	1
3_92	4	*Fraxinus excelsior*	26	2	2	1

3_92	5	*Prunus avium*	27	2	1	1
3_92	6	*Fraxinus excelsior*	15	2	2	2
3_92	7	*Prunus avium*	14	2	2	1
3_92	8	*Fraxinus excelsior*	21	2	2	1
3_92	9	*Fraxinus excelsior*	13	2	1	1
3_93	1	*Quercus petraea*	45	1	1	1
3_93	10	*Quercus petraea*	30	1	2	1
3_93	2	*Quercus petraea*	49	2	1	1
3_93	3	*Fagus sylvatica*	65	2	1	1
3_93	4	*Fagus sylvatica*	40	2	1	1
3_93	5	*Quercus petraea*	25	2	1	1
3_93	6	*Quercus petraea*	34	2	1	1
3_93	7	*Quercus petraea*	27	1	1	1
3_93	8	*Quercus petraea*	28	1	1	1
3_93	9	*Fagus sylvatica*	6	1	1	1
3_94	1	*Fagus sylvatica*	9	2	1	1
3_94	10	*Fagus sylvatica*	7	2	1	1
3_94	2	*Fagus sylvatica*	3	1	1	1
3_94	3	*Fagus sylvatica*	7	2	1	1
3_94	4	*Fagus sylvatica*	28	2	1	1
3_94	5	*Fagus sylvatica*	17	2	1	1
3_94	6	*Fagus sylvatica*	24	1	1	1
3_94	7	*Fagus sylvatica*	14	2	1	1
3_94	8	*Fagus sylvatica*	5	2	1	1
3_94	9	*Fagus sylvatica*	7	1	1	1
3_95	1	*Quercus petraea*	17	2	1	
3_95	10	*Carpinus betulus*	30	2	1	
3_95	2	*Fagus sylvatica*	17	1	1	
3_95	3	*Fagus sylvatica*	36	1	1	
3_95	4	*Acer pseudoplatanus*	5	2	1	1
3_95	5	*Acer pseudoplatanus*	19	1	1	1
3_95	6	*Quercus petraea*	19	2	1	
3_95	7	*Fagus sylvatica*	45	1	1	
3_95	8	*Fagus sylvatica*	31	1	1	1
3_95	9	*Quercus petraea*	9	2	1	
3_96	1	*Carpinus betulus*	29	2	1	2
3_96	10	*Carpinus betulus*	55	2	1	1
3_96	2	*Fagus sylvatica*	38	2	1	1

3_96	3	*Carpinus betulus*	23	2	1	1
3_96	4	*Sorbus aucuparia*	28	2	1	1
3_96	5	*Carpinus betulus*	24	2	1	1
3_96	6	*Carpinus betulus*	39	2	1	1
3_96	7	*Carpinus betulus*	45	2	1	1
3_96	8	*Quercus petraea*	29	2	1	1
3_96	9	*Carpinus betulus*	24	2	1	1
3_97	1	*Fagus sylvatica*	60	1	1	1
3_97	10	*Carpinus betulus*	24	3	1	1
3_97	2	*Fagus sylvatica*	5	2	1	1
3_97	3	*Carpinus betulus*	11	2	1	1
3_97	4	*Carpinus betulus*	6	2	1	1
3_97	5	*Carpinus betulus*	9	2	1	1
3_97	6	*Fagus sylvatica*	2	2	1	1
3_97	7	*Carpinus betulus*	19	2	1	1
3_97	8	*Fagus sylvatica*	19	1	1	1
3_97	9	*Carpinus betulus*	8	3	1	
3_98	1	*Quercus robur*	27	2	2	1
3_98	10	*Quercus petraea*	47	2	1	1
3_98	2	*Sorbus torminalis*	42	1	1	1
3_98	3	*Fagus sylvatica*	48	2	1	1
3_98	4	*Fagus sylvatica*	20	2	1	1
3_98	5	*Quercus petraea*	25	1	2	1
3_98	6	*Prunus avium*	6	2	1	
3_98	7	*Sorbus aucuparia*	16	2	1	2
3_98	8	*Quercus petraea*	41	2	1	1
3_98	9	*Quercus petraea*	40	1	1	1
3_99	1	*Acer pseudoplatanus*	16	2	1	1
3_99	10	*Acer campestre*	5	1	1	
3_99	2	*Acer pseudoplatanus*	18	1	1	1
3_99	3	*Acer campestre*	10	1	1	1
3_99	4	*Acer campestre*	34	1	1	1
3_99	5	*Corylus avellana*	36	2	1	1
3_99	6	*Acer pseudoplatanus*	26	2	1	1
3_99	7	*Acer pseudoplatanus*	10	2	1	2
3_99	8	*Acer pseudoplatanus*	9	1	1	1
3_99	9	*Acer platanoides*	11	1	1	1
5_10	1	*Betula pendula*	11	2	2	2

5_10	10	*Betula pendula*	30	1	2	2
5_10	2	*Rhamnus carthaticus*	20	2	2	2
5_10	3	*Betula pendula*	18	2	2	2
5_10	4	*Rhamnus carthaticus*	18	1	2	2
5_10	5	*Betula pendula*	20	2	2	3
5_10	6	*Betula pendula*	30	2	2	
5_10	7	*Betula pendula*	25	2	1	1
5_10	8	*Rhamnus carthaticus*	22	2	2	2
5_10	9	*Betula pendula*	14	2	2	2
5_12	1	*Fagus sylvatica*	43	2	1	1
5_12	2	*Carpinus betulus*	65	2	1	1
5_12	3	*Fagus sylvatica*	23	1	1	1
5_12	4	*Rhamnus carthaticus*	6	2	1	2
5_12	5	*Carpinus betulus*	33	1	1	1
5_12	6	*Fagus sylvatica*	37	1	1	1
5_12	7	*Carpinus betulus*	37	1	2	1
5_12	8	*Fagus sylvatica*	38	1	1	1
5_2	1	*Ulmus glabra*	58	2	1	2
5_2	10	*Ulmus glabra*	25	2	1	1
5_2	2	*Ulmus glabra*	35	2	1	
5_2	3	*Ulmus glabra*	65	2	1	2
5_2	4	*Ulmus glabra*	50	3	1	1
5_2	5	*Ulmus glabra*	40	2	1	1
5_2	6	*Ulmus glabra*	25	2	1	2
5_2	7	*Ulmus glabra*	25	2	1	1
5_2	8	*Fraxinus excelsior*	35	3	3	
5_2	9	*Ulmus glabra*	15	2	1	2
5_3	1	*Cornus sanguinea*	35	2	1	1
5_3	2	*Fraxinus excelsior*	40	2	1	2
5_3	3	*Ulmus glabra*	30	2	1	1
5_3	4	*Ulmus glabra*	30	2	1	1
5_3	5	*Fraxinus excelsior*	20	1	1	1
5_3	6	*Ulmus glabra*	40	2	1	1
5_3	7	*Crataegus spec.*	40	2	1	1
5_3	8	*Ulmus glabra*	20	2	1	1
5_3	9	*Fraxinus excelsior*	15	1	1	2
5_4	1	*Fagus sylvatica*	20	2	2	2
5_4	10	*Fagus sylvatica*	23	2	2	2

