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Forest structures and carbon storage in managed and unmanaged forests along an altitudinal gradient in a central European low mountain range

Waldstrukturen und Kohlenstoffvorräte in bewirtschafteten und unbewirtschafteten Wäldern entlang eines Höhengradienten in einem mitteleuropäischen Mittelgebirge

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Abstract

Along an altitudinal gradient in the Bavarian Forest, a German low mountain range, forest structures on 144 sampling plots located in eight strict forest reserves and nearby managed forest stands were investigated. Live woody biomass volumes increased with decreasing altitude, whereas deadwood volumes did not show a dependency on elevation. Mean wood volumes were on average around 40 % higher in strict forest reserves than in managed forest stands, with decreasing discrepancies at higher altitudes. Silvicultural management had a strong impact on deadwood volumes, leading to higher mean deadwood volumes in the strict forest reserves than in managed forests. Probability of presence models for the main tree species indicated shifts of the curve maxima towards higher altitudes for beech and silver fir in the strict forest reserves, when data from 2009 and 2018 were compared. Total carbon stores in the strict forest reserves increased from the first survey in 2009 to 2018 in most cases, on average by around 40 to/ha. The two reserves at the highest altitudes (1,174 and 1,211 m a.s.l.), however, suffered from recent storm damages and severe spruce bark beetle outbreaks, which led to decreased above ground carbon stores but increased coarse woody debris carbon stores.

Keywords: *Strict forest reserves, altitudinal gradient, climate change, tree species distribution, carbon balance*

Zusammenfassung

Entlang eines Höhengradienten im Bayerischen Wald, einem deutschen Mittelgebirge, wurden Waldstrukturen auf 144 Probeflächen in acht Naturwaldreservaten und benachbarten Wirtschaftswäldern untersucht. Das Biomassevolumen des lebenden Baumbestandes stieg mit abnehmender Meereshöhe, während die Totholzvorräte keine Höhentendenz zeigten. Die Holzvorräte waren in den Naturwaldreservaten im Mittel rund 40 % höher als in den Wirtschaftswäldern, mit zunehmender Angleichung der Vorräte in den höheren Lagen. Bewirtschaftung hatte einen starken Einfluss auf die Totholzvorräte, mit im Mittel höheren Totholzvorräten in den Naturwaldreservaten als in den Wirtschaftswäldern. Die modellierte Auftretenswahrscheinlichkeit der Hauptbaumarten in den Naturwaldreservaten der Aufnahmejahre 2009 und 2018 im Vergleich ließ eine Verschiebung der Kurvenmaxima in Richtung höherer Lagen bei Buche und Tanne erkennen. Die Kohlenstoffvorräte in den Naturwaldreservaten stiegen in den meisten Fällen von 2009 bis 2018, im Mittel um rund 40 to/ha. In den beiden höchstgelegenen Naturwaldreservaten (auf 1.174 und 1.211 m ü. NN) führten Sturmschäden und Borkenkäfermassenvermehrungen der letzten Jahre jedoch zu einer Abnahme der oberirdischen Kohlenstoffvorräte im lebenden Baumbestand und zu einer Zunahme der Kohlenstoffvorräte in Form von Totholz.

Schlüsselwörter: Naturwaldreservate, Höhengradient, Klimawandel, Baumartenverbreitung, Kohlenstoffbilanz

1 Introduction

Climate change is one of the major challenges humankind has to cope with in the 21st century. Due to anthropogenic activities, the atmospheric CO_2 level has increased to 407.4 ppm in 2018 compared to around 280 ppm in the preindustrial era (Blunden & Arndt, 2019), causing a global mean temperature increase of 1.0 °C, which is predicted to further rise to +1.5 °C by 2030–2052 (IPCC, 2018). Besides an essential reduction of CO_2 emissions, the idea of enhancing and optimizing the CO_2 binding capacities of global CO_2 sinks to fight climate change gains more and more attention. Forests pose a huge global CO_2 sink, whose latent potential for solving the climate crisis was brought into public focus only recently by Bastin et al. (2019). Although controversially discussed with regard to putative methodical issues, the key message of this study remains indisputably a wake up-call by emphasizing the importance of forest ecosystems in the global carbon cycle and the potential of reforestation for carbon sequestration. However, forests are much more than just CO_2 sinks, they are complex ecosystems, which, in turn, are also subject to climate change effects. Counting on and with forests as CO_2 sinks requires a deep understanding of these ecosystems and how climate change affects the individual components and their interactions. Climate warming is expected to have a strong impact on forest ecosystems since important aspects of the tree life cycle as bud burst, winter dormancy and growth rate are regulated by temperature (Asse et al., 2018). Especially in mountainous regions, shifts of species distribution ranges to higher altitudes in response to upward shifts of their temperature optima are anticipated and have already been demonstrated for several plant and animal species (Pauli et al., 2007; Bässler et al., 2013). The differences in the speed of these migrations, caused by different dispersal potentials, may lead to altered species compositions in mountainous ecosystems, triggering new interspecific dynamics with unknown outcome (Corlett & Westcott, 2013). Shifts of key species as trees in forest ecosystems, which determine the habitat properties for connected organisms, are of particular interest. However, other factors as management practice and forest life stage may interfere with climate change effects, and the complexity of forest ecosystems is challenging for studies, which aim to trace tree species and forest ecosystem responses to climate warming.

The presented study was conducted to answer the following key questions:

1. Are elevational gradients with their climatic conditions suitable to study climate change effects on forest structures?
2. Is there a masking effect of altitude-dependent forest structures due to management practice or other factors in comparison to unmanaged forests?
3. Are changes in forest structure in unmanaged forests observable within a time frame of 10 years and can these changes be linked to altitude-dependent climate parameters?

2 Materials and methods

2.1 *Study area*

The altitudinal gradient was installed in the Bavarian Forest, a German low mountain range at the border to the Czech Republic, covering a region from about 300 meters above sea level (m a.s.l.) to 1,400 m a.s.l. The mean annual temperature ranges from 9.1 °C in the area of the rivers Donau and Inn (ca. 300 m a.s.l) to 3.8 °C in the Arber region (ca. 1,400 m a.s.l.). Mean annual precipitation ranges from 875 to 1,663 mm/m² during the year and between 417 and 697 mm/m² during the vegetation period (extrapolation of climate data derived from the National Climate Data Centre, Germany, to individual sampling plots according to Kaspar et al. (2013), Maier et al. (2003) and Müller-Westermeier (1995)). Soils are predominantly nutrient-poor over granite or gneiss bedrock, in the lowland forests with a layer of aeolian silt deposits. At medium and high altitudes, many sites are characterized by scattered boulders and thin layers of topsoil (Bayerisches Geologisches Landesamt, 1996).

Due to the lack of resource deposits, forestry use started comparatively late in the Bavarian Forest, where the first sawmills were not raised before the first half of the 19th century. Furthermore, the harsh climate accounted for people's avoidance of the central ridges of the mountain range over

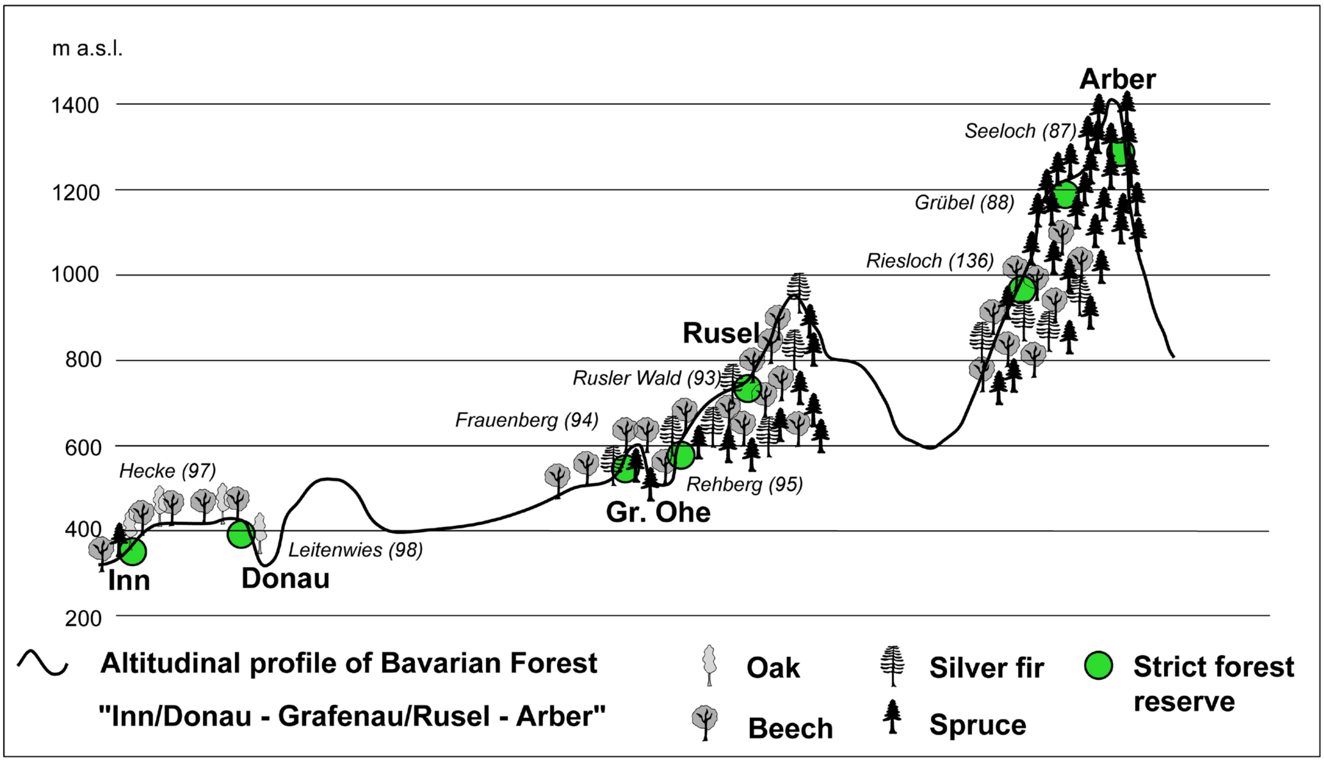

Fig. 1: Altitude profile of the study area and location of the investigated forest reserves (Table 1).

Abb. 1: *Höhenprofil des Untersuchungsgebietes und Lage der untersuchten Naturwaldreservate (Tabelle 1).*

the centuries, leading to a remnant, broad mountain belt in the border region between Bavaria and Bohemia after the late medieval colonization and forest clearances (Naturpark Bayerischer Wald, 2016). Numerous near-natural forest stands without substantial human impact are therefore preserved, especially in the inner Bavarian Forest. Since 1978, several strict forest reserves have been established, representing the natural forest communities typical for their respective ecological niches. This conservation category bans wood harvesting as well as infrastructure provision and maintenance in the reserve area. Exceptionally, sanitary measures are allowed in the case of disease outbreaks, which may compromise nearby managed forests (BayWaldG Art. 12a, 2005).

