Published in final edited form as:
For Ecol Manage. 2017 March 15; 388: 3–12. doi:10.1016/j.foreco.2016.11.030.

Assessing the resilience of Norway spruce forests through a model-based reanalysis of thinning trials☆

Rupert Seidl[a,*], **Friedrich Vigl**[a], **Günter Rössler**[b], **Markus Neumann**[b], and **Werner Rammer**[a]

[a]Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU), Vienna, Austria

[b]Department of Forest Growth and Silviculture, Austrian Research Center for Forests (BFW), Vienna, Austria

Abstract

As a result of a rapidly changing climate the resilience of forests is an increasingly important property for ecosystem management. Recent efforts have improved the theoretical understanding of resilience, yet its operational quantification remains challenging. Furthermore, there is growing awareness that resilience is not only a means to addressing the consequences of climate change but is also affected by it, necessitating a better understanding of the climate sensitivity of resilience. Quantifying current and future resilience is thus an important step towards mainstreaming resilience thinking into ecosystem management. Here, we present a novel approach for quantifying forest resilience from thinning trials, and assess the climate sensitivity of resilience using process-based ecosystem modeling. We reinterpret the wide range of removal intensities and frequencies in thinning trials as an experimental gradient of perturbation, and estimate resilience as the recovery rate after perturbation. Our specific objectives were (i) to determine how resilience varies with stand and site conditions, (ii) to assess the climate sensitivity of resilience across a range of potential future climate scenarios, and (iii) to evaluate the robustness of resilience estimates to different focal indicators and assessment methodologies. We analyzed three long-term thinning trials in Norway spruce (*Picea abies* (L.) Karst.) forests across an elevation gradient in Austria, evaluating and applying the individual-based process model iLand. The resilience of Norway spruce was highest at the montane site, and decreased at lower elevations. Resilience also decreased with increasing stand age and basal area. The effects of climate change were strongly context-dependent: At the montane site, where precipitation levels were ample even under climate change, warming increased resilience in all scenarios. At lower elevations, however, rising temperatures decreased resilience, particularly at precipitation levels below 750–800 mm. Our results were largely robust to different focal variables and resilience definitions. Based on our findings management can improve the capacity to recover from partial disturbances by avoiding overmature and overstocked conditions. At increasingly water limited sites a strongly decreasing resilience of Norway spruce will require a shift towards tree species better adapted to the expected future conditions.

---

[*]Corresponding author. rupert.seidl@boku.ac.at (R. Seidl).

☆This article is part of the special issue: "Ecology of Mountain Forest Ecosystems in Europe" published in the journal Forest Ecology and Management 388, 2017.

Keywords

Climate change; Disturbance; Recovery; Engineering resilience; Picea abies, iLand

1 Introduction

Climate change is increasingly altering forest ecosystem dynamics, yet the impacts of warming vary strongly between ecosystems. While some areas benefit from a prolonged growing season and CO_2 fertilization (Reyer et al., 2014), others are experiencing an increase in drought stress (Allen et al., 2015) as a result of the ongoing climatic changes. The vulnerability to climate is expected to be particularly high in areas that are exposed to disproportionally large changes in the climate system (Lindner et al., 2010). An example are the European Alps, which have warmed twice as much as the northern hemisphere over the past decades (Auer et al., 2007). Furthermore, particular vulnerability is expected for species that are at the margins of their natural range, or have been cultivated outside their realized niche (Hanewinkel et al., 2013; Seidl et al., 2011). Here, a prominent example is Norway spruce (*Picea abies* (L.) Karst.): The species is natural to Europe's mountain forests (Bebi et al., 2017) and high latitudes, but has been planted widely also in low elevation areas of Central Europe, where it is expected to be particularly vulnerable to climate change (Boden et al., 2014; Hlásny and Turčáni, 2013; Lindner et al., 2010).

In response to growing concerns about climate change the resilience of forest ecosystems has received increasing attention recently, and has been proposed as an important factor for addressing future uncertainties in ecosystem management (Biggs et al., 2012; Seidl, 2014). Resilience can broadly be defined as the ability of a system to recover from disturbance and persist in the face of perturbations (Carpenter et al., 2001). The theory of resilience in ecosystems has made considerable progress recently (Reyer et al., 2015; Scheffer et al., 2015). Yet, the operational assessment and quantification of resilience in real world systems has remained challenging. One reason for why applications lag behind theory developments is that many indicators of resilience require long-term data over a wide gradient of perturbations that are not commonly available in forest ecosystems. To address the need for long time-series in determining resilience, dendroecological analyses have recently been used to assess the resilience to climatic extremes (Boden et al., 2014; Lloret et al., 2011). While allowing important insights into the plasticity and response of trees to changes in climate, these studies rely on past extremes for inferring resilience, and thus are not necessarily representative for the conditions that are expected for the future (Radeloff et al., 2015). Furthermore, the individual tree resilience inferred from tree rings might differ substantially from stand- to landscape level resilience, with the latter being the primary focal scales of forest management.

While no long-term stand-level resilience experiments exist to date, forest research has accumulated a wealth of experimental data over the past decades. An important category of such existing long-term experiments are thinning trials. These are experiments that have been designed to understand how different thinning regimes influence the growth, stability, timber quality, and mortality of trees (Pretzsch, 2005; Zeide, 2001). They usually span a wide gradient of removal levels and intervention intervals, and include replications as well as untreated control plots in order to deduce thinning effects with a high degree of statistical rigor. Over the last decades these trials have provided important information on improving the productivity, structure, and composition of forest ecosystems through management. More recently, these studies have also been used to inform management responses to a changing climate (D’Amato et al., 2011; Kerhoulas et al., 2013; Neill and Puettmann, 2013), particularly focusing on the question whether reduced tree density can alleviate increasing drought stress (D’Amato et al., 2013; Elkin et al., 2015; Gebhardt et al., 2014).

From an ecological perspective, the wide range of thinning interventions implemented in thinning trials represents an experimental gradient of disturbance. Yet, to the best of our knowledge, these experimental gradients of perturbation have to date not been used to assess forest resilience. Here, we reanalyze thinning trials with the aim to quantitatively assess the resilience of forest ecosystems. In this context it is important to note that different dimensions of resilience exist: Engineering resilience describes the ability of a system to recover from disturbance (Holling, 1996), while ecological resilience refers to a system remaining within its prevalent domain and not shifting to an alternative ecological state in response to a perturbation (Gunderson, 2000). Determined by the nature of thinnings, which are non-stand replacing interventions, we here focus solely on recovery after partial disturbance, and thus address engineering resilience in this contribution (henceforward referred to resilience for the sake of readability).

The resilience of a system is not static over time but changes *inter alia* in response to a changing climate (Seidl et al., 2016). In the context of management this means that managers need to embrace the fact that resilience as a management goal is a moving target. Moreover, whether the expected future climate conditions will erode or bolster a systems’ resilience needs to be factored into management considerations. Studying the effect of future no-analog conditions (Radeloff et al., 2015) on resilience requires the use of process-based forest ecosystem models. In contrast to empirical models, which have been frequently used in the analysis of thinning responses previously, process-based approaches simulate system trajectories based on ecological mechanisms, and are thus robust also under scenarios that represent novel future conditions (Gustafson, 2013). Many process-based models, however, do not operate at the appropriate scale to capture thinning responses (Petritsch et al., 2007; Seidl et al., 2013), making a process-based reanalysis of thinning trials challenging. A thorough evaluation of the applied models is thus of paramount importance. Long-term trials offer a powerful means in this regard, allowing models to be tested across a wide gradient of experimentally manipulated conditions.

Here, our objective was to assess the resilience of Norway spruce forests in Central Europe to non-stand-replacing disturbance by re-analyzing thinning trials under both historic climate and a range of climate change scenarios. Specifically, our aims were (i) to evaluate an individual-based process model of forest dynamics with regard to its ability to reproduce observed responses to thinning interventions, (ii) to demonstrate how engineering resilience can be derived from stand-level recovery after thinning at three experimental sites distributed across an elevation gradient in Austria, (iii) to assess the climate sensitivity of resilience across a range of climate scenarios, and (iv) to evaluate the robustness of resilience estimates to different focal indicators and assessment methodologies. Previous research has shown that Norway spruce is increasingly climatically limited in low elevation areas and close to the timberline, with optimal performance in the montane elevation belt (Ponocná et al., 2016; Primicia et al., 2015). We thus hypothesized resilience to decline from the montane to the submontane elevation belt, i.e. from the center of the species' niche to its warm and dry edge. Furthermore, given the increasing level of stress introduced by a changing climate, we hypothesized resilience to decrease with progressing climate change. This hypothesis is based on findings by Zang et al. (2014), among others, indicating that increased temperature and water stress negatively impacts the recovery of Norway spruce. Lastly, we hypothesized that quantitative estimates of resilience would vary strongly across different focal variables of the assessment (Carpenter et al., 2001).

