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Climate change and disturbances will shape future temperate forests in the transition zone between Central and SE Europe

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Abstract It is expected that climate change as well as abiotic and anthropogenic disturbances will strongly influence temperate forests. Besides changes in the main climate variables, various disturbance factors may significantly worsen conditions for mesic Slovenian forests (SE Europe) dominated by European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and European silver fir (*Abies alba*). In Slovenia, the climate has warmed in recent decades, with an average annual rate of increase of about 0.4°C per decade or even more than 0.5°C per decade in summer. In addition, disturbances have caused considerable damage to trees in the most extensive forest types in Slovenia, starting with a widespread ice storm in 2014, followed by bark beetle outbreaks, windthrows and salvage logging interventions. After 2014, salvage logging increased from about one third to two thirds of the total annual felling. Over the last two decades, we have observed a decline in Norway spruce growing stock, with the highest rate of decrease in areas below 500 m a.s.l., and an increasing trend for European beech. Overall, the three dominant species (beech, spruce, silver fir), which together account for more than 70% of the total growing stock, have shown a declining trend over the last 20 years. The patterns observed are broadly consistent with earlier predictions developed for different climate change scenarios and with those reported in many other European countries. Adaptive forest management, which implements close-to-nature silviculture, has been traditionally practised in the region under study and has the potential to play an important role in reducing the risks associated with the impacts of climate change and disturbances in the future.

Keywords: climate warming; disturbance factors; ice storm; bark beetle outbreaks; spruce decline; salvage logging; tree species composition; temperate forest, Slovenia

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Introduction

Forests in Europe will have to adapt to changes in mean climate variables and to their increased variability, with a higher risk of extreme weather events, such as prolonged summer droughts, windstorms and floods (IPCC 2001, 2007, 2014, Lindner et al. 2010, Blennow et al. 2010).

In the twentieth century, climate change (hereafter CC) has obviously also increased the probability of large-scale, intensified disturbances such as windthrows and snow and ice breaking (Schelhaas et al. 2003), and CC is likely to increase forest disturbance hazard in the future (Thom et al. 2017). Disturbances and climate change are highly likely to interact, which can lead to synergistic or antagonistic ecological effects that are difficult to predict (Brook et al. 2008). Parallel to global warming, natural and anthropogenic disturbance regimes have changed significantly, so that these two driving forces of ecosystem dynamics can often mask or modify the effects of the other (Danneyrolles et al. 2019). Furthermore, the interactions between multiple abiotic and biotic stressors are not well understood, which further complicates the possible outcomes of direct and indirect CC effects (Chmura et al. 2011, Boisvert-Marsh et al. 2014).

Natural and human disturbances can be defined as relatively discrete events in time that disrupt the ecosystem and cause pronounced changes in resource availability or the physical environment (White & Pickett 1985, Attiwill 1994), and they are a major driver of forest community dynamics (Goldblum & Rigg 2010). Although highly variable in space and time, disturbances can have a lasting effect on forests and are increasingly affecting forest management (Seidl et al. 2011a, Grecs & Kolšek 2017, Danneyrolles et al. 2019). Disturbances must therefore be taken into account when attempting to understand and predict the effects of CC on tree species distribution and forest formation (Bouchard et al. 2019), as they have been shown to enhance the response of tree communities to CC (Brice et al. 2019). Warmer and drier conditions are likely to favour fires, drought and insect disturbances in the future, while warmer and wetter conditions could increase wind and pathogen disturbances (Seidl et al. 2017).

The main components of a forest disturbance regime include disturbance type and frequency, severity, and spatial extent (Runkle 1985). All these descriptors are modulated by changing responses to current and future CC. An increasing frequency of large-scale disturbance events has been documented over the last decade, and this is expected to further increase in the future (Seidl et al. 2014). In Europe, damage caused by wind, insect outbreaks and forest fires has increased in forests over the course of the twentieth century. In addition, the synergistic interaction of various disturbance factors has been enhanced, e.g. drought increases the intensity of fires, and insect damage increases vulnerability to storms. These strong linkages are usually expressed as a cascade that occurs when abiotic disturbances are followed by insect outbreaks (Kausrud et al. 2012, de Groot et al. 2018). Widespread interactions between different abiotic and biotic agents are likely to increase the intensity and spatial extent of disturbances (Seidl et al. 2017), further strengthening the role of disturbances as critical drivers of forest ecosystem composition, structure and functioning (Bengtsson et al. 2000, Schelhaas et al. 2003, Seidl et al. 2011b, 2014, 2017, Thom & Seidl 2016, Nagel et al. 2017).

Extreme weather events, such as extensive summer droughts, have a much greater effect on tree growth and survival than gradual changes in average climate conditions (Lindner et al. 2010). Warmer and drier conditions will lead to more frequent and extended droughts throughout Europe. Regions most vulnerable to increasing drought risk are the Mediterranean and some continental parts of Central and Eastern Europe, which could experience an increase in droughts and fire hazards by the end of the 21st century (Polemio & Casarano 2004, Goldammer et al. 2005, Good et al. 2006, Moriondo et al. 2006, IPCC 2007, 2014).

Future CC and associated changes in the disturbance regime are likely to be most pronounced in coniferous forests (Seidl et al. 2017), especially where conifers have been artificially introduced. Conifers are expected to decline due to water limitations (Lasch et al. 2002, Lexer et al. 2002, Martínez-Vilalta & Pińol 2002) and higher temperatures (Pretzsch & Dursky 2002), especially Norway spruce (*Picea abies*) and European silver fir (*Abies alba*). These native conifers will probably be replaced by broadleaved tree species in Western and Central Europe (Maracchi et al. 2005, Koca et al. 2006, Kutnar & Kobler 2011). However, drought may also negatively impact mesic deciduous forests (Broadmeadow et al. 2005, Kutnar & Kobler 2011, 2014, Stojanović et al. 2013, 2014). Other abiotic threats to forests are likely to increase, although the expected impacts are regionally specific and will largely depend on the forest management system implemented (Kellomäki & Leinonen 2005, Dobor et al. 2020).