In this study, eight strict forest reserves (SFR) along the altitudinal gradient were chosen to represent lowland forests, strongly dominated by beech (*Fagus sylvatica* L.) with an admixture of oak (*Quercus robur* L., and *Q. petraea* (Matt.) Liebl.), common ash (*Fraxinus excelsior* L.) and maple (*Acer pseudoplatanus* L., and *A. platanoides* L.), mixed mountain forests, composed of beech (*Fagus sylvatica*), silver fir (*Abies alba* Mill.) and spruce (*Picea abies* (L.) Karst.), as well as high altitude forests, characterized by a strong domination of spruce *(Picea abies*), associated with mountain ash (*Sorbus aucuparia* L.) in the understory (Tab. 1). The strict forest reserves remained unmanaged since their declaration in 1978 (seven forest reserves) and 1989 (forest reserve “Riesloch”), except for repeated sanitary measures over the last several years in the two high altitude reserves, “Grübel” and “Seeloch”, due to spruce bark beetle outbreaks. Figure 1 shows an altitude profile of the study area and the location of the investigated forest reserves. Reference plots were located in nearby managed forest stands.

2.2 Sampling design and data collection

2.2.1 Selection of sampling plots

Forty-eight sampling plots in eight strict forest reserves (six plots each) distributed along the altitudinal gradient were investigated, following the sampling plot selection of a previous study in 2009 (Blaschke et al., 2011). In order to compare the data from these near-natural forests with managed forest stands, two further sets of 48 sampling plots each were investigated, one set containing spruce-dominated reference plots and a second set containing beech-dominated reference plots. For each sampling plot in a strict forest reserve, the two reference plots in managed forest stands were selected within a 3,000 m radius of the respective forest reserve. A similarity matrix was used for sampling plot selection, which considered soil characteristics (moisture regime and soil properties), altitude as well as tree species composition and basal areas based on the state forest company inventory data. Plots near forest edges were excluded. For the lowland forests and mixed mountain forests, reference plots with similar tree species composition as the respective sampling plot in the forest reserve were designated with “A”, whereas managed reference plots with a higher proportion of conifers were designated with “B”. Selection criteria for B-plots consisted of a by half reduced beech proportion (basal area) compared to the respective sampling plot in the strict forest reserve and a spruce content, which was enhanced by this respective reduction in the beech content. In the high altitude forests in the region of the reserves “Grübel” and “Seeloch” with mean altitudes above 1,150 m, which are naturally dominated by spruce (Walentowski et al., 2020), reference plots resembling the sampling plots in the strict forest reserves were designated with “B” due to the high proportion of spruce in these forests. Reference plots designated with “A” were characterized by a by half reduced spruce content and an accordingly enhanced proportion of beech trees.

2.2.2 Data collection

Data on forest structure were collected from March till November 2018, considering live and dead trees, snags, as well as downed deadwood on circular sampling plots covering an area of 500 m². Positions and data of measured trees and deadwood items were recorded with the silvicultural data collection software FieldMap (IFER - Monitoring and Mapping Solutions, Ltd., Jilove u Prahy, Czech Republic) on

Tab. 1: Specifications of the strict forest reserves investigated in this study.

Tab. 1: *Basisdaten zu den untersuchten Naturwaldreservaten.*

Strict forest reserve (name, ID)	Reserve establishment	Size [ha]	Size of permanent monitoring area (PMA) [ha]	altitude [m a.s.l.]	forest community
Hecke (97)	1978	15.6	0.57	310–405	beech forests
Leitenwies (98)	1978	12.8	1.01	370–420	beech and oak mixed forests
Frauenberg (94)	1978	19.4	0.21	460–650	beech forests
Rehberg (95)	1978	24.9	0.91	510–620	mixed mountain forests
Rusler Wald (93)	1978	23.3	0.97	700–815	mixed mountain forests
Riesloch (136)	1989	47.6	no PMA installed	775–1035	mixed mountain forests
Grübel (88)	1978	56.2	1.09	1,170–1,260	mixed mountain forests and high altitude spruce forests
Seeloch (87)	1978	130.1	0.50	915–1,430	mixed mountain forests and high altitude spruce forests

a portable field computer (Getac Technology, Düsseldorf, Germany). The demarcated center of the circular sampling plot served as reference point, from which distance and angle to trees within the plot were measured with a TruPulse 360 Laser Rangefinder (Laser Technology, Inc., Centennial, USA). Within the sampling plots, all standing trees with a minimum diameter at breast height (DBH) of 7 cm, snags with a mid-diameter of at least 10 cm, and downed deadwood with a minimum length of 1 m, a minimum mean diameter of 10 cm and not less than 7 cm in diameter at the thinner end were mapped. DBH of standing trees was measured with a DBH tape. Trees at the outer border of the sampling plot were recorded if at least half of their diameter at breast height was located within the sampling plot. Diameters of snags and downed deadwood were measured using a slide caliper. Diameters of downed deadwood were measured at both ends. The length was calculated by the software from distance and angle measurements from the central reference point. In addition to size measurements, the decomposition stage of standing and downed deadwood was classified in four decomposition classes, based on visual assessment (Table 2) (Albrecht 1990). The tree species of each tree and deadwood item was recorded, if possible. In cases, where highly decomposed deadwood was not identified to the species level, these items were assigned to either coniferous wood or hardwood. For the sampling plots located in strict forest reserves, data collected in 2009, applying the same procedures as described above, was available (Blaschke et al., 2011) and used for comparative analysis.

In seven out of eight strict forest reserves, permanent monitoring areas of 0.2 ha to 1.0 ha are installed (Table 1) and data on forest structure was available from repeated recordings during the last four decades. Data on standing trees and standing as well as downed deadwood was collected as described above, with measurements of distance and angle of live trees and deadwood items from a reference tree with known position. Data on downed deadwood was not available in all datasets. Carbon stores of living trees as well as standing and downed deadwood (if available) were calculated for the respective year of recording (Klein & Schulz 2012) and compared to the values obtained from the sampling plots.

2.2.3 Recording of climate data

On ten sampling plots distributed along the altitudinal gradient, data on temperature and relative air humidity were recorded with Hobo U23 Pro v2 Data loggers (Onset Computer Cooperation, Bourne, USA). Recordings started in March 2018 on the lower sites near the rivers Donau and Inn. At the high altitudes in the Arber region, recording of climate data did not start before May 2018 because of inaccessibility of these plots due to the snow depth. Measurement stations were installed on a peg with 1.5 m height, located on or in the immediate vicinity of selected sampling plots in the eight forest reserves. The chosen positions of the measuring stations were equal to those used in a research project in 2009 in order to enable a comparison to climate data collected at identical locations almost ten years ago.

2.3 Data analyses

Data collected on sampling plots as well as permanent observation areas in the forest reserves was transformed to ha-based values in a MS Access database.

Statistical analyses were carried out in R 3.6.2 (Cran-R-Project 2018), using the package vegan. Wood volumes were calculated using tree height curves derived from the forest reserve monitoring areas. Calculation of carbon balances was performed according to Zell (2008), with a correction for oak and silver fir according to Klein and Schulz (2012).

3 Results

3.1 Forest structure

3.1.1 Wood volumes, basal areas and number of trees

In the strict forest reserves, mean volumes of living wood per ha declined with increasing altitude (Figure 3). A similar, though less distinct trend was observed in managed forests dominated by spruce. Beech-dominated, managed forests showed no clear tendency with respect to the altitudinal gradient. Wood volumes were on average higher in the strict forest reserves than in the managed forest stands. However, the differences between managed and unmanaged forests decreased at higher altitudes, leading to very similar wood biomass amounts at 1,000 m a.s.l. and above. Tree height curves, based on data derived from the permanent monitoring areas in the forest reserves, showed declining tree heights with increasing altitude (Figure 2).

In contrast to wood volumes, no influence of the altitudinal gradient on the basal areas per ha was observed, neither in the strict forest reserves nor in managed forest stands. However, considerable differences in the number of trees per ha were apparent in forest reserves with similar basal area values, reflecting the developmental stages of the respective

Tab. 2: Deadwood decomposition classes according to Albrecht (1990).

Tab. 2: *Zersetzungsgrade für Totholz nach Albrecht (1990).*

Decomposition class	Description	Criteria
1	fresh dead	wood still firm, not extensively decorticated
2	beginning decomposition	sapwood or heartwood soft, in parts still firm, bark partially or completely dropped
3	advanced decomposition	sapwood and heartwood (partially) soft, complete or near-complete decortication
4	rotten	structures of heart wood extensively degraded

forest communities. While the forest reserve "Hecke" was dominated by large old trees, resulting in a rather low tree number of about 450 trees per ha, the forest reserve "Rehberg", which showed a very similar basal area value, was characterized by nearly 1,000 trees per ha, with almost half of the trees measuring 15 cm DBH or less. Figure 3 shows wood volumes and number of trees per ha for the investigated plot groups over the course of the altitudinal gradient.

3.1.2 Deadwood

The analysis of data collected on standing and downed deadwood (hereinafter referred to as coarse woody debris, CWD) showed no clear influence of altitude on the amount of deadwood biomass. In the strict forest reserves, the proportion of CWD classified "fresh dead" decreased with increasing altitude, whereas the proportion of CWD with beginning decomposition increased, except for the reserve "Rusler Wald", which showed comparatively low amounts

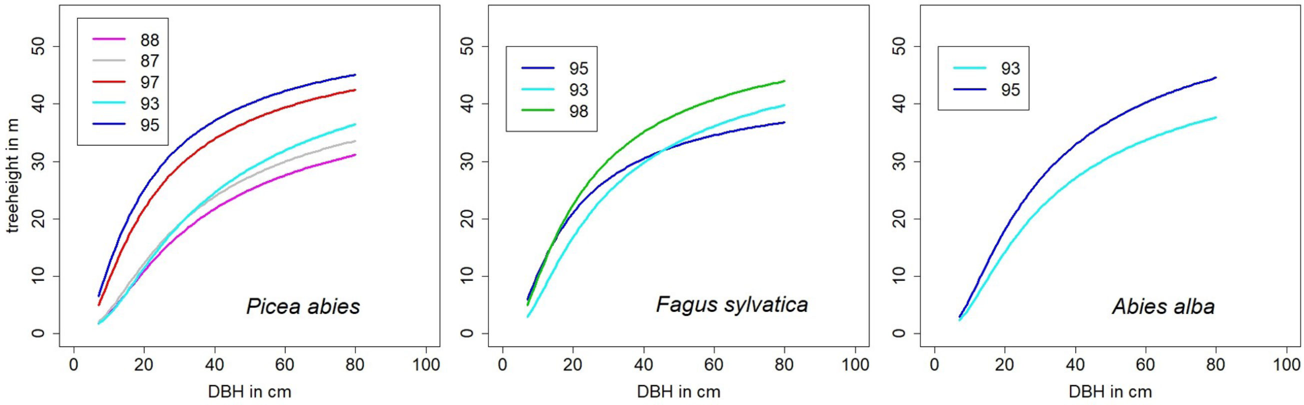

Fig. 2: Tree height curves for Norway spruce (*Picea abies*), beech (*Fagus sylvatica*) and silver fir (*Abies alba*) calculated with data from permanent monitoring areas in the investigated forest reserves (SFR IDs see table 1).