5_4	2	*Fagus sylvatica*	37	2	1	1
5_4	3	*Carpinus betulus*	8	1	1	1
5_4	4	*Carpinus betulus*	20	2	2	2
5_4	5	*Corylus avellana*	20	2		3
5_4	6	*Carpinus betulus*	14	2	1	2
5_4	7	*Fagus sylvatica*	27	2	1	1
5_4	8	*Carpinus betulus*	20	2	1	
5_4	9	*Malus sylvestris*	15	3	3	3
5_6	1	*Frangula alnus*	16	2	1	1
5_6	10	*Frangula alnus*	31	2	1	1
5_6	2	*Frangula alnus*	30	2	1	1
5_6	3	*Sorbus aucuparia*	31	2	2	2
5_6	4	*Quercus robur*	25	1	1	1
5_6	5	*Prunus serotina*	33	3	3	3
5_6	6	*Sorbus aucuparia*	21	2	2	2
5_6	7	*Frangula alnus*	33	3	3	3
5_6	8	*Quercus robur*	27	2	2	2
5_6	9	*Frangula alnus*	32	2	1	2
5_7	1	*Sorbus aucuparia*	26	2	2	1
5_7	10	*Corylus avellana*	20	2	1	1
5_7	2	*Sambucus nigra*	21	2	3	3
5_7	3	*Corylus avellana*	14	2	1	2
5_7	4	*Quercus robur*	35	2	2	1
5_7	5	*Sorbus aucuparia*	25	2	1	1
5_7	6	*Prunus serotina*	31	2	2	2
5_7	7	*Crataegus spec.*	33	2	2	1
5_7	8	*Sambucus nigra*	35	2	2	2
5_7	9	*Crataegus spec.*	50	1	2	2
5_8	1	*Fagus sylvatica*	50	1	1	1
5_8	2	*Fagus sylvatica*	36	2	2	2
5_8	3	*Fagus sylvatica*	22	2	2	3
5_8	4	*Fagus sylvatica*	70	2	2	2
5_8	5	*Fagus sylvatica*	40	1	1	1
5_8	6	*Fagus sylvatica*	17	2	1	1
5_9	1	*Acer pseudoplatanus*	30	1	1	
5_9	10	*Acer spec.*	34	1	1	1
5_9	2	*Acer pseudoplatanus*	45	1	1	1
5_9	3	*Sorbus aucuparia*	47	1	1	2

5_9	4	*Sambucus nigra*	28	1	2	1
5_9	5	*Acer pseudoplatanus*	28	1	1	1
5_9	6	*Acer pseudoplatanus*	45	1	1	1
5_9	7	*Prunus avium*	40	2	1	1
5_9	8	*Acer pseudoplatanus*	13	2	1	1
5_9	9	*Sorbus aucuparia*	23	1	2	2

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8. Appendix

In the appendix, the database used in subchapter 3.6.2 is presented (Table A1). In addition, I listed my publications and manuscripts not included in the dissertation. The talks and posters I presented at national and international scientific conferences are listed under "Other Academic Activities", in Subsection 8.3. Furthermore, I included my teaching activities, participation in summer schools, and my activities as a scientific reviewer for peer-reviewed journals while working on my dissertation (Subsection 8.3).

8.1. Database on treeline dynamics in Europe

Table A1. Database used for the analysis of treeline dynamics in Europe (Section 3.6.2).

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Aakala et al. 2014	Scandes	Advance	1.17	60	400	Pinaceae	altitudinal	67.7300	29.6300
Ameztegui et al. 2016	Pyrenees	Advance	0.80	50	2300	Pinaceae	altitudinal	42.5725	0.9297
Ameztegui et al. 2016	Pyrenees	Stationary	0.00	50	2300	Pinaceae	altitudinal	42.4386	1.5931
Arekhi et al. 2018	Tourus	Advance	2.50	43	2442	Pinaceae	altitudinal	37.2449	34.4706
Aune et al. 2011	Scandes	Advance	NA	120	306	Betulaceae	altitudinal	69.1200	17.1900
Aune et al. 2011	Scandes	Stationary	0.00	120	310	Betulaceae	altitudinal	70.2700	24.4700
Aune et al. 2011	Scandes	Stationary	0.00	120	348	Betulaceae	altitudinal	69.5500	25.1300
Aune et al. 2011	Scandes	Stationary	0.00	90	626	Betulaceae	altitudinal	68.5100	19.4200
Aune et al. 2011	Scandes	Stationary	0.00	90	244	Betulaceae	altitudinal	68.5000	34.4400
Aune et al. 2011	Scandes	Advance	NA	50	534	Betulaceae	altitudinal	67.4200	33.4600
Autio 2006	Scandes	Advance	NA	4	473	Mixed	altitudinal	67.5000	27.0400
Autio 2006	Scandes	Stationary	0.00	4	450	Mixed	altitudinal	67.5000	27.0400
Batllori & Guiterrez 2007	Pyrenees	Advance	NA	50	2329	Pinaceae	altitudinal	42.3100	0.4500
Batllori & Guiterrez 2008	Pyrenees	Advance	NA	50	2105	Pinaceae	altitudinal	42.2800	0.4900
Batllori & Guiterrez 2008	Pyrenees	Advance	NA	50	2389	Pinaceae	altitudinal	42.3300	0.5600
Batllori & Guiterrez 2008	Pyrenees	Advance	NA	50	2350	Pinaceae	altitudinal	42.3300	1.2500
Batllori & Guiterrez 2008	Pyrenees	Advance	NA	50	2386	Pinaceae	altitudinal	42.2600	1.3200
Batllori & Guiterrez 2008	Pyrenees	Advance	NA	50	2336	Pinaceae	altitudinal	42.2300	2.0800

