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What drives the future supply of regulating ecosystem services in a mountain forest landscape?

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Abstract

Forest ecosystems provide a wide variety of ecosystem services to society. In harsh mountain environments, the regulating services of forests are of particular importance. Managing mountain forests for regulating services is a cost- and labor intensive endeavor. Yet, also unmanaged forests regulate the environment. In the context of evidence-based decision making it is thus important to scrutinize if current management recommendations improve the supply of regulating ecosystem services over unmanaged development trajectories. A further issue complicating decision making in the context of regulating ecosystem services is their high sensitivity to climate change. Climate-mediated increases in natural disturbances, for instance, could strongly reduce the supply of regulating services from forests in the future. Given the profound environmental changes expected for the coming decades it remains unclear whether forest management will still be able to significantly control the future trajectories of mountain forest development, or whether the management effect will be superseded by a much stronger climate and disturbance effect. Here, our objectives were (i) to quantify the future regulating service supply from a 6456 ha landscape in the Stubai valley in Tyrol, Austria, and (ii) to assess the relative importance of management, climate, and natural disturbances on the future supply of regulating ecosystem services. We focused our analysis on climate regulation, water regulation, and erosion regulation, and used the landscape simulation model iLand to quantify their development under different climate scenarios and management strategies. Our results show that unmanaged forests are efficient in providing regulating ecosystem services. Both climate regulation and erosion regulation were higher in unmanaged systems compared to managed systems, while water regulation was slightly

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enhanced by management. Overall, direct effects of climate change had a stronger influence on the future supply of regulating services than management and natural disturbances. The ability of management to control ecosystem service supply decreased sharply with the severity of future climate change. This finding highlights that forest management could be severely stymied in the future if climate change continues to proceed at its current rate. An improved quantitative understanding of the drivers of future ecosystem service supply is needed to more effectively combine targeted management efforts and natural ecosystem dynamics towards sustaining the benefits society derives from forests in a rapidly changing world.

Keywords

Mountain forests; Silviculture; Climate change impacts; Erosion protection; Carbon storage; Water regulation; iLand; Natural disturbances; LTER

1 Introduction

Forest ecosystems have a high capacity to regulate natural processes. They constitute the largest terrestrial carbon (C) storage, and currently take up a substantial share of the anthropogenic C emissions to the atmosphere (Pan et al., 2011). Potential forest C stocks are considerably higher than current C stocks in many parts of the world (Erb et al., 2018), underlining the strong potential of forests to mitigate climate change in the coming decades (Griscom et al., 2017). In addition to global climate regulation, forest ecosystems are also central elements of the local water cycle. Due to their ability to intercept water in the canopy and free up soil water storage via root water uptake forests act as buffers between precipitation and runoff. This buffering effect is particularly relevant in the context of local flood risk following extreme precipitation events. Several studies show that the degree of forest canopy closure is a strong determinant of this risk (Bradshaw et al., 2007; Moos et al., 2018). Furthermore, forests protect the soil from water and wind erosion, and thus effectively regulate soil losses from ecosystems (Altieri et al., 2018; Lü et al., 2012; Panagos et al., 2015). This is a particularly important role of forests given the long time scales of soil formation. In summary, forests contribute substantially to human well-being by providing regulating services to society (MA, 2005).

The regulating services provided by forests are of particular relevance in mountainous areas (Forest Europe, 2015). These areas are characterized by strong topographic gradients and high relief energy, which steeply increase the propensity for soil loss through erosion (Panagos et al., 2015) as well as gravitational processes such as rockfall, avalanches and snow gliding (Leitinger et al., 2018; Rammer et al., 2015). Furthermore, mountain topography often facilitates heavy local precipitation events and thunderstorms, and human infrastructure is often restricted to flood-prone river valley bottoms. As a consequence, the green infrastructure provided by forests is particularly relevant in mountainous countries; in Austria, for instance, 30.1% of the forest area is primarily designated to protect humans against natural hazards or to prevent soil erosion (BMLFUW, 2015). Due to their importance in buffering humans from harsh mountain environments, mountain areas frequently have a substantially higher forest share than low elevation areas (EEA, 2010). They constitute

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regional hotspots of forest C storage (Nabuurs et al., 2008), and are estimated to contain 11% of current global biomass stocks (Erb et al., 2018). In addition to providing regulating services to local communities, mountain forests are thus also relevant for the global climate system.

The continuous supply of regulating ecosystem services from forests is challenged by the increasingly changing environmental conditions. Climate warming can, for instance, lead to a considerable decrease in the ecosystem services provided by mountain forest ecosystems (Elkin et al., 2013; Seidl et al., 2011a). The mountain forests of the Alps are disproportionally exposed to warming temperatures (Auer et al., 2007), and further changes in the climate system could fundamentally alter their composition and structure, with significant negative impacts on the regulating services they provide (Maroschek et al., 2015; Obojes et al., 2018; Thom et al., 2017b). Furthermore, future conditions could substantially reduce the temporal stability of ecosystem service provisioning (Albrich et al., 2018), e.g. due to increasing natural disturbances such as strong winds or bark beetle outbreaks (Seidl et al., 2017a). While mountain forests develop slowly over decades to centuries, disturbances cause a rapid (hours to few years) decrease in canopy cover and live tree biomass (White and Jentsch, 2001). This, in turn, has largely negative effects on ecosystem service supply in general (Thom and Seidl, 2016), and on regulating ecosystem services in particular (Badoux et al., 2006; Kurz et al., 2008; Litschert et al., 2014; Simard and Lajeunesse, 2015).

Managing mountain forests for the supply of regulating services aims at maintaining a relatively continuous forest cover while enhancing resistance and resilience to disturbances (Brang et al., 2006; Dorren et al., 2004). The state-of-the-art silvicultural approach in the Alps consists of small, irregular patch cuts for regenerating the forest and maintaining a high level of forest canopy cover in space and time (Cordonnier et al., 2008; Streit et al., 2009). However, management is complicated by steep terrain and low accessibility, which requires highly specialized harvesting technologies (e.g., skyline systems) and results in high management costs (Jandl et al., 2018). Furthermore, in contrast to many provisioning ecosystem services (e.g., timber production) also unmanaged forests provide regulating services (Castro et al., 2015; Irauschek et al., 2017; Langner et al., 2017; Mina et al., 2017). The added value of costly management interventions is thus not always clear. Furthermore, given the strong expected climate change effects, it remains uncertain whether management will be able to significantly modulate the future trajectories of mountain forest development, or whether the management effect will be superseded by a much stronger climate and disturbance effect (Ammer et al., 2018). It is thus important to quantify the effect of management on regulating services relative to the effects of changes in the climate and disturbance regimes. In other words: How much leverage does forest management have, and would no management be equally effective in providing regulating services in mountain forests?