Abb. 2: *Höhenkurven für Fichte, Buche und Tanne, berechnet mit Daten von Repräsentationsflächen der untersuchten Naturwaldreservate (NWR IDs s. Tabelle 1).*

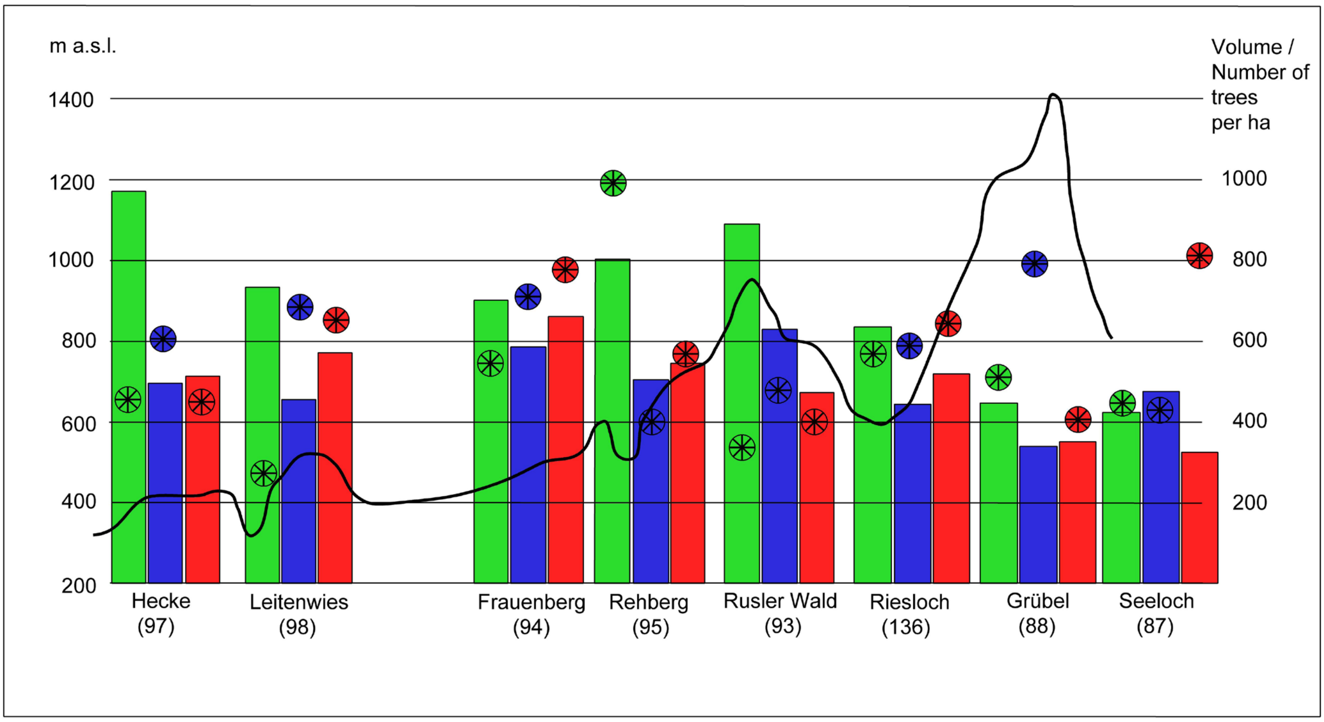

Fig. 3: Wood volumes and number of trees per ha per plot group (n = 6) and approximate location on the altitudinal gradient. Black line – altitude profile; bars – wood volume [m³/ha]; circles – number of trees per ha; green – strict forest reserve; blue – managed forest, beech-dominated ("A"); red – managed forest, spruce-dominated ("B").

Abb. 3: *Holzvorräte und Stammzahlen pro ha und Plotgruppe (n = 6) mit ungefährem Standort im Höhengradienten. Schwarze Linie – Höhenprofil; Balken – Holzvorrat [Vfm/ha]; Kreise – Stammzahl pro ha; grün – Naturwaldreservat; blau – Wirtschaftswald, Buchen-dominiert ("A"); rot – Wirtschaftswald, Fichten-dominiert ("B").*

of deadwood in this decomposition classes. For the fresh dead wood in managed forests, a similar though less distinct tendency was observed as in the forest reserves. Silvicultural management had a considerable impact on the amount of CWD in the investigated forests. Seven out of eight strict forest reserves were ranked among the top ten of the deadwood-richest sampling plot groups (Figure 4). An exception was the forest reserve "Rehberg", which ranged among the managed forest stands with moderate CWD stocks. The forest reserve "Leitenwies" showed the highest CWD stocks with more than 200 m³ deadwood biomass per ha. This strict forest reserve also showed the lowest numbers of living trees

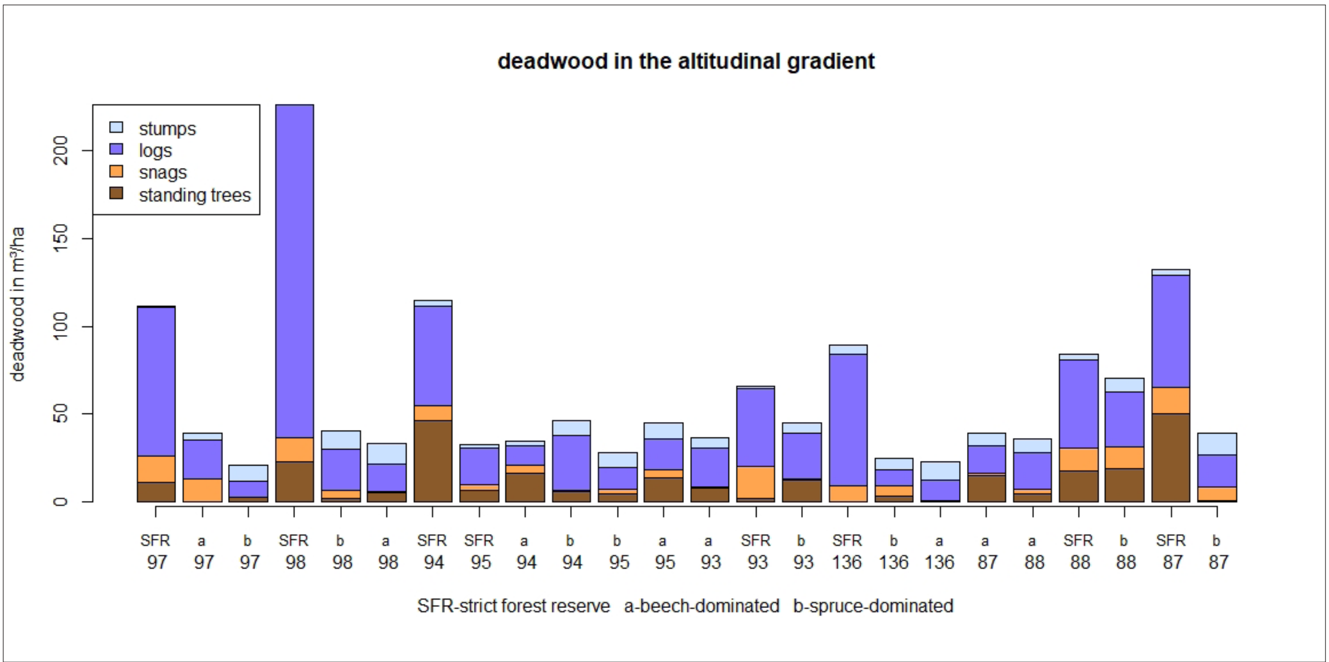

Fig. 4: CWD loads per ha in four CWD types per plot group (n = 6, increasing altitude on x-axis from left to right).

Abb. 4: *Totholzvorräte pro ha in vier Totholztypen pro Plotgruppe (n = 6, zunehmende Meereshöhe auf der X-Achse von links nach rechts).*

Tab. 3: Total and mean volumes per ha of different CWD types in the investigated forest types.

Tab. 3: *Gesamtvolumen und mittleres Volumen pro ha der verschiedenen Totholztypen in den untersuchten Waldtypen.*

Forest type	CWD type	Total vol/ha	Mean vol/ha
NWR	snags	579.4	15.6
NWR	downed deadwood	3503.0	72.9
NWR	fallen trees	2.6	1.3
NWR	standing dead trees	937.8	29.3
NWR	stumps	116.6	2.8
a	snags	161.4	6.2
a	downed deadwood	824.4	17.1
a	fallen trees	1.8	1.8
a	standing dead trees	384.2	15.3
a	stumps	349.2	7.2
b	snags	212.6	11.1
b	downed deadwood	967.0	20.5
b	fallen trees	22.8	3.8
b	standing dead trees	298.0	12.4
b	stumps	416.2	8.6

per ha, whereas "Rehberg" showed the highest log numbers per ha.

The distribution of deadwood volumes to CWD types showed marked differences between managed and near natural forests. In the strict forest reserves, mean volume of downed deadwood per ha was more than 3.5-fold higher than in managed forests (Table 3). Mean deadwood volumes per ha recorded as standing trees were 2-fold higher in strict forest reserves than in managed forest stands. Deadwood recorded as snags occurred with more than 2-fold higher mean volumes per ha in the forest reserves than in beech-dominated managed forests, but with similar volumes in spruce-dominated managed forest stands. On the other hand, stumps were recorded with more than 2-fold and more than 4-fold higher volumes in beech-dominated and spruce-dominated managed forests, respectively, than in the strict forest reserves.

