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Master thesis

*Resistance, resilience and recovery to drought periods in  
European mixed forest stands.*

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## ABSTRACT

The study of how forest tree species react to drought events is becoming more and more important; these stress associated phenomena have increased at accelerated rates in the last decades because of climate change. Therefore, understanding how forest species react, adapt and grow in a limited or prolonged period of drought is important in order to adopt new approaches to forest management, taking in account the occurrence of these stress events.

A many studies have been carried out about reaction to these disruptive periods of pure forest stands, especially composed by productive species such as Norway spruce (*Picea abies* [L.] H. Karst) and European beech (*Fagus sylvatica* L.), by shifting the focus on mixed forest stands, we may amplify our knowledge regarding trees ecological strategies and implementation to cope with drought stress. In particular, how the analysis of tree resistance and resilience can show different response patterns. In our study we measured tree rings on cores from increment boring of 1826 trees of European beech, Norway spruce and silver fir (*Abies alba* Mill.) of mixed forest stands belonging to 28 long-time experimental plots of 8 different European countries. Following, indices for resistance, recovery and resilience were applied to compute short-term drought responses, considering drought events occurring from 1950 to 2016 for most of the samples, and from 1950 to 2010 for Slovakia samples. Thereafter, linear mixed effect analysis was carried out to investigate which ecological factor is key as a driving-covariate for the indices considered. The research was conducted to find out species-specific stress reactions and how they change along an ecological gradient. We showed that Norway spruce performed the highest recovery but the lowest resistance and resilience, whereas conversely, European beech was more resistant and resilient on facing droughts but quite weak in terms of recovery. Differently, Silver fir resulted in high level of recovery, but at the same time, it conserved remarkable performance in both resistance and resilience. We found out also that growth indices are mainly influenced by regional climatic conditions. We further discussed how a trees dimensions and geographical position can partially affect species ecological responses.

## RIASSUNTO

Negli ultimi anni si è assistito ad una crescente attività di ricerca mirata ad analizzare in che misura le specie forestali reagiscono ad eventi di siccità. Ciò è dovuto al fatto che è stato constatato come, negli ultimi decenni, questi fenomeni di stress siano aumentati ad un ritmo accelerato a causa del cambiamento climatico. Difatti, comprendere come le specie forestali reagiscono, si adattano e crescono in un periodo limitato o prolungato di siccità è importante per adottare nuovi approcci di gestione forestale, che dovrebbero tener conto del verificarsi di questi eventi di stress.

Poiché molti studi sono stati condotti per determinare come soprassuoli forestali tendenzialmente puri si comportino al verificarsi di tali periodi perturbativi, con particolare riguardo per le specie definite produttive quali l'abete rosso (*Picea abies* [L.] H. Karst) e il faggio (*Fagus sylvatica* L.), abbiamo deciso di focalizzare l'attenzione su cenosi forestali miste, poiché riteniamo che in questo modo si possano ampliare le nostre conoscenze sull'attuazione di strategie ecologiche messe in atto dagli alberi per far fronte allo stress in questione. In particolare, la resistenza e la resilienza delle diverse specie possono mostrare modelli diversi di reazione. Nel nostro studio abbiamo misurato gli anelli degli alberi su carotine prelevate da 1826 alberi di faggio, abete rosso e abete bianco (*Abies alba* Mill.) di boschi misti appartenenti a 28 aree di saggio permanenti di 8 diversi paesi europei. Di seguito sono stati applicati gli indici di resistenza, recupero e resilienza per calcolare le risposte a breve termine allo stress analizzato, considerando gli eventi di siccità verificatisi dal 1950 al 2016 per la maggior parte dei campioni, e dal 1950 al 2010 per i campioni della Slovacchia. Successivamente, sono state condotte analisi lineari ad effetto misto per indagare quale fattore ecologico gioca un ruolo chiave per gli indici considerati. La ricerca è stata condotta per scoprire le reazioni specie specifiche al verificarsi dello stress e come queste cambino lungo un gradiente ecologico. Abbiamo dimostrato che l'Abete rosso presenta i livelli più alti in termini di recupero ma denota basse capacità di resistenza e resilienza, mentre al contrario, il Faggio è più resistente e resiliente nel rispondere ad eventi di siccità ma risulta piuttosto carente in termini di recupero. Diversamente, per l'Abete bianco è stato riscontrato un alto livello di recupero, ma allo stesso tempo, ha preservato notevoli capacità sia in termini di resistenza che di resilienza. Abbiamo anche scoperto che gli indici di crescita sono influenzati principalmente dalle condizioni climatiche regionali, ma si è ulteriormente discusso di come le dimensioni degli alberi e la posizione geografica possono influenzare in parte le risposte ecologiche della specie.

# 1. INTRODUCTION

In recent decades, due to rising global temperature we have experienced a general increase of drought stress regime, which has grown in intensity and frequency promoting evapotranspiration and causing soil water depletion (Dai, 2013). Keeping on the current climatic trend, several forest ecosystems are becoming more vulnerable to drought and further causing reduction in forest growth and survival as shown by the increasing die-off episodes (Allen, Breshears, & McDowell, 2015; Allen et al., 2010). In this fast-changing context, tree species experience different adaptation strategies to cope with new climatic conditions.

Drought is a common term generally used to indicate a period without significant rainfall (Jaleel et al., 2009). This atmospheric condition enhances evaporation and transpiration processes, which are responsible of a continuous soil water loss from a specific land area. The perpetuation of this condition causes various effects on plants such as reduction of water content, drop of leaf water potential, cell turgor loss, stomata closure and limitation of gas exchanges. As a consequence, depending on drought severity, photosynthetic activity and plant metabolism may be profoundly compromised (Jaleel et al., 2008). In the prospective to find out how forest ecosystems response to this type of stress events, many studies have been conducted, which generally agree to state that species diversity seems to increase forest resilience against several type of natural disturbance (Hooper et al., 2005), allowing plants to better perform when facing adverse phenomena, drought stress included (Grossiord, 2019).

Further studies have shown how species mixing may provide several benefits to whole forest stands, such as increasing water and resources availability, decreasing solar radiation, improving the resources supply and resources transport through ectomycorrhizal communities, with the final result of enhancing trees growth (H. Pretzsch et al., 2014; H. Pretzsch et al., 2013; H. Pretzsch et al., 2018). The main reason to explain the occurrence of these mechanisms is that mixed forests seems to better promote niche differentiation of the plant species they host, which allow the efficient allocation of available resources and thus, decreasing the competition rate (Morin et al., 2011). One example may be given by mixed stands of Norway spruce (*Picea abies* [L.] H. Karst) and European beech (*Fagus sylvatica* L.), which manage to use water in different times. Indeed, at the beginning of vegetative season Norway spruce starts to uptake water quite earlier compared to European beech, thus benefiting from greater supply. Vice versa, in case of drought event, the coniferous species tends to immediately stop water consumption whereas the deciduous one keeps on absorbing water despite the stress (Mcdowell, 2008).

Furthermore, even facilitation mechanisms such as resources sharing through anastomoses and hydraulic lift (H. Pretzsch et al., 2013) seem to occur in mixed stands, especially under unfavourable growth conditions, as stated by stress-gradient hypothesis (Callaway & Walker, 1997).

Therefore, the analysis of mixed forest stands responses to drought stress may disclose interesting tree species-specific behaviour that occur in these conditions and thus, increases knowledge about forest ecology to improve forest management.

### *1.1 Mountain mixed forests of European beech, silver fir and Norway spruce: basics on ecology and functioning*

Mountain mixed forests composed by European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* [L.] H. Karst) are generally found on very fertile sites, where the environmental conditions allow to the three tree species to well grow but without significantly promoting one of them, thus none of them can prevail over the others. In Italy for instance, they can be found in mountain areas within an elevation range that reflects the ecological characteristic of silver fir (500 – 2000 m a.s.l.) and manly located at altitudes which correspond to the central transverse part of the Alps.

The ecological and functional interpretation of these mixed stands is quite complicated as several aspects have to be considered. First of all, it is necessary to analyse the competitive relationships established between the species, which are not always univocal and result in specific mechanisms of natural regeneration. The regeneration pattern in turn lead to different vertical structures of these forests, which, in the last 50 years, have been also affected more or less heavily by the anthropogenic pressure, providing changes in terms of composition and structure (manly promoting Norway spruce). The mechanisms of natural regeneration of these forest communities are mainly regulated by the interaction of four elements. These include latitude, nature of the substrate, elevation range and composition. It follows that their growth-pattern can be very different from stand to stand. Nevertheless, it is possible to summarize the general model of these mechanisms and of the resulting vertical structure in the following base functioning: the general turnover occurs when small gaps (100-200 m<sup>2</sup>) are opened, created by death of large individuals or a group of few trees. The result is therefore a stratified vertical distribution structure, with regular canopy cover from full to scarce and fine texture, called "uneven-aged for single tree". Further and deep explanation about the ecology and



functioning of mountain mixed forests of European beech, Norway spruce and silver fir can be found in Portoghesi, (2006).

## *1.2 Research objective*

The analysis of how mountain forest ecosystems response to drought phenomena and the management practices which may enhance the forest resilience to stress occurrence, are two of the main targets of Climate-Smart Forestry in Mountain Region project (COST Action CA15226 CLIMO), under which this study was developed. Indeed, CLIMO aims “to define CSF (Climate-Smart Forestry) in the European context, which will require the identification of key silvicultural characteristics and the harmonisation of CSF in mountain areas to create a common knowledge at European level”.

Therefore, in the current study, in order to enhance knowledge regarding the drought stress reactions of European Beech, Norway spruce and silver fir implement in mountain mixed forest stands, we analysed the respective past growth response of all three species. In this prospective, we tried to address the following targets:

- 1) To find out if the tree species considered shows species-specific stress reactions;
- 2) To understand how their stress reactions differ along an ecological gradient.

Actually, there is no standard procedure to estimate how disturbance impacts on ecosystems (Hooper et al., 2000; Kaufman, 1982; Orwin & Wardle, 2004; Sousa, 1980). Nevertheless, taking into account that the manifestation of stress is indicated by a significant deviation from the optimal condition of growth, which can concern both the single tree species and the whole stand (Larcher, 2003), we assume that a reasonable method to investigate the relative species responses is the analysis of tree resistance and resilience.

Therefore, we decided to analyse trees chronologies in order to point out short-term stress reactions of tree species during past drought events. This allowed finding out how resistance capacity is implemented by tree species, i.e. to estimate their tendency to remain in its reference state when facing drought condition. In a second step also the resilience, defined as the rate at which a system returns to a reference state after any type of disruption (Chapin III, Matson, & Mooney, 2002), thus in our case, the capacity of tree species to maintain their functions and structures after have faced several drought events, was estimated.

## 2. MATERIALS AND METHODS

### 2.1 Study sites and increment cores collection

The study was carried out over a large latitudinal transect from South to Central Europe, ranging for almost eight degree of latitude ( $41^{\circ}91'$  –  $49^{\circ}09'$ ) and including eight European Countries and three Ecological Zones as described by FAO as follow: Temperate oceanic forest, Temperate mountain system and Temperate continental forest. 27 study plots have been selected in different number for each country according with the availability of the partner universities, as reported in Table 1. Detailed information can be found in Hilmers et al., (2019). One study plot located in “Cansiglio Forest”, Italy ( $N 46^{\circ}06'$ ,  $O 12^{\circ}27'$ ) was later added for the thesis development. All the study sites were selected in the typical mixed mountain forest altitude (600 – 1800 m) where Norway spruce, silver fir and European beech, or at least two of the species naturally coexist. Moreover, the sites selected belong to long-term experimental plots, many of which are non-managed and fully stocked, whereas only a few are just moderately thinned. The study focused on mature and/or old-growth forest stands, where all the species are present in the upper canopy. Exposition and soil type have been not taken in consideration as parameters for the sites selection. It is further possible to notice from Table 1 that most of the study sites directly correspond to the long-experimental plots but, in some cases, they have been set up considering tree samples from different plots spatially close each other.

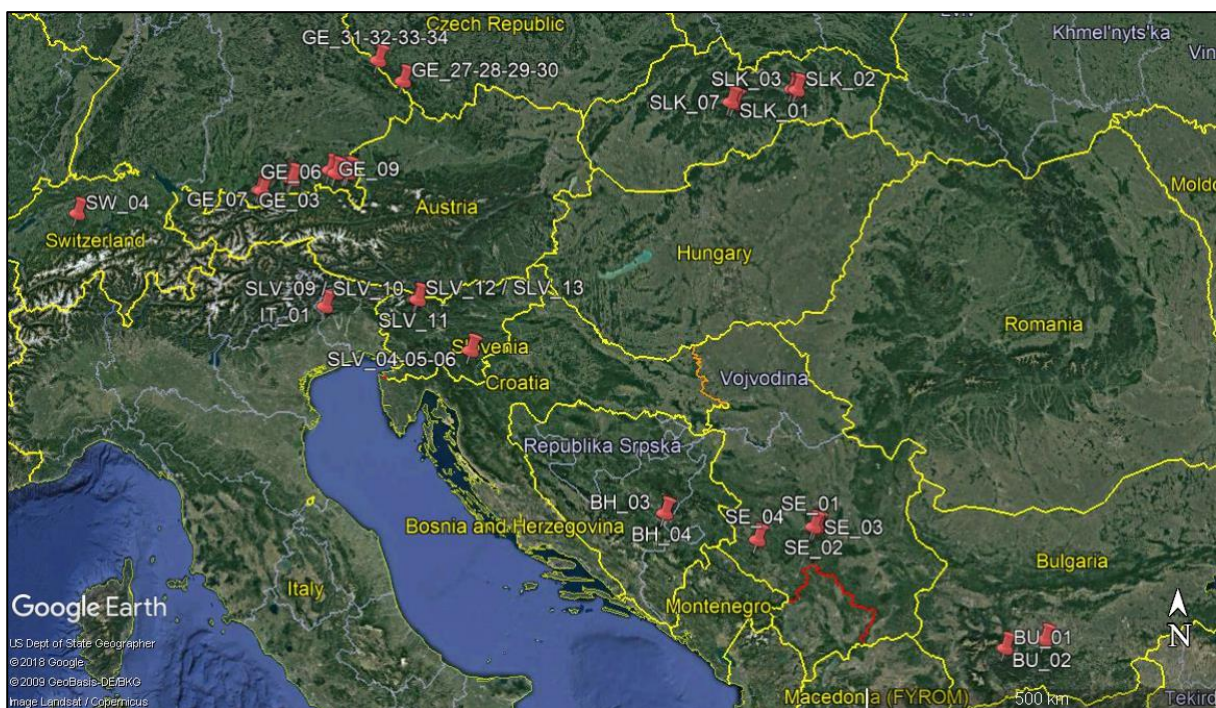


Figure 1: CLIMO study 1 plot distribution.



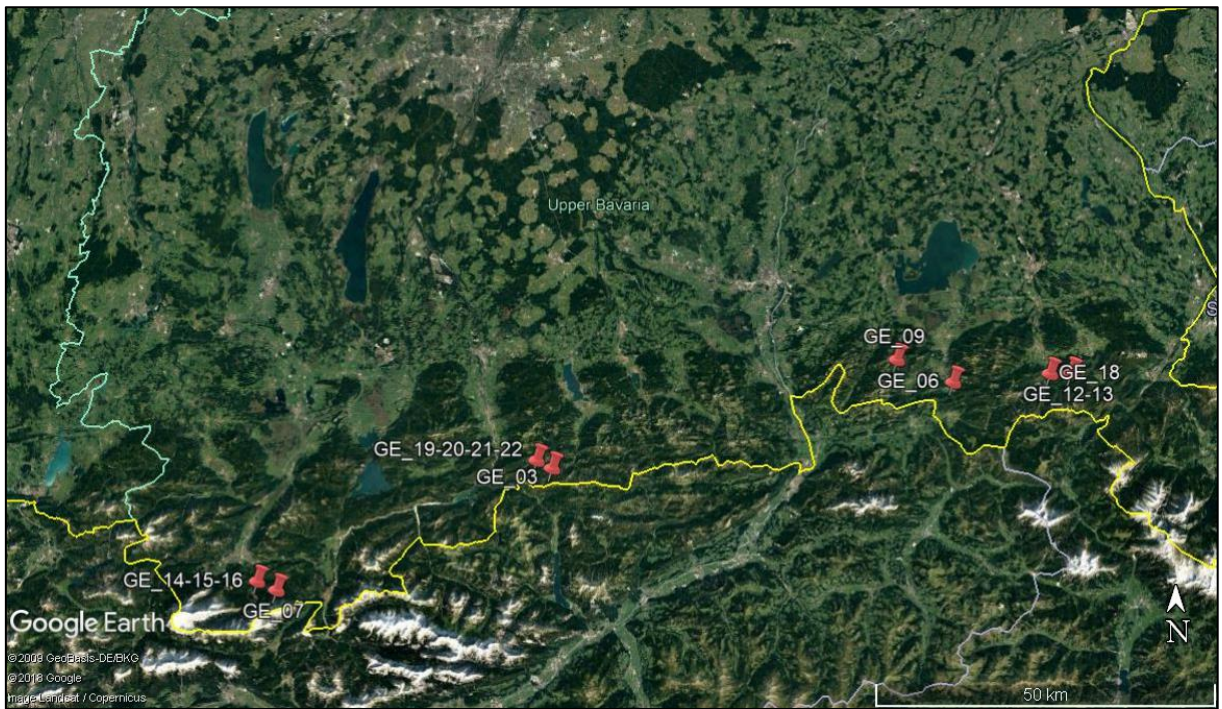


Figure 2 - CLIMO study 1 South Germany plot distribution.

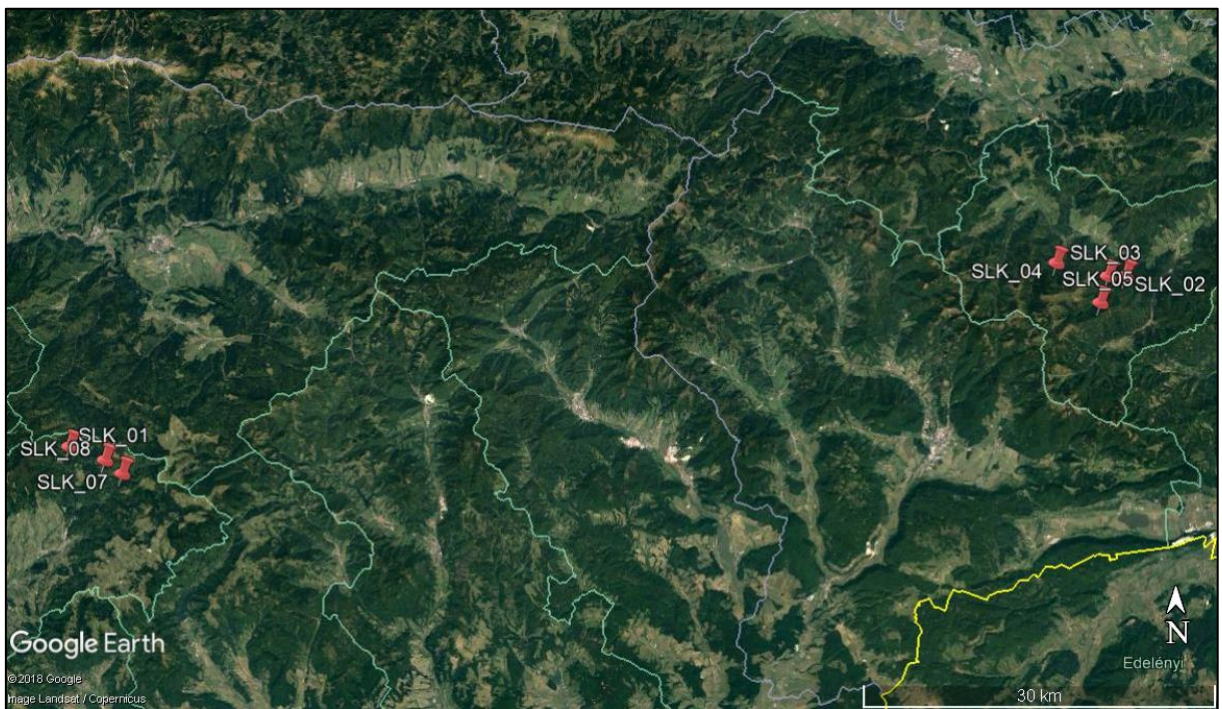
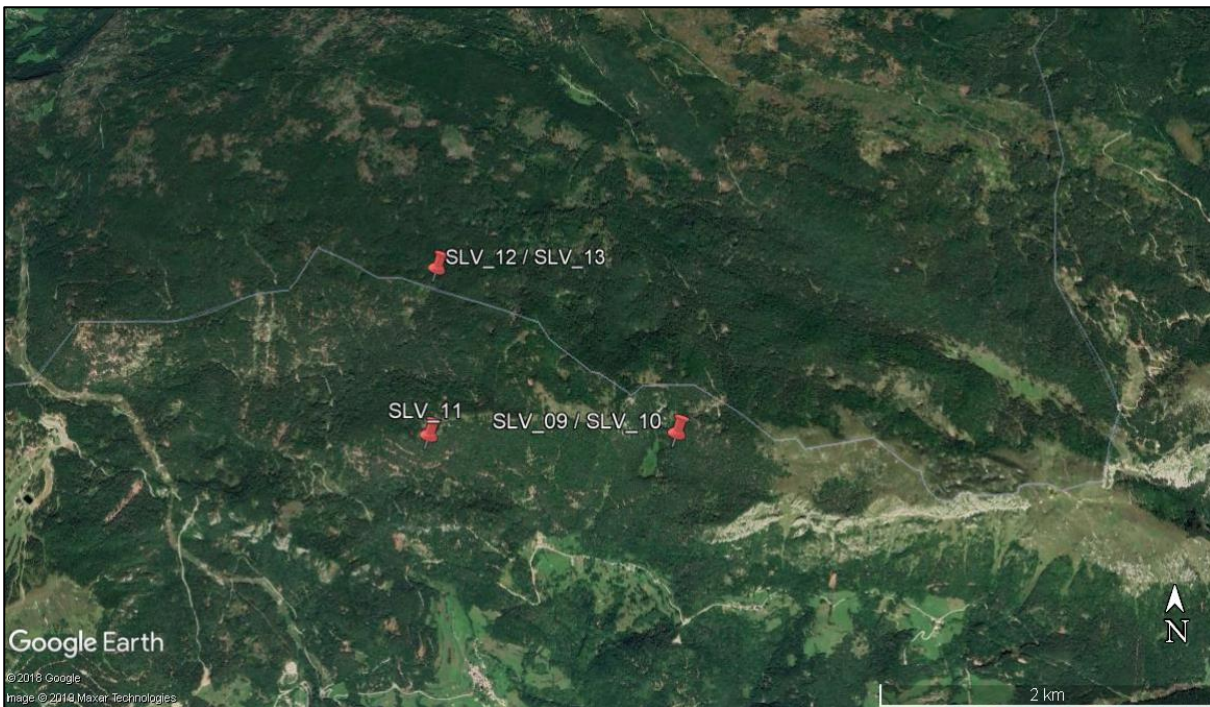


Figure 3 - CLIMO study 1 Slovakia plot distribution.





