The role of herbaceous vegetation in forest landscape dynamics

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The role of herbaceous vegetation in forest landscape dynamics

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Summary

Forest ecosystems play an integral role in the earth system (e.g., by regulating biogeochemical cycles) and provide a wide range of services to human societies. It is therefore of crucial importance to understand the effects of a changing climate and changing disturbance regimes on forest dynamics. To date, most studies of forest dynamics have focused on trees, thus neglecting the herbaceous understorey (e.g., grass, ferns, herbs) although an increasing number of empirical studies suggest that the interaction between herbs and trees can profoundly alter forest dynamics. In particular, competition for light and water by the herbaceous understorey has been shown to change the structure and composition of tree regeneration, and thus to delay and potentially even arrest forest succession. When ignoring this interaction, thresholds in ecosystem responses to changing climate and disturbance regimes may remain undetected. However, due to the restrictions of empirical studies little is known on the implications of overstorey-understorey interactions for forest dynamics at larger spatio-temporal scales.

Dynamic vegetation models (DVMs) have been developed to overcome this restriction and explore vegetation dynamics at large temporal scales (>100 years). Among the various types of DVMs, forest landscape models (FLMs) are specifically designed to investigate vegetation interactions under changing climate and disturbance regimes at large spatial scales (typically $10^3$ – $10^6$ ha). I used the process-based FLM LandClim to investigate the long-term effect of overstorey-understorey interactions on forest dynamics in central European landscapes, specifically focusing on (1) competition for light in mesic forest landscapes, (2) competition for water under present and future climate conditions in a drought-prone landscape, and (3) the potential of disturbances (browsing, windthrow, timber harvest) to promote delayed and arrested succession.

In Chapter I, I implemented an understorey component in the FLM LandClim, with a focus on competition for light as the main mode of interaction. Simulation results for two mesic landscapes in Central Europe (Feldberg in the Black Forest and Dischma valley in the central Alps) showed spatio-temporal patterns that were in line with trends reported in empirical studies from chronosequences and species elevation distributions. The presence of an herbaceous understorey had a strong impact on tree regeneration and forest growth during early succession, but a much smaller effect on the late-successional stage. Also, the strength of overstorey-understorey interactions varied considerably across the landscape, causing large delays in forest growth at low and mid-elevations. Furthermore, the understorey was found to act as a differential filter for tree establishment, inducing a shift towards more shade-tolerant species, which translated into altered overstorey composition for up to 200 years. I was thus able to upscale the effects of understorey competition that are evident from empirical studies at the plot level (i.e., a few square metres) and at the short time scale (<10 years), and provide support for the long-standing claim that herbaceous vegetation can alter successional trajectories also at large spatio-temporal scales.
In Chapter II, I extended the water balance model of LandClim to explore the long-term implications of competition for water between herbs, saplings and adult trees for forest structure and composition under present and future climate scenarios (RCP 4.5 and RCP 8.5). The new water balance model captured the main empirical patterns of the understorey contribution to stand evapotranspiration across a European gradient. When applied to the drought-prone study landscape Valais in southwestern Switzerland, the new version of LandClim produced changes in regeneration density and biomass as well as shifts in tree species that were consistent with empirical data and expected trends for the region. Under present climate, herbaceous understorey affected tree regeneration mainly at the most drought-prone landscape positions (i.e., south-facing, low-elevation slopes). Under future climate change, in particular under the RCP8.5 scenario, extreme drought events caused extensive overstorey mortality and induced a phase of intensive competition between trees and herbaceous vegetation. At the driest landscape positions, this led to the formation of an open, savannah-like vegetation. Overall, I demonstrated in this chapter that water competition by the herbaceous understorey can cause long-lasting legacy effects on forest structure and composition, and thus I conclude that DVMs that do not consider the herbaceous understorey are at risk of underestimating the impacts of severe drought events.

In Chapter III, I used this new LandClim version to systematically explore the effect of different disturbances on competition between herbaceous vegetation and trees across four study landscapes representing a trans-Alpine environmental gradient. Specifically, I investigated which abiotic, biotic and disturbance conditions are most important for causing arrested succession, and which time scale needs to be considered to differentiate between delayed and arrested succession. The results suggest that arrested succession as a stable herbaceous state is indeed possible in temperate forests, particularly when herbaceous competition and browsing jointly induce a strong establishment filter. Overall, abiotic conditions consistently influenced the probability of arrested succession, which became increasingly likely towards warmer, drier conditions. Furthermore, I was able to identify a time scale to distinguish between arrested and delayed succession: if a forested state (in terms of ≥ 10% canopy cover) is not reached within 100 years after a disturbance, there is a high likelihood of permanently arrested succession. This chapter thus provides an important step towards resolving the controversy about the existence of arrested succession in temperate forests, and clarifying its distinction from delayed succession.

In this thesis, I was able to demonstrate the importance of the often neglected herbaceous understorey by bridging the gap between the small-scale vegetation interaction between herbs and trees and its large-scale implication for forest landscape dynamics. Based on my results, I recommend considering herbaceous understorey in DVMs, particularly if they are applied in the context of (1) early successional dynamics, (2) impacts of climatic extreme events, particularly drought, (3) the long-term effect of browsing, and (4) effects of overstorey disturbances. Herbaceous vegetation is an integral component of forest ecosystems, and studies neglecting its influence are likely to overlook an essential vegetation interaction which can lead to drastically different forest responses to changing climate and disturbance regimes.
Zusammenfassung


Um Vegetationsdynamik über längere Zeiträume (> 100 Jahre) zu untersuchen, wurden Dynamische Vegetationsmodelle (DVM) entwickelt. Unter den verschiedenen DVM-Ansätzen sind insbesondere Waldlandschaftsmodelle dazu geeignet, Vegetationsinteraktionen unter verschiedenen Klimabedingungen und Störungsregimen auf grosser räumlicher Skala \(10^3-10^6\) ha zu untersuchen. Aus diesem Grund wurde in der vorliegenden Doktorarbeit das prozessbasierte Waldbauernschaftsmodell LandClim verwendet, um die langfristige Auswirkung von Interaktionen zwischen Baum- und Krautschicht auf die Waldbauernschaftsdynamik zu analysieren. Zentrale Aspekte der Untersuchung waren dabei (1) die Auswirkung der Konkurrenz um Licht auf die Dynamik mesischer Waldbauernschaften, (2) die Konkurrenz um Wasser und ihre Auswirkung auf trockenheitsbeeinflusste Wälder unter gegenwärtigem und zukünftigem Klima und (3) die Bedeutung von Störungsereignissen (Wildverbiss, Windwurf und Holzeinschlag) für die Interaktion zwischen Baum- und Krautschicht im Hinblick auf das Auftreten von „arrested succession“.

In Kapitel I wurde das Waldbauernschaftsmodell LandClim um eine Krautschicht-Komponente erweitert, welche mit Bäumen um Licht konkurriert. Modellergebnisse aus zwei mesischen Waldbauernschaften (Feldberg im Schwarzwald und Dischmatal in den Zentralalpen) wiesen gleiche Muster auf, wie sie in empirischen Chronosequenz-Studien und Vegetationserhebungen entlang von Höhengradienten gefunden worden waren. Die Auswirkung der Krautschicht auf die Baumverjüngung war während des frühen Sukzessionsstadiums am stärksten und nahm in späteren Sukzessionsstadien deutlich ab. Zudem zeigte sich, dass die Verzögerung der Wiederbewaldung stark von der jeweiligen
Höhenlage in der Landschaft abhing, und stärkste Effekte generell in tiefen bis mittleren Lagen auftraten. Die Ergebnisse zeigten zudem eine Artverschiebung zu schattentoleranteren Baumarten, welche die Waldzusammensetzung über einen Zeitraum von bis zu 200 Jahre hinweg prägte. Im vorliegenden Kapitel konnte daher aufgezeigt werden, dass die Unterwuchsvegetation von zentraler Bedeutung für die langfristige Walddynamik ist. Durch den vorliegenden Modellansatz wurde somit die Verbindung zwischen kleinskaligen empirischen Messungen und der Walddynamik auf grossen räumlichen und zeitlichen Skalen hergestellt.


General Introduction

Forest ecosystems provide a wide range of functions and services and are thus of central importance for the earth system (e.g., with respect to global biogeochemical cycles) and for human societies (e.g. production of wood, energy, fibre, as well as protection from natural hazards) (MEA, 2005; EEA, 2010). Forests are however facing an uncertain future with rapidly changing climate and disturbance regimes projected for the 21st century (IPCC, 2013, 2014). Understanding how forests respond to these driving forces is thus of fundamental importance and a core objective for environmental research (Bugmann, 2014). To date, most studies of long-term forest dynamics have focused solely on trees (Bugmann, 2001; Li et al., 2012). However, an increasing number of studies demonstrated that herbaceous vegetation can significantly interfere with tree regeneration and could thereby alter long-term forest dynamics (George and Bazzaz, 2003; Gilliam, 2007). This is a critical point since thresholds in ecosystem responses to changing climate and disturbance regimes may remain undetected or misinterpreted if essential vegetation interactions are ignored (Keane et al., 2015).

The role of herbaceous understorey in temperate forest ecosystems

Herbaceous vegetation is of outstanding importance for biodiversity, ecosystem structure and functioning in forests (Gilliam and Roberts, 2003). However, due to its small stature its ecological importance is frequently overlooked and widely neglected in studies of forest dynamics (George and Bazzaz, 2003; Keane et al., 2008). The herbaceous understorey (defined as vascular, predominantly non-woody species of less than 1 m height, Gilliam, 2007) contains on average more than 80% of plant diversity of temperate forests and provides habitat, food and shelter for a wide range of animals (Weisberg and Bugmann, 2003; Gilliam, 2007). Most studies of the herbaceous understorey have therefore focused on the response of herbaceous diversity to shifts in overstorey structure and composition (Hart and Chen, 2006; Gilliam, 2007; Bartels and Chen, 2013). Much less attention has been given to the reciprocal effects between trees and herbaceous vegetation, generally referred to as ‘overstorey-understorey interactions’ (Li et al., 2012). Overstorey trees determine the growing conditions for the herbaceous layer, by controlling the amount of sunlight that reaches the forest floor (Lieffers and Stadt, 1994; Gilliam, 2007). Herbaceous vegetation forms a sub-canopy stratum above the forest floor that further reduces light availability at the ground, and strongly draws upon soil resources (Balandier et al., 2006). Herbaceous plants can thereby impact tree establishment and have the potential to alter forest composition and succession in the long term (George and Bazzaz, 2003; Royo and Carson, 2006). It would thus be short-sighted to perceive the link between overstorey and understorey vegetation in a one-way ‘top-down’ direction only; rather, it constitutes an interaction where herbs also have a ‘bottom-up’ effect on succession trajectories of the tree overstorey.

Unfortunately, the magnitude of this ‘bottom-up’ effect is largely unknown. As reviewed by Li et al. (2012), only ≈ 6.5% of publications about plant interactions in forests address the
effect of understory on overstorey trees. A number of seminal experiments investigated the interference of herbaceous understory on tree regeneration (e.g., George and Bazzaz, 1999a, 1999b; Den Ouden, 2000) and provided compelling evidence that the herbaceous understory can strongly influence the emergence, growth and survival of tree seedlings by competing with them for above- and belowground resources. This led to the conclusion that the herb stratum represents an important ‘understorey filter’ for tree establishment (George and Bazzaz, 2003). The reduction of light availability is considered to be the primary influence of herbaceous vegetation on tree establishment (Horsley, 1993; Gilliam, 2007). At sites where water and nutrient availability constrain plant growth, the herbaceous understory can also compete intensively for belowground resources (e.g., Putz and Canham, 1992; Nambiar and Sands, 1993). Further interference mechanisms (e.g., allelopathy, mechanical inhibition) may also play a role under specific conditions, but their effect is more controversial (e.g., Priewasser, 2013), difficult to generalize and mostly considered to have a smaller impact than resource competition (Den Ouden, 2000; George and Bazzaz, 2003).

The impact of understory vegetation on tree regeneration can alter successional trajectories in terms of (1) delayed or (2) arrested succession, and (3) by changing tree species composition (Royo and Carson, 2006), as reviewed below. First, there is abundant evidence that understory vegetation can significantly delay forest succession by inhibiting tree establishment for years or decades until trees eventually emerge through a dense understory canopy (e.g., Lieffers et al., 1993; Balandier et al., 2006; del Rio, 2006). The higher seedling mortality and decreased growth can lead to stands with significantly lower stem densities that take a longer time to develop into a closed-canopy, mature forest (Balandier et al., 2006; Wagner et al., 2006). Among others, this has important consequences for mountain forests that provide protection from gravitational natural hazards such as avalanches or rockfall, where rapid forest re-growth after disturbance events is of critical importance (Frehner et al., 2005). Second, cases where tree regeneration was found to be entirely excluded for prolonged periods (e.g., Niering and Goodwin, 1974) have been suggested to represent arrested succession in a stable herbaceous state (Stromayer and Warren, 1997; Royo and Carson, 2006). However, it is unclear whether the long-term dominance of herbaceous vegetation actually represents a self-perpetuating alternative stable state, or whether additional processes such as continuous browsing or disturbances are required for its maintenance (Stromayer and Warren, 1997; Mallik, 2003; Royo and Carson, 2006). Solid empirical or experimental studies in this respect are limited due to the long time scales involved (Stromayer and Warren, 1997), such that conclusive information on the prevalence and importance of arrested succession is lacking. Lastly, understory vegetation may act as a selective filter for tree establishment, thereby altering species composition in favour of shade-tolerant (George and Bazzaz, 1999a) and possibly also drought-tolerant species. Over the last decades, evidence has been mounting that the understory impacts species composition of the advance regeneration in forests worldwide, for example in South and North America, Europe, Asia and Oceania (Horsley and Marquis, 1983; Taylor and Qin, 1988; Widmer, 1998; Den Ouden, 2000; Standish et al., 2001; González et al., 2002; Coomes et al., 2005). Overall, there is compelling evidence that the understory vegetation interacts strongly with tree regeneration. However, the role of specific processes, the overall magnitude of the effects, and the long-term impact of the
herbaceous understorey on forest dynamics remain unclear due to the complexity of interactions as well as the limited time scale that can be addressed by empirical means.

Herbaceous vegetation and its effect on tree regeneration vary substantially over time and space, depending on climate, site conditions and overstorey development (Alaback, 1984; Hart and Chen, 2006; Halpern and Lutz, 2013). While early successional stages are typically dominated by highly competitive light-demanding pioneer plants (such as many grass and forb species, e.g., *Calamagrostis*, Ellenberg, 1996), the importance of understorey competition usually decreases as trees emerge above the understorey layer, and ultimately close the overstorey canopy (Balandier et al., 2006). Although very few studies about overstorey-understorey interactions have exceeded a time frame of 30 years (e.g., Halpern and Lutz, 2013), there is some evidence from chronosequence studies that the importance of the herbaceous understorey can increase again as forests mature and enhanced tree mortality opens up the canopy (Alaback, 1982). This has also been reported for drought-prone stands, where the contribution of the herb layer to forest water uptake increases with stand age and decreasing stand density (Delzon and Loustau, 2005). Due to the small number of chronosequence studies that investigated overstorey-understorey interactions, and taking into account the limitations inherent to the chronosequence approach (Walker et al., 2010), little is known about the generality of these long-term patterns under different environmental conditions (Hart and Chen, 2006).

Similar to the scarcity of information at large temporal scales, few studies have addressed the change of patterns along environmental gradients. The existing studies showed that understorey vegetation can change strongly in its structure and composition, most of all along elevational or latitudinal gradients (Hart and Chen, 2006; Wilson and Nilsson, 2009; Patsias and Bruelheide, 2013). Some studies reported a decreasing herbaceous biomass with increasing elevation (e.g., Raich et al., 1997; De Long et al., 2015), but the opposite trend was reported as well (e.g., Siccama et al., 1970); these patterns probably depend on the biogeographical region, changes in the overstorey structure as well as the extent of the climatic gradient that is considered. Landscape-level studies have also highlighted the importance of topography for the herbaceous understorey (McCarthy et al., 2001; Halpern and Lutz, 2013). Aspect and slope determine the degree of exposure to incident radiation and thus influence the availability of soil moisture at a given site (Zou et al., 2007), which is usually associated with changes in understorey biomass and composition (e.g., Halpern and Lutz, 2013). Plant-available water is furthermore controlled by soil water holding capacity, which is an additional important factor for overstorey-understorey interactions (Balandier et al., 2006). Thus at the landscape scale, the herbaceous understorey strongly depends on climate, soil, topography and overstorey stand structure (e.g., Ford et al., 2000), but the general patterns and linkages between overstorey and understorey at this scale remain elusive (Gilliam and Roberts, 2003).
Global change impacts on overstorey-understorey interactions

Ongoing global change has profoundly affected forests worldwide and caused unprecedented loss of forest cover and changes in species composition (FAO, 2015). In Europe, extreme climatic events and disturbances (e.g., storms, fires, pest outbreaks, etc.) have caused considerable damage to forests over the last decades (Schelhaas et al., 2003; Allen et al., 2010; Seidl et al., 2011). With the progression of climate change, these events are likely to become more frequent and intense, and are expected to exert a stronger control on future forest dynamics (Rigling and Schaffer, 2015). Forests in mountain regions are especially vulnerable to climate change impacts, since the temperature increase in mountain regions is substantially above the global average (Price et al., 2011; Pepin et al., 2015). Rising temperatures and increasing frequency and severity of drought events are likely increasing the risk of forest mortality (IPCC, 2014), which may result in rapid shifts in understorey composition (e.g., Kane et al., 2011) and potentially alter overstorey-understorey interactions. However, little is known about the long-term consequences of these extreme climatic events for forest ecosystems (Anderegg et al., 2013), particularly at the landscape scale (Elkin et al., 2013).

In this context, a consideration of long-term forest dynamics that neglects the potential role of herbaceous understorey may be at risk of inadequately capturing its response to changing climate and disturbance regimes. Herbaceous vegetation may react differently to global change drivers than trees, and will likely play a more important role under an intensified disturbance regime, for the following reasons:

1. While distributions of tree species to changing climates are relatively slow and often occur with considerable time lags (as for instance at the tree-line, Harsch et al., 2009), herbaceous vegetation usually reacts much faster, as shown by the upward spread along elevation gradients (Lenoir et al., 2008; Küchler et al., 2015). A warming climate may thus result in an increasing importance of herbaceous vegetation for successional trajectories of high-elevation mountain forests.

2. With rising temperatures and decreasing precipitation, as projected for many areas worldwide, water limitation is becoming an issue of increasing concern for forests in the future (Allen et al., 2010). Competition between herbs and trees for soil water (particularly in the regeneration stage) may thus intensify.

3. Increasing frequency and severity of climatic extremes (e.g., drought events) and natural disturbances (e.g., catastrophic windthrow) are likely to affect forests in the future (Rigling and Schaffer, 2015) and potentially cause large-scale overstorey mortality (Allen et al., 2010). This is expected to increase light availability at the forest floor and thus enhance the growth of herbaceous vegetation (Patsias and Bruelheide, 2013) as long as enhanced drought is not overcompensating this effect. In either case, these processes are likely to enhance the importance of overstorey-understorey competition.

4. The combination of novel disturbance regimes may change competition between trees and herbaceous vegetation, as found for eastern deciduous forests of North America (e.g., de la Cretaz and Kelty, 2002; Royo and Carson, 2008; Royo et al., 2010). In these forests, dense understorey vegetation is considered as a key factor causing the observed insufficient regeneration rates (McWilliams et al., 1995; Royo and Carson, 2006). Some experimental
studies (e.g., Horsley and Marquis, 1983; Nuttle et al., 2013) suggest that the failure of tree regeneration is particularly severe when different disturbance types act in combination (Royo and Carson, 2006), especially when intensive ungulate browsing is involved (Nuttle et al., 2013). Due to the difficulties in simultaneously manipulating different disturbance factors, their relative importance remains however largely unknown (Nuttle et al., 2013).

Empirical studies mostly investigate rather short periods (usually <10 years), while questions about forest dynamics would require a time scale of many decades to several centuries (Stromayer and Warren, 1997). Thus, there is a critical deficiency of knowledge on the long-term impacts of a changing climate and changing disturbance regimes on overstorey-understorey interactions.

Using a forest landscape model approach to investigate overstorey-understorey interactions

To overcome the empirical limitations in exploring forest dynamics and disturbance effects at large spatial and temporal scales, dynamic forest landscape models (FLMs) have been developed (Mladenoff, 2004; Perry and Enright, 2006). Overall, FLMs share two common features, i.e. the simulation of forest dynamics at large spatiotemporal scales (typically $10^3$ – $10^6$ ha, and more than 100 years) and the explicit representation of spatial processes (such as fire, windthrow, insect outbreaks, harvest and seed dispersal) (He, 2008). Typically, this distinguishes them from so-called ‘forest gap models’ (Bugmann, 2001), which simulate vegetation dynamics at smaller scales usually without spatially interactive processes; from ecosystem process models, which focus on mass and energy fluxes within ecosystems (e.g., Friend et al., 1993); and from dynamic global vegetation models, which typically represent vegetation dynamics at the level of broad plant categories at a much larger scale (e.g., Sato et al., 2007). More recently, forest landscape models have been developed that link vegetation dynamics with an ecosystem process model approach (e.g., Seidl et al., 2012; Gustafson et al., 2016). Some FLMs represent successional dynamics in a way that is similar to forest gap models (i.e., they consider establishment, growth and mortality of individual trees within small patches of land), but use simplified process representations due to computational limitations at large spatial scales (see also He, 2008, for a detailed discussion of this topic). The key advantage of this mechanistic approach is its ability to represent competition-driven, transient vegetation dynamics as well as complex and interacting effects under changing (and potentially ‘no-analogue’) climatic conditions (Perry and Enright, 2006; Gustafson, 2013).

This more mechanistic type of FLMs (e.g, LandClim, Schumacher et al., 2004; LANDIS-II, Scheller et al., 2007) is increasingly used to explore ecological processes and their interactions at different spatio-temporal scales, such as theories of disturbances, effects of spatial heterogeneity as well as equilibrium and non-equilibrium vegetation dynamics (He, 2008; Henne et al., 2015; Perry et al., 2016). In particular in mountain forests, which are typically characterized by steep topographic and edaphic gradients, FLMs allow for the investigation of vegetation interactions under past, present and future climate conditions, as for instance shown with the FLM LandClim for the Central European Alps (e.g., Schumacher et al., 2006; Henne et al., 2011). Overall, FLMs are suitable tools to systematically explore
vegetation interactions at large spatio-temporal scales in order to obtain a better understanding of past, present and future forest dynamics.