2 Materials and methods

2.1 Thinning trials

We reanalyzed three thinning trials in even-aged Norway spruce forests in Austria, maintained and re-measured by the Austrian Research Center for Forests, Vienna (Table 1). They were selected for analysis here because they span a wide gradient of thinning interventions and environmental conditions, were initiated approximately at the same time, and focus on the same tree species (Norway spruce). The trial Eibiswald (46.726N, 15.048E) is situated in the montane elevation belt (1250 m asl) at the south-eastern rim of the Alps (ecoregion western Styrian mountains, (Kilian et al., 1994)). Although the coolest site studied here, temperatures are relatively mild for the elevation and precipitation is ample (Table 1), resulting in near-optimal growing conditions for Norway spruce. Consequently, Norway spruce is the dominant tree species of the natural vegetation composition at Eibiswald (Kilian et al., 1994). Six thinning variants (including an untreated control) were implemented in 1000 m^2 blocks, each replicated three times, and separated by a 5 m buffer zone that was treated but not analyzed. The initial age of the stands was 40 years in 1968, and the observation period was 45 years. The second thinning trial is located near Karlstift in northern Austria (Waldviertel ecoregion) at 930 m asl (48.575N, 14.773E). It is characterized by cool temperatures and moderate precipitation levels, whereof more than 50% accrue during spring and summer. Also at Karlstift, Norway spruce is the dominant species of the natural vegetation composition (Kilian et al., 1994). The trial studied four thinning variants in 1200 m^2 blocks with four replicates per treatment. The first measurements were taken in 1974 in the then 27 year old Norway spruce stands. The third thinning trial is located approximately 40 km east of the Karlstift trial, close to the village of Ottenstein (48.615N, 15.324E). Although being situated in the same ecoregion as Karlstift, its lower elevation results in considerably warmer and drier climate (Table 1). Consequently, the natural vegetation composition is dominated by European beech (*Fagus sylvatica* L.), with Norway spruce being at the margin of its realized niche. At Ottenstein nine different thinning variants were implemented in 1000 m^2 blocks, separated by 5 m treated buffers and replicated twice. The trial was initiated in 1969 and the last remeasurement was in 2012. A limited number of blocks were affected by snow breakage, resulting in the highest maximum removal rates at Ottenstein. At all three sites selective thinning regimes were implemented, i.e. future crop trees were identified and competitors removed. The removals are thus predominately thinnings from above. In total, we here analyzed more than 300 individual thinning interventions, distributed over 51 stands and three sites, with an observation period from 1968 to 2013.

2.2 Simulation model

Simulation modeling was used to reanalyze the three thinning trials in the context of resilience (see also Dymond et al., 2015), and to quantify the sensitivity of resilience to changing climate conditions. With regard to the particular objectives of this contribution the rationale for using a simulation approach were threefold: First, simulation modeling allowed us to study forest recovery at high temporal resolution, which is a prerequisite for robustly deriving recovery times particularly when considering the nonlinear responses of forests to disturbance. Second, the application of a process-based simulation framework enabled us to make inferences on important ecosystem indicators that were not measured through the course of the trials (e.g., net primary productivity, NPP). Finally, simulation modeling allowed us to address the climate sensitivity of resilience via a re-analysis of the trials under a range of different potential future climate conditions.

The model used was iLand, the individual-based forest landscape and disturbance model (Seidl et al., 2012). iLand is a process-based model that operates at the level of individual trees. Competition for resources is simulated explicitly in space using ecological field theory, an approach that is sensitive to thinning-related changes in resource availability through a release from competitors. The resources available for a tree in combination with its species-specific responses to environmental drivers are used to estimate productivity in iLand, employing a resource use efficiency approach (Landsberg and Waring, 1997). Allocation of carbohydrates to tree compartments is modeled based on species-specific allometric ratios and is sensitive to environmental conditions. Furthermore, the partitioning into above- and below-ground compartments as well as into height and diameter growth is dynamically adapted to the competitive situation experienced by a tree. Mortality probability is derived based on an individuals' carbon balance and also accounts for species-specific traits such as longevity. iLand was recently extended to include a flexible, agent-based forest management module that allows the implementation of complex management interventions from tree to landscape scale (Rammer and Seidl, 2015). iLand has been parameterized for Central European tree species, and was previously tested and applied successfully in mountain forest ecosystems in the Eastern Alps (Thom et al., in press a). Furthermore, previous analyses support the utility of iLand for assessing the resilience of forest ecosystems (Seidl et al., 2014; Silva Pedro et al., 2015).

2.3 Scenarios of climate change

As we here were particularly interested in the climate sensitivity of forest resilience, we extended the climate gradient represented by the three thinning experiments by studying a range of climate change scenarios (Table 2). Three regional climate change scenarios, representing different combinations of global and regional circulation models under SRES A1B forcing (IPCC, 2000), were studied: ALADIN (Radu et al., 2008) driven by the global climate models (GCM) ARPEGE and REMO (Jacob, 2001), as well as RegCM3 (Pal et al., 2007) driven by the GCM ECHAM5. The three selected SRES scenarios fall into the envelope of the newer CMIP 5 climate scenarios, and no significant ecological differences between the scenario families were found in a previous analysis (Thom et al., in press b). Each of the scenarios used here was downscaled statistically to 1 km horizontal resolution and bias-corrected using observational data of the Austrian meteorological station network. The grid cell center point closest to the respective thinning trial location was used for further analysis. Within each scenario we here studied two time slices, representing the projected climate for the mid and late 21st century (i.e., years 2041–2060 and 2081–2100, respectively). The atmospheric CO_2 level was identical across scenarios, averaging 522 ppm in 2041–2060 and 674 ppm in 2081–2100. Representative climate conditions for each period were derived by randomly sampling years with replacement from the downscaled climate record of the respective time window. The three thinning trials were subsequently re-analyzed under historical climate conditions as well as under the resulting six climate change forcings. For the latter the observed thinning interventions were simulated under the climatic conditions projected for 2041–2060 and 2081–2100 by three different climate models (Table 2).

2.4 Analyses

A key element of our model-based reanalysis was to test whether iLand was able to reproduce the thinning responses observed in the studied thinning trials. To that end we set up the model using the tree coordinates and dimensions recorded in the first inventory of each trial, and simulated the trial by mimicking removals with regard to timing and tree identity. We ran simulations under past climate conditions for the respective trial period and site, and compared simulation results to observations. Specifically, we were interested whether the model was able to reproduce the observed stand development trajectories over the wide range of implemented thinning interventions. To further our insights into model performance we not only evaluated iLand at the stand level (i.e., the spatial level of the subsequent resilience analysis), but also compared simulations to observations at the level of individual trees. Here we particularly focused on the diameter at breast height (DBH) as response variable, as DBH is highly sensitive to different thinning regimes. For all evaluation exercises the entire range of thinning variants – including the unthinned control stands – were analyzed. Subsequently, with thinning response being a key variable for our analyses, we explicitly tested the response of stands to thinning interventions. We related the basal area at the first re-measurement after an intervention (typically after 2–5 years) to the basal area in the year of the intervention. The thus obtained indicator of basal area change after thinning was also extracted from the simulated stand trajectories, and simulations compared to observations across all interventions and sites. For all analyses, the comparison between observed and simulated data was conducted via a linear regression of predicted over observed data, with the explained variation in the observed data calculated by means of analysis of variance.