For Slovenia, which is located in the transition area between three major geographic regions of SE Europe (Alps and Dinaric Mountains, Mediterranean Region, and the Pannonian Basin), various climate envelope models (Box et al. 1999, Pearson & Dawson 2003, Hijmans & Graham 2006) have been developed to predict the effects of CC on forests and tree species distribution (Kutnar & Kobler 2011, 2013, 2014). By the end of the 21st century, mesic forests with predominant European beech (*Fagus sylvatica*) could be affected by changing environmental conditions (Thom et al. 2020). Under various climate warming scenarios, the proportion of dominant beech forests is likely to decrease, and the area of warmth-tolerant thermophilic forests and tree species will increase significantly (Kutnar & Kobler 2011, 2014). In the coming decades, the distribution range and abundance of Norway spruce (Kutnar & Kobler 2014) and European silver fir (Anić et al. 2009, Ficko et al. 2011) are likely to decrease. It is expected that the distribution areas of the currently dominant tree species will expand northwards and/or to higher altitudes and shrink at their marginal edges (Boisvert-Marsh et al. 2014, Thurm et al. 2018, Bouchard et al. 2019). All these expected changes are consistent with general observations related to global warming.

Besides the long-term shifts in tree species composition and forest distribution caused by changes in climate variables, CC-driven changes in forest disturbance patterns have to be considered. Natural and anthropogenic disturbance factors alone and together have caused considerable damage to Slovenian forests in recent years. Therefore, the objectives of this study are to assess i) changes in key climate variables over the last decades; ii) the effects of different disturbance factors on forests, a with special emphasis on a massive ice storm disturbance; and iii) the resulting changes in tree species composition in Slovenia.

Materials and Methods

Study area

Slovenian forests cover a total area of 1.2 million ha, which corresponds to 58% of the country's total area (ZGS 2005-2019). Due to its heterogeneous relief, its climate, and the legacy of former forest management, Slovenian forests consist of a diverse mosaic of forest types, ranging from lowland floodplain forests to widespread mesic mixed forests dominated by beech at medium altitudes and to mountainous coniferous forests at higher altitudes. In lowland areas that experience periodical flooding, forest stands occur in narrow strips along rivers and streams and are dominated mainly by willows (*Salix* sp.), alders (*Alnus glutinosa*, *A. incana*), ashes (*Fraxinus excelsior, F. angustifolia*) and common oak (*Quercus robur*). In the hilly areas above the floodplains, mixed forests of sessile oak (*Quercus petraea*) and hornbeam (*Carpinus betulus*) are the predominant forest type.

Most of the mountain areas are covered by forests of European beech (*Fagus sylvatica*) with mixtures of various broadleaved trees (e.g. *Acer pseudoplatanus*, *Fraxinus excelsior*, *Ulmus glabra*) and conifers (*Abies alba*, *Picea abies*). Dinaric forest of European beech and European silver fir (*Abies alba*) is one of the most extensive forest types in the country, covering more than 10% of the total forest area (Dakskobler 2008). In the Alpine region, various European beech forests mixed with Norway spruce (*Picea abies*), European silver fir, and European larch (*Larix decidua*) reach the timberline up to the belt of dwarf mountain pine (*Pinus mugo*).

Scots pine (*Pinus sylvestris*) forests can be found throughout the interior of the country on nutrient-poor soils. Austrian pine forests (*Pinus nigra*) grow on some extreme slopes of the continental part of the country with a warmer (micro)climate; this tree species was also planted over the greater part of south-western Slovenia, in the Karst region. All over the country, forests and shrubby vegetation of various thermophilic deciduous species (e.g. *Ostrya carpinifolia*, *Fraxinus ornus*, *Quercus pubescens*, *Q. cerris*, *Sorbus aria*) extend mainly on limestone and dolomite rocks on warm south-facing slopes.

In its natural range, Norway spruce grows more abundantly only in the Alps in the north of the country and to a much lesser extent in cold valleys and karst depressions in the Dinaric region in the southern part of the country. However, in past centuries spruce was one of the most anthropogenically favoured tree species in Slovenia, as it was intensively introduced and planted in many regions because of its timber. In areas which lie outside its natural distribution, spruce is much more sensitive to extreme weather events, and widespread bark beetle infestation is more frequent, especially at lower altitudes (de Groot 2014, de Groot et al. 2016, Ogris & Grecs 2016).

The dominant tree species in Slovenia in 2018 were *Fagus sylvatica* with 32.4% (Fig. 1), *Picea abies* with 30.6% (Fig. 2) and *Abies alba* with 7.4% of the total growing stock (ZGS 2005-2019). The management of Slovenian forests is based on sustainable, close-to-nature and multi-purpose principles. The relatively low intensity and un-even aged silviculture is mostly oriented towards near-natural tree species composition (Diaci 2006).

Analysis of meteorological and climatic data

We analysed meteorological data for Slovenia from the data archive of the Slovenian Environment Agency (hereafter ARSO) (ARSO 2019). We analysed the mean annual temperature (°C) and annual precipitation (mm), number of days with snow cover

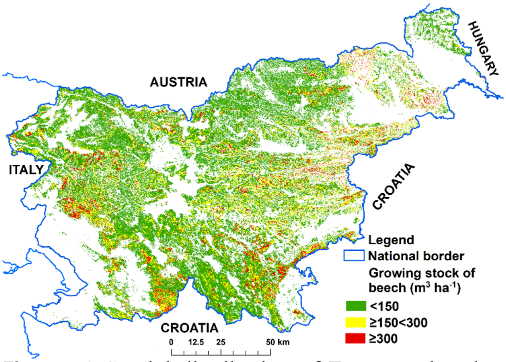

Figure 1 Spatial distribution of European beech (*Fagus sylvatica*) growing stock in Slovenia (Data source: ZGS 2018a).

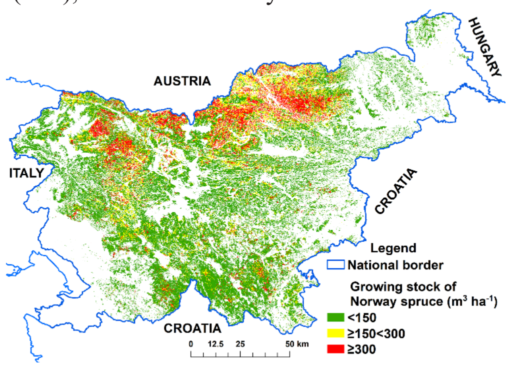

Figure 2 Spatial distribution of Norway spruce (*Picea abies*) growing stock in Slovenia (Data source: ZGS 2018a).

and maximum snow cover (cm), and their linear trends for the last 60 years (1959-2018). Continuous meteorological measurements for the period 1959-2018 were available for only five meteorological stations, namely Ljubljana (299 m a.s.l.), Brnik (384 m), Šmartno (452 m), Rateče (864 m) and Kredarica (2513 m) (ARSO 2019).