The vast majority of FLMs (and other forest models) consider interactions among tree species only. Despite repeated requests to account for the herbaceous understory as an important component of forest ecosystems (Maguire and Forman, 1983; George and Bazzaz, 2003; Royo and Carson, 2006; Keane et al., 2008) herbaceous vegetation has been largely ignored in most forest models. The few existing examples focused on the response of herbaceous species to changes in the overstorey canopy (Kellomäki and Väisänen, 1991; Khanina et al., 2007; Meen et al., 2012), or were designed to evaluate grassland-shrubland or grassland-savannah transitions in arid regions (e.g., Peters, 2002). In order to better understand temperate forest dynamics and to increase the robustness and reliability of model projections under changing disturbance and climate conditions, it is thus of key importance to address the topic of overstorey-understorey interactions in temperate forest ecosystems.

In my dissertation, I thus developed a herbaceous understory module for the FLM LandClim (Schumacher, 2004) to explore the landscape-scale implications of competition between herbs and trees for long-term dynamics of temperate forests in Central Europe. LandClim provides a suitable framework for investigating overstorey-understorey interactions since it incorporates competition-driven forest dynamics and is well-tested in Central Europe (e.g., Schumacher et al., 2004; Elkin et al., 2012; Schwörer et al., 2014; Henne et al., 2015). Furthermore, its ability to represent disturbances of natural as well as anthropogenic origin makes it a suitable candidate to systematically explore overstorey-understorey interactions under changing disturbance conditions.

**Aims and structure of the thesis**

The objective of this thesis is to explore the effect of interactions between the herbaceous understory and trees on temperate forest dynamics at large spatial (i.e., landscapes of $\geq 10^3$ ha) and temporal (i.e. $\geq 100$ yrs) scales. In particular, the thesis focuses on the implications of overstorey-understorey interactions for forest dynamics under changing climate and disturbance conditions, which have been suggested to play a key role in mediating the competition balance between herbs and trees. I systematically explore the interaction between herbs and trees (Fig. 1) with respect to:

1. the effect of *competition for light*, focusing on how this interaction delays succession and alters species composition along a large elevational gradient.

2. the effect of *competition for water* on the dynamics of drought-prone forest landscapes, with a focus on changes in forest structure and composition under present and future climate conditions,

3. the influence of *disturbances* (browsing, timber harvest, windthrow) on delayed and arrested succession.
Consequently, the thesis is structured into the following parts:

**Chapter I**

Light competition has been suggested as the main mode of interaction between the overstorey and the understorey in temperate forests (e.g., Gilliam, 2007). In order to explore its consequences on forest dynamics at large spatio-temporal scales, I developed a sub-model representing herbaceous vegetation and its competition for light in LandClim. I applied the new model version to two mesic study landscapes at Mt. Feldberg (in the Black Forest, Germany) and the Dischma valley (Central Alps, Switzerland) representing a large elevational gradient. Model performance was evaluated in three steps: (1) a sensitivity analysis of the growth parameters for the four herbaceous plant functional types (PFTs) grass, forbs, ferns, herbs, (2) a comparison of the simulated overstorey and understorey dynamics with patterns reported in chronosequence studies (Alaback, 1984; Jules et al., 2008), and (3) comparing elevational distribution patterns of herbaceous PFTs with empirical data from Priewasser (2013). Following these evaluation steps, I analysed the effect of herbaceous understorey on forest growth and tree species composition by comparing scenarios excluding and including understorey. Furthermore, I explored the effect of two windthrow scenarios to test how understorey reacts to overstorey disturbances.
Chapter II

Competition between trees and herbs for soil water is frequently ignored (cf. Chapter I), even in studies of drought impacts on temperate forests. However, several empirical studies suggest that this interaction can significantly reduce tree growth and regeneration and thereby impact forest structure and composition (e.g., Picon-Cochard et al., 2006; Giuggiola, 2016). Overstory-understorey interactions may therefore become more important in a future climate characterized by an increased frequency and severity of drought events. In order to explore the consequences of this interaction on forest dynamics, I extended the water balance submodel of LandClim to incorporate competition for soil water between herbs, saplings and adult trees. This new water balance model was evaluated with empirical data from five sites across Europe. Then, I applied the new model to explore overstorey-understorey interactions under present climate and scenarios of future climate change (RCP4.5 and RCP8.5 scenarios) for a drought-prone study landscape around Visp in the Valais, Switzerland.

Chapter III

Disturbances are a key factor influencing overstorey-understorey interactions (Hart and Chen, 2006) and have been suggested to exacerbate the reduction of tree regeneration by understorey vegetation (Royo and Carson, 2006). The combined occurrence of different disturbances is considered as a particularly important mechanism potentially leading to arrested succession (Stromayer and Warren, 1997; Royo and Carson, 2006). However, due to the complexity of interacting factors and the large spatio-temporal scales involved, it is highly challenging to study arrested succession by empirical approaches alone. In this chapter, I therefore used the new version of LandClim (including competition for light and water) to study the long-term effects of understorey competition in combination with different disturbances on forest succession. In particular, I (1) systematically explored the relative importance of different abiotic, biotic and disturbance factors for the occurrence of arrested succession, and (2) tested whether combinations of understorey competition with disturbances increased the probability of arrested succession. The model was applied to four study landscapes representing a cross-Alpine transect in Central Europe in order to cover a large bioclimatic gradient and arrive at conclusions relevant for a wide range temperate forests.
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Chapter I

Herbaceous understorey – an overlooked player in forest landscape dynamics?


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Abstract

Dense herbaceous understorey layers can impact tree regeneration and thereby affect forest succession. However, the implications of this interaction on large spatial and temporal scales are not well understood. To analyze the role of overstorey-understorey interactions for forest dynamics, we implemented an understorey layer (composed of the plant functional types grasses, forbs, ferns, herbs and shrubs) in the forest landscape model LandClim, focusing on competition for light as the main mode of interaction. The model was used to simulate post-disturbance dynamics over an elevational gradient of 560 to 2800 m a.s.l. in Central Europe. Simulation results showed strong impacts of the herbaceous understorey on tree regeneration within the first decades, but generally little effect on late-succession forests, i.e. not providing any evidence for ‘arrested’ succession. The results also demonstrated varying overstorey-understorey interactions across the landscape: strongest effects were found at low to mid elevations of the study landscapes, where tree establishment was substantially delayed. At high elevations, tree growth and establishment were more limited by low temperatures, and the effect of light competition from the understorey was negligible. Although the inclusion of large windthrow disturbances increased the biomass of herbaceous understorey across the landscape, this had only a small impact on the overstorey due to the presence of advance regeneration of trees. Overall, our results demonstrate that the herbaceous understorey can have a significant impact for forest landscape dynamics through light competition, and that non-woody plants should not be neglected in forest modelling.

Keywords: herbaceous vegetation, overstorey understorey interaction, arrested succession, Black Forest, Dischma valley, Central Alps, dynamic vegetation model
Introduction

Biotic interactions are increasingly recognized as key mechanisms that influence vegetation dynamics at larger scales (e.g., Nieto-Lugilde et al., 2015). In forests, the study of biotic interactions has mostly focused on competition between woody species (Bugmann, 2001; Gilliam, 2007) and plant-animal interactions (e.g., Kupferschmid et al., 2015). The interaction between the herbaceous understorey and the woody overstorey is usually considered as a one-way interaction, i.e., overstorey trees determine the composition of understorey herbs by controlling the amount of light reaching the forest floor (Gilliam, 2007; Li et al., 2012). However, an increasing number of empirical studies have demonstrated that the herbaceous understorey can significantly interfere with tree regeneration and therefore impact the composition and dynamics of the overstorey (George and Bazzaz, 1999a; Royo and Carson, 2006). Thus, it is important to consider not only the ‘top down’ effect of trees on the herbaceous layer, but rather a two-way interaction where herbs can also have a ‘bottom up’ effect on tree population dynamics.

The herbaceous understorey has a range of effects on tree regeneration, but a general understanding of the underlying mechanisms is only beginning to emerge (Balandier et al., 2006; Royo and Carson, 2006; Li et al., 2012). In temperate forests, competition for light is thought to be the most important factor (Nabuurs, 1996; George and Bazzaz, 2003), although competition for water and/or nutrients may have a strong influence under dry and/or poor soil conditions (Coomes and Grubb, 2000).

The magnitude of light competition between the overstorey and the understorey varies over time. Early successional, open sites are typically dominated by light-demanding grasses, forbs and shrubs (Lieffers et al., 1993; Ellenberg, 1996). As the canopy closes, these are subsequently replaced by more shade-tolerant herbaceous species (Alaback, 1984; Hart and Chen, 2006). Within the first 15 to 20 years, the effect of the herbaceous layer on tree regeneration is usually considered to be strongest (Balandier et al., 2006). However, extreme cases have been described where the herbaceous layer diminishes tree regeneration to such an extent that the ecosystem becomes ‘trapped’ in an open herbaceous/shrub stage and does not revert to forest (termed ‘arrested succession’; Niering and Goodwin, 1974). Other studies have shown that herbaceous vegetation can significantly delay tree regeneration even under closed-canopy conditions (e.g., George and Bazzaz, 1999a, 1999b). Thus, while it is clear that the effect of the herbaceous layer is not restricted to the first years of succession, its magnitude remains somewhat elusive.

Compared to our knowledge on temporal dynamics, much less is known how overstorey-understorey interactions vary across space, i.e. at the landscape scale. The composition and biomass of the understorey may change in response to soil depth, slope and overstorey stand structure (Hart and Chen, 2006). As canopy conditions become more open, herbaceous biomass typically increases (Alaback, 1984; Ellenberg, 1996). This effect becomes particularly evident in mountain forests, where increasingly open forest canopies at higher elevations result in the formation of dense herbaceous layers that can impede tree regeneration (e.g., Ott et al., 1997; Frehner et al., 2005). At the landscape scale, disturbances are central
for structuring spatial heterogeneity and driving ecosystem dynamics (Turner et al., 2001). Large-scale disturbances such as windthrow and wildfires are of particular importance for the herbaceous layer, since they produce an environment with favourable conditions for pioneer species (Turner et al., 1997). The interaction between the herb and the tree layer can therefore be expected to intensify in areas with frequent disturbances, or under scenarios of future conditions that feature an increased disturbance frequency (IPCC, 2013). The restricted spatial and temporal context at which herbaceous understorey effects are usually investigated (McCarthy, 2003) poses a severe obstacle to the generalisation of overstorey-understorey interactions. By using dynamic forest landscape models, the constraints of long time spans and large spatial extents can be overcome (Bugmann, 2001; Mladenoff, 2004). In particular, mechanistic (so called ‘process-based’) models enable us to explore and disentangle complex ecological interactions (e.g., of climate, biotic interactions, disturbances and land-use change).

Despite repeated pleas to include a herbaceous layer in dynamic models of forest growth (e.g., Maguire and Forman, 1983; Weisberg et al., 2003; McKenzie et al., 2009), there are only a few process-based forest models that have put this into practice (e.g., Kellomäki and Väisänen, 1991). Dynamic global vegetation models (DGVMs) generally include herbaceous and shrubby components (e.g., LPJ-GUESS, Smith et al., 2001; SEIB-DGVM, Sato et al., 2007), but their modelling is coarse, geared towards the continental- to global-scale distribution of broad plant categories and the general implications for land surface processes (e.g., Hickler et al., 2012). To our knowledge, no process-based forest model has been used specifically to investigate the two-way interactions between the overstorey and understorey layer. Here, we introduce a dynamic understorey layer in the forest landscape model LandClim (Schumacher, 2004) to investigate how competition for light influences overstorey-understorey interactions at large spatial and temporal scales. Specifically, we address the following questions:

1. To what extent does herbaceous vegetation delay overstorey tree succession? Can intense light competition by the herbaceous understorey result in ‘arrested’ succession?
2. How do overstorey-understorey interactions vary over time and across elevational gradients? In particular, do low-elevation forests differ from high-elevation forests?
3. To what extent does the occurrence of large windthrow disturbances intensify overstorey-understorey interactions at the landscape scale?

**Material and Methods**

**The forest landscape model**

LandClim is a forest landscape model that simulates competition-driven dynamics in complex topography (Schumacher, 2004; Schumacher et al., 2004). LandClim has been used to study forest dynamics under past, present and future climate conditions across a range of landscapes in temperate forests in central and southern Europe (Schumacher et al., 2004; Henne et al., 2013), North America (Schumacher and Bugmann, 2006) and New Zealand (Thrippleton et al., 2014). Landscapes are represented in LandClim in the form of raster grids (25 x 25 m²)
with specific environmental conditions for each grid cell (i.e., aspect, slope, soil and climate). Within each grid cell, stand-scale processes are simulated, i.e. the establishment, growth and mortality of tree cohorts (groups of even-aged trees of the same species). Intra- and inter-specific competition for light and soil water is taken into account. LandClim also incorporates landscape-scale processes such as seed dispersal, windthrow, fire and bark beetle dynamics.

Light extinction through the canopy is modelled using the Lambert-Beer Law (Bugmann, 2001; Monsi and Saeki, 2005). Light limitation reduces tree growth and influences the probability of regeneration as well as the density and biomass of new tree cohorts. The fate of young tree cohorts is tracked over ten years before these trees are considered as successfully established. During this time, the number of years with suitable conditions for establishment (e.g., light availability above a species-specific threshold) and actual tree growth performance determine establishment probability. The density of actually established trees is influenced by light availability at the forest floor (see Schumacher et al., 2004). Thus, unfavourable light conditions (such as due to herbaceous competition) can stop tree regeneration and theoretically halt succession. A more detailed description of LandClim can be found in Schumacher (2004).

**Representation of herbaceous understory**

Due to the high species diversity in the understory, we chose to represent it as Plant Functional Types (PFTs), i.e. species groups based on similar architecture and ecological strategies (e.g., Weisberg et al., 2003; Balandier et al., 2006). We focus on four groups of herbaceous PFTs (listed according to increasing shade tolerance, cf. Appendix A1): grasses, tall forbs, ferns, and small herbs. A shrub PFT was also included to represent *Rubus* spp., for comparison with the empirical data by Priewasser (2013) (cf. section ‘Model evaluation’ and Appendix A1). Details on the parameterization of the understory PFTs are provided in Appendix A1.

Each understory PFT is represented in LandClim as a single cohort per grid cell. Because LandClim has an annual time step and does not consider growth dynamics within the growing season, understory PFTs can be assumed to be present all the time, i.e. from the point of view of the model they are perennial, even though from a botanical point of view they may of course be annual plants. Their annual growth rate was modelled using a logistic growth equation, similar to the one used for tree growth (Schumacher et al., 2004). In contrast to trees, however, negative growth is possible for herbaceous PFTs. Herbaceous cohorts can therefore lose biomass from one year to the next if environmental conditions (light, water, temperature) are deteriorating.

The herbaceous understory casts shade on the forest floor in addition to the shading exerted by the tree layers. Light extinction by herbs is calculated analogously as for trees, using the Lambert-Beer Law (Monsi and Saeki, 2005), which is a function of leaf area index (LAI) and a light extinction coefficient (0.6; Pitman, 2000). The LAI of each herbaceous PFT was calculated in two steps for each grid cell. First, LAI for each herbaceous cohort was calculated
from cohort biomass using an allometric function (Eq. 1) that was derived by fitting a linear model to empirical data (cf. Appendix A3). Second, herbaceous vegetation cover (cover\textsubscript{Herb}) was considered as an additional, down-weighting factor in the calculation of the grid cell LAI for each cohort (Eq. 2), to account for the patchiness of the herbaceous vegetation at scales of a few meters (George and Bazzaz, 2003). The percentage of ground cover by each PFT was calculated using allometric equations from different empirical studies (cf. Appendix A4).

\begin{align*}
\text{LAI}_{\text{Herb}} &= 0.7442 \cdot \text{Biomass}_{\text{Herb}} \quad \text{(Eq. 1)} \\
\text{LAI}_{\text{Herb, cohort}} &= \text{LAI}_{\text{Herb}} \cdot \text{cover}_{\text{Herb}} \quad \text{(Eq. 2)}
\end{align*}

**Sensitivity analysis for herbaceous growth parameters**

The herbaceous growth parameters (maximum growth rate ‘\(R_{\text{max}}\)’ and maximum biomass ‘\(K_{\text{max}}\)’) are decisive for determining the outcome of competition with trees, but their values are subject to considerable uncertainty (cf. Appendix 1). Thus, these parameters were studied in more detail using a sensitivity analysis. Parameters were varied within ranges informed by empirical measurements (cf. Appendix A3). Maximum biomass was varied from 16 to 800 g·m\(^{-2}\) (i.e., 0.16 to 8 t·ha\(^{-1}\)), and maximum growth rate varied from 0.01 to 1 yr\(^{-1}\) (equivalent to \(>50\) and \(<10\) years to reach maximum biomass, respectively). For the sensitivity analysis, a Latin Hypercube sampling design was used to create 2500 parameter combinations. Simulations were performed with all four herbaceous PFTs (grass, forb, fern, herb) in competition with 16 tree species for 400 simulation years. We used a representative subset of the study landscape in the Black Forest (elevation bands 600, 1000 and 1400 m a.s.l.; see next section).

**Case study landscapes**

We applied the model to two case study landscapes, the St. Wilhelm valley (47° 52’ N, 7° 58’ E; total area 1218 ha) on the slopes of Mt. Feldberg in the Black Forest, Germany (referred to as ‘Feldberg landscape’ below), and the Dischma valley (46° 47’ N, 9° 51’E; total area 1700 ha) in the central Alps near Davos, Switzerland. Both landscapes have a high annual precipitation sum of \(>1000\) mm (Bogenrieder and Rasbach, 1982; Schumacher et al., 2004) and were selected because together they represent a large elevation range from 560 m to \(>2800\) m a.s.l.. The landscapes are characterized by mesic forests. Light and temperature are the main limiting factors, whereas water limitation plays a minor role only. Climate data and lapse rates for temperature and precipitation for the Feldberg landscape were generated from weather stations in Freiburg i.Br. (236 m a.s.l.) and at the top of Mt. Feldberg (1490 m a.s.l.) from 1949-2012 (DWD, Deutscher Wetterdienst; https://werdis.dwd.de/, July 2014). Details on the topographic and soil input maps for Feldberg are given in Appendix A2. Information regarding the climate and soil data for the Dischma landscape can be found in Schumacher et al. (2004).
Simulation experiments

For analysing the spatio-temporal patterns at the landscape scale, LandClim was run for 400 years of forest succession for the Feldberg and Dischma landscapes. This is equivalent to the time scale of the chronosequence by Jules et al. (2008), which was used for model evaluation (see below). Growth parameters for the herbaceous species were based on empirical studies of post-windthrow vegetation dynamics in the Black Forest (Sayer and Reif, 1999) (cf. Appendix A1). To evaluate the effect of understorey vegetation on forest succession, simulations were run for both landscapes in two scenarios: (1) only trees, and (2) trees and understorey vegetation. All scenarios were simulated with 10 iterations to account for stochastic variability in the model. For each model iteration, the climate records for the landscapes of Mt. Feldberg and Davos were re-sampled with replacement, so as to generate a 400-year climate sequence representing present-day climate.

To analyse the impact of windthrow disturbances, three scenarios were compared: (1) control, no disturbances; (2) windthrow disturbances with a 600-yr rotation period; and (3) windthrow disturbances with a rotation period of 400 yrs (representing ‘intermediate’ and ‘strong’ windthrow disturbance scenarios, see Schumacher, 2004). Average and maximum windthrow sizes were based on windthrow reports from the Black Forest by Fischer (1999) (average = 2 ha, maximum = 73.8 ha). Windthrow simulations were performed for the Feldberg landscape only, as this disturbance type plays a minor role in the Dischma landscape.

Model evaluation

The simulated temporal patterns of overstorey-understorey development were compared to a 420-yr chronosequence by Jules et al. (2008) that used forest sites of different ages under otherwise similar abiotic conditions to study successional dynamics. Chronosequences are appropriate for describing the aggregated characteristics of plant communities (Walker et al., 2010) and can provide qualitative information on the long-term interaction between tree overstorey and herbaceous understorey.

Three stages of herbaceous succession are evident from the study of Jules et al. (2008): stage 1 – an understorey peak (mostly grasses and shrubs) within the first 25 yrs; stage 2 – a gradual decline towards a minimum cover around yr 80-100; and stage 3 – an increase in herb cover thereafter. Since other long-term studies described similar qualitative patterns (Oliver, 1981; Alaback, 1982; Alaback, 1984), we considered these three stages as robust results for the model evaluation, despite potential complications from land use history.

The ecological differences between the study region of Jules et al. (2008) and the Black Forest landscape, however, restricted the comparison to a qualitative evaluation of broad trends in tree and understorey succession.

Simulated spatial patterns were compared to vegetation data from herbaceous species on 90 post-windthrow plots across the Northern Swiss Alps by Priewasser (2013), which covered an elevation range from 370 to 1800 m a.s.l.. Vegetation data had been collected in 2011 on
windthrow sites affected by the storm Vivian (1990) and Lothar (1999), thus providing a detailed and highly accurate picture of herbaceous vegetation composition approximately 10 and 20 yrs after disturbance (for details cf. Priewasser, 2013; Kramer et al., 2014). Trends in elevational distribution of dominant herbaceous vegetation were similar at both storm sites, and were therefore combined for an evaluation of the model (Figure 3i). To ensure that elevational trends are due to climatic constraints and not confounded by varying pH and overstorey vegetation, only data from acidic sites within former spruce forests were included. Analyses of all model outputs were performed in the statistical software \textit{R}, version 3.1.2 (R Development Core Team, 2014).
Chapter I

Results

Sensitivity Analysis

The sensitivity analysis showed consistent patterns for all herbaceous PFTs over time (Figure 1). Understorey effects on forest biomass were strongest in the first 100 years of succession, but they practically disappeared by the year 400. The parameter $R_{\text{max}}$ (maximum growth rate) influenced the results only when it was $>0.2 \text{ yr}^{-1}$, while the parameter $K_{\text{max}}$ (maximum biomass) had a strong effect throughout the investigated parameter range. Very high $K_{\text{max}}$ values resulted in a strong delay of tree biomass development up to the year 100, particularly for the more shade-tolerant PFTs (i.e., ferns and herbs; Figure 1c-d).

Figure 1: Sensitivity analysis of the herbaceous growth parameters ‘maximum biomass’ (g·m$^{-2}$) and ‘maximum growth rate’ (yr$^{-1}$) for the four simulated plant functional types. Shown is the impact of the herbaceous layer on forest biomass development (expressed as biomass relative to equilibrium biomass, i.e. 400 t/ha). Orange points mark the parameters of each PFT used in the following landscape simulations (see also Table A1.1). The ‘No Understorey’ results show the forest biomass growth of a single scenario in the absence of herbaceous understorey (thus no parameters were varied here).
**Landscape simulations – temporal patterns**

The understorey PFTs showed a peak at the beginning of succession, which decreased to a rather low level after 20-30 years at low elevations (Feldberg, 600 m a.s.l.; Figure 2c) and after 40-50 years at high elevations (Dischma, 1800 m a.s.l.; Figure 2d). This difference was caused by much faster tree succession at low elevations (Feldberg, 600 m; Figure 2a,b).