After model evaluation we analyzed the resilience of the studied ecosystems. We here defined resilience as the rate of recovery after disturbance (Scheffer et al., 2015), with the thinning trials representing a standardized and replicated experiment imposing a range of disturbance severities and frequencies on our study systems. We calculated the time needed to recover the predisturbance state after a thinning event, standardized by the relative disturbance severity of the respective event (Eq. (1)).

$$T_R = \frac{Recovery\ time\ (years)}{Disturbance\ severity\ (\%)} \quad (1)$$

Resilience (R_R) is inversely related to this standardized recovery time (T_R), and represents the amount of disturbance loss that can be recovered by the system within one unit of time (Eq. (2)). Higher values of R_R indicate faster recovery and thus higher resilience.

$$R_R = \frac{1}{T_R} = \frac{Disturbance\ severity\ (\%)}{Recovery\ time(years)} \quad (2)$$

R_R was calculated at the level of individual thinning interventions within each stand. Disturbance severity was derived as the percentage of growing stock (GS) removed through a thinning intervention, and recovery time was defined as the number of years that the stand required to reach (or exceed) the GS level prior to disturbance. Growing stock (here measured as total stem volume) was chosen as focal variable because it is an important indicator in the context of timber production, and correlates strongly with above-ground live carbon stores in forest ecosystems. Furthermore, it is a variable widely available from forest inventory and analysis programs. Using relative values in the definition of R_R controlled for differences in productivity between sites, and facilitates a generalized interpretation in the context of widely reported disturbance indicators (see e.g., Thom et al., 2013). However, resilience can be expected to vary with target variable, rendering the question “resilience of what?” (Carpenter et al., 2001) of central importance for the quantification of resilience. To evaluate the sensitivity of our findings to the selection of a different focal indicator we replicated the analysis also for leaf area index (LAI) (see Supplementary Material).

R_R was subsequently analyzed by means of multiple linear regression and analysis of variance across all sites and climate scenarios to assess how stand, soil, and climate factors influence resilience. With regard to stand attributes we focused on stand age, stand basal area, and recent disturbance history (i.e., percent of GS removed in the previous ten years) as potential explanatory variables. The soil parameters included as potential explanatory variables were effective soil depth and plant-available nitrogen. To better understand the climate sensitivity of forest resilience we also included mean annual temperature and precipitation sum as well as their interaction term as potential explanatory variables. Residual analysis was used to determine whether predictors required transformation to conform to the assumptions of linear regression analysis. Multicollinearity was evaluated via the variance inflation factor (VIF). Candidate models for all possible combinations of the eight predictor variables were fitted, and the model most strongly supported by the data determined via Akaike’s Information Criterion (AIC). Variables with a VIF > 5 were omitted. For the final model, the contribution of each predictor to the overall variance explained was determined by means of analysis of variance. All statistical analyses were conducted using the R language and environment for statistical computing (R Development Core Team, 2016).

To corroborate our analysis of resilience and assess its robustness we also calculated an alternative measure of resilience from our simulations focusing on the temporal variation in NPP. Theory suggests that systems with high resilience have low temporal variation, and that variation over time increases with decreasing resilience (Scheffer et al., 2015). We thus calculated an alternative, variation-based indicator of resilience (R_V) as the inverse of the coefficient of variation in annual NPP (Eq. (3)).

$$R_V = \frac{1}{cv(NPP)} = \frac{mean(NPP)}{sd(NPP)} \qquad (3)$$

To enable the comparison between trials we controlled for differences in stand age by restricting the analysis of R_V to a common range of between 40 and 56 years. Differences were tested by means of Wilcoxon's signed rank sum test. All analyses regarding resilience were based solely on simulated data.

3 Results

3.1 Model evaluation

iLand was well able to reproduce the main growth patterns observed at the three sites (Fig. 1, Appendix A in the Online Supplementary Material). The model tracked the change in mean diameter over time well for Eibiswald and Karlstift, with an average deviation of the mean DBH across all stands and remeasurements of −3.4% and +2.8%, respectively. Also at Ottenstein, simulated mean DBH compared reasonably well to observations (−8.2%). iLand moderately underestimated tree heights at all three sites (−8.2% at Eibiswald, −7.4% at Karlstift, and −12.8% at Ottenstein), but overestimated stand basal area at Karlstift in the first half of the study period (+31%) (Fig. 1, Appendix A).

As expected, tree diameter increment responded particularly strongly to the different treatments experimentally implemented in the thinning trials. For instance, the diameter range at the beginning of the trial was only between 5.0 cm and 6.5 cm between stands at Ottenstein, but responded to the various treatments by expanding to a range of 23.8 cm to 43.7 cm at the end of the study period (Karlstift: 27.8–33.2 cm, Eibiswald: 25.1–33.6 cm). Overall, the model captured this strong response of Norway spruce to thinning satisfactorily. In the final year of the trial, iLand predicted a diameter range of between 21.0 cm and 40.5 cm at Ottenstein (Karlstift: 31.3–35.0 cm, Eibiswald: 22.8–33.9 cm). iLand explained 78.6%, 66.2%, and 87.8% of the observed between-stand variation in mean DBH at the end of the trial period at Ottenstein, Karlstift, and Eibiswald. In addition to this stand level evaluation we also conducted a pairwise comparison at the level of individual trees. The goodness of fit between the simulated and the observed individual tree diameter increments was lower than that of stand level state variables. The mean bias was statistically significant but ecologically negligible, amounting to +0.01, −0.10, and +0.08 cm yr^{-1} at Eibiswald, Karlstift, and Ottenstein. Root-mean-square errors were between 0.13 cm and 0.19 cm, and

19.2%, 47.1%, and 41.1% of the variation in individual tree DBH increment was explained by the model at Eibiswald, Karlstift, and Ottenstein, respectively. (Fig.1d–f).

Analyzing model performance with regard to the simulated response to individual thinning inte entions showed that the relative basal area change after thinning was faithfully reproduced by iLand. Overall, 84.5% of the short-term (2–5 years) variation in basal area was captured by iLand, with no significant bias of the simulated basal area change across all sites and interventions (Fig. 2). The largest deviations between simulated and observed thinning responses were found for the first two decades at Karlstift, where the model overestimated the growth boost after thinnings (see also Fig. 1b).

3.2 Stand level drivers of resilience

Both site and stand level predictors significantly influenced the resilience of Norway spruce forests to non-stand replacing disturbances (Table 3). The AIC-selected final model across all study sites, thinning interventions, and climate scenarios included six predictors and one interaction term, and was able to explained 85.5% of the variation in R_R of GS. Stand-level predictors not only included age (log-transformed) but also the disturbance history of a stand, here described by the stand basal area and the amount of GS affected by disturbance in the last ten years. Multicollinearity between stand-level indicators was found to be acceptable, with variance inflation factors ranging from 1.37 to 4.98. Overall, our analysis suggested that stand level factors had a considerably stronger influence on resilience than site factors, together accounting for 77.4% of the explained variation (with age alone contributing 66.9%). Resilience was found to decrease with increasing age and basal area (Fig. 3). Also higher levels of recent previous disturbance moderately reduced the capacity to recover. Under the climate conditions representing the site Karlstift, for instance, R_R of GS decreased by 46.5% from age 30 to age 60. This reduction in resilience could be compensated by reducing the basal area level from 48 m^2 to 27.6 m^2 for a 50 year old stand.

3.3 Climate sensitivity of resilience

Although less influential in explaining the variation in resilience than stand variables, also climate factors significantly affected resilience. Notably, the distinctly different climatic conditions at the three trial sites resulted in widely different recovery rates after disturbance, and thus different levels of R_R. After controlling for site-specific differences in stand and soil attributes the highest resilience was found at Eibiswald, and the lowest values of R_R were calculated for Ottenstein. For 50 year old stands with an effective soil depth of 120 cm, a basal area of 40 m^2, and 20% of GS disturbed in the previous 10 years resilience was 5.0, 4.9, and 4.3% GS yr^{-1} at Eibiswald, Karlstift, and Ottenstein respectively, assuming past climatic conditions. This suggests that Norway spruce stands at Eibiswald recover 18.1% faster from disturbances than those at Ottenstein.

The response of resilience to climate change was found to be strongly conditional on the prevailing site conditions. At the cool and wet site Eibiswald the higher temperatures and CO_2 levels projected for the future increased resilience in all scenarios, regardless of the directionality and change in precipitation (Fig. 4). Overall, the capacity to recover from disturbance increased from 5.5% yr^{-1} under baseline climate to on average of 7.7% yr^{-1} in the period 2081–2100 at Eibiswald. Conversely, resilience decreased under all simulated climate change scenarios at the warm and dry site Ottenstein, with the strongest loss in resilience under the driest scenario ALADIN-ARPEGE. Here the capacity to recover from disturbances was estimated to drop to 3.3% GS yr^{-1} on average under the climate expected for the end of the 21st century, compared to 4.7% GS yr^{-1} under baseline climate. Our model-based synthesis across sites and scenarios showed that the transition from an increase in resilience in response to warming to a decrease was strongly determined by water availability, with an inflection point at around 800 mm annual precipitation (Fig. 4). The site Karlstift was situated close to this inflection point: Here, warming alone had only very little influence on resilience, while a warming in combination with decreasing precipitation levels resulted in decreasing levels of resilience. Generally, we found that the effect of precipitation on resilience increased with increasing temperatures.