Here, our objective was to assess the relative importance of management, climate, and natural disturbances on the future supply of regulating ecosystem services. Focusing on the services climate regulation, water regulation, and erosion regulation our specific objectives were (i) to quantify future regulating service supply in a mountain forest landscape in

Austria, (ii) to determine the relative influence of management, climate change, and natural disturbances on the future variation in the supply of regulating services, and (iii) to assess how the management effect is modulated by site conditions and land-use legacies, in order to identify priority areas for ecosystem management. We hypothesized that climate change has a stronger influence on regulating services than management (Albrich et al., 2018), and that management is more influential than natural disturbances (Thom et al., 2018). Furthermore, we expected water regulation to be more strongly climate driven than erosion regulation and climate regulation, as canopy and soil water storage show strong saturating effects (Waring and Running, 2007). Finally, we hypothesized that climate is a more important driver of future ecosystem service supply close to the timberline (i.e., in strongly cold-limited environments), and that management is a more important driver under better growing conditions in lower elevation ranges. Likewise, we hypothesized that past land-use legacies reduce the future leverage of management.

2 Methods and materials

2.1 Study area

We here focused on the forest ecosystems of the Stubai valley, located in the province of Tyrol in western Austria. The landscape is situated in the western subcontinental inner Alps (ecoregion 1.2 according to Kilian et al. (1994)), and covers a total area of 6456 ha with a stockable forest area of 4811 ha. The Stubai valley is in many ways representative for the mountain forest landscapes of the Eastern Alps (Pecher et al., 2013; Zimmermann et al., 2010): With the valley bottom at ~900 m asl and the current timberline at approximately 2000 m asl (the highest mountain peaks surrounding the valley are > 3000 m asl) the landscape is characterized by steep terrain and strong ecological gradients (Fig. 1). Climate conditions are strongly determined by these topographic gradients, with mean annual temperature (1961–2010) decreasing with elevation from 6.8 to 1.1 °C, and mean annual precipitation sum increasing from 850 to 1087 mm over the same elevation gradient. The bedrock is predominately crystalline, with dominant soil types being Cambisols and Podzols (Hotter et al., 2013). The natural vegetation in the montane elevation belt (i.e., areas below ~1600 m asl) consists of Norway spruce (*Picea abies* (L.) Karst.) forests, while in the subalpine elevation belt the dominance of Norway spruce recedes, with Swiss stone pine (*Pinus cembra* L.) and European larch (*Larix decidua* Mill.) forming the timberline (Hotter et al., 2013). While montane forests form closed canopies, subalpine forests are naturally open, with trees clustered in favorable micro-sites. The current tree species composition does not differ strongly from the natural vegetation. Current forest structure, however, is substantially influenced by past land-use. In the montane elevation belt, forests have been used to provide wood for fuel and construction materials for several centuries. In the subalpine elevation belt, substantial parts of the landscape have been used as high pastures for livestock in the past, a land-use practice that has ceased in importance over the last century (Niedertscheider et al., 2017; Tasser et al., 2017). Today, these areas still have lower canopy cover (Fig. 1), and are characterized by a small number of old European larch trees (which were kept to provide shelter for the livestock) and a regenerating cohort of Norway spruce (and to a lesser degree Swiss stone pine). The historic natural disturbance regime of the area consists of infrequent wind storms, as well as avalanches in local avalanche tracks.

Biotic disturbances such as bark beetles did not play a major role historically, but have been gaining importance in recent years due to climate warming.

2.2 Simulation model

We quantitatively studied future forest development under different climate, management, and disturbance scenarios as well as the resulting changes in regulating service supply using the individual-based forest landscape and disturbance model iLand (Seidl et al., 2012a). iLand is a process-based model of forest landscape dynamics operating at the grain of individual trees. It is a spatially explicit model, simulating the local interactions between individual trees as well as the landscape-scale spread of disturbances and tree seeds. Primary production is modeled using a modified light-use efficiency approach (Landsberg and Waring, 1997). Environmental limitations to light use are considered at daily time step, with vegetation structure updated annually in the simulation. C allocation within a tree is based on a functional balance approach informed by allometric ratios between tree components (Duursma et al., 2007). Trees adapt dynamically to their environment, e.g. by changing their allocation priorities from height growth to diameter growth when being released from competitors (Seidl et al., 2012a). Single tree mortality is computed based on the C balance of an individual, with mortality probability increasing with C starvation. In addition, different life history strategies of trees are considered via an increasing mortality probability as trees approach their species-specific maximum age and/or maximum size. Regeneration is simulated at a grain of 2 m cells. The presence of seeds, light availability, and environmental filters determine the establishment success of trees.

iLand simulates a closed C cycle by accounting for C in live and dead organic material as well as in soil organic matter (Seidl et al., 2012b; Thom et al., 2017b). The water cycle accounts for water interception in the canopy, snow water storage and melting, water storage in the soil, evaporation from soil and leaves, transpiration of trees (based on the Penman-Monteith equation), as well as runoff. iLand also includes a detailed, agent-based model of forest management (Rammer and Seidl, 2015), allowing the implementation of a wide variety of realistic silvicultural strategies in the simulation. The model was extensively tested in forest ecosystems in Central Europe (Seidl et al., 2017b; Thom et al., 2017a), and was previously applied to simulate forest dynamics (Thom et al., 2017c), forest management alternatives (Seidl et al., 2018), and the provisioning of a range of ecosystem services (Albrich et al., 2018; Thom et al., 2017b) in European mountain forest ecosystems. However, the model was not previously applied at the Stubai valley landscape, which is why we conducted extensive model tests against independent data prior to our analyses (see Supplementary Material S1).

The model was initialized based on data describing the current vegetation structure and composition. Inventory data were available from local forest authorities for 839 angle count sample plots, distributed systematically throughout the landscape on a 100 m raster. These data were combined with information from wall-to-wall forest type mapping (Hotter et al., 2013) and a canopy height model derived from LiDAR for determining the current forest structure and composition in each of the 3031 forest stands (mean stand size: 1.61 ha). The model was subsequently initialized via a legacy spin-up procedure (Thom

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et al., 2018), which ensures that the initialized stand corresponds to the observational data (thus preserving past management legacies throughout the spin-up) while producing stand conditions that are consistent with the model-internal logic (e.g., with regard to the positioning and arrangement of individual trees). The average initial basal area on the landscape was 43.1 m^2ha^{-1}, with Norway spruce contributing 91.3%, and European larch and Swiss stone pine 5.2% and 2.8%, respectively (see Supplementary Material S2 for details). Soil data for the simulations were derived from combining local forest type mapping (Hotter et al., 2013) with quantitative information derived from the Austrian Forest Soil Survey (Seidl et al., 2009) for the parameters effective soil depth, soil physical properties (sand, silt and clay content) and plant-available nitrogen (as an indicator of soil fertility).