For the period from 2000 to 2018, 25 ARSO meteorological stations throughout Slovenia provided data for the following climate variables: mean temperature (T_{avg}), mean daily temperature maximums (T_{max}), relative humidity (RH) and amount of precipitation (P) (ARSO 2019). The distribution of meteorological stations among altitudinal belts was as follows: < 500 m a.s.l.: 16 stations; >500 m and <1000 m: 5 stations; > 1000 m: 4 stations. We compared the changes in climate variables and their linear trends for annual data (12-month average) and separately for the summer period (average for June, July, August) (ARSO 2019). Five meteorological stations were used for evaluation of climate variables in a 60-year period (1959-2018), and a subset of the series of 25 stations was used for analysis of a 19-year period (2000-2018). We used all available meteorological stations in Slovenia with complete data series and continuous measurement for both periods.

Analysis of disturbance effects for Slovenian forests

The forest damage caused by various abiotic and biotic disturbances was estimated at the compartment level (ZGS 2015, 2005-2019). The compartment is the smallest spatial organisational unit in forest management planning in Slovenia, with an average size of 22 ha (ZGS 2018b). The negative impacts of various disturbances in Slovenian forests were assessed on the basis of the amount of salvage logging in the forests over a 15-year period (2004-2018). In this analysis six different disturbance factors were distinguished: i) insect infestation, ii) diseases and fungal pathogens, iii) windthrows, iv) snow-breakage, v) ice storms, and vi) other factors, e.g. logging of decaying and physiologically weakened trees, tree damage caused by regular forest operations, local emissions, wildlife, avalanches and landslides. We compared the annual volume of salvaged timber from damaged and removed coniferous and broadleaved tree species. All data were compiled from the annual reports of the Slovenia Forest Service (ZGS 2005-2019).

Using ArcMap software (ESRI 2018), we analysed forest damage caused by a large-scale ice storm event in 2014, and the decrease in the growing stock of Norway spruce based on data from 2010 and 2018. The effects of the massive ice storm disturbance on forest trees and stands were analysed by distinguishing between severely damaged forests (more than 10% of all trees were damaged) and damaged forests (less than 10% and more than 0% of all trees were damaged). The intensity of the damage was compared at the level of forest types.

For the analysis of changes in Slovenian forests, extensive data on more than 335,000 forest stands and more than 53,700 forest compartments from the Slovenia Forest Service were used (ZGS 2010a, 2010b, 2018a, 2018b). The forest stand is a relatively homogeneous part of the forest in terms of tree species composition, developmental stage or age of the predominant trees, etc., and corresponds to the spatial unit that is important for forest inventory, planning, and management unit consisting of several different stands. From the forest stand data, we calculated the average growing stock (m^3 ha^{-1}) of Norway spruce for each compartment. The analyses included compartments where spruce growing stock in the year 2010 was equal to or higher than 20 m^3 ha^{-1}. We prepared a spatial map showing the decline of the spruce growing stock in each compartment. We distinguished between three classes of decline: i) < 25%, ii) ≥ 25% < 50%, and iii) ≥ 50%. We also calculated the average altitude of each compartment. Of all compartments, 40% were located in the lowest altitudinal belt (< 500 m), 45% in the middle altitudinal belt (≥ 500 m < 1000 m) and 15% in the highest altitudinal belt (≥ 1000 m).

Statistical analyses

Linear models were used to test trends in climate variables (temperature, precipitation) during the entire period from 1959 to 2018. Separate models were fitted for the first 30-year period (1959-1988) and second 30-year period (1989-2018). These models indicate whether the slope of the regression line is significantly ($p < 0.05$) different from zero. The coefficient of determination (R^2) was used as an overall measure of goodness-of-fit. Linear models were also constructed for T_{avg}, T_{max}, RH and P for the period from 2000 to 2018.

For salvage logging data, differences in percentages of damaged trees (% of the total growing stock per year) were tested between three 5-year periods (2004-2008, 2009-2013, 2014-2018) using a non-parametric Kruskal-Wallis rank sum test with Dunn's post-hoc test and Bonferroni correction for multiple comparisons. For the entire period (2004-2018), a linear model was applied to each disturbance factor (insects, diseases and fungi, windthrow, snow, ice storm) and tree species group (conifers, broadleaves, all species). These models indicate whether the slope of the regression line is significantly ($p < 0.05$) different from zero. The coefficient of determination (R^2) was used as an overall measure of goodness-of-fit.

For the period 1999-2018, linear models were fitted to examine changes in the share of the main tree species (spruce, beech, fir) and species groups (conifers, deciduous, dominant tree species together). A separate model was used for the first 10-year period (1999-2008) and the second 10-year period (2009-2018). The models indicate whether the slope of the regression line is significantly ($p<0.05$) different from zero. The coefficient of determination (R^2) was used as an overall measure of goodness-of-fit.

For each compartment, relative change in the spruce growing stock (GS, $m^3\ ha^{-1}$) from 2010 to 2018 was calculated with the formula:

$$((GS_{2018} - GS_{2010}) / GS_{2010}) \times 100.$$

Compartments with negative relative change (i.e. decrease) in spruce growing stock were considered for further analysis. Differences in the relative decrease in spruce among three altitudinal belts were tested with a one-way Analysis of Variance (ANOVA).

All described statistical analyses were conducted with the R software version 3.5.2 (R Core Team 2018). The *agricolae* package (de Mendiburu 2020) was used for statistical procedures. In all statistical tests, the significance level was set at $\alpha = 0.05$.