3.4 Resilience of what

Results with regard to the key drivers of R_R and the ranking of resilience between sites were robust to changing the focus of the analysis from the recovery of GS to recovery of LAI (see Appendix B in the Online Supplementary Material for details). The wet and cool site Eibiswald was the most resilient also in terms of LAI, while the warm and dry site Ottenstein was the least resilient. Also, stand variables and among them particularly stand age were confirmed to be highly relevant drivers of R_R of LAI. Site factors were relatively more important in the context of LAI compared to GS, accounting for 25.2% of the explained variation. Consequently, also the climate sensitivity of R_R was elevated for LAI, and particularly the effect of varying precipitation levels amplified. However, the precipitation-mediated inflection point between warming-induced increases and decreases of resilience was only slightly lower for the R_R of LAI relative to GS.

3.5 Robustness of resilience assessment

The spatial trends and climate sensitivities of resilience estimated from recovery after thinning (R_R) were largely in agreement with changes in the temporal variability of the system (R_V), which is an alternative indicator of resilience. Also for R_V, here analyzed as the temporal variation of annual NPP, resilience was found to increase with elevation: While Eibiswald had the highest resilience (i.e., temporal variation in NPP low), Ottenstein showed the lowest level of resilience (i.e., temporal variation in NPP high) (Fig. 5). Resilience at Karlstift was found to be slightly lower than at Eibiswald, yet differences between these two sites were not statistically significant ($p = 0.826$). In compliance with R_R, the warm and dry low elevation site Ottenstein had a significantly lower R_V compared to the two other sites ($p < 0.001$). Also with regard to the effects of potential future climates the analysis of R_V did generally confirm the signals revealed by the recovery-based resilience indicator R_R: At the cool and wet site Eibiswald, R_V almost doubled from the baseline value of 5.6–10.9 for 2081–2100, while at Ottenstein R_V decreased from 7.1 to 5.2 over the same period.

4 Discussion and conclusions

The ongoing and expected changes in climate (Lindner et al., 2010) make resilience a key attribute of future forest ecosystems. Yet, despite theoretical advances regarding the assessment of resilience (Scheffer et al., 2015), the application of the concept in ecosystem management has progressed only slowly, hampered *inter alia* by the availability of appropriate data and indicators of resilience. Here, we have conducted a novel reanalysis of thinning trials, reinterpreting the wide range of thinning removals as an experimental disturbance gradient and quantifying resilience as the recovery rate from these perturbations.

4.1 Study limitations

While the studied thinning trials comprise a wide range of thinning intervals and intensities, they only represent a subset of the natural disturbance regime of Norway spruce forests (Bebi et al., 2017; Janda et al., 2017; Kulakowski et al., 2017). Specifically, they correspond to low to moderately severe canopy disturbances returning with relatively high frequency. However, also rare but extensive high severity events are an important part of the natural disturbance regime in Central Europe (Čada et al., 2013; Thom et al., 2013). As disturbance severity and disturbance legacies strongly determine post-disturbance development (Halpin and Lorimer, 2016; Seidl et al., 2014), recovery from large and severe events might follow distinctly different trajectories than those determined here for non-stand-replacing events. Nonetheless, theory suggests that even small perturbations can give insights into the overall resilience of a system (Scheffer et al., 2015). We thus suggest our results to be an initial quantification of the resilience of Norway spruce forests in Central Europe, yet recommend corroborating our findings with further analyses, particularly focusing on complementary large and severe natural disturbance events.

Further uncertainties remain with regard to the simulation approach used here. Specifically, we combined empirical information with simulation modeling to derive resilience indicators. Simulation modeling allowed us to analyze crucial variables of ecosystem functioning not routinely measured in forests (e.g., LAI, NPP) with the high temporal resolution needed to calculated recovery-related resilience indicators. Tests of the applied model document its ability to approximate stand development and disturbance responses for the studied systems. The tree and standlevel variation explained by iLand is well in the range of accuracies achieved with other process-based forest ecosystem models (e.g., Collalti et al., 2014; Seidl et al., 2005). Furthermore, iLand was well able to capture the responses of individual trees to a wide range of thinnings. The latter is a particularly relevant finding, as modeling thinning responses has been found to be challenging for process-based ecosystem models (Petritsch et al., 2007). Nonetheless, deviations of the simulated stand development trajectories from observations, such as at Karlstift in the middle part of the trial period (see Fig. 1c), highlight the inherent limitations of using simulation models. Nonetheless, the use of a process-based model also offers potential avenues for future application: Using highly scalable simulation tool such as iLand, the stand level results analyzed here could consistently be scaled up to larger areas such as landscapes and regions (Seidl et al., 2013), aiding the quantification and mapping of future climate risks.

4.2 Quantifying resilience

Here we demonstrated how to deduce resilience from thinning trials, and showed that recovery after moderate management interventions, as implemented regularly throughout forests in the temperate and boreal zone, can readily be used to quantify forest resilience. We corroborated our recovery-related assessment of resilience with a different resilience indicator based on system-level variance of ecosystem carbon fluxes (NPP). Finding good agreement between these two indicators underlines the robustness of our assessment, and is noteworthy also from an applications perspective: In the context of operational forest management, the variance-based indicators of resilience derived from theoretical considerations (Scheffer et al., 2015) are difficult to implement, as they require long-term data monitored at high temporal resolution in order to achieve a satisfactorily signal-to-noise ratio in quantifying variance. Recovery from human perturbations, on the other hand, could be more easily assessed in practice, as variables already monitored currently in forest planning might be sufficient to quantify and compare resilience across forest types. In addition, remote-sensing based indicators of recovery after disturbance could be utilized to address large-scale trends, and obtain consistent estimates were management records are lacking (Bartels et al., 2016). Furthermore, the wide range of thinning trials implemented across the globe (e.g., Ares et al., 2009; D'Amato et al., 2013; Fernández-de-Uña et al., 2015; Gebhardt et al., 2014; Wallentin and Nilsson, 2013) could be utilized in the future to gain a better understanding of differences in resilience between regions and forest types.

An important finding of our study in the context of management is that resilience is not a static property of a forest ecosystem, but changes significantly with a changing climate (see also Seidl et al., 2016). We here found that the climate conditions expected for the 21st century could either increase or decrease resilience, depending on the current site conditions and changes in temperature and precipitation. Our initial hypothesis on a general decrease of the resilience of Norway spruce forests with climate warming thus has to be rejected. Targeting resilience in forest management will not only have to consider the current resilience of a given system, but also needs to consider its potential future changes. Despite efforts to obtain a better description and quantification of resilience it will remain a moving target for management also in the future.

Here, we have focused solely on engineering resilience, which is only one dimension of the resilience of forest ecosystems. Management considerations should also include aspects of ecological resilience and social-ecological resilience (Biggs et al., 2012; Gunderson, 2000; Johnstone et al., 2016; Seidl et al., 2016). In this context it is important to note that a swift recovery (and thus high engineering resilience) might not always be in congruence with high ecological resilience (Holling, 1996). While a swift recovery from disturbance can, for instance, be desirable from the perspective of production forestry, variable recovery rates and a prolonged maintenance of open conditions after perturbations are likely to benefit biodiversity (Swanson et al., 2011; Thom et al., in press a) and can dampen and delay the risk from future disturbances (Seidl et al., in press).

4.3 Managing for resilience

A number of conclusions for resilience-focused management can be deduced from our results: First, the finding that stand variables have a stronger influence on resilience than climatic drivers suggests that management has a strong leverage on resilience. Our results highlight that particularly age is of critical importance, and that old and overstocked conditions have especially low resilience to perturbations. Avoiding these conditions could help to counteract some of the negative climate change impacts that are expected in Norway spruce forests particularly at dry, low-elevation sites. Furthermore, also multi-aged stands could be a silvicultural means to counteract the decreasing resilience with stand age (Kuuluvainen et al., 2012; Lafond et al., 2014). However, as our experimental data contained exclusively homogeneous and evenaged stands, the hypothesis of higher resilience in multi-aged stands should be tested more thoroughly in future work.