**Figure 4:** *CLIMO study 1 Slovenia - distribution of the long-experimental plots used for study site SLV\_09-10-11-12-13.*

Thereafter, the CLIMO project original protocol provided to sample between twenty to thirty trees per tree species from each study sites, or the maximum number available where it was not possible to comply with that quota. The following has been carried out by extracting with Pressler increment borer two radial cores per tree, from northern and eastern direction, at breast height (1.30 m), together with the collection of height (m) and diameter at breast height (cm). Unfortunately, since part of core data belong to a previous research project, not all the study sites respect the original proportion of tree per species. A total of 1826 trees were sampled, respectively distributed as follows: 727 of European beech, 714 of silver fir and 385 of Norway spruce. The discrepancy between Norway spruce and the other two species in terms of number of trees sampled is due to the fact that incremental data coming from Slovakia plots had previously been collected for another research project that did not include Norway spruce. Following Table 2 gives an overview of the total number of tree sampled and how they are partitioned among the species for each stand. Therefore, for the aforementioned reason, the year of sampling is not the same for all the sites. In particular, seven of the eight forest stands from Slovakia were sampled in 2010, while one in 2011. For the rest of the sites the cores collection was conducted in 2017. Finally, the Italian plot was sampled in 2019.

**Table 1** - CLIMO Study 1: sites description. It is possible to note the presence of some study sites that have been set up by considering trees of different plots which are quite close in space.

Site	Plot	Country	Latitude N (°)	Longitude O (°)	Elevation (m)
BH_03	Bosnia_Herzegovina_03	Bosnia_Herzegovina	43.76	18.24	1270
BH_04	Bosnia_Herzegovina_04	Bosnia_Herzegovina	43.74	18.25	1291
BU_01	Bulgaria_01	Bulgaria	41.91	23.84	1569
BU_02	Bulgaria_02	Bulgaria	41.96	24.52	1391
GE_03	Germany_03	Germany	47.59	11.69	1271
GE_06	Germany_06	Germany	47.7	12.47	860
GE_07	Germany_07	Germany	47.43	11.16	1463
GE_09	Germany_09	Germany	47.73	12.36	902
GE_12-13-18	Germany_12	Germany	47.71	12.7	973
GE_12-13-18	Germany_13	Germany	47.71	12.7	973
GE_14-15-16	Germany_14	Germany	47.44	11.12	1235
GE_14-15-16	Germany_15	Germany	47.44	11.12	1235
GE_14-15-16	Germany_16	Germany	47.44	11.12	1235
GE_12-13-18	Germany_18	Germany	47.71	12.66	884
GE_19-20-21-22	Germany_19	Germany	47.6	11.66	1091
GE_19-20-21-22	Germany_20	Germany	47.6	11.66	1091
GE_19-20-21-22	Germany_21	Germany	47.6	11.66	1091
GE_19-20-21-22	Germany_22	Germany	47.6	11.66	1091
GE_27-28-29-30	Germany_27	Germany	48.85	13.58	743
GE_27-28-29-30	Germany_28	Germany	48.85	13.58	743
GE_27-28-29-30	Germany_29	Germany	48.85	13.58	743
GE_27-28-29-30	Germany_30	Germany	48.85	13.58	743
GE_31-32-33-34	Germany_31	Germany	49.09	13.09	951
GE_31-32-33-34	Germany_32	Germany	49.09	13.09	951
GE_31-32-33-34	Germany_33	Germany	49.09	13.09	951
GE_31-32-33-34	Germany_34	Germany	49.09	13.09	951
SE_01	Serbia_01	Serbia	43.55	20.73	869
SE_02	Serbia_02	Serbia	43.55	20.78	1067
SE_03	Serbia_03	Serbia	43.53	20.76	1236
SE_04	Serbia_04	Serbia	43.42	19.8	1270
SLK_01	Slovakia_01	Slovakia	48.64	19.53	803
SLK_02	Slovakia_02	Slovakia	48.77	20.74	773
SLK_03	Slovakia_03	Slovakia	48.77	20.72	738
SLK_04	Slovakia_04	Slovakia	48.78	20.66	621
SLK_05	Slovakia_05	Slovakia	48.75	20.71	845
SLK_07	Slovakia_07	Slovakia	48.62	19.59	786
SLK_08	Slovakia_08	Slovakia	48.63	19.57	733
SLV_04-05-06	Slovenia_04	Slovenia	45.66	15	910
SLV_04-05-06	Slovenia_05	Slovenia	45.66	15	910
SLV_04-05-06	Slovenia_06	Slovenia	45.66	15	910
SLV_09-10-11-12-13	Slovenia_09	Slovenia	46.24	14.06	1426
SLV_09-10-11-12-13	Slovenia_10	Slovenia	46.24	14.06	1375

SLV_09-10-11-12-13	Slovenia_11	Slovenia	46.24	14.04	1443
SLV_09-10-11-12-13	Slovenia_12	Slovenia	46.25	14.04	1421
SLV_09-10-11-12-13	Slovenia_13	Slovenia	46.25	14.04	1375
SW_04-05	Switzerland_04	Switzerland	46.95	7.77	890
SW_04-05	Switzerland_05	Switzerland	46.95	7.77	890
IT_01	Italy_01	Italy	46.06	12.27	1150

**Table 2 - CLIMO Study 1: number of tree species per study site with the respective year of sampling.**

Site	Country	E. Beech	S. Fir	N. Spruce	Sampling year
BH_03	Bosnia_Herzegovina	29	30	27	2017
BH_04	Bosnia_Herzegovina	30	16	16	2017
BU_01	Bulgaria	20	23	27	2017
BU_02	Bulgaria	29	30	NA	2017
GE_03	Germany	28	28	19	2017
GE_06	Germany	30	7	29	2017
GE_07	Germany	4	11	29	2017
GE_09	Germany	20	14	20	2017
GE_12-13-18	Germany	20	20	20	2017
GE_14-15-16	Germany	27	30	30	2017
GE_19-20-21-22	Germany	20	20	20	2017
GE_27-28-29-30	Germany	8	20	20	2017
GE_31-32-33-34	Germany	17	20	20	2017
SE_01	Serbia	27	27	NA	2017
SE_02	Serbia	31	30	NA	2017
SE_03	Serbia	23	24	NA	2017
SE_04	Serbia	NA	27	29	2017
SLK_01	Slovakia	27	29	30	2017
SLK_02	Slovakia	26	36	NA	2010
SLK_03	Slovakia	56	50	NA	2010
SLK_04	Slovakia	17	64	NA	2011
SLK_05	Slovakia	37	31	NA	2010
SLK_07	Slovakia	76	52	NA	2010
SLK_08	Slovakia	43	7	NA	2010
SLV_04-05-06	Slovenia	21	19	3	2017
SLV_09-10-11-12-13	Slovenia	26	21	30	2017
SW_04-05	Switzerland	16	14	16	2017
IT_01	Italy	19	14	NA	2019



Figure 5 – 6: silver fir - Northern and Eastern cores extraction with Pressler increment borer in *Cansiglio\_01* study plot.

## 2.2 Core data elaboration

### 2.2.1 Core samples preparation

The measurement procedure following described was applied to Italy study site core samples. Nevertheless, the same protocol was carried out by the respective tree ring providers. The Core samples preparation was conducted according to the standard procedures used in dendrochronology (Blasing & Fritts, 1976; Schweingruber, 1989). Woody cores were left drying for two weeks after collection, in order to avoid crack generation due to shrinkage occurring as they dried if immediately mounted on the mount. Thereafter, each couple of cores was adjacently glued on a prefabricated wooden support taking care that the inclination of the fibres was perpendicular to the support, so as to have a cross sectional view facing up, otherwise the ring boundaries could be not so visible after sanding (Speer, 2009). The sanding was carried out with a planer and abrasive paper of increasingly fine grain. This allowed a correct, easy counting and measurement of the rings (Fig. 6).



Figure 7: woody core samples glued on the prefabricated support. The samples come from the *Cansiglio\_01* study plot: it is possible to appreciate the difference in rings clearness between the silver fir (top support) and European beech (bottom support).



### 2.2.2 Cross-dating and synchronization

In order to appreciate in detail the increment differences among years, ring width were measured with digital positiometer (Biritz GmbH, Gerasdorf bei Wien, Austria) with an accuracy of 0.01 mm. Following cross-dating and synchronization of the tree chronologies were carried out using Excel 2013.



**Figure 8 – 9:** Cores measuring by Biritz GmbH with accuracy of 0.01 mm. Annual rings are considered reliable until their inclination does not exceed 70°, represented by the black lines outside the screen.

Cross-dating is the process facilitating the accurate matching of ring width to the calendar year by using similar oscillation of several ring chronologies. This is fundamental when comparison between ring-width measurements and annual phenomena such as meteorological data is planned. In the current study, the cross-dating was conducted by using the list method, a fast procedure that works only if the outside date of the sample is known. It is further advisable to build up the master list only from good quality cores in which the ring sequences are complete. Small and big rings rings have to be used as reference to produce a list of marker rings. Finally, those rings that are mostly noted between samples are assumed to be reliable and thus, they can be used to date other cores (Speer, 2009).

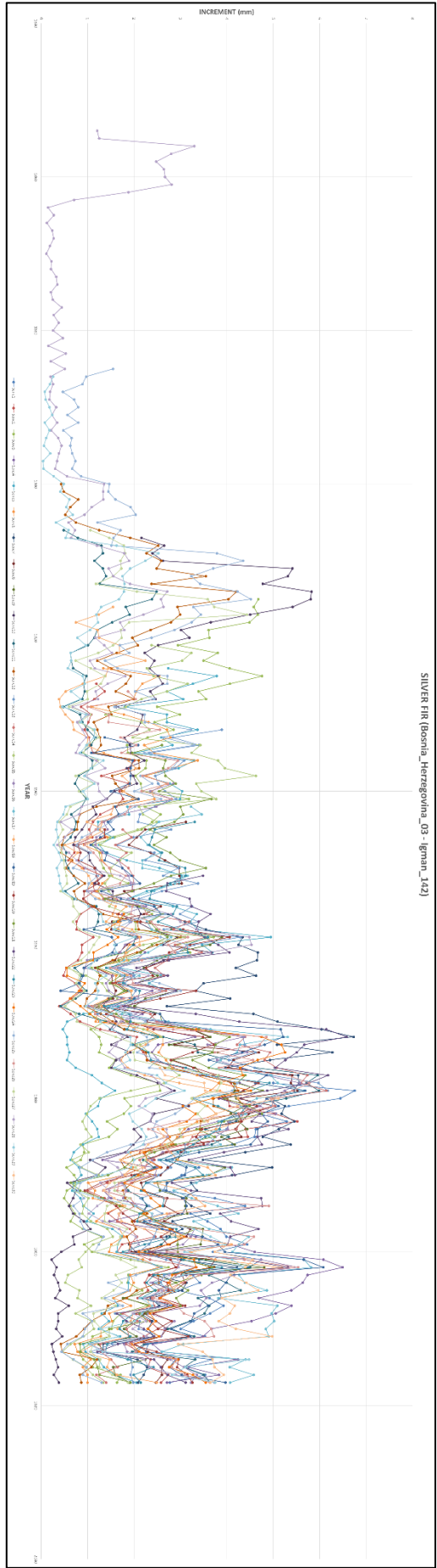
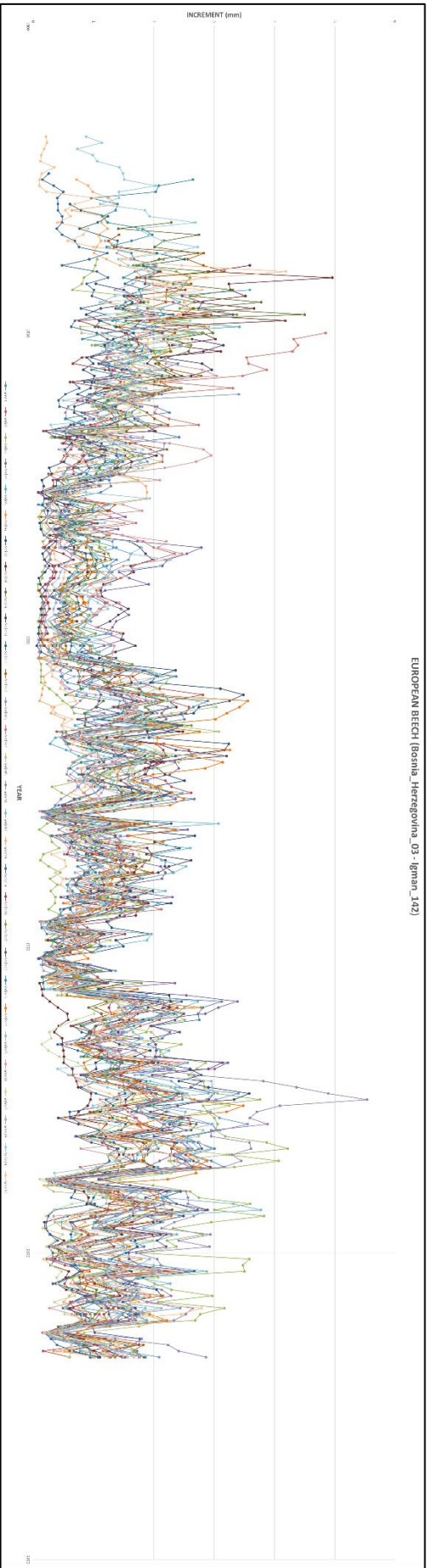
As two cores for each tree have been collected, cross-dating was firstly carried out between the core sample series of each tree (Northern and Eastern), in order to get a master list of mean value for each tree. Following, the second cross-dating was conducted between the mean core series of each tree for each species within the same study site. In this way the synchronization between the tree-species core series was performed as showed in the following graphs realized for the *Bosnia Herzegovina 03* study site. Here the incremental data are plotted separately for each tree species after having been cross-dated. (From this moment, the *Bosnia Herzegovina 03* study site will be taken as example for all the elaborations conducted in the same way for all other study areas). The first Graphs display the growth

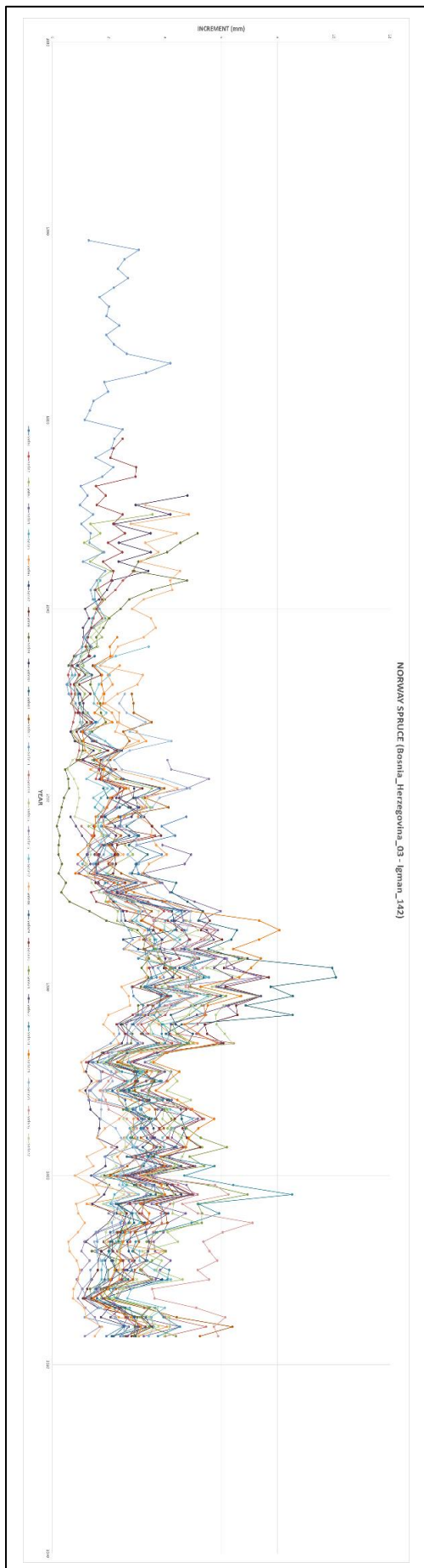


trend entirely, highlighting as the synchronization decreases moving backwards in time. As a consequence, it was decided to focus the following analyses considering the 1950 as start-reference year. Therefore, three time periods has been defined depending on the cores sampling year:

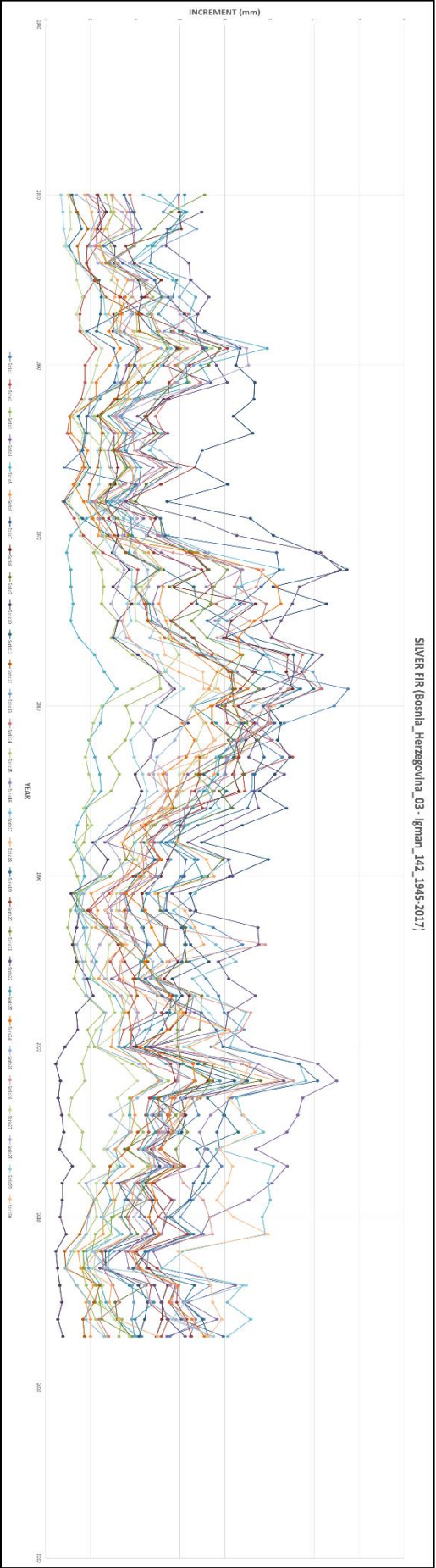
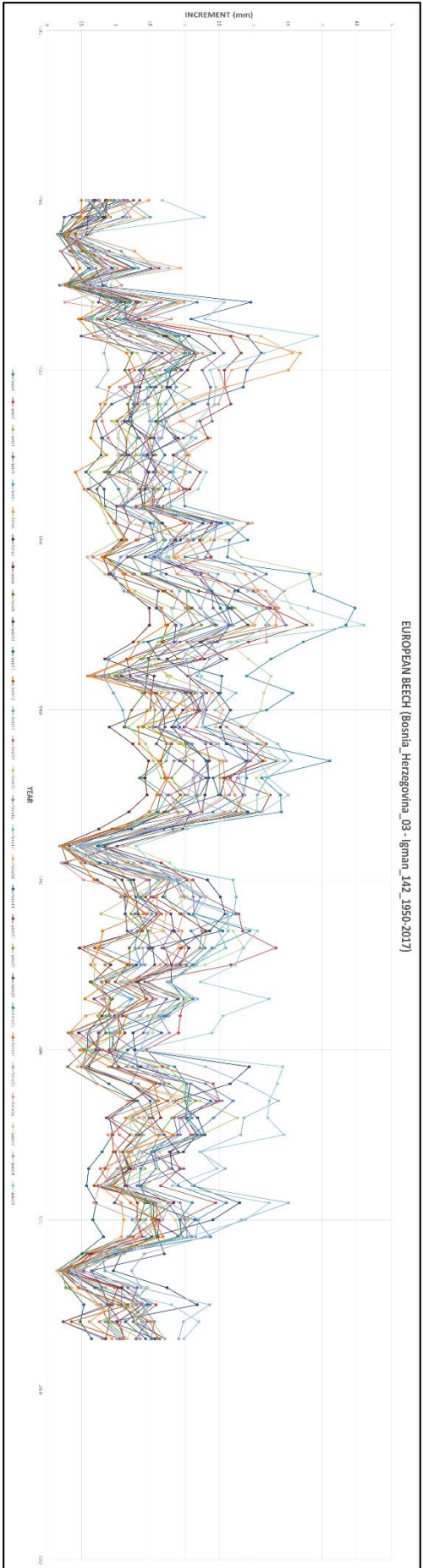
- From 1950 to 2016 for most of core increment time series;
- From 1950 to 2010 for datasets coming from the sampling of Slovakia study sites;
- From 1950 to 2018 for core increment time series coming from Italian stand.

In this way, it was possible to better emphasize the common negative peaks of tree growth trend, which resulted in a first overview of the possible pointer years which have been computed as following.

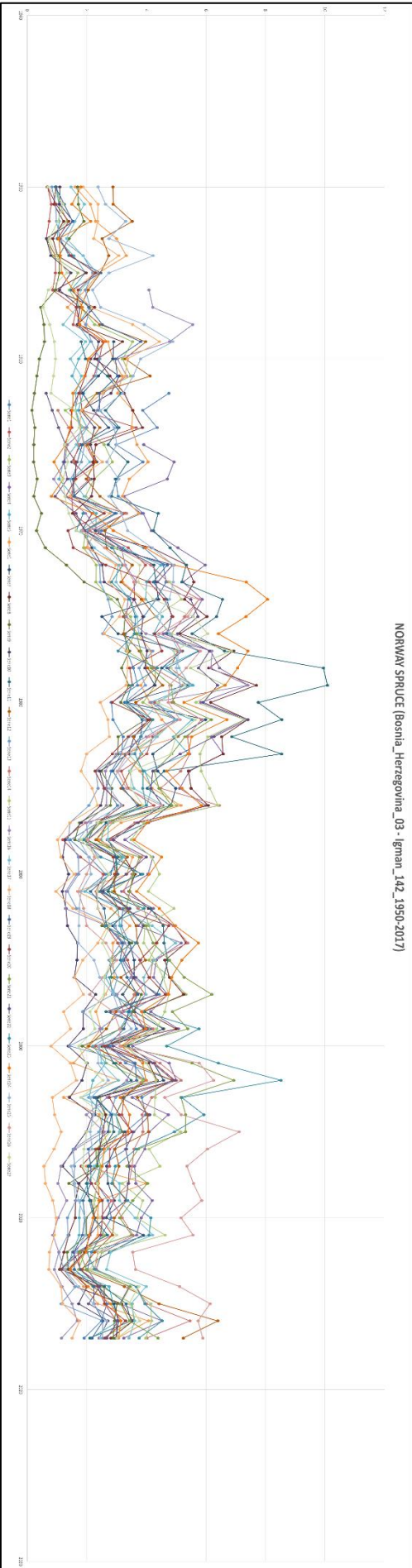




**Graph 1, 2 and 3 - European Beech, silver fir and Norway Spruce from Bosnia Herzegovina 03 study site. Tree samples growth trend entirely represented.**



**Graph 4, 5 and 6 - European Beech, silver fir and Norway Spruce from Bosnia Herzegovina 03 study site. Tree samples growth trend from 1950 to 2017.**



### 2.2.3 Data standardization

As established by the dendrochronological Principle of Aggregate Tree Growth Model (Cook, 1985) each individual tree-growth series depends on a complex matrix of environmental factors, both natural and human, that affected the patterns of tree growth over time. This conceptual model results in the following equation:

$$R_t = f(G_t, C_t, D1_t, D2_t, E_t) \text{ with } E_t = N_t + CA_t + EQ_t + E_t$$

Where:

$R_t$  is ring width at year  $t$ .