At low elevations, the three broad stages of understorey succession were visible in the simulation results: a pronounced peak of understorey vegetation (mainly grass, ferns and *Rubus*), followed by a biomass drop in the first century, and the occasional re-occurrence of the pioneer PFT *Rubus* after around year 150 (Figure 2c).

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**Figure 2**: Succession of tree species and understorey in the study landscapes (a, c) Feldberg at 600 m a.s.l. and (b, d) Dischma at 1800 m a.s.l. For clarity, the y-axis was rescaled by a factor of 10 above the horizontal dashed line.
Landscape simulations – spatial patterns

Understorey vegetation followed clear elevational trends in both landscapes (Figure 3). Elevations <1000 m were dominated by *Rubus*, fern and grass in the first 20 simulation years (Figure 3a,c). At elevations from 1100 to 2000 m, grass became increasingly important in terms of relative biomass. Herbs and forbs were consistently present at low biomass across the elevation gradient. Notably, elevational patterns shifted over time. Whereas elevations <1000 m were strongly affected by shading from canopy trees already at years 20 and 30, mid and high elevations still had higher levels of herbaceous biomass (Figure 3c,e). This herbaceous peak shifted upwards with the progression of succession (Figure 3e-h). Empirical data from Priewasser (2013) about vegetation composition at years 10 to 20 showed a dominance of *Rubus* and fern at lower elevations and forbs and grasses at higher elevations (Figure 3i).

![Figure 3](image)

**Figure 3**: Distribution of understorey plant functional types along an elevation gradient for Feldberg and Dischma. For clarity, the y-axis was rescaled by a factor of 10 above the horizontal dashed line. Cross marks in panel i show the number of study sites within each 200 m elevation belt. Sites shown in panel i represent the composition of herbaceous vegetation at an age of approximately 10 to 20 years.
Understorey impact on forest dynamics

At low elevations, the presence of understorey vegetation delayed forest succession by several years and decreased initial tree biomass by 32% (Figure 4a,c). With increasing elevation, the difference in total tree biomass between scenarios with or without understorey diminished (Figure 4b,d) and became negligible at elevations above 1900 m (Figure 4e-h). Across all elevations, the understorey effect diminished after a few decades, and simulated biomass was virtually the same after approximately 70 years (Figure 4c,d). Correspondingly, within the first decade available light at the forest floor was reduced by the introduction of herbaceous vegetation by 30% at Feldberg (600 m a.s.l.) and 8% at Dischma (1800 m a.s.l.), but became negligible at both landscapes by the year 400 (results not shown).

Figure 4: Effect of understorey vegetation on forest biomass development with time (a-d) for Feldberg at 600 m and Dischma at 1800 m, and across the elevational gradient at year 30 (e-h). In both cases, the top panels (a, b, e, and f) illustrate the absolute biomass values and the bottom panels (c, d, g, and h) show the percent difference between the two lines (with and without understorey).
Despite the decreasing impact on total tree biomass with time, the introduction of herbaceous vegetation did induce a long-lasting shift in dominant tree species throughout the landscape (Figure 5). This was particularly apparent for low and mid elevations in the Feldberg landscape (Figure 5a,b), where light-demanding species such as *Betula* and *Salix* were replaced by more shade-tolerant species (mostly *Fagus sylvatica*). The effect of the understorey on tree species dominance was less pronounced in the Dischma landscape (Figure 5c,d), although there was a discernible decrease of *Larix decidua* in favour of *Picea abies*. Differences in terms of dominant tree species distribution were still evident up to the simulation year 200 (cf. Appendix A5).

**Figure 5**: Maps of dominant species for the Feldberg and Dischma landscapes at year 50 of the succession, excluding and including understorey vegetation.
Effects of windthrow

The occurrence of large windthrow disturbances strongly increased average herbaceous biomass across the landscape (up to 56%; Figure 6). Windthrow disturbances also reduced mean tree biomass across the landscape. Including herbaceous understorey in the simulations slightly enhanced the understorey effect on the tree overstorey, although it was relatively small (Figure 6, difference between ‘tree biomass – no herb layer’ and ‘tree biomass - with herb layer’).

Figure 6: Effects of simulating windthrow disturbances on the understorey and the tree layer (elevation band 600 m in the Feldberg landscape) for two different windthrow scenarios (rotation period of 600 years and 400 years, based on Schumacher 2004). The results indicate the percentage change compared to the simulation without windthrow disturbances.
Discussion

The understorey layer as implemented in LandClim produced simulation results that were not only realistic and plausible, but also consistent with the broad patterns evident from empirical data. Below, we discuss in more detail (1) the effects of herbaceous understorey on delaying forest succession (with particular consideration of ‘arrested’ succession), (2) emerging spatio-temporal patterns (comparing low-elevation with high-elevation forests), and (3) the importance of disturbance events for overstorey-understorey interactions. Notably, the simulation results consider light competition as the predominant interference mechanism between trees and herbs (as suggested by Horsley, 1993; Den Ouden, 2000; George and Bazzaz, 2003).

Can light competition with herbaceous understorey arrest forest succession?

In the sensitivity analysis, we studied the effect of the herbaceous understorey on delaying forest succession and tested whether the case of ‘arrested succession’ occurs. We showed that the model simulates significantly delayed forest succession when herbaceous vegetation has high maximum biomass (Figure 1), so that even after 100 years practically no forest had established. This finding is consistent with studies from Den Ouden (2000) and Koop and Hilgen (1987), who described a stagnation of forest succession for several decades due to interactions between the herbaceous understorey and tree regeneration. However, as shown by George and Bazzaz (1999b), a small fraction of trees are able to survive phases of strong herbaceous competition and become established. Therefore, after several decades some trees eventually emerge above the herbaceous canopy and progressively shade out understorey vegetation (e.g., Lieffers et al., 1993). In a similar manner, the herbaceous understorey greatly reduced the success of tree establishment in our simulations, but ultimately could not stop reforestation in the long term (400 years). Our results thus suggest that even though an ecosystem may appear to be in a state of ‘arrested’ succession, this may simply be a matter of perspective and the relatively short lifespan of humans (and their lack of patience) compared to forests (cf. Hiltbrunner et al., 2014).

There are, however, several ecological processes that are not considered in the model that may influence the interaction between trees and understorey. They include (1) competition for water and nutrients (e.g., Provendier and Balandier, 2008), although forests in the mesic landscapes studied here are unlikely to be strongly constrained by these factors (Bogenrieder and Rasbach, 1982; Schumacher et al., 2004); (2) enhanced seed predation, but little quantitative knowledge is available on this (Royo and Carson, 2008); (3) allelopathic effects (e.g., Nilsson and Wardle, 2005), which are hard to study experimentally (Priewasser, 2013); (4) mechanical inhibition of seedling germination and growth (e.g., Dolling, 1996); and (5) interactions with browsing animals (e.g., Stromayer and Warren, 1997).

The interference of browsing deer and herbaceous understorey is considered to be particularly important for ‘arrested’ succession (Stromayer and Warren, 1997; Royo and Carson, 2006). Continuous browsing pressure results in the suppression of tree establishment and a
depauperation of the herbaceous understorey (Royo and Carson, 2006). Only few unpalatable herbaceous species remain unaffected by browsing and can subsequently form a dense understorey (e.g. the ferns Dennstaedtia punctilobula and Pteridium aquilinum; de la Cretaz and Kelty, 1999; Den Ouden, 2000). It remains unclear, however, how persistent those dense understorey layers are in the long term and in the absence of additional disturbance processes (Royo and Carson, 2006). There is some empirical evidence showing that after reduction of deer browsing, trees gradually re-established despite competition with a dense herbaceous understorey (de la Cretaz and Kelty, 2002). Thus, even though light competition can substantially reduce tree regeneration it appears unlikely that this mechanism alone could result in arrested succession.

**Emerging temporal and spatial patterns of overstorey-understorey interactions**

Early successional dynamics were affected most strongly by the presence of herbaceous understorey vegetation. Using the herbaceous growth parameters derived from the Black Forest data set, the model produced an understorey biomass (herbaceous and Rubus PFTs) comparable to measurements from temperate and boreal regions (e.g., 5.2 t/ha, Alaback, 1982; 6.9 t/ha, Lieffers et al., 1993; 1.5-5.7 t/ha for Rubus, Kowalenko, 2003). In the model, the simulated understorey biomass resulted in a 30% reduction of light availability at the forest floor, which is a realistic but somewhat low estimate (compared to empirical data, which measured light reductions of 30-85%; Shropshire et al., 2001). The simulated delay of forest succession by 10 years at lower elevations of the Feldberg landscape matches empirical data well, reporting delays of 10 – 20 years (Balandier et al., 2006). Some studies found longer lasting delays (e.g., 20 - 30 years in boreal forests, Lieffers et al., 1993; Royo and Carson, 2006), which could be simulated with a relatively minor increase in the $K_{max}$ (‘maximum biomass’) parameter of the herbaceous PFTs (see Figure 1). Overall, the model produced simulation results that were in agreement with empirical patterns of early successional dynamics.

Long-term successional patterns of herbaceous understorey are often described in three broad stages (e.g., Alaback, 1982; Alaback, 1984; Jules et al., 2008): (1) an initial biomass peak, followed by (2) a phase of low biomass, and (3) understorey re-initiation. These patterns emphasize the importance of the overstorey canopy for controlling understorey growth trends (Lieffers et al., 1993; Hart and Chen, 2006). LandClim simulated the first two phases in good accordance with empirical observations, i.e. the initial peak and decrease of understorey biomass associated with the development of the overstorey. However, understorey re-initiation occurred only weakly in the simulation results (i.e., the re-appearance of pioneer PFT Rubus at year 200, Figure 2c). This was mostly due to the aggregation of the results to the landscape level. Individual grid cells in LandClim may differ strongly from each other in terms of environmental conditions and stochastic processes (e.g., establishment, mortality), more so later in the simulation than at the beginning, thus resulting in different forest structures at any one time and a strong dilution of the visibility of understorey re-initiation (cf. Appendix 6). The first two phases were detected clearly because the simulation was started from bare ground, leading to the synchronous development of these stages across the entire
landscape. Thus, the simulated long-term successional trends of the herbaceous understorey are consistent with empirical studies, although the distinctness of late-successional patterns may depend on the level of spatial aggregation of the data.

The most prominent spatial pattern across the simulated landscape was the change in species abundance with elevation due to temperature limitation. The empirical data from Priewasser (2013) showed a similar elevational pattern for Rubus, whereas ferns and forbs were more evenly distributed in the simulation results than in the data. At high elevations (>1200 m a.s.l.), grass increased in relative importance in the model as well as in the empirical data, although it must be noted that only three study sites were located at elevations >1600 m (see Figure 3i). In the model, the elevational distribution of the species is driven largely by the parameter minDD (‘minimum degree-day sum’), which was derived from literature and based on a broad set of herbaceous species (e.g., Laurent et al., 2004 see Appendix A1). Generally, our parameter estimates reflect the maximum climatic niches of the PFT groups, thus the actual climatic niches of the species that are present in our study landscapes may have been narrower. Across the simulated elevation gradient, decreasing temperature strongly influenced overstorey-understorey interactions. On the one hand, low temperature led to a prolonged initial peak of herbaceous biomass at higher elevations due to the slower growth of the overstorey. On the other hand, cold conditions also resulted in a substantial decrease of herbaceous biomass. It was this latter effect that was predominant in the model, thus leading to a smaller impact of the herbaceous layer on tree regeneration in the high-elevation Dischma landscape compared to the Feldberg landscape. Relatively few empirical studies exist that have examined overstorey-understorey interactions across elevations.

At the upper treeline, herbaceous vegetation had either neutral or even slightly positive effects on conifer seedling survivorship (Maher et al., 2005). Yet, Kupferschmid and Bugmann (2005) found that spruce establishment was limited by strong competition with ferns and particularly Calamagrostis grasses in the higher subalpine sites compared to montane forests. Weisberg et al. (2003) showed that in patches of higher light availability at subalpine sites, Calamagrostis and other graminoid species strongly increased in ground cover and outcompeted other PFTs. Notably, Calamagrostis competes not only for light, but can also form impermeable mats due to the accumulation of dead biomass over several years, which hinders conifer regeneration (mostly Picea abies) particularly at high elevations (Ott et al., 1997). Confounding interference mechanisms such as this one make it challenging to evaluate the elevational patterns of light competition directly. As the production of aboveground biomass in herbaceous plants is positively correlated with temperature (e.g., Raich et al., 1997; De Long et al., 2015), a reduction of herbaceous biomass and thus light competition at higher elevations, as simulated by the model, is consistent with broad empirical patterns.

Individual tree species had different responses to the herbaceous understorey, depending on their shade tolerance. The strongest shift in tree species dominance occurred at low elevations, where shade-tolerant species (mostly Fagus sylvatica) were favoured at the expense of light-demanding species (e.g., Betula, Salix). A number of studies report similar findings (e.g., Koop and Hilgen, 1987; George and Bazzaz, 1999a), where establishment of light-demanding species, in particular Betula, was drastically reduced by the presence of an herbaceous
understorey, whereas more shade-tolerant species (e.g. *Acer, Picea, Fagus*) were less affected. The simulation results further emphasize the long-term effect (up to 200 years) of the relatively short peak of herbaceous understorey during the first 10 – 20 years. Considering the entire range of spatial and temporal scales simulated, the impact of understorey competition on tree regeneration was found to be strongest during early succession and at lower elevations. However, the model also demonstrated that understorey competition can have a much longer-lasting impact on tree species composition.

**Importance of disturbance events**

Disturbances (of both human and natural origin) have been suggested to alter the strength of overstorey-understorey interactions (Royo and Carson, 2006). In the simulations, large windthrow disturbances strongly favoured the herbaceous layer locally, and this increase in herbaceous biomass was visible even at the landscape scale. This effect is in accordance with the literature, demonstrating the strong impact of disturbance size on the understorey response (George and Bazzaz, 2003). Large disturbances generally lead to a proliferation of herbaceous species, in particular those with a pioneer strategy (Alaback, 1984; Hart and Chen, 2006). The quick exploitation of resources available after a disturbance by herbaceous vegetation may have consequences for tree succession. For example, large disturbances due to forest fires in Yellowstone National Park resulted in abundant herbaceous vegetation that precluded tree establishment for several decades (Turner et al., 1997). After large-scale disturbances, surviving vegetation as well as the availability and dispersal of seeds from nearby sources can play a major role in controlling the rate of forest development (Turner et al., 1997; Dale et al., 2005). For determining light competition between trees and herbs, the presence of advance regeneration (i.e., juvenile trees) is of particular importance since it can substantially accelerate forest regeneration (George and Bazzaz, 2003; Schwitter et al., 2015). Simulated windthrows in LandClim affect only larger-sized trees (Schumacher, 2004); thus younger cohorts survive the disturbance event and rapidly shade out the herbaceous layer. The consistent presence of advance regeneration in our simulations was the main reason why the herbaceous layer had a rather small impact on tree biomass in both windthrow scenarios.

Large-scale, ‘stand replacing’ disturbances where vegetation is entirely removed would most likely have produced a much stronger effect on both the understorey and the overstorey, but they were not simulated here because they are not important in the two case study landscapes. Wildfires in particular have been shown to result in the proliferation of understorey vegetation (Hart and Chen, 2006), and a dense herbaceous cover can furthermore lead to positive feedbacks on fire spread across the landscape (Allen, 2007). Timber harvest can also produce prolonged understorey responses and is replacing wildfire as the most important disturbance type in boreal forests (Hart and Chen, 2006).

Even more than a single disturbance type, the co-occurrence of different disturbances (e.g. windthrow, harvest, fire, browsing) has been highlighted as a key mechanism in the formation of dense understorey layers (Royo and Carson, 2006). Although the empirical study of the effects of multiple interacting disturbances is highly challenging (e.g., Allen, 2007), forest
landscape models provide a particularly helpful tool to explore the implications of cross-scale interactions between disturbance regimes (Temperli et al., 2013). With the inclusion of herbaceous vegetation as described here, LandClim offers a consistent framework to study the consequences of multiple interacting disturbances on overstorey-understorey dynamics.

**Conclusion**

Including herbaceous PFTs in a dynamic forest landscape model allowed us to study the interactive effects of light competition between trees and herbs. We found that forest succession can be significantly delayed by the herbaceous understory, although there was no evidence for ‘arrested’ succession in the long term. Our results suggest that the strongest impact of understory on the development of total forest biomass will be found at lower elevations and during early succession.

Furthermore, light competition with herbaceous plants favours more shade-tolerant tree species, and this shift in species composition was discernible for up to 200 years. The occurrence of large-scale disturbances (here, windthrow) increased herbaceous biomass across the landscape, but did not enhance the understory effect on tree regeneration as strongly as we expected, due to the consistent presence of advance tree regeneration in the simulations.

Overall, the simulation results emphasize the importance of considering the herbaceous layer when modelling forest dynamics, particularly with respect to understanding (1) the spatial and temporal patterns of early succession, and (2) the impacts of large-scale disturbances.

Recognizing that the herbaceous understory can alter tree species composition and understanding the mechanisms that cause this shift may be especially important for forest management and biodiversity conservation. However, additional ecological processes that are exerted or at least influenced by the understory layer (e.g., competition for water, mechanical inhibition) may be pivotal for the dynamics of some forest ecosystems, but are not included in LandClim yet. Integrating these would allow the model to be applied in ecosystems where factors other than light competition (co-)limit tree regeneration. A better understanding of the factors that influence tree regeneration across temporal and spatial scales will improve our ability to predict tree responses to changes in the environment or management regimes.

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References


Appendix

Appendix 1: Parameters of understorey PFTs

This section describes the choice of life-history parameters for the four understorey plant functional types (PFTs; grasses, tall forbs, ferns, small herbs) and the shrub PFT (*Rubus* spp.). Herbaceous cohorts are not subject to the mortality routines of trees. We assumed a continuous presence of all herbaceous PFTs throughout the simulation, which may occur at very low biomass when conditions are unfavourable. Due to the ubiquitous presence of the herbaceous layer, seed dispersal and vegetative resprouting was not considered either. Understorey PFTs were assumed to be unaffected by minimum winter temperatures, therefore a universal low value (-99) was assigned to all herbaceous PFTs. Since disturbances by browsing and fire were not considered in this study, the parameters ‘browsing tolerance’ and ‘fire tolerance’ were set to an intermediate value of 3 for all understorey PFTs. The life-history traits of the understorey PFTs are summarized in Table A1.1.

Grasses

Grass was implemented to represent a fast-growing, light-demanding pioneer PFT. The genus *Calamagrostis* was used to parameterize this PFT, due to its relatively well-studied ecology as a typical pioneer grass and its importance as a competitor with tree seedlings (Brumelis and Carleton, 1989; Hogg and Lieffers, 1991; Lieffers et al., 1993; Cater and Chapin, 2000; Küßner et al., 2000; Shropshire et al., 2001; Hart and Chen, 2006). Humbert et al. (2007) classified *Calamagrostis canadensis* as a very light-demanding species (class 9 of 9), corresponding to the LandClim shade tolerance level of 1 (very low shade tolerance). The grass PFT was assigned a high drought tolerance (0.33) (Ellenberg, 1996) and a minimum growing degree-day value of 200 (Fosaa et al., 2004).

Tall Forbs

Tall forbs represented a similar life strategy as grasses, including a rapid growth rate and high demand for light. For this PFT, the genus *Epilobium* served as a model organism (e.g., Dyrness, 1973; Lieffers et al., 1993; Küßner et al., 2000; Shropshire et al., 2001; Hart and Chen, 2006). Tall forbs were also assigned a shade tolerance level of 1 (very low shade-tolerance) (Humbert et al., 2007). Tall forbs tend to be more restricted to sites with good water supply (Ott et al., 1997), and thus were assigned a low drought tolerance (0.17) in LandClim. A minimum growing degree-day value of 650 was used based on measurements for the germination of *Epilobium angustifolium* by Mercier and Langlois (1993).

Ferns

Ferns represented a fast-growing herbaceous PFT, which is more shade tolerant and reaches higher biomasses than forbs. The assumption of higher shade tolerance is based on Alaback (1984), being supported by a number of studies observing abundant fern covers under closed-canopy forests (e.g., Alaback, 1982; Gilliam and Turrill, 1993; Hill and Silander, 2001; de la
Parameters for this PFT were based on the widespread bracken fern (*Pteridium aquilinum*), which can have severe effects on tree regeneration (George and Bazzaz, 1999a, 1999b; Royo and Carson, 2006). Although *Pteridium* is generally considered as a light-demanding pioneer (Barkham, 1978; Dolling, 1996), Den Ouden (2000) found that *Pteridium* is actually well-adapted to grow under a forest canopy, and Humbert et al. (2007) classified it as an intermediate light-demanding species (class 6 out of 9). This corresponds approximately to the LandClim shade tolerance class 3 (intermediate shade-tolerance). Ferns tend to be more prevalent on colder and moist sites (often on North-facing slopes, Neufeld and Young, 2003) and are sensitive to low moisture, where they are less competitive (Ellenberg, 1996). Therefore an intermediate drought tolerance was assigned, between the levels of grasses and forbs. A minimum growing degree-day value of 500 was assigned based on the COBRA-X model for *Pteridium aquilinum* by Pakeman and Marrs (1996) (Appendix 2 therein).

**Small herbs**

Small herbs were intended to represent plants of small stature, low biomass, but high shade tolerance. Numerous small herbaceous species exist in forest ecosystems, which comprise a wide variety of life-history traits (Bierzychudek, 1982), but unfortunately mostly lack systematic investigations. We therefore chose to define herbs as a late-successional life type (as for example found in the long-term study of Alaback, 1982) but acknowledge the restrictions of this assumption. A similar low drought tolerance (0.17) as for tall forbs was assigned to small herbs. A minimum growing degree-day value of 480 was assigned based on the information given in Laurent et al. (2004).