3.1.3 Tree species distribution

In the strict forest reserves, the influence of altitude on the abundance of a tree species, represented by its respective mean volume per ha, was apparent for beech (*Fagus sylvatica*), spruce (*Picea abies*) and silver fir (*Abies alba*) (Figure 5). Wood volumes of beech were highest in the forest reserve "Hecke", located near the river Inn at about 300 m a.s.l., and declined considerably with increasing altitude. An exception was the reserve "Rusler Wald" in the middle of the altitudinal gradient, which showed high amounts of beech stocks, comparable to values of the lowland forests. In the uninfluenced, near-natural forests, wood volumes of spruce

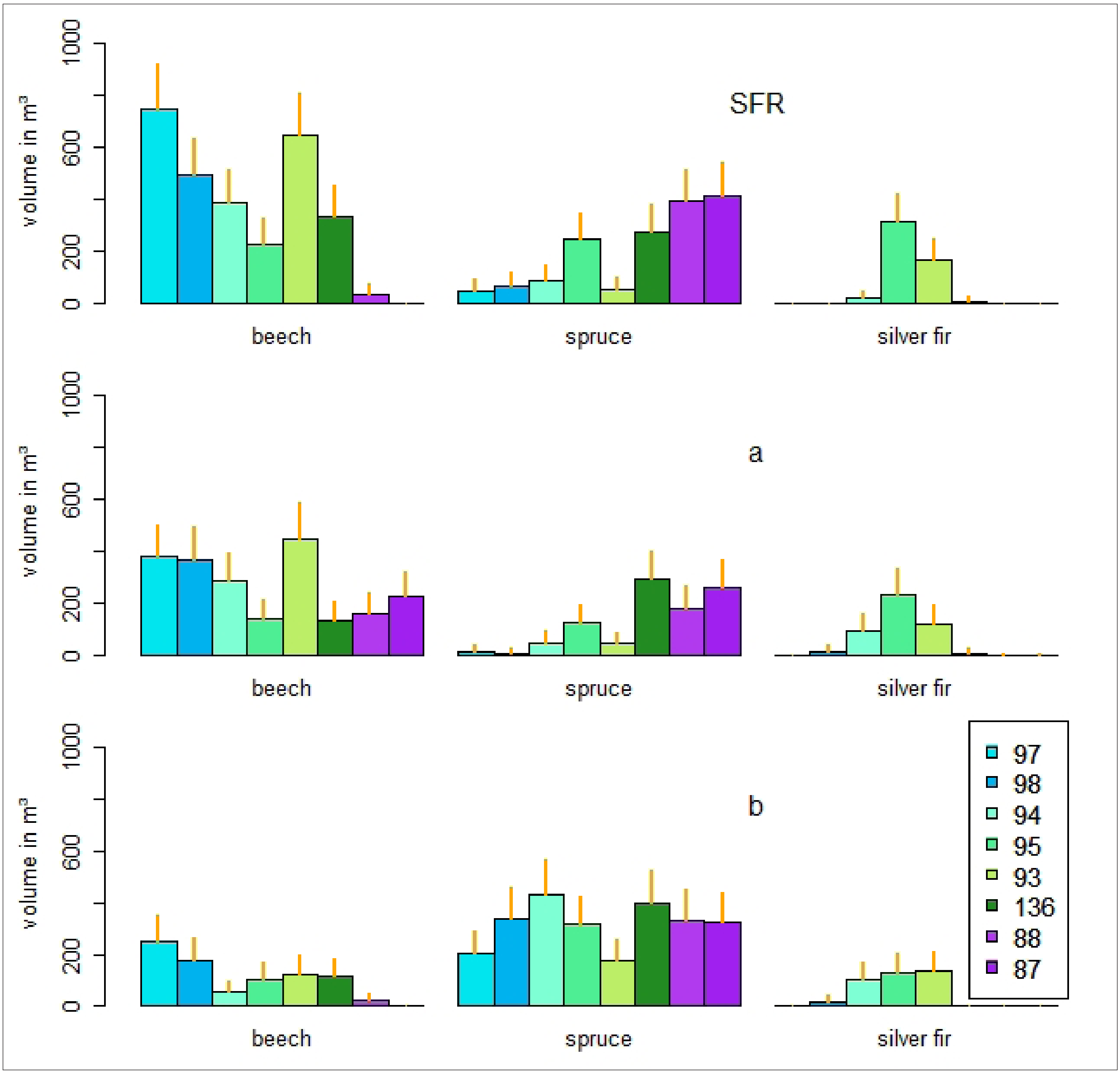

Fig. 5: Wood volumes/ha of the three main tree species per plot type along the altitudinal gradient (increasing altitude on x-axis from left to right).

Abb. 5: *Holzvorräte in Vfm pro ha der drei Hauptbaumarten nach Plottyp entlang des Höhengradienten (zunehmende Meereshöhe auf der X-Achse von links nach rechts).*

declined with decreasing altitude, from the high mountainous forests, where spruce was the sole dominant species, to the sampling plots near the rivers Donau and Inn, where spruce trees rarely occurred in the beech-dominated forest reserves. Silver fir showed the highest wood volumes in the middle of the altitudinal gradient. Due to the mode of selection of the reference plots in managed forest stands, the influence of altitude on the abundance of beech and spruce in managed forests was far less distinct than in the strict forest reserves. Silver fir, however, showed a similar pattern of wood volume amounts along the altitudinal gradient in the managed forest stands compared to the strict forest reserves.

The collected data on tree species occurrence on the sampling plots was transformed to presence-absence data in order to calculate the probability of presence of a given tree species depending on the altitude. Calculating with data from all sampling plot types, the probability of presence of beech amounted to more than 90 % below 1,000 m a.s.l. and progressively declined above this altitude (Figure 6a). At 1,400 m a.s.l., its probability of presence decreased to less than 10 %. The probability of presence curve generated only with data from the strict forest reserve plots showed an almost identical course (Figure 6b).

Norway spruce strongly dominated on the sampling plots at high altitudes in the Arber region. From 1,400 m a.s.l. down to about 900 m a.s.l., the probability of presence for spruce was more than 90 %. In the lowland forests in the region of the rivers Donau and Inn, the probability for the presence of spruce was still around 40 % (Figure 6a). Considering only data from the forest reserves, the probability of presence for spruce declined rapidly from over 90 % at 900 m a.s.l. and above to 20 % at 300 m a.s.l. (Figure 6b).

With almost 70 %, silver fir attained its maximum probability of presence on the sampling plots located in the middle of the altitudinal gradient (Figure 6a). However, management practice had a strong influence on the occurrence of silver fir. In managed forest stands dominated by conifers, the maximum probability of presence values amounted to 60 % at medium altitudes, whereas in the strict forest reserves located in the same region, the probability of presence of silver fir reached almost 100 %. In managed forest stands dominated by deciduous trees, silver fir occurred mainly in lowland forests located at about 400 m a.s.l. (Figure 6b). In contrast, silvicultural management had considerably less influence on the probability of presence values of beech and spruce (Figure 6b). Due to the selection criteria of forest stands dominated by deciduous and coniferous trees, respectively, the probability of presence of beech in forests

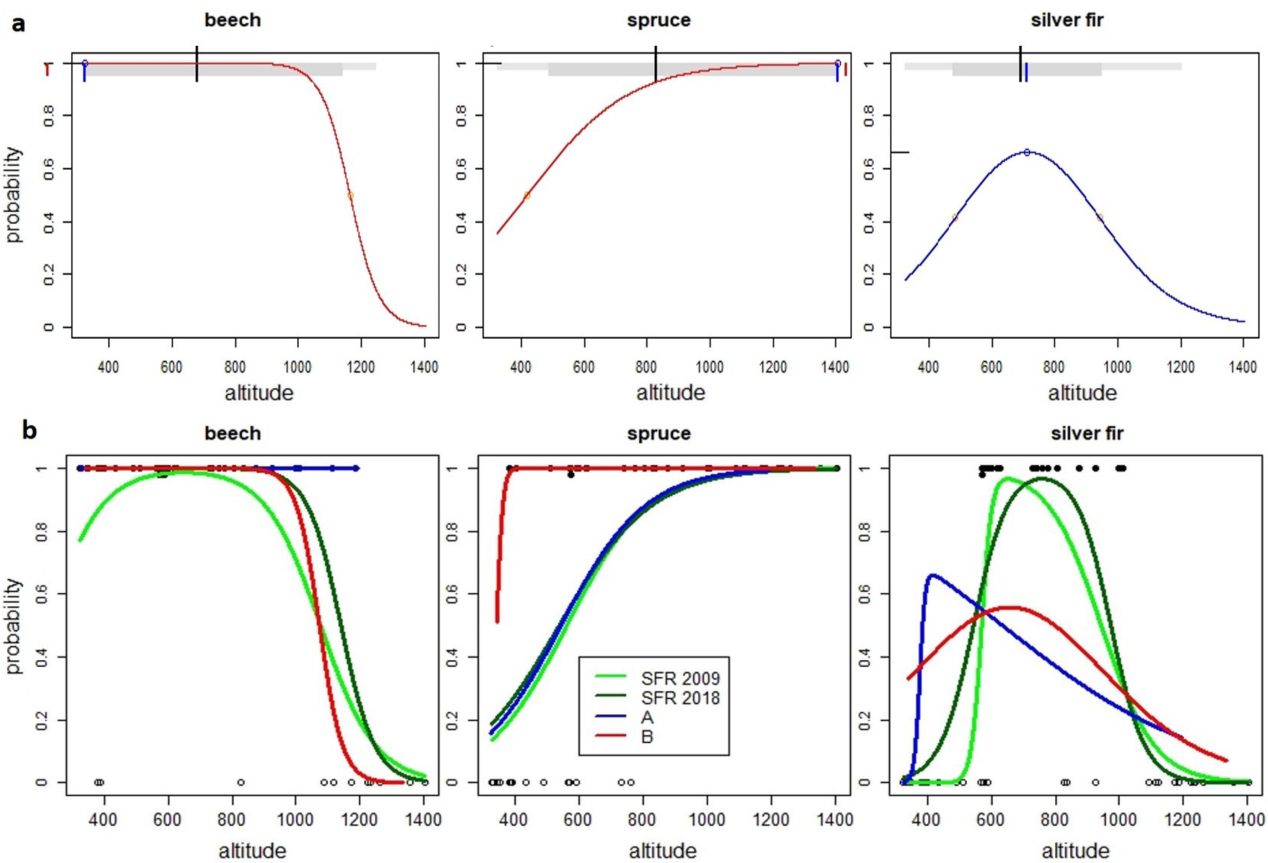

Fig. 6: Probability of presence of the three main tree species beech, spruce and silver fir along the altitudinal gradient, calculated for all plot types (**a**) and separately for plots in strict forest reserves (2009 vs. 2018), in managed forests dominated by beech (A) and in managed forests dominated by spruce (B) (2018) (**b**).