$G_t$  is the age (or size)-related growth trend.

$C_t$  is climate at year  $t$ .

$D1_t$  is the endogenous disturbance within the stand.

$D2_t$  is the exogenous disturbance from outside the stand.

$E_t$  is the error term incorporating all of the signal that is not controlled for by the above variables, some of which can be summarised by the following factors:

- $N_t$  is the annual variability in nutrient availability;
- $CA_t$  is the annual variability in carbon allocation within a tree;
- $EQ_t$  is the error made by the operator.

Thereafter, in order to detect the climate related growth reaction from the chronologies (factor  $C_t$ ), each individual tree core series resulting from synchronization was standardized through two following steps. The standardization works in order to remove the tree's natural biological growth which the radial stem growth is subjected and which negatively influences the increment levels due to climate events such as drought events (Thurm, Uhl, & Pretzsch, 2016).

Firstly, the ring width series were converted in basal area increment (BAI) series ( $cm^2 \cdot year^{-1}$ ) using *bai.in* function of R package *dplR* (*Dendrochronology Program Library* in R) (Biondi, 1999; Biondi & Qeadan, 2008; R Core Team, 2013). The conversion, which is based on the distance between the innermost measured ring and the pith of the tree, works with the following formula developed by Biondi & Qeadan, (2008):

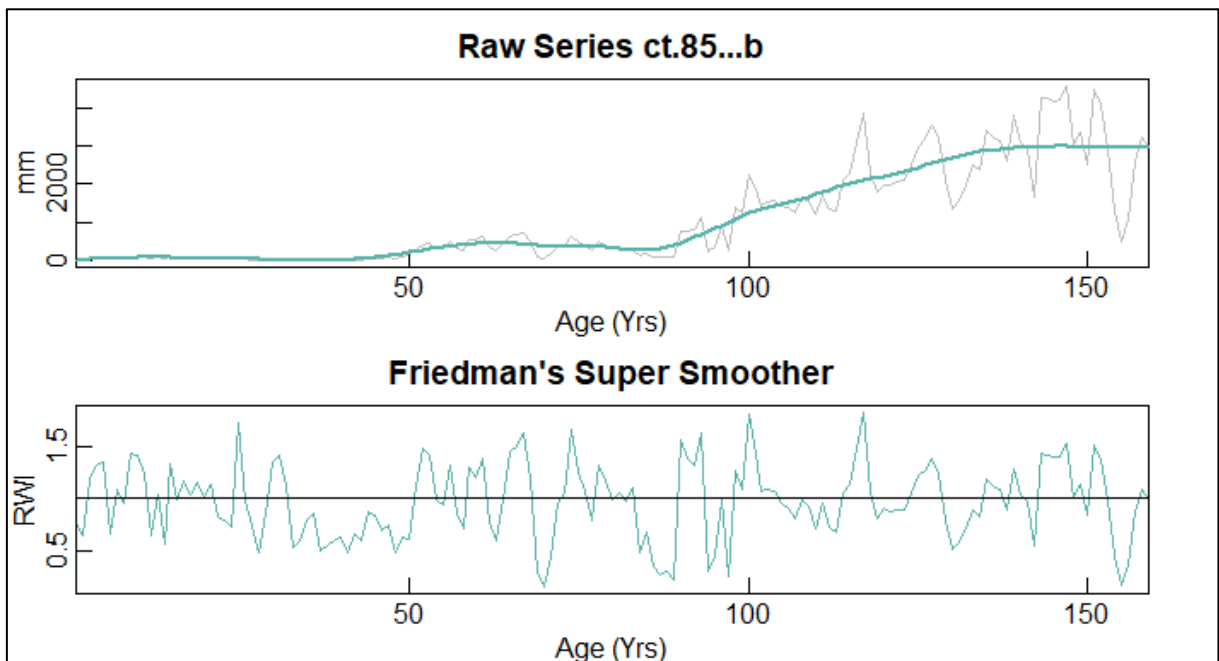
$$BAI_t = \pi(w_t^2 + 2w_tR_{t-1})$$



where  $w_r$  is the ring width as defined by Blasing & Fritts, (1976) and  $R_{t-1}$  is the radial increment since the beginning of the series.

It is almost an unavoidable passage dictated by the fact that two-dimensional measurement better interprets the volumetric growth of tree compared to one-dimensional growth computed through the tree ring width (Biondi & Qeadan, 2008).

Afterward, a detrending procedure was applied to standardize the BAI time series, in order to remove the possible age-related effects or other biological factors that can influence the radial stem growth. For the current study, we applied the Friedman's Super Smoother function (Friedman, 1984) and the standardization was carried out by dividing each time series by the growth trend to produce units in the dimensionless ring-width index (RWI). As reported in Graphs 7 and 8, an example of detrending process for European beech with mean BAI time series belongs to Bosnia Herzegovina 03 study site.



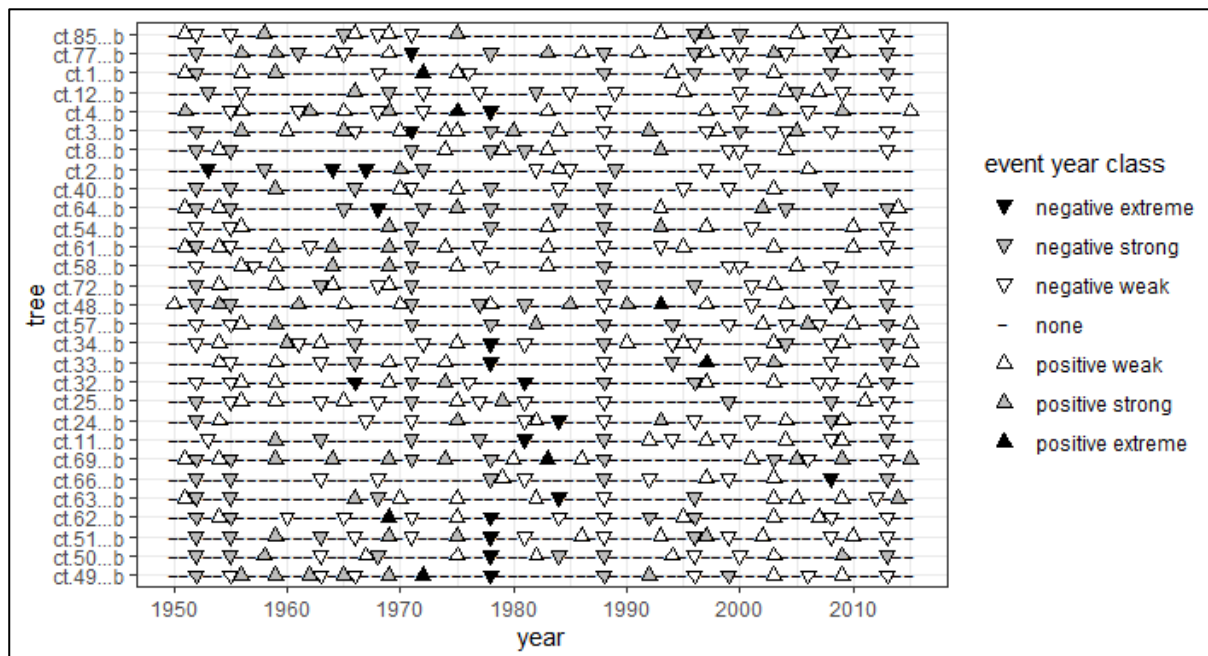
**Graph 7:** mean basal area increment (BAI) calculated on the mean of two cores per tree of *E. beech* samples – *Bosnia Herzegovina 03* study site.

**Graph 8:** detrending application - Growth trend estimated according to Friedman's Super Smoother function.

## 2.2.4 Event years and Pointer years computation

Through the results of mean basal area increment series standardization, was subsequently possible to compute the effective event years and thus, the relative pointer years, which could be assumed to be related to drought phenomena.

Firstly, the event years, defined as a pronounced features, detected within a limited section of an individual tree-ring series, highlights a remarkable growth increase or decrease at individual-tree level (Schweingruber, 1989). These were computed with the normalization in a moving window method through the *pointer.norm* function (*point.Res* R package), proposed by Cropper, (1979) and followingly improved by Neuwirth et al., (2007). Basically, the elaboration transforms tree-ring series in year  $i$  within a symmetric moving window of  $n$  years, hence generating the number of standard deviations that tree growth deviated in individual years also called Cropper values (C). To identify event years the number of standard deviations are related to three intensity classes defined as weak, strong and extreme, as reported in Graph 9 that shows the event years for each individual European beech sampled in *Bosnia Herzegovina 03* study site.

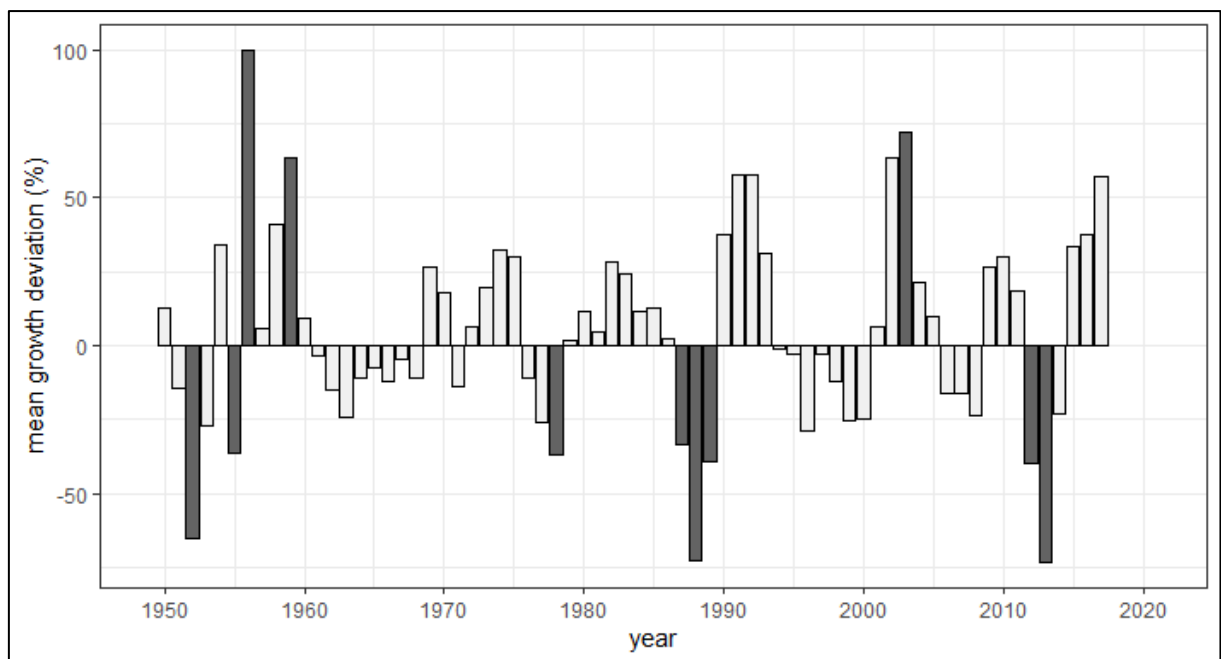


Graph 9: Event years computation of *E. beech* individual trees - *Bosnia Herzegovina 03* study site.

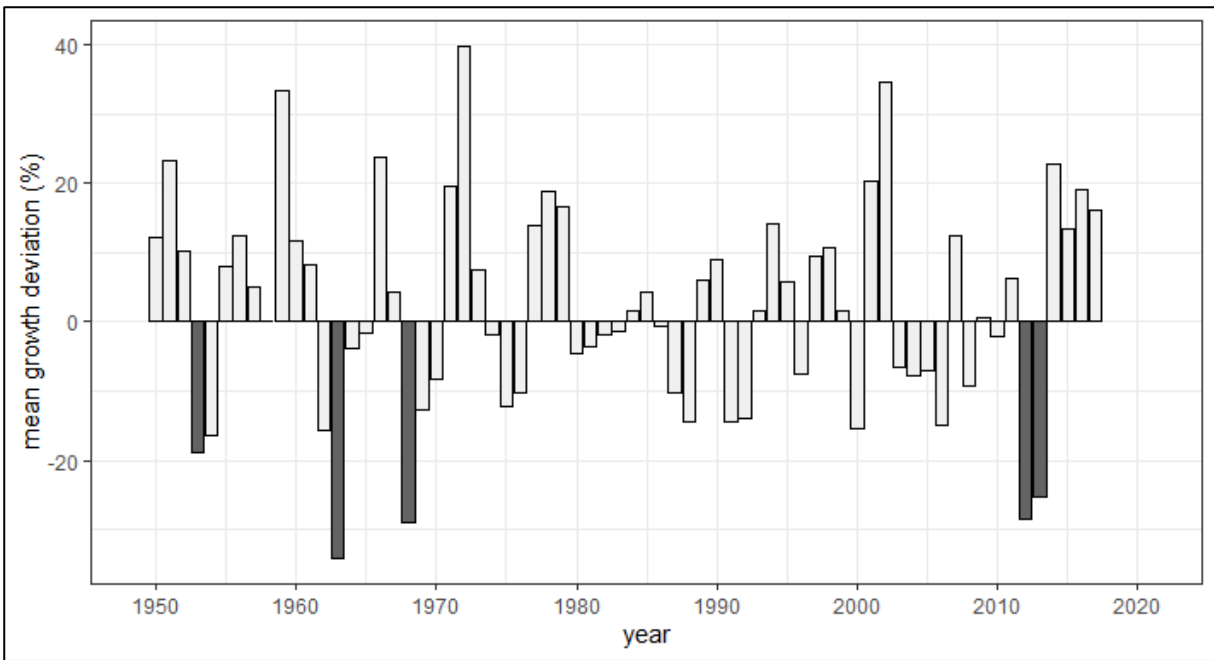
Thereafter, the computation of pointer years was carried out. Pointer years are defined as the concentration of cross-dated event years within a group of trees, which thus provide a significant growth response at stand level (Schweingruber, et al., 1990). Their analysis was



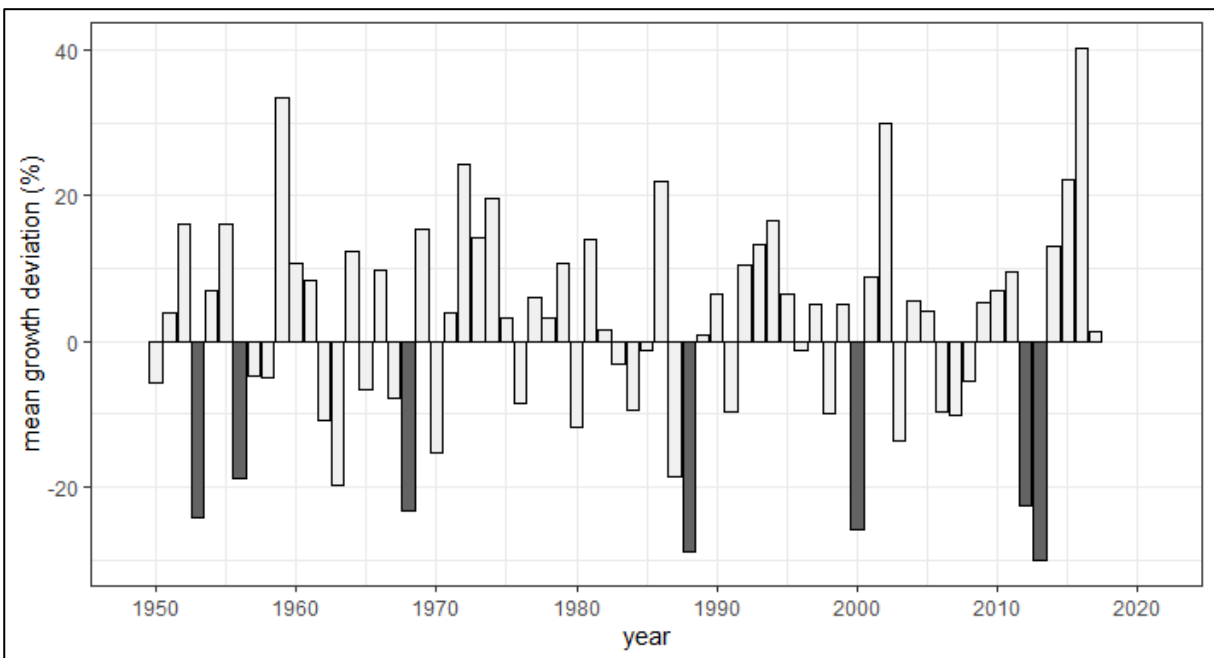
conducted by using the relative growth change method through the *pointer.rgc* function (*point.Res* R package) proposed by Schweingruber et al., (1990). The function computes the ratio of each tree ring in year  $i$  and the average growth of  $n$  preceding years for individual trees, with  $n = 4$  for the current study (selected as default). Following, resulting relative growth changes are used to identify event years for trees, and these event years to provide pointer years for the stand. This method allows to set the threshold of standard deviation from the average growth to define pointer years. Since the European beech responses are more sensible than those ones of silver fir and Norway spruce, the current elaboration has been carried out fixing the threshold for E. beech equal to 30%, while the negative mean growth deviation selected as remarkable for coniferous species has been fixed equal to 20%. As a consequence, Graphs 10, 11 and 12, show respectively the pointer years calculated for European beech, silver fir and Norway spruce of mixed forest stand of *Bosnia Herzegovina 03* study site, and all the years with a negative mean growth deviation greater than thresholds values are expressed as extreme negative pointer years. Finally, a summary including only the extreme negative pointer years identified for each stand with the relative mean growth deviation, and partitioned for each tree species is provided in Table 3.



**Graph 10:** Pointer years computation with relative growth method (neg. threshold = 40) of E. beech - *Bosnia Herzegovina 03* study site.



**Graph 11:** Pointer years computation with relative growth method (neg. threshold = 20) of *s. fir* - *Bosnia Herzegovina 03* study site.



**Graph 12:** Pointer years computation with relative growth method (neg. threshold = 20) of *N. spruce* - *Bosnia Herzegovina 03* study site.

**Table 3:** Extreme negative Pointer years of all mixed forest stands determined with relative growth change (RGC) method. Here are portioned for each tree species. This method allows to compute growth change of a specific year  $i$  performing the ratio among tree ring of the considered year and the mean growth of preset number of previous years. It is applied at individual tree level. The resulting event years are following use to detect pointers years at stand level. In our case, negative threshold of RGC for *E. beech* is fixed to -30%, whereas for *S. fir* and *N. spruce* we selected a negative threshold of -20%. In few cases (Italy and Slovakia), since there were not mean growth deviation value under these limits, the closest values have been showed.