2.3 Climate

An important prerequisite for the faithful representation of forest dynamics at Stubai valley in simulations is the characterization of the high topographically-mediated climate variability throughout the landscape. This was achieved by developing a downscaled climatology at 100 m horizontal resolution for the period 1961–2015 from nearby weather station data and gridded climate products (see Supplementary Material S3). Results were evaluated against *in situ* climate observations from an elevational transect across the central Stubai valley. The climate variables considered were minimum and maximum temperature, precipitation, global radiation, vapor pressure deficit, and maximum gust wind speed at daily temporal resolution. A stable 200 year climate record representing historic climate was derived by randomly drawing from the years 1961–2000 with replacement.

Climate change was represented via four alternative future climate trajectories, derived from different GCM-RCM combinations and RCPs that were statistically downscaled to the study area. From an initial screening of 26 future climate trajectories (i.e., 13 GCM-RCM combinations for the RCPs 4.5 and 8.5) we chose (1) a moderate climate scenario, corresponding to a temperature increase of +2.6 °C in 2081–2100 relative to historic climate and no significant changes in precipitation (EC-EARTH and KNMI-RACMO22E under RCP4.5), (2) a warm scenario (EC-EARTH and KNMI-RACMO22E under RCP8.5), corresponding to a temperature increase of +4.7 °C, also with no significant changes in precipitation, (3) a warm and wet scenario (IPSL-CM5A-MR and IPSL-INERIS-WRF331F under RCP8.5) representing an increase in temperature and precipitation by +4.6 °C and +6.2%, respectively, and (4) a hot and dry scenario (HadGEM2-ES and CLMcom-CCLM4-8-17 under RCP8.5) with a temperature increase of +6.3 °C and a precipitation decrease of –18.3%. In all scenarios, climate change progressed transiently throughout the 21st century, and was assumed to stabilize at the level of 2080–2100 during the 22nd century (years sampled with replacement).

2.4 Management

We simulated a detailed rendering of mountain forest management based on the current management recommendations of the local forest authority (Hotter et al., 2013). Specifically, the management system is a slit cut system (Streit et al., 2009), in which small, irregular openings (~550 m^2 in size) along skyline tracks (oriented roughly at a 90° angle

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to the direction of the slope) are used to regenerate the forest (see Supplementary Material S4). In an approximate interval of 40 years the area adjacent to previous skyline tracks is treated, resulting in a hypothetical rotation period of between 120 and 160 years (dependent on stand size). Target tree species follow the potential natural vegetation under current environmental conditions (Hotter et al., 2013; Kilian et al., 1994) and thus correspond to the current tree species composition. Overall, the system aims to generate a fine-grained mosaic of forest development stages on the landscape. It has been found to be successful in regenerating mountain forests of the Alps, while providing high levels of regulating services in previous analyses (Irauschek et al., 2017; Streit et al., 2009). The specific rendering of the management regime in the simulation varied with site type, with gap sizes as well as the share of European larch and Swiss stone pine increasing with elevation. In line with the Austrian Forest Act trees killed by wind or bark beetles were salvage harvested in the year of mortality (assumed detection probability in the simulation: 90%).

2.5 Disturbances

We here considered the two most important natural disturbance agents in the mountain forests of the Alps, wind and bark beetles (Kulakowski et al., 2017; Thom et al., 2013). Both disturbance agents as well as their interactions and responses to climate change were dynamically simulated in iLand. Wind disturbances are driven by maximum gust wind speeds in iLand (here derived from climate models), and are modulated by soil frost (increasing anchorage) as well as the structure and composition of the forest landscape (Seidl et al., 2014). The critical windspeeds for windthrow and wind breakage are calculated at the level of individual trees, accounting for the effects of upwind gap size and local sheltering by neighboring trees. Stand structure is dynamically updated during an individual wind event, with downed or broken trees creating new wind-exposed edges (Seidl et al., 2014). Downed and broken Norway spruce trees also provide breeding material for the European spruce bark beetle (*Ips typographus* L.) (henceforth in short referred to as bark beetle). The development of bark beetles is simulated using a phenology-based approach in iLand, considering the possibility of multivoltinism and sister broods (Seidl and Rammer, 2017). Beetles disperse spatially explicitly in the landscape and actively search for suitable host trees within their perception range. A trees' capacity to defend against an attack from bark beetles depends on its non-structural carbohydrate reserves in iLand, and is thus reduced if trees experience drought stress. Both wind and bark beetle modules were evaluated previously, indicating that iLand is able to reproduce expected spatio-temporal disturbance patterns in the mountain forests of the Alps (Seidl and Rammer, 2017; Thom et al., 2018).

2.6 Analyses

A main objective of our study was to quantify the relative importance of management, climate change, and natural disturbances on the future variation of regulating ecosystem services. To that end, we conducted a factorial simulation experiment varying these three factors over two levels per factor. Specifically, the three factors were management (levels: management, no management), climate change (levels: future climate, historic climate), and natural disturbances (levels: natural disturbances simulated, natural disturbances not simulated). Simulations for each combination of factors were run over 200 years. To account

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for the stochasticity of the employed disturbance modules each simulation was replicated 20 times.

We analyzed indicators of three regulating services of mountain forests, i.e. climate regulation, water regulation, and erosion regulation. Each indicator was derived from two sub-indicators to increase the robustness of the assessment. The indicators used were total ecosystem carbon as indicator of climate regulation (subindicators live tree carbon and carbon in soil and detrital matter), total ecosystem water storage potential as indicator of water regulation (subindicators canopy water storage potential and soil water storage potential), and effective canopy cover as indicator of erosion regulation (subindicators canopy cover and mean tree diameter). Given that biophysical effects of forests on climate via changes in albedo and latent heat flux are of only moderate importance in the temperate forests of Central Europe (Thom et al., 2017b) we chose total ecosystem C storage as indicator of climate regulation (Smith et al., 2014). Total ecosystem C storage was derived as the sum of the sub-indicators live tree C and C stored in deadwood, litter, and soil. Higher values of total ecosystem C storage (reported as the mean C density in Mg C ha^{-1}) indicate an increasing climate regulation function of the forest landscape.

Water regulation was quantified via total ecosystem water storage potential. It describes the buffering capacity of the ecosystem towards heavy rain events, and consists of canopy water storage and soil water storage. Canopy water storage potential was calculated as the amount of rain that the canopy can intercept, while soil water storage potential denotes the amount of additional water that the soil can hold before runoff occurs. Soil water storage potential thus includes the effect of vegetation water uptake and use via transpiration (calculated using the Penman-Monteith equation (Waring and Running, 2007)). Both canopy and soil water storage potential were calculated on a daily basis in iLand, by subtracting the current level of water stored in the canopy and soil from the maximum amount of water that could be retained in these pools. Subsequently, the daily values were averaged over the year to derive the average daily buffering capacity of the system against heavy rain (measured in mmd^{-1}), with higher values indicating an increasing regulating service supply.