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Batllori & Guiterrez 2008	Pyrenees	Stationary	0.00	50	2395	Pinaceae	altitudinal	42.3000	0.5300
Batllori & Guiterrez 2008	Pyrenees	Stationary	0.00	50	2473	Pinaceae	altitudinal	42.3100	1.2100
Batllori & Guiterrez 2008	Pyrenees	Stationary	0.00	50	2532	Pinaceae	altitudinal	42.3300	1.2300
Batllori & Guiterrez 2008	Pyrenees	Stationary	0.00	50	2356	Pinaceae	altitudinal	42.3400	1.3700
Batllori & Guiterrez 2008	Pyrenees	Stationary	0.00	50	2432	Pinaceae	altitudinal	42.2700	1.4400
Batllori & Guiterrez 2008	Pyrenees	Stationary	0.00	50	2299	Pinaceae	altitudinal	42.2400	2.1900
Bello-Rodríguez et al. 2019	Canary Islands	Advance	1.88	53	2460.00	Pinaceae	altitudinal	28.1998	-16.6571
Bello-Rodríguez et al. 2019	Canary Islands	Advance	1.88	53	2300.00	Pinaceae	altitudinal	28.2275	-16.5799
Beloiu & Beierkuhnlein 2019	Carpathians	Advance	NA	1	2058	Pinaceae	altitudinal	45.3761	22.8904
Beloiu & Beierkuhnlein 2019	Carpathians	Stationary	0.00	1	1820	Pinaceae	altitudinal	45.3372	23.6823
Beloiu et al. 2021	Crete	Stationary	0.00	70	1527	Mixed	altitudinal	35.3355	24.1214
Beloiu et al. 2021	Crete	Stationary	0.00	70	1663	Mixed	altitudinal	35.2818	24.1306
Beloiu et al. 2021	Crete	Stationary	0.00	70	1894	Mixed	altitudinal	35.2661	24.0086
Beloiu et al. 2021	Crete	Stationary	0.00	70	1830	Mixed	altitudinal	35.2738	23.9378
Camarero & Gutierrez 2004	Pyrenees	Advance	0.02	145	2430	Pinaceae	altitudinal	42.2800	-1.3800
Camarero & Gutierrez 2004	Pyrenees	Advance	0.02	145	2360	Pinaceae	altitudinal	42.3600	-1.0300
Camarero & Gutierrez 2004	Pyrenees	Stationary	0.00	145	2110	Pinaceae	altitudinal	42.3700	-0.0200
Camarero & Gutierrez 2007	Pyrenees	Advance	NA	48	2040	Pinaceae	altitudinal	42.0100	2.4400
Compostella & Caccianiga 2017	Alps	Advance	NA	100	2350	Pinaceae	altitudinal	46.3600	10.4800
Compostella & Caccianiga 2017	Alps	Advance	NA	100	2320	Pinaceae	altitudinal	46.4000	10.5700
Compostella & Caccianiga 2017	Alps	Advance	NA	100	2320	Pinaceae	altitudinal	46.3600	10.5000

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Compostella & Caccianiga 2017	Alps	Stationary	0.00	100	2320	Pinaceae	altitudinal	46.2700	10.5000
Compostella & Caccianiga 2017	Alps	Stationary	0.00	100	2300	Pinaceae	altitudinal	46.2900	10.5500
Compostella & Caccianiga 2017	Alps	Stationary	0.00	100	2340	Pinaceae	altitudinal	46.2900	10.5100
Compostella & Caccianiga 2017	Apennines	Stationary	0.00	100	1725	Fagaceae	altitudinal	44.2900	10.3900
Compostella & Caccianiga 2017	Apennines	Stationary	0.00	100	1713	Fagaceae	altitudinal	44.2800	10.4000
Compostella & Caccianiga 2017	Apennines	Stationary	0.00	100	1724	Fagaceae	altitudinal	44.2800	10.3800
Compostella & Caccianiga 2017	Apennines	Stationary	0.00	100	1765	Fagaceae	altitudinal	44.2900	10.3800
Compostella & Caccianiga 2018	Apennines	Stationary	0.00	100	1720	Fagaceae	altitudinal	44.2900	10.4000
Dai et al. 2017	Apennines	Advance	1.21	53	2587	Pinaceae	altitudinal	42.1188	14.1252
Dai et al. 2017	Apennines	Advance	0.66	53	2640	Pinaceae	altitudinal	42.0986	14.0691
Dalen & Hofgaard 2005	Scandes	Retreat	NA	100	423	Betulaceae	altitudinal	69.4000	23.5800
Dalen & Hofgaard 2005	Scandes	Retreat	NA	100	791	Betulaceae	altitudinal	69.4000	23.5800
Dalen & Hofgaard 2005	Scandes	Retreat	NA	100	460	Betulaceae	altitudinal	69.4000	23.5800
Dalen & Hofgaard 2005	Scandes	Retreat	NA	100	772	Betulaceae	altitudinal	69.4000	23.5800
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	1140	Betulaceae	altitudinal	68.1000	18.8500
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	698	Betulaceae	altitudinal	68.1000	18.8500
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	1156	Betulaceae	altitudinal	68.1000	18.8500
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	740	Betulaceae	altitudinal	68.1000	18.8500
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	1114	Betulaceae	altitudinal	62.1000	9.2300
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	1210	Betulaceae	altitudinal	62.1000	9.2300
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	1121	Betulaceae	altitudinal	62.1000	9.2300