Site	Country	E. Beech		S. Fir		N. Spruce	
		Year	RGC (%)	Year	RGC (%)	Year	RGC (%)
BH_03	Bosnia_Herzegovina	2013	-73.27	1963	-34.18	2013	-30.05
		1988	-72.88	1968	-29.07	1988	-28.81
		1952	-65.35	2012	-28.48	2000	-25.78
		2012	-39.7	2013	-25.29	1953	-24.12
		1989	-39.33			1968	-23.19
		1978	-37			2012	-22.58
		1955	-36.16				
		1987	-33.55				
BH_04	Bosnia_Herzegovina	1988	-71.75	1963	-39.46	1988	-34.75
		2013	-69.62	1962	-31.32	1953	-28.31
		1952	-63.98	1954	-30.79	1987	-24.79
		1989	-44.38	2012	-26.56	1957	-22.44
		2012	-36.75	2013	-24.7	2000	-20.56
		1996	-33.16	1982	-22.96		
		1963	-30.18	2000	-22.1		
				1968	-20.56		
BU_01	Bulgaria	1952	-68.61	2003	-20.28	1994	-21.98
		1955	-60.4	1989	-20.12	1989	-21.95
		1978	-52.91			2003	-20.76
		2004	-51.42				
		1999	-36.61				
		1989	-32.16				
BU_02	Bulgaria	1978	-61.67	1968	-20.29	/	/
		1989	-52.96				
		2012	-35.47				
		1991	-32.97				
GE_03	Germany	1977	-44.64	2013	-26.28	1976	-29.77
		1996	-40.92	1976	-26.15	2013	-21.17
		1978	-36.84	1956	-20.18		
		1953	-34.52				
		1968	-31.98				
		2011	-31.79				
GE_06	Germany	1976	-38.39	1976	-29.68	1992	-40.23

		1992	-32.41	1974	-21.57	1976	-30.61
		1950	-23.34			2009	-26.74
						2003	-25.64
						2004	-24.88
						2015	-20.46
						1954	-20.35
<b>GE_07</b>	<b>Germany</b>	1978	-57.49	1956	-23.55	1954	-24.9
		1977	-48.86	1981	-21.8	1980	-21.2
		1968	-47.57				
		1995	-42.88				
		1953	-41.2				
		1996	-41.07				
		2012	-32.07				
<b>GE_09</b>	<b>Germany</b>	1953	-37.44	1976	-34.53	2003	-37.08
				2013	-33.18		
<b>GE_12-13-18</b>	<b>Germany</b>	2011	-49.32	1976	-28.7	1976	-29.99
		1978	-34.96	2013	-26.36	2003	-28.08
		1996	-30.62	1981	-22.39	1991	-21.51
				1956	-22.04	1992	-21.21
						1995	-21.12
<b>GE_14-15-16</b>	<b>Germany</b>	1978	-54.85	1956	-42.44	2003	-23.9
		1977	-50.52	1976	-22.34	1992	-22.25
		1953	-48.47			1976	-21.94
		1996	-46.68				
		2011	-45.77				
		1956	-32.27				
		1968	-30.52				
<b>GE_19-20-21-22</b>	<b>Germany</b>	1953	-57	1956	-28.34	1976	-22.98
		2011	-36.04	2013	-26.25	2013	-21.66
		1977	-30.03	1976	-20.13		
				1963	-20.11		
<b>GE_27-28-29-30</b>	<b>Germany</b>	1978	-70.64	1974	-29.07	1992	-38.21
		1984	-40.1	1973	-25.91	2003	-30.4
		1979	-39.94	2011	-24.53	1971	-25.85
		1996	-36.5	2000	-24.41	1962	-25.51
		2016	-33.2	2006	-22.43	1951	-24.87
<b>GE_31-32-33-34</b>	<b>Germany</b>	1996	-42.76	1974	-33.68	1992	-24.21
		2011	-39.36	1996	-31.62	2003	-22.67

		1985	-34.89	1950	-27.75		
		1978	-33.04	1975	-26.43		
				1976	-25.88		
				2005	-20.8		
<b>SE_01</b>	<b>Serbia</b>	2013	-69.76	2013	-47.59	/	/
		1994	-38.44	1968	-31.22		
		2001	-32.01	2012	-25.47		
		2012	-30.21	1989	-22.86		
		2006	-30.18	1958	-20.48		
<b>SE_02</b>	<b>Serbia</b>	1978	-60.59	2013	-44.37	/	/
		1988	-38.44	1968	-27.22		
		2013	-31.94	1980	-25		
				1963	-23.55		
				2010	-22.57		
				2003	-22.05		
				1964	-22		
				1991	-21.52		
				1954	-20.49		
				2012	-20.08		
<b>SE_03</b>	<b>Serbia</b>	1977	-75.82	2013	-35.12	/	/
		1978	-54.8	1968	-30.16		
		1988	-35.21	1954	-20.67		
		2013	-30.26				
<b>SE_04</b>	<b>Serbia</b>	/	/	2012	-32.79	2013	-40.11
				2013	-32.67	2000	-31.79
				1954	-26.8	1958	-31.3
				1963	-25.14	2012	-28.77
				1989	-22.47	1963	-23.81
				1962	-22.22	1954	-21.64
				1968	-21.6		
<b>SLK_01</b>	<b>Slovakia</b>	1980	-54.59	2013	-30.6	1962	-34.11
		1952	-40.18	1974	-20.35	1950	-32.06
		1987	-39.75			2003	-31.9
		2016	-33.27			1951	-30.82
		1979	-33.09			2015	-26.89
						2000	-25.06
						1958	-21.41
<b>SLK_02</b>	<b>Slovakia</b>	1987	-33.04	1967	-27.66	/	/

<b>SLK_03</b>	<b>Slovakia</b>	1993	-33.11	1976	-15.75	/	/
<b>SLK_04</b>	<b>Slovakia</b>	1987	-29.54	1976	-30.95	/	/
				1963	-27.04		
				1992	-26.64		
				1977	-26.35		
				1950	-25.06		
				1965	-22.23		
<b>SLK_05</b>	<b>Slovakia</b>	1987	-36.23	1996	-27.64	/	/
		1980	-33.8	2003	-21.95		
<b>SLK_07</b>	<b>Slovakia</b>	1996	-27.12	1996	-30.73	/	/
				1962	-21.97		
<b>SLK_08</b>	<b>Slovakia</b>	1987	-32.42	1970	-31.3	/	/
				2010	-23.57		
				2011	-23.51		
				1989	-23.16		
				2007	-22.65		
				1983	-22.32		
				1969	-22.14		
<b>SLV_04-04-06</b>	<b>Slovenia</b>	1953	-49.95	2006	-26.84	1950	-32.09
				2013	-26.25	1963	-31.26
				1968	-24.2	1962	-25.76
				1993	-22.84	2002	-22.77
				1976	-22.33	2006	-22.55
				1957	-22.19	1988	-22.26
						2013	-22.23
						1967	-22.11
						2003	-20.06
<b>SLV_09-10-11-12-13</b>	<b>Slovenia</b>	1952	-57.8	2006	-25.57	2006	-28.16
		2007	-33.23	2013	-25.32	2013	-20.51
		1970	-30.3				
<b>SW_04-05</b>	<b>Switzerland</b>	2016	-46.3	1957	-22.91	1974	-26.59
		1956	-34.64	1968	-20.21	1962	-24.15
		1963	-30.17			2006	-21.07
<b>IT_01</b>	<b>Italy</b>	1996	-28.71	1962	-35.17	/	/
				2003	-23.01		

## 2.3 Climate data

The climatic data collection was mostly based on the local weather station of each study site area. Nevertheless, in some cases where data retrieval was not available, or at least data was missed just for a specific time period, the datasets provided by the Climatic Research Unit (CRU) of University of East Anglia (UK) were used to cope with the lack of data (CRUTEM4.2.0.0-2013-03, 2013; Hulme, 1992; Hulme, Osborn, & Johns, 1998). In this case, the datasets are homogenized and spatialized on a  $0.5^\circ \times 0.5^\circ$  of latitude grid (Mitchell, et al., 2004). The grid was realized by using a system of spatial interpolation, through which, the specific climate datum for a point is computed considering the existing data collected by the closest weather stations and applying a weighting system that assigns less importance to the stations furthest from the point (New, et al., 2000). Specifically, since for the current study mean monthly temperature and monthly cumulative precipitation for each forest stand site have been gathered for the time span 1901 – 2016, historical series taken from CRU databases were considerably useful for the first half of the century.

### 2.3.1 Drought index computation: the SPEI

To find out the effective drought years within the time span considered from 1950 to 2016, the Standardized Precipitation – Evapotranspiration Index (aka SPEI) was adopted. It is a detailed drought index based on precipitation and temperature data that, in order to estimate and take in account the evapotranspiration occurrence, it incorporates for computation a climatic water balance, the accumulation of deficit/surplus at different time scales and the adjustment to a log-logistic probability distribution (Vicente-Serrano, Beguería, & López-Moreno, 2010). It is extremely accurate since it is defined for monthly data.

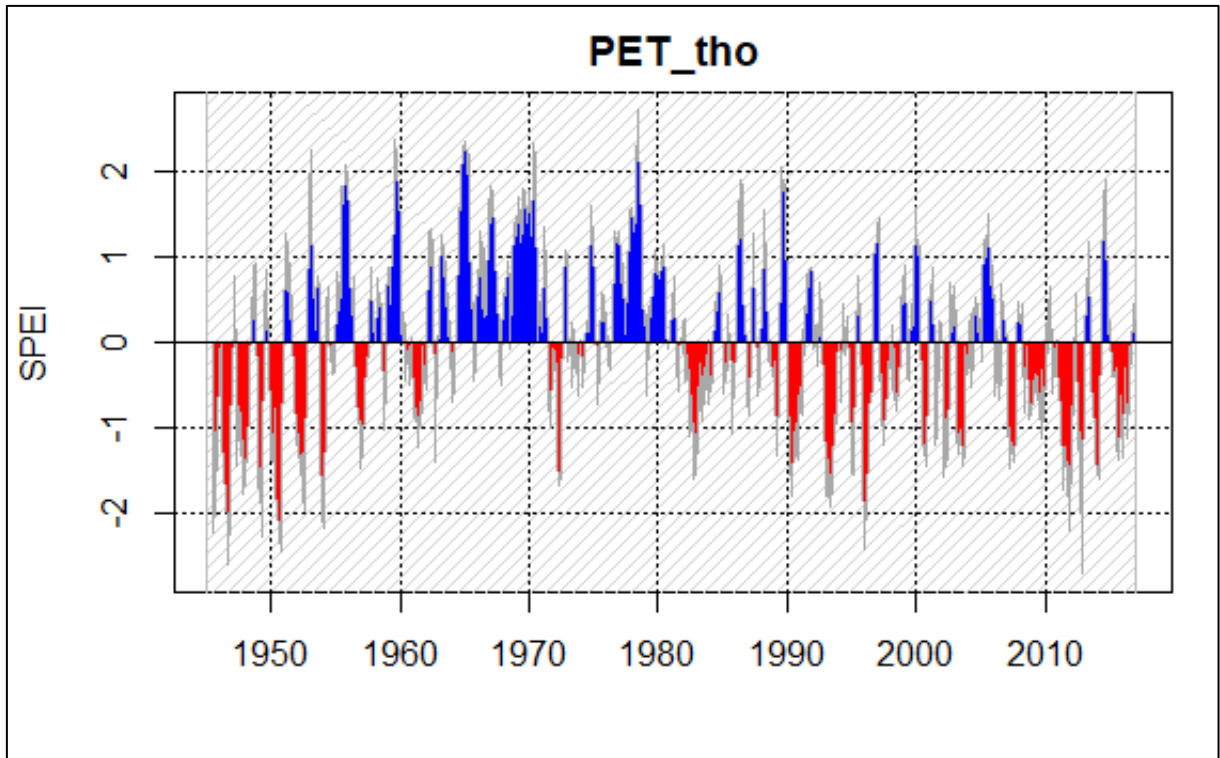
For the current study, all the following elaborations were conducted using the R package *SPEI*. The first step was to compute the potential evapotranspiration (PET) of each study site location based on average monthly air temperature data according to Thornthwaite equation (Thornthwaite, 1948). Thereafter, since the index considers the difference between precipitation and the relative evapotranspiration as the meteorological variable of interest, the SPEI value was performed as the difference between the cumulative monthly precipitation and the estimated cumulative monthly evapotranspiration for each location. A factor that must not to be underestimated is the reference period over which the SPEI is performed. As suggested by the World Meteorological Organization, (2012), the minimum length of data time series to be considered is 30 years. For the current study, three time series have been

selected according with the time periods defined for the pointers years elaboration, which depend on the cores year of sampling.

The SPEI value for a specific month is computed taking in account the precipitation series and the evapotranspiration series respectively recorded and estimated for the same month of the past years. Therefore, we decided to extend the reference periods aforementioned, considering the 1945 as start-reference year. We also opted to not involve weather data since the early beginning of the 1900s to avoid overly influencing the time span of interest.

Another aspect to highlight, is the possibility to consider different time scales for the index computation (Vicente-Serrano et al., 2010). This allow to model the influence of the variables values of past months, which are considered by the index algorithm to better weight the output value for a given month. For instance, a time scale of nine would imply that data from the current month and of the past eight months will be used for performing the SPEI value for a given month. Therefore, we selected month-based time scales belonging to average periods of time aggregation (from three to twelve month). They provide information about reservoirs capacity to store water, which are essential to detect drought-stress condition over forest stands. Specifically, SPEI values have been initially computed considering time scales of six, nine and twelve months for each forest stand location, as the response to drought impact changes according to species characteristic and site conditions (Pasho, Camarero, de Luis, & Vicente-Serrano, 2011). Later, the most correlated SPEI time scale was selected for each study site by performing correlation analyses between mean value chronologies computed over already detrended ring-width series, which represent tree growth, and monthly SPEI series representing drought severity for the period 1950–2016, 1950-2010 and 1950-2018, always according to the different sampling years of the forest stands. To compute the mean value chronologies the *chron* function (*dplR* R package) (Cook et al., 1990) was used, whereas the next correlation was carried out using the *rcorr* function of R package *Hmisc* (*Harrell Miscellaneous*) (Hollander, Wolfe, 1973), which adopts Pearson's rank correlation coefficients. Moreover, as it is possible to appreciate in *Graph 13*, which reports the SPEI values for the *Bosnia Herzegovina 03* forest study site, the drought index severity ranges from an extreme dry value of  $-3$  to an extreme humid value of  $+3$ . Considering that SPEI index was also developed as an improvement of the already existing *SPI* index (*Standardized Precipitation Index*), it is logical to assume that the *SPI* severity scale (*Tab. 4*) as defined by World Meteorological Organization (2012), may be also applied to SPEI index. Finally, a summary of the SPEI time scales selected for each forest stand is reported in *Tab. 5*.





Graph 13

SPI VALUE	CATEGORY
$SPI \geq 2$	Extreme wet
$1.5 \leq SPI < 2.0$	Severe wet
$1.0 < SPI < 1.5$	Moderate wet
$-1.0 < SPI < 1.0$	Average
$-1.5 < SPI \leq -1.0$	Moderate dry
$-2.0 < SPI \leq -1.5$	Severe dry
$SPI \leq -2.0$	Extreme dry

**Table 4:** severity of the dry and wet events according to SPI index as defined by WMO. The same classes have been assumed valid for SPEI index.

## 2.4 Drought year analysis

### 2.4.1 Drought year selection

The selection of drought years was previously characterized by a manual clustering based on process that lead to set up 14 groups of study sites (Fig. 9). The groups were made taking into consideration the distances among plot based on the criterion that it has not be longer than 1 degree in terms of latitude and longitude, and always according with the SPEI index similarity degree. This allowed selecting common drought years among the forest stands included in the same group.

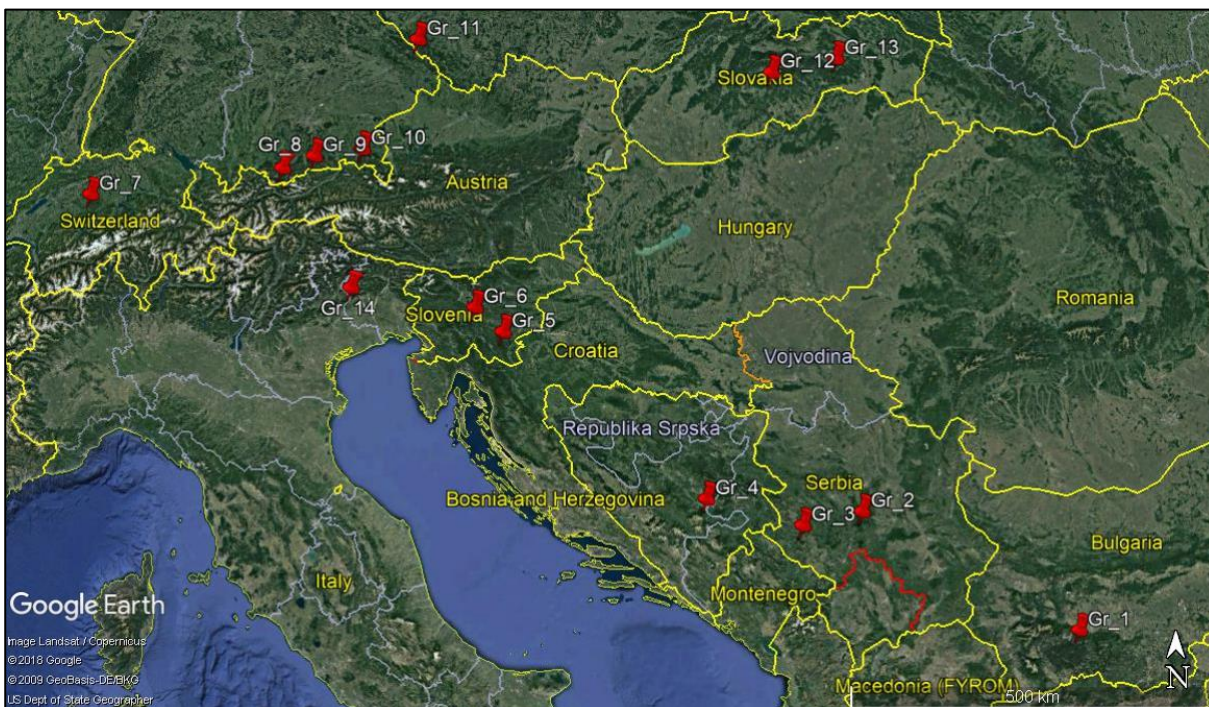


Figure 10: Study sites groups distribution according to the clustering process performed based on the distance among forest stands.

Following, to better assess the tree species response to effective drought stress, three of the most drought years were chosen for each study site group by matching the pointer years previously performed and SPEI index results. Specifically, it has been observed if, most negative Spei years have been considered, there was a correspondance with the pointer years of all the forest stands incorporated in the same group.

Of course, it was not possible to select common drought years considering all the tree species object of study, since as reported by Tab. 3, the differences in terms of pointer years, especially between the coniferous species and European beech, are remarkable. This is probably due to the fact that the tree species analysed perform different drought prevention strategies: from one side Norway spruce, and more generally silver fir are isohydric species, while the same can not be said for European beech that show a more anisohydric behaviour (H. Pretzsch et al., 2013). Consequently, as drought condition occurs, Norway spruce takes up

isohydric regulation of water status through immediate stomata closure to avoid hydraulic failure (McDowell et al., 2008). This mechanism generates a reduction of carbon photosynthetic uptake which is reflected by low growth rates occurring usually in the first phase of drought episode. Differently, European beech as anisohydric species tends to keep on growing and transpiring until the water is available, leaving the stoma open despite the stress condition (McDowell et al., 2008). Therefore, a reduction in ring width is usually observable in the period following the drought event. This is due to the fact that, depends on drought severity, the tree has to spend time and energy to restore the possible damages due to the eventual hydraulic failure (McDowell et al., 2008; Pretzsch et al., 2013).

Therefore, the coupling of the years showing the most negative SPEI values and the pointer years was carried out taking in consideration the output of negative mean growth deviation computation for Norway spruce and, in its absence, of silver fir, as they better reflect the timing of drought occurrence. In this way, three of the most driest years have been chosen for each study site.

#### 2.4.2 Drought indices

The investigation of tree species response to drought stress was carried out by applying the drought indices provided by Lloret et al., (2011), which define tree – ring growth patterns during and after drought events, allowing for intra-specific and inter-specific comparison. Specifically, the indices are able to exhibit and estimate the ecological tendencies of tree organism related to drought stress distinguishing in *resistance* ( $R_t$ ), *recovery* ( $R_c$ ) and *resilience* ( $R_s$ ), taking in consideration the mean annual or periodic values of basal area increment as following described:

- *PreDr* (pre-drought growth) is the mean basal area increment computed for a period of  $n_{PreDr}$  years before the drought period;
- *Dr* (drought growth) is the basal area increment computed for a period of  $n_{Dr}$  years during the drought period;
- *PostDr* (post-drought growth) is the mean basal area increment computed for a period of  $n_{PostDr}$  years after the drought period.

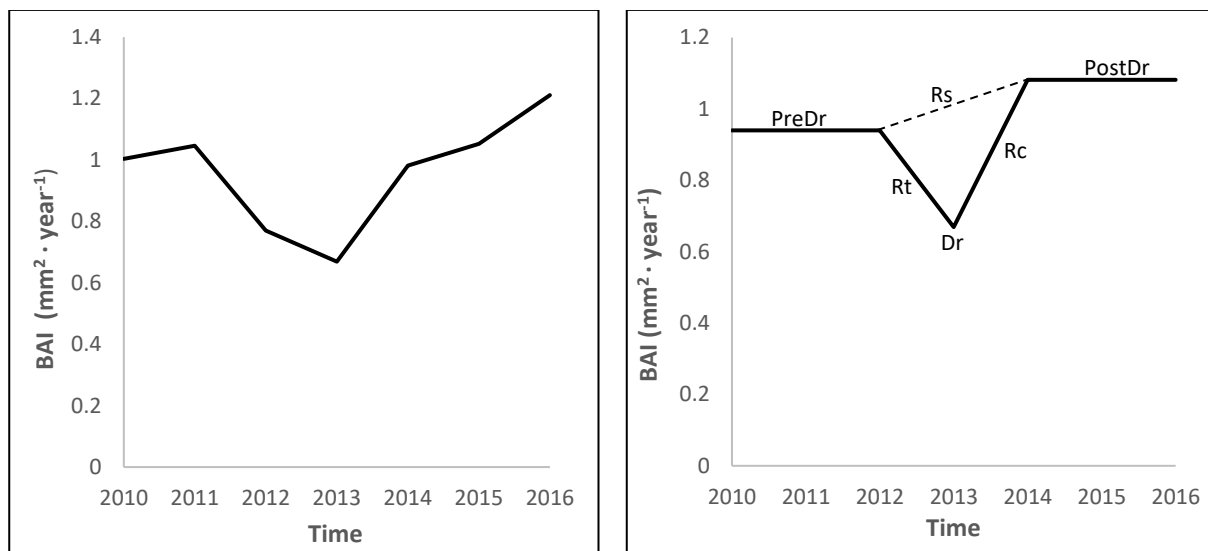
Therefore, the resistance index, assumed as the reversal of the general decrease of physiological performance during disturbance, is reckoned as the ratio between the

performance during and before the disturbance (Kaufman, 1982; Lloret et al., 2011):  $R_t = Dr/PreDr$ . When  $R_t = 1$  indicates the complete resistance whereas, as the value decreases below 1, the resistance response correspondently drop as well.

Differently, recovery mirrors the capacity to recover from the eventual damage provided by the disturbance and is thus computed as the ratio between performance after and during the disturbance (Lloret et al., 2011):  $R_c = PostDr/Dr$ . In this case,  $R_c = 1$  indicates a continuation of low growth performance after the drought event, whereas just in case of  $R_c > 1$  there is evidence of a recovery process. Conversely,  $R_c < 1$  denotes weak recovery but not necessarily an increasing decline of the system.

Finally resilience, defined as the ability and also the rate at which the system restores his functions reaching the pre-disturbance growth levels, is estimated as the ratio between the performance after and before disturbance (Sousa, 1980):  $R_s = PostDr/PreDr$ .  $R_s \geq 1$  indicates full restoration after the drought stress, whilst  $R_s < 1$  testifies low resilience and growth – decline.

To better explain the indices function, Graph 14 shows the basal area growth pattern for Norway spruce in Bosnia Herzegovina 03 stand for the time span 2009 – 2015, within which a drought event occurs in 2013.



**Graph 14:** basal area increment pattern of Norway spruce in *Bosnia Herzegovina 03* mixed stand within the time span 2010-2016. The indices of resistance, recovery and resilience are used to describe the drought stress response. Firstly, the mean basal area increments are computed considering three year before and three year after the drought year, resulting as follow:  $PreDr = 0.94$ ,  $Dr = 0.67$  and  $PostDr = 1.08$ . Thereafter, the indices are elaborated considering the aforementioned relations:  $R_t = Dr/PreDr = 0.71$ ;  $R_c = PostDr/Dr = 1.61$ ;  $R_s = PostDr/PreDr = 1.15$ . The results indicate a drought response characterized by high resilience, high recovery and medium resistance.

Consequently, the drought indices have been computed using the average annual basal increment of three years before the drought event, the basal area increment of dry year selected with the negative SPEI – pointer years margining approach, and the average annual basal increment of three years after drought event. We assumed that three years are sufficient to identify tree ecological reactions to the abiotic stress as well as to avoid the possibility of low-growth period overlap, as also reported in (H. Pretzsch et al., 2013). In addition, other studies show that the choice of a period of 3 years after and prior to the stress event, is a good compromise between the duration of the drought and the short-term growth response (Gazol et al., 2017).

## 2.5 statistical elaborations

The indices values computed are used to answer the research questions as elaborated below. A large dataset comprising the Rt, Rc and Rs has been build up, further including as covariates the basal area of each trees and the SPEI index value of each site both relative to the years considered for drought indices computation, the  $\Delta$ SPEI index value defined as the difference between the value of SPEI for drought year and the mean values of the same index for the following three years, and the plot characteristics data relative to latitude, longitude and elevation.