Furthermore, we found that having already experienced disturbances in the recent past decreases the resilience to further disturbances. Shorter disturbance return intervals in response to climate change could thus further reduce the recovery capacity of forest ecosystems, suggesting a compounding effect of multiple disturbances that occur in short succession (Buma, 2015). Management that aims to anticipate and mitigate the impacts of such intensifying disturbance regimes thus also helps for maintaining the resilience of forests. Finally, we found support for our hypothesis that the resilience of Norway spruce forests decreases towards the margins of its realized niche. Specifically, our results show that Norway spruce stands on sites with precipitation levels below 750–800 mm will particularly suffer from climate change. Under these conditions, already moderate warming or further deceases in precipitation lead to a decline in resilience (cf. Fig. 4). While future precipitation changes are still uncertain, virtually all climate models and scenarios available today agree on a continued warming over the coming decades, regardless of emission pathway (IPCC, 2013; Solomon et al., 2009). For dry sites, our results thus suggest that tree species change will be necessary to maintain a minimum recovery capacity towards perturbations also in the future.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

W. Rammer, F. Vigl, and R. Seidl acknowledge funding from the Austrian Climate Research Program under grant ACRP5-MOCCA-KR12AC5K01104. R. Seidl received further support from a European Commission’s Marie Curie Career Integration Grant (PCIG12-GA-2012-334104) as well as from the Austrian Science Fund (FWF) through START grant Y895-B25. We thank four anonymous reviewers for helpful comments on earlier versions of the manuscript.

References

Allen CD, Breshears DD, McDowell NG. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere. 2015; 6 art129.

Ares A, Berryman SD, Puettmann KJ. Understory vegetation response to thinning disturbance of varying complexity in coniferous stands. Appl Veg Sci. 2009; 12:472–487.

Auer I, Reinhard B, Jurkovic A, Lipa W, Orlik A, Potzmann R, Schöner W, Ungersböck M, Matulla C, Briffa K, Jones P, et al. HISTALP – historical instrumental climatological surface time series of the Greater Alpine Region. Int J Climatol. 2007; 27:17–46.

Bartels SF, Chen HYH, Wulder MA, White JC. Trends in post-disturbance recovery rates of Canada’s forests following wildfire and harvest. For Ecol Manage. 2016; 361:194–207.

Bebi P, Seidl R, Motta R, Fuhr M, Firm D, Krumm F, Conedera M, Ginzler C, Wohlgemuth T, Kulakowski D. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. For Ecol Manage. 2017; 388:43–56.

Biggs R, Schlüter M, Biggs D, Bohensky EL, BurnSilver S, Cundill G, Dakos V, Daw TM, Evans LS, Kotschy K, Leitch AM, et al. Toward principles for enhancing the resilience of ecosystem services. Annu Rev Environ Resour. 2012; 37:421–448.

Boden S, Kahle H-P, Von Wilpert K, Spiecker H. Resilience of Norway spruce (*Picea abies* (L.) Karst) growth to changing climatic conditions in Southwest Germany. For Ecol Manage. 2014; 315:12–21.

Buma B. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere. 2015; 6 art70.

Čada V, Svoboda M, Janda P. Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. For Ecol Manage. 2013; 295:59–68.

Carpenter S, Walker B, Anderies JM, Abel N. From metaphor to measurement: resilience of what to what? Ecosystems. 2001; 4:765–781.

Collalti A, Perugini L, Santini M, Chiti T, Nolè A, Matteucci G, Valentini R. A process-based model to simulate growth in forests with complex structure: evaluation and use of 3D-CMCC forest ecosystem model in a deciduous forest in Central Italy. Ecol Modell. 2014; 272:362–378.

D'Amato AW, Bradford JB, Fraver S, Palik BJ. Forest management for mitigation and adaptation to climate change: insights from long-term silviculture experiments. For Ecol Manage. 2011; 262:803–816.

D'Amato AW, Bradford JB, Fraver S, Palik BJ. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol Appl. 2013; 28:1735–1742.

Dymond CC, Spittlehouse DL, Tedder S, Hopkins K, McCallion K, Sandland J. Applying resilience concepts in forest management: a retrospective simulation approach. Forests. 2015; 6:4421–4438.

Elkin C, Giuggiola A, Rigling A, Bugmann H. Short- and long-term efficacy of forest thinning to mitigate drought impacts in mountain forests in the European Alps. Ecol Appl. 2015; 25:1083–1098. [PubMed: 26465044]

Fernández-de-Uña L, Cañellas I, Gea-Izquierdo G. Stand competition determines how different tree species will cope with a warming climate. PLoS ONE. 2015; 10:e0122255. [PubMed: 25826446]

Gebhardt T, Häberle K-H, Matyssek R, Schulz C, Ammer C. The more, the better? Water relations of Norway spruce stands after progressive thinning. Agric For Meteorol. 2014; 197:235–243.

Gunderson LH. Ecological resilience – in theory and application. Annu Rev Ecol Syst. 2000; 69:425–439.

Gustafson EJ. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landsc Ecol. 2013; 28:1429–1437.

Halpin CR, Lorimer CG. Trajectories and resilience of stand structure in response to variable disturbance severities in northern hardwoods. For Ecol Manage. 2016; 365:69–82.

Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE. Climate change may cause severe loss in the economic value of European forest land. Nat Clim Change. 2013; 3:203–207.

Hlásny T, Turcčáni M. Persisting bark beetle outbreak indicates the unsustainability of secondary Norway spruce forests: case study from Central Europe. Ann For Sci. 2013; 70:481–491.

Holling, CS. Engineering resilience versus ecological resilience. Engineering within Ecological Constraints. Schulze, PC., editor. National Academy Press; Washington DC, USA: 1996. p. 31-44.

IPCC. Emissions scenarios. Intergovernmental Panel on Climate Change. Cambridge University Press; Cambridge, UK: 2000.

IPCC. Working Group I contribution to the IPCC fifth assessment report. Intergovernmental Panel on Climate Change. Climate Change 2013: the physical science basis. Cambridge University Press; Cambridge, UK: 2013.

Jacob D. A note to the simulation of the annual and inter-annual variability of the water budget over the Baltic Sea drainage basin. Meteorol Atmos Phys. 2001; 77:61–73.

Janda P, Trotsiuk V, Mikoláš M, Bace R, Nagel TA, Seidl R, Seedre M, Morrissey RC, Kucbel S, Jaloviar P, Jasík M, et al. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. For Ecol Manage. 2017; 388:67–78.

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, et al. Changing disturbance regimes, climate warming and forest resilience. Front Ecol Environ. 2016; 14:369–378.

Kerhoulas LP, Kolb TE, Hurteau MD, Koch GW. Managing climate change adaptation in forests: a case study from the U.S. Southwest J Appl Ecol. 2013; 50:1311–1320.

Kilian, W., Müller, F., Starlinger, F. Die forstlichen Wuchsgebiete Österreichs Eine Naturraumgliederung nach waldökologischen Gesichtspunkten. FBVA-Berichte 82. Forstliche Bundesversuchsanstalt; Vienna, Austria: 1994.

Kulakowski D, Seidl R, Holeksa J, Kuuluvainen T, Nagel TA, Panayotov M, Svoboda M, Thorn S, Vacchiano G, Whitlock C, Wohlgemuth T, Bebi P. A walk on the wild side: disturbance dynamics and the conservation and management of European mountain forest ecosystems. For Ecol Manage. 2017; 388:120–131.

Kuuluvainen T, Tahvonen O, Aakala T. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio. 2012; 41:720–737. [PubMed: 22581386]

Lafond V, Lagarrigues G, Cordonnier T, Courbaud B. Uneven-aged management options to promote forest resilience for climate change adaptation: effects of group selection and harvesting intensity. Ann For Sci. 2014; 71:173–186.

Landsberg JJ, Waring RH. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For Ecol Manage. 1997; 95:209–228.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M, Lexer MJ, et al. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manage. 2010; 259:698–709.

Lloret F, Keeling EG, Sala A. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. Oikos. 2011; 120:1909–1920.

Neill AR, Puettmann KJ. Managing for adaptive capacity: thinning improves food availability for wildlife and insect pollinators under climate change conditions. Can J For Res. 2013; 440:428–440.

Pal JS, Giorgi F, Bi X, Elguindi N, Solmon F, Rauscher SA, Gao X, Francisco R, Zakey A, Winter J, Ashfaq M, et al. Regional climate modeling for the developing world: the ICTP RegCM3 and RegCNET. Bull Am Meteorol Soc. 2007; 88:1395–1409.

Petritsch R, Hasenauer H, Pietsch SA. Incorporating forest growth response to thinning within biome-BGC. For Ecol Manage. 2007; 242:324–336.

Ponocná T, Spyt B, Kaczka R, Büntgen U, Treml V. Growth trends and climate responses of Norway spruce along elevational gradients in East-Central Europe. Trees Struct Funct. 2016; 30:1633–1646.

Pretzsch H. Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.): evidence from long-term experimental plots. Eur J For Res. 2005; 124:193–205.

Primicia I, Camarero JJ, Janda P, Čada V, Morrissey RC, Trotsiuk V, Bače R, Teodosiu M, Svoboda M. Age, competition, disturbance and elevation effects on tree and stand growth response of primary *Picea abies* forest to climate. For Ecol Manage. 2015; 354:77–86.