Erosion regulation was quantified via forest structure, assuming that soil loss is minimized if the soil is sheltered by a closed forest canopy of mature trees. Specifically, we followed the guidelines of Frehner et al. (2005) in defining the effective canopy cover for protection against soil loss as the canopy cover of all trees in pole-stage stands and bigger. As threshold for pole-stage stands we used a mean tree diameter of 10 cm. A sensitivity analysis of the effect of this threshold value is presented in Supplementary Material S5. The two sub-indicator used to describe the regulation of soil loss were canopy cover and mean tree diameter. Higher levels of effective canopy cover (measured in percent of canopy cover of all forests with a mean diameter ≥10 cm) indicate an improved protection against soil loss. All ecosystem service indicators were directly derived from iLand output, and were analyzed in simulation years 50, 100, 150, and 200, in order to control for effects of temporal autocorrelation.

To address our first objective (i.e., quantifying future regulating service supply) we report simulated indicator values for the different levels of our factorial experiment. For our

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second objective (i.e., determining the relative influences of management, climate change, and natural disturbances on the future variation in the supply of regulating services) we followed the approach of Nishina et al. (2015) and partitioned the simulated variation in landscape-scale service supply using analyses of variance. Specifically, the relative influence of the three factors of our factorial design was derived by relating their respective sum of squares (SS) to the total SS (SS_{Total}), calculated following Eq. (1):

$$SS_{Total} = SS_{Mgmt} + SS_{CC} + SS_{Dist} + SS_{CC \times Dist} + SS_{Residual} \quad (1)$$

In addition to the main factors management (SS_{Mgmt}), climate change (SS_{CC}), and natural disturbances (SS_{Dist}) we also considered the interaction between climate change and disturbances ($SS_{CC \times Dist}$), as we expected natural disturbances to be climate-sensitive (Seidl et al., 2017a). How strong the overall variation in simulated regulating services is driven by these three factors can be gauged by the residual sum of squares ($SS_{Residual}$), with lower $SS_{Residual}$ indicating an overall higher influence of management, climate, and disturbances on future ecosystem service supply in the simulations. Eq. (1) was applied to all simulated factor combinations and replicates after averaging the data over all analyzed time points and grid cells. In order to retain a balanced design in the analysis of our factorial experiment and quantify the effect of different climate futures, analyses were conducted separately for each of the four climate change scenarios described above.

To address our third objective (i.e., assessing how the management influence is modulated by site conditions and land-use legacies) we replicated the above described variance partitioning approach at the level of regular 100 m grid cells for the entire landscape. The thus derived local effect of management on the overall variation in ecosystem service supply was first investigated visually using maps. Subsequently, the management leverage was related to indicators of topography (i.e., elevation, aspect) and land-use legacies (i.e., canopy cover and mean tree diameter at breast height in the initial year of the analysis, both being inversely related to past land-use intensity) to elucidate the influence of these factors on the effectiveness of management to influence the supply of regulating ecosystem services. The strength of influence of site and legacy variables was assessed using Spearmans correlation coefficient (r_S). All analyses were conducted using R (R Development Core Team, 2017), specifically employing the packages dplyr (Wickham et al., 2017) and raster (Hijmans, 2017). The simulation results were stored in an online repository (Seidl et al., 2019).

3 Results

3.1 Future supply of regulating ecosystem services

The future supply of all three regulating services – climate regulation, water regulation, and erosion regulation – was sensitive to climate change. Climate regulation increased considerably under warmer and wetter future conditions (+ 9.9% relative to a continuation of historic conditions, based on simulations including management and natural disturbances), but sharply declined under the hot and dry climate scenario (–22.2%, Table 1). This response of total ecosystem C storage to climate was mainly driven by strong changes in live tree C

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stocks on the landscape, which decreased by 38.3% under the hot and dry climate scenario (resulting from decreased tree growth and increased mortality due to water limitation).

Conversely, water regulation was highest in the hot and dry climate scenario. Here, the increasing plant water demand in combination with decreasing precipitation levels strongly increased the soil water storage potential of the landscape (+ 64.0%). This effect overcompensated a decreasing canopy water storage potential (–7.0%), and resulted in an overall increase in water regulation (+ 30.1%). The total ecosystem water storage potential was moderately higher than under a continuation of historic climate also in all other simulated climate change scenarios (Table 1).

Of all the ecosystem service indicators studied, erosion regulation responded least strongly to climate change. This was the result of diverging climate effects on the two underlying sub-indicators, with canopy cover generally increasing under climate change (due to longer growing seasons and increased tree growth), and mean tree diameters moderately decreasing in most scenarios (as a result of increasing disturbances under climate change). Overall, the effective canopy cover protecting against soil loss was between +3.0% and +16.5% higher under climate change compared to historic climate.

Both management and natural disturbances had an overall negative effect on the climate regulation provided by the landscape, relative to unmanaged and undisturbed conditions (Fig. 2). Effects of management and disturbance were of similar magnitude, reducing total ecosystem C storage by on average −44.5 Mg C ha^{-1} and −43.1 Mg C ha^{-1}, respectively (mean over all analyzed climate scenarios). Forest management was moderately able to dampen the negative effect of natural disturbances, with a 16% reduced C loss from disturbances in managed vs. unmanaged simulations. This dampening effect was, however, largely compensated by an increased C sink of the tree cohorts regenerating after disturbances. Also erosion regulation was highest in unmanaged and undisturbed simulations (Fig. 2). Both management and disturbances reduced the effective canopy cover by 4.0 percentage points, respectively. In contrast, the effect of management and disturbances on ecosystem water storage potential was weak but positive (up to +0.24 mm d^{-1}), with increasing water use of younger forests overcompensating a reduced canopy water storage potential.

3.2 Drivers of future ecosystem service supply

Across all three regulating ecosystem services, the influence of management on future service supply was lower than the influence of climate. Management on average explained 29.2% (range 0.3–63.1%) of the variation in regulating ecosystem service supply, while the main effect of climate accounted for 47.3% (0.2–98.5%). The management effect was strongest for climate regulation, and least pronounced for water regulation. For both of these services, the management effect decreased sharply with increasing severity of climate change, i.e. being highest under moderate climate change and lowest in the hot and dry climate scenario (Fig. 3). Conversely, the management effect on erosion regulation was strongest in the hot and dry scenario. The main disturbance effect was lower than the effect of management across all scenarios and ecosystem services (11.1%, range 0.2–29.0%). However, if the amplifying interactions from climate change are considered, the influence of future disturbances on ecosystem service supply increased considerably (17.8%, range 0.4–47.0%).