Thereafter, we used R (R Core Team, 2013) and *lmer* function from *lme4* package (Bates, et al., 2014) in conjunction with *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017) to perform linear mixed effect analysis pointing out how each drought indice varies among tree species. Moreover, we emphasized the relationships which show how the drought ecological response changes according to the trees size and the site climatic characteristics for each tree species. In addition, the condition of absence of collinearity is defined as the possibility of correlation between covariates (Zuur, Ieno, & Elphick, 2010) and previously checked, since more driving-response covariates have been considered to carry out mixed effects models. The collinearity analysis results are available in Table A2 in the *Appendix*.

The main model has been realized entering as fixed effects on tree species, basal area and SPEI index, setting the last two ones as interaction terms. As random effect only plot was put on intercept, omitting to add also the tree number, since it has been observed that there was no relevant influence at single tree level. In order to verify if the model (Eq.1) was well fitted to the ecological variables, the Akaike information criterion (AIC) has been used as fitting

criterion comparing similar models (Eq.2, Eq.3, Eq.4) for each of the drought indices. The respective AIC values are observable in Table A3, reported in the *Appendix*.

Furthermore, a visual inspection of residual plots has been carried out showing that there were not any significant deviations in terms of homoscedasticity. These are fundamental assumptions to check whenever a linear model is performed, especially the absence of heteroscedasticity, which is defined as the condition of approximate equality of the variance of the data across the range of the respective predicted value (Winter, 2013). The relative residual plots have been reported in the *Appedix*.

Finally, p-values were obtained by using the aforementioned lmerTest R-package that applies the Satterthwaite's degrees of freedom method.

In a second step, the same model (Eq.1) was run for a downsized dataset considering only trees with a basal area lower than 1.1 m<sup>2</sup>. Furthermore, a similar model (Eq.5) has been performed only for Rc index replacing SPEI index values with ΔSPEI index value for a following comparison.

In the end, the secondary models (Eq.6, Eq.7 and Eq.8) have been performed in order to highlight how Rt Rc and Rs change in relation to geographical position and altitude. In this case, the use of three distinct models was necessary because of the high collinearity detected among latitude, longitude and altitude, as reported in Table A2.

$$(1) \quad Rt, Rc, Rs \sim Species \cdot (Spei + BA) + (1|Plot)$$

$$(2) \quad Rt, Rc, Rs \sim Species + BA + Spei + (1|Plot)$$

$$(3) \quad Rt, Rc, Rs \sim Species \cdot BA + Spei + (1|Plot)$$

$$(4) \quad Rt, Rc, Rs \sim Species \cdot Spei + BA + (1|Plot)$$

$$(5) \quad Rc \sim Species \cdot (\Delta Spei + BA) + (1|Plot)$$

$$(6) \quad Rt, Rc, Rs \sim Species \cdot Elevation + (1|Plot)$$

$$(7) \quad Rt, Rc, Rs \sim Species \cdot Longitude + (1|Plot)$$

$$(8) \quad Rt, Rc, Rs \sim Species \cdot Latitude + (1|Plot)$$

### 3. RESULTS

#### *3.1 Generic drought stress responses as Resistance, Recovery and Resilience*

The linear mixed effects analysed clearly showed species-specific differences in drought response concerning resistance. Firstly, it has been observed that European beech is generally more resistant compared to the coniferous species, as proved by Graph 15. However, it is also noted that although European beech is characterized by higher resistance coefficient (1.25), at the same time it also shows high variability of the same index, especially when compared with Norway spruce. For what concerns the coniferous species the estimate for silver fir is slightly lower than European beech (1.06) whereas the difference is more accentuated for Norway spruce (0.95), as showed in Graph 16.

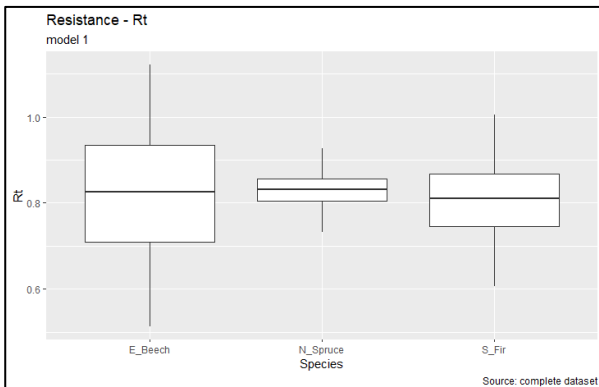
The results perfectly fit with the average resistance value respectively computed for beech, fir and spruce as follow:  $R_t = 0.95, 0.90$  and  $0.87$ .

Conversely to what was observed for the resistance index, the analyses carried out for the recovery index presents significantly different ecological behaviours according to the tree species. In fact, as shown in Graphs 17 and 18, a faster recovery is outlined by coniferous species, also highlighting a better performance of Norway spruce (1.17) compared to silver fir (1.09). On the other hand, the European beech exhibits a lower reactivity in terms of recovery to stress occurrence (0.89) indicating a lower average growth rate in the period immediately following the drought event.

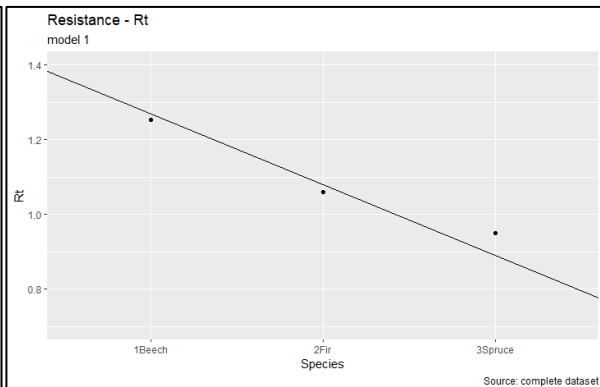
Another aspect to put in evidence is the difference in terms of variability of the index analysed. In fact, Norway spruce and European beech describe a wide range of recovery reactions. Differently, silver fir shows almost punctual response to the large spectrum of drought events considered, even despite the number of samples analysed exceeds 700 units and the collection area falls within a range of 8 degrees of latitude.

Finally, the model developed for the resilience index shows a situation that tends to be flatter and does not show remarkable variations between species, although species-specific differences persist. Graphs 19 and 20 show a good restoration of the ecological functions exercised by European beech (1.11) and silver fir (1.11), while Norway spruce (1.05), despite overcame a level of  $R_s = 1$ , reveals a slight difficulty in returning to a functional reference state after the stress occurrence. Even in this case European beech exhibits great variability of

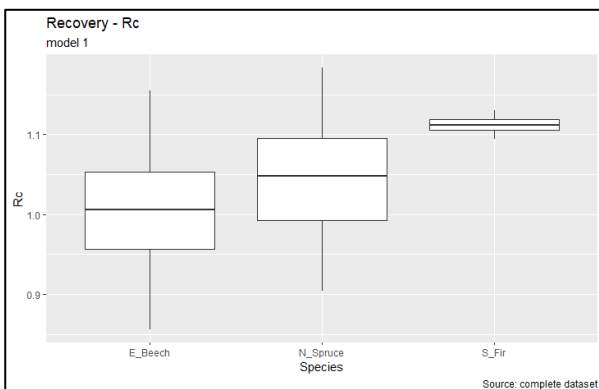
resilience level, followed by Norway spruce. Differently, silver fir still shows a certain stationarity, albeit in lesser terms compared to the situation observed for recovery index.



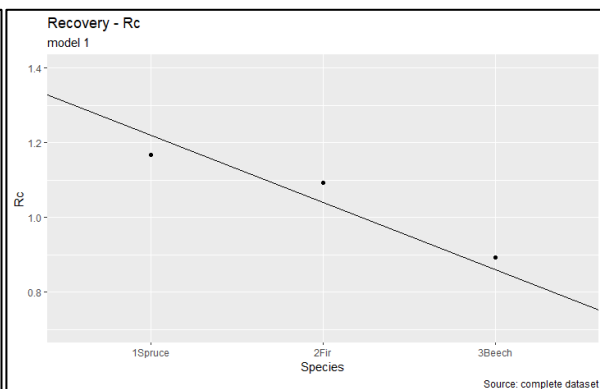
**Graph 15:** Resistance coefficients for European beech, Norway spruce and silver fir performed with linear mixed model.



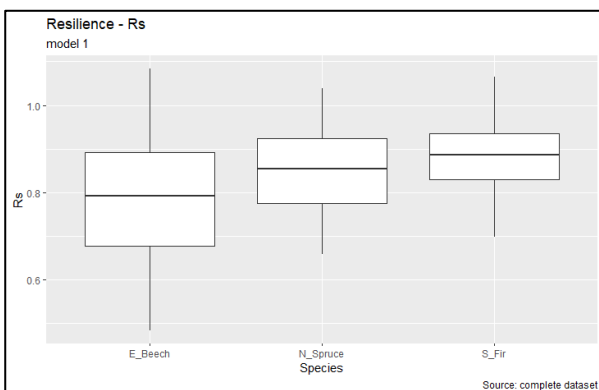
**Graph 16:** Estimated Rt values for European beech, Norway spruce and silver fir using linear mixed effects model. The species are plotted in descending order to show the distances among tree species in terms of drought resistance.



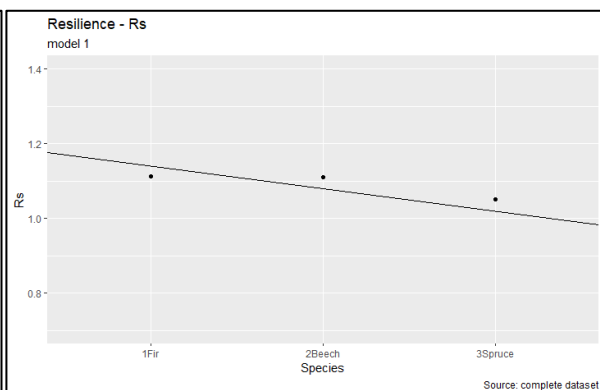
**Graph 17:** Recovery coefficients for European beech, Norway spruce and silver fir performed with linear mixed model.



**Graph 18:** Estimated Rc values for European beech, Norway spruce and silver fir using linear mixed effects model. The species are plotted in descending order to show the distances among tree species in terms of drought recovery.



**Graph 19:** Resilience coefficients for European beech, Norway spruce and silver fir performed with linear mixed model.



**Graph 20:** Estimated Rc values for European beech, Norway spruce and silver fir using linear mixed effects model. The species are plotted in descending order to show the distances among tree species in terms of drought recovery.



**Table 6:** Coefficients of Estimate, Standard error and P-value respectively computed for the linear mixed effects models Eq.4 and Eq.5 of Rt, Rc and Rs. Here European beech was set as the intercept while the other species show the respective deviation from it.

Formula				Rt Species · (Spei + BA) + (1 Plot)				Dt. 1		Formula				Rc Species · (Spei + BA) + (1 Plot)				Dt. 1	
				Estimate	Std. Error	P-value								Estimate	Std. Error	P-value			
<i>E_Beech</i>				1.13035	0.0186	< 2e-16	***		<i>E_Beech</i>				1.02E+00	2.07E-02	< 2e-16	***			
<i>N_Spruce</i>				-0.2005	0.02235	< 2e-16	***		<i>N_Spruce</i>				1.70E-01	2.89E-02	4.37E-09	***			
<i>S_Fir</i>				-0.12009	0.01616	1.25E-13	***		<i>S_Fir</i>				9.31E-02	2.09E-02	8.76E-06	***			
<i>Spei</i>				0.19597	0.01305	< 2e-16	***		<i>Spei</i>				-6.95E-02	1.69E-02	3.75E-05	***			
<i>BA</i>				-0.07271	0.02369	0.00219	**		<i>BA</i>				-5.24E-02	2.92E-02	0.07357	.			
<i>N_Spruce:Spei</i>				-0.14515	0.02481	5.21E-09	***		<i>N_Spruce:Spei</i>				1.15E-01	3.22E-02	0.00037	***			
<i>S_Fir:Spei</i>				-0.08629	0.01809	1.89E-06	***		<i>S_Fir:Spei</i>				5.87E-02	2.35E-02	0.01234	*			
<i>N_Spruce:BA</i>				0.04155	0.02112	0.04914	*		<i>N_Spruce:BA</i>				-9.15E-03	2.74E-02	0.73839				
<i>S_Fir:BA</i>				0.01304	0.02011	0.5168			<i>S_Fir:BA</i>				4.76E-02	2.61E-02	0.06834	.			
Formula				Rs Species · (Spei + BA) + (1 Plot)				Dt. 1		Formula				Rc Species · (ΔSpei + BA) + (1 Plot)				Dt. 1	
				Estimate	Std. Error	P-value								Estimate	Std. Error	P-value			
<i>E_Beech</i>				1.08972	0.01621	< 2e-16	***		<i>E_Beech</i>				1.07E+00	1.96E-02	< 2e-16	***			
<i>N_Spruce</i>				-0.04677	0.02032	0.02139	*		<i>N_Spruce</i>				5.05E-02	2.53E-02	0.046	*			
<i>S_Fir</i>				-0.0194	0.0147	0.18686			<i>S_Fir</i>				4.71E-02	2.01E-02	0.0194	*			
<i>Spei</i>				0.132	0.01186	< 2e-16	***		<i>ΔSpei</i>				-4.65E-03	1.25E-02	0.7104				
<i>BA</i>				-0.11019	0.02132	2.88E-07	***		<i>BA</i>				-3.71E-02	2.90E-02	0.2018				
<i>N_Spruce:Spei</i>				-0.05213	0.02257	0.02092	*		<i>N_Spruce:ΔSpei</i>				3.30E-02	2.28E-02	0.1477				
<i>S_Fir:Spei</i>				-0.03365	0.01645	0.04088	*		<i>S_Fir:ΔSpei</i>				1.50E-03	1.76E-02	0.9321				
<i>N_Spruce:BA</i>				0.03788	0.01921	0.04865	*		<i>N_Spruce:BA</i>				-3.25E-02	2.68E-02	0.2253				
<i>S_Fir:BA</i>				0.05337	0.0183	0.00355	**		<i>S_Fir:BA</i>				3.40E-02	2.57E-02	0.1857				
Formula				Rt Species · (Spei + BA) + (1 Plot)				Dt.2		Formula				Rc Species · (Spei + BA) + (1 Plot)				Dt.2	
				Estimate	Std. Error	P-value								Estimate	Std. Error	P-value			
<i>E_Beech</i>				1.11621	0.01899	< 2e-16	***		<i>E_Beech</i>				1.02165	0.02175	< 2e-16	***			
<i>N_Spruce</i>				-0.19611	0.02463	2.09E-15	***		<i>N_Spruce</i>				0.17105	0.03201	9.55E-08	***			
<i>S_Fir</i>				-0.11252	0.01775	2.51E-10	***		<i>S_Fir</i>				0.10546	0.02311	5.14E-06	***			
<i>Spei</i>				0.19337	0.01329	< 2e-16	***		<i>Spei</i>				-0.07052	0.01726	4.46E-05	***			
<i>BA</i>				0.02093	0.06863	0.76			<i>BA</i>				-0.13091	0.0892	0.14228				
<i>N_Spruce:Spei</i>				-0.15396	0.02533	1.30E-09	***		<i>N_Spruce:Spei</i>				0.12598	0.03301	0.00014	***			
<i>S_Fir:Spei</i>				-0.09187	0.01856	7.63E-07	***		<i>S_Fir:Spei</i>				0.06293	0.02419	0.00931	**			
<i>N_Spruce:BA</i>				-0.05913	0.08941	0.508			<i>N_Spruce:BA</i>				0.07313	0.11601	0.52844				
<i>S_Fir:BA</i>				-0.09174	0.07875	0.244			<i>S_Fir:BA</i>				0.03001	0.10247	0.76965				
Formula				Rs Species · (Spei + BA) + (1 Plot)															
				Estimate	Std. Error	P-value	Dt.2		Estimate	Std. Error	P-value	Dt.2							
<i>E_Beech</i>				1.08E+00	1.64E-02	<2e-16	***												
<i>N_Spruce</i>				-4.66E-02	2.24E-02	0.0371	*		<i>N_Spruce:Spei</i>				-5.09E-02	2.30E-02	0.0271	*			
<i>S_Fir</i>				-9.47E-03	1.61E-02	0.5568			<i>S_Fir:Spei</i>				-3.39E-02	1.69E-02	0.0444	*			
<i>Spei</i>				1.27E-01	1.21E-02	<2e-16	***		<i>N_Spruce:BA</i>				4.33E-02	8.11E-02	0.5932				
<i>BA</i>				-1.02E-01	6.23E-02	0.1027			<i>S_Fir:BA</i>				-5.35E-03	7.15E-02	0.9403				
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1																			

### *3.2 Differences in Resistance, Recovery and Resilience according to regional climatic conditions and individual basal area*

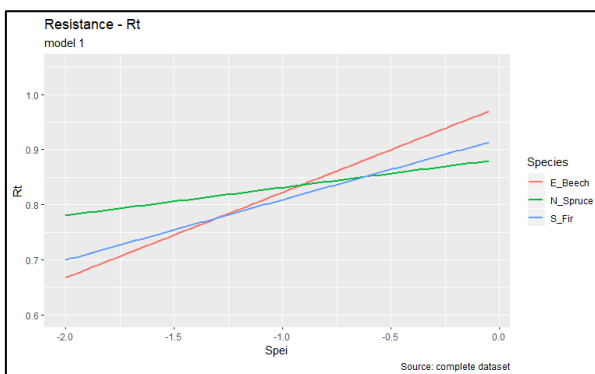
The linear mixed effects analysis underline also the relation existing between the ecological responses of tree species to drought stress and regional climatic conditions, expressed as variations of the Standardised Precipitation - Evapotranspiration Index (SPEI).

Concerning the resistance capacity, it is possible to observe how all three forest species considered, benefit from a progressive increase in water availability until the average level of the precipitation-temperature ratio is reached, which corresponds to a value of SPEI close to 0 (World Meteorological Organization, 2012). However, there are substantial differences between tree species. Specifically, it is observed that silver fir and even more European beech see their own resistance increasing considerably as the climatic conditions improve, starting from levels of  $R_t < 0.7$  for  $SPEI = -2$  (sever dry), to then reach  $R_t$  values respectively greater than 0.9 and close to 1.0 at  $SPEI = 0$ . Norway spruce reacts differently. Indeed, even if it shows an increase in its ability to remain unperturbed by drought events proportional to the occurrence of more favourable climatic conditions, the rate of improvement in resistance remains low on average. In fact, the index shifts from values of  $R_t \leq 8$  for  $SPEI = -2$  to  $R_t < 9$  for  $SPEI = 0$ , as reported by Graph 21.

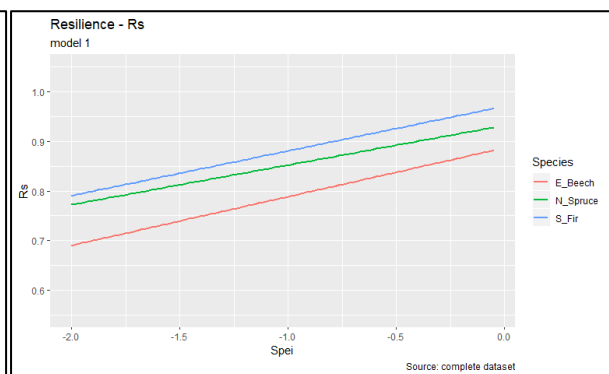
A similar trend is noted for the resilience index, which also tends to increase for all three tree species in parallel with the stabilization of the SPEI at average values. In this case, Norway spruce and silver fir show almost the same positive degree of slope, slightly accentuated for the second one as depicted in Graph 22. The European beech post-drought reaction appears more pronounced, showing more marked increase in resilience according with the improvement of climatic conditions.

Contrasting results are finally observed for the recovery index. In the period immediately following the drought, silver fir and European beech do not seem to benefit from the increase in water availability, albeit in a different way. Indeed, while for silver fir there is a slightly negative trend according to a general improvement of climatic conditions, European beech shows a significant worsening of the recovery coefficient for SPEI values tending to 0. On the contrary, Norway spruce is the only species to show a significant increase in its ability to recover for climatic conditions on average more favourable, as evidenced by Graph 23. In this case, a further linear mixed effects analysis was performed using the Eq.5 by replacing SPEI index with the respective  $\Delta SPEI$ , defined as the difference between the value of SPEI for

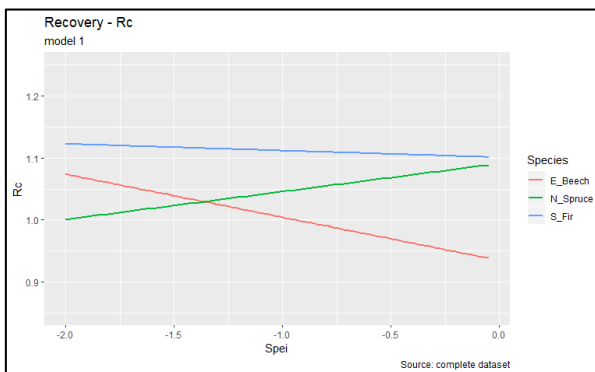
drought year and the mean values of the same index for the following three years. As a consequence, the respective slopes of silver fir and European beech, have been considerably reduced, resulting in an almost stationary situation of the recovery index despite the climatic conditions change. Nevertheless, a slight negative trend persisted in both cases. In this context, as shown in Graph 24, the trend of Norway spruce has not changed. However, the use of  $\Delta$ SPEI does not lead to significant coefficient, testifying that SPEI index should show the right correlation with basal area increment.



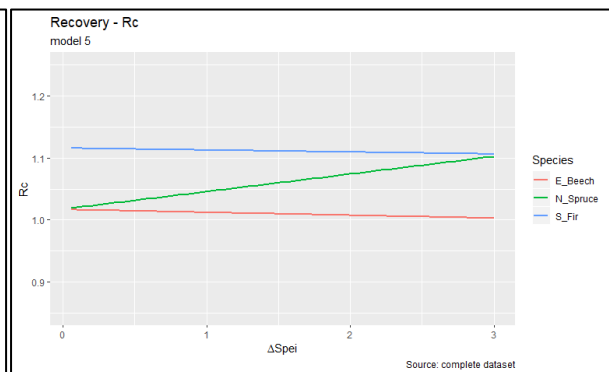
**Graph 21:**  $R_t$  – SPEI relationship performed with linear mixed effects model Eq. 1 (Formula:  $R_t \sim \text{Species} \cdot (\text{Spei} + \text{BA}) + (1|\text{Plot})$ ).



**Graph 22:**  $R_s$  – SPEI relationship performed with linear mixed effects model Eq. 1 (Formula:  $R_s \sim \text{Species} \cdot (\text{Spei} + \text{BA}) + (1|\text{Plot})$ ).



**Graph 23:**  $R_c$  – SPEI relationship performed with linear mixed effects model Eq. 1 (Formula:  $R_c \sim \text{Species} \cdot (\text{Spei} + \text{BA}) + (1|\text{Plot})$ ).