Radeloff VC, Williams JW, Bateman BL, Burke KD, Sarah CK, Childress ES, Cromwell KJ, Gratton C, Hasley AO, Kraemer BM, Latzka AW, et al. The rise of novelty in ecosystems. Ecol Appl. 2015; 25:2051–2068. [PubMed: 26910939]

R Development Core Team. A language and environment for statistical computing. R Foundation for Statistical Computing; Vienna, Austria: 2016.

Radu R, Déqué M, Somot S. Spectral nudging in a spectral regional climate model. Tellus A. 2008; 60:898–910.

Rammer W, Seidl R. Coupling human and natural systems: simulating adaptive management agents in dynamically changing forest landscapes. Glob Environ Chang. 2015; 35:475–485.

Reyer C, Lasch-Born P, Suckow F, Gutsch M, Murawski A, Pilz T. Projections of regional changes in forest net primary productivity for different tree species in Europe driven by climate change and carbon dioxide. Ann For Sci. 2014; 71:211–225.

Reyer CPO, Brouwers N, Rammig A, Brook BW, Epila J, Grant RF, Holmgren M, Langerwisch F, Leuzinger S, Lucht W, Medlyn B, et al. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J Ecol. 2015; 103:5–15.

Scheffer M, Carpenter SR, Dakos V, van Nes E. Generic indicators of ecological resilience: inferring the chance of a critical transition. Annu Rev Ecol Evol Syst. 2015; 46:145–167.

Seidl R. The shape of ecosystem management to come: anticipating risks and fostering resilience. Bioscience. 2014; 64:1159–1169. [PubMed: 25729079]

Seidl R, Donato DC, Raffa KF, Turner MG. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proc Natl Acad Sci USA. in press.

Seidl R, Eastaugh CS, Kramer K, Maroschek M, Reyer C, Socha J, Vacchiano G, Zlatanov T, Hasenauer H. Scaling issues in forest ecosystem management and how to address them with models. Eur J For Res. 2013; 132:653–666.

Seidl R, Lexer MJ, Jäger D, Hönninger K. Evaluating the accuracy and generality of a hybrid patch model. Tree Physiol. 2005; 25:939–951. [PubMed: 15870060]

Seidl R, Rammer W, Lexer MJ. Climate change vulnerability of sustainable forest management in the Eastern Alps. Clim Change. 2011; 106:225–254.

Seidl R, Rammer W, Scheller RM, Spies TA. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol Modell. 2012; 231:87–100.

Seidl R, Rammer W, Spies TA. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol Appl. 2014; 24:2063–2077. [PubMed: 27053913]

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol. 2016; 53:120–129. [PubMed: 26966320]

Silva Pedro M, Rammer W, Seidl R. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. Oecologia. 2015; 177:619–630. [PubMed: 25526843]

Solomon S, Plattner G-K, Knutti R, Friedlingstein P. Irreversible climate change due to carbon dioxide emissions. Proc Natl Acad Sci USA. 2009; 106:1704–1709. [PubMed: 19179281]

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, DellaSala DA, Hutto RL, Lindenmayer DB, Swanson FJ. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front Ecol Environ. 2011; 9:117–125.

Thom D, Rammer W, Dirnböck T, Müller J, Kobler J, Katzensteiner K, Helm N, Seidl R. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. J Appl Ecol. in press.

Thom D, Rammer W, Seidl R. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob Change Biol. in press b.

Thom D, Seidl R, Steyrer G, Krehan H, Formayer H. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. For Ecol Manage. 2013; 307:293–302.

Wallentin C, Nilsson U. Storm and snow damage in a Norway spruce thinning experiment in southern Sweden. Forestry. 2013; 87:229–238.

Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A. Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Glob Change Biol. 2014; 20:3767–3779.

Zeide B. Thinning and growth: a full turnaround. J For. 2001; 99:20–25.

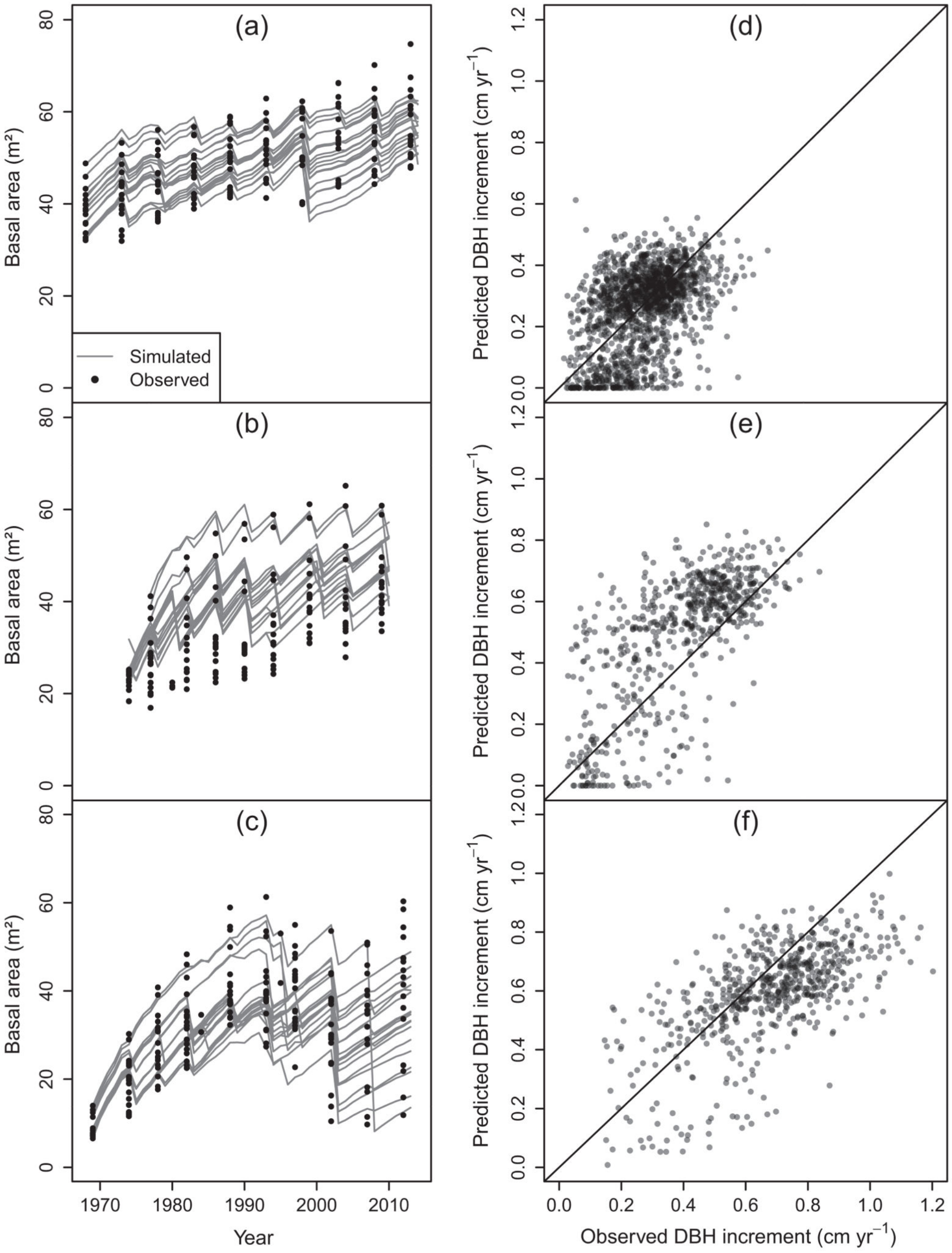

Fig. 1.

Evaluation of iLand against independent data from thinning trials. Panels (a) through (c) compare simulated stand basal area trajectories to periodic observations at the trial sites. Panels (d) through (f) compare simulated to observed individual-tree DBH increment for trees that were retained over the entire trial period. Top row (panels a, d): Eibiswald, center row (panels b, e): Karlstift, bottom row (panels c, f): Ottenstein. DBH = diameter at breast height.