Results

Changes in the main climate variables in Slovenia in the last decades

In Slovenia, several climate variables have changed significantly over the last six decades (Fig. 3, Fig. 1S, 2S, and 3S). On average, the annual temperature calculated for five meteorological stations has increased over the last 60 years (1959-2018). The temperature increase ranged from 0.31°C per decade (Kredarica station at 2513 m) to 0.46°C per decade (Ljubljana station at 299 m), and the average rate of temperature increase was 0.38°C per decade ($p < 0.001$, $R^2 = 58.1\%$). On average, the temperature increased non-significantly ($p > 0.05$) by 0.02°C per decade in the period 1959-1988, and significantly ($p < 0.001$, $R^2 = 31.9\%$) by 0.41°C per decade in the period 1989-2018 (Fig. 3). Average annual precipitation (mm) over the last 60 years (1959-2018) decreased non-significantly ($p > 0.05$) by 0.4% per decade, but if only the period 1989-2018 is considered, it actually increased at an average rate of 2.2% per decade (Fig. 1S). In contrast to changes in average annual temperatures, trends in annual precipitation amount were not statistically significant. On average, the number of days with snow cover decreased (5.2 days per decade;

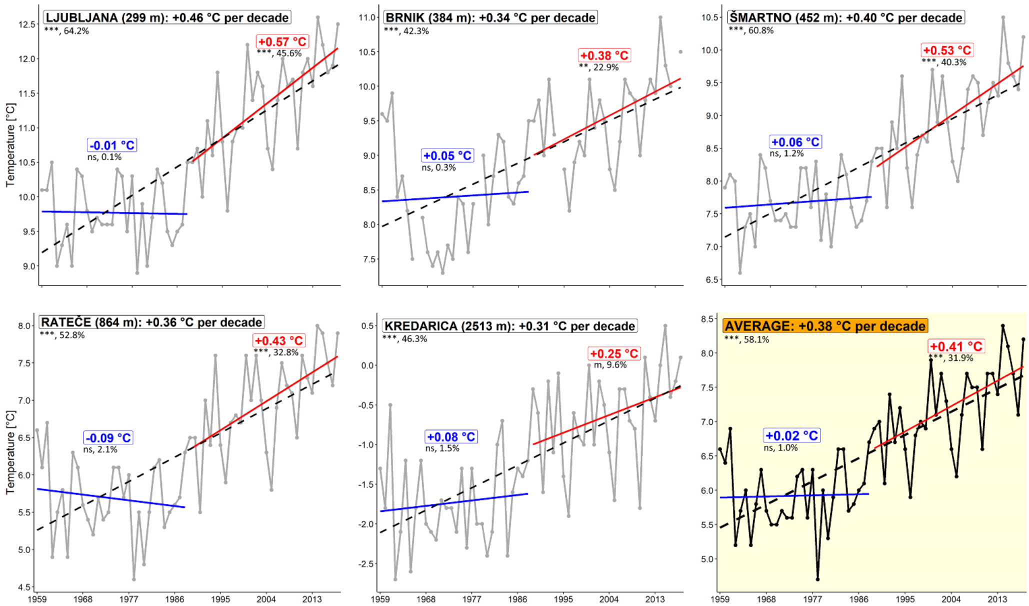

Figure 3 Mean annual temperature (°C) for five Slovenian meteorological stations and their average (bottom-right panel) over the last 60 years and (1959-2018) (Data source: ARSO 2019).

Fig. 2S) and maximum snow cover decreased (2.7 cm per decade; Fig. 3S) in the period under study, except for the Kredarica station, which exhibited a slightly increasing trend for maximum snow cover.

We also observed changes in meteorological variables for the period from 2000 to 2018 (Fig. 4). For the set of 25 meteorological stations in Slovenia, the mean annual temperature ranged between -0.5°C (Kredarica, 2513 m a.s.l.) and 14.0°C (Portorož, 2 m) and the mean annual precipitation between 768.9 mm (Lendava, 190 m) and 2859.3 mm (Vogel, 1535 m). On average, the values of all climate variables, i.e. T_{avg}, T_{max}, RH and P, have shown an increasing trend over the last two decades. Results from the linear models indicate that all trends in these variables were statistically non-significant. Mean annual temperature (T_{avg}) exhibited the most pronounced increasing trend (marginally significant, $p < 0.1$). T_{avg} (Fig. 4a) and T_{max} (Fig. 4b), calculated from 12 months of data, increased by 0.44°C per decade. The increase in mean and maximum temperature during the summer period (average for June, July, August) was more than 0.5°C per decade (Fig. 4a, 4b). Relative humidity increased by 3.0% (annual average) and by 2.6% (summer average) per decade. On average, P increased by 7.9% (annual average) and by 1.4% (summer average) per decade (Fig. 4d).

Effects of large-scale disturbances on forest stands

A variety of disturbance factors, such as windstorms, ice storms and insect outbreaks, caused damage to Slovenia's forests (Fig. 5). After the ice storm, the share of salvage logging in the total annual felling increased from about one third to two thirds. In the period 2004-2013, the amount of salvage logging was between 0.7 and 1.3 million m³ of damaged trees per year. In the period 2014-2018, it increased to a level between 2.6 and 4.2 million m³ per year. In 2014, more than three million m³ of wood damaged by the ice was logged. During the ice storm event, trees were either uprooted or snapped, or their crowns were slightly to severely damaged. The amount of salvage

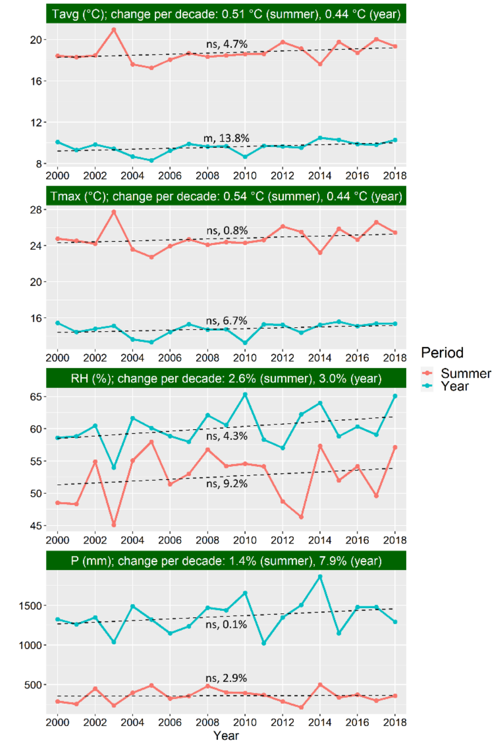

Figure 4 Mean temperature (T_{avg}), mean daily temperature maximums (T_{max}), relative humidity (RH), and precipitation (P) for 25 meteorological stations (ARSO) in Slovenia, for the period 2000 to 2018 (Data source: ARSO 2019).

logging due to bark beetle outbreaks increased significantly, as almost 6 million m^3 wood was damaged in the period 2014-2018 (ZGS 2005-2019). Other abiotic and biotic factors, such as windthrows, tree diseases and heavy snow, caused additional damage and increased salvage logging in the years after 2014 (Fig. 5). Linear models revealed that in the period 2014-2018, the share of trees damaged by insects increased marginally significantly ($p < 0.1$, $R^2 = 20.7\%$). The share of trees damaged by other disturbance factors also increased during this period (except for damage caused by diseases and fungi), but these trends were not significant ($p > 0.05$). Overall, the share of damaged conifers ($p < 0.01$, $R^2 = 46.4\%$), deciduous trees ($p < 0.05$, $R^2 = 30.1\%$) and all tree species ($p < 0.01$, $R^2 = 47.6\%$) increased in the studied period.