Abb. 6: *Präsenzwahrscheinlichkeit der drei Hauptbaumarten Buche, Fichte und Tanne entlang des Höhengradienten, berechnet für alle Plottypen (**a**) und separat für Plots in Naturwaldreservaten (2009 vs. 2018), in Buchen-dominierten Wirtschaftswäldern (A) und in Fichten-dominierten Wirtschaftswäldern (B) (2018) (**b**).*

dominated by deciduous trees amounted to 100 % along the entire altitudinal gradient. The same value was obtained for spruce in forest stands dominated by coniferous trees from the lowland forests up to the highest altitudes. The values for spruce in managed forests dominated by deciduous trees mainly corresponded to the values obtained from the strict forest reserves along the altitudinal gradient. The probability of presence of beech in conifer-dominated forests was over 90 % from the lowland forests up to 1,000 m a.s.l.

Since for the sampling plots in the strict forest reserves, data collected in 2009 were available, the probability of presence values were calculated and compared to the values obtained for 2018. For spruce, no changes along the altitudinal gradient were observed (Figure 6b). Beech and silver fir, however, showed subtle shifts of the probability of presence curve maxima towards higher altitudes (Figure 6b).

3.2 Carbon stores

3.2.1 Forest reserves: Data from sampling plots 2009 vs. 2018

In the strict forest reserves, total C stocks declined with increasing altitude, ranging from 348.7 to/ha in the forest reserve “Hecke” at 352 m a.s.l. to 139.5 to/ha in the reserve “Seeloch” at 1,211 m a.s.l. An exception was the reserve “Rusler Wald” at 757 m a.s.l., which exhibited carbon stores in the range of the lowland forest reserves. A comparison with data collected in 2009 showed an increase of total carbon stores in all forest reserves except for the reserve “Seeloch”. In this forest reserve, live wood C stores declined and CWD C stores increased, resulting in a decline of total carbon stores since 2009. Over all forest reserves, total carbon stores increased on average by around 40 to/ha compared to 2009, ranging from -10.6 to/ha (“Seeloch”) to +82.9 to/ha (“Frauenberg”).

3.2.2 Data from sampling plots 2018: forest reserves vs. managed forest stands

Similar to the strict forest reserves, managed forest stands showed a decrease of total C stores with increasing altitude, although less pronounced than in the forest reserves (Figure 7). The impact of silvicultural management on aboveground biomass C declined with increasing altitude. Mean C stock density was 246.7 to/ha in the forest reserves and 162.2 to/ha in the managed forests. CWD C stores in managed forests were lower than in the forest reserves in most cases.

3.2.3 Forest reserves: Data from sampling plots vs. permanent monitoring areas

Carbon stores of the forest reserves as calculated from the data collected on the sampling plots were compared to data obtained from the permanent monitoring areas (Figure 8). The mean deviation of aboveground biomass carbon values (AGC values) obtained from sampling plots and permanent monitoring areas within at most 3 years was 7.2 to/ha, corresponding to the carbon stored in three beech trees with a DBH of 40 cm. However, considerable over- as well as underestimation of AGC stores calculated from data of several sampling plots occurred with respect to the respective permanent monitoring area. In the forest reserve “Frauenberg”, AGC stores were underestimated by almost 50 % in 2009. Values calculated for 2018 based on sampling plot data still

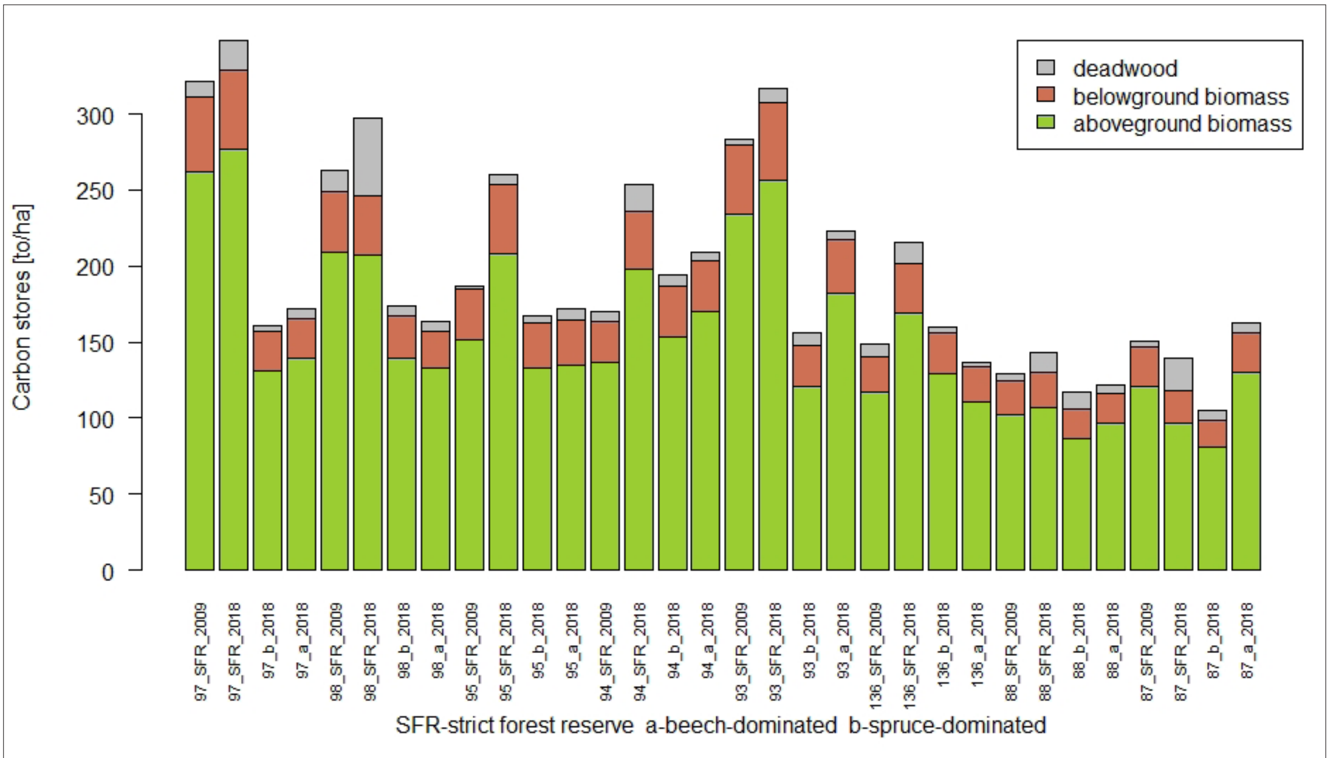

Fig. 7: Carbon stores per ha in managed forest stands (2018) and in strict forest reserves (2009 vs. 2018), calculated with data from sampling plots (increasing altitude on x-axis from left to right).

Abb. 7: *Kohlenstoffvorräte pro ha in Wirtschaftswäldern (2018) und in Naturwaldreservaten (2009 vs. 2018), berechnet mit Daten von Probekreisen (zunehmende Meereshöhe auf der X-Achse von links nach rechts).*

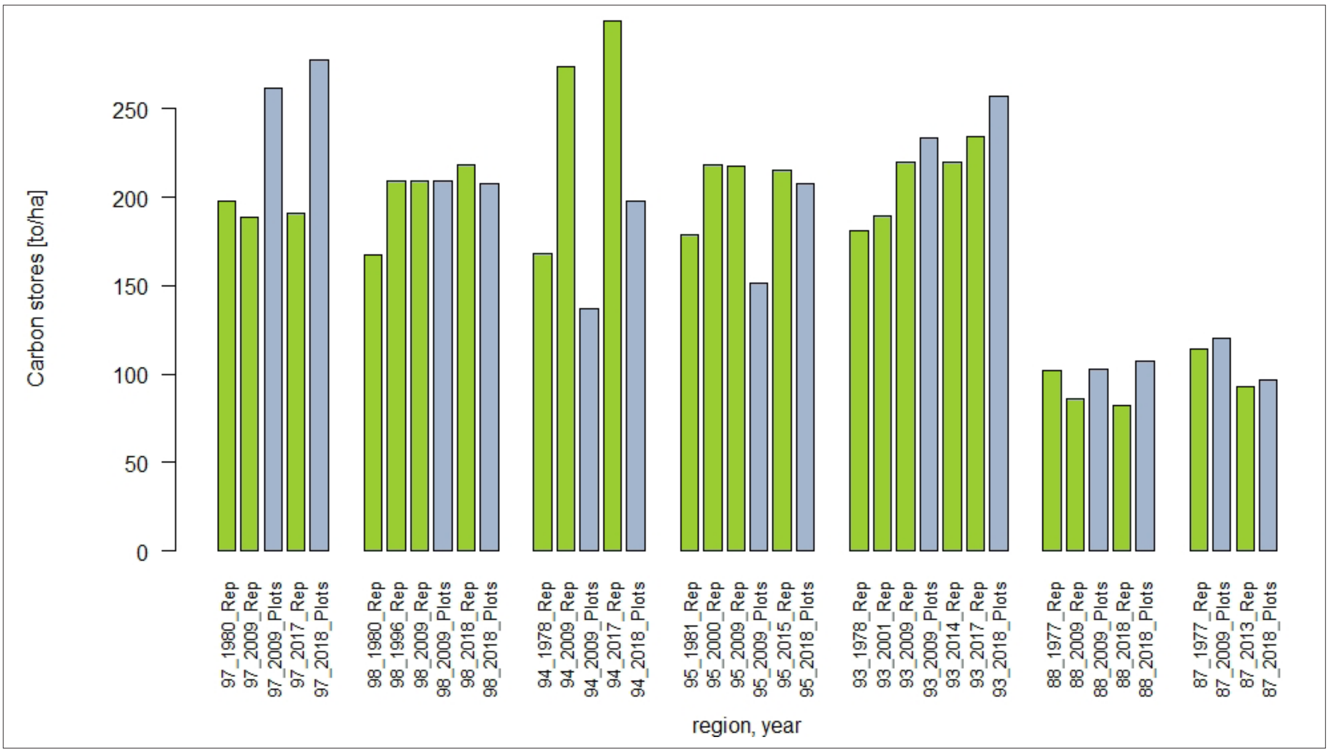

Fig. 8: Live tree C stores per ha in the strict forest reserves calculated with data from sampling plots in comparison to data from permanent monitoring areas collected during the last four decades. Green bars (Rep) – permanent monitoring areas; blue bars (Plots) – sampling plots (increasing altitude on x-axis from left to right).