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Dalen & Hofgaard 2005	Scandes	Stationary	0.00	100	700	Betulaceae	altitudinal	62.1000	9.2300
Devi et al. 2020	Ural	Advance	0.43	115	310	Pinaceae	altitudinal	66.9555	65.8007
Devi et al., 2008	Ural	Advance	0.396	100	299	Betulaceae	altitudinal	66.81	65.58
Diaz-Varela et al. 2010	Alps	Advance	2.36	46	2100	Pinaceae	altitudinal	46.2637	9.6269
Diaz-Varela et al. 2010	Alps	Retreat	-2.56	46	2108	Pinaceae	altitudinal	46.2273	9.5882
Didier 2001	Alps	Stationary	0.00	51	1500	Pinaceae	altitudinal	45.1600	6.4800
Dinca et al. 2017	Alps	Advance	3.86	44	2122	Pinaceae	altitudinal	46.9031	13.7276
Dinca et al. 2017	Carpathians	Advance	2.18	44	1580	Mixed	altitudinal	48.9464	19.6019
Dinca et al. 2017	Carpathians	Advance	2.14	44	1884	Pinaceae	altitudinal	45.2878	22.8573
Dinca et al. 2017	Pyrenees	Advance	0.73	44	2145	Pinaceae	altitudinal	42.6400	-0.0161
Dullinger et al. 2003	Alps	Advance	NA	50	1900	Pinaceae	altitudinal	47.4000	15.5000
Esper & Schweingruber 2004	Ural	Advance	NA	100	950	Pinaceae	latitudinal	61.2600	59.4300
Feuillet et al. 2020	Pyrenees	Advance	0.73	62	2300	Pinaceae	altitudinal	42.5185	2.4518
Fomin et al. 2020	Ural	Advance	NA	55	286	Pinaceae	latitudinal	66.8196	65.5391
Gehrig-Fasel et al. 2007	Alps	Advance	NA	12	2450	Mixed	altitudinal	46.1200	7.3000
Gervais & MacDonald 2000	Scandes	Advance	NA	107	300	Pinaceae	latitudinal	68.2400	35.1600
Grace & Norton 1990	Scotland	Stationary	0.00	85	600	Mixed	altitudinal	57.0800	-3.5000
Hagedorn et al. 2014	Ural	Advance	0.53	57	1586	Mixed	latitudinal	54.5000	58.8167
Hagedorn et al. 2014	Ural	Advance	0.86	49	1569	Mixed	latitudinal	59.5000	59.0000
Hagedorn et al. 2014	Ural	Advance	0.69	42	1236	Mixed	latitudinal	66.7833	65.4333
Hagedorn et al. 2014	Ural	Advance	0.79	39	1608	Mixed	latitudinal	63.5087	59.4555

Study ID	Location	Dynamics	Shift (m/y)	Study duration (year)	Elevation max (masl)	Species family	Treeline type	Lat °	Long °
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2140	Pinaceae	altitudinal	46.6000	10.0000
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2300	Pinaceae	altitudinal	46.7000	10.1000
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2200	Pinaceae	altitudinal	46.8000	10.2000
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2250	Pinaceae	altitudinal	46.4000	9.8000
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2110	Pinaceae	altitudinal	46.6000	9.7000
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2150	Pinaceae	altitudinal	46.2000	7.5000
Hättenschwiler & Körner 1995	Alps	Stationary	0.00	9	2300	Pinaceae	altitudinal	46.0000	7.0000
Hedenås et al. 2011	Scandes	Advance	NA	13		Betulaceae	altitudinal	68.2000	18.5000
Hofgaard 1997	Scandes	Stationary	0.00	55	650	Betulaceae	altitudinal	64.4000	15.5000
Hofgaard et al. 1991	Scandes	Advance	NA	29	1170	Pinaceae	altitudinal	62.3000	8.5000
Hofgaard et al. 2013	Scandes	Advance	340.00	95	360	Betulaceae	latitudinal	70.0781	24.7492
Hofgaard et al. 2013	Scandes	Advance	2.29	95	150	Pinaceae	latitudinal	70.3160	25.6419
Jonsson 2004	Iceland	Stationary	0.00	80	200	Betulaceae	latitudinal	65.5647	-17.7773
Juntunen et al. 2002	Scandes	Advance	NA	16	275	Pinaceae	altitudinal	69.4000	26.5800
Juntunen et al. 2002	Scandes	Advance	NA	16	410	Pinaceae	altitudinal	66.1300	28.3300
Juntunen et al. 2002	Scandes	Stationary	0.00	16	420	Pinaceae	altitudinal	68.0200	24.0500
Juntunen et al. 2002	Scandes	Stationary	0.00	16	465	Pinaceae	altitudinal	67.3400	24.1100
Kern & Popa 2008	Carpathians	Advance	1.00	96	1902	Pinaceae	altitudinal	47.0984	25.2356
Kjällgren & Kullman 1998	Scandes	Advance	NA	55	948	Betulaceae	altitudinal	63.0000	13.0000
Kjällgren & Kullman 1998	Scandes	Advance	NA	55	920	Betulaceae	altitudinal	63.0000	13.0000
Kjällgren & Kullman 1998	Scandes	Advance	NA	55	920	Betulaceae	altitudinal	63.0000	13.0000

Study ID	Location	Dynamics	Shift (m/y)	Study duration (year)	Elevation max (masl)	Species family	Treeline type	Lat °	Long °
Kjällgren & Kullman 1998	Scandes	Advance	NA	55	895	Betulaceae	altitudinal	63.0000	13.0000
Kullman & Öberg, 2009	Scandes	Advance	0.978	92	820	Pinaceae	altitudinal	62.25	12.61
Kullman & Öberg, 2009	Scandes	Advance	0.806	92	720	Pinaceae	altitudinal	62.25	12.61
Kullman & Öberg, 2009	Scandes	Advance	0.741	92	800	Betulaceae	altitudinal	62.25	12.61
Kullman 1986	Scandes	Advance	0.819	60	910	Pinaceae	altitudinal	62.63	12.8
Kullman 1993a	Scandes	Advance	3.125	16	700	Pinaceae	altitudinal	62.7300	12.7500
Kullman 1993a	Scandes	Advance	2.812	16	700	Pinaceae	altitudinal	62.5700	12.2700
Kullman 1993a	Scandes	Advance	2.5	16	700	Pinaceae	altitudinal	63.2000	12.2000
Kullman 1993a	Scandes	Advance	2.5	16	685	Pinaceae	altitudinal	63.2190	12.7793
Kullman 1993a	Scandes	Advance	2.187	16	700	Pinaceae	altitudinal	63.2400	12.4600
Kullman 1993a	Scandes	Advance	1.875	16	700	Pinaceae	altitudinal	63.6900	12.5100
Kullman 1993a	Scandes	Advance	1.25	16	700	Pinaceae	altitudinal	63.2000	12.2900
Kullman 1993a	Scandes	Advance	1.25	16	700	Pinaceae	altitudinal	63.1800	12.3100
Kullman 1993a	Scandes	Advance	0.937	16	700	Pinaceae	altitudinal	62.5500	14.2300
Kullman 1993a	Scandes	Advance	0.937	16	700	Pinaceae	altitudinal	63.1800	12.4300
Kullman 1993a	Scandes	Advance	0.937	16	700	Pinaceae	altitudinal	63.1900	12.9300
Kullman 1993a	Scandes	Advance	0.625	16	700	Pinaceae	altitudinal	63.3100	12.3600
Kullman 1993a	Scandes	Advance	0.625	16	700	Pinaceae	altitudinal	63.1600	12.4100
Kullman 1993a	Scandes	Advance	0.625	16	700	Pinaceae	altitudinal	63.2000	14.4600
Kullman 1993a	Scandes	Stationary	0.00	16	860	Pinaceae	altitudinal	63.1840	12.3522
Kullman 1993a	Scandes	Stationary	0.00	16	700	Pinaceae	altitudinal	63.3500	12.1000