In the last 15 years, insects represented the most influential disturbance factor in Slovenian forests, with bark beetles causing the highest tree mortality (Table 1). Other significant disturbing factors were ice damage and windthrows. On average, all disturbances caused damage amounting to 1.9 million m^3 per year, which corresponds to 0.56% of the total growing stock. We found that the share of damaged trees by insects was significantly higher in the 5-year period 2014-2018 compared to the period 2009-2013 (Table 1).

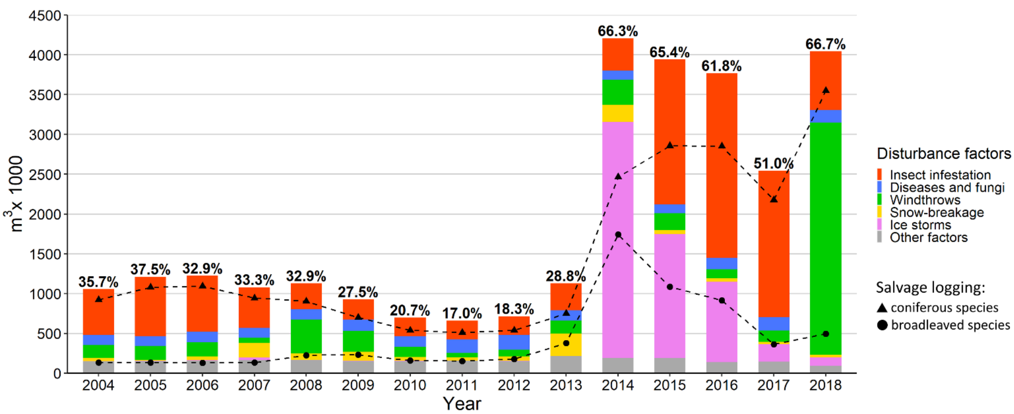

Figure 5 The volume of salvage logging ($m^3 \times 1{,}000$) in Slovenian forests over the last 15 years (2004-2018). The percentages above each bar indicate the proportion of salvage logging in the total annual felling (Data source: ZGS 2005-2019).

Table 1 Share of damaged trees by main disturbance factors (in % of the total growing stock per year).

	insects		diseases and fungi		windthrow		snow-breakage		ice storm		conifers		broadleaves		all species	
period	aver.	p = 0.008	aver.	p = 0.232	aver.	p = 0.386	aver.	p = 0.763	aver.	p = 0.028	aver.	p < 0.001	aver.	p = 0.006	aver.	p < 0.001
2004-2008	0.19	ab	0.04	a	0.07	a	0.02	a	0	a	0.32	a	0.05	a	0.37	a
2009-2013	0.08	a	0.05	a	0.04	a	0.03	a	0	a	0.18	a	0.07	a	0.25	a
2014-2018	0.41	b	0.04	a	0.21	a	0.02	a	0.34	b	0.79	b	0.26	b	1.06	b
2004-2018	**0.22**	/	**0.04**	/	**0.11**	/	**0.03**	/	**0.11**	/	**0.43**	/	**0.13**	/	**0.56**	/

A significant difference was also detected for ice damage. The share of damaged trees by other disturbance factors did not differ significantly between the three 5-year periods. The share of damaged conifers, deciduous trees and all tree species together was significantly higher in the last 5-year period (2014-2018) compared to the period 2009-2013 and 2004-2008. Overall, forest disturbances damaged a significantly higher proportion of trees in the last 5-year period (2014-2018; 1.06% of total growing stock per year) compared to the first 5-year period (2004-2008; 0.37%). The damaging effects for all main disturbance factors increased from the first to the last period, from 0.19% to 0.41% of the growing stock per year for insects, from 0.07% to 0.21% for wind, and from 0.00% to 0.34% for ice (Table 1).

Effects of massive ice storm disturbance on forests

In the period between January 30th and February 10th, 2014, an extreme ice storm caused extensive damage to Slovenian forests. In terms of its spatial extent and the total amount of damaged wood, this event was the most catastrophic natural disturbance ever recorded in Slovenia. More than half of Slovenia's forests (609,413 ha) were damaged during the ice storm event (ZGS 2015). Within these disturbed areas, the proportion of damaged trees varied considerably, ranging from 0.1% to 85.0%. In forest areas with a total area of 105,856 ha, more than 10% of the trees were either uprooted or snapped, or their crowns were damaged (Fig. 6), and forests with more than 50% damaged trees covered an area of 6,749 ha.

The ice disturbance and resulting tree damage occurred in a variety of forests on different bedrocks, mostly in the submontane to montane belt. (Fig. 6). In terms of the extent of area damaged by the ice, Dinaric fir-beech forests were the worst affected forest type. More than 60% of Dinaric fir-beech forests (146,608 ha in total) were damaged, and 13.5% of these forests were severely damaged (more than 10% of all trees damaged) (Fig. 6). Acidophilic beech forests (431,702 ha in total) were among the significantly disturbed forests. In total, 41.0% of these forests were damaged and 4.6% were severely damaged. Almost 60% of submontane beech forests (60,326 ha in total) were damaged, and 10.9% of the total area was severely damaged (Fig. 6).

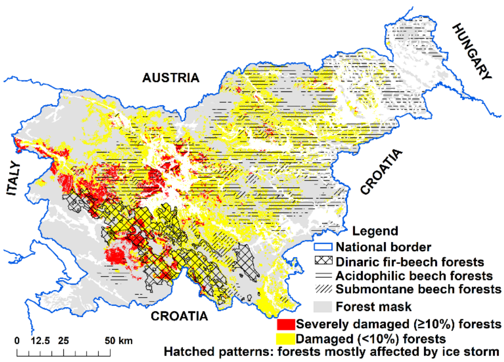

Figure 6 Slovenian forests mostly affected by the large-scale ice storm event in 2014 (Data source: ZGS 2015, Čarni et al. 2002).

Changes in tree species composition

The proportion of Norway spruce (Fig. 7a) in the growing stock decreased significantly over the period 1999-2018 ($p < 0.001$, $R^2 = 94.6\%$). In 1999, Norway spruce was the most common tree species in the growing stock with 32.5%.