Abb. 8: *Kohlenstoffvorräte des lebenden Bestandes pro ha in den Naturwaldreservaten, berechnet mit Daten von Probekreisen im Vergleich mit Daten von Repräsentationsflächen aus den letzten vier Jahrzehnten. Grüne Balken (Rep) – Repräsentationsflächen; blaue Balken (Plots) – Probekreise (zunehmende Meereshöhe auf der X-Achse von links nach rechts).*

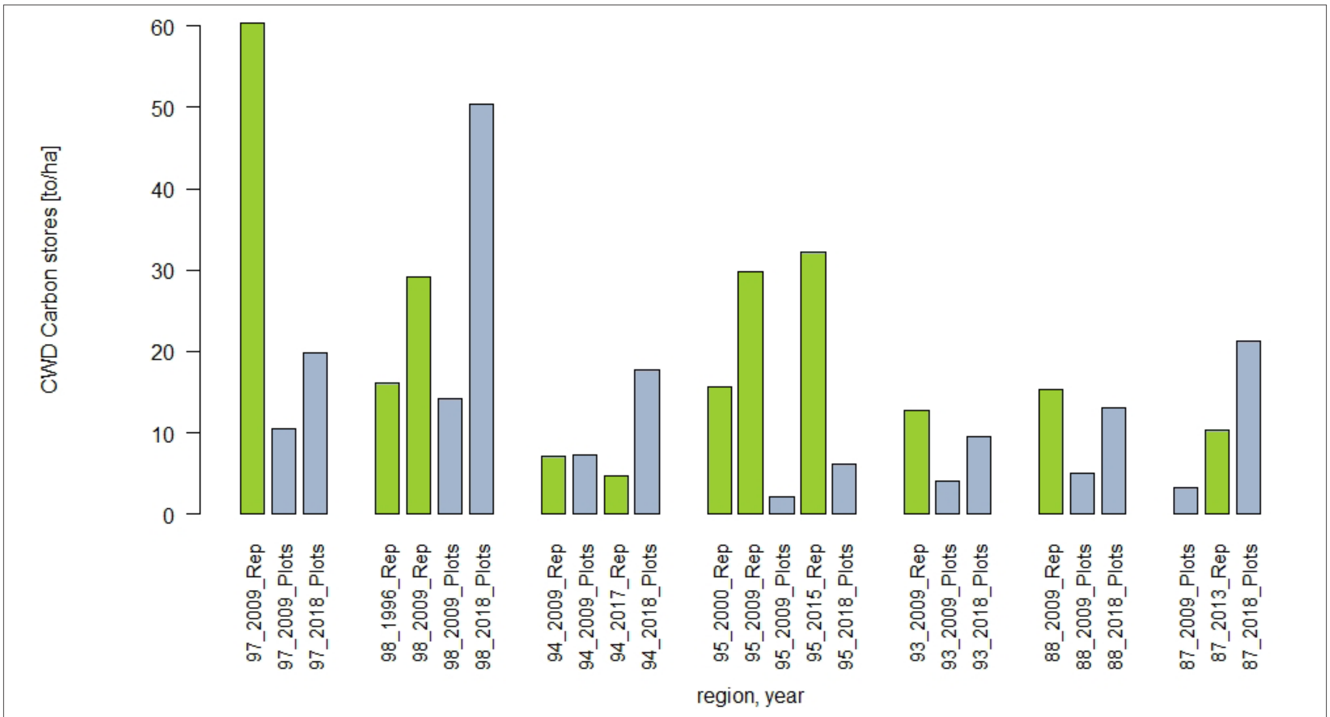

Fig. 9: CWD C stores per ha in the strict forest reserves calculated with data from sampling plots in comparison to data from permanent monitoring areas collected during the last three decades. Green bars (Rep) – permanent monitoring areas; blue bars (Plots) – sampling plots (increasing altitude on x-axis from left to right).

Abb. 9: *Kohlenstoffvorräte im Totholz pro ha in Naturwaldreservaten, berechnet mit Daten von Repräsentationsflächen aus den letzten drei Jahrzehnten. Grüne Balken (Rep) – Repräsentationsflächen; blaue Balken (Plots) – Probekreise (zunehmende Meereshöhe auf der X-Achse von links nach rechts).*

showed a discrepancy of 34 % with regards to the permanent monitoring area. In the forest reserve "Hecke", carbon store values were overestimated with sampling plot data in both 2009 and 2018 by 40 % and 45 %, respectively. Most of the observed deviations, however, ranged on a more moderate level (0.1 to 18.7 %).

The development of AGC stores over time as calculated with data from the permanent monitoring areas showed an increase of C storage since the establishment of the forest reserves in four out of seven reserves. A decrease of C stores was observed in two forest reserves located at high altitudes in the Arber region ("Seeloch" and "Grübel") and one located near the river Inn ("Hecke"). C stores calculated from sampling plot data for 2009 and 2018 mirrored the tendencies observed in the permanent monitoring areas, except for the reserve "Grübel" where the sampling plots showed a slight increase of C stores in contrast to the permanent monitoring area, as well as in the case of the reserve "Leitenwies", where a minor reduction of AGC stores was apparent on the sampling plots in 2018 compared to 2009, whereas the permanent monitoring area showed an increase of C storage in the same period.

CWD C stores were underestimated with sampling plot data in most of the forest reserves. However, the sampling plot data showed an increase of CWD C stores in all forest reserves from the first survey in 2009 to the recent investigation in 2018 (Figure 9). Since data on downed deadwood in permanent monitoring areas was not available for more than one date in four out of seven forest reserves, comparing the development of CWD C stores over time was not possible. In the strict forest reserves "Rehberg" and "Leitenwies", where data on downed deadwood in the permanent monitoring areas was available for three and two data collections in different years, respectively, an increase of CWD C stores was observed as well.

3.3 *Local climate data*

Altitude had a significant impact on mean daily temperature along the elevational gradient. The mean temperature difference between the highest and lowest measurement sites (forest reserves "Hecke" and "Seeloch") was 4.6 °C for data collected from the 7th of May till 31st of December in 2018, with a maximum temperature difference of 9.4 °C in mid-June. Figure 10 shows the course of mean daily temperatures for the two highest and the two lowest measurement sites in the measurement period 2018.

A comparison of the temperature data from 2018 with data collected in 2009 on identical measurement sites is shown in Figure 11. The mean temperature deviation between 2009 and 2018 for the measured period ranged from +1.3 °C at the two measurement stations in the lowest forest reserves "Leitenwies" and "Hecke", and +2.3 °C at the measurement station in the reserve "Riesloch" at the flank of the Arber. The highest reserve, "Seeloch" showed a mean temperature deviation of +2.1 °C for the measured period. The length of the vegetation period defined as the number of days with a mean daily air temperature of 10 °C or more was at least 24 days longer in 2018 than in 2009 at the highest measurement station on the mountaintop of the Arber (here, measurements did not start before 7th of May in 2018, when mean daily air temperatures already exceeded 10 °C), and 13 days longer at the lowest measurement station in the reserve "Hecke".

Over all sites, the year 2018 was dryer than 2009 (Figure 12). Mean difference of air humidity between 2009 and 2018 was +3.8 % at the lowest and +7.9 % at the highest measurement station (2009–2018, i.e. 2009 displayed a higher mean air humidity than 2018).

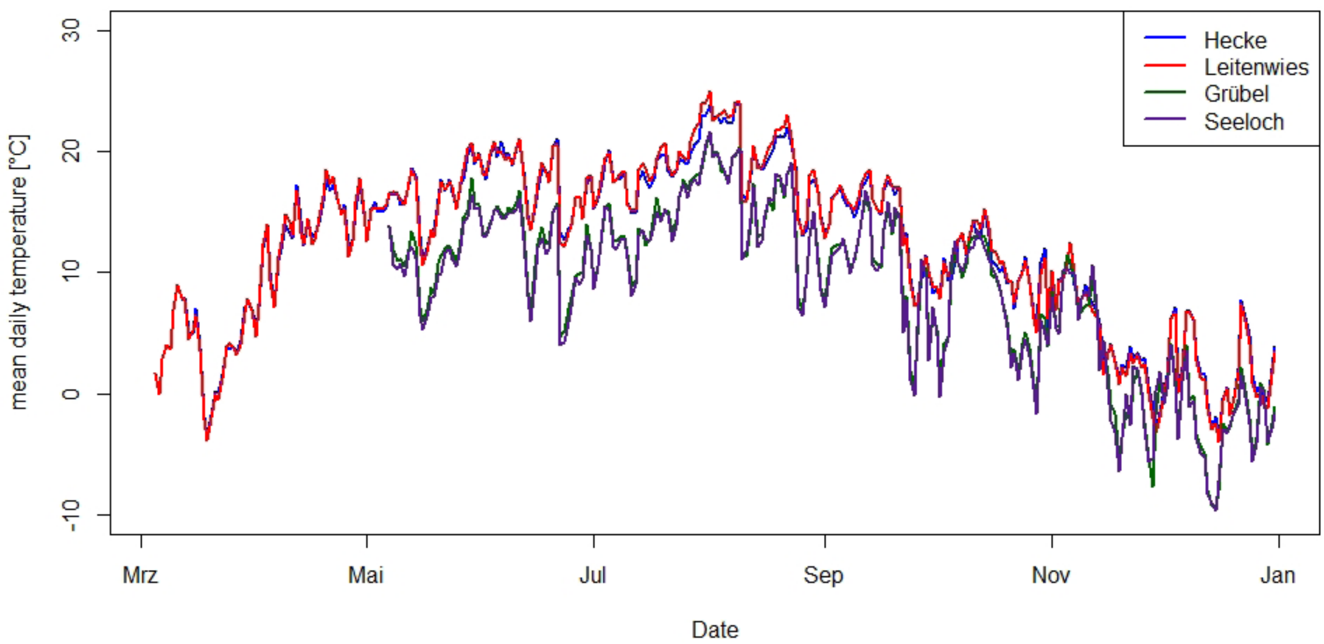

Fig. 10: Mean daily air temperature from March to December 2018 at the two lowest („Hecke" and „Leitenwies") and the two highest („Grübel" and „Seeloch") measurement stations.