Study ID	Location	Dynamics	Shift (m/y)	Study duration (year)	Elevation max (masl)	Species family	Treeline type	Lat °	Long °
Kullman 1993a	Scandes	Stationary	0.00	16	700	Pinaceae	altitudinal	63.2000	12.1800
Kullman 1993a	Scandes	Stationary	0	16	700	Pinaceae	altitudinal	63.2000	12.2300
Kullman 1993a	Scandes	Stationary	0	16	700	Pinaceae	altitudinal	63.2400	12.3200
Kullman 1993a	Scandes	Stationary	0	16	700	Pinaceae	altitudinal	62.8700	12.8600
Kullman 1993a	Scandes	Stationary	0	16	700	Pinaceae	altitudinal	62.5700	12.2700
Kullman 1993b	Scandes	Advance	NA	20	915	Betulaceae	altitudinal	63.1000	12.2100
Kullman 1996	Scandes	Advance	NA	9	891	Mixed	altitudinal	63.1500	12.2600
Kullman 2000	Scandes	Advance	0.36	84	1090	Betulaceae	altitudinal	61.5800	12.5200
Kullman 2001	Scandes	Advance	0.80	60	1100	Mixed	altitudinal	62.2000	13.3500
Kullman 2002	Scandes	Advance	7.50	50	1370	Rosaceae	altitudinal	63.4284	13.1031
Kullman 2002	Scandes	Advance	6.80	50	1375	Pinaceae	altitudinal	63.4281	13.1027
Kullman 2002	Scandes	Advance	6.30	50	1410	Betulaceae	altitudinal	63.4333	13.1000
Kullman 2002	Scandes	Advance	4.80	50	1410	Pinaceae	altitudinal	63.4315	13
Kullman 2002	Scandes	Advance	2.40	50	1390	Salicaceae	altitudinal	63.4281	13.1027
Kullman 2003	Scandes	Advance	1.25	60	880	Betulaceae	altitudinal	63.1300	12.2300
Kullman 2004	Scandes	Advance	1.59	88	975	Pinaceae	altitudinal	62.0700	12.2700
Kullman 2004	Scandes	Advance	1.53	88	115	Pinaceae	altitudinal	61.5500	12.5300
Kullman 2004	Scandes	Advance	1.14	88	975	Pinaceae	altitudinal	62.0400	12.2500
Kullman 2004	Scandes	Advance	0.97	88	1090	Betulaceae	altitudinal	61.5900	12.5100
Kullman 2005	Scandes	Advance	1.63	89	940	Pinaceae	altitudinal	61.3800	12.4000
Kullman 2005	Scandes	Advance	1.24	89	930	Pinaceae	altitudinal	61.3800	12.4000

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Kullman 2005	Scandes	Advance	0.79	89	940	Betulaceae	altitudinal	61.3800	12.4000
Kullman 2005	Scandes	Advance	NA	50	670	Pinaceae	altitudinal	63.1400	12.2500
Kullman 2007	Scandes	Advance	1.46	89	940	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.29	89	920	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.24	89	920	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.18	89	935	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.12	89	915	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.12	89	920	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.07	89	930	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.07	89	890	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.07	89	930	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	1.01	89	890	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	0.96	89	890	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2007	Scandes	Advance	0.90	89	890	Betulaceae	altitudinal	63.1100	12.1900
Kullman 2018	Scandes	Advance	2.21	97	945	Betulaceae	altitudinal	63.1833	12.3167
Kullman 2018	Scandes	Advance	1.40	97	755	Betulaceae	altitudinal	63.1646	12.2842
Kullman 2018	Scandes	Advance	1.03	97	830	Pinaceae	altitudinal	63.1646	12.2842
Kullman 2018	Scandes	Advance	0.77	97	775	Pinaceae	altitudinal	63.1646	12.2842
Leonelli et al., 2011	Alps	Advance	1.16	99	2505	Pinaceae	altitudinal	45.79	7.36
Linderholm 2002	Scandes	Stationary	0.00	96	700	Pinaceae	altitudinal	63.1000	13.0500
Martazinova et al. 2011	Carpathians	Advance	0.66	70	1393	Pinaceae	altitudinal	48.6408	23.2362

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Martazinova et al. 2011	Carpathians	Advance	0.50	70	1448	Pinaceae	altitudinal	48.0100	24.4000
Martazinova et al. 2011	Carpathians	Advance	0.36	70	1370	Pinaceae	altitudinal	48.1500	24.4900
Martazinova et al. 2011	Carpathians	Advance	0.13	70	1105	Pinaceae	altitudinal	48.1612	24.3878
Martazinova et al. 2011	Carpathians	Retreat	-0.20	70	1169	Pinaceae	altitudinal	49.0500	22.3400
Mathisen et al., 2014	Ural	Advance	0.57	50	535	Betulaceae	latitudinal	67.7	33.77
Mathisen et al., 2014	Ural	Advance	0.53	50	400	Pinaceae	latitudinal	67.7	33.23
Meshinev et al. 2000	Balkans	Advance	3.02	43	2100	Pinaceae	altitudinal	42.7530	24.4102
Middleton et al. 2008	Scandes	Advance	1.785	56	510	Pinaceae	altitudinal	67.9884	24.1688
Middleton et al. 2009	Scandes	Advance	1.07	56	510	Betulaceae	altitudinal	67.9918	24.1647
Mietkiewicz et al. 2017	Alps	Advance	0.89	100	2160	Pinaceae	altitudinal	46.6880	9.7954
Mietkiewicz et al. 2017	Alps	Stationary	0.00	100	2160	Pinaceae	altitudinal	46.7473	9.9105
Mihai et al. 2007	Carpathians	Advance	0.14	16	2100	Pinaceae	altitudinal	45.4588	24.9385
Moiseev & Shiyatov, 2003	Ural	Advance	1.142	70	1330	Pinaceae	altitudinal	54.3200	58.5100
Moiseev & Shiyatov, 2003	Ural	Advance	1.142	70	1330	Pinaceae	altitudinal	66.4600	65.3600
Moiseev & Shiyatov, 2003	Ural	Advance	0.985	70	1330	Pinaceae	altitudinal	54.5300	58.8500
Moiseev & Shiyatov, 2003	Ural	Advance	0.571	70	1330	Pinaceae	altitudinal	54.3200	58.5100
Moiseev & Shiyatov, 2003	Ural	Advance	NA	35	1330	Pinaceae	altitudinal	66.5500	65.4900
Motta & Nola 2001	Alps	Advance	NA	90	2489	Pinaceae	altitudinal	44.3700	7.0500
Motta et al. 2002	Alps	Advance	NA	94	1980	Mixed	altitudinal	46.1700	11.4400
Motta et al. 2002	Alps	Stationary	0.00	94	1890	Mixed	altitudinal	46.1700	11.4500
Nicolussi et al 2005	Alps	Advance	0.5	130	2285	Pinaceae	altitudinal	46.5200	10.4400