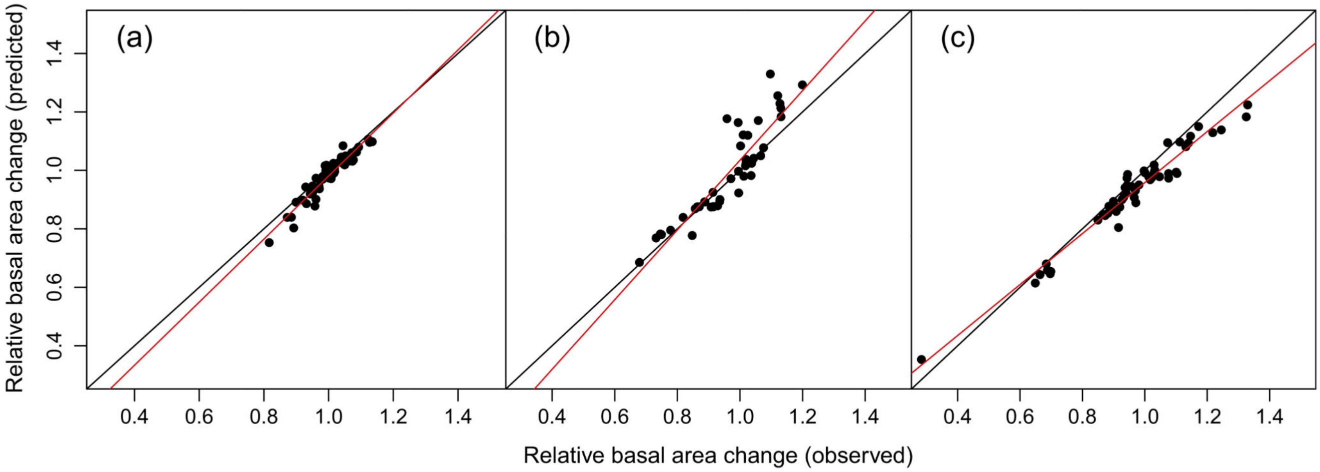

Fig. 2.

Observed versus simulated relative basal area change after thinning at (a) Eibiswald, (b) Karlstift, and (c) Ottenstein. Relative basal area change was derived as the ratio between the basal area at the first re-measurement after a thinning relative to the basal area observed at or before the thinning. The red line indicates a linear regression between simulated and observed values, the black line is the 1:1 line.

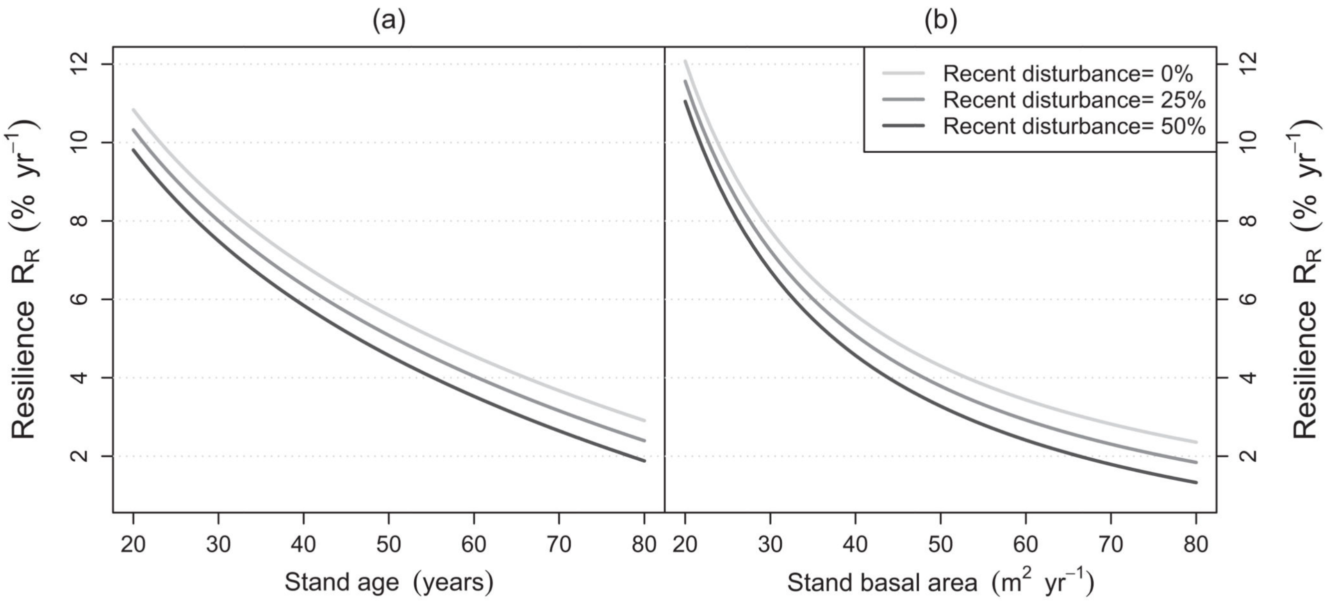

Fig. 3.

The sensitivity of resilience to stand attributes and recent disturbance. Resilience R_R here describes the capacity to recover from non-stand-replacing disturbance, measured as the amount of disturbance (in percent of growing stock) that is recovered per year. Curves are derived from a multiple linear model fit to simulation data reanalyzing thinning trials under current and future climate conditions (see Table 3). Panel (a) shows the change of resilience over stand age for a constant basal area level of 40 m^2. Panel (b) shows the sensitivity to changing stand basal area for a 50 year old stand. The effect of different recent disturbance levels (in% GS disturbed over the preceding 10 years) is indicated via different lines. Mean annual temperature was set to 6 °C, precipitation sum to 1000 mm yr^{-1}, and the effective soil depth to 120 cm.

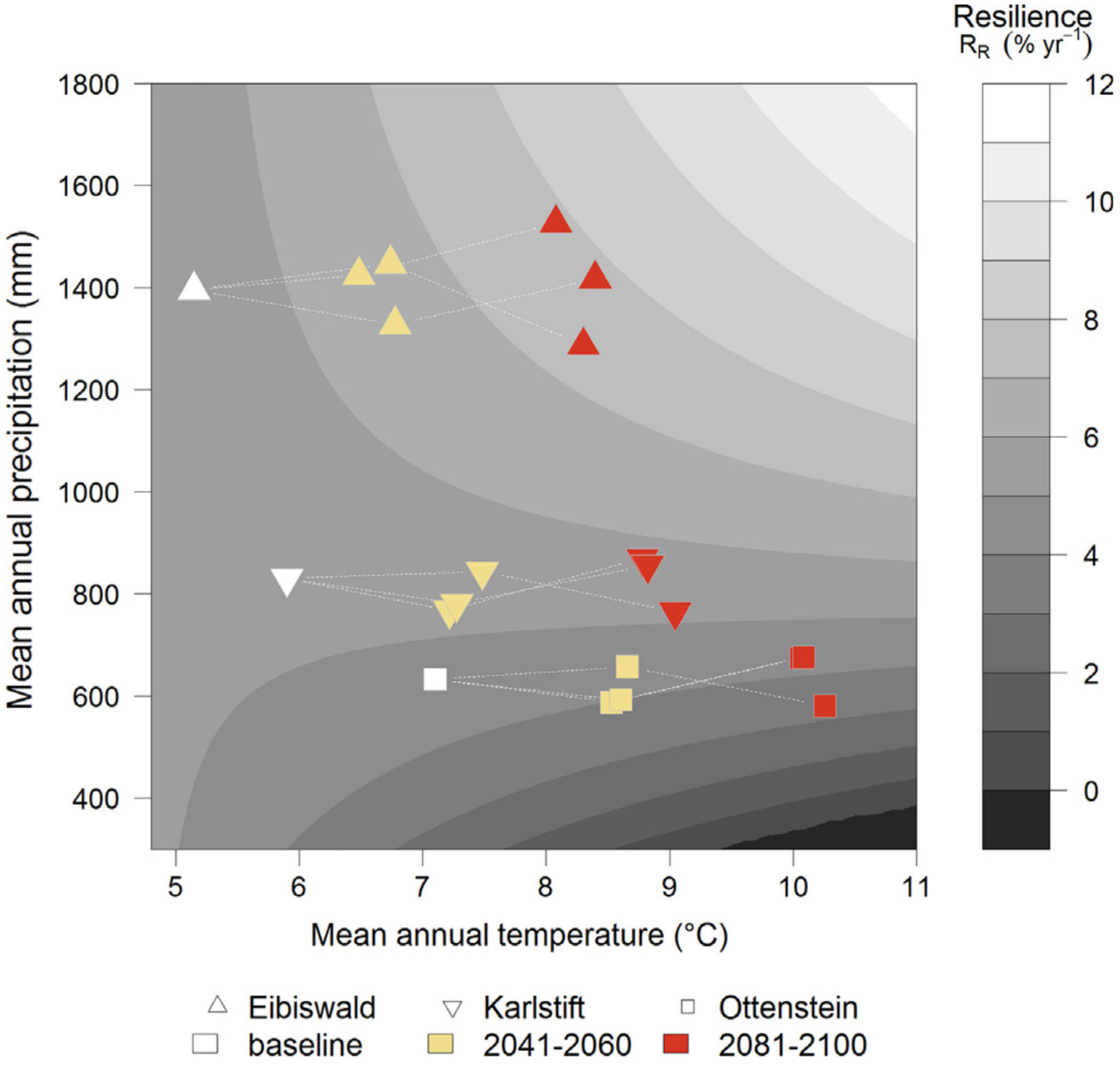

Fig. 4.