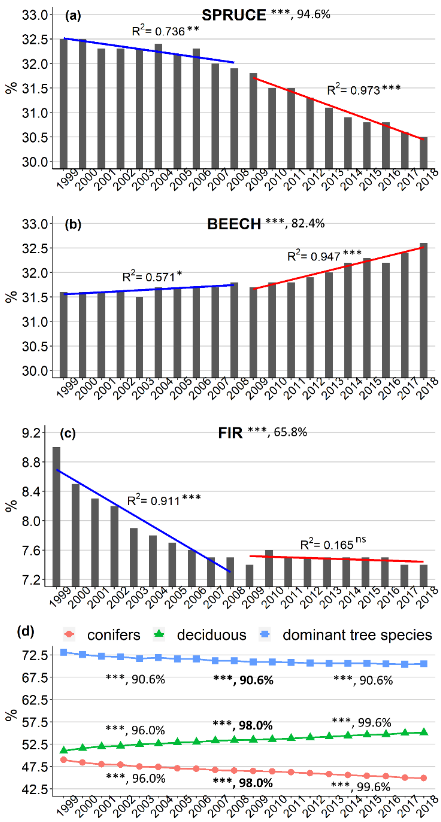

Figure 7 Temporal changes in the proportion of three dominant tree species (a to c) and cumulative for the groups of different tree species (d) in the total growing stock of Slovenian forests in the last 20 years (1999-2018) (Data source: ZGS 2005-2019).

Twenty years later, its share decreased to 30.5%. This decline was particularly evident in the last 10 years (2009-2018). In contrast to spruce, the proportion of European beech (Fig. 7b) increased significantly ($p < 0.001$, R^2 = 82.4%), with the rate of increase accelerating in the last 10 years. The growing stock of European beech remained at a similar level for almost 15 years (about 31.7%) and then gradually increased to 32.6% in 2018. The share of silver fir significantly ($p < 0.001$, R^2 = 65.8%) decreased by 1.6 percentage points between 1999 and 2018. However, its decrease was significant only in the first half of the period under study (1999-2008), while the decline in the second half was not statistically significant (Fig. 7c).

In line with the changes described for the main tree species, the ratio between coniferous and broadleaves in the growing stock also changed significantly over the period 1999-2018. The share of coniferous species (Norway spruce, European silver fir and other) significantly decreased ($p < 0.001$, R^2 = 98.0%) from over 49% to about 45%, while the share of broadleaved species (European beech and other broadleaves) significantly increased by about 4 percentage points (Fig. 7d). The linear models revealed a significant declining trend ($p < 0.001$, R^2 = 90.6%) for the proportion of the three dominant tree species, i.e. cumulative % for beech, spruce and fir (Fig. 7d).

In the period from 2010 to 2018, Norway spruce growing stock decreased in 17,570 compartments with a total area of 611,148 ha. The strongest decline in Norway spruce growing stock (≥ 50%) took place in 108,000 ha of the examined forests (Fig. 8, Table 2). Of these, 52% were located in the lowest (< 500 m a.s.l.), 40% in the middle (≥ 500 m < 1000 m) and only 8% in the highest altitudinal belt (≥ 1000 m).

There was an intermediate decline in Norway spruce growing stock (≥ 25% < 50%) on 122,100 ha. Half of these forest areas were located in the lowest, 39% in the middle and 11% in the

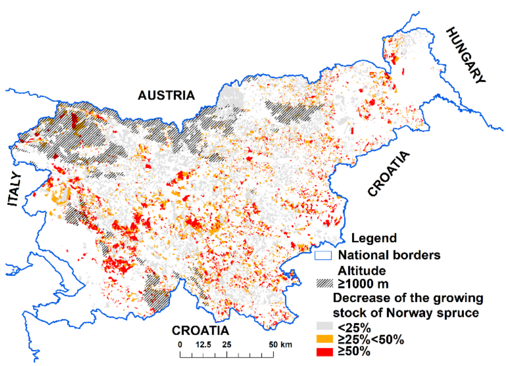

Figure 8 Decrease in the spruce growing stock from 2010 until 2018 (Data source: ZGS 2010a, 2010b, 2018a, 2018b, EUROSTAT 2018).

highest altitudinal belt. The lowest level of spruce decline (less than 25%) mainly occurred in compartments located in the middle altitudinal belt (Fig. 8, Table 2).

The highest proportion of forests with higher rates of spruce decline was observed in the lowest belt (< 500 m) (Fig. 9). Relative spruce decline at lower altitudes was significantly higher compared to the other two belts (Fig. 10).

Table 2 Decline classes in the growing stock (GS) of Norway spruce, according to data from 2010 and 2018 (Data source: ZGS 2010a, 2010b, 2018a, 2018b, EUROSTAT 2018).

Decline in GS (%)	Altitudinal belt (m a.s.l.)	Area (x 1000 ha)	Proportion (%)
≥ 50	< 500	56.5	52
≥ 50	≥ 500 < 1000	43.3	40
≥ 50	≥ 1000	8.2	8
Total (≥ 50)		108.0	100
≥ 25 < 50	< 500	61.0	50
≥ 25 < 50	≥ 500 < 1000	47.7	39
≥ 25 < 50	≥ 1000	13.4	11
Total (≥ 25 < 50)		122.1	100
< 25	< 500	151.8	40
< 25	≥ 500 < 1000	175.5	46
< 25	≥ 1000	53.8	14
Total (< 25)		381.1	100

Discussion

Long- and short-term variation in crucial climate variables

In the age of CC, forest ecosystems worldwide are under enormous pressure. Changes in climatic conditions and an increase in the frequency and severity of forest disturbances and other stress factors (drought and heat stress) could fundamentally alter the composition, structure and biogeography of forests in many regions. A continuation of the 60-year trends analysed for Slovenia suggests an increase in mean temperature of 3.0°C and a decrease in precipitation of about 3% by the end of this century. However, the current 20-year trend assumes an even stronger increase in mean annual temperature in this region, and maximum summer temperatures could be 4.3°C higher by the end of the century. In contrast to a steady rise in temperature, the changes in precipitation proved to be more variable and therefore less predictable. The 60-year trend indicates a decreasing amount of precipitation. In recent decades, however, the amount of precipitation has actually increased. Higher precipitation and relative humidity could be related to the occurrence of extreme weather events, although high spatial variability in precipitation (due to the complex terrain) could most likely offset the general

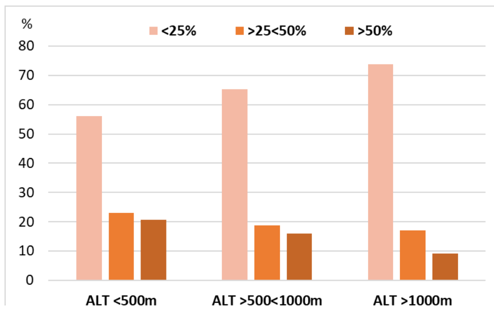

Figure 9 Relative proportion of the decline classes of spruce growing stock in three altitudinal belts (Data source: ZGS 2010a, 2010b, 2018a, 2018b, EUROSTAT 2018).