Abb. 10: *Mittlere Tages-Lufttemperatur von März bis Dezember 2018 an den zwei tiefsten („Hecke" und „Leitenwies") und den zwei höchsten („Grübel" und „Seeloch") Messstationen.*

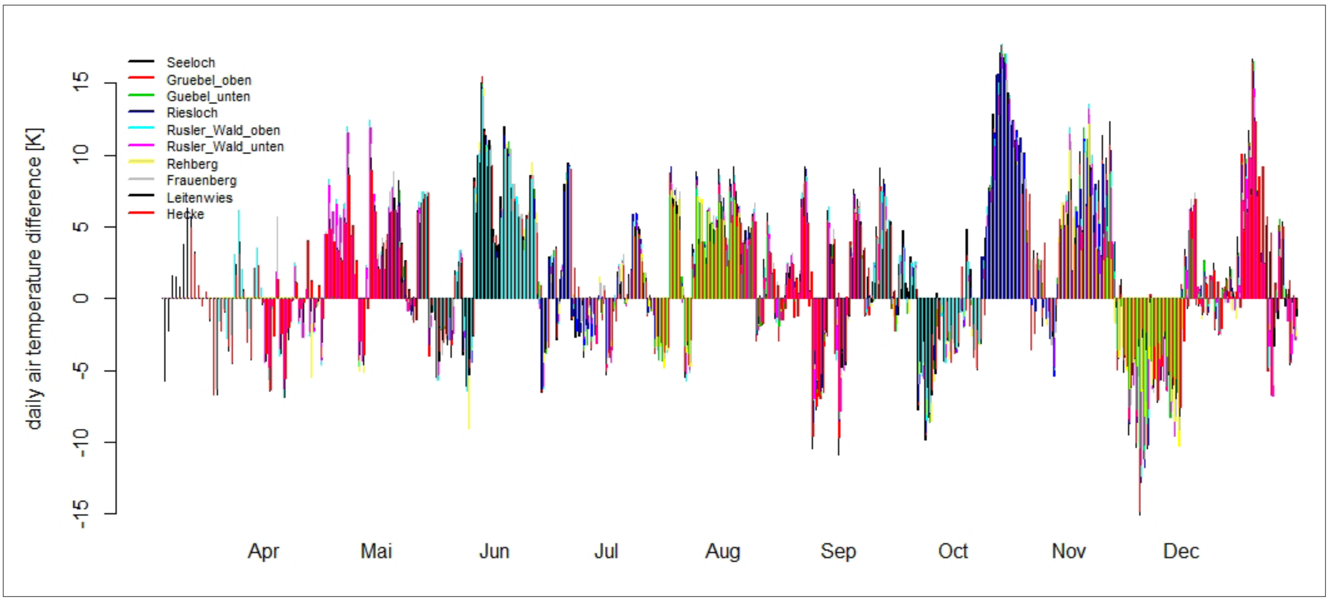

Fig. 11: Mean daily air temperature difference between 2009 and 2018 for all measurement stations along the altitudinal gradient. Positive bars depict warmer days, negative bars colder days in 2018 compared to 2009.

Abb. 11: *Differenzen der mittleren Lufttemperaturen pro Tag zwischen 2009 und 2018 für alle Messstationen entlang des Höhengradienten. Positive Balken entsprechen wärmeren Tagen, negative Balken kälteren Tagen in 2018 als in 2009.*

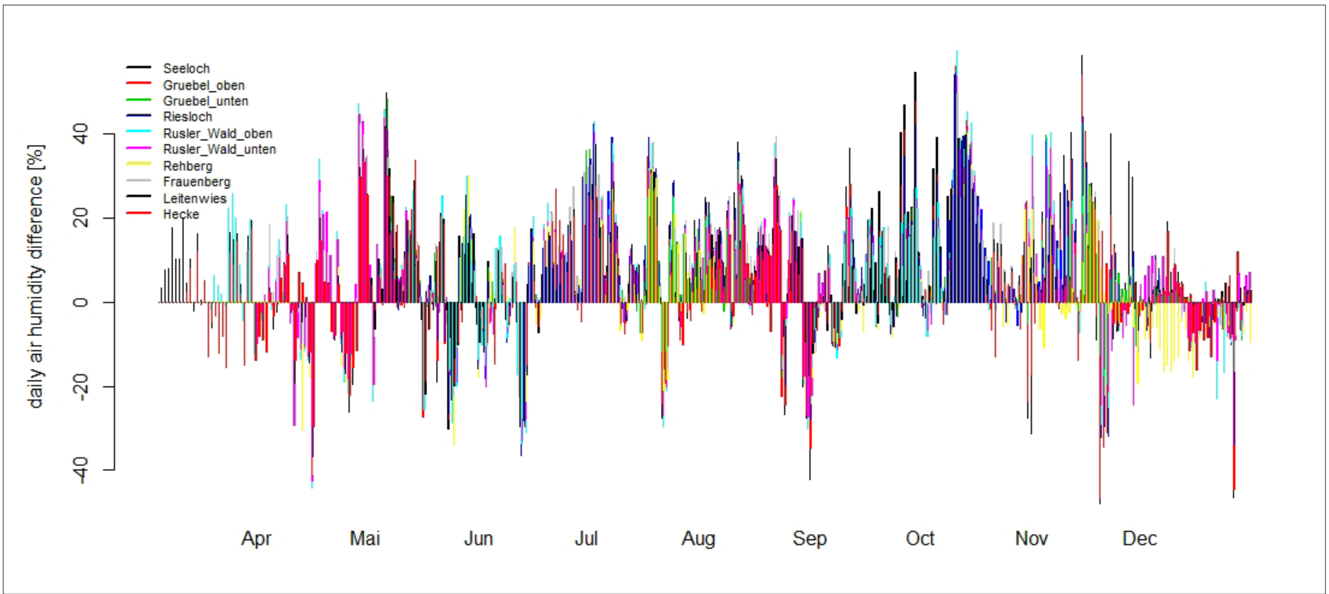

Fig. 12: Mean daily air humidity difference between 2009 and 2018 for all measurement stations along the altitudinal gradient. Positive bars depict dryer days, negative bars days with higher air humidity in 2018 compared to 2009.

Abb. 12: *Differenzen der mittleren Luftfeuchte pro Tag zwischen 2009 und 2018 für alle Messstationen entlang des Höhengradienten. Positive Balken entsprechen trockeneren Tagen, negative Balken Tagen mit höherer Luftfeuchte in 2018 als in 2009.*

4 Discussion

In this study, the impact of altitude and thereby associated climate parameters as mean annual temperature and length of the vegetation period on temperate forest ecosystems incentral Europe was investigated by means of 144 sampling plots in managed and near-natural forests along an altitudinal gradient ranging from 300 m a.s.l. to 1,400 m a.s.l. Data on live trees and coarse woody debris on sampling plots in strict forest reserves were compared to data obtained in 2009 on identical locations, to data from reference plots in nearby managed forest stands, as well as to data from permanent observation areas in the respective strict forest reserves, which were available for several dates in the past 40 years.

4.1 Influence of altitude, management practice and life stage on forest structures, CWD loads and carbon stores

The influence of altitude on live woody biomass stores was apparent in the sampling plot groups located in strict forest reserves as well as in managed forest stands dominated by spruce, although less pronounced in the latter. Mean volumes of live woody biomass per hectare declined with increasing altitude, leading to decreasing AGC values with increasing altitude as well. A similar trend was found by Holeksa et al. (2007) in spruce forests of the Western Carpathians, Slovakia, Coomes and Allen (2007) in mountain *Nothofagus* Bl. forests in New Zealand, Zhu et al. (2010) in temperate forests along an altitudinal gradient on Mount Changbai, Northeast China, as well as by Seedre et al. (2015) in old-growth Norway spruce stands in the Bohemian Forest, Czech Republic. The fact that temperature as tree growth-limiting factor not only determines the position of the treeline in high alpine zones but also limits forest productivity at high elevations in low mountain ranges below the treeline has repeatedly been demonstrated for temperate ecosystems at various scales (e.g. Gindl et al., 2001; Savva et al., 2006; Coomes et al., 2007; Sidor et al., 2015). The differentiated response of radial growth to temperature depending on the altitude was shown for Norway spruce and beech in low mountain ranges and the Alps in southern Germany (Dittmar & Elling, 1999), as well as for Norway spruce in the Carpathian mountains, Romania (Sidor et al, 2015), and the Tatra Mountains, Poland (Savva et al., 2006). Oladi et al. (2010) investigated wood formation in *Fagus orientalis* Lipsky at different elevations in the Alborz Mountains, Iran, and reported a ten-day delay of cambium reactivation in spring at 1,600 m a.s.l. compared to lower sites at 1,100 and 650 m a.s.l. Moreover, the authors showed that trees at the high-elevation site entered cambium dormancy earlier in autumn than did trees at lower elevations. Rossi et al. (2007) investigated cambial activity and cell differentiation in conifers at the treeline in the Alps and reported threshold temperatures for wood formation to be in the range of 6 °C to 8 °C mean daily air temperature for all tree species studied.

In this study, climate data obtained from measurements in 2009 and 2018 pointed towards mean temperature increases to be more pronounced at high elevations than at low-elevation sites. The length of the vegetation period (number of days with a temperature >10 °C) was 24 days longer in 2018 than in 2009 in the strict forest reserve “Seeloch” at the mountaintop of the Arber, whereas at the lowest measurement site, the vegetation period was only 13 days longer. Furthermore, measurements of relative air humidity showed that the year 2018 was drier than the year 2009, with a higher mean deviation at high altitudes compared to the lower sites. Indeed, climate warming appears to be accelerated with increasing elevation (Mountain Research Initiative, 2015). However, the observed extended vegetation period has been suggested to trigger an increased net C uptake, leading to a negative feedback to climate warming (Keenan et al., 2014).

The reduction of forest productivity at high altitudes as expressed by live woody biomass stores along the altitudinal gradient was not reflected by the respective mean basal areas per ha. This finding is in contrast to Jafari et al. (2013) who reported a negative correlation of mean basal areas with altitude in the Alborz Mountains, Iran. Wilcke et al. (2008), who also found decreasing basal areas with increasing altitude in tropical montane forests in Ecuador, furthermore reported decreasing tree heights with increasing altitude. Similarly in the present study, the tree-height curves obtained from permanent observation areas in the investigated forest reserves showed a decline of tree heights with increasing altitude, which resulted in the observed reduction of live woody biomass stores, as was also reported by Coomes and Allen (2007) and Holeksa et al. (2007). The missing correlation of basal area values with altitude is probably due to the predominating effect of the successional stages of the investigated forests over the influence of altitude on basal areas. This assumption was confirmed by a comparison of tree densities and assignment of tree numbers to diameter classes, which reflected the respective successional stages. Indeed, forest life stage had a significant impact on the investigated structure parameters. Old forests were characterized by low tree densities and high numbers of large old trees, whereas middle-aged and young forests showed high tree densities with lower numbers of large trees. However, although the basal areas were similar, declining tree heights with increasing altitude led to clearly different wood volumes in these cases, indicating that the effect of altitude and thereby temperature predominated over forest life stage with regard to this structure parameter.

Mean volumes of living trees per ha as well as mean AGC values were higher in strict forest reserves than in managed forest stands. This is in agreement with other studies, which compared (modeled) tree biomass and carbon stores in managed and unmanaged forests (Thornley & Cannell, 2000; Mund & Schulze, 2006; Klein et al., 2013; Suberi et al., 2018; Nord-Larsen et al., 2019). The impact of silvicultural management on live woody biomass stores was least at high altitudes, whereas biomass stores at low-elevation sites were considerably lower in managed forests than in the strictly protected forest reserves. The approximation of biomass stores in managed forests at high elevations to amounts observed in the strict forest reserves is probably due to two independent factors: First, the lower forest productivity at the high elevation sites was apparently taken into consideration in the management plans, leading to a lower logging intensity than at the low elevation sites. Second, the Arber region faced a number of severe storm damages and bark beetle outbreaks during the last years, affecting managed forest stands and protected areas likewise, which might have led to similar residual live woody biomass stores. Furthermore, it should be noticed that in the case of bark beetle outbreaks in the forest reserves, the protection of surrounding managed forests from damage due to bark beetle attacks is prioritized over the abandonment of the forest reserves, enabling sanitary measures as clearing and decorticating of infested trees in the unmanaged reserve areas.