The climate sensitivity of resilience as predicted by a multiple linear regression model synthesizing a wide range of ecological conditions simulated with iLand (see Table 3). The background indicates the change in resilience R_R with temperature and precipitation, and indicates the amount of non-stand-replacing disturbance (in % of growing stock removed) that can be recovered per year. The symbols represent the locations of the three study sites in climate space (upright triangles: Eibiswald, inverted triangles: Karlstift, rectangles: Ottenstein) in three periods (white: baseline, yellow: 2041–2060, red: 2081–2100) for the three different climate scenarios (see Table 2 for details). Stand attributes were set to age = 50 years, basal area = 40 m^2, recent disturbances = 0%, and effective soil depth = 120 cm.

(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

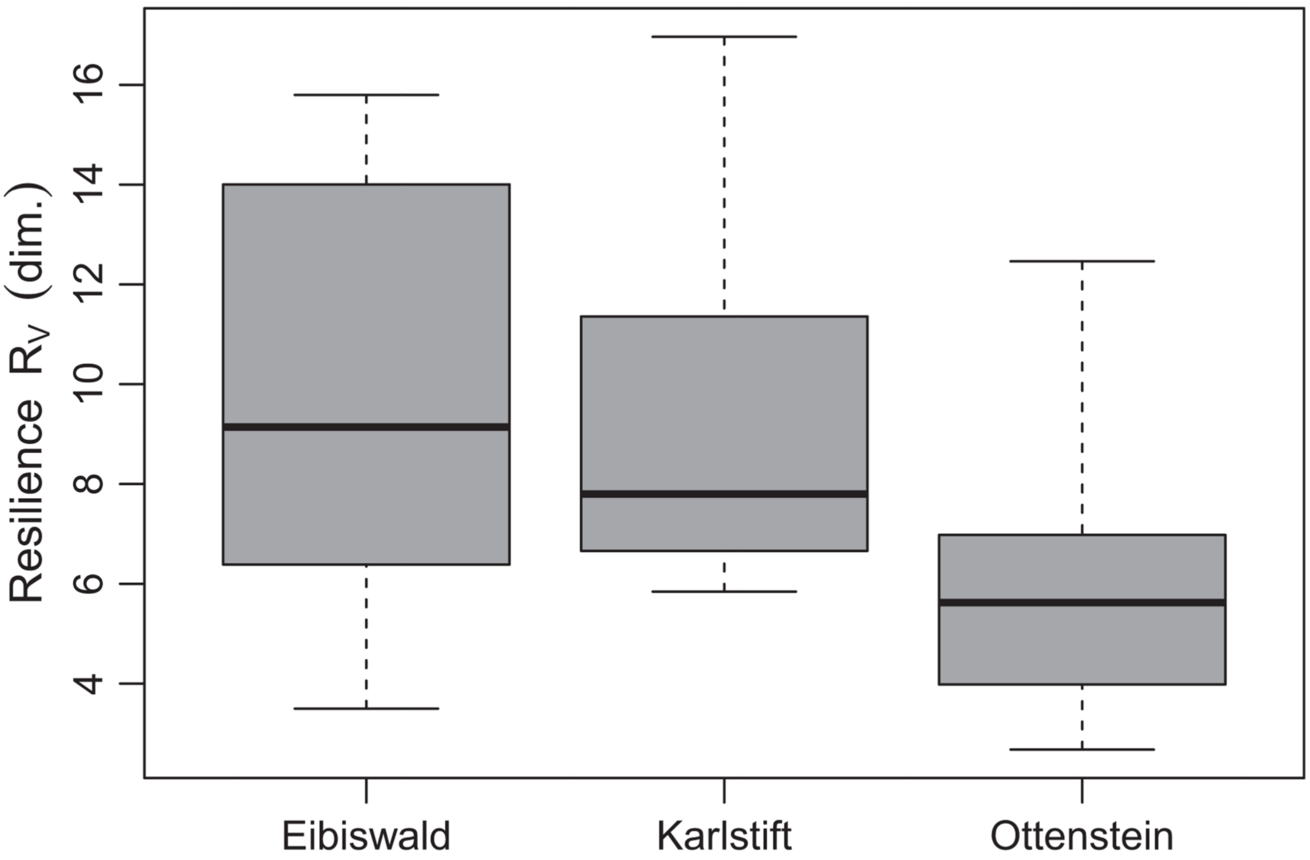

Fig. 5.

Resilience R_V based on the temporal variation of NPP over all scenarios for the three sites. Higher values indicate higher resilience (lower temporal variation of NPP).

Table 1

Description of the three thinning trials investigated. DBH = diameter at breast height.

		Eibiswald	**Karlstift**	**Ottenstein**
Site description	Elevation (m)	1,250 m	930 m	540 m
	Mean annual temperature (°C)	5.1	5.9	7.1
	Mean annual precipitation sum (mm)	1394	831	633
	Mean daily radiation April – September (MJ m^{-2})	18.9	17.4	17.9
	Mean daily vapor pressure deficit April – September (kPa)	0.39	0.37	0.52
	Soil type	Cambisol	Dystric cambisol	Cambisol
	Effective soil depth (cm)	149	150	23
	Plant-available nitrogen (kg ha^{-1} yr^{-1})	60	45	62
Initial conditions	Year of initiation	1968	1974	1969
	Age at initiation	40	27	13
	Mean DBH (cm) [a]	13.9 ± 2.0	9.1 ± 1.7	5.9 ± 0.4
	Stem density per ha [a]	2461 ± 852	4191 ± 2709	3043 ± 1058
	Basal area (m^2 ha^{-1}) [a]	38.0 ± 5.0	26.11 ± 7.0	8.7 ± 2.3
Experimental design	Number of stands	18	16	17
	Number of re-measurements	12	12	14
	Year of last re-measurement	2013	2009	2012
	Number of thinning variants	4–8	4–9	5
	Percent of growing stock removed per intervention (mean; min–max)	9.6; 2.0–42.7	21.5; 2.9–50.2	33.2; 1.9–93.9

[a] Mean and standard deviation over all plots at the given site.

Table 2

The site-specific changes in mean annual temperature (ΔT, absolute change in C°) and annual precipitation sum (ΔP, relative change in percent) in the studied climate scenarios relative to baseline climate (i.e., the observed climate of the years between the initiation of a trial and its last re-measurement, cf. Table 1).

Climate models	**Period**	**Eibiswald**		**Karlstift**		**Ottenstein**	
		ΔT (°C)	**ΔP (%)**	**ΔT (°C)**	**ΔP (%)**	**ΔT (°C)**	**ΔP (%)**
ALADIN-ARPEGE	2041–2060	+1.59	+3.7	+1.58	+1.7	+1.56	+3.9
	2081–2100	+3.16	−7.7	+3.14	−8.0	+3.16	−8.2
REMO-ECHAM5	2041–2060	+1.63	−4.8	+1.37	−5.9	+1.50	−6.4
	2081–2100	+3.25	+1.5	+2.92	+3.1	+2.99	+6.9
RegCM3-ECHAM5	2041–2060	+1.34	+2.1	+1.32	−7.5	+1.43	−7.1
	2081–2100	+2.93	+9.4	+2.88	+4.7	+2.96	+6.6

Table 3

Coefficients of the final linear model describing the resilience of Norway spruce forests to non-stand replacing disturbance. The response variable is resilience, measured as the amount of disturbance (in percent of growing stock removed) that is recovered per year (R_R). Data are based on simulated stand trajectories under current and future climate conditions (n = 1438).

Parameter	**Coefficient**	**P-value**
Log (age) (years)	−5.719	<0.001
1/basal area (m^2)	259.209	<0.001
Recent disturbance (%)	−0.0205	<0.001
Temperature (°C)	−7.946	<0.001
Log (precipitation) (mm)	−5.739	<0.001
Interaction temperature: log (precipitation)	1.193	<0.001
Effective soil depth (cm)	0.0139	<0.001
Intercept	57.673	<0.001