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Normark 2012	Scandes	Advance	0.76	98	100	Betulaceae	altitudinal	69.6407	19.0631
Öberg & Kullman 2012	Scandes	Advance	11.25	4	975	Betulaceae	altitudinal	63.1200	12.2100
Öberg & Kullman 2012	Scandes	Advance	10	4	975	Betulaceae	altitudinal	63.1000	12.1900
Öberg & Kullman 2012	Scandes	Advance	7.5	4	970	Betulaceae	altitudinal	62.4400	12.4400
Öberg & Kullman 2012	Scandes	Advance	6.25	4	870	Betulaceae	altitudinal	63.1300	12.1300
Öberg & Kullman 2012	Scandes	Advance	6.25	4	930	Betulaceae	altitudinal	63.1400	12.2000
Öberg & Kullman 2012	Scandes	Advance	5	4	950	Betulaceae	altitudinal	63.1000	12.1800
Öberg & Kullman 2012	Scandes	Advance	3.75	4	975	Betulaceae	altitudinal	63.1100	12.1000
Öberg & Kullman 2012	Scandes	Advance	3.75	4	845	Betulaceae	altitudinal	63.1700	12.0200
Öberg & Kullman 2012	Scandes	Advance	3.75	4	905	Betulaceae	altitudinal	63.1000	12.2000
Öberg & Kullman 2012	Scandes	Advance	3.75	4	985	Betulaceae	altitudinal	63.1000	12.2400
Öberg & Kullman 2012	Scandes	Advance	3.75	4	1025	Betulaceae	altitudinal	63.0900	12.2400
Öberg & Kullman 2012	Scandes	Advance	3.75	4	920	Betulaceae	altitudinal	63.0900	12.1900
Öberg & Kullman 2012	Scandes	Advance	2.5	4	825	Betulaceae	altitudinal	63.1300	12.1300
Öberg & Kullman 2012	Scandes	Advance	2.5	4	940	Betulaceae	altitudinal	63.1200	12.2700
Öberg & Kullman 2012	Scandes	Advance	1.25	4	730	Betulaceae	altitudinal	63.1800	12.2100
Öberg & Kullman 2012	Scandes	Advance	1.25	4	930	Betulaceae	altitudinal	63.1200	12.2200
Öberg & Kullman 2012	Scandes	Advance	1.25	4	975	Betulaceae	altitudinal	63.1300	12.2100
Öberg & Kullman 2012	Scandes	Advance	1.25	4	845	Betulaceae	altitudinal	63.0800	13.0200
Öberg & Kullman 2012	Scandes	Advance	1.25	4	925	Betulaceae	altitudinal	63.0900	12.1900
Öberg & Kullman 2012	Scandes	Advance	1.25	4	950	Betulaceae	altitudinal	62.4400	12.4400

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Öberg & Kullman 2012	Scandes	Advance	1.25	4	1100	Betulaceae	altitudinal	61.5800	12.5100
Öberg & Kullman 2012	Scandes	Stationary	0.00	4	1010	Betulaceae	latitudinal	63.2400	13.0400
Öberg & Kullman 2012	Scandes	Stationary	0	4	845	Betulaceae	latitudinal	63.1700	12.0200
Öberg & Kullman 2012	Scandes	Stationary	0	4	920	Betulaceae	latitudinal	63.1100	12.2700
Öberg & Kullman 2012	Scandes	Stationary	0	4	835	Betulaceae	latitudinal	63.0800	13.0200
Öberg & Kullman 2012	Scandes	Stationary	0	4	940	Betulaceae	latitudinal	63.0500	12.2900
Öberg & Kullman 2012	Scandes	Stationary	0	4	995	Betulaceae	latitudinal	62.5200	12.4200
Öberg & Kullman 2012	Scandes	Stationary	0	4	995	Betulaceae	latitudinal	62.3600	12.2200
Öberg & Kullman 2012	Scandes	Stationary	0	4	1080	Betulaceae	latitudinal	62.3400	12.3400
Öberg & Kullman 2012	Scandes	Stationary	0	4	1085	Betulaceae	latitudinal	62.3300	12.1600
Öberg & Kullman 2012	Scandes	Stationary	0	4	940	Betulaceae	latitudinal	62.2700	13.5700
Öberg & Kullman 2012	Scandes	Stationary	0	4	1135	Betulaceae	latitudinal	62.2500	12.2300
Öberg & Kullman 2012	Scandes	Stationary	0	4	1140	Betulaceae	latitudinal	62.2500	12.2200
Öberg & Kullman 2012	Scandes	Stationary	0	4	980	Betulaceae	latitudinal	62.1600	13.2800
Öberg & Kullman 2012	Scandes	Stationary	0	4	1135	Betulaceae	latitudinal	62.1400	13.3200
Öberg & Kullman 2012	Scandes	Stationary	0	4	1040	Betulaceae	latitudinal	62.1800	13.3300
Öberg & Kullman 2012	Scandes	Stationary	0.00	4	965	Betulaceae	latitudinal	61.5400	12.5200
Öberg & Kullman 2012	Scandes	Stationary	0.00	4	945	Betulaceae	latitudinal	61.3700	12.3800
Öberg & Kullman 2012	Scandes	Stationary	0.00	4	874	Betulaceae	latitudinal	61.1000	13.0700
Öberg & Kullman 2012	Scandes	Retreat	-1.25	4	935	Betulaceae	latitudinal	63.1100	12.2100
Öberg & Kullman 2012	Scandes	Retreat	-1.25	4	1055	Betulaceae	latitudinal	62.3400	12.1700