**Graph 24:**  $R_c$  –  $\Delta$ SPEI relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_c \sim \text{Species} \cdot (\Delta\text{Spei} + \text{BA}) + (1|\text{Plot})$ ).

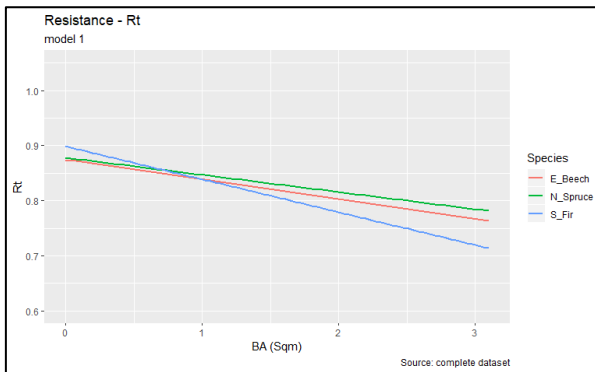
Subsequently, possible relationships that describe how drought indices vary according to the tree's basal area were analysed. It should be remembered that most of the samples come from individuals belonging to the dominant and codominant layer. Nevertheless, the range of basal

area detected is very wide. For this reason, it was appropriate to run the model on two separate datasets: the first complete dataset (Dt.1) already used for the analysis of the effect of climatic conditions; the second (Dt.2) obtained by considering trees with a basal area lower than 1.1 square meters. This selection was also applied due to the fact that individuals with an extremely larger basal area are relatively few compared to the total number of trees sampled. It was therefore decided to verify that the presence of a high-size small group of trees was not significantly influencing the ecological relationship analysed.

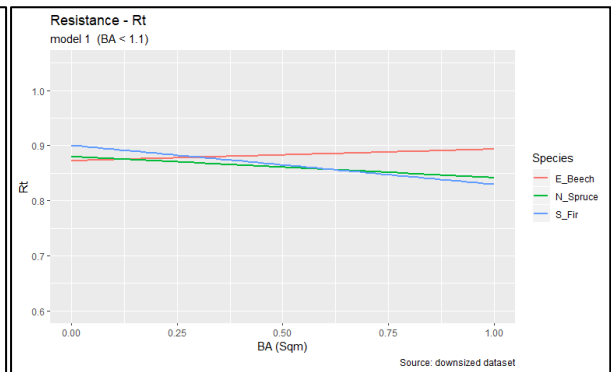
The analysis of the resistance index carried out on Dt.1 shows that, as the size of the basal area increases, the three tree species considered denote a progressive decrease in the ability to cope with the impact of drought stress, more marked for silver fir. Alternatively, if we consider only the individuals of moderate size (Dt.2), it is observed how the trends of silver fir and European beech assume a less steep slope, showing less sensibility to basal area change, while Norway spruce responds in a completely different way, assuming a positive trend (Graphs 25 and 26). However, the coefficients elaborated for Dt.2 resulted no particularly significant, as reported in Table 6.

With regard to the recovery index, it can be observed that both Norway spruce and European beech respond negatively to the increase in basal area regardless of the dataset considered, although a less steep slope is noted for areas lower than 1.1 square meters. In contrast, silver fir seems to behave almost steadily in Dt.1, while it also tends to react more slowly after drought stress for trees with more moderate basal areas (Dt.2), as shown by Graph 27 and 28. However it is necessary to specify that recovery index appears non-significantly affected by basal area factor, regardless of the dataset used.

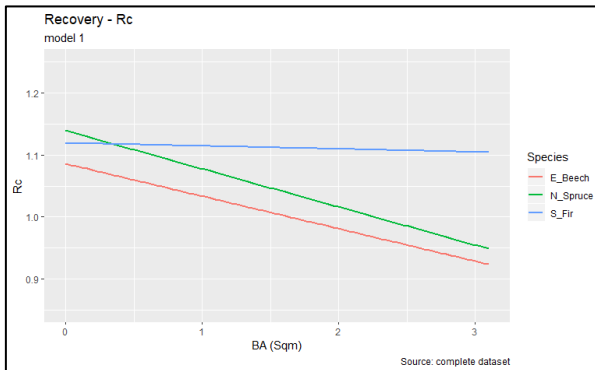
Finally, the analysis carried out for the resilience index shows that as the basal area increases, the ability to return to the reference functional state before the drought period decreases proportionally, with a less marked slope for individuals with a lower basal area (Dt.2). A further aspect to emphasize is that in the analysis performed on Dt.1 Norway spruce is more affected at bigger diameters than the silver Fir (Graph 29). Nonetheless, even in this case the analysis conducted over the Dt.2 was not significant.



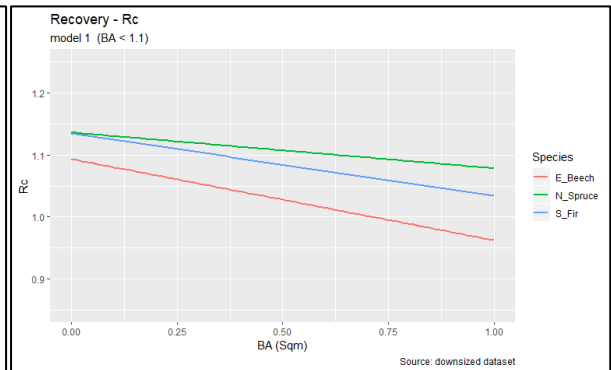
**Graph 25:**  $R_t - BA$  relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_t \sim \text{Species} \cdot (\text{Spei} + BA) + (1|Plot)$ ).



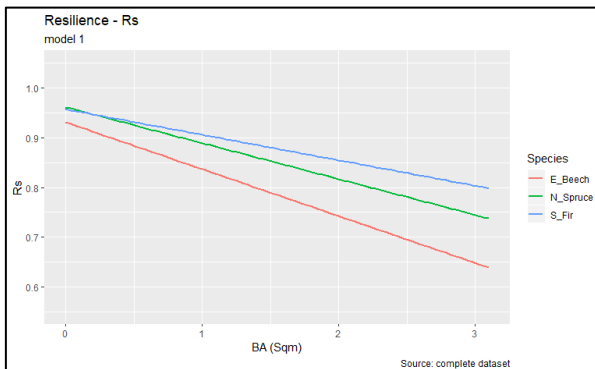
**Graph 26:**  $R_t - BA$  relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_t \sim \text{Species} \cdot (\text{Spei} + BA) + (1|Plot)$ ) considering trees with  $BA < 1.1 \text{ m}^2$ .



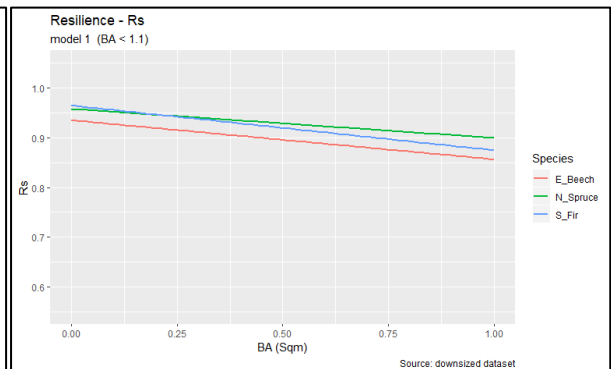
**Graph 27:**  $R_c - BA$  relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_c \sim \text{Species} \cdot (\text{Spei} + BA) + (1|Plot)$ ).



**Graph 28:**  $R_c - BA$  relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_c \sim \text{Species} \cdot (\text{Spei} + BA) + (1|Plot)$ ) considering trees with  $BA < 1.1 \text{ m}^2$ .



**Graph 29:**  $R_s - BA$  relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_s \sim \text{Species} \cdot (\text{Spei} + BA) + (1|Plot)$ ).



**Graph 30:**  $R_s - BA$  relationship performed with linear mixed effects model Eq. 5 (Formula:  $R_s \sim \text{Species} \cdot (\text{Spei} + BA) + (1|Plot)$ ) considering trees with  $BA < 1.1 \text{ m}^2$ .

### *3.3 Analysis of Resistance, Recovery and Resilience according to elevation and geographical position*

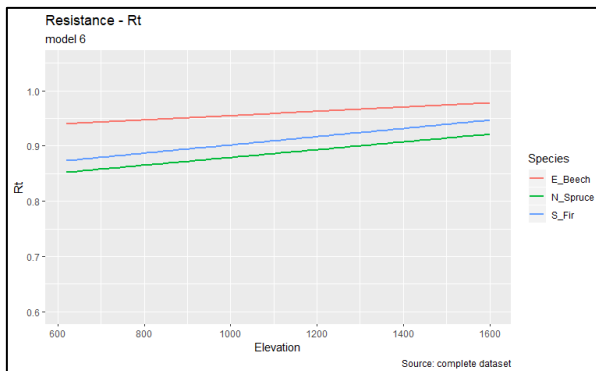
As the last step, the drought indices have been correlated with elevation, latitude and longitude of the respective study sites, in order to better investigate how ecological responses of mixed forest stands change according to different geographical locations. However, it should be noted that the following elaborations have been carried out only to provide further explanatory support to the models previously described, i.e. to better analyse the influences of environmental factors on the ecological strategies of the tree species investigated. Indeed, it was not possible to include the aforementioned covariates in the previous models because of their strong collinearity, as described in *chapter 2.5*. Therefore, it was decided to elaborate simpler models (Eq.6, Eq.7 and Eq. 8), one for each covariate, to observe the only influence of geographical position (latitude and longitude) and altitude. As a consequence, the use of simple models led to the elaboration of non-significant results in several cases (Table 7). Nevertheless, some of the information obtained was also interesting and thus, they provide additional support in explaining the ecological reactions analysed.

The analyses conducted show that the resistance index resulted positively correlated with the site elevation for all the tree species, which improves their own capacity to cope with drought stress as the altitude increases within the range considered (600 – 1600), as shown by Graph 30. Conversely, for what concern the geographical position influence, opposite effects have been found. Specifically, European beech and silver fir slightly increase resistance capacity as latitude increases as well, while it can be observed that the same capacity drop as we move toward higher values of longitude. A completely different behaviour is manifested by Norway spruce, which, on the contrary, tends to decrease resistance reaction moving in Northern direction, whereas it seems to lightly rise up as longitude increases, as illustrated in Graph 31 and 32. It should be underlined that only the correlation of Norway spruce with longitude covariate is statistically significant, as reported in Table 7.

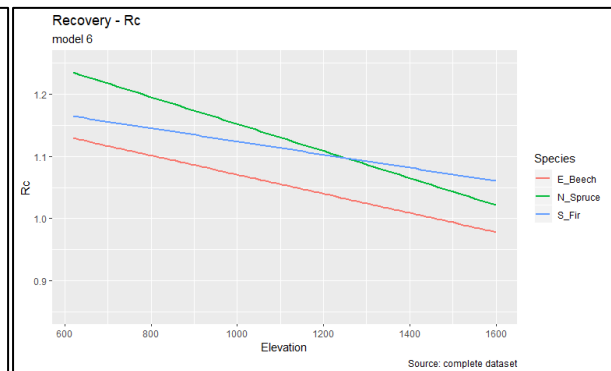
In contrast to what was observed for resistance, it is noted that the recovery capacity of tree species analysed tends to decrease significantly as the elevation increases, with particular relevance for Norway spruce (Graph 33). The three forest species, on the other hand, seem to benefit in terms of recovery when they are in northern geographical areas, always considering the latitudinal range interested (41°91' – 49°09'). Finally, European beech and silver fir still show a positive trend when correlated with longitude, whereas Norway spruce recovery drastically drops as it moves towards eastern regions (Graph 35). In this context, only Norway

spruce is well correlated with covariates of latitude and longitude, while the elevation only shows a weak correlation with all three species.

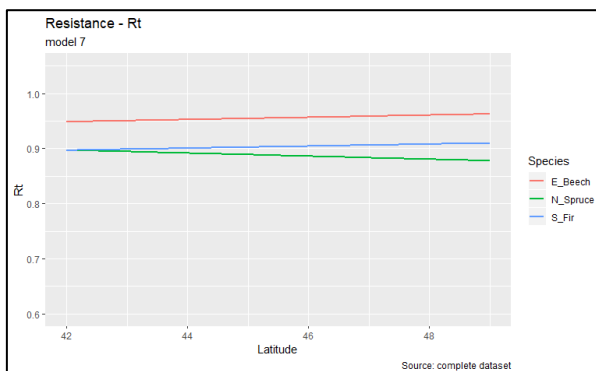
In the final analysis, it is observed that the resilience of European beech and Norway spruce shows a slightly negative trend if correlated with altitude while the silver fir remains almost stationary. The correlation with latitude, on the other hand, indicates a modest improvement in the resilience capacity of tree species as we move to the northernmost areas. Finally, the relationship conducted with longitude shows that, while silver fir and Norway spruce are characterized by a proportionally negative trend, especially for the latter, European beech tends to remain unchanged regardless the degree of longitude, showing a slight improvement only in the more eastern areas. In this case, only the longitude correlation does not report significant value.



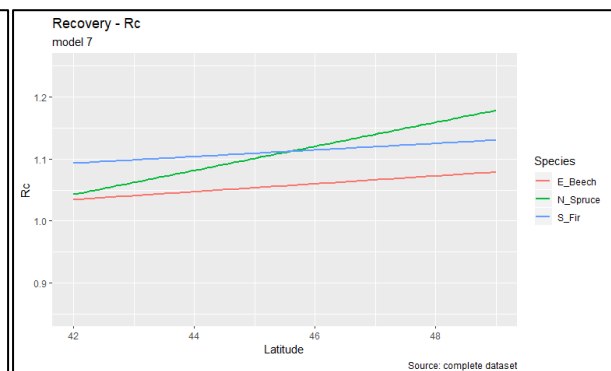
**Graph 30:**  $R_t$  – Elevation (m) relationship performed with linear mixed effects model Eq. 6 (Formula:  $R_t \sim \text{Species} \cdot \text{Elevation} + (1|\text{Plot})$ ).



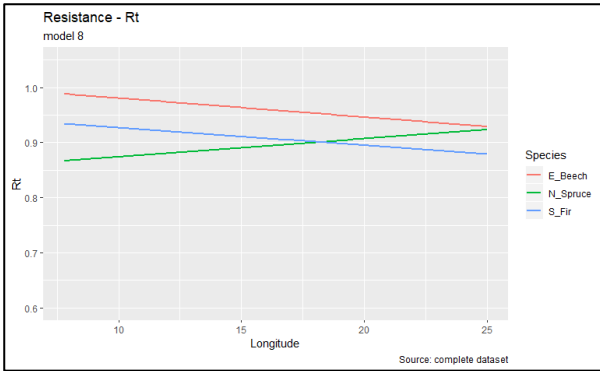
**Graph 33:**  $R_c$  – Elevation (m) relationship performed with linear mixed effects model Eq. 6 (Formula:  $R_c \sim \text{Species} \cdot \text{Elevation} + (1|\text{Plot})$ ).



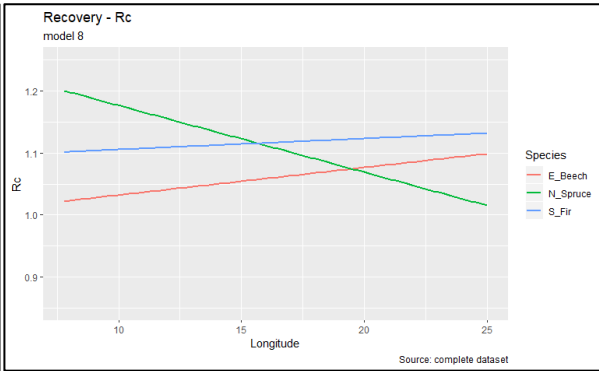
**Graph 31:**  $R_t$  – Latitude (°) relationship performed with linear mixed effects model Eq. 7 (Formula:  $R_t \sim \text{Species} \cdot \text{Lat} + (1|\text{Plot})$ ).



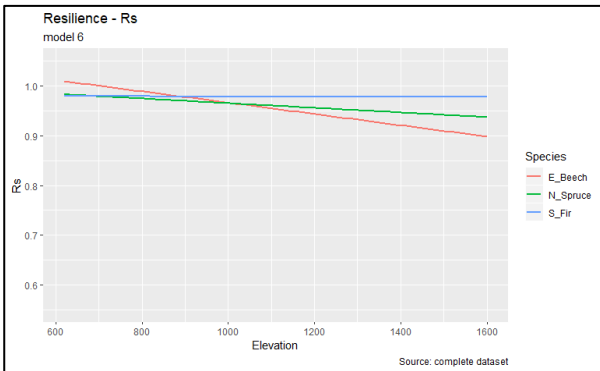
**Graph 34:**  $R_c$  – Latitude (°) relationship performed with linear mixed effects model Eq. 7 (Formula:  $R_c \sim \text{Species} \cdot \text{Lat} + (1|\text{Plot})$ ).



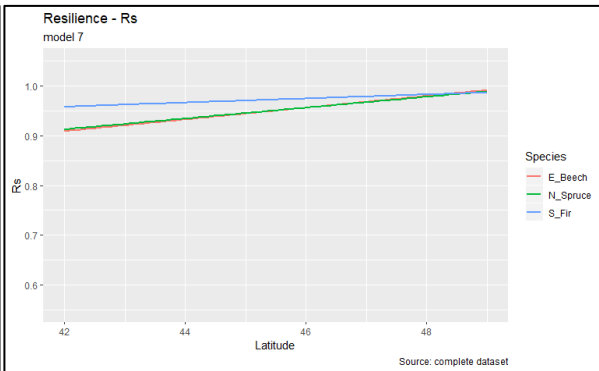
**Graph 32:**  $R_t$  – Longitude ( $^{\circ}$ ) relationship performed with linear mixed effects model Eq. 8 (Formula:  $R_t \sim \text{Species} \cdot \text{Lon} + (1|\text{Plot})$ ).



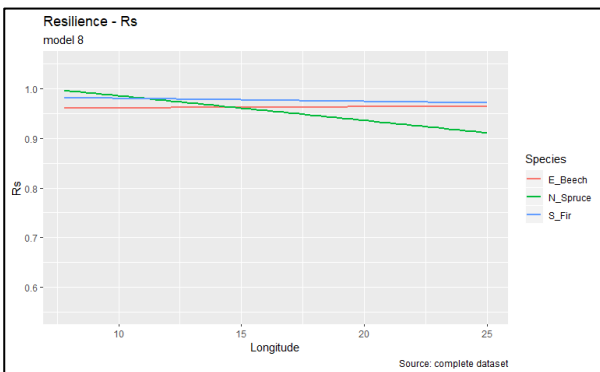
**Graph 35:**  $R_c$  – Longitude ( $^{\circ}$ ) relationship performed with linear mixed effects model Eq. 8 (Formula:  $R_c \sim \text{Species} \cdot \text{Lon} + (1|\text{Plot})$ ).



**Graph 36:**  $R_s$  – Elevation (m) relationship performed with linear mixed effects model Eq. 6 (Formula:  $R_s \sim \text{Species} \cdot \text{Elevation} + (1|\text{Plot})$ ).



**Graph 37:**  $R_s$  – Latitude ( $^{\circ}$ ) relationship performed with linear mixed effects model Eq. 7 (Formula:  $R_s \sim \text{Species} \cdot \text{Lat} + (1|\text{Plot})$ ).



**Graph 38:**  $R_s$  – Longitude ( $^{\circ}$ ) relationship performed with linear mixed effects model Eq. 8 (Formula:  $R_s \sim \text{Species} \cdot \text{Lon} + (1|\text{Plot})$ ).



**Table 7:** Coefficients of Estimate, Standard error, Degree of freedom and P-value respectively computed for the linear mixed effects models Eq.6, Eq.7 and Eq.8 of Rt, Rc and Rs..