**Rubus**

The PFT of *Rubus* was implemented as a fast-growing pioneer shrub, based on descriptions by Balandier et al. (2013). In contrast to the herbaceous vegetation, *Rubus* was represented as an evergreen shrub growth type, as previously been implemented in LandClim by Henne et al. (2013). Functionally, the *Rubus* PFT resembles a small tree with a maximum height of 2 meters, and thus its establishment, growth and mortality is tracked in LandClim using the standard rules for tree species. Since the main focus was on the shading effect of herbs and shrubs, we performed a preliminary analysis on the behaviour of *Rubus* (results not shown) and found LAI to be simulated reasonably well by LandClim (maximum LAI was simulated to be 4.5; observed maximum LAI was 3.75; Balandier et al., 2006). *Rubus* was assumed to be rather drought tolerant (Balandier et al., 2013), therefore the same high drought tolerance as for grasses (0.33) was assigned. The $K_{\text{max}}$ parameter of *Rubus* was set to 500 g·m$^{-2}$, which corresponds to a maximum biomass of 5 t·ha$^{-1}$ (Kirby, 1980). However, the low shade tolerance (Balandier et al., 2013) prevents the species from maintaining such high biomass once it is overtopped by trees. A maximum age of 25 years was assigned (Davison and Forman, 1982; Alaback, 1984), although the actual longevity of individual *Rubus*-canes is lower. It is important to note, however, that the focus of our study was on the phenomenological description of a shrub layer within a larger cell of 25x25 m$^2$, not an accurate simulation of *Rubus* individuals. A minimum growing degree-day value of 898 was
assigned, based on the bioclimatic affinity grouping by Laurent et al. (2004). The original value from Laurent et al. (2004) given for the group of Rubus (Group 18) was 1290. However, with this assumption Rubus was virtually absent within the study landscape of Mt. Feldberg. Since Laurent et al. (2004) assigned Rubus to the same bioclimatic affinity group as Sorbus, the same minimum degree day value as for Sorbus aria (which is already parameterised in LandClim) was chosen. This assumption yielded more realistic results, with Rubus occurring up to 1100 m a.s.l. (see Figure 3 and respective discussion in the main manuscript). Data for minimum temperature tolerance (-18 °C) were based on descriptions by Laurent et al. (2004).

**Determination of herbaceous growth parameters**

Herbaceous growth parameters ‘Maximum biomass’ (K_{max}) and ‘Maximum growth rate’ (R_{max}) were determined based on post-windthrow vegetation data from the Black forest, following the storm events Vivian and Wiebke in February 1990 (Sayer and Reif, 1999). The parameter K_{max} was calculated by converting measured herbaceous cover for the sites ‘Enzklösterle’ and ‘Rippoldsau’ into biomass via allometric functions given by Turner et al. (2004) (for equations cf. Appendix 4). Since late-successional herbs were not explicitly distinguished in the measurements, the same K_{max} value as for forbs was assumed. The parameter R_{max} was tested within reasonable ranges in a preliminary analysis, ranging from values of 0.2 (>50 years to reach maximum biomass) to 1 (<10 years to reach maximum biomass). It was assumed that herbaceous pioneer PFTs (grasses, forbs) had the highest growth rate, followed by ferns and small, late-successional herbs.

Table A1.1: Summary of Life History Traits of Simulated Understorey PFTs

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Grass</th>
<th>Forb</th>
<th>Fern</th>
<th>Herb</th>
<th>Rubus</th>
</tr>
</thead>
<tbody>
<tr>
<td>lifeForm</td>
<td>Herbaceous</td>
<td>Herbaceous</td>
<td>Herbaceous</td>
<td>Herbaceous</td>
<td>Shrub</td>
</tr>
<tr>
<td>lifeCycle</td>
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<td>PERENNIAL</td>
<td>PERENNIAL</td>
<td>PERENNIAL</td>
<td>PERENNIAL</td>
</tr>
<tr>
<td>ShadeTolerance</td>
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<td>1</td>
<td>3</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>DroughtTolerance</td>
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<td>0.17</td>
<td>0.25</td>
<td>0.17</td>
<td>0.33</td>
</tr>
<tr>
<td>minTemperature (°C)</td>
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<td>-99</td>
<td>-99</td>
<td>-99</td>
<td>-18</td>
</tr>
<tr>
<td>minDegreeDay (d)</td>
<td>200</td>
<td>650</td>
<td>500</td>
<td>480</td>
<td>898</td>
</tr>
<tr>
<td>K_{max} (g m^{-2})</td>
<td>128</td>
<td>32</td>
<td>96</td>
<td>32</td>
<td>500</td>
</tr>
<tr>
<td>R_{max} (yr^{-1})</td>
<td>1</td>
<td>0.8</td>
<td>0.2</td>
<td>0.2</td>
<td>0.5</td>
</tr>
</tbody>
</table>
Appendix 2: Topography and soil maps for the Feldberg landscape

Input maps for the topography of the St. Wilhelm valley were derived from a digital elevation model (SRTM, Shuttle Radar Topography Mission, Version 4; http://srtm.csi.cgiar.org/, July 2014). Aspect and slope were calculated from the elevation data using the package ‘raster’ in R (R Development Core Team, 2014). Edaphic conditions were represented by a map of soil bucket size (see also Bugmann and Cramer, 1998 for an explanation of the ‘Bucket Size’ concept). Bucket size (BS in cm, i.e. water volume relative to soil surface, cm³·cm⁻²) is calculated from soil depth (D in cm) and available water content (AWC, volumetric water content in cm³·cm⁻³), as:

\[ BS = D \times AWC \]  

(Eq. A2.1)

Following the method described in Henne et al. (2013), a topographic wetness index (TWI, also referred to as the ‘compound topographic index’, CTI) was calculated for the St. Wilhelm catchment in the Black Forest with SAGA-GIS (Conrad et al., 2015). The TWI calculates catenary landscape positions based on the slope and the flow accumulation (Gessler et al., 2000) and has been shown to correlate well with soil variables determining BS (i.e., soil depth, content of silt and organic matter, Henne et al., 2013). Next, the TWI map was used to derive a landscape gradient of soil depth, ranging from shallow soils (D = 30 cm) to well-developed soils (D = 150 cm), as described for soils of the southern Black Forest region in Zöttl (1979). Based on the soil maps (BK 50) of the Landesamt für Geologie, Rohstoffe und Bergbau Baden Württemberg (LGRB, 2014, http://www.lgrb-bw.de/, July 2014) and from soil profiles of the Feldberg region (Zöttl, 1979), an AWC of 28% was estimated.
Appendix 3: Data and function for LAI-Biomass relationship

Empirical data relating leaf area index (LAI) and aboveground biomass (dry weight) were collected from the following studies: Friedl et al. (1994); Cayrol et al. (2000); Knops and Reinhart (2000); Spehn et al. (2000); Mirzaei et al. (2008); Vescovo and Gianelle (2008); Vohland and Jarmer (2008); Butterfield and Malmstrom (2009); Cerabolini et al. (2010). These data comprised study sites from North and Central America as well as Europe (Germany, Italy and Switzerland). The functional relationship is thus representative for temperate and Mediterranean conditions. Studies from the tropics (e.g., tall grass steppe) were not included. Furthermore, the majority of the data originated from graminoid species, due to their high economic importance for livestock feeding. Very little data were available for LAI and biomass for other herbaceous species. However, the few studies for ferns (e.g., Pitman, 2000) and tall forbs (e.g., Cerabolini et al., 2010; Inauen et al., 2013) indicate a similar functional relationship as for grasses. We therefore applied the following relationship to calculate LAI from biomass (in tons per ha) for all herbaceous groups:

\[
\text{LAI} = 0.7442 \cdot \text{biomass} \quad \text{(Eq. A3.1)}
\]

Due to the lack of data for biomass values >7.2 t·ha\(^{-1}\), we decided to assign an LAI cap of 5.4 to the herbaceous species to avoid unjustified extrapolations (cf. Fig. A3.1).

Figure A3.1: Allometric relationship between LAI and biomass, fitted to data from various sources: Friedl et al. (1994); Cayrol et al. (2000); Knops and Reinhart (2000); Spehn et al. (2000); Mirzaei et al. (2008); Vescovo and Gianelle (2008); Vohland and Jarmer (2008); Butterfield and Malmstrom (2009); Cerabolini et al. (2010).
Appendix 4: Allometric relationships between herbaceous cover and biomass

The following allometric functions express the relationship between herbaceous ground cover (in percent) and biomass (in t·ha⁻¹).

**Type Grass** (Turner et al., 2004, *Calamagrostis*)

\[
\text{cover}_\text{Grass} = \left( \frac{\text{biomass}_\text{Grass}}{0.04} + 1.0525 \right) / 0.5395 \\
\text{Eq. A4.1}
\]

**Type Forb** (Turner et al., 2004, *Epilobium*)

\[
\text{cover}_\text{Forb} = \left( \frac{\text{biomass}_\text{Forb}}{0.04} + 0.3088 \right) / 0.541 \\
\text{Eq. A4.2}
\]

**Type ’Fern’** (Pitman, 1989; Blackburn and Pitman, 1999; Pitman, 2000, *Pteridium*)

\[
\text{cover}_\text{Fern} = 100 \cdot (1 - \exp(-1.457 \cdot \text{biomass}_\text{Fern} \cdot 0.61825)) \\
\text{Eq. A4.3}
\]

**Type ’Herb’** (Turner et al., 2004, *Fragaria*)

\[
\text{cover}_\text{Herb} = \left( \frac{\text{biomass}_\text{Herb}}{0.04} \cdot 0.1136 \right) / 0.3598 \\
\text{Eq. A4.4}
\]
Appendix 5: Distribution of dominant tree species at Feldberg study site

Figure A5.1: Maps of dominant vegetation (in terms of species biomass per grid cell), in the absence (left) and presence (right) of herbaceous understorey for different times of succession.
Appendix 6: Herbaceous succession at different spatial scales

Figure A6.1: Effect of spatial aggregation on visibility of herbaceous succession stages for the Feldberg study landscape. Mean herbaceous biomass is shown for large scale (i.e. the entire landscape; a), intermediate scale (b) and nine individual grid cells (c). Maps on the right side show the forest biomass at year 400 for the respective spatial scales. The different scales shown in a-c refer to changes in spatial extent only, whereas grain (i.e. cell size) remains constant.
Appendix References


Chapter II

Overstorey-understorey interactions intensify after drought-induced forest die-off: long-term effects for forest structure and composition

Thripleton, T.; Bugmann, H.; Folini, M.; Snell, R.S. (2017)

_Ecosystems_

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Abstract

Severe drought events increasingly affect forests worldwide, but little is known about their long-term effects at the ecosystem level. Competition between trees and herbs (‘overstorey-understorey competition’) for soil water can reduce tree growth and regeneration success and may thereby alter forest structure and composition. However, these effects are typically ignored in modelling studies.

To test the long-term impact of water competition by the herbaceous understorey on forest dynamics, we incorporated this process in the dynamic forest landscape model LandClim. Simulations were performed both with and without understorey under current and future climate scenarios (RCP4.5 and RCP8.5) in a drought-prone inner-Alpine valley in Switzerland.

Under current climate, herbaceous understorey reduced tree regeneration biomass by up to 51%, particularly in drought-prone landscape positions (i.e., south-facing, low-elevation slopes), where it also caused a shift in forest composition towards drought-tolerant tree species (e.g., Quercus pubescens). For adult trees, the understorey had a minor effect on growth. Under future climate change scenarios, increasing drought frequency and intensity resulted in large-scale mortality of canopy trees, which intensified the competitive interaction between the understorey and tree regeneration. At the driest landscape positions, a complete exclusion of tree regeneration and a shift towards an open, savannah-like vegetation occurred.

Overall, our results demonstrate that water competition by the herbaceous understorey can cause long-lasting legacy effects on forest structure and composition across drought-prone landscapes, by affecting the vulnerable recruitment phase. Ignoring herbaceous vegetation may thus lead to a strong underestimation of future drought impacts on forests.

Keywords: dynamic vegetation model; understorey layer; soil water competition; vegetation shift; Valais; central Alps
Introduction

Drought severely affects the dynamics, structure and biodiversity of forests as well as most of the ecosystem services that they provide (Clark et al., 2016). Under climate change, novel combinations of precipitation and temperature are likely to cause unprecedented drought conditions in forested ecosystems (Dai, 2013; Clark et al., 2016). Already under present climate, extensive drought events have triggered large-scale forest die-off in many regions worldwide, with far-reaching ecological consequences (Allen et al., 2010; Anderegg et al., 2013). In particular, the long-term consequences of such severe drought events on forest ecosystems remain poorly understood (Anderegg et al., 2013; Anderegg et al., 2015).

From a meteorological perspective, drought is a prolonged period of below-average precipitation, often in connection with above-normal temperatures (Clark et al., 2016). The severity of drought experienced by vegetation, however, depends also on site conditions (e.g., slope, aspect, soil) and interactions among the vegetation itself (Cáceres et al., 2015). Inference about drought effects at larger spatial extents is thus challenging, as the impact of drought varies with local climate, but also with spatial heterogeneity of site conditions and vegetation structure (Cáceres et al., 2015). This is particularly important in mountain landscapes, where steep topographic gradients result in highly variable site conditions and differences in climatic conditions (Schumacher et al., 2004). Topography is furthermore important as it co-determines local irradiation and thus drought (McCarthy et al., 2001; Zou et al., 2007).

In addition to abiotic factors, competition with neighbouring vegetation will ultimately determine drought experienced by individual plants. This effect has been well documented by thinning experiments in xeric forests, where trees experience substantial growth releases due to enhanced water availability in thinned stands (e.g., Giuggiola et al., 2013). Previous research has predominantly focused on trees, but there is increasing awareness that the herbaceous understorey (i.e., grasses, forbs, ferns and herbs) can also be an important competitor for soil water (Balandier et al., 2006; Gobin et al., 2015). Despite its small stature, it can develop dense root systems in the topsoil, with rooting densities one to two orders of magnitude greater than trees (Nambiar and Sands, 1993). Measurements of total evapotranspiration demonstrate that the herbaceous understorey contributes on average 30% in boreal and temperate forests, and can reach even higher values during summer droughts (Jarosz et al., 2008; Gobin et al., 2015). Competition for water by herbaceous vegetation tends to be particularly strong for saplings, as small trees have not developed deep roots yet (Nambiar and Sands, 1993; Balandier et al., 2006). Although understorey competition is primarily an issue for tree regeneration (Balandier et al., 2006), the understorey can also exacerbate drought for mature trees at xeric sites (Richardson, 1993). If this effect is ignored, as done in most modelling efforts to date, the impacts of drought may be severely underestimated.

Neglecting the effect of understorey may be particularly problematic in the case of landscape-scale tree mortality (so called ‘forest die-off’, see also Allen et al., 2010) triggered by extreme climate events. Since understorey abundance is strongly coupled to canopy cover, overstorey
die-off promotes the growth of understorey vegetation (Anderegg et al., 2012). As a result, water competition between herbs and trees (particularly in early life stages) can be expected to intensify and potentially shift the species composition of tree regeneration. However, such vegetation shifts are mostly undocumented, and little is known about the long-term effects on successional trajectories (Anderegg et al., 2013).

Drought-related overstorey die-off and corresponding vegetation shifts have been reported for the Swiss Rhone valley (Valais) in the central Alps (Bigler et al., 2006; Rigling et al., 2013). This area represents one of the driest inner-Alpine landscapes and is considered as highly vulnerable to extreme climatic events under future climate change (Elkin et al., 2013). Increasing mortality of pine forests at low elevations and a shift to oak-dominated stands have been observed under present climate (Rigling et al., 2013). Within the same area, water competition by the understorey has been shown to reduce tree regeneration (Moser et al., 2010) as well as adult tree growth (Giuggiola, 2016). However, the impact of overstorey-understorey competition on future forest dynamics remains unclear.

Since empirical experiments are restricted in the spatiotemporal scales they address, dynamic vegetation models (DVMs) have been developed to explore the effect of specific processes at these large scales (Bugmann, 2001). Forest landscape models, a subset of DVMs, have been developed to investigate forest dynamics under changing climate and disturbance regimes (Schumacher et al., 2004). With their explicit representation of topography, soil, climate and vegetation dynamics, these models are suitable to investigate the spatially heterogeneous nature of climate change impacts on mountain landscapes (Schumacher and Bugmann, 2006; Henne et al., 2015). The DVM LandClim has recently been extended by an herbaceous understorey module (Thrippleton et al., 2016) and thus provides the opportunity to explore the impact of overstorey–understorey water competition on forest dynamics under climate change. We use the model in a study landscape in the Valais, Switzerland, to address the following questions:

1. How does water competition by the understorey affect drought as experienced by trees across the landscape?
2. What are the consequences of these overstorey-understorey interactions on forest structure and composition?
3. How do overstorey-understorey interactions change under future climate conditions?
Methods

Forest landscape model LandClim

LandClim is a spatially explicit, process-based forest landscape model that incorporates competition-driven stand dynamics and disturbance processes (e.g. fire, bark-beetle infestations, windthrow). The model has been used to study forest dynamics under past, present and future climate conditions across a range of landscapes in temperate forests in central and southern Europe (Schumacher et al., 2004; Henne et al., 2015), North America (Schumacher and Bugmann, 2006; Schwörer et al., 2016) and New Zealand (Thrippleton et al., 2014). Landscapes are represented as rasters (25 m × 25 m) with specific environmental conditions for each grid cell (i.e., aspect, slope, soil and climate). Within each grid cell, stand-scale processes are simulated, i.e. the establishment, growth and mortality of tree cohorts (groups of even-aged trees of the same species). Herbaceous understorey has recently been added to LandClim and was successfully used to address questions on the role of light competition between trees and herbs over a large elevational gradient (Thrippleton et al., 2016).

Development of water competition module between trees and herbs

Original water submodel of LandClim

The simulation of drought in LandClim is based on the water balance calculated for each grid cell in the landscape, accounting for precipitation, temperature, slope/aspect, and soil conditions. The original water balance in LandClim (Bugmann and Cramer, 1998) calculates supply and demand at a monthly resolution. Water supply is controlled by incoming rainfall reaching the soil surface ($P_{\text{soil}}$, monthly precipitation minus canopy interception), whereas demand is driven by evapotranspiration. Lateral water flow between grid cells is not considered, as it has been shown to play a relatively minor role compared to the representation of soil properties (Wolf, 2011). Stand evapotranspiration (ET) is the lesser of evapotranspirative demand (D) and water supply from the soil (S) following the approach of Federer (1982) (Eq. 1).

$$\text{ET} = \min (S, D) \quad \text{(Eq. 1)}$$

The soil is represented as a single soil layer, with a specific water holding capacity (WHC) depending on texture, depth, stone content and organic content of the soil (Henne et al., 2011). The soil layer is filled by water reaching the soil surface ($P_{\text{soil}}$) and depleted by evapotranspiration (ET). The model calculates a drought index (DI) for each month as:

$$\text{DI} = 1 - \frac{\text{ET}}{\text{D}} \quad \text{(Eq. 2)}$$

For annual and seasonal drought stress, a mean DI is calculated for the respective months (growing season is assumed as the months from April to October with average temperatures above 5.5°C).

Drought experienced by a tree cohort is represented as a drought reduction factor that is calculated from the site-specific DI and the species-specific drought tolerance using an
empirical reduction function (Schumacher et al., 2004). The drought reduction factor reduces tree growth and regeneration success, and increases mortality of adult trees (Schumacher et al., 2004).

**New overstorey-understorey water submodel**

To explicitly consider water competition between herbs and trees, the framework of Bugmann and Cramer (1998) was extended by calculating supply and demand for three separate groups: (1) herbaceous vegetation, (2) saplings (defined in the model as trees <10 years old), and (3) trees (Fig.1).

![Figure 1: Representation of water competition in LandClim, between the three groups herbs (represented by different functional types; cf. Thrippleton et al., 2016), saplings (i.e. tree age <10 years) and adult trees. Boxes represent variables, solid arrows links between variables, and dotted arrows the impact of drought indices (abbreviated as ‘DI’) on processes at the stand and landscape levels.](image)

The calculation of stand demand was based on Bugmann and Cramer (1998) and Elkin et al. (2015). Elkin et al. (2015) introduced a coupling between evapotranspiration and vegetation, which was not considered in the original model by Bugmann and Cramer (1998). Based on the approach by Elkin et al. (2015), an updated function connecting stand demand with leaf area index was included in the new water balance model, which improved the model performance and maintained its capacity to capture effects of thinning to mitigate drought impacts as described in Elkin et al. (2015). Further details are given in Appendix S1.
The relative fraction of total stand demand ($D_{\text{stand}}$) for each group was based on their amount of foliage weight (folW), since foliage characteristics determine transpiration to a large extent (Schulze et al., 2005):

$$D_{\text{Herb}} = D_{\text{stand}} \cdot \left( \frac{\text{folW}_{\text{Herb}}}{\text{folW}_{\text{Stand}}} \right) \quad \text{(Eq. 3)}$$

$$D_{\text{Sapling}} = D_{\text{stand}} \cdot \left( \frac{\text{folW}_{\text{Sapling}}}{\text{folW}_{\text{Stand}}} \right) \quad \text{(Eq. 4)}$$

$$D_{\text{Tree}} = D_{\text{stand}} \cdot \left( \frac{\text{folW}_{\text{Tree}}}{\text{folW}_{\text{Stand}}} \right) \quad \text{(Eq. 5)}$$

Foliage weights (folW) were calculated from biomass using allometric equations. For trees, those from Schumacher (2004) were used as implemented in the original version of LandClim. For saplings, we assumed a foliage weight of 40% (for evergreen trees) and 20% (for deciduous trees) of total aboveground biomass (based on Nelson et al., 2014). For herbs, we assumed that 50% of aboveground biomass was attributed to foliage (based on Niinemets, 2010).

The strategies for water uptake and root distribution often differ between herbs and trees, especially under water limited conditions (Balandier et al., 2006). Herbs and saplings concentrate their roots close to the soil surface (Balandier et al., 2006), where herbs often exceed root densities of trees by an order of magnitude (Nambiar and Sands, 1993; Moreno et al., 2005). In contrast, adult trees can access deeper layers of the soil where they preferentially take up water when root competition in the topsoil is high (Balandier et al., 2006). To account for this vertical stratification in water uptake, the single-layer soil model of LandClim was replaced by a two-layer model (the two layers are referred to as topsoil and subsoil in the following). It was assumed that herbs and saplings have access only to the topsoil layer while adult trees can access both layers. This two-layer model is frequently used for savannah ecosystems (Ward et al., 2013) and a variety of other process-based vegetation models (e.g. LPJ-Guess, Gerten et al., 2004).

Precipitation reaching the soil surface ($P_{\text{soil}}$) infiltrates into the topsoil layer and becomes available to herbs and saplings. Since soil evaporation in forests is usually negligible (Black and Kelliher, 1989, see also explanation below), all water that is not transpired by herbs and saplings is transferred to the subsoil layer. Adult trees have access to the remaining water in both topsoil and subsoil. At the end of each time step (i.e., each month), all remaining water is stored in the subsoil layer, filling from the bottom up (i.e., only after the water holding capacity of the subsoil layer is exceeded, water is stored in the topsoil layer, thus implicitly mimicking percolation). During months with no precipitation it is thus possible that the topsoil dries out, while water in the subsoil is still available for adult trees. When the amount of soil water exceeds the water holding capacity of the soil (i.e. WHC$_{\text{tot}}$), excess water is lost from the system.