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Öberg & Kullman 2012	Scandes	Retreat	-3.75	4	1000	Betulaceae	latitudinal	62.1600	13.2800
Öberg & Kullman 2012	Scandes	Retreat	-5	4	965	Betulaceae	latitudinal	62.5600	12.5100
Öberg & Kullman 2012	Scandes	Retreat	-8.75	4	990	Betulaceae	latitudinal	62.3400	12.1800
Paulsen et al. 2000	Alps	Stationary	0.00	216	2320	Pinaceae	altitudinal	46.5000	11.0100
Paulsen et al. 2000	Alps	Stationary	0.00	216	2140	Pinaceae	altitudinal	46.5400	11.0300
Paulsen et al. 2000	Alps	Stationary	0.00	216	2150	Pinaceae	altitudinal	47.2000	11.3000
Paulsen et al. 2000	Alps	Stationary	0.00	216	2370	Pinaceae	altitudinal	46.1200	7.3000
Paulsen et al. 2000	Alps	Stationary	0.00	216	2380	Pinaceae	altitudinal	46.1200	7.3000
Paulsen et al. 2000	Alps	Stationary	0.00	216	2510	Pinaceae	altitudinal	46.1200	7.3000
Paulsen et al. 2000	Alps	Stationary	0.00	216	2100	Pinaceae	altitudinal	46.3200	7.3800
Paulsen et al. 2000	Alps	Stationary	0.00	216	2050	Pinaceae	altitudinal	46.2300	7.0800
Paulsen et al. 2000	Alps	Stationary	0.00	216	2050	Pinaceae	altitudinal	46.2300	7.0800
Pears 1968	Scotland	Advance	NA	7	490	Mixed	altitudinal	57.0600	-3.4900
Pears 1968	Scotland	Stationary	0.00	7	640	Mixed	altitudinal	57.0600	-3.4900
Peñuelas et al. 2007	Pyrenees	Advance	0.37	83	1712	Fagaceae	altitudinal	41.5200	2.1600
Piermattei et al. 2016	Apennines	Advance	NA	1	2060	Pinaceae	altitudinal	42.8100	13.2600
Piermattei et al. 2016	Apennines	Advance	NA	1	1940	Pinaceae	altitudinal	42.4500	13.3800
Piermattei et al. 2016	Apennines	Advance	NA	1	2040	Pinaceae	altitudinal	42.1500	13.6000
Piermattei et al. 2017	Apennines	Advance	NA	1	1920	Pinaceae	altitudinal	42.1500	13.2700
Shiryaev et al., 2019	Ural	Advance	0.426	60	257	Pinaceae	altitudinal	66.92	65.65
Shiyatov 2003	Ural	Advance	0.60	92	350	Pinaceae	latitudinal	66.5000	65.5000

Study ID	**Location**	**Dynamics**	**Shift (m/y)**	**Study duration (year)**	**Elevation max (masl)**	**Species family**	**Treeline type**	**Lat °**	**Long °**
Shiyatov et al. 2005	Ural	Advance	0.670	90	410	Pinaceae	latitudinal	66.8158	65.3933
Shiyatov et al. 2007	Ural	Advance	0.285	90	410	Pinaceae	latitudinal	66.8578	65.6141
Shiyatov & Mazepa 2015	Ural	Advance	0.693	100	340	Pinaceae	altitudinal	66.9	65.73
Šrůtek et al. 2002	Canary Islands	Stationary	0.00	1	2020	Pinaceae	altitudinal	28.3000	-16.6000
Sutinen et al. 2012	Scandes	Advance	0.75	120	475	Pinaceae	altitudinal	67.9967	24.1583
Tomiolo 2008	Alps	Advance	NA	108	2370	Pinaceae	altitudinal	46.1400	10.2600
Tomiolo 2008	Alps	Stationary	0.00	108	2455	Pinaceae	altitudinal	46.1000	9.4300
Treml & Chuman 2015	Carpathians	Advance	0.28	69	1602	Pinaceae	altitudinal	50.0827	17.2304
Treml & Chuman 2015	Carpathians	Advance	0.26	69	1602	Pinaceae	altitudinal	50.7363	15.7398
Truong et al. 2007	Scandes	Advance	NA	1	750	Betulaceae	altitudinal	68.3344	18.5011
Van Bogaert et al. 2011	Scandes	Advance	1.49	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Advance	0.62	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Advance	0.52	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Advance	0.52	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Advance	0.41	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Stationary	0.00	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Stationary	0.00	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Stationary	0.00	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Stationary	0.00	97	700	Betulaceae	altitudinal	68.2500	19.0000
Van Bogaert et al. 2011	Scandes	Retreat	-1.24	97	700	Betulaceae	altitudinal	68.2500	19.0000
Vittoz et al. 2008	Alps	Advance	NA	95	2350	Pinaceae	altitudinal	46.1500	7.4700

Study ID	Location	Dynamics	Shift (m/y)	Study duration (year)	Elevation max (masl)	Species family	Treeline type	Lat °	Long °
Vittoz et al. 2008	Alps	Advance	NA	95	2580	Pinaceae	altitudinal	46.1100	7.5100
Wallentin et al. 2008	Alps	Advance	2.80	52	2093	Mixed	altitudinal	47.0377	10.9397
Zindros et al. 2020	Olympus	Retreat	NA	60	2696	Pinaceae	altitudinal	40.0905	22.3338
Zindros et al. 2020	Olympus	Advance	5.96	60	2696	Pinaceae	altitudinal	40.0193	22.3860

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8.2. List of publications and manuscripts not included in this dissertation

Published:

- Bennett, J.M., Thompson, A., Goia, I., Feldmann, R., Ştefan, V., Bogdan, A., Rakosy, D., **Beloiu, M.**, Biro, I.-B., Bluemel, S., Filip, M., Madaj, A.-M., Martin, A., Passonneau, S., Kalisch, D.P., Scherer, G., & Knight, T.M. 2018. A review of European studies on pollination networks and pollen limitation, and a case study designed to fill in a gap. *AoB PLANTS* 10. https://doi.org/10.1093/aobpla/ply068

- Kattge J, Bönisch G, Díaz S, et al. 2020; contribution, data support: **Beloiu, M.** TRY plant trait database - enhanced coverage and open access. *Glob Chang Biol*. 26(1):119-188. https://doi.org/10.1111/gcb.14904

- Kidane, Y.O., Hoffmann, S., Jaeschke, A., **Beloiu, M.**, Beierkuhnlein, C. 2022. Ericaceous vegetation of the Bale Mountains of Ethiopia will prevail in the face of climate change. *Scientific reports* 12: 1858. https://doi.org/10.1038/s41598-022-05846-z

- Hanz, D.M., **Beloiu, M.,** Wipfler, R., Beierkuhnlein, C., Field, R., Jentsch, A., Vetaas, O.R., & Irl, S.D.H. High intraspecific trait variation in endemic species assemblages along a circuminsular environmental gradient. *Journal of Vegetation Science* 33: e13120. https://doi.org/10.1111/jvs.13120

In preparation:

- Lux, M.A., Hoffmann, S., **Beloiu, M.,** Beierkuhnlein, C. Bioindication and forest drought response: Assessing the relation between Ellenberg Indicator Values and post-drought vitality of temperate forests. *Ecological Processes* (in prep.)