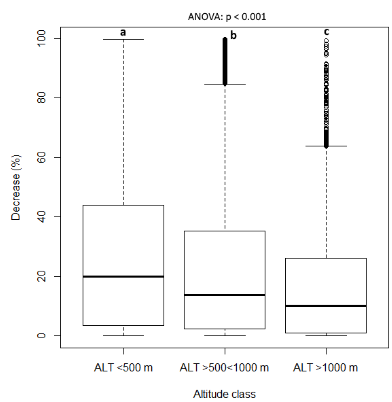

Figure 10 Relative decrease (%) in spruce growing stock for different altitudinal belts (Data source: ZGS 2010a, 2010b, 2018a, 2018b, EUROSTAT 2018).

trends locally, which would make the future responses of forests even more uncertain.

We can state with greater certainty that rising temperatures could have an adverse effect on tree growth and survival. Extreme events such as extreme droughts and heat waves are important drivers of tree mortality and are expected to increase in frequency and intensity with CC. When high temperatures are combined with low soil water availability, the effects of droughts can be amplified by increased evapotranspiration, and trees can die rapidly (Taccoen et al. 2019). The warming of the future climate with higher average temperatures and even more extreme summer temperatures will also lead to further disturbance events. Overall, disturbance regimes have proved to be very sensitive to both climate means and extremes (Thom et al. 2013).

Changes in tree species composition

It has been shown that forest disturbances are one of the most important factors determining the rate of shift in tree species distribution with CC (Vanderwel & Purves 2014, Seidl et al. 2017). Our study showed that Slovenian forests have undergone profound changes in their structure and composition in recent years. Both natural disturbances and salvage logging have caused considerable damage to overstory trees and also damage to forest soils. Disturbances have resulted in a high proportion of degraded forests with many larger canopy gaps and openings, where younger developmental phases occur. Various disturbance factors have changed the tree species composition towards an increased proportion of broadleaved species. In total, the proportion of the three dominant tree species (beech, spruce, silver fir) has decreased in Slovenian forests during the last two decades.

In the last 15 years, insect and wind damage has affected on average 0.22% and 0.11% of the growing stock per year, respectively, which is comparable to Austrian forests (Thom et al. 2013). However, most of the damage has occurred in recent years. Large-scale disturbances, beginning with the severe ice storm in 2014 and subsequent bark beetle outbreaks and windthrows, caused severe damage, especially to forest types with a higher proportion of Norway spruce introduced by humans. This tree species has suffered the greatest decline; its share has decreased by 1.3 percentage points over the last ten years. If this current downward trend in spruce continues, its share in the total growing stock will only be about 20% by the end of the century. However, the constantly increasing temperature and climate extremes with CC-induced disturbances could further accelerate the decline of spruce in the coming decades. In contrast, European beech has increased its share of the total growing stock, which is mainly due to the decline of Norway spruce and silver fir. However, for Slovenia (Kutnar & Kobler 2011, 2014) and Europe (Hanewinkel et al. 2013), it is predicted that even beech will start to lose its share in the second half of the 21st century.

The expected decline of spruce and the current changes in tree species composition indicate changes in Slovenian forests that are consistent with CC predictions for Slovenian forests that were made ~10 years ago (Kutnar & Kobler 2011, 2014). The majority changes in the observed forest stands and tree species have been in accordance with predictions. Furthermore, the results of the present study suggest that the magnitude of these changes has been amplified by increasing disturbance effects.

The significant decline in spruce is mainly due to the high spruce damage during the ice storm in 2014 (Nagel et al. 2016) and the particularly widespread bark beetle outbreaks in the following years. Crown damage and negative influences on the root system weakened their ability to cope with abiotic and biotic stressors. In addition, the predicted increase in summer temperatures and, as a consequence, prolonged droughts increased their vulnerability and contributed to higher tree mortality. It is expected that rising temperatures will accelerate the development cycle of the spruce bark beetle (*Ips typographus* L.) and increase its reproductive potential, i.e. the formation of several generations during a single growing season (Temperli et al. 2015). Most importantly, bark beetle outbreaks and the associated decline in spruce stands occurred mainly in the lowland areas of Slovenia, where spruce does not grow naturally, which is consistent with our results of the decline in the growing stock of spruce according to the data from 2010 to 2018. In total, the most severely damaged forest compartments with the largest decrease in spruce growing stock were located at altitudes below 500 m. In these low-altitude forests, forest managers, private owners and even foresters forced the introduction of Norway spruce, largely ignoring the important criteria of (un) suitable local site conditions. Norway spruce is a typical example of how economically valuable tree species were largely favoured and planted beyond their natural ecological niche but are now under severe pressure (Vitasse et al. 2019). However, monospecific spruce stands in unsuitable locations, such as steep, south facing slopes with shallow soils, can also be exposed to spruce decline even at higher altitudes. Such monospecific spruce stands are particularly susceptible to disturbances such as storms (windthrows), drought and insect outbreaks (Lindner et al. 2010). Therefore, management systems that promote forest diversity significantly reduce the degree of disturbance (Dobor et al. 2020). Forest structure and composition, which are associated with management measures such as the promotion of coniferous trees and an increase in timber volume as well as the lack of appropriate silvicultural measures in the younger developmental phases, are highly susceptible to disturbances in forest stands (Seidl et al. 2011b).

At the European level and in Slovenia, European beech and Norway spruce are the two most important tree species in temperate and boreal forests. It is predicted that these species will lose large parts of their potential distribution range and be replaced by species with a more thermophilic character (Hanewinkel et al. 2013). Recently, however, it has been shown that CC in Austria even favours European beech and oak species (Thom et al. 2017), and the proportion of beech has also increased in Slovenia. In the long term, beech forests are likely to be threatened (Kutnar & Kobler 2011, 2014, Hanewinkel et al. 2013). The physiological performance, growth and competitiveness of beech can be impaired by such altered (micro)climatic conditions (Peuke et al. 2002, Geßler et al. 2007, Stojanović et al. 2013).