It was assumed that the WHC of the topsoil (WHC$_{\text{top}}$) comprises the soil volume where most herb roots are located, which is typically within the upper centimetres (Roberts et al., 1980; Jackson et al., 1996). Due to the lack of detailed information of soil texture at the landscape
scale, an average water holding capacity of 6 cm was assumed for the topsoil layer, based on Henne et al. (2011).

\[ \text{WHC}_{\text{top}} = \min(6, \text{WHC}_{\text{tot}}) \]  
(Eq. 6)

The WHC of the subsoil (WHC_{\text{sub}}) is defined as the remainder of WHC_{\text{tot}}, i.e.:

\[ \text{WHC}_{\text{sub}} = \text{WHC}_{\text{tot}} - \text{WHC}_{\text{top}} \]  
(Eq. 7)

As a consequence, the subsoil will have no water holding capacity if WHC_{\text{tot}} of the soil is equal or less than 6 cm.

The actual transpiration (T) of herbs, saplings and trees are defined as the lesser of their respective water supply (S) and demand (D), analogous to the original model (Eq. 1):

\[ T_{\text{Herb}} = \min (S_{\text{Herb}}, D_{\text{Herb}}) \]  
(Eq. 8)

\[ T_{\text{Sapling}} = \min (S_{\text{Sapling}}, D_{\text{Sapling}}) \]  
(Eq. 9)

\[ T_{\text{Tree}} = \min (S_{\text{Tree}}, D_{\text{Tree}}) \]  
(Eq. 10)

Due to the higher rooting density of herbaceous vegetation in the topsoil (Nambiar and Sands, 1993; Moreno et al., 2005), it was assumed that the herbaceous understorey has priority for water uptake in the topsoil layer. In addition, herbaceous vegetation can take up to 50% of incoming precipitation reaching the soil surface (Knoop and Walker, 1985). Thus, the equation for soil water supply for herbs (S_{\text{Herb}}) is:

\[ S_{\text{Herb}} = 0.5 \cdot \text{P}_{\text{soil}} + \text{Water}_{\text{top}} \]  
(Eq. 11)

Where Water_{\text{top}} is the amount of water stored in the topsoil layer. Compared to herbs, saplings are inferior competitors in terms of rooting densities and water uptake (Balandier et al., 2006). It was thus assumed that saplings only have access to the water in the topsoil layer that has not already been removed (i.e. transpired) by herbs:

\[ S_{\text{Saplings}} = 0.5 \cdot \text{P}_{\text{soil}} + \text{Water}_{\text{top}} - T_{\text{Herb}} \]  
(Eq. 12)

Based on the concept of vertical niche separation for water uptake (see above) it was assumed that mature trees are least competitive in the topsoil and preferentially access water in the subsoil. The uptake of the water therefore follows a hierarchical order from herbs to saplings and adult trees. Thus, the supply for adult trees is the water in both soil layers (Water_{\text{tot}}) that has not been removed by herbs and saplings:

\[ S_{\text{Trees}} = \text{Water}_{\text{tot}} - (T_{\text{Herb}} + T_{\text{Sapling}}) \]  
(Eq. 13)

Overall, stand evapotranspiration (ET) thus includes evaporation of intercepted water (P_{\text{i}}) and transpiration from vegetation (T_{\text{Herb}}, T_{\text{Saplings}}, T_{\text{Tree}}).
Chapter II

Analogous to the original formulation (Eq. 2), the drought index (DI) for herbs, saplings and adult trees is calculated as:

\[
\text{DI}_{\text{Herb}} = 1 - \left( \frac{T_{\text{Herb}}}{D_{\text{Herb}}} \right)
\]  
\text{(Eq. 14)}

\[
\text{DI}_{\text{Sapling}} = 1 - \left( \frac{T_{\text{Sapling}}}{D_{\text{Sapling}}} \right)
\]  
\text{(Eq. 15)}

\[
\text{DI}_{\text{Tree}} = 1 - \left( \frac{T_{\text{Tree}}}{D_{\text{Tree}}} \right)
\]  
\text{(Eq. 16)}

The model only considers negative interactions (i.e. competition) between trees and herbs, and does not account for facilitative effects (e.g., protection from desiccation via shading, hydraulic redistribution) under extremely dry conditions. We acknowledge the importance of facilitation under harsh conditions, but consider competition as the dominant interaction between herbs and trees for most temperate forests (Balandier et al., 2006).

Evaporation from the soil was furthermore assumed to be negligible compared to transpiration from the herbaceous understory (Black and Kelliher, 1989; Schaap and Bouten, 1997). Soil evaporation is effectively determined by the amount of solar radiation reaching the soil surface (Baldocchi et al., 2000). The presence of vegetation shields the soil surface from radiation, reduces ventilation and can additionally insulate the soil surface by deposited litter (Baldocchi et al., 2000). Since our landscape was covered by a dense vegetation (ranging from closed canopy forest to dense grassland), we considered the assumption of a negligible soil evaporation as reasonable.

**Model evaluation**

To evaluate the new water submodel, we compared LandClim results to empirical data from five study sites across Europe (Fig. 2a). They were selected based on the availability of evapotranspiration measurements for both overstorey and understory, and as a representation of different climatic and site conditions. Data were taken from (1) Constantin et al. (1999) for Norunda, Sweden; (2) Roberts et al. (1980) for Thetford Chase, UK; (3) Jarosz et al. (2008) for Le Bray, France; (4) Giuggiola (2016) for the Valais, Switzerland; and (5) Joffre and Rambal (1993) for Sierra Norte de Sevilla, Spain (cf. Fig. 2). Each simulation was based on present climate (see Appendix S2, Table S2.1) and 10 replicates on an area of 400 grid cells (i.e., 25 ha). Forest growth was simulated for each site with site-specific climate, species and management regimes (see Appendix S2). LandClim consistently reproduced the characteristics of the forest stands as reported in empirical studies (see Appendix S2 for further information). When the forest reached the same age as described in the respective study, the simulated understory contribution to stand evapotranspiration was compared to empirical measurements. For additional model evaluation, the effect of understory on tree growth was simulated (see Appendix S2, S4). Since understory removal experiments were not conducted at these sites (with the exception of the Valais site), we were unable to compare the simulated effect of understory water competition on tree growth with empirical data (but see Appendix S2 for further details).
Model application

Study landscape

To examine the impact of overstorey-understorey water competition across a landscape gradient covering a wide range of environmental conditions, we chose the dry inner-alpine Rhone valley around Visp in Valais, Switzerland (46°11’ N and 7°93’ E, see Fig. 2b). The dry-subcontinental climate of the valley bottom is characterized by low precipitation (below 600 mm/year) and relatively high mean annual temperature (9.5 °C, climate station Visp at 650 m a.s.l.) (Bigler et al., 2006). At the highest elevation, low temperature strongly limits plant growth and upper treeline is located at around 2300 m a.s.l.. The wide range of environmental conditions is reflected in the tree species dominating the different elevational zones: low elevations are dominated by *Pinus sylvestris*, which is currently experiencing drought-related decline (Rigling et al., 2013) and is expected to be impacted even more strongly by future climate change (Elkin et al., 2013). Higher elevations are dominated by *Picea abies* (from 1200-1800 m) and *Pinus cembra* as well as *Larix decidua* close to treeline (Elkin et al., 2013). Forests in the Valais are generally managed for their protective function against gravitational hazards (rockfall, avalanches). Further details about the study landscape are given in Elkin et al. (2013) and in Appendix S3 (Fig. S3.1).

Simulation experiments

An initial forest state was created with spin-up simulations as described in Elkin et al. (2013), under present climate conditions (MeteoSwiss; http://www.meteoswiss.admin.ch/, August 2015). The entire landscape was assumed to be forested, so as to include the complete spectrum of elevation and topographic conditions. Simulations included an herbaceous understorey consisting of the plant functional types grass, forb, fern and herb, as implemented in Thrippleton et al. (2016). To account for variability of the initial forested state, the spin-up simulations were replicated 10 times, each using different present climate time series (randomly re-sampled with replacement from present climate records).

![Figure 2](image.png)

**Figure 2**: Location of (a) the five study sites across Europe used for model evaluation and (b) the main study landscape around Visp in the Valais, Switzerland.
For studying the long-term effects of understorey-overstorey water competition, simulations were carried out either including or excluding the herbaceous understorey. Simulations, both with and without understorey, started from the initial forest state and ran for 100 years under current and future climatic conditions (corresponding to the time span of year 2000 to 2100).

For future climate, ten downscaled and bias-corrected regional climate model (RCM) scenarios for the Visp climate station were used (Rajczak et al., 2016). Each scenario was aggregated to a monthly resolution to derive climate change scenarios for the years 2000 to 2100. Among these ten regional climate change scenarios, two scenarios were chosen that represent the maximum range between a ‘low impact’ (ICHEC-EC EARTH-DMI, RCP 4.5) and a ‘high impact’ scenario (ICHEC-EC EARTH-CLMcom, RCP 8.5). Scenarios from two GCM-RCM model chains were used since they represented a wider climatic range than the difference between emission scenarios within a single model chain.

To evaluate the impact of herbaceous water competition, the changes in DI were assessed relative to the scenario without understorey at each grid cell of the study landscape. Effects on forest structure were analysed by calculating mean tree biomass and stem density for three representative elevation levels (700 m, 1200 m, 1900 m) for the north- and south-facing slopes of the study landscape. Species shifts were analysed in terms of mean biomass change relative to the ‘no understorey’ scenario across the entire elevation gradient to account for gradual elevation shifts with climate change. All simulations were carried out with LandClim version 1.7, analyses were done with R, version 3.3.0 (R Development Core Team, 2016).
Results

Model evaluation

In general, the simulated understorey contribution to total stand evapotranspiration followed the same pattern as in the empirical data (Fig. 3). LandClim yielded the lowest understorey contribution for the site Norunda (14%), an intermediate contribution for the sites Thetford Chase, Le Bray and Valais (18-30%) and the highest understorey evapotranspiration for the two sites in Sierra Norte de Sevilla (40-70%). Measured understorey contribution was within the range of simulated values for all sites, with the exception of the high-elevation Sierra Norte de Sevilla site, where the model underpredicted the understorey contribution. Across the European sites, herbaceous understorey competition reduced adult tree growth by 2 – 15% (Appendix S4, Fig. S4.1).

![Figure 3: Measured (red triangles) and simulated (box plots) understorey contribution to stand evapotranspiration (ET) at five European sites (note that Sierra Norte de Sevilla contained two study sites: ‘low elevation’ stand at 280 m, ‘high elevation’ stand at 580 m a.s.l.). Boxplots show results of 10 simulation runs. Empirical data from: (1) Constantin et al. (1999); (2) Roberts et al. (1980); (3) Jarosz et al. (2008); (5,6) Joffre & Rambal (1993). For the Valais (4), understorey contributions were not measured directly but estimated indirectly based on difference in soil water availability between understorey removal and control plots (Giuggiola, 2016). Standard deviations for the measured values are not included since they were mostly not available.]
**Understorey impact on drought for trees across the landscape**

Under current climate, understorey competition for water increased the drought experienced by saplings on south-facing slopes at low elevations (DI increase by 0.2-0.5; Fig. 4a). At elevations above 1200 m a.s.l. and on most north-facing slopes, the understorey had practically no impact on drought for saplings. For adult trees, competition by the herbaceous understorey caused a small increase in the DI across the landscape (Fig. 4b). In contrast to elevation and aspect, soil WHC only had a minor influence on changes to the DI (see Appendix S4, Table S4.1).

![Figure 4](image_url): Understorey effect on the drought index (shown as difference between scenarios including and excluding herbaceous understorey) for saplings (i.e. tree age <10 years) and adult trees across the study landscape of Visp, Valais. Results show the final simulation year (i.e. 2100 AD) under current climate and future climate change (‘Low Impact CC’: ICHEC-EC EARTH-DMI RCP 4.5 and ‘High Impact CC’: ICHEC-EC EARTH-CLMcom RCP 8.5).

Under the ‘low impact’ (RCP 4.5) climate change scenario, there was little difference to current conditions in terms of sapling and tree DI (Fig. 4c,d). However, understorey water competition had a considerably stronger impact on sapling drought in the ‘high impact’
scenario (RCP 8.5) with an increase of DI by >0.5 (Fig. 4e). The most prominent pattern was an increase in DI for saplings across the entire valley bottom. Furthermore, there was an upward elevation shift of areas affected by water competition between herbs and tree saplings (Fig. 4e). Under the ‘high impact’ scenario, elevations up to 1100 m. a.s.l. were impacted by drought compared to merely 800 m. a.s.l. under the present climate. For adult trees, the ‘high impact’ scenario resulted in a larger area affected by an increase in drought due to herb competition, although the magnitude of drought did not differ substantially from the ‘present climate’ conditions (Fig. 4b,f).

**Overstorey-understorey effects on forest structure**

While tree overstorey and herb understorey biomass remained largely constant in the simulation under the current climate, future climate change caused substantial tree mortality and a corresponding response in the understorey (Fig. 5). Total aboveground biomass of trees decreased during the 21\textsuperscript{st} century for both the ‘low impact’ (loss of 50 t ha\textsuperscript{-1} in 2030, Fig. 5b) and the ‘high impact’ (loss of 110 t ha\textsuperscript{-1} in 2080, Fig. 5c) climate change scenario, due to increasing drought intensity and frequency (Appendix S4, Fig. S4.2). Herbaceous understorey responded strongly to the simulated overstorey die-off, as shown by an increase in herb biomass (Fig. 5e,f). While the effect was smaller and rather ephemeral for the ‘low impact’ scenario, the understorey biomass doubled in the ‘high impact’ scenario (Fig. 5f).

![Figure 5: Development of tree overstorey (a-c) and herbaceous understorey (d-f) shown as landscape mean for present climate, ‘Low Impact’ and ‘High Impact’ future climate change scenarios (ICHEC-EC EARTH-DMI RCP 4.5 and ICHEC-EC EARTH-CLMcom RCP 8.5, respectively). Black line represents the mean biomass, shaded areas indicate the 90% confidence interval.]
Higher understorey biomass increased competition with saplings and thus caused a strong decrease in *regeneration* biomass (up to -51% under present climate and -58% for the ‘high impact’ climate change scenario, with regeneration referred to young trees at the age of 10 years) and density (-46% under present and -48% under ‘high impact’ climate scenario) at low-elevation, south-facing slopes for the year 2100 (Tables 1, 2). North-facing slopes and higher elevations were much less affected. The understorey effect on *total* tree biomass and density was substantially smaller, but showed the same pattern in terms of aspect and elevation.

At the species level, understorey competition for water caused a shift by reducing the regeneration of *Abies*, *Acer*, *Picea*, *Pinus* and *Larix* at elevations <1000 m a.s.l., which in turn favoured the more drought-tolerant species *Quercus pubescens* and *Sorbus aria* (Fig. 6). This effect was substantial for south-facing slopes (Fig. 6a-c) but minor for north-facing slopes (Fig. 6d-f). An upward extension of areas affected by the species shift occurred for the ‘high impact’ Scenario (Fig. 6a-c).

![Figure 6](image-url): Difference in the species-specific regeneration biomass (i.e. young trees at the age of 10 years) relative to the scenario without herbaceous understorey across the elevation gradient for south-facing (a-c) and north-facing slopes (d-f) under different climate scenarios. ‘Low Impact CC’ and ‘High Impact CC’ refer to the ICHEC-EC EARTH-DMI RCP 4.5 and ICHEC-EC EARTH-CLMcom RCP 8.5 climate change scenarios, respectively.
Under the ‘high impact’ scenario, competition by the herbaceous understorey was so severe that tree regeneration was entirely inhibited in parts of the landscape (red areas in Fig. 7c). In the absence of tree regeneration after overstorey die-off (Fig. 7a), the vegetation shifted to an open, savannah-like landscape (Fig. 7e), dominated by the light-demanding grass PFT.

Figure 7: Biomass distribution of trees (a,b: all trees, c,d: regeneration, i.e. young trees at the age of 10 years) and herbs (e) across the study landscape in Visp (Valais, Switzerland) for the year 2100 under the ‘High Impact’ scenario (ICHEC-EC EARTH-CLMcom RCP 8.5), including and excluding the herbaceous understorey. Red colour indicates areas of low forest biomass (< 30 t ha$^{-1}$ in a,b) and a lack of regeneration (c,d), respectively.
Table 1: Tree biomass (all trees and regeneration, i.e. young trees at age of 10 years) for the year 2100 under scenarios with and without herbaceous understorey competition for different aspect, elevation and climate change scenarios. ‘Low Impact CC’ refers to the ICHEC-EC EARTH-DMI RCP 4.5 scenario, ‘High Impact CC’ refers to the ICHEC-EC EARTH-CLMcom RCP 8.5 climate change scenarios.

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<th>High Impact CC</th>
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Table 2: Stem density (all trees and regeneration, i.e. young trees at age of 10 years) for the year 2100 under scenarios with and without herbaceous understorey for different aspect, elevation and climate change scenarios. ‘Low Impact CC’ refers to the ICHEC-EARTH-CLMcom RCP 4.5 climate change scenarios, ‘High Impact CC’ refers to the ICHEC-EARTH-EC ECHAM6-HAM2.0 RCP 8.5 climate change scenarios.

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Chapter II

Discussion

Our results demonstrated the long-term implications of water competition between overstorey and understorey, indicating strong impacts on the structure and composition of drought-prone forests under future climate change. Below, we discuss our findings with respect to (1) the contribution of the understorey to stand evapotranspiration; (2) landscape patterns of the understorey effects on the drought experienced by trees; and (3) their long-term impacts on forest structure and composition. Ultimately, we address (4) the implications of climate change for overstorey-understorey feedbacks.

Understorey contribution to stand evapotranspiration

Empirical studies have shown that fluxes from the forest understorey are generally lower in dense forests (Schaap and Bouten, 1997), and increase considerably as the canopy opens (Black and Kelliher, 1989; Baldocchi et al., 2000; Iida et al., 2009). In savannahs, the understorey contribution to total evapotranspiration can reach 40 to 60% of the total (Baldocchi et al., 2004). Empirical data at our five European study sites showed a similar pattern, which was reproduced by the model consistently (Fig. 3). In LandClim, the main factor for understorey biomass (and thus its contribution to stand evapotranspiration) was available light at the forest floor (Thrippleton et al., 2016). The increasing understorey contribution across the European stands also corresponds to an increase in canopy openness, with Norunda having the densest stands and the savannah-like oak stands in southern Spain having by far the lowest stand density. This linkage between overstorey openness and understorey contribution has been shown in several temperate and boreal forest stands worldwide (Jarosz et al., 2008; Iida et al., 2009). At the global scale, the understorey of temperate and boreal forests contributes on average one-third to total stand evapotranspiration (Gobin et al., 2015), with closed-canopy forests showing averages below this value (3-21%) and more open-canopy forests frequently ranging between 20 and 40% (Jarosz et al., 2008). LandClim captured these trends well, and additionally provides us the means to explore how understorey contributes to drought impacts for trees as a function of topography, soil conditions and climate.

Landscape patterns of understorey effects on drought experienced by trees

Topography is known to mediate the impacts of drought (Adams et al., 2014), with aspect being particularly important (Johnstone et al., 2010). Our simulations showed a strong impact of both elevation and aspect: low-elevation, south-facing slopes had increased herbaceous water competition, resulting in higher drought indices, lower tree cover and higher understorey biomass dominated by light-demanding early-successional grass PFTs. Similar patterns were reported for drought-affected forests, where more open, south-facing stands are typically characterized by an understorey of early-successional herbs and shrubs (Halpern and Lutz, 2013; Saura-Mas et al., 2015). The vigorous understorey at these landscape positions is often considered problematic for tree regeneration (e.g., McCarthy et al., 2001). In extreme cases of overstorey mortality (e.g. due to wildfire), tree regeneration can be severely inhibited by herbaceous water competition on sun-facing slopes (Moser et al., 2010).
Edaphic conditions also co-determine drought severity across larger scales, i.e. landscape to regional extents (Cáceres et al., 2015). Interactions with the understorey are generally increasing in importance as soils get shallower or poorer in water retention (Balandier et al., 2006; Provendier and Balandier, 2008). Contrary to this expectation, the simulated understorey effect on drought experienced by trees was largely independent of soil water holding capacity (WHC). This is likely due to two main reasons: estimates of WHC were generally high for the entire landscape (>9 cm) and unevenly distributed across the landscape (Appendix S3, Fig. S3.1d). Due to our assumption of a fixed topsoil layer of 6 cm WHC, a substantial portion of water was stored in the subsoil layer. While herbs were thus competing strongly with saplings in the topsoil, adult trees had access to deeper water sources and were less affected by herbaceous competition. An empirical study by Rigling et al. (2002) from sites close to our study landscape reported soils of partially lower WHC than those in our soil map, but noted that trees roots can grow into rock crevices. It is thus likely that our WHC estimates were overestimated for parts of the landscape. The accurate determination of soil WHC is however difficult in complex and heterogeneous landscapes and provides a general obstacle for assessments of drought impacts on forests (Cáceres et al., 2015).

**Understorey competition effects on forest structure and composition**

Understorey water competition is widely viewed as an important process reducing regeneration density and growth in both coniferous (Richardson, 1993; Picon-Cochard et al., 2006) and broadleaved forests (Balandier et al., 2006; Provendier and Balandier, 2008). In our simulations, regeneration biomass was reduced by up to 51% at drought-prone landscape positions under present climate, which is in a similar range as found by empirical studies from the USA and Europe, showing reductions of regeneration biomass by 50 – 85% due to understorey water competition (Morris et al., 1993; Nambiar and Sands, 1993; Picon-Cochard et al., 2006). Most studies suggest that herbaceous competition becomes negligible as trees overtop the herbaceous layer and develop deeper roots (Balandier et al., 2006). In accordance with this expectation, our simulation results showed little effect of understorey water competition on adult trees (Fig. 4). In the long term, however, the interactions during the regeneration stage are known to reduce forest production (Balandier et al., 2006), which was also evident from our simulations. This effect has been highlighted particularly in production forests, where understorey competition can result in a strong reduction of long-term timber yield (Wagner et al., 2006), although we caution the perception of herbaceous understorey as merely undesirable ‘weed’ and emphasize its importance for biodiversity and ecosystem functioning (see Gilliam, 2007).

The herbaceous understorey is furthermore important as a filter for tree establishment and may shift species composition by selecting for specific traits (George and Bazzaz, 1999a). In our simulations, competition with herbaceous vegetation increased the impact of drought and thus mortality of drought-sensitive species, which led to a shift towards more drought-tolerant tree species. The simulated increase in *Quercus pubescens* in our climate change scenarios corresponds well to currently observed drought-induced vegetation shifts from *Pinus* sp. towards the more drought-tolerant *Quercus* sp. in the Valais (Rigling et al., 2013) and in
Mediterranean forests (Galiano et al., 2013). However, most empirical studies of forest dynamics and composition do not account for the role of herbaceous understory (McCarthy, 2003). In an experimental study, Davis et al. (1998) showed that tree seedling mortality during drought is in fact more likely due to herbaceous competition than to the direct effect of drought itself. In accordance with this finding, our simulation results suggest that herbaceous understory exacerbates the effect of drought on tree regeneration, and thus has the potential to induce long-lasting imprints on forest biomass and species composition.