3.3 Modulating effects of site conditions and land-use legacy

The effect of management generally decreased with elevation for all three regulating ecosystem services investigated (r_S between −0.22 and −0.36). This decrease was nonlinear, and was particularly pronounced for elevations > 1500 m asl (Fig. 4). The leverage of management was also strongly related to legacies of past land-use. Across all three ecosystem services, the effect of management over the 200 year study period increased with the initial canopy cover of a stand (r_S between + 0.16 and +0.38). In areas which experienced a strong influence of livestock grazing in the past, and which are still characterized by a fairly open canopy today, the influence of management on regulating services supply over the next 200 years is considerably reduced. In considering the effects of site conditions and land-use legacies it is important to note that stands that were strongly grazed in the past are frequently also situated in the subalpine zone, i.e. site effects and land-use legacy influences are not independent (r_S of –0.47). The aspect of a site did not have a strong systematic influence on the management effect. Also, the initial development stage of a stand (here described by its mean tree diameter) and thus its harvesting history was only moderately related to the management effect on regulating services (r_S between + 0.14 and +0.24).

4 Discussion and conclusions

Forest ecosystems make an important contribution to human well-being via regulating the environment (MA, 2005). In mountainous areas, regulating services are frequently the economically most important category of ecosystem services (Häyhä et al., 2015). However, regulating service supply will likely change in the future, as forest ecosystems respond to climate change (Lindner et al., 2010). Our results indicate that both positive and negative climate change impacts are possible, depending on the severity of the future changes in the climate system and the ecosystem service considered (Elkin et al., 2013; Seidl et al., 2011a). Water and erosion regulation, for instance, benefited from climate change in our study landscape, regardless of the scenario considered. However, our findings of positive climate change effects strongly depend on the context of our study landscape, which – in the past – was strongly limited by cold temperatures and short vegetation periods (Jolly et al., 2005; Oberhuber, 2004). Moderate climate change relaxes these limitations and leads to an overall increase in tree growth and canopy closure (Kulakowski et al., 2011; Pretzsch et al., 2014), with positive effects on the supply of regulating ecosystem services. However, if water becomes increasingly limiting, the effects of climate change might become negative (Allen et al., 2015; Pichler and Oberhuber, 2007), as is the case for climate regulation in the hot and dry climate scenario studied here. In this regard it is important to note that projections of local changes in precipitation in mountainous areas still remain uncertain, yet are crucial for determining climate change impacts on forest ecosystems. The same holds true for projections of extreme wind events, which are important triggers of the disturbance regime in our study region. Consequently, the uncertainty in these important drivers also imposes uncertainty on our simulated future forest trajectories (Lindner et al., 2014).

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Here we showed that unmanaged forests are efficient in providing regulating ecosystem services (see also Irauschek et al., 2017; Langner et al., 2017; Mina et al., 2017). Both climate regulation and erosion regulation were higher in unmanaged systems compared to systems implementing current management recommendations, with only a weak positive management signal for water regulation (Fig. 2). This finding suggests that reducing management intensity or phasing out management entirely will not endanger the regulating services that mountain communities depend upon. As unmanaged forests are increasingly valued for their benefits in the context of biodiversity conservation (Paillet et al., 2010), we here show that increasing their share on the landscape will not necessarily lead to a reduction in important regulating ecosystem services. It is important to note, however, that many rural mountain communities not only depend on regulating ecosystem services but also generate a substantial part of their income and livelihood from managing natural resources (Häyhä et al., 2015). Not managing forests might thus negatively affect rural communities and result in the loss of other important ecosystem services such as the supply of timber and biomass for bioenergy.

Another important consideration pertains to the temporal scale of analysis: We studied forest development over 200 years, which is roughly 50% of the maximum life span of the tree species prevalent in the mountain forest ecosystems studied here. We thus cannot rule out that a continuation of unmanaged forest development beyond our study horizon would eventually lead to the emergence of terminal stages of forest development (i.e., low canopy closure, big but few live trees) over large parts of the landscape, with potential negative implications for some regulating services.

While forest management did have an effect on service provisioning, its influence was considerably smaller than the effect of climate change. This finding is consistent with previous results of a strong climate effect on landscape development in general (Schumacher and Bugmann, 2006; Tasser et al., 2017), and on regulating ecosystem services in particular (Albrich et al., 2018). It also supports our hypothesis of only moderate management leverage regarding these services. It has to be noted, however, that our finding of a comparatively low effect of management relative to climate change is contingent on the specific management regime considered here. Large-scale clear-cutting, for instance, would very likely have resulted in a higher relative effect of management on the overall variation in service provisioning than our small-scale, gap-oriented mountain forest management. As large-scale clearcutting would have strong negative impacts on regulating ecosystem services (Frehner et al., 2005), and is prohibited in dedicated protection forests by the Austrian Forest Act, we consider its application in the context of our study landscape unrealistic. We note, however, that changes in future land-use policy and societal preferences for ecosystem services exert considerable uncertainties on our simulation of future forest development (see also Seidl and Lexer, 2013). While the management regime studied here mimics current management recommendations in a highly realistic manner, it was applied uniformly across all simulated climate scenarios. This approach ensured that the factors in our factorial analysis are indeed independent, but also disregards potential adaptive measures of managers (Yousefpour et al., 2017), which are increasingly likely as climate change impacts worsen (Blennow et al., 2012; Seidl et al., 2016). A change in tree species composition towards more mixed forests with a higher share of broadleaved trees is, for instance, often discussed as climate change adaptation strategy in these forest types (Hotter et al., 2013; Seidl et al., 2011b), but was not considered in the current simulations.

An important limitation of our study lies in the fact that not all potentially relevant regulating ecosystem services were considered. In addition to climate, water, and erosion regulation, for instance also the protection of society and its artifacts against avalanches and rockfall is an important regulating service in mountain forests of the Alps (Bebi et al., 2009; Rammer et al., 2015). Furthermore, the indicators considered here are only proxies for the respective services, and differ with regard to how closely they resemble the relevant underlying processes. Forest C cycling is modeled at a high level of detail in iLand, based on current process understanding of C uptake and release. In the context of our finding of decreasing C stocks with forest management we note, however, that the C stored in wood removals is not immediately released back into the atmosphere, but can be partially stored in long-lived wood products (Lippke et al., 2011). Also the water regulation indicator used here is based on highly detailed process-based modeling, simulating canopy water interception, throughfall, snow water storage, soil water storage, plant water uptake and transpiration, as well as runoff at daily time step. Issues not considered here but of importance particularly in mountain watersheds are, for instance, subsurface water routing (Tague et al., 2009). In contrast to the process-based climate and water regulation indicators, erosion regulation was quantified using a phenomenological approach largely based on expert knowledge (Frehner et al., 2005), yet widely applied throughout the Alps (Elkin et al., 2013; Maroschek et al., 2015; Mina et al., 2017). Future work should aim to incorporate a more process-based perspective of soil loss and erosion (Altieri et al., 2018; Barik et al., 2017), in order to strengthen the robustness of assessments particularly under no-analog future conditions.