Changes in forest stands

Slovenia lies in the transition zone where different geographical regions meet (e.g. Mediterranean, Alps and Dinaric Mountains, Pannonian Basin). Therefore, different natural conditions have the potential to experience different types of disturbances and natural hazards. Apart from episodic disturbance events, the most serious threat to Slovenian forests could lie in the vicinity of the Mediterranean, where CC is expected to increase the negative effects of adverse climatic conditions (e.g. summer droughts, heat-induced stress, forest fires) on forest growth and health (Pereira et al. 2005, Moriondo et al. 2006).

Spatial modelling of the future distribution of tree species forest types based on different climate scenarios for Slovenia shows a significant potential reduction in mesic forest types, in which European beech, silver fir and Norway spruce are the dominant tree species in the overstory layer. These forest types and tree species are known for their vulnerability to extreme climatic events such as high mean summer temperatures and drought stress. The future success of these species is endangered in the context of CC, while other forest types and tree species (with lower forest economic value and higher fire risk), e.g. thermophilus broadleaves and drought-tolerant forests, are likely to extend their distribution range in

Slovenia (Kutnar & Kobler 2011) and Europe (Hanewinkel et al. 2013).

In the context of forest disturbance effects, cascade or domino effects are of particular importance when there are multiple interactions between abiotic and biotic disturbance factors (Kausrud et al. 2012, Seidl et al. 2017, de Groot et al. 2018). In forests where the decline in net primary production is extreme or persists over several growing seasons, increased susceptibility to insects or diseases is possible. The dominant tree species studied in this research (Norway spruce, European beech, European silver fir) are relatively unspecific with respect to soil and terrain conditions (Zupančič 1999, Dakskobler 2008); therefore, their distribution is mainly determined by climatic constraints (Falk & Hempelmann 2013). CC will favour forests with tree species that are not predominant under current environmental conditions.

Disturbances and CC will not only change the distribution of tree species and forests, but they will also change understory vegetation (Stevens et al. 2015, Kutnar et al. 2019) and interrupt the sustainable provision of forest ecosystem services (Thom & Seidl 2016), as well as result in the loss of economic value (Hanewinkel et al. 2013). For example, Dinaric fir-beech forest, which is one of the most extensive forest types in Slovenia (Dakskobler 2008), has also been one of the most severely damaged forests in this area in recent years. These forests are important for their role in timber production and for providing many other ecosystem services. Due to their location in limestone karst areas, their ecological and biodiversity aspects are of great importance. These forests are the habitat of many species of European interest (Habitat Directive, 1992), and a large part of them has been designated as part of the Natura 2000 network (Skoberne 2004, Kutnar et al. 2011). The significant alteration or even loss of Dinaric fir-beech forests may lead to the loss of species habitats and the potential extinction of many key forest species in this area. Since many forest-dwelling species are highly dependent on the predominant tree species, a delayed response to a changing climate may contribute to an extinction debt and climate-induced loss of biodiversity (Thom et al. 2017). CC has already caused numerous shifts in species abundance and distribution (Parmesan & Yohe 2003) and will be a major driver of species extinction in the near future (Thomas et al. 2004).

Future perspective of forest management in view of CC and disturbances

Possible increases in tree mortality associated with rising temperatures, climate-induced physiological stress and interactions with other climate-induced processes such as insect outbreaks are of particular concern for the future (Allen et al. 2010). The management systems aimed at maintaining the dominance of Norway spruce in the forest fail in the context of CC, and none of the measures applied have been able to mitigate the effects of disturbances (Dobor et al. 2020).

The persistence of local and regional tree populations, for which the role of phenotypic variation may be an important factor, will be challenged due to warmer and drier climate conditions (Chmura et al. 2011). Bouchard et al. (2019) emphasized that the persistence of tree species is the key factor in forest changes. However, the response of tree populations exposed to unusually warm and dry conditions is still relatively poorly known for most species.

Since sustainable close-to-nature forest management is based on the imitation of less intensive disturbances, little attention has been paid to restoring more severe disturbance areas within forest landscapes (Diaci et al. 2017). However, research on adaptation to CC and disturbances has become increasingly important over the last two decades. Disturbances promote the reorganization of ecosystems since the increasing frequency and severity of disturbances are likely to accelerate the adaptation of forest ecosystems to CC, but the increasing size of disturbances may have the opposite effect on forests (Thom et al. 2017). Forest conversion with warm-adapted tree species goes hand in hand with a loss of total growth performance compared to the current species composition. The question of which tree species should be promoted in view of CC and increasing harmful disturbances is an ongoing debate in forest ecology and management (Thurm et al. 2018). Foresters from many countries are looking for tree species or provenances able to cope with expected CC. Forest managers need to know to what extent and on which sites the tree species predominant in our study area, such as European beech, Norway spruce, and silver fir, can sustain viable populations in the coming decades and in which cases they should consider or promote alternative species (Vitasse et al. 2019, Thurm et al. 2018).

Conclusions

We discussed current changes in temperate forests in Slovenia (in the transition zone between Central Europe to SE Europe) caused by global warming and various disturbance factors in relation to climate change (CC) predictions, and the main findings are as follows:

- CC and disturbances cause major alterations in the forest structure and species composition of temperate forests.
- The climate in the investigated region has warmed by about 0.4°C per decade.
- Various disturbance factors, which currently damage more than 1% of the total growing stock per year, are accelerating the changes in forests.
- After the severe ice storm in 2014 and associated bark beetle outbreaks and windthrows in the following years, salvage logging increased from about one third to two thirds of the total annual logging.
- Spruce has recently declined significantly in Slovenian forests, especially in low-elevation areas where it has been planted outside its natural range and where the climate has become unsuitable for spruce.

The results of our study complement existing knowledge on possible CC impacts on tree species and forest stands and contribute to the general understanding of forest dynamics in a time of rapid global environmental changes. On a shorter timescale, changes induced by disturbance factors represent stronger drivers of forest dynamics than the direct effect of CC. As there are no severe stand-replacing disturbances where a natural succession of ageing forest stands occurs, the effects of CC are expected to be experienced much more slowly. However, large-scale forest disturbances are able to accelerate the effects of CC. The restoration of forest stands after intensive natural disturbances is becoming more frequent and more difficult under global changes. One of the future challenges will be to integrate multiple disturbance processes into forest management models, and for these purposes, understanding the forest dynamics affected by CC and disturbances will be essential.

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