**Climate change-induced overstorey-understorey feedbacks**

A number of studies have demonstrated the response of understory vegetation to drought-induced overstorey die-off, but little is known about the long-term consequences of such vegetation shifts for successional trajectories (Anderegg et al., 2013). Our results show that drought-related overstorey die-off can induce a phase of intense competition between tree regeneration and understory vegetation, thereby exacerbating the legacy effects of drought on forest structure and composition. Under the ‘high impact’ climate scenario, our simulations suggest that the feedback between overstorey and understory can result in fundamental vegetation shifts up to the point where closed forest is replaced by open, grass-dominated vegetation. Empirical studies from the Valais have shown substantial drought-related tree mortality already under present climate conditions (Bigler et al., 2006; Rigling et al., 2013). Moser et al. (2010) investigated post-disturbance tree regeneration in the presence of competing herbaceous vegetation in the Valais, concluding a high risk of shifts towards forest-free vegetation with increasing frequency of drought events, which supports our simulation results. Various studies from temperate forests have shown the high potential of herbaceous understory to inhibit tree regeneration for prolonged periods, but it is unclear whether this corresponds to a change of land cover that is stable in the long-term (Royo and Carson, 2006). Our results showing that strong competition by the herbaceous understory was able to exclude tree regeneration until the end of the 21st century suggest that this is the case indeed. The increasing importance of the light-demanding and drought-tolerant grass PFT under the ‘high impact’ climate change scenario furthermore underlines the differentiated effect of climate change on herbaceous PFTs (e.g., Patsias and Bruelheide, 2013). It has to be noted, however, that in the present model version, compositional shifts in the understory only result in an altered competition with trees if herbaceous biomass (i.e., foliage weight) changes.

On a global level, several observations indicate that drought-induced forest die-off has led to changes in the regeneration layer that were influenced by understorey water competition (e.g., Suarez and Kitzberger, 2008 from South America; Anderegg et al., 2012 from North America; Saura-Mas et al., 2015 from Europe). With more frequent extreme drought events and associated forest die-off in the future (Allen et al., 2010), the tree regeneration stage will be of increasing importance under climate change (Galiano et al., 2013). In line with these studies, our results highlight the importance of herbaceous competition with tree regeneration following overstorey mortality and draw particular attention on the long-term impacts that are likely to occur under future climate change.
Climate change-induced vegetation shifts, such as the increase of drought-tolerant oak *Quercus pubescens* in our study, mark substantial changes for an ecosystem and the services it provides. Changes in forest structure and tree species composition following drought-related overstorey mortality are often associated with altered community structure and can have cascading effects on ecosystem function (Anderegg et al., 2013). Furthermore, a conversion towards more open, oak-dominated landscapes may have substantial economic consequences due to a reduction of forest biomass and shifts away from commercially valuable coniferous timber (Hanewinkel et al., 2013). Additionally, in mountain landscapes, forest structure and composition have implications for protective ecosystem services (Schuler et al., 2016). For our study region, forests are of high importance as protection primarily against rockfall (Elkin et al., 2013), and a persistent loss of tree cover or conversion to grassland would severely deteriorate this function.

Overall, we demonstrated that herbaceous understorey can exacerbate legacy effects of drought in temperate forests. We therefore caution against neglecting the herbaceous understorey in assessments of vegetation dynamics under future climatic conditions, as this may lead to a critical underestimation of the long-term effects of drought.

**Acknowledgements**

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References


Appendix

Appendix 1: Linkage of stand demand to vegetation structure

The water balance submodule of LandClim calculates a drought index based on evapotranspirative demand (D) and water supply from the soil (S) following the approach of Federer (1982). In the original formulation of the water balance submodel, the drought index was calculated independently of vegetation structure (Bugmann and Cramer, 1998). To account for the effect of vegetation, Elkin et al. (2015) included the leaf area index (LAI) in the calculation of the drought index. In the approach of Elkin et al. (2015), stand water use was lowest at a LAI of 0 (unvegetated condition), and increased by 25% at a LAI of 8 (dense stand), based on empirical data from Moreno and Cubera (2008).

Preceding the present study, the water submodel developed by Bugmann and Cramer (1998) and extended by Elkin et al. (2015) had been investigated in detail and evaluated with empirical data from 25 FLUXNET sites across Europe and North America (Folini, 2015). The submodel performed reasonably well, but deviated from empirical measurements in sites where trees had access to ground water sources (not considered in LandClim) and where water storage in snowpack is important. The latter issue has since been addressed by Schwörer et al. (2016).

However, the approach of Elkin et al. (2015) functionally coupled the vegetation LAI only to the supply-side, making it unsuitable to our approach, which needs to account for the contribution of understorey to stand demand as well. We thus based our approach on the original model version by Bugmann and Cramer (1998) and developed a new function linking stand demand to vegetation LAI via a vegetation-dependent demand factor ($F_{vegetation}$) (see Fig. S1.1), based on the empirical relationship between stand water use and LAI used in Elkin et al. (2015). In the new model, stand demand ($D_{stand}$) is then calculated as:

$$D_{stand} = (PET \cdot F_{vegetation}) - P_i$$  \hspace{1cm} (Eq. S1.1)

Where PET is the potential evapotranspiration (based on the approach of Thornthwaite and Mather, 1957) and $P_i$ is the amount of intercepted precipitation (see Bugmann and Cramer, 1998, for further details).
This assumption essentially implies that a dense vegetation canopy transpires more water than sparse vegetation. On a broad level, this is in line with the finding that the biological regulation of stand transpiration is mainly due to stand LAI and stomatal conductance (Granier et al., 2000). It has to be noted, that stand transpiration is a much more complex process and generalisations at larger scales are usually difficult to obtain (Granier et al., 2000; Schulze et al., 2005). Our simplified relationship between stand demand and LAI is however consistent with patterns at the catchment level (Brown et al., 2005; Komatsu et al., 2007; Marc and Robinson, 2007), which we considered as a reasonable phenomenological representation at a coarse scale.

In order to evaluate the effect of the old and the new Demand-LAI relationship (Fig. S1.1) on the model performance, we used published evapotranspiration data from forests that differed in terms of their LAI, but were similar in terms of other environmental conditions (climate, soil, etc.). The studies by Stoy et al. (2006) and Sun et al. (2008) provided suitable data sets in this respect and covered a rather wide range of LAI (Tab. S1.1). We applied the water balance submodel to the study locations (Duke Forest, North Carolina and Chequamegon-Nicolet National Forest, Wisconsin, USA) and measured the model performance in terms of the percentage bias (i.e. the deviation between measured and simulated monthly evapotranspiration). The simulations were carried out with both model versions, which were then compared to each other. As shown in Tab. S1.1, the new model version was consistently closer to measured values for all sites. We therefore considered our new formulation of stand demand as an improvement compared to the previous version.
Table S1.1
Model evaluation: site characteristics and model performance. Model performance was measured using the percentage bias (i.e., the deviation between measured and simulated monthly evapotranspiration).

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<th>Study Site</th>
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Appendix 2: Study design for European Sites

Five study sites across Europe were selected (Fig. 2, main manuscript), where empirical data about the understorey contribution to stand evapotranspiration was available. The aim was to test (1) whether the model simulated realistic understorey contribution to stand evapotranspiration and (2) whether the resulting tree growth reduction was in a reasonable range.

Simulation experiment

The simulation experiments were carried out in two phases (see also Fig. S2.1):

(1) A ‘stand development’ phase, where forest growth was simulated using site specific species composition and management until the forest age was reached that was equivalent to the empirical data (see Table S2.1). For the evaluation of understorey contribution to stand evapotranspiration, the annual means from the final decade of the ‘stand development’ phase were compared to empirical data.

(2) An ‘understorey removal’ phase, where scenarios including understorey were compared to scenarios where the understory was removed. This phase was simulated for 10 years, since empirical understorey removal experiments are usually only a few years (e.g., Moreaux et al., 2011). For quantifying the understorey effect on tree growth, the simulated biomass of dominant trees from the beginning and end of this simulation period were compared between scenarios (i.e. including and excluding understorey). As empirical understorey removal experiments are rare for mature stands (see e.g., Richardson, 1993), we were not able to compare simulated results for each site with a comparable empirical data set.

Figure S2.1 Concept of stand development and understorey removal simulations.
For each study site, a landscape of 400 grid cells (i.e. 25 ha) was simulated to account for stochastic variability between individual grid cells. Monthly climate data from nearby climate stations (see Table S2.1) was obtained from the KNMI Climate explorer (http://climexp.knmi.nl/, accessed 27.5.2016). Climate data from observation years since 1950 was used to create a ‘present climate’ input by randomly sampling observation years. For each site and scenario, the model was run with 10 iterations with different random climates (i.e., the same climate data, but randomly resampled in different orders). A summary of climatic and soil conditions as well as species composition and forest age is given in Table S2.1.

The simulated characteristics of tree overstorey and herbaceous understorey were compared to empirical measurements, which were consistently reproduced by the model. For the tree overstorey, empirical data included species composition, basal area and density of the stand (Roberts et al., 1980 for Thetford Chase; Joffre and Rambal, 1993 for Sierra Norte de Sevilla; Jansson et al., 1999 for Norunda; Delzon and Loustau, 2005 for Le Bray; Giuggiola, 2016 for Valais). For herbaceous understorey, empirical data included biomass and/or leaf area index (Roberts et al., 1980 for Thetford Chase; Loustau et al., 1991; Delzon and Loustau, 2005 for Le Bray; Giuggiola, 2016 for Valais). For sites where no data about understorey biomass was reported (i.e. Norunda and Sierra Norte de Sevilla), model results were compared to empirical data from the same ecosystem type (i.e., Baldocchi et al., 2004 for grass leaf area index in an oak-grass savannah; Nilsson and Wardle, 2005 for biomass of Vaccinium understorey in Swedish boreal forests).

**Study site Norunda, Sweden**

The forest stand at Norunda is located near the southern border of the boreal forest. The stand has an age of approximately 100 years and is dominated by *Pinus sylvestris* (80%) and *Picea abies* (19%), with a dense understorey of ericaceous dwarf shrubs (mainly *Vaccinium myrtillus*). Soils in Norunda are gravelly tills with several deep boulders (Constantin et al., 1999). The stand has been subject to conventional forest management with a typical rotation period of 100 years (Jansson et al., 1999). We therefore started the simulation from bare ground without further management intervention for 100 years. Additional details can be found in Lundin et al. (1999), Jansson et al. (1999), Moderow et al. (2009), and Constantin et al. (1999).

**Thetford Chase, UK**

The study site consists of an approximately 50 year old *Pinus sylvestris* stand (at the time of measurement by Roberts et al., 1980) with a dense understorey of bracken fern (*Pteridium aquilinum*). The sandy soils at this site have an approximate depth of 1 m (Roberts et al., 1980). Since the stand structure was relatively similar to the pine plantation in Le Bray (see next section), the same management was applied for both study sites. This simulated management resulted in a realistic stand characteristics as described in Roberts et al. (1980).
Further descriptions of the study site and the empirical measurements can be found in Roberts et al. (1980).

**Le Bray, France**

The study site in the Landes forest is a plantation of *Pinus pinaster*, characterized by dense understorey of *Molinia coerulea* L. Moench (Jarosz et al., 2008). The soil of the study region is a sandy humic podzol with a cemented B horizon that limits root extension to a depth of 80 cm (Delzon and Loustau, 2005). The stand is subject to successive thinnings, described in more detail in Delzon and Loustau (2005). The harvest routine of LandClim was adjusted to cause a similar development of stand density as described by Delzon and Loustau (2005) from chronosequences in the Landes forest. Details about the empirical measurements are given in Jarosz et al. (2008).

**Valais, Switzerland**

The study site is dominated by *Pinus sylvestris* and is located at a south facing slope in the Swiss Rhone valley in the Valais (Giuggiola, 2016). The soil at this site is a shallow rendzic leptosol with a maximum depth of 80 cm. However, the depth of the rooting zone of trees is very difficult to estimate since tree roots are frequently growing into crevices (Rigling et al., 2002). We thus estimated a higher soil WHC than measured for the soil profiles by Rigling et al. (2002), acknowledging that the soil WHC is however uncertain at this site. Further details can be found in Rigling et al. (2002) and Giuggiola (2016).

**Sierra Norte de Sevilla, Spain**

The study sites of Joffre and Rambal (1993) are located in the ‘Dehesa’ rangeland ecosystems in the region of Andalucia in southern Spain. These ecosystems are characterized by low density of trees (mainly *Quercus ilex* and *Quercus suber*; 50-60 trees per ha), dominated by a dense grass cover (Joffre and Rambal, 1993). For the simulation experiment, two of the study sites of Joffre and Rambal (1993) were selected, i.e. Castilblanco de los Arroyo (lowest elevation, driest site dominated by *Quercus ilex*) and Cazalla de la Sierra (highest elevation site with more precipitation, dominated by *Quercus suber*). Soils are sandy loam in Castilblanco and silty loam in Cazalla with soil depths of > 150 cm and generally high WHC (Joffre and Rambal, 1988). Since LandClim builds on the assumption that vegetation (woody and/or herbaceous) covers the landscape (cf. section ‘Methods’ in the main manuscript), a simulated removal of herbaceous vegetation (and thus practically all vegetation cover) would not be feasible for the Sierra Norte de Sevilla sites. Therefore only simulated evapotranspiration including herbaceous understorey was considered. Further details about the study site and the measurements are given in Joffre and Rambal (1993).
Table S2.1 Site characteristics, dominant tree and understorey species for the five European case study sites. WHC refers to water holding capacity of the soil.

<table>
<thead>
<tr>
<th>Site</th>
<th>Lat.</th>
<th>Lon.</th>
<th>Elevation (m a.s.l.)</th>
<th>Dominant species</th>
<th>Understorey species</th>
<th>WHC (cm)</th>
<th>Forest age (years)</th>
<th>Precip. (mm)</th>
<th>Temp. (°C)</th>
<th>Climate station</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Norunda</td>
<td>60.5°N</td>
<td>17.3°E</td>
<td>45</td>
<td>Pinus sylvestris, Picea abies</td>
<td>Dwarf shrubs (Vaccinium)</td>
<td>9</td>
<td>100</td>
<td>527</td>
<td>5.5</td>
<td>Uppsala</td>
<td>Constantin et al. (1999), Lundin et al. (1999)</td>
</tr>
<tr>
<td>Thetford</td>
<td>52.4°N</td>
<td>0.7°E</td>
<td>45</td>
<td>Pinus sylvestris</td>
<td>Picea abies</td>
<td>40</td>
<td>100</td>
<td>549</td>
<td>9.4</td>
<td>Mildenhall</td>
<td>Roberts et al. (1980), Beadle et al. (1982)</td>
</tr>
<tr>
<td>Forest age</td>
<td></td>
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<td></td>
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<tr>
<td>Precip. (mm)</td>
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<td>Climate station</td>
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</tr>
</tbody>
</table>
Species parameters

For tree species, parameters from Schumacher et al. (2004) (for *Pinus sylvestris*, *Picea abies*) and Henne et al. (2013) (for *Quercus ilex*, *Quercus suber*) were used. Parameters for understorey vegetation were used as described in Thrippleton et al. (2016). Since two species (*Pinus pinaster* and *Vaccinium myrtillus*) were not present in the LandClim species set, these were parameterised for the present study.

*Pinus pinaster*

Maritime pine (*Pinus pinaster*) is a shade-intolerant pioneer species that grows well under poor site conditions (Pimont et al., 2011). A low shade tolerance (1) was therefore assigned to the species. Furthermore, the species has been described as very drought tolerant (Bogino and Bravo, 2008), thus a high drought tolerance value (0.40) was assigned. For the dispersal and foliage parameters as well as the browsing tolerance and minimum degree days, the same values as for *Pinus halepensis* were assumed based Henne et al. (2013) (and supplementary materials therein). The maximum age of maritime pine was estimated as 300 years (Schütt, 2008), age at maturity as 10 years (Richardson, 2000) and maximum height was set to 35 m (Pimont et al., 2011). The parameters ‘maximum growth rate’ and ‘maximum biomass’ were estimated as 0.12 and 2, based on empirical data by Lara et al. (2013) and Ritson and Sochacki (2003).

*Ericaceous dwarf shrub*

This newly implemented PFT was parameterized to resemble the ecology of the dwarf shrub *Vaccinium myrtillus*, which plays an important role in the understorey of many boreal forests, such as in our study site Norunda (Constantin et al., 1999). Shade tolerance was set to a value of 2 (i.e. low to intermediate level; Hester et al., 1991). ‘Maximum biomass’ was estimated as 250 g m\(^{-2}\) (Wardle et al., 2003), minimum degree days were set to 400 (Fosaa et al., 2004), and drought tolerance was estimated as 0.3 (medium to high level; Jäderlund et al., 1997; Mäkipää, 1999). All other parameters were the same as the generic ‘herb’ PFT from Thrippleton et al. (2016).
Appendix 3: Landscape maps Valais

Figure S3.1 Landscape maps for (a) the digital elevation model, (b) aspect, (c) slope and (d) soil water holding capacity for the study landscape around Visp in the Valais, Switzerland. The map of soil WHC was calculated based on topography for a previous study (Briner et al., 2012), assuming that areas with increasing steepness have shallower soils and thus a lower soil WHC. Similar topography-based estimates have shown to adequately reproduce soil characteristics in mountain landscapes and coincide well with empirical data (Henne et al., 2013; Schwörer et al., 2014).
Appendix 4: Additional simulation results

Figure S4.1 Change in tree biomass growth after removal of understorey vegetation (relative to the scenario where understorey was not removed) for the European case study sites. Note that the site ‘Sierra Norte de Sevilla’ was not considered in the understorey removal experiments (see Appendix S2). The impact of understorey removal is mostly due to the species-specific drought stress experienced at each site, and not as much due to the understorey contribution to evapotranspiration (see Fig. 3 in main manuscript).

Figure S4.2 Drought index of trees for three elevation belts, i.e. ‘Low elevation’ (700-800 m a.s.l.), ‘Mid elevation’ (1200-1300 m a.s.l.) and ‘High elevation’ (1900-2000 m a.s.l.) for present and future climate (Low Impact CC - ICHEC-EC EARTH-DMI RCP 4.5 and High Impact CC - ICHEC-EC EARTH-CLMcom RCP 8.5).
Table S4.1 Relationship between drought index (for saplings and adult trees) and different variables, shown as Spearman's rank correlation coefficient. WHC: water holding capacity of the soil.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Sapling Drought Index</th>
<th>Tree Drought Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbaceous biomass</td>
<td>0.59</td>
<td>0.20</td>
</tr>
<tr>
<td>Tree biomass</td>
<td>-0.43</td>
<td>-0.58</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.45</td>
<td>-0.85</td>
</tr>
<tr>
<td>Aspect</td>
<td>0.13</td>
<td>0.29</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.18</td>
<td>-0.07</td>
</tr>
<tr>
<td>Soil WHC</td>
<td>0.12</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Appendix References


Herbaceous competition and browsing may induce arrested succession in central European forests

Thripleton, T.; Bugmann, H.; Snell, R.S. (2017)

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Abstract

Arrested succession, i.e. an ecosystem permanently halted in an early successional, typically non-forested state, has been suggested to result from intense competition by understorey vegetation, high browsing pressure and additional disturbances, but the relative importance of these factors is unclear. In addition, distinguishing between permanently arrested succession or merely delayed succession may be highly challenging, if not impossible, due to the large time scales involved.

We used the dynamic vegetation model LandClim to systematically explore the effect of multiple factors on delayed and arrested succession over a time span of 1000 years, starting from an unforested state. We included abiotic and biotic factors as well as large-scale overstorey disturbance, in four Central European landscapes.

Arrested succession occurred in 1 to 14% of the simulations. Among the non-arrested simulations, 95% reached a forested state (defined as $\geq 10\%$ canopy cover) within 100 years. Large herbaceous biomass was the most important predictor for arrested succession, followed by browsing and large-scale disturbances. Combinations of factors were important at particular locations in the landscape, where understorey competition and browsing jointly induced a strong establishment filter. Abiotic conditions consistently influenced the probability of arrested succession, with a low probability under mesic conditions and increased likelihood in more xeric parts of the landscapes.

Synthesis We demonstrated that permanently arrested succession has the potential to occur in temperate forests, particularly under a combination of high amounts of herbaceous biomass and ungulate browsing in drought-constrained landscape positions. We thus conclude that considering environmental heterogeneity at the landscape scale is key for understanding the conditions that lead to delayed and arrested succession.

KEYWORDS: arrested succession, delayed succession, forest landscape model, plant-plant interactions, recalcitrant understorey layer, ungulate browsing
Introduction

The persistence of herbaceous communities in areas otherwise dominated by closed-canopy forests has induced considerable research in (sub-)tropical ecosystems (e.g., Hirota et al., 2011; Gunaratne et al., 2014). Despite some seminal earlier works (e.g., Niering and Goodwin, 1974; Putz and Canham, 1992), much less attention is currently paid to this phenomenon in temperate ecosystems, although evidence is increasing that intense understorey competition in combination with browsing and disturbance (e.g., timber harvest, fire) can severely reduce or even completely prevent tree regeneration (Royo and Carson, 2006). In temperate ecosystems, the prevailing paradigm is that succession typically returns back to a forested state, although significant delays are possible (i.e., the ecosystem remains in an herbaceous state for some time before reverting back to a forest)(Ellenberg, 1996). However, examples from the Central European Alps show remarkably stable herbaceous vegetation persisting in areas otherwise dominated by trees, such as grass-dominated savannahs on south-facing slopes in dry inner-alpine valleys (Braun-Blanquet, 1961; Ellenberg, 1996) or disturbance sites at high elevations (e.g., Geissler and Hartmann, 2000). These examples raise the question whether particular sets of conditions could result in arrested succession (i.e., an ecosystem permanently stopped in an early-successional, non-forest state) in temperate regions.

Persistent understorey vegetation has been suggested to develop preferentially when several disturbance types occur jointly (Stromayer and Warren, 1997; Royo and Carson, 2006). Large-scale, exogenous disturbances such as windthrow or timber harvest increase light levels at the forest floor, thereby favouring the establishment of a highly competitive early successional understorey vegetation (Lieffers et al., 1993; Hart and Chen, 2006). In the presence of sufficient advance regeneration, canopy openings are usually closed within a relatively short time (e.g., Messier et al., 1999). However, increasing ungulate population densities, as observed in many forests worldwide, can cause a chronic biotic disturbance that severely inhibits tree regeneration (Côté et al., 2004; Beguin et al., 2016) and favours the development of a dense herbaceous layer (e.g., Rooney, 2009). Particularly in parts of the landscape where trees are under considerable environmental stress (e.g., close to the dry or cold treeline), combinations of herbaceous competition and different disturbance types may have the potential to promote a persistent, non-forested state.