Several important implications follow from our results. First, it is of paramount importance for ecosystem service supply in mountain forests to limit climate change to moderate levels (see also Elkin et al., 2013). Specifically, our analyses showed that while the management leverage is still considerable under moderate climate change, severe climate change will strongly supersede the effects of management on ecosystem service supply. Only under moderate levels of climate change the potential to proactively manage ecosystems for meeting societal demands is retained. Under more severe levels of climate change the impacts of climate change are strongly dominating ecosystem service supply, largely reducing management to reactively battling climate change impacts. Second, a prioritization of areas where considerable silvicultural leverage is available is advisable in ecosystem management. We found support for our hypothesis that management has a stronger influence on sites that are less constrained by the prevailing environmental conditions (here: especially the mid-elevation portions of the landscape). Also in line with our hypotheses, areas that are still recovering from past land-use have a lower potential to be influenced by future management. As also many other temperate forest ecosystems are currently recovering from past land use (Bebi et al., 2017; Duveneck and Thompson, 2019), these insights could be of broad importance for considerations of future forest management. In the specific context of our study landscape such spatially explicit information could be used to increase the efficiency of forest management (Seidl et al., 2018), given that mountain forest management is highly cost and labor intensive (Jandl et al., 2018). In doing so it is important to note that management decisions frequently create long-lasting legacies on the landscape

(Niedertscheider et al., 2017; Thom et al., 2018), which in turn influence the future ability to react to change. Ecosystem management should thus aim for an evidence-based combination of active interventions and natural ecosystem dynamics towards sustaining the regulating services forests provide to society also in a rapidly changing world.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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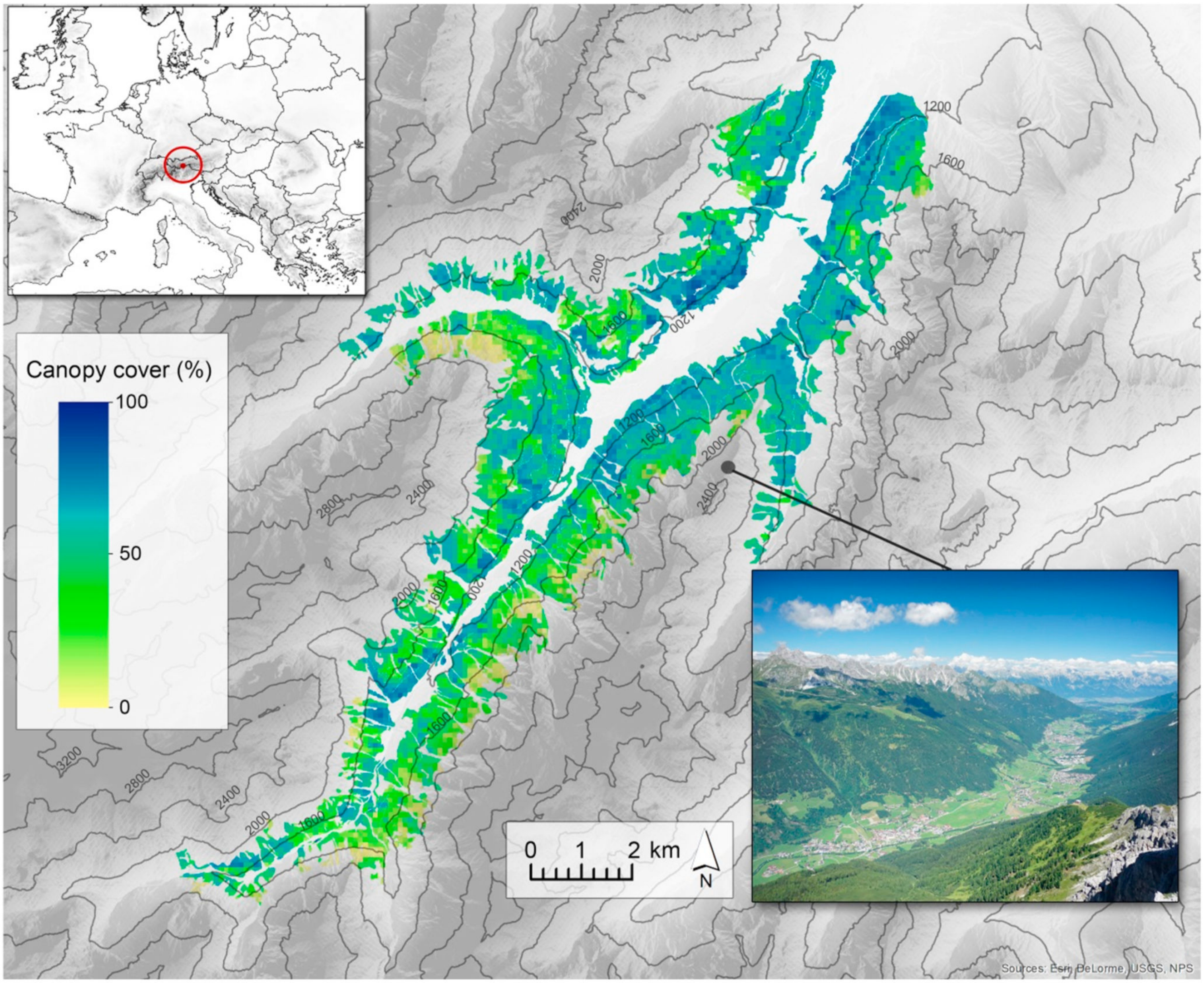

Fig. 1.

The study landscape in the Stubai valley, Tyrol, Austria. The forest area studied is highlighted in color, indicating the variation in current forest canopy cover. The topography of the landscape is illustrated via 400 m isolines. The insert map gives the location of the landscape in Europe. The insert photo shows the northern portion of the valley as seen from the southern flank. Insert photo credit: Matthias Frank CC BY-SA 4.0. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