8.3. Other academic activities

In the following, I would like to list some of my academic activities that are directly or indirectly related to my thesis.

Conferences

Parts of this thesis and other scientific work done during the PhD was presented by me at various conferences:

Talk: 02.08.2021 - 06.08.2021 - Annual Meeting of the Ecological Society of America (ESA) Annual Meeting, Harnessing the ecological data revolution, Salt Lake City, Utah, (online), "*Slow sapling recovery leads to mortality rather than acclimation*" Beloiu, M; Stahlmann, R; Beierkuhnlein, C.

Talk: 19.04.2021 – 30.04.2021 - vEGU21, the 23rd EGU General Assembly (online), "*Using high resolution aerial imagery and deep learning to detect tree spatio-temporal dynamics at the treeline*" Beloiu, M.; Poursanidis, D; Hoffmann, S; Chrysoulakis, N; Beierkuhnlein, C.

Talk: 29.10.2020 - BayCEER Workshop 2020, Bayreuth, Germany, (online), "*Drought impacts on Central European forests: the remote sensing perspective*" Beloiu, M; Stahlmann, R; Weiser, F; Beierkuhnlein, C.

Talk: 03.08.2020 - 06.08.2020 - Annual Meeting of the Ecological Society of America (ESA) Annual Meeting, Harnessing the ecological data revolution, Salt Lake City, Utah, (online), "*Surprising recovery of saplings to severe drought in temperate forests*" Beloiu, M; Stahlmann, R; Weiser, F; Beierkuhnlein, C.

Poster: 01.10.2019 - 05.10.2019 - The International Society for Ecological Modelling Global Conference 2019, Salzburg, Austria, "*Differences in the spatial structure of two Pinus cembra L. populations in the Carpathian Mountains*" Beloiu, M; Beierkuhnlein, C.

Talk: 25.09.2019 - 30.09.2019 - Deutscher Kongress für Geographie, Kiel, Germany, "*Spatial patterns of Pinus cembra L. in Carpathian Mountains protected areas*" Beloiu, M; Beierkuhnlein, C.

Talk: 07.04.2019 - 12.04.2019 - 21st European Geosciences Union (EGU) General Assembly, Kiel, Germany, "*Assessing the performance of various machine learning algorithms for forest disturbance mapping*" Sandric, I; Plesoianu, A; Beloiu, M; Carlan, I; Stefan, A.

Talk: 10.01.2019 - IBS, Malagá, Spain, "*From coast to coast -How environment drives functional diversity in an insular system*" Hanz, D; Beloiu, M; Wipfler, R; Beierkuhnlein, C; Field, R; Vetaas, OR; Irl, SDH.

Talk: 21.06.2018 - 22.06.2018 - 27. Anwendertreffen AG GIS-Küste & ESRI Usergroup Küste, Fa. Conterra, Münster, Germany, "*Traits under the magnifying glass - How do environmental gradients drive functional diversity?*" Beloiu, M; Hanz, D; Wipfler, R.

Poster: 28-30.09.2017 - The Second Interdisciplinary Symposium devoted to the Biogeography of the Carpathians, Cluj-Napoca, Romania, "*Vulnerability of Pinus cembra L. in the Carpathian Mountains under the impact of climate change*"

Teaching

- Spatial Ecology
- Modelling of Spatial Ecological Processes
- Foundations of Biogeographical Modelling, a course for M.Sc. Global Change Ecology and others, covering the basics of handling spatial data in R, species distribution modelling, home range estimations, etc.
- Introduction to R, a course for 1st semester M.Sc. Global Change Ecology and others, covering the basics of the statistical programming language R.
- Statistical Modelling with R, a course for 1st semester M.Sc. Global Change Ecology and others, covering statistical tests (e.g., ANOVA) and statistical models from simple linear regression models to more advances GLMER.
- Remote Sensing in Landscape Ecology
- Field Quantification of Biodiversity, field course for students of M.Sc. Global Change Ecology and similar programs, covering the basics of forest inventory, soil sampling, and tree species mapping in different forest types.
- Biogeographie des globalen Wandels (one session)
- Allgemeine Biogeographie (one session)

Science / Summer schools

- 08 - 12.07.2019 **Data and Models in Ecology and Evolution**, Summer school, Institut Pascal - University of Paris-Saclay
- 19 - 24.05.2019 **Functional Traits of Organisms**, Summer school, Porquerolles (Var), France
- 19 - 24.08.2018 **“CARSEQ”: Carbon Sequestration in Forest Ecosystems**, Summer school, Davos, Switzerland
- 03.2018 - **H2020 ECOPOTENTIAL Science School**, La Palma, Canary Islands

Reviewer activities

I peer-reviewed one manuscript for each of the following journals:

- Forests
- Sustainability
- Land

9. Acknowledgment

On our life's journey we meet many people, most of whom pass through our lives only temporarily as we pass through theirs, but they shape our thoughts and influence our development. There is no achievement without failure and no progress without constant dedication. However, having the right people around can help us enormously to move forward on the mountain of knowledge. I am very grateful for all the wonderful people I have met and the opportunities I have had so far to develop into the 2.9 version of myself.

I would like to thank Prof. Dr. Carl Beierkuhnlein for accepting me as a Ph.D. student, allowing me to work on subjects I am passionate about, and giving me the opportunity to teach various courses. I am deeply grateful for the opportunity to learn from him. I particularly appreciate his excellent scientific knowledge and holistic perspectives. I admire that he leads a whole master's programme, Global Change Ecology, which gives students from abroad the opportunity to pursue their dreams. That makes him a great role model for me. As Wilhelm von Humboldt said, "…education is liberty". Hence, I am deeply grateful and fortunate that Prof. Dr. Carl Beierkuhnlein was my Ph.D. supervisor.

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Finally, I would like to thank the examination committee and the reviewers for their constructive feedback and the Graduate School for the financial support that enabled me to attend the summer schools and conferences I wanted.

10. (Eidesstattliche) Versicherungen und Erklärungen

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

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Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.

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Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. –vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.

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Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung der Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.

(§ 8 Satz 2 Nr. 8 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.

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