The relative importance of the factors that lead to a persistent herbaceous state is poorly known and mostly speculative, since strictly controlled experiments have rarely been performed (Royo and Carson, 2006). Also, most field experiments have <10 years of data and are site- and/or species-specific. As competitive interactions between trees and the understorey change over time (Hart and Chen, 2006), it is difficult to extrapolate from short-term experiments to larger temporal scales. Thus, large time scales need to be considered, which typically exceed the capacity of field observations and experimental studies (Schumacher et al., 2004).

Process-based dynamic vegetation models (DVMs) can overcome these limitations and provide insights on vegetation patterns emerging at large spatio-temporal scales (Bugmann,
Although global-scale DVMs typically include a grass plant functional type (e.g., LPJ-GUESS, Smith et al., 2001; SEIB-DGVM, Sato et al., 2007), surprisingly few DVMs that are applied at the forest stand or landscape level have included an herbaceous layer (e.g., Kellomäki and Väisänen, 1991; Riggs et al., 2015). Previous studies have explored the effect of single and multiple disturbances (e.g., fire, windthrow and bark beetle infestations, Henne et al., 2013; Temperli et al., 2013), but none of these accounted for interactions between trees and herbaceous vegetation. Thrippleton et al. (2016) demonstrated the importance of herbaceous competition on long-term forest dynamics and species composition using a simulation approach, but did not account for browsing and anthropogenic overstorey disturbances such as timber harvest, or their combined effects.

We aim to extend the scientific understanding of the processes that lead to delayed and arrested succession across large spatio-temporal scales in central Europe. We use a landscape-scale DVM to systematically explore the relative contribution of the ecological factors that have been hypothesized to lead to arrested succession. As windthrow (Schelhaas et al., 2003), timber harvest, and browsing (Weisberg and Bugmann, 2003) have been identified as the major large-scale disturbances influencing tree regeneration in this area, they were included in our simulations. Specifically, we addressed the following questions:

1. Which biotic (i.e., herbaceous understorey and browsing) and large-scale disturbance factors (i.e., timber harvest and windthrow) are most important for delayed and arrested succession?
2. How do abiotic conditions influence the probability of arrested succession?
3. Is arrested succession more likely to occur under a combination of these factors?

We hypothesized that arrested succession may occur in central Europe at environmentally constrained landscape positions accompanied by intensive disturbances, which grant understorey vegetation a competitive advantage over trees.
Material and Methods

The forest landscape model LandClim

LandClim is a spatially explicit, process-based landscape model that incorporates competition-driven vegetation dynamics as a function of climate, topography and large-scale, exogenic disturbances (Schumacher et al., 2004). The landscape is represented as a grid of raster cells (25 x 25 m²) with specific environmental conditions for each cell (i.e., climate, soil, topography). Within each cell, a simplified forest gap model (Bugmann, 2001) is employed to represent establishment, growth and mortality of tree cohorts (i.e., groups of trees of the same age). New cohorts establish once a decade, but the establishment probability and density of tree regeneration is determined by the environmental conditions (i.e., light, water and temperature) and browsing pressure that prevailed during the previous 10 years. Mortality of adult trees is determined by growth-dependent stress, age-dependent senescence, as well as exogenic disturbances. Cohorts compete with each other for light and water. Simulated forest dynamics are an emergent property of the model, driven primarily by species-specific-traits of shade tolerance, drought tolerance and temperature constraints on establishment and growth (Schumacher et al., 2004). A more detailed description of the design of the model and its representation of forest landscape dynamics is provided in Appendix S1.

LandClim was originally developed to represent vegetation dynamics in central Europe (Schumacher, 2004), but has since been applied across a wide range of environmental conditions from the Mediterranean basin (Henne et al., 2015) and dry continental conditions in the US Rocky Mountains (Temperli et al., 2015) to humid temperate rainforests in the northwestern US (Schwörer et al., 2016) and New Zealand (Thrippleton et al., 2014).

Herbaceous understorey vegetation has recently been included in LandClim and here is represented as a single plant functional type (PFT; Thrippleton et al., 2016). This PFT is represented in the model as a single cohort in each raster cell, with PFT-specific variables describing maximum biomass, growth rate and bioclimatic limitations. Understory cohorts are present at all times, but their realized biomass depends on the degree to which environmental conditions (i.e., light, water, temperature) decrease its maximum biomass. The leaf area index of the understorey layer (calculated via an allometric function from biomass, see Thrippleton et al., 2016) decreases the amount of light available for tree regeneration. Furthermore, biomass of the herbaceous understorey determines the amount of water removed from the topsoil, thus increasing the drought experienced during the regeneration stage (Thrippleton et al., 2017). Overstorey trees affect herbaceous biomass by decreasing light availability in the understorey, thus leading to minimal herbaceous biomass under a dense canopy (Thrippleton et al., 2016). Additional information on the interaction between herbaceous understorey and trees is given in Appendix S1 and Thrippleton et al. (2016; 2017).

LandClim includes various large-scale, exogenic disturbance processes (hereafter referred to as ‘disturbances’), among which we focus on the three main disturbances affecting central European forests: (1) windthrow, as the main natural large-scale overstorey disturbance
(Schelhaas et al., 2003), (2) timber harvest, as the main anthropogenic disturbance that has shaped central European forests for centuries to millennia, and (3) browsing, as a major biotic disturbance to the tree regeneration layer (Weisberg and Bugmann, 2003).

The performance of LandClim has previously been evaluated at various spatio-temporal scales by confronting model outputs with palaeoecological, chronosequence, and forest inventory data (e.g., Henne et al., 2011; Elkin et al., 2012; Elkin et al., 2015; Thrippleton et al., 2016), where it consistently reproduced empirical patterns of forest dynamics and vegetation composition. Furthermore, the processes of large-scale disturbances, browsing and understorey competition have been thoroughly tested in previous studies (Schumacher et al., 2004; Henne et al., 2013; Temperli et al., 2013; Elkin et al., 2015; Thrippleton et al., 2016, 2017), making LandClim highly suitable to address the processes and spatial scales that are relevant for this study. Below, we briefly describe how LandClim represents each factor.

Please note, that for consistency, we refer to the model parameters that were varied between the simulations as ‘variables’ in the statistical analysis.

**Abiotic, biotic and disturbance factors**

*a) Abiotic conditions*

To cover the wide range of bioclimatic conditions typical for central European forests, we selected four study landscapes that represent a trans-Alpine environmental gradient (Fig.1, Table 1), including two mesic forests (1: Feldberg, Black Forest; Thrippleton et al., 2016; 2: Jura, pre-Alpine Jura mountains; Snell et al., 2017), a high-elevation landscape limited by temperature (3: Dischma valley in the central Alps; Thrippleton et al., 2016), and a drought-limited landscape (4: Valais, located in the southern-Alpine Valais region; Thrippleton et al., 2017).
Figure 1. Location of the study landscapes in Switzerland and Southern Germany (Source: EU-DEM, EEA (2015)).

Climatic input data were based on the temperature and precipitation records from climate stations located within each study landscape and adjusted for elevation using empirically derived lapse rates (cf. Schumacher et al., 2004). Since temperature and precipitation strongly co-vary in the study landscapes, elevation was used as a proxy for climatic conditions in the following analyses (see Table 1). The length of the climate records for each landscape varied from 30 to 70 years (see Schumacher et al., 2004 for Dischma; Thrippleton et al., 2016 for Feldberg; Snell et al., 2017 for Jura; Thrippleton et al., 2017, for Valais), and were randomly re-sampled with replacement for each simulation to generate 1000-year time series.

In addition to climate and elevation, aspect and soil water holding capacity (WHC) are important abiotic variables that may influence the degree of delayed or probability of arrested succession. WHC represents total available water to trees and the understory, and strongly influences drought occurrence. We used a two-layer soil module developed by Thrippleton et al. (2017) where herbaceous understorey and tree regeneration have access to water in the topsoil only whereas adult trees have access to water in all soil layers. Total WHC was varied from 6 to 18 cm, representing a range of very low to high WHC values (Henne et al., 2011). Topography also impacts the calculation of drought in LandClim, by changing incident solar radiation. For the simulations, we assumed a constant slope of 35° and varied aspect from 0 to 360°, thus covering the full range of possible aspects (see Schumacher, 2004 for details). The ranges of all abiotic variables tested are provided in Table 1.
b) **Herbaceous understorey**

Herbaceous understorey was represented by a generic, fast-growing, light demanding plant functional type (PFT) (based on the grass PFT of Thrippleton et al., 2016). This generic understorey PFT has a wide range of environmental tolerances, allowing it to grow across the climate gradient covered by the four landscapes. Furthermore, we assumed the understorey PFT to be unpalatable for browsing ungulates (e.g., Rooney, 2009). To evaluate the degree of competition between trees and herbaceous understorey, we varied the model parameter maximum herbaceous biomass from 0 to 800 g m\(^{-2}\) (Table 1), based on typical ranges observed in empirical studies from temperate and Mediterranean ecosystems (see Thrippleton et al., 2016). This represents the maximum biomass that is reached under optimal growing conditions, thus determining understorey competitive strength (Thrippleton et al., 2016).

c) **Browsing**

Ungulate browsing is represented as a filter for tree establishment, where the establishment probability depends on local browsing pressure and the browsing tolerance of a species (Henne et al., 2013). Browsing pressure (on a scale between 0 and 1) was varied between no browsing (0) up to severe browsing (0.9), based on the wide range of possible browsing pressures observed in central European mountains (e.g., Kupferschmid et al., 2015). Browsing pressure was assumed to be constant throughout each simulation, and effects of forest structure and composition on browsing intensity were not considered. The aim of this simplified approach was to provide a parsimonious baseline scenario that allowed us to systematically investigate browsing effects on forest succession.
Table 1: Abiotic, biotic and large-scale disturbance factors and their variable ranges used in the simulation study. For minimum and maximum elevations, annual mean temperatures and precipitation sums are given in brackets.

<table>
<thead>
<tr>
<th>Factors</th>
<th>Variable</th>
<th>Site</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Sample interval</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abiotic (environmental)</td>
<td>Elevation (a.s.l.)</td>
<td>Feldberg</td>
<td>600</td>
<td>(8.9°C, 1147 mm)</td>
<td>1500</td>
<td>(3.6°C, 1743 mm)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Jura</td>
<td>900</td>
<td>(7.0°C, 1430 mm)</td>
<td>1500</td>
<td>(4.1°C, 1918 mm)</td>
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<tr>
<td></td>
<td></td>
<td>Dischma</td>
<td>1500</td>
<td>(3.5°C, 1032 mm)</td>
<td>2500</td>
<td>(-1.4°C, 1236 mm)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Valais</td>
<td>600</td>
<td>(8.8°C, 649 mm)</td>
<td>2300</td>
<td>(0.4°C, 1213 mm)</td>
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<tr>
<td></td>
<td>Aspect</td>
<td>all sites</td>
<td>0</td>
<td>360</td>
<td></td>
<td>1 ° (degree)</td>
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<tr>
<td></td>
<td>Soil WHC</td>
<td>all sites</td>
<td>6</td>
<td>18</td>
<td></td>
<td>1 cm</td>
</tr>
<tr>
<td>Biotic</td>
<td>Max.Underst.Biom.</td>
<td>all sites</td>
<td>0</td>
<td>800</td>
<td></td>
<td>1 g m⁻²</td>
</tr>
<tr>
<td></td>
<td>Browsing pressure</td>
<td>all sites</td>
<td>0</td>
<td>0.9</td>
<td></td>
<td>0.01 -</td>
</tr>
<tr>
<td>Large-scale disturbance</td>
<td>Windthrow rot. period</td>
<td>all sites</td>
<td>200</td>
<td>1000</td>
<td></td>
<td>1 yr (years)</td>
</tr>
<tr>
<td></td>
<td>Harvest target area</td>
<td>all sites</td>
<td>0</td>
<td>0.9</td>
<td></td>
<td>0.01 -</td>
</tr>
</tbody>
</table>
d) **Windthrow**

Windthrow events are simulated stochastically and occur as spatially explicit patches. A windthrow event starts from a randomly chosen location in the landscape and spreads until it reaches an area of a certain size, sampled from a user-defined size distribution. Within each affected grid cell, mortality by windthrow is calculated as a function of tree diameter at breast height, with an increasing probability of death for larger size classes. Consequently, windthrow disturbances in LandClim have a smaller impact on juvenile trees, i.e. advance regeneration (see Appendix S1 and Schumacher et al., 2004 for further details). Windthrow parameters defined by the user are the rotation period (i.e., the mean time required to disturb an area equivalent to the total study area) and the size distribution of the wind events. We chose to vary the rotation period (Table 1) as it approximates disturbance frequency within a grid cell, with value ranges based on Schumacher (2004). Windthrow size distributions (i.e., minimum size 0.06 ha, average 2 ha, maximum 73.8 ha) were based on empirical data from reports of large-scale windthrow events (Fischer, 1999).

e) **Timber harvest**

In contrast to the wind disturbances that are simulated stochastically in their spatio-temporal occurrence and primarily affect large trees, the harvest module of LandClim allows for specific forest management interventions (Schumacher et al., 2004; Temperli et al., 2012). We defined a simplified harvest regime to represent an anthropogenic overstorey disturbance type using identical harvest rules for all landscapes (rather than more realistic scenarios that consider specific tree species, environmental conditions and management objectives), thus assuring the comparability of harvest effects across study landscapes.

The management regime was defined to harvest 100% of adult trees (i.e., ≥ 10 years old) in all size classes in a certain percentage of grid cells across the landscape. A harvest interval of 100 years was selected based on typical harvest intervals in temperate coniferous mountain forests (Ott et al., 1997; Elkin et al., 2013). The grid cells chosen for harvest were determined by ranking the stands by stem density (i.e., preferentially harvesting dense stands). The percentage of cells that are harvested is defined by the parameter **target area** and varied between 0 and 0.9 (Table 1), representing no harvest (0%) to 90% of the total area being harvested. The aim of this particular harvest regime was to provide a functionally contrasting disturbance type to windthrow, which would allow us to determine the importance of surviving younger age cohorts (i.e., ‘advance regeneration’) for post-disturbance dynamics.

**Simulation studies and sampling design**

a) **Systematic exploration of factors**

To explore the range of all variables and the possible interactions that may lead to delayed and arrested succession (Table 1), we used Latin Hypercube Sampling (LHS). LHS creates variable combinations using stratified random sampling, that efficiently explores the
multivariate space with fewer combinations than a full factorial design (Stein, 1987). For each of the four study landscapes, 2500 variable combinations were created using LHS.

As the real landscapes do not necessarily include all combinations of abiotic variables (e.g., every combination of aspect and WHC at every elevation), we created artificial landscape subsets, each representing a specific combination of abiotic variables determined by the LHS design. This approach allowed us to systematically explore forest succession under clearly defined abiotic conditions, which greatly facilitated the statistical analysis of the results. Each subset consisted of a rectangle of 2500 grid cells (i.e., 156 ha), providing a sufficiently large area to account for stochastic variability between grid cells and to simulate landscape-scale disturbance events. Each subset was representative for a specific elevation, with a constant aspect and soil WHC in all grid cells. The four landscapes were represented by 2500 subsets (i.e., simulations) each.

b) Reference simulations

A set of reference simulations were created to investigate forest growth under all combinations of abiotic variables (i.e., elevation, aspect, WHC), but in the absence of understorey competition, browsing and large-scale, exogenic disturbances. These reference simulations served two purposes: (1) to identify the abiotic conditions where forest growth is prevented, and (2) to provide a baseline for quantifying the effect of herbaceous understorey, browsing, windthrow and timber harvest on forest biomass growth.

**Simulation protocol**

The simulation experiments were started from bare ground, assumed unlimited seed dispersal, and were run for 1000 years. Each simulation included 31 common central European tree species (Schumacher et al., 2004; Henne et al., 2011, see also Appendix Table S1.1 for species traits). Simulations for the systematic exploration of all factors included the understorey PFT as well as browsing, windthrow and harvest.

**Model outputs**

Simulation results were used to (1) identify cases of arrested succession, (2) calculate the number of years that succession was delayed, and (3) determine the change in forest biomass growth rate. Arrested succession was defined as having a mean tree canopy cover permanently below 10% (FRA, 2012) throughout the entire 1000 years. Mean canopy cover was calculated using an empirical relationship between diameter at breast height and crown projection area (Shimano, 1997). Simulations were classified as either non-arrested (0) or arrested (1). Using forest biomass instead of canopy cover to identify arrested succession yielded similar results. The reference simulations were used to identify those conditions where forests were prevented from establishing due to abiotic constraints. This was only the case for sites above 2200 m a.s.l. in Dischma due to low temperatures at upper treeline. These locations were removed from the analyses.
The simulations that were classified as non-arrested were further analysed for delayed succession and the change in growth rate. Delayed succession was defined as the difference in time of forest establishment (i.e. mean canopy cover of 10% reached, FRA, 2012) between a simulation and its respective reference. Since all reference simulations reached the forested state within the first decade of the simulation, the delay measure thus essentially corresponds to the time from the beginning of succession until the forested state.

For forest growth, we focused on growth rate rather than the development of forest biomass, since we were interested in the process of forest recovery rather than a comparison of long-term biomass trajectories. The forest biomass growth rate was defined as mean aboveground forest biomass in quasi-equilibrium divided by the length of time to reach this biomass (which typically required a century or more), and was calculated for all non-arrested simulations. Change in forest growth was defined as the difference in forest biomass growth rate relative to its respective reference simulation.

**Analysis of results**

The effect of each variable on the probability of arrested succession was analysed with a logistic regression model for each study landscape. All variables in Table 1 were included as predictors, as well as two-way, multiplicative interactions between understorey and browsing or large-scale disturbances, respectively. Three-way interactions were not included as their effect was found to be insignificant. For the statistical analysis, aspect was recalculated into an East-West (EW, with 1 representing east and -1 west) and a North-South gradient (NS, with 1 representing north and -1 south), as described in Bigler (2016). The inverse of the windthrow rotation period was used to facilitate the interpretation of the variable (i.e., an increasing value of the variable represents increasing disturbance pressure). Since the estimate of each variable depends on its unit, the predictors were standardized (i.e. centering and scaling of all predictors to a mean of 0 and a standard deviation of 1) to allow for a direct comparison of the factors. The Dischma and Jura landscapes had too few cases of arrested succession to fit logistic models, thus they were excluded from this analysis. To illustrate the combined effect of different factors, the logistic regression models were used to predict the probability of arrested succession (cf. Fig. 3) using the non-standardized variable values to display actual variable ranges and units.

The effect of all variables on delayed succession was analysed using linear regression models, but no significant relationships were found since the majority of simulations that were non-arrested had already reached the forest state within the first few decades (see Appendix S2, Fig. S2.2). The change in forest biomass growth rate was analysed for each landscape using linear regression models with biotic and disturbance variables as predictors. Abiotic variables were not considered since we quantified forest growth relative to the reference simulations, which had the same abiotic conditions. To compare the effects of each factor on forest growth, the standardised slope (β) was used, based on Nakagawa and Cuthill (2007). β represents the change in the response associated with a unit change in the predictor
(Nakagawa and Cuthill, 2007). All simulations were performed with LandClim Version 1.7, and statistical analyses were performed with the software R (Version 3.3.2, R Development Core Team, 2016). Summaries of statistical models are given in Appendix S2, Table S2.1 and S2.2.

**Results**

**Factors increasing the probability of arrested succession**

Only a minority (i.e., <15%) of the simulations were identified as being in a state of arrested succession, although each landscape featured different proportions (i.e., 4% in Feldberg, 2% in Jura, 1% in Dischma, and 14% in Valais). Due to the scarcity of arrested succession in Dischma and Jura, these two landscapes were excluded from further analyses.

Logistic regression using the standardized variables showed that maximum herbaceous biomass was most important among the biotic and disturbance factors for increasing the probability of arrested succession, followed by browsing intensity and the two-way interaction between herbaceous biomass and browsing (Fig. 2). The simulated timber harvest had a smaller impact but consistently increased the probability of arrested succession in both landscapes. The effect of windthrow was less consistent, showing an increasing probability for Valais, but a decreasing probability for Feldberg. Among the abiotic variables, the probability decreased from southwest- to northeast-facing slopes. Increasing WHC and increasing elevation also reduced the probability of arrested succession (Fig. 2).

![Figure 2](image-url)  
**Figure 2.** The probability of arrested succession, analysed using logistic regression. Odds Ratios >1 (black line marks an odds ratio of 1) indicate an increasing probability of arrested succession, and values <1 indicate a decreasing probability with increasing variable value. Points indicate mean values and vertical lines 95% confidence intervals. Variables were standardized to allow for the direct comparison of all factors. NS represents a gradient from South-facing slopes (lowest values) to North-facing slopes (highest values). EW represents a gradient from West (lowest values) to East (highest values). ‘Max.Underst.Biom’ represents the maximum biomass that is reached by herbaceous vegetation under optimal growing conditions.
The interaction terms were less important when considered across the entire landscape (Fig. 2). The predictions of the logistic regression models (Fig. 3, Fig. S2.1) illustrate that the combined effect of high understorey biomass, browsing and timber harvest was mostly additive, and substantially enhanced the probability of arrested succession at specific elevations. This environmental differentiation was particularly evident for the Valais (Fig. 3), where the simulated probability was generally low at high elevations (1900 m, Fig. 3a-c), but increased substantially at mid (1200 m) and low elevations (700 m), especially when the factors occurred in combination (Fig. 3d-i). At low elevations (Fig. 3g), high understorey biomass alone increased the probability of arrested succession by 40%. When high herbaceous biomass coincided with high browsing pressure, the probability of arrested succession was virtually 100%, even if no large-scale, exogenic overstorey disturbances were included (Fig. 3i). At low to intermediate browsing levels, the probability was further increased by disturbances due to timber harvest (Fig. 3g,h). Results for Feldberg showed a similar pattern, but it was apparent only under intermediate to high browsing pressure combined with high understorey biomass (Appendix S2, Fig. S2.1).

Figure 3. Combined effects of maximum understorey biomass, browsing and timber harvest (set to a level of 0.9; cf. Methods section) on the probability of arrested succession for three elevations and three browsing levels in the Valais (prediction from the logistic regression model fit for the landscape). Other abiotic factors were set to their mean values for comparability.
Factors contributing to delayed succession

No relationship was found between the number of years that succession was delayed and the various abiotic, biotic and disturbance factors in our model. This is likely because the majority of the simulations that were non-arrested reached a forest state (i.e., mean canopy cover of ≥10%, FRA, 2012) within the first few decades (see Appendix S2, Fig. S2.2, S2.3). Across all sites, 80% of the simulations that were non-arrested had reached a forest state by the year 50, and 95% by the year 100. Only a very small percentage (2.2%) of the simulations had delays lasting >200 years. In general, simulations with delays > 100 years were mostly likely to remain in the state of arrested succession for the entire 1000-year simulation.