Formula				Dt. 1	Formula				Dt. 1
<i>Rt ~ Species · Elevation + (1 Plot)</i>					<i>Rc ~ Species · Elevation + (1 Plot)</i>				
	Estimate	Std. Error	P-value			Estimate	Std. Error	P-value	
<i>E_Beech</i>	9.16E-01	4.83E-02	< 2e-16	***	<i>E_Beech</i>	1.23E+00	5.50E-02	<2e-16	***
<i>N_Spruce</i>	-1.07E-01	4.39E-02	0.0147	*	<i>N_Spruce</i>	1.45E-01	5.54E-02	0.00895	**
<i>S_Fir</i>	-8.87E-02	3.07E-02	0.0039	**	<i>S_Fir</i>	5.56E-03	3.89E-02	0.88626	
<i>Elevation</i>	3.89E-05	4.48E-05	0.3913		<i>Elevation</i>	-1.54E-04	5.13E-05	0.00432	**
<i>N_Spruce:Elevation</i>	3.14E-05	3.87E-05	0.4168		<i>N_Spruce:Elevation</i>	-6.34E-05	4.89E-05	0.19432	
<i>S_Fir:Elevation</i>	3.57E-05	2.95E-05	0.2261		<i>S_Fir:Elevation</i>	4.79E-05	3.74E-05	0.19984	
Formula				Dt. 1	Formula				Dt. 1
<i>Rt ~ Species · Lat + (1 Plot)</i>					<i>Rc ~ Species · Lat + (1 Plot)</i>				
	Estimate	Std. Error	P-value			Estimate	Std. Error	P-value	
<i>E_Beech</i>	8.64E-01	2.52E-01	0.0015	**	<i>E_Beech</i>	7.67E-01	3.11E-01	0.0183	*
<i>N_Spruce</i>	1.51E-01	2.09E-01	0.4716		<i>N_Spruce</i>	-5.40E-01	2.65E-01	0.0414	*
<i>S_Fir</i>	-4.49E-02	1.49E-01	0.7629		<i>S_Fir</i>	1.03E-01	1.89E-01	0.5856	
<i>Latitude</i>	2.02E-03	5.40E-03	0.7108		<i>Latitude</i>	6.36E-03	6.67E-03	0.3469	
<i>N_Spruce:Latitude</i>	-4.81E-03	4.49E-03	0.2841		<i>N_Spruce:Latitude</i>	1.31E-02	5.68E-03	0.0215	*
<i>S_Fir:Latitude</i>	-1.61E-04	3.19E-03	0.9598		<i>S_Fir:Latitude</i>	-1.05E-03	4.04E-03	0.7948	
Formula				Dt. 1	Formula				Dt. 1
<i>Rt ~ Species · Lon + (1 Plot)</i>					<i>Rc ~ Species · Lon + (1 Plot)</i>				
	Estimate	Std. Error	P-value			Estimate	Std. Error	P-value	
<i>E_Beech</i>	1.02E+00	4.78E-02	< 2e-16	***	<i>E_Beech</i>	9.88E-01	6.04E-02	<2e-16	***
<i>N_Spruce</i>	-1.74E-01	3.69E-02	#####	***	<i>N_Spruce</i>	2.97E-01	4.67E-02	2.29E-10	***
<i>S_Fir</i>	-5.65E-02	3.25E-02	0.082	.	<i>S_Fir</i>	1.00E-01	4.11E-02	0.0148	*
<i>Longitude</i>	-3.44E-03	2.78E-03	0.2236		<i>Longitude</i>	4.45E-03	3.51E-03	0.2128	
<i>N_Spruce:Longitude</i>	6.74E-03	2.34E-03	0.004	**	<i>N_Spruce:Longitude</i>	-1.52E-02	2.96E-03	2.78E-07	***
<i>S_Fir:Longitude</i>	2.65E-04	1.79E-03	0.8819		<i>S_Fir:Longitude</i>	-2.68E-03	2.26E-03	0.2357	
Formula				Dt. 1	Formula				Dt. 1
<i>Rs ~ Species · Elevation + (1 Plot)</i>					<i>Rs ~ Species · Lat + (1 Plot)</i>				
	Estimate	Std. Error	P-value			Estimate	Std. Error	P-value	
<i>E_Beech</i>	1.08E+00	4.27E-02	< 2e-16	***	<i>E_Beech</i>	4.11E-01	2.12E-01	0.06026	.
<i>N_Spruce</i>	-6.81E-02	3.96E-02	0.0852	.	<i>N_Spruce</i>	4.33E-02	1.89E-01	0.81856	
<i>S_Fir</i>	-1.01E-01	2.77E-02	0.0003	***	<i>S_Fir</i>	3.74E-01	1.34E-01	0.00535	**
<i>Elevation</i>	-1.14E-04	3.97E-05	0.0066	**	<i>Latitude</i>	1.19E-02	4.55E-03	0.01326	*
<i>N_Spruce:Elevation</i>	6.69E-05	3.49E-05	0.0556	.	<i>N_Spruce:Latitude</i>	-9.40E-04	4.04E-03	0.81608	
<i>S_Fir:Elevation</i>	1.13E-04	2.66E-05	#####	***	<i>S_Fir:Latitude</i>	-7.74E-03	2.88E-03	0.00713	**
Formula					Formula				
<i>Rs ~ Species · Lon + (1 Plot)</i>					<i>Rs ~ Species · Lon + (1 Plot)</i>				
	Estimate	Std. Error	P-value	Dt. 1		Estimate	Std. Error	P-value	Dt. 1
<i>E_Beech</i>	9.59E-01	4.21E-02	< 2e-16	***	<i>Longitude</i>	2.24E-04	2.45E-03	0.9274	
<i>N_Spruce</i>	7.67E-02	3.34E-02	0.0216	*	<i>N_Spruce:Longitude</i>	-5.20E-03	2.11E-03	0.0138	*
<i>S_Fir</i>	2.77E-02	2.94E-02	0.3459		<i>S_Fir:Longitude</i>	-8.40E-04	1.61E-03	0.6029	
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1									

## 4. DISCUSSION

Our results show that the three species considered implement species-specific strategies when facing droughts. First of all, the analysis of the resistance index shows how European beech differs from the coniferous species by its anisohydric character, while the latter tend to preserve an isohydric behaviour. As anticipated in chapter 2.4.1, in case of drought occurrence an anisohydric tree species tends to keep on growing and transpiring until the water is available, leaving the stomata open despite the stress condition and running the risk of hydraulic failure occurrence (McDowell et al., 2008). Conversely, the isohydric tree species implements defence actions against excessive transpiration by immediately closing its own stomata (McDowell et al., 2008). As suggested by Klein, (2014), to assert if a tree species has isohydric or anisohydric properties it is necessary to refer to the stomatal conductance of leaf water potential at 50% of the maximum ( $\varphi_{g_s50}$ ). However, the fact that European beech and Norway spruce are diametrically opposed in this respect has already been amply demonstrated by previous studies (H. Pretzsch et al., 2013; Schäfer et al., 2017). According to Guicherd, (1994),  $\varphi_{g_s50}$  of silver fir computed for forest stands in French Alpine region, ranges from -0.2 to -0.4. A completely different magnitude is shown by the  $\varphi_{g_s50}$  calculated for European beech, which varies between -2.12 and -3.17 (Aranda, Gil, & Pardos, 2000). Given the distinction between species in terms of ecological strategies, we can therefore attribute the highest level of resistance of European beech to its ability to maintain physiological activities despite the stress condition, thus maintaining diametric growth at standard values. In addition, in the context of mixed stands, European beech is further favoured by the presence of coniferous species, because, as already pointed out by Pretzsch et al., (2013), the earlier stop of water consumption by Norway spruce and silver fir should increase water and further mineral resources availability for the deciduous species.

Further proof of the above is offered by the recovery index results, which, on the contrary, see coniferous species as favoured with the primacy of Norway spruce. Indeed, this can be partially attributed to the anisohydric trait of European beech that, in the period immediately after the stress occurrence, it should spend a modest share of resources and energy to restore the eventual damage provided by hydraulic failure (McDowell et al., 2008) saving on growth. Indeed, according to severity of drought, cavitation of water conducting pipes can be generated, which in turn lead to losses of leaves and fine roots (Pretzsch et al., 2013).

It should also be noted that, given the same vegetative vigour, Norway spruce and silver fir tend to start growing earlier than European beech, even by one month in certain cases.

Therefore, as also suggested by Thurm et al., (2016), in a context of mixed forest, the coniferous species could benefit from a temporary greater availability of resources at the beginning of the growing season, regardless of whether a drought event has occurred in the previous year. Moreover, since silver fir and Norway spruce have different root system structures, i.e. quite deep and following well branched for the first one and more shallow but still quite ramified from the second one, we can assume that these tree species are able to exploit separate soil levels. In addition, silver fir may also further provide indirect water to Norway spruce through the ecological mechanism known as “hydraulic lift”. Indeed, wood plants under dry conditions can draw and acquire water from particularly deep roots which is then released overnight into the surface soil layers of lower water potential as an external reservoir (Caldwell & Richards, 1998). All of these circumstances would explain the inter-specific difference obtained for recovery rate.

To complete the answer to the first research question, it is necessary to take into account the results obtained for the resilience index. Similar to that observed for the resistance capacity we can note that European beech and silver fir show again a better performance than Norway spruce. This is perfectly in line with previous studies (H. Pretzsch et al., 2014, 2013) where it was observed that, in the comparison of different tree species, those that have high recovery rates tend on average to be lacking in terms of resistance and resilience, vice versa, species characterized by low recovery standards show good performance in withstanding the impact of drought and restoration the pre-stress functional levels.

However, two important aspects resulted from this research has be highlighted. First of all, it should be noted that silver fir, despite having the same isohydric traits similar to Norway spruce, it maintains high standards both in terms of resistance and resilience. In second instance, it can be observed that Norway spruce, despite having the lowest level of resilience, remains above the threshold of  $R_s = 1$ , indicating a slower but full recovery of pre-stress functional standards. This general ability to respond energetically to the occurrence of drought stress should perhaps be sought in the context of a mixed forest. A significant example is provided by Lebourgeois et al., (2013), who shows how silver fir trees growing in mixed stands can better cope with summer droughts compared to those ones growing in pure stands. Similarly it has been stated for European beech (H. Pretzsch et al., 2013), Douglas fir (Thurm et al., 2016) and silver fir (Gazol & Camarero, 2016). It could be assumed that mixed forests are well suited to promoting facilitation mechanisms and strategies of complementarity between the species they host. Complementarity describes the condition for which different plant species with different morphological and physiological properties are able to use

environmental resources in different ways allowing more than one species to acquire the same resource (Westoby & Wright, 2006). In our case we have already appreciated complementary and facilitation occurrence: firstly among European beech and coniferous species that, during drought occurrence they use water in different time; later a similar condition we assume to happen between Norway spruce and silver fir that may exploit soil resources from different areas, whereas silver fir may also increase water availability in shallow soil horizons.

Following, the results relative to the correlation performed between drought indices and SPEI values seem to be perfectly in line with the relationship above described. Indeed, the fact that resilience and resistance show similar species-specific responses is also emphasized by the regional climatic condition correlation, which prove that the three tree species are generally more favored to cope with drought events in more moist environment on average. Nonetheless, a different situation is exposed by the recovery index, for which, firstly, European beech and then, secondly, silver fir show a negative correlation to the improvement of climatic conditions. This situation could be explained by the fact that, under certain circumstances, unfavourable regional climatic characteristics have led to the development of specific plant adaptation strategies, for which a better resilience in broad sense can be expressed by trees located in drier sites. This condition would be also in line with the stress gradient hypothesis, which states that facilitation mechanisms are more likely to occur on unfavorable growing conditions (Callaway & Walker, 1997). One example can be provided by some pure European beech stands analysed by (Schäfer et al., 2017). Moreover, it should be also taken into account that evapotranspiration rate changes may have contrasting effects on tree species growth, depending on site conditions, forest type and the amount of precipitation fallen (Vicente-Serrano et al., 2010). Indeed, in already dry areas or even in temperate sites an increase in the evapotranspiration would negatively affect tree functionality, whereas in areas characterized by high moisture conditions, vegetative activities may be enhanced by an increasing in evapotranspiration rate. However, our results indicate that, in general, tree species tend to express a better reaction to drought phenomena as a function of a climatic gradient, for which better moisture conditions correspond to better resistance and resilience performance.

Moreover, the fact that the three tree species generally exhibit better response to drought stress in environments where dry weather conditions do not usually occur is also confirmed by the correlation with latitude that shows how resilience generally increases in the northernmost regions. Naturally, this observation must be contextualized to the latitudinal range available for study, limited to a scale of almost 8 degrees (41°91' – 49°09') that falls

within three major Ecological Zones aforementioned in the *Introduction*. From further outputs it is also observed that drought reaction tends to be disadvantaged by an increasing elevation, probably due to the decrease of soil resources availability. Differently, longitude variation seems to significantly influence Norway spruce behaviour, which shows better resistance capacity as we move toward eastern regions, probably due to its continental traits but, at the same time, it seems to suffer in terms of recovery and resilience in the same locations.

Finally the outputs of individual basal area correlation have highlighted that the tree species drop both in resistance and resilience for generally increased in dimension. This could be due to the fact that relative smaller trees are more covered by the larger neighbours, enabling them to less transpire in case of particularly dry condition because less exposed to sun radiation (Aussenac, 2000). Similar results have been found out by Hans Pretzsch et al., (2018). Moreover, if we generally assume that larger trees in terms of basal area should be even the tallest, it is also possible to consider that high-dimension trees are supposed to be more subject to hydraulic constraints, as reported by Carrer & Urbinati, (2004), which could promote phenomena of hydraulic failure in case of drought occurrence.

The different results provided by this study were able to satisfied the initial research questions. Nevertheless it should be considered that resistance, recovery and resilience of tree species capacity are influenced by several factors, both environmental (climatic condition, stational characteristics, biotic and abiotic agents) and physiological. Therefore, even if the models performed can provide a general understanding of the ecological properties investigated, it should be remembered that ecosystems in reality are always more complex, and therefore requires continuous studies and updates.

## 5. CONCLUSIONS

The current study conducted over a large number of mixed forest stands of European beech, Norway spruce and silver fir, confirmed that tree species considered perform species-specific short-term reactions when drought stress occurs. Our results provide evidence that Norway spruce tends to perform high recovery simultaneously with low resistance and resilience, whereas conversely, European beech generally show remarkable level of resistance and resilience to coping with droughts but it turns out to be weak in terms of recovery, as highlighted by previous studies in similar context (H. Pretzsch et al., 2014, 2013). The outputs concerning silver fir have revealed that, despite being a coniferous species, it preserved a high standard of all indices computed, showing impressive capacity of resilience that we assume is partially due to its well-developed deep-rooting system. Moreover, we can further assume that Norway spruce benefits from being mixed with European beech but especially with silver fir, since despite showing lower level of resilience, it remains on average above the threshold of  $R_s = 1$ , indicating full recovery of pre-stress reference state in relative short period. We assume that this is probably due to the combination of complementarity and facilitation factors which likely occur in mixed forest stands, here significantly enhanced by the presence of silver fir.

Furthermore, the possibility to conduct mixed analysis over a wide spectrum of latitude, has led to the conclusion that regional climatic condition is one of the major driving factors that influence the species drought event response and that tree species generally profit of better climatic regimes.

In addition, the study allowed us to highlight how tree species tend to reduce both their resistant and resilient performance as individual basal area increases, outlining how dimension is significant when dealing with drought stress.

Nevertheless, more ecological factors that may affect tree species drought-facing strategies should be considered in future research to improve forest modelling in this context, especially site-specific aspects such as soil properties and the competition index.

Moreover, a following step to better address the role of mixed forest stands in coping with drought stress, should be to conduct similar analysis consider pure stands of Norway spruce and European beech close to the mixed stands analysed in the current study. This should allow to carefully outline the differences in terms of growth indices by using the triplet

approach, as already applied in previous studies (H. Pretzsch et al., 2014, 2013; Thurm et al., 2016).

However, the current study highlights specific ecological functions inherent in the ecosystems analysed, which show how mixed forests stands offer real advantages in terms of climate change effects mitigation. Therefore, foresters should take in consideration the outputs of the recent research relative to this context to improve forest management practices also concerning the target to increase wood productivity. In this prospective, mixed forests should be enhanced, not necessary in against-monoculture sense, but even just by promoting their spread over the land surfaces where they should be naturally present would be a first step toward smart forestry.





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Finally, I would like to thank all my friends, many of whom have been part of this adventure called University and with whom I have shared unique experiences, which only happen in this moment of our lives. Some of them have become a second family, irreplaceable, and linked by something indissoluble that I hope will accompany us for many years.

# APPENDIX

Table A1: *Climo 1 –Plot groups distribution.*

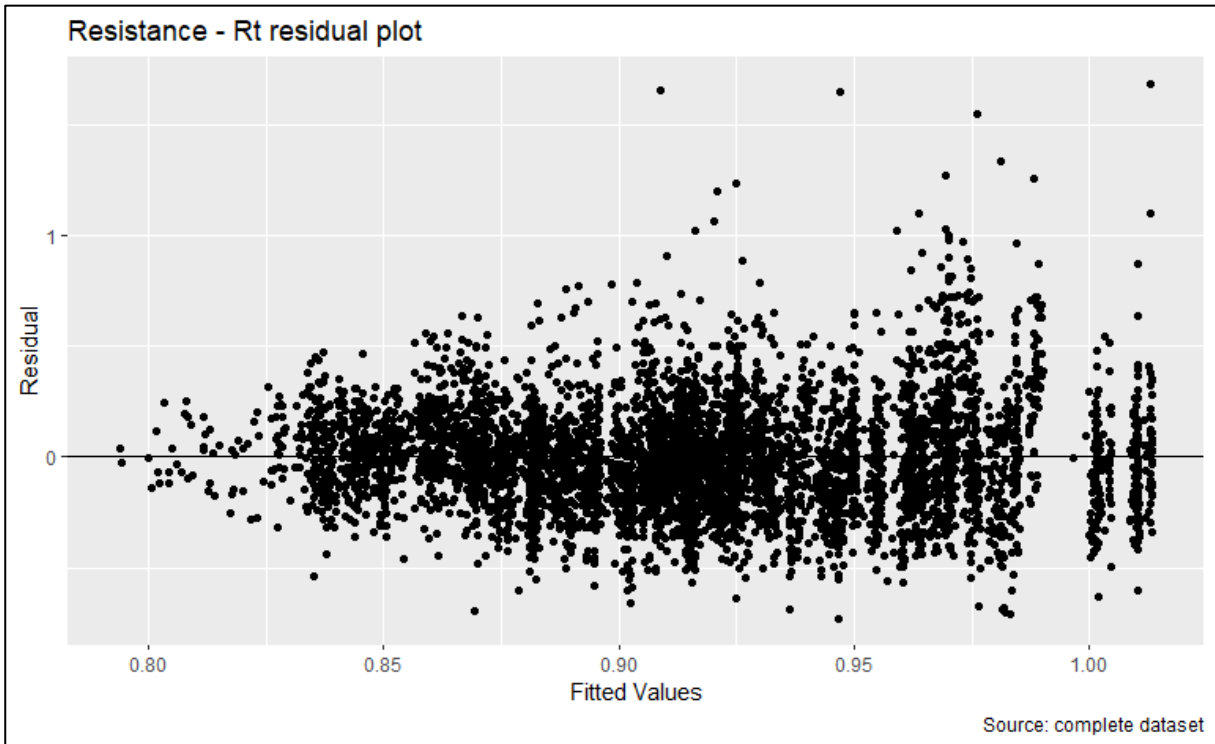
Group	Site	Plot	Country	Latitude N (°)	Longitude E (°)	Elevation (m)
Gr_4	BH_03	Bosnia_Herzegovina_03	Bosnia_Herzegovina	43.76	18.24	1270
	BH_04	Bosnia_Herzegovina_04	Bosnia_Herzegovina	43.74	18.25	1291
Gr_1	BU_01	Bulgaria_01	Bulgaria	41.91	23.84	1569
	BU_02	Bulgaria_02	Bulgaria	41.96	24.52	1391
Gr_9	GE_03	Germany_03	Germany	47.59	11.69	1271
Gr_10	GE_06	Germany_06	Germany	47.7	12.47	860
Gr_8	GE_07	Germany_07	Germany	47.43	11.16	1463
Gr_10	GE_09	Germany_09	Germany	47.73	12.36	902
	GE_12-13-18	Germany_12	Germany	47.71	12.7	973
	GE_12-13-18	Germany_13	Germany	47.71	12.7	973
Gr_8	GE_14-15-16	Germany_14	Germany	47.44	11.12	1235
	GE_14-15-16	Germany_15	Germany	47.44	11.12	1235
	GE_14-15-16	Germany_16	Germany	47.44	11.12	1235
Gr_10	GE_12-13-18	Germany_18	Germany	47.71	12.66	884
Gr_9	GE_19-20-21-22	Germany_19	Germany	47.6	11.66	1091
	GE_19-20-21-22	Germany_20	Germany	47.6	11.66	1091
	GE_19-20-21-22	Germany_21	Germany	47.6	11.66	1091
	GE_19-20-21-22	Germany_22	Germany	47.6	11.66	1091
Gr_13	GE_27-28-29-30	Germany_27	Germany	48.85	13.58	743
	GE_27-28-29-30	Germany_28	Germany	48.85	13.58	743
	GE_27-28-29-30	Germany_29	Germany	48.85	13.58	743
	GE_27-28-29-30	Germany_30	Germany	48.85	13.58	743
	GE_31-32-33-34	Germany_31	Germany	49.09	13.09	951
	GE_31-32-33-34	Germany_32	Germany	49.09	13.09	951
	GE_31-32-33-34	Germany_33	Germany	49.09	13.09	951
Gr_3	SE_01	Serbia_01	Serbia	43.55	20.73	869
	SE_02	Serbia_02	Serbia	43.55	20.78	1067
	SE_03	Serbia_03	Serbia	43.53	20.76	1236
Gr_2	SE_04	Serbia_04	Serbia	43.42	19.8	1270
Gr_11	SLK_01	Slovakia_01	Slovakia	48.64	19.53	803
Gr_12	SLK_02	Slovakia_02	Slovakia	48.77	20.74	773
	SLK_03	Slovakia_03	Slovakia	48.77	20.72	738
	SLK_04	Slovakia_04	Slovakia	48.78	20.66	621
	SLK_05	Slovakia_05	Slovakia	48.75	20.71	845
Gr_11	SLK_07	Slovakia_07	Slovakia	48.62	19.59	786
	SLK_08	Slovakia_08	Slovakia	48.63	19.57	733
Gr_5	SLV_04-05-06	Slovenia_04	Slovenia	45.66	15	910
	SLV_04-05-06	Slovenia_05	Slovenia	45.66	15	910
	SLV_04-05-06	Slovenia_06	Slovenia	45.66	15	910
Gr_6	SLV_09-10-11-12-13	Slovenia_09	Slovenia	46.24	14.06	1426

Gr_6	SLV_09-10-11-12-13	Slovenia_11	Slovenia	46.24	14.04	1443
	SLV_09-10-11-12-13	Slovenia_12	Slovenia	46.25	14.04	1421
	SLV_09-10-11-12-13	Slovenia_13	Slovenia	46.25	14.04	1375
Gr_7	SW_04-05	Switzerland_04	Switzerland	46.95	7.77	890
	SW_04-05	Switzerland_05	Switzerland	46.95	7.77	890
Gr_14	IT_01	Italy_01	Italy	46.06	12.27	1150

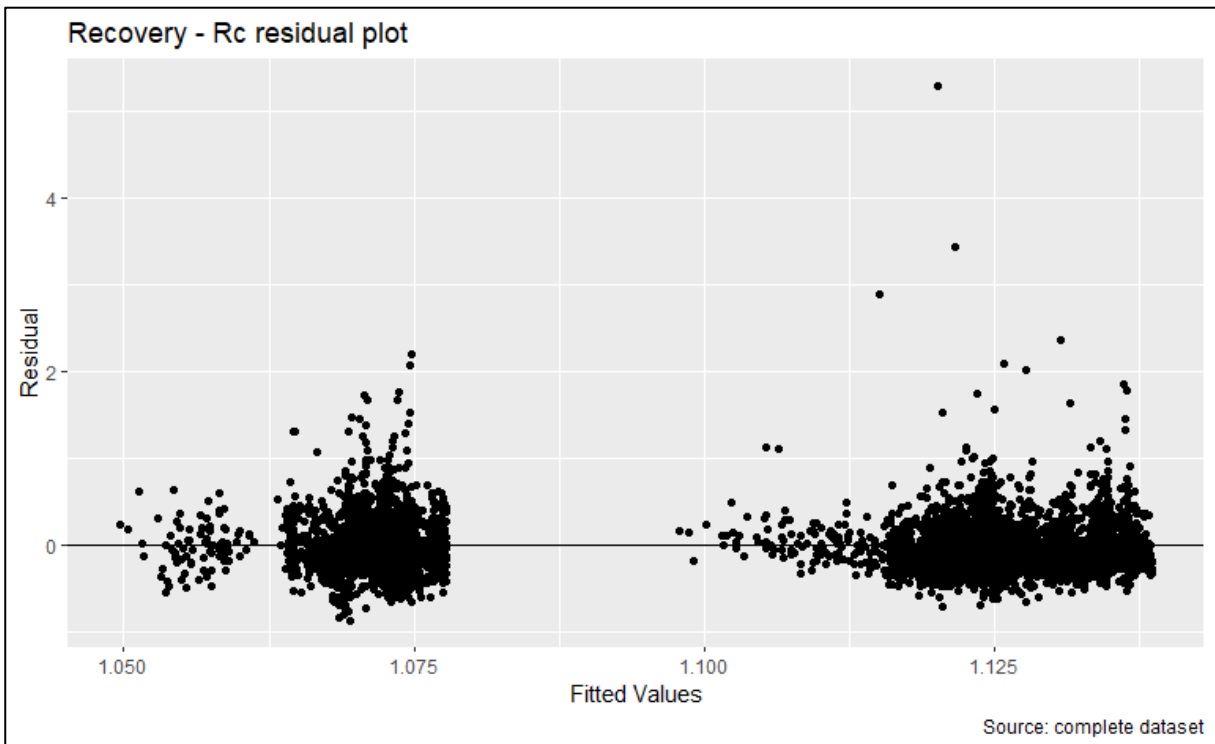
**Table A2:** Collinearity assessment of the covariates used for linear mixed effects analysis. 1 or -1 is complete collinearity whereas the further away the value from the unit, the lower the collinearity among the covariates will be.