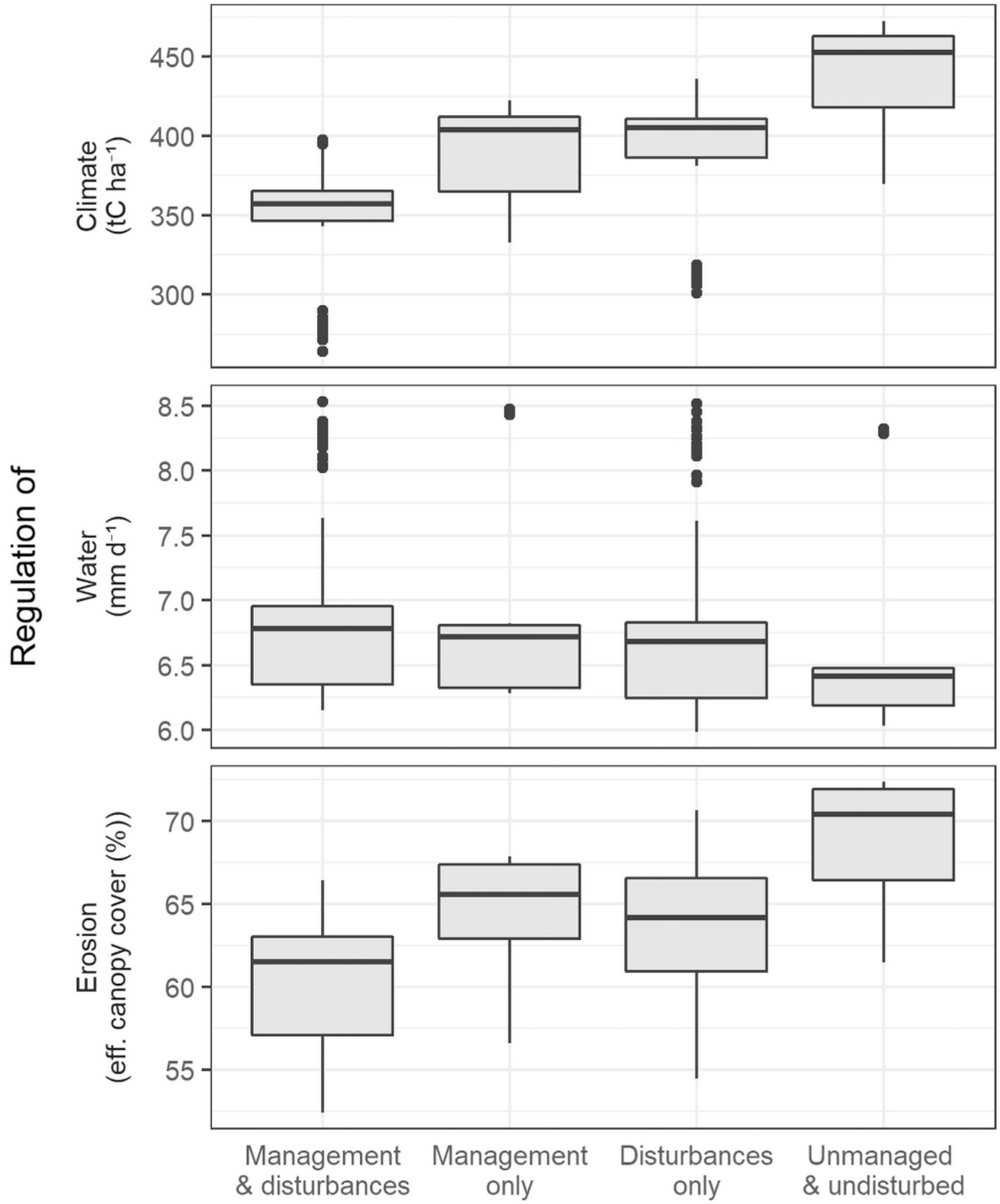

Fig. 2.
Management and disturbance effects on the supply of regulating ecosystem services. Effects are shown for all combinations of management and disturbances. Values are averages over the four studied time points, and comprise all five climate scenarios investigated (i.e., a continuation of historic climate and four scenarios of future climate change). Boxes indicate the interquartile range, with the bold horizontal line giving the median value. Whiskers extend to the largest and smallest values within 1.5 times the interquartile range, respectively. All larger and smaller values are indicated as points.

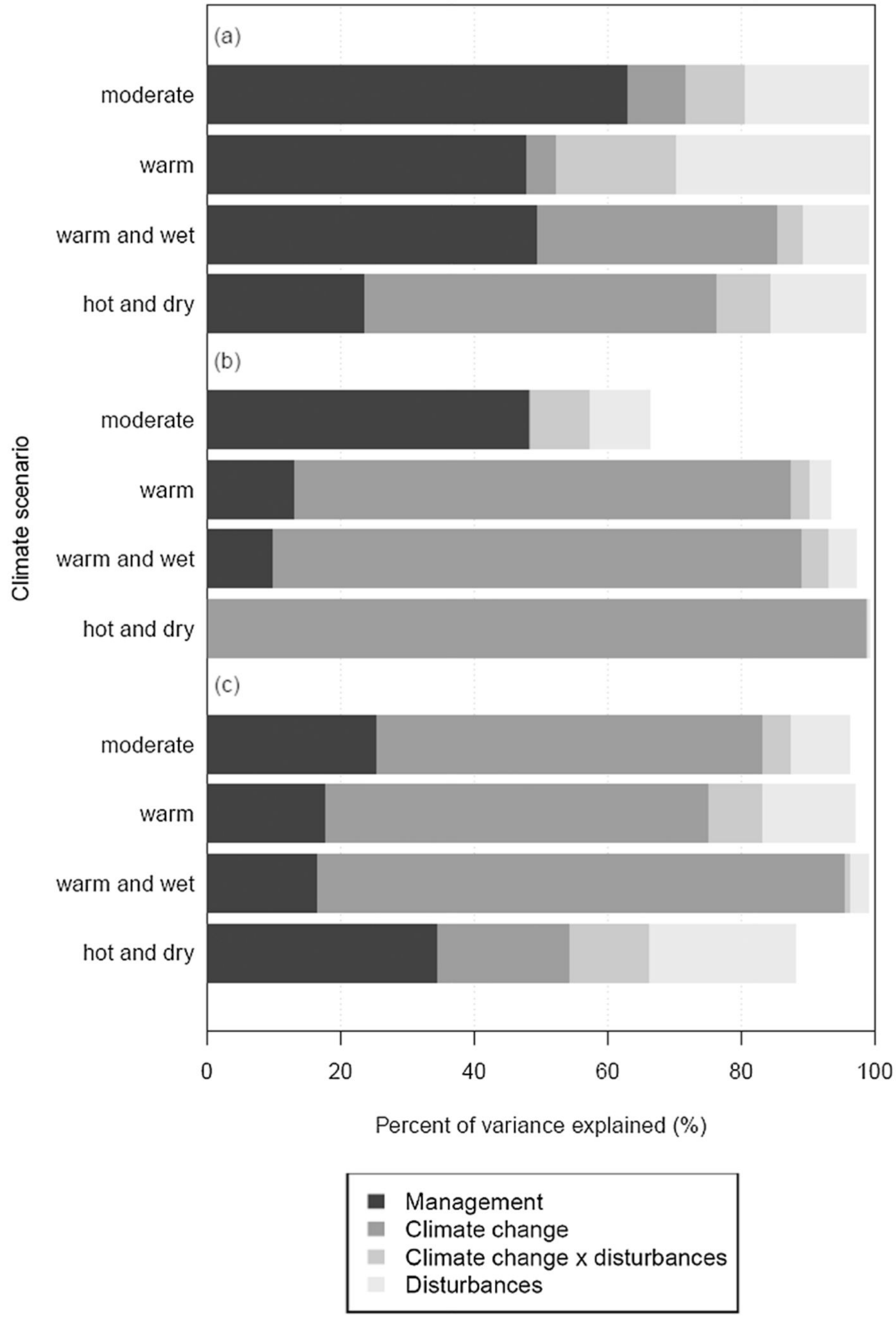

Fig. 3.