Mean CWD loads were higher in strict forest reserves than in managed forest stands, which is in agreement with other studies, which compared protected areas with managed forests (Bobiec, 2002; Mund & Schulze, 2006; Nord-Larsen et al., 2019). CWD volumes in strict forest reserves were fairly within published ranges for protected forest areas in Europe (Christensen et al., 2005; Bujoczek et al., 2018; Oettel et al., 2020). In contrast to other studies (Kueppers et al., 2004), no distinct influence of altitude on the amount of deadwood biomass was observed, although the highest CWD loads were recorded in the lowest forest reserves. Holeksa et al. (2007) reported insignificant declines of CWD stores with increasing altitude in the Western Carpathians. Bujoczek et al. (2018) found deadwood volumes to be highest at medium altitudes (600 – 1,000 m a.s.l.) in protected primeval forests in Poland. Christensen et al. (2005) reported CWD loads to be higher in montane than in lowland and submontane European beech forest reserves. However, forest life stage had a strong impact on CWD amounts in the investigated strict forest reserves, leading to deadwood volumes comparable to managed forest stands in the middle-aged forest reserve "Rehberg". The abundance of different CWD types differed between managed and near natural forests, with standing dead trees and downed deadwood being more abundant in strict forest reserves than in managed forest stands, whereas stumps occurred with higher volumes in the latter. Snags were recorded with the highest mean volumes per ha in strict forest reserves. However, spruce-dominated managed forests showed almost comparable values, indicating that mortality due to bark beetle attacks in combination with stem breaks caused by wind were the main sources of snags in these ecosystems.

A comparison of carbon stores recorded on sampling plots in the strict forest reserves in the years 2009 and 2018 showed mean increases of C stored in deadwood as well as AGC in most cases, which is in line with observations of Nord-Larsen et al. (2019) in beech-dominated forests in Denmark. Data from permanent monitoring areas, however, showed decreasing AGC stores over time in the two highest reserves, undoubtedly due to enhanced mortality as a result of spruce bark beetle attacks, as well as in the lowest reserve "Hecke", where the permanent monitoring area was installed in an over-mature part of the forest. The comparison of carbon store values calculated with data from sampling plots (500 m²) and permanent monitoring areas ((0.2) 0.5 to 1 ha) in the strict forest reserves showed considerable discrepancies in some cases, proving that data on woody biomass and carbon stores calculated thereof have to be interpreted with caution as sampling design has a considerable impact on the validity of extrapolation to hectare-based values. In unmanaged forests, multiple structures may develop on a small scale, leading to a patchy and irregular pattern of forest structures. A higher impact of this patchiness on the reliability of the obtained data is considered to occur with comparatively small sampling plots, and will decline with increasing size. However, it should be noted that permanent monitoring areas in the strict forest reserves were deliberately installed in mature parts of the forests, potentially yielding distorted results for the entire reserve. Smaller sampling plots randomly distributed over the full range of a protected area might yield data with higher variability but this approach appears more suitable to represent the full range of habitats in a naturally inhomogeneous ecosystem.

4.2 Tree species distribution and probability of presence models

The distribution of the main tree species beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and silver fir (*Abies alba*) in the forest reserves along the altitudinal gradient as expressed by their wood volumes per ha corresponded to their natural occurrence in the forest communities of the respective altitudinal belts (Walentowski et al., 2020). Wood volumes of beech declined with increasing altitude, whereas spruce stocks increased towards the higher altitudes of the Arber region, where mountainous forest ecosystems are naturally dominated by Norway spruce. Silver fir showed the highest wood volumes at medium altitudes, which are naturally covered with mixed mountainous forests, composed of beech, spruce and fir. The observed preferences for certain altitudinal zones are correlated with species-specific temperature optima for tree growth, as demonstrated by Cailleret & Davi (2011) for beech and silver fir. Furthermore, the authors found significant increases of radial growth at high altitudes in both tree species and assigned this to climate warming effects. Similarly, Dulamsuren et al. (2017) found growth increases in beech at high altitudes in the Black Forest in south-west Germany, but a growth decline at low elevations since the 1980s, which they supposed to be caused by elevated spring and summer temperatures together with decreased precipitation in these seasons. In general, upward shifts of plant species distributions in mountain regions are expected in response to climate change-related temperature increases (Jump & Penuelas, 2005). A comparison of modeled probability of presence for the examined tree species on sampling plots in strict forest reserves in 2009 and 2018 showed shifts of curve maxima to higher altitudes for beech and silver fir, possibly indicating uphill movements of these species, whereas Norway spruce did not show a response in the considered time span. Hanewinkel et al. (2013) and Dyderski et al. (2018) predicted range expansions for beech and silver fir to higher latitudes and altitudes in response to climate warming, whereas net range contractions were expected for Norway spruce due to the lack of colonisable areas. Although there were no signs of range contraction of spruce at low and medium altitudes in this study, proving that the species was still present with the same probability as in 2009 over the altitudinal gradient, severe bark beetle outbreaks during the last several years strongly decimated Norway spruce populations at all elevations in the investigated area. In general, higher summer temperatures enable a shortening of the spruce bark beetle generation time (Marini et al., 2017), leading to the establishment of multiple broods during hot summers. High summer temperatures in combination with drought stress have been shown to favor mass outbreaks of spruce bark beetles (Netherer et al., 2019). In 2018, completion of two spruce bark beetle generations and establishment of a third generation, together with multiple sister broods, were observed all over Bavaria (Triebenbacher et al., 2019). Increasing numbers of spruce bark beetle generations and a higher risk of mass infestations in Central Europe are predicted for the near future due to climate warming (Jakoby et al., 2019; Netherer et al., 2019). Indeed, the future of Norway spruce as dominating tree species in Central European lowland managed forests appears to be uncertain in the face of climate change, which affects the trees both directly by increasing frequency and duration of drought events and other weather extremes as well as indirectly by climate warming-promoted bark beetle mass infestations. Beech, on the other hand, is considered to be more tolerant to dry conditions and supposed to replace Norway spruce in the Central European lowlands (Falk & Hempelmann, 2013). Results of Dulamsuren et al. (2016), who reported growth declines of beech trees at low elevations and increased radial growth at high elevations in south-western Germany since the 1980s, rather point to an upward shift of the climatic envelope of beech, which might be supported by the findings presented herein. Movements of beech forests to higher altitudes have already been demonstrated in the Montseny Mountains, Spain, at the southernmost limit of distribution (Penuelas & Boada, 2003; Penuelas et al., 2017). Mátyás et al. (2010) reported mass mortality in beech stands in the southwest of Hungary, at low elevation sites and at the xeric limit of distribution, as a result of consecutive drought episodes in the years 2000–2004. The authors outlined that extreme weather events as drought rather than the changing climatic means might trigger range contractions at the trailing edge of the distribution. A similar situation was reported from the xeric limit of distribution of silver fir in the Spanish Pyrenees (Hernández et al., 2019), where increased mortality rates were observed since the 1980s (Linares & Camarero, 2012). However, the authors stated that the trees appeared to suffer from drought stress caused by high temperature conditions rather than by a precipitation deficit in this area. Tinner et al. (2013) showed that silver fir forests existed in southern Europe around 6,000 years ago under climatic conditions with 700–800 mm annual precipitation, comparable to today, and by 5–7 °C higher summer temperatures (July means) than today, suspecting that silver fir may withstand increasing temperatures due to climate warming unless annual precipitation does not drop below 700 mm. Zang et al. (2014) investigated the drought tolerance of beech, Norway spruce and silver fir, and reported Norway spruce to be the species the least tolerant to drought stress, whereas they considered silver fir as the most drought-resistant of the three species examined. In contrast, Cailleret et al. (2014) stated the drought tolerance of *Abies alba* to be low, predicted a large dieback of silver fir and Norway spruce in the area of the Bavarian Forest National Park and their progressive replacement by *Fagus sylvatica*. However, the responses of trees and entire forest ecosystems are highly complex, and many contradicting studies and predictions have been published. Furthermore, observed altitudinal shifts of trees claimed to be due to climate warming have repeatedly been questioned, as forest life stage and land use changes (as well as other biotic interactions) may interfere with or predominate over climate change effects (Bodin et al., 2013; Máliš et al., 2016). An intensive monitoring of mountainous ecosystems and a careful monitoring design are therefore of paramount importance for a better understanding of climate change effects on forest ecosystems, which is the prerequisite for robust recommendations to forest practitioners.

5 Conclusions

Forests at high altitudes are particularly sensitive to temperature fluctuations and will probably respond with enhanced growth rates to rising temperatures as they are predicted due to global climate change (Savva et al., 2006; Hartl-Meier et al., 2014), unless precipitation amounts decline simultaneously and take over as growth-restricting factor. Additionally, rising average temperatures at high altitudes will also result in longer growing periods, as threshold temperatures for tree growth will be reached earlier in spring and will be delayed in autumn as already indicated by the climate recordings in this study. However, life stage, management regime and large-scale pathogen attacks fueled by climate change may interfere with forest ecosystem responses to climate warming. Therefore, data on forest structure have to be interpreted with caution when it comes to the question of climate change effects. The consideration of other factors influencing the productivity of forest ecosystems, especially biotic and human factors, and their interaction with climate warming, is indispensable for robust and reliable forecasts of forests responses to climate change. In mountainous regions, upward shifts of tree species distribution ranges are expected and have already been demonstrated for several species in European mountain ranges. The present study yields further signs for an upward-moving altitudinal distribution of beech and silver fir in Central Europe. Changes in mean wood volumes and CWD loads observed in the strict forest reserves within a time frame of nine years were primarily due to stand maturation after the abandonment of forest management. However, direct and indirect climate warming effects were visible at the highest sites, where increased incidences of storm damage and bark beetle outbreaks led to an enhanced mortality of Norway spruce and corresponding changes in the amounts of live and dead woody biomass. Silver fir proved to be a viable element of the mixed mountain forests at medium altitudes with the potential of an uphill range expansion. Further support of this robust tree species, especially at higher altitudes, may save a conifer component in mountain forests in the face of climate change. The comparative investigation of sampling plots in managed and protected forests along an altitudinal gradient proved to be a useful approach for the investigation of elevation-dependent temperature effects on forest structures and the impact of management and life stage on climate warming responses.

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