	Plot	Lat	Lon	Elevation	Nr	Artcode	ACS	H
Plot	1	0.895517	-0.61944	-0.61232	0.008282	-0.05578	-0.51381	0.137703
Lat	0.895517	1	-0.78194	-0.57473	0.071564	-0.10495	-0.61293	0.133819
Lon	-0.61944	-0.78194	1	0.282191	-0.27658	0.086788	0.568326	0.15314
Elevation	-0.61232	-0.57473	0.282191	1	-0.15162	-0.03924	0.058992	-0.31339
Nr	0.008282	0.071564	-0.27658	-0.15162	1	-0.00471	-0.09509	-0.00079
Artcode	-0.05578	-0.10495	0.086788	-0.03924	-0.00471	1	0.078012	-0.3287
ACS	-0.51381	-0.61293	0.568326	0.058992	-0.09509	0.078012	1	0.099938
H	0.137703	0.133819	0.15314	-0.31339	-0.00079	-0.3287	0.099938	1
Year	-0.18915	-0.24474	0.222269	0.091187	-0.03419	0.063049	0.14791	-0.11334
Dbh	-0.0678	-0.1439	0.0799	0.080813	-0.09314	-0.11034	0.132542	0.099962
BA_m	-0.11444	-0.19448	0.100994	0.107019	-0.0528	-0.05967	0.156917	-0.00953
BAI	-0.13052	-0.20787	0.130059	0.012466	0.061979	-0.12465	0.220824	0.073392
Spei	0.251996	0.298983	-0.2044	-0.08946	-0.0946	-0.07393	-0.19937	-0.03549
PostSpei	0.061002	0.171527	-0.07925	-0.31266	0.068814	-0.02896	0.115983	0.128327
DSpei	-0.10296	-0.00103	-0.02214	-0.1647	0.113391	0.015114	0.145482	0.135223
Py	-0.05253	-0.04495	0.008986	0.117031	0.068156	0.21411	-0.01425	-0.06284
	Year	Dbh	BA_m	BAI	Spei	PostSpei	DSpei	Py
Plot	-0.18915	-0.0678	-0.11444	-0.13052	0.251996	0.061002	-0.10296	-0.05253
Lat	-0.24474	-0.1439	-0.19448	-0.20787	0.298983	0.171527	-0.00103	-0.04495
Lon	0.222269	0.0799	0.100994	0.130059	-0.2044	-0.07925	-0.02214	0.008986
Elevation	0.091187	0.080813	0.107019	0.012466	-0.08946	-0.31266	-0.1647	0.117031
Nr	-0.03419	-0.09314	-0.0528	0.061979	-0.0946	0.068814	0.113391	0.068156
Artcode	0.063049	-0.11034	-0.05967	-0.12465	-0.07393	-0.02896	0.015114	0.21411
ACS	0.14791	0.132542	0.156917	0.220824	-0.19937	0.115983	0.145482	-0.01425
H	-0.11334	0.099962	-0.00953	0.073392	-0.03549	0.128327	0.135223	-0.06284
Year	1	0.304609	0.209536	0.183848	-0.29514	0.189051	0.220247	-0.13702
Dbh	0.304609	1	0.961594	0.710189	-0.20077	-0.0131	0.100507	-0.07031
BA_m	0.209536	0.961594	1	0.695205	-0.18383	-0.05421	0.053795	-0.06441
BAI	0.183848	0.710189	0.695205	1	-0.12528	0.031192	0.077382	0.131283
Spei	-0.29514	-0.20077	-0.18383	-0.12528	1	-0.07472	-0.69733	0.180035
PostSpei	0.189051	-0.0131	-0.05421	0.031192	-0.07472	1	0.644421	-0.16601
DSpei	0.220247	0.100507	0.053795	0.077382	-0.69733	0.644421	1	-0.22784
Py	-0.13702	-0.07031	-0.06441	0.131283	0.180035	-0.16601	-0.22784	1

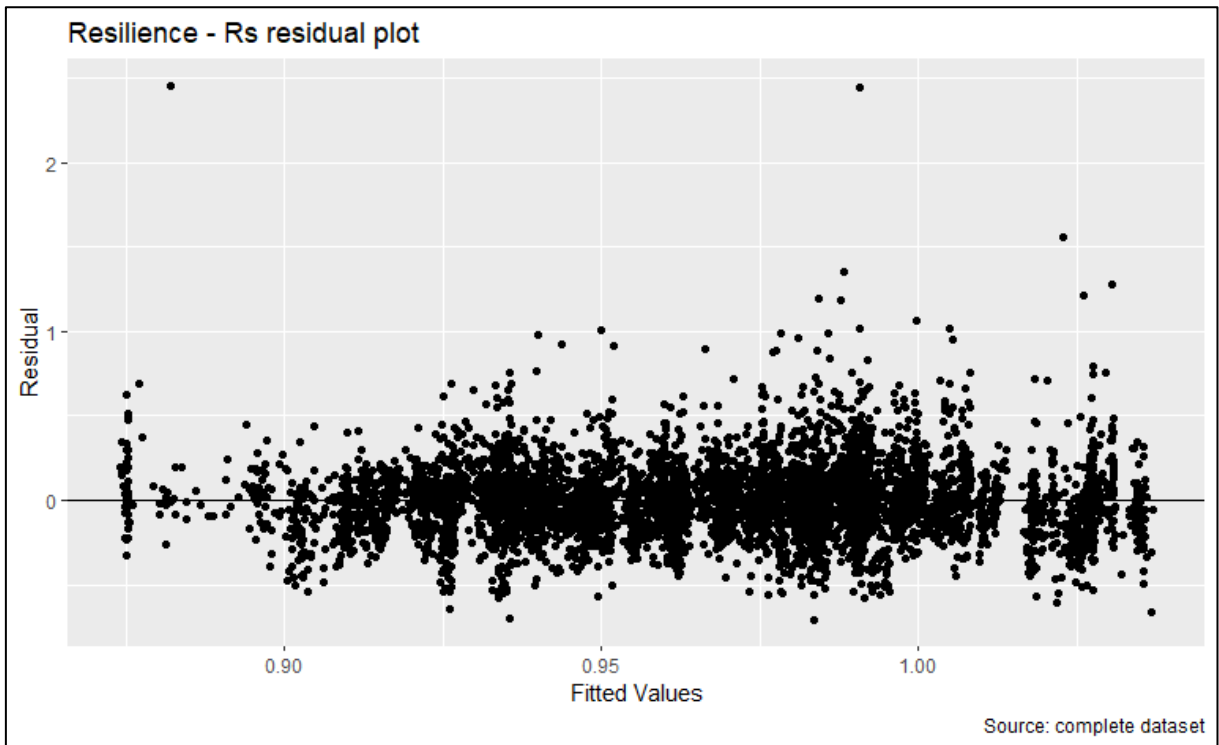
*Residual plots*



**Graph A1:** residual plot of linear mixed effects model Eq.1 for  $R_t$  analysis.



**Graph A2:** residual plot of linear mixed effects model Eq.1 for  $R_c$  analysis.



Graph A3: residual plot of linear mixed effects model Eq.1 for Rs analysis.

Table A3: Akaike information criterion (AIC) performed for comparing linear mixed effects model Eq.1 with the models respectively identified as Eq.2, Eq.3 and Eq.4.

<i>RT GENERAL MODEL Eq.2:</i>	Rt ~ Species + BA + Spei + (1 Plot)							
<i>RT GENERAL MODEL Eq.1:</i>	Rt ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RT GENERAL MODEL Eq.2</i>	7	-340	-294	177.06	-354.13			
<i>RT GENERAL MODEL Eq.1</i>	11	-387.41	-315	204.71	-409.41	55.283	4	2.83E-11 ***
<i>RT GENERAL MODEL Eq.3:</i>	Rt ~ Species · BA + Spei + (1 Plot)							
<i>RT GENERAL MODEL Eq.1:</i>	Rt ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RT GENERAL MODEL Eq.3</i>	9	-347.43	-288.2	182.72	-365.43			
<i>RT GENERAL MODEL Eq.1</i>	11	-387.41	-315	204.71	-409.41	43.981	2	2.82E-10 ***
<i>RT GENERAL MODEL Eq.4:</i>	Rt ~ Species · Spei + BA + (1 Plot)							
<i>RT GENERAL MODEL Eq.1:</i>	Rt ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RT GENERAL MODEL Eq.4</i>	9	-387.42	-328.2	202.71	-405.42			
<i>RT GENERAL MODEL Eq.1</i>	11	-387.41	-315	204.71	-409.41	3.9875	2	0.1362
<i>RC GENERAL MODEL Eq.2:</i>	Rc ~ Species + BA + Spei + (1 Plot)							
<i>RC GENERAL MODEL Eq.1:</i>	Rc ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RC GENERAL MODEL Eq.2</i>	7	2401.6	2447.7	-1193.8	2387.6			
<i>RC GENERAL MODEL Eq.1</i>	11	2388.7	2461.1	-1183.3	2366.7	20.963	4	0.000322 ***

<i>RC GENERAL MODEL Eq. 3:</i>	Rc ~ Species · BA + Spei + (1 Plot)							
<i>RC GENERAL MODEL Eq. 1:</i>	Rc ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RC GENERAL MODEL Eq. 3</i>	9	2399.6	2458.9	-1190.8	2381.6			
<i>RC GENERAL MODEL Eq. 1</i>	11	2388.7	2461.1	-1183.3	2366.7	14.934	2	0.000572 ***
<i>RC GENERAL MODEL Eq. 4:</i>	Rc ~ Species · Spei + BA + (1 Plot)							
<i>RC GENERAL MODEL Eq. 1:</i>	Rc ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RC GENERAL MODEL Eq. 4</i>	9	2389.9	2449.2	-1185.9	2371.9			
<i>RC GENERAL MODEL Eq. 1</i>	11	2388.7	2461.1	-1183.3	2366.7	5.2154	2	0.0737 .
<i>RS GENERAL MODEL Eq. 2:</i>	Rs ~ Species + BA + Spei + (1 Plot)							
<i>RS GENERAL MODEL Eq. 1:</i>	Rs ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RS GENERAL MODEL Eq. 2</i>	7	-1392.2	-1346	703.09	-1406.2			
<i>RS GENERAL MODEL Eq. 1</i>	11	-1404.2	-1332	713.1	-1426.2	20.013	4	0.000496 ***
<i>RS GENERAL MODEL Eq. 3:</i>	Rs ~ Species · BA + Spei + (1 Plot)							
<i>RS GENERAL MODEL Eq. 1:</i>	Rs ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RS GENERAL MODEL Eq. 3</i>	9	-1400.8	-1342	709.42	-1418.8			
<i>RS GENERAL MODEL Eq. 1</i>	11	-1404.2	-1332	713.1	-1426.2	7.342	2	0.02545 *
<i>RS GENERAL MODEL Eq. 4:</i>	Rs ~ Species · Spei + BA + (1 Plot)							
<i>RS GENERAL MODEL Eq. 1:</i>	Rs ~ Species · (Spei + BA) + (1 Plot)							
	<b>Df</b>	<b>AIC</b>	<b>BIC</b>	<b>logLik</b>	<b>deviance</b>	<b>Chisq Chi</b>	<b>Df</b>	<b>P-value</b>
<i>RS GENERAL MODEL Eq. 4</i>	9	-1399.2	-1340	708.63	-1417.2			
<i>RS GENERAL MODEL Eq. 1</i>	11	-1404.2	-1332	713.1	-1426.2	8.9364	2	0.01147 *
<b>Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</b>								

## REFERENCES

- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), 1–55. <https://doi.org/10.1890/ES15-00203.1>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... Cobb, N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Aranda, I., Gil, L., & Pardos, J. A. (2000). Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees - Structure and Function*, 14(6), 344–352. <https://doi.org/10.1007/s004680050229>
- Aussenac, G. (2000). Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, 57(3), 287–301. <https://doi.org/10.1051/forest:2000119>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <http://CRAN.R-project.org/package=lme4>. *R Package Version*.
- Biondi, F. (1999). Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecological Applications*, 9(1), 216–227. [https://doi.org/10.1890/1051-0761\(1999\)009\[0216:CTRCAR\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0216:CTRCAR]2.0.CO;2)
- Biondi, F., & Qeadan, F. (2008). A theory-driven approach to tree-ring standardization Defining the biological trend expected basal area increment.pdf, 64(2), 81–96.
- Blasing, T. J., & Fritts, H. C. (1976). Reconstructing past climatic anomalies in the North Pacific and western North America from tree-ring data. *Quaternary Research*. [https://doi.org/10.1016/0033-5894\(76\)90027-2](https://doi.org/10.1016/0033-5894(76)90027-2)
- Caldwell, M. M., & Richards, J. H. (1998). Hydraulic lift: consequences of water efflux from the roots of plants, 151–161. <https://doi.org/10.1007/s004420050363>
- Callaway, R. M., & Walker, L. R. (1997). Competition and facilitation: A synthetic approach to interactions in plant communities. *Ecology*, 78(7), 1958–1965. [https://doi.org/10.1890/0012-9658\(1997\)078\[1958:CAFASA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2)
- Carrer, M., & Urbinati, C. (2004). Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology*, 85(3), 730–740. <https://doi.org/10.1890/02-0478>



- Chapin III, F. S., Matson, P. A., & Mooney, H. A. (2002). *Principles of terrestrial ecosystem ecology*—Springer-Verlag. New York, USA.
- Cook, E. R. (1985). A time series analysis approach to tree ring standardization.
- Cropper, J. (1979). Tree-Ring Skeleton Plotting by Computer.
- CRUTEM4.2.0.0-2013-03. (2013). Data availability and File Format explained.
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*. <https://doi.org/10.1038/nclimate1633>
- Friedman, J. H. A variable span smoother, *J. Am. Stat. Assoc.* § (1984).  
<https://doi.org/10.21236/ada148241>
- Gazol, A., & Camarero, J. J. (2016). Functional diversity enhances silver fir growth resilience to an extreme drought. *Journal of Ecology*, *104*(4), 1063–1075.  
<https://doi.org/10.1111/1365-2745.12575>
- Gazol, A., Ribas, M., Gutiérrez, E., & Camarero, J. J. (2017). Aleppo pine forests from across Spain show drought-induced growth decline and partial recovery. *Agricultural and Forest Meteorology*, *232*, 186–194.  
<https://doi.org/10.1016/J.AGRFORMET.2016.08.014>
- Grossiord, C. (2019). Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytologist*. <https://doi.org/10.1111/nph.15667>
- Guicherd, P. (1994). Water relations of European silver fir (*Abies alba* Mill) in 2 natural stands in the French Alps subject to contrasting climatic conditions. *Annales Des Sciences Forestieres*, *51*(6), 599–611. <https://doi.org/10.1051/forest:19940606>
- Hilmers, T., Avdagić, A., Bartkowicz, L., Bielak, K., Binder, F., Bončina, A., ... Pretzsch, H. (2019). The productivity of mixed mountain forests comprised of *Fagus sylvatica*, *Picea abies*, and *Abies alba* across Europe. *Forestry: An International Journal of Forest Research*, 1–11. <https://doi.org/10.1093/forestry/cpz035>
- Hooper, D. U., Bignell, D. E., Brown, V. K., Brussaard, L., Dangerfield, J. M., Wall, D. H., ... Wolters, V. (2000). Aboveground and Belowground Biodiversity in Terrestrial Ecosystems : Patterns , Mechanisms , and. *BioScience*, *50*(12), 1049–1061.  
[https://doi.org/10.1641/0006-3568\(2000\)050](https://doi.org/10.1641/0006-3568(2000)050)
- Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel P, Lawton JH, Lodge DM, Loreau M, N. S. et al. (2005). EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING:A CONSENSUS OF CURRENT KNOWLEDGE. *America*, *75*(July 2004), 3–35. <https://doi.org/10.1890/04-0922>
- Hulme, M. (1992). A 1951-80 global land precipitation climatology for the evaluation of

- general circulation models. *Climate Dynamics*, 7(2), 57–72.  
<https://doi.org/10.1007/BF00209609>
- Hulme, M., Osborn, T. J., & Johns, T. C. (1998). Precipitation sensitivity to global warming: Comparison of observations with Had CM2 simulations. *Geophysical Research Letters*, 25(17), 3379–3382. <https://doi.org/10.1029/98GL02562>
- Jaleel, C. Abdul, Manivannan, P., Lakshmanan, G. M. A., Gomathinayagam, M., & Panneerselvam, R. (2008). Alterations in morphological parameters and photosynthetic pigment responses of *Catharanthus roseus* under soil water deficits. *Colloids and Surfaces B: Biointerfaces*, 61(2), 298–303.  
<https://doi.org/10.1016/J.COLSURFB.2007.09.008>
- Jaleel, Cheruth Abdul, Manivannan, P., Wahid, A., Farooq, M., Al-Juburi, H. J., Somasundaram, R., & Panneerselvam, R. (2009). Drought stress in plants: A review on morphological characteristics and pigments composition. *International Journal of Agriculture and Biology*, 11(1), 100–105.
- Kaufman, L. H. (1982). Stream aufwuchs accumulation: Disturbance frequency and stress resistance and resilience. *Oecologia*, 52(1), 57–63. <https://doi.org/10.1007/BF00349012>
- Klein, T. (2014). The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Functional Ecology*, 28(6), 1313–1320. <https://doi.org/10.1111/1365-2435.12289>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models . *Journal of Statistical Software*, 82(13).  
<https://doi.org/10.18637/jss.v082.i13>
- Larcher, W. (2003). *Physiological plant ecology. Ecophysiology and stress physiology of the functional groups. Annals of Botany*.
- Lebourgeois, F., Gomez, N., Pinto, P., & Mérian, P. (2013). Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecology and Management*, 303, 61–71. <https://doi.org/10.1016/J.FORECO.2013.04.003>
- Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12), 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>
- Mitchell, T. D., Carter, T. R., Jones, P. D., Hulme, M., & New, M. (2004). A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed record (1901-2000) and 16 scenarios (2001-2100). *Geography*, (July).
- Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness

promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14(12), 1211–1219. <https://doi.org/10.1111/j.1461-0248.2011.01691.x>

- Nate, M., McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., ... Yepez, E. A. (2008). McDowell mechanisms of plants mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178(4), 719–739. <https://doi.org/10.1016/j.biocon.2016.01.028>
- Neuwirth, B., Schweingruber, F. H., & Winiger, M. (2007). Spatial patterns of central European pointer years from 1901 to 1971. *Dendrochronologia*, 24(2–3), 79–89. <https://doi.org/10.1016/J.DENDRO.2006.05.004>
- New, M., Hulme, M., & Jones, P. (2000). Representing twentieth-century space-time climate variability. Part II: Development of 1901–96 monthly grids of terrestrial surface climate. *Journal of Climate*, 13(13), 2217–2238. [https://doi.org/10.1175/1520-0442\(2000\)013<2217:RTCSTC>2.0.CO;2](https://doi.org/10.1175/1520-0442(2000)013<2217:RTCSTC>2.0.CO;2)
- Orwin, K. H., & Wardle, D. A. (2004). New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. *Soil Biology and Biochemistry*. <https://doi.org/10.1016/j.soilbio.2004.04.036>
- Pasho, E., Camarero, J. J., de Luis, M., & Vicente-Serrano, S. M. (2011). Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. *Agricultural and Forest Meteorology*, 151(12), 1800–1811. <https://doi.org/10.1016/j.agrformet.2011.07.018>
- Portoghesi, L. (2006). *European Forest Types. Categories and types for sustainable forest management reporting and policy. Forest@ - Rivista di Selvicoltura ed Ecologia Forestale* (Vol. 3). <https://doi.org/10.3832/efor0425-003>
- Pretzsch, H., Rötzer, T., Matyssek, R., Grams, T. E. E., Häberle, K. H., Pritsch, K., ... Munch, J. C. (2014). Mixed Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* [L.]) stands under drought: from reaction pattern to mechanism. *Trees - Structure and Function*, 28(5), 1305–1321. <https://doi.org/10.1007/s00468-014-1035-9>
- Pretzsch, H., Schütze, G., & Uhl, E. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation. *Plant Biology*, 15(3), 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>
- Pretzsch, Hans, Schütze, G., & Biber, P. (2018). Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest*

- Ecosystems*, 5(1). <https://doi.org/10.1186/s40663-018-0139-x>
- Schäfer, C., Grams, T. E. E., Rötzer, T., Feldermann, A., & Pretzsch, H. (2017). Drought stress reaction of growth and  $\delta^{13}\text{C}$  in tree rings of European beech and Norway spruce in monospecific versus mixed stands along a precipitation gradient. *Forests*, 8(6). <https://doi.org/10.3390/f8060177>
- Schweingruber, F. H. (1989). Tree rings - basics and applications of dendrochronology. Kluwer Academic Publishers. ISBN 90277244 58. 276 pages. Price: £84.00. *Journal of Tropical Ecology*, 5(3), 352–352. <https://doi.org/10.1017/S026646740000376X>
- Schweingruber, F. H., Eckstein, D., & Serre-Bachet, F. (1990). Identification, Presentation and Interpretation of Event Years and Pointer Years in Dendrochronology. *Dendrochronologia*.
- Sousa, W. P. (1980). The Responses of a Community to Disturbance: The Importance of Successional Age and Species' Life Histories, 81, 72–81.
- Speer, B. J. H. (n.d.). Fundamentals of Tree-Ring Research.
- Team, R. C. (2013). R Development Core Team. *R: A Language and Environment for Statistical Computing*.
- Thorntwaite, C. W. (1948). An Approach toward a Rational Classification of Climate. *Journal of Nuclear Materials*, 41(2), 161–166. [https://doi.org/10.1016/0022-3115\(71\)90076-6](https://doi.org/10.1016/0022-3115(71)90076-6)
- Thurm, E. A., Uhl, E., & Pretzsch, H. (2016). Mixture reduces climate sensitivity of Douglas-fir stem growth. *Forest Ecology and Management*, 376, 205–220. Retrieved from <https://www.sciencedirect.com/science/article/abs/pii/S0378112716303176>
- Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscale drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *Journal of Climate*, 23(7), 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- Westoby, M., & Wright, I. J. (2006, May 1). Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*. Elsevier Current Trends. <https://doi.org/10.1016/j.tree.2006.02.004>
- Winter, B. (2013). Linear models and linear mixed effects models in R with linguistic applications, 1–22. Retrieved from <http://arxiv.org/abs/1308.5499>
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. <https://doi.org/10.1111/j.2041-210x.2009.00001.x>