Drivers of future regulating ecosystem service supply for (a) climate regulation, (b) water regulation, and (c) erosion regulation. The importance of drivers is expressed as the percent of variance in ecosystem service supply explained by each factor in a factorial simulation experiment. Climate change × disturbances denotes the interaction effect between these two factors.

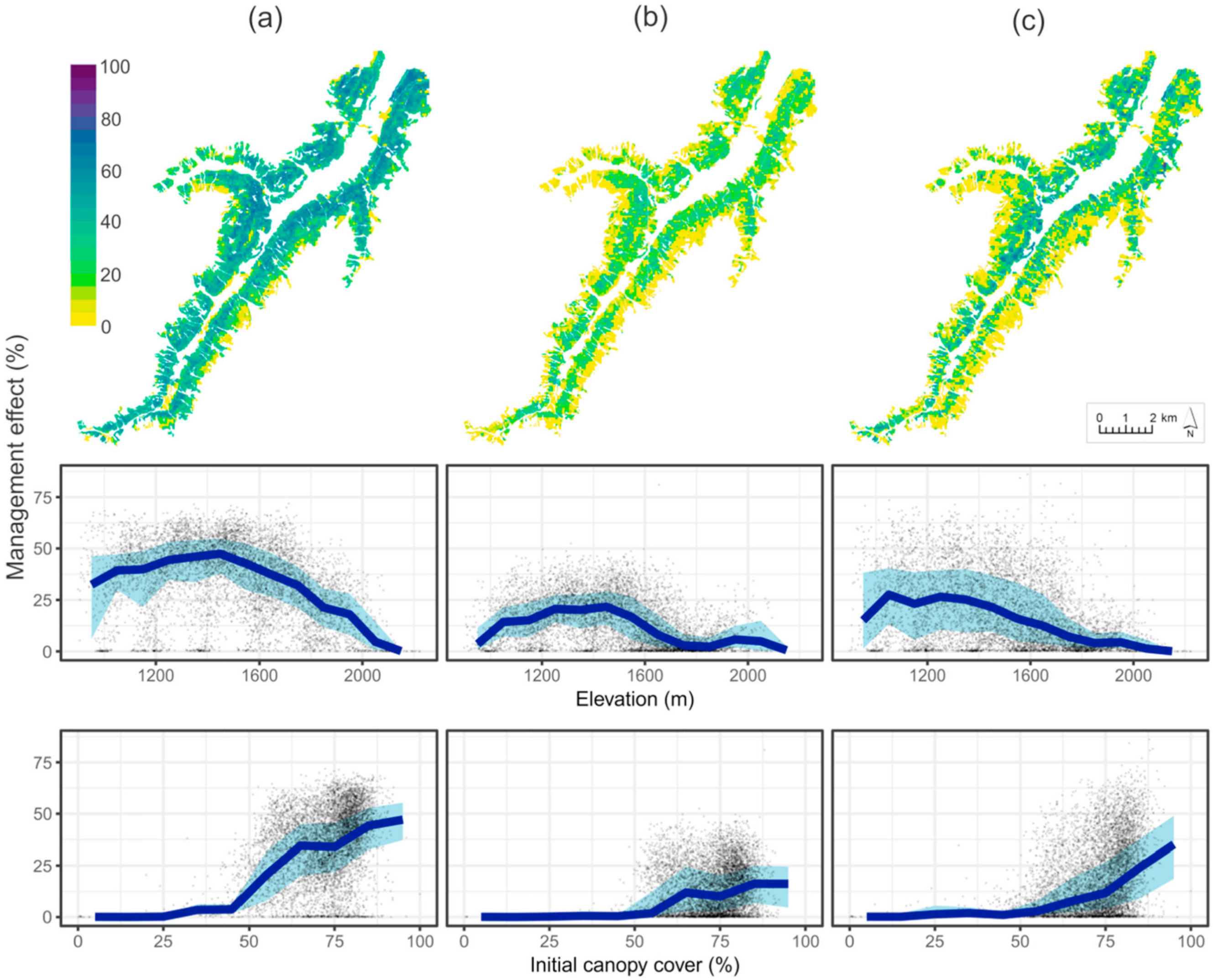

Fig. 4.

The effect of management on the supply of (a) climate regulation, (b) water regulation, and (c) erosion regulation, and its covariation with elevation (as an indicator of local site conditions) and initial canopy cover (as an indicator of land-use history). Shown is the mean over all four climate change scenarios, with the effect of management being described as the percent of variance in ecosystem service supply explained by management in an analysis of variance. Lines give the median value in 100 m elevation bands and 10% canopy cover classes, respectively, with ribbons indicating the interquartile range of the data.

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Table 1

The effect of different climate scenarios on the supply of regulating ecosystem services. Values are averaged over the 200 year simulation period, and the standard deviation over 20 replicates and four time points is given in parenthesis. Results pertain to landscape development implementing current management recommendations, with natural disturbances being dynamically simulated.

Ecosystem service	Indicator	Climate scenario				
		Historic	Moderate	Warm	Warm & wet	Hot & dry
Climate regulation	Total ecosystem carbon [$MgCha^{-1}$]	357.4 (9.7)	362.6 (21.6)	347.6 (12.8)	392.8 (14.0)	278.0 (20.8)
	Live tree carbon [$MgCha^{-1}$]	152.3 (4.7)	162.6 (19.3)	163.4 (15.2)	204.4 (21.1)	94.0 (17.8)
	Carbon in soil and detrital matter [$MgCha^{-1}$]	205.1 (6.6)	200.0 (5.0)	184.2 (8.6)	188.5 (10.5)	184.0 (7.1)
Water regulation	Total ecosystem water storage potential [mmd^{-1}]	6.31 (0.59)	6.37 (0.50)	6.79 (0.78)	6.94 (0.40)	8.21 (0.97)
	Canopy water storage potential [mmd^{-1}]	3.00 (0.06)	3.23 (0.18)	3.19 (0.13)	3.37 (0.10)	2.79 (0.18)
	Soil water storage potential [mmd^{-1}]	3.39 (0.60)	3.22 (0.35)	3.69 (0.78)	3.66 (0.46)	5.56 (0.95)
Erosion regulation	Effective canopy cover [%]	56.2 (2.6)	61.8 (6.3)	62.0 (5.2)	65.5 (4.3)	57.9 (7.4)
	Canopy cover [%]	56.4 (2.6)	61.9 (6.2)	62.1 (5.1)	65.6 (4.2)	58.2 (7.3)
	Mean tree diameter [cm]	25.2 (2.0)	24.9 (1.9)	24.8 (1.3)	28.3 (2.5)	18.2 (1.5)