Factors contributing to changes in forest growth rate

Forest growth rate decreased substantially with increasing herbaceous competition, browsing and large-scale disturbances in all landscapes (mean decrease of forest growth rate by 0.9 t·ha⁻¹·yr⁻¹ for Dischma, 1.8 t·ha⁻¹·yr⁻¹ for Feldberg, 1.4 t·ha⁻¹·yr⁻¹ for Jura and 1.3 t·ha⁻¹·yr⁻¹ for Valais; cf. Appendix S2, Fig.S2.4). Generally, single variables had the largest effect, but two-way interactions between understorey biomass and browsing, or between understorey biomass and large-scale disturbances further decreased forest growth rates (Fig. 4). Maximum herbaceous biomass had the largest effect in all four landscapes, followed by browsing pressure (for all landscapes except Dischma), and then by harvest and windthrow. The patterns were consistent for all landscapes, with the strongest relative effects of biotic and disturbance factors at Feldberg and Jura, and smaller effects for Dischma and Valais.

![Figure 4. Effect of different variables on forest biomass growth rate (expressed as β, the standardised slope of the linear models). Forest growth is measured as the change of tree biomass growth rate (t·ha⁻¹·yr⁻¹) relative to the reference scenario (same abiotic conditions, but no understorey and no disturbances). A negative β indicates a negative effect on forest biomass growth.](image-url)
Discussion

Due to the large time scales involved, it is challenging to empirically test whether forest succession is merely delayed or permanently arrested. Identifying the factors underlying the persistence of understorey vegetation is additionally complicated in empirical studies due to the complexity of interwoven processes (Royo and Carson, 2006). A simulation study can provide comprehensive, transparent and systematic insights into the processes that cause delayed and arrested succession, and helps to extend the conclusions of empirical studies over longer time scales and across large environmental gradients. Below, we discuss (1) the most important biotic and disturbance factors (alone and combination) that led to decreased forest growth, delayed and arrested succession, (2) the influence of environmental conditions on the probability of arrested succession, and (3) underline the importance of using adequate spatio-temporal scales for studies of delayed and arrested succession.

Relative importance of factors for delayed and arrested succession

In our simulations, maximum herbaceous biomass was the most important factor for reducing forest growth rates and increasing the likelihood of arrested succession. During the early stage of tree establishment, competition with herbaceous vegetation is often reported as the first ‘filter’ that trees have to overcome (George and Bazzaz, 1999a). Empirical studies that report reduced tree survival even under moderate levels of understorey competition (Wagner et al., 1989) are thus consistent with our findings. In our simulation results, the probability of arrested succession was very low when herbaceous biomass was <200 g·m⁻², but increased substantially above this value, particularly at low elevations of the Valais (Fig. 3). Several empirical studies reported little or no tree regeneration at an herbaceous biomass >300 g·m⁻² (e.g., Lieffers et al., 1993; Bergquist et al., 1999). Standish et al. (2001) studied the relationship between herbaceous biomass (Tradescantia fluminensis) and tree regeneration, and found sufficient regeneration at an herbaceous biomass <200 g·m⁻², but very low probability of seedling survival at >400 g·m⁻². A herbaceous understorey with a biomass of 100 – 200 g·m⁻², as typically observed in temperate forest ecosystems (e.g., Halpern and Lutz, 2013) is thus unlikely to halt succession for a prolonged period of time, but both empirical studies and our results indicate a disproportionally higher inhibition of tree regeneration when herbaceous biomass exceeds 400 g·m⁻².

Browsing pressure was identified as the second most important factor for forest growth rate and arrested succession. Ungulates browse preferentially on saplings that have just emerged above the herbaceous layer (Côté et al., 2004), thereby reducing the presence of advance regeneration and delaying forest succession (Beguin et al., 2016). Empirical and process-based modelling studies however suggest that forest regeneration can occur even under very high browsing pressure (Kienast et al., 1999; Brüllhardt et al., 2015), thus supporting our projections for the Valais and Feldberg (Fig. 3, Fig.S2.1). Yet, at specific places in the landscape, in particular the most xeric low elevations, a combination of high browsing pressure with intense understorey competition caused an effective dual establishment filter for tree regeneration in our simulations, enhancing the probability of arrested succession.
Similarly, a number of empirical studies suggested that ungulate herbivory in combination with competition by a resistant grass layer may lead to a long-term persistence of an open grassland state (e.g., Rooney, 2009).

While the analysis of arrested succession and forest growth showed clear patterns for the influence of herbaceous biomass and browsing, this was not the case for the analysis of delayed succession. This was likely due to our definition of delay, as the time required to reach a forested state using a threshold of 10% canopy cover (following FRA, 2012). Since this low threshold was typically reached in a short period of time, no clear patterns emerged. However, the analysis of forest growth rate was able to identify the factors that decrease forest biomass growth and thereby delay the development of a mature forest.

Our assumption that the understorey PFT was unaffected by browsing ungulates (as often observed for unpalatable species, e.g., Bergquist et al., 1999) was helpful to disentangle the effect of different factors in our experiment, but real feedbacks between vegetation and browsing are typically more complex. A more sophisticated approach could take into account the effect of herbivory on understorey vegetation (which plays an important role in the formation of recalcitrant understorey layers, see Royo and Carson, 2006) as well as the dynamic response of deer population density to changes in food supply (which is particularly important for long-term dynamics, Weisberg and Bugmann, 2003). These aspects have recently been included in other landscape models (e.g., FireBGCv2, Riggs et al., 2015; LANDIS-II, De Jager et al., 2017), which we welcome as important steps towards further exploring the complex feedbacks between ungulate population and vegetation dynamics at the landscape scale.

Besides ungulate browsing, seed-predation by small mammals can play a significant role for inhibiting tree regeneration (George and Bazzaz, 1999a) and may be an important additional process delaying succession (e.g., Acacio et al., 2007). For instance, studies in temperate forests of New Zealand have shown that exotic seed predators play a key role in preventing native tree regeneration (e.g., Perry et al., 2015). This also underlines the potential for invasive species to enhance the degree of delayed or the probability of arrested succession.

Large-scale disturbances are generally thought to play a significant role in the long-term dominance of understorey vegetation (Royo and Carson, 2006). In our simulations, disturbances by windthrow and harvest were important for the reduction of forest growth rate (Fig. 4), but their direct effect on the probability of arrested succession was relatively small (Fig. 2). By starting our simulations from bare ground instead of a closed forest, it is possible that we minimized the importance of large-scale disturbances. Under these conditions, simulations with high understorey competition and/or browsing pressure more frequently remained in a state of arrested succession, and therefore disturbances that remove the overstorey were irrelevant at this point.

For delaying forest growth rate, timber harvest had a higher impact than windthrow (Fig. 4), which was likely due to our assumption that harvest affects all trees (≥ 10 years old), whereas windthrow preferentially removes larger trees (see Appendix S1). While the representation of
this disturbance is highly simplified, it allowed us to explore the possible role of surviving advance regeneration after a disturbance event, suggesting its key importance for post-disturbance succession (e.g., George and Bazzaz, 2003). Furthermore, two-way interactions between herbaceous understorey and harvest decreased forest growth, thus suggesting that intense understorey competition could reverse the beneficial effects of gaps for tree regeneration, as observed in empirical studies (e.g., Kern et al., 2012).

**The importance of environmental drivers for arrested succession**

Climatic and soil conditions are important for determining the degree that understorey vegetation is able to inhibit tree regeneration (Mallik, 1995). In our simulations, elevation-dependent climatic conditions strongly influenced the probability of arrested succession. In LandClim, warmer conditions at low elevations produce faster growth of both trees and herbs as long as soil moisture is not limiting. However, the herbaceous understorey had a superior growth rate during the first years of succession and was therefore able to counteract the beneficial climatic effects on tree establishment (Thrippleton et al., 2016). The elevation/climate effect also explained site differences on forest growth rates (Fig. 4): Jura and Feldberg comprise elevations up to 1500 m a.s.l. only, whereas the Valais and Dischma extend to much higher elevations (>2200 m a.s.l., cf. Tab.1), where tree growth was strongly limited by low temperature. The effect of biotic and large-scale disturbance factors was negligible in these high-elevation parts of the landscapes, thus diminishing their overall effect for Valais and Dischma. Despite these differences, the general patterns were consistent across all four landscapes, which underlines the robustness of our results across a wide environmental gradient.

We found the highest probability of arrested succession at the lowest elevations in the Valais, which is particularly dry and experiences severe seasonal droughts (Bigler et al., 2006). Under these conditions, herbaceous understorey had an additional advantage in our simulations compared to trees, as the PFT has a high drought tolerance (Thrippleton et al., 2016) and is able to remove substantial amounts of water from the upper soil layer (Thrippleton et al., 2017). Under present climatic conditions, low elevations in the Valais are characterized by a transition from forest to open, steppe-like vegetation and remarkably stable herbaceous-dominated communities on the most drought-prone south-facing slopes (Braun-Blanquet, 1961; Ellenberg, 1996). Furthermore, strong reductions in tree regeneration due to understorey competition have been reported by empirical studies, indicating a potential future shift towards a more savannah-like vegetation with increasing droughts (Moser et al., 2010). Our simulation results showing persistent herbaceous vegetation at the most drought-prone landscape positions are thus in agreement with present observations, indicating that herbaceous competition may lead to arrested succession under intense water competition.

Previous work from subtropical and tropical ecosystems has furthermore shown that stable grasslands can prevent tree establishment under low soil moisture content and/or low amounts of precipitation (e.g., Baudena et al., 2015; Veldman et al., 2015). A similar interference mechanism may inhibit tree regeneration in temperate forests, particularly under dry
conditions, as shown in a number of empirical studies (e.g., Picon-Cochard et al., 2006; Provendier and Balandier, 2008) and our simulation results.

Under conditions of high precipitation and low temperature, as for high elevations of the Valais and most parts of the landscapes Feldberg, Jura and Dischma, arrested succession was unlikely to occur. Yet, empirical evidence indicates that understorey vegetation can severely delay and potentially arrest succession under cold conditions (e.g., Liefers et al., 1993; Mallik, 1995). Our simulations showed decreasing herbaceous biomass and competition with increasing elevation, which is in agreement with patterns reported in empirical studies (e.g., Maher et al., 2005; Wilson and Nilsson, 2009). The consequence for our study was that arrested succession became much less likely at colder, high-elevation locations. However, other inhibition processes by the herbaceous layer not included in LandClim may play an important role in cold climates, including competition for nutrients (e.g., Liefers et al., 1993), allelopathy (Mallik, 1995) and the accumulation of slowly decaying litter that can cause mechanical inhibition of tree regeneration (Ott et al., 1997). Thus, our results likely represent a conservative estimate of understorey competition in cold climates, and additional interference mechanisms may need to be considered if species with peculiar traits are known to be present (e.g., Calamagrostis forming dense, impermeable grass mats in mountain forests, Ott et al., 1997).

**Advancing the concept of arrested succession – the role of spatio-temporal scales**

The term ‘arrested succession’ is often used with a relatively vague definition, which can cause misconceptions and hinder the development of ecological theory. Besides clarifying the relative importance of different factors for causing arrested succession in temperate forests, our simulation study underlines the key importance of considering appropriate spatio-temporal scales when studying delayed and arrested succession.

With respect to the temporal scale, the distinction between delayed succession and arrested succession is particularly unclear. Royo and Carson (2006) explored definitions of both terms, although it remained unresolved as to the exact time scale that each term refers to (cf Stromayer and Warren, 1997). Our simulation study indicates that if a forested state (in terms of ≥ 10% canopy cover) was not reached within 100 years, there was a high likelihood of permanently arrested succession. We thus suggest that the term ‘delayed succession’ should refer to decadal time scales, while ‘arrested succession’ is better reserved for the centennial time scale.

With respect to the spatial scale, we found that it was instrumental to examine this phenomenon at the landscape scale, where topographic, climatic and edaphic differences can cause a highly heterogeneous set of environmental conditions. Our simulation study supports the conclusions by Reynolds and Pacala (1993) who found that arrested succession may be difficult to detect and often obscured by the scale of environmental heterogeneity. Although arrested succession was not a common phenomenon within our four landscapes, our simulations suggest that specific landscape positions (in particular xeric south-facing slopes at
low elevations) were far more prone to arrested succession. Thus, focusing on scales that are too large (e.g., on a regional average) or too small (e.g., a few mesic sites in a landscape) may significantly underestimate the degree of delayed and probability for arrested succession in the temperate zone. This is particularly critical since our simulation results indicate that the probability of arrested succession may increase with changing environmental and disturbance conditions. Thus, even though a landscape may appear to be at very low risk for arrested succession under present conditions, this could change considerably under intensified disturbance regimes (Seidl et al., 2011) or under more frequent and severe drought events, which are likely to affect central European forests in the future (Trnka et al., 2013).

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References


Chapter III


Appendix

Appendix S1: Additional Information

Model description

LandClim is a process-based forest landscape model designed to simulate forest dynamics under the influence of exogenic disturbances on large spatial (10^3 to 10^6 ha) and long temporal scales (i.e. hundreds to thousands of years) (Schumacher et al., 2004).

LandClim is based on the LANDIS landscape model (Mladenoff, 2004) and was extended to incorporate a more realistic representation of stand scale processes by integrating a forest gap model approach (cf. Bugmann, 2001). Landscapes in LandClim are represented in the form of a grid of raster cells (25 x 25 m^2), with each grid cell characterized by specific environmental conditions (i.e., climate, soil, topography). The model represents processes at (1) the stand-scale, i.e. forest dynamics simulated at the level of each grid cell and (2) the landscape-scale, i.e. large-scale disturbances and seed dispersal.

Forest dynamics at the stand scale are determined by environmental conditions and competition between vegetation cohorts (groups of the same species and age) for available resources (i.e., light and water). Light extinction through the canopy is modelled using the Lambert-Beer Law (Monsi and Saeki, 2005), i.e., larger cohorts diminish the availability of light for smaller cohorts (Bugmann, 2001). Water availability is determined by precipitation, soil water holding capacity and evapotranspiration (Bugmann and Cramer, 1998; Thrippleton et al., 2017). Tree demography is represented in terms of (1) establishment, (2) growth and (3) mortality, with each process influenced by light, water and temperature conditions via empirically derived reduction functions (see Schumacher et al., 2004). Since establishment and mortality of trees include stochastic process components, the outcome of the simulated forest dynamic is not deterministic, but an emergent property driven by abiotic conditions and biotic interactions.

Establishment

Establishment of new tree cohorts occurs on 10-year time steps, with the probability of regeneration determined by tracking annual environmental conditions and browsing pressure within each decade (see Schumacher et al., 2004 for further details). This environmental ‘filter’ approach for tree regeneration is used in most forest gap models (e.g., Shugart and Noble, 1981; Bugmann, 1996) and accounts for species-specific requirements for light, water and temperature conditions as well as for browsing tolerance (see Table S1.1 below). Establishment probabilities are used with a random number generator, resulting in stochastic establishment events that are more likely to occur when conditions are favourable. If a cohort establishes, establishment density is calculated as a function of available light at the forest floor (Schumacher et al., 2004), thus leading to lower establishment densities under denser canopies.
**Growth**

The calculation of tree growth is based on a logistic growth function. The shape of the growth function is determined by the parameters ‘maximum growth rate’ and ‘maximum biomass’ representing growth conditions for a specific species under optimum environmental conditions (Schumacher et al., 2004). Actual growth is calculated as optimum growth constrained by environmental reduction factors (i.e. light reduction, temperature reduction and drought reduction). The growth reduction functions are empirically derived and reported in detail in Schumacher et al. (2004). Previous studies have evaluated simulated tree growth in LandClim and found good agreement with measured growth at the individual tree level (Elkin et al., 2012) and forest biomass at the landscape scale (Temperli et al., 2013b).

**Mortality**

Tree mortality can occur as a result of (1) growth-dependent stress mortality, (2) age-related senescence mortality, as well as (3) ‘exogenic’ mortality resulting from large-scale disturbances (cf. Schumacher et al., 2004 for a detailed description). The representation of endogenous mortality in LandClim includes stochastic processes and follows common assumptions implemented in forest gap models (see Bugmann, 1996). Growth-dependent stress mortality assumes that only 1% of trees would survive 10 years of consecutive stress conditions (with ‘stress’ defined as conditions where the growth-reduction factor drops below a threshold value, cf. Schumacher et al., 2004). Stress mortality occurs only after more than 3 consecutive years of stress. Age-related mortality is represented by a constant probability of death throughout the lifespan of a tree, assuming that 1% of the trees can reach their maximum age (parameter Maximum age). The simulated mortality rates have been shown to coincide well with mortality rates observed in long-term forest monitoring plots (Elkin et al., 2015). Mortality due to exogenous, large-scale disturbance processes occurs once per decade and removes trees depending on the characteristics of the disturbance regimes (see below).

**Herbaceous understorey**

LandClim has recently been extended to include herbaceous understorey vegetation (cf. Thrippleton et al., 2016 for a detailed description). Herbaceous vegetation is included as plant functional types (PFTs), i.e species sharing similar architecture and ecological strategies. Each herbaceous understorey PFT is present as a single cohort per grid-cell of the landscape. Annual growth is simulated using a logistic growth function (as for trees, see section ‘Growth’ above), but allows for negative growth in years with unfavourable conditions. Herbaceous understorey competes with trees for light (Thrippleton et al., 2016) and water (Thrippleton et al., 2017).

In terms of competition for light, herbaceous understorey diminishes the availability of light at the forest floor, which decreases tree regeneration success. Light extinction by herbs is based on the Lambert-Beer Law (Monsi and Saeki, 2005) and is a function of herbaceous leaf
area index (LAI) and a light extinction coefficient (0.6, Pitman, 2000). Herbaceous LAI is calculated from herbaceous biomass, using an allometric relationship based on data from empirical studies of temperate and Mediterranean regions (see Thrippleton et al., 2016 and Appendix 3 therein).

In terms of competition for water, herbaceous understorey removes available water from the topsoil layer and thereby increases drought experienced by tree regeneration and adult trees (Thrippleton et al., 2017). Water uptake by the herbaceous layer is based on the amount of herbaceous foliage biomass, which determines its contribution to total stand demand. Simulated herbaceous contribution to stand evapotranspiration was evaluated at several sites across Europe where the model consistently reproduced patterns reported in empirical studies (Thrippleton et al., 2017).

The effect of overstorey-understorey interactions was evaluated using empirical data from chronosequence studies, long-term forest observation plots (Alaback, 1982; Jules et al., 2008) and empirical understorey removal experiments (e.g., George and Bazzaz, 1999a; Giuggiola, 2016). When understory was included in LandClim, the model reproduced patterns reported for shifts in species composition, as well as reductions of density and biomass of tree regeneration (Thrippleton et al., 2016; Thrippleton et al., 2017).

Large-scale disturbances

The occurrence of landscape-scale disturbances events (e.g., windthrow, fire and bark-beetle outbreaks) play a key role for shaping mountain forest dynamics in Central Europe (Seidl et al., 2011). LandClim allows to simulate large-scale disturbances by windthrow, timber harvest (Schumacher et al., 2004), wildfire (Schumacher et al., 2006) and bark-beetle outbreaks (Temperli et al., 2013a) in a stochastic, spatially explicit manner at a decadal timescale. The disturbances used in the present study (i.e., windthrow, timber harvest and browsing) interact only with trees, i.e. there is no direct interaction with abiotic factors.

Windthrows account for more than 50% of total damage to forests throughout Europe, and are especially important disturbance agents in mountainous areas (Schelhaas et al., 2003). In LandClim, windthrows occur as spatially explicit patches in the landscape, with the probability of tree mortality depending on tree diameter. The function linking tree diameter to probability of mortality by windthrow was derived from empirical data for temperate forests (Canham et al., 2001). A detailed description of windthrow disturbances, including a sensitivity analysis of windthrow parameters is given in Schumacher (2004).

Forest management plays an important economic role in Europe (FAO, 2015) and is especially relevant in mountain regions of Central Europe, where forests cover more than half of the total mountain area (EEA, 2010). In LandClim, timber harvest allows the user to assign management areas with specific management objectives (Schumacher, 2004). The order in which stands are harvested is based on a stand ranking algorithm, which allows to prioritize stands by specific criteria (e.g., stand age, biomass or stand density). Details about different
harvest types and the timber harvest module is given in Schumacher (2004) and Temperli et al. (2013b). An application of different timber harvest regimes and comparison with empirical data is provided in Temperli et al. (2013b).

**Browsing**

Browsing has become an increasingly important chronic disturbance in mountain forests of Central Europe due to a strong increase in ungulate populations during the 20th century (Kupferschmid et al., 2015). The most important ungulate browsers in the central Alps are European roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and chamois (*Rupicapra rupicapra*) (Kupferschmid et al., 2015). A swiss-wide survey found significant browsing impacts on forest regeneration at all altitudinal zones and regions of the country (Kupferschmid et al., 2015).

In LandClim, browsing by ungulates is simulated as a process reducing the probability of establishment of tree regeneration (see section ‘Establishment’ above). The browsing impact depends on species-specific browsing tolerances (see Table S1.1) and a user-define browsing intensity. The relationship between browsing pressure and probability of establishment is described by an incomplete beta function (Press et al., 1992). The shape parameters of this function are defined for each browsing tolerance class and are described in detail in Henne et al. (2013) and supplementary material therein. Species-specific browsing tolerances were derived from Bugmann (1994). The LandClim browsing module has been applied to temperate and Mediterranean forests, where the model reproduced present landscape patterns and past vegetation dynamics in line with reconstructions from palynological studies (Henne et al., 2011; Henne et al., 2013).
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Table S1.1b Parameters of 31 central European tree species (Schumacher, Bugmann & Mladenoff 2004; Henne et al. 2011).

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Appendix S2: Additional Results

**Figure S2.1** Combined effects of understorey biomass, browsing and harvest (set to a level of 0.9) on the probability of arrested succession for three different elevations and three different browsing levels at the study landscape Feldberg (prediction from the logistic regression model fit for the landscape). Other abiotic factors were set to their means for comparability.
Figure S2.2 Relationship between delay of forest succession (defined as time between start of simulation and time when mean canopy cover of 10% was reached) and Maximum understorey biomass for the four study landscapes (colour indicates point density, i.e. number of simulations, with dark grey indicating highest density). Side figures show the distribution of delays for all simulations per site. Note that 95% of all (i.e. non-arrested) simulations showed a delay of ≤ 100 years.
Figure S2.3 Relationship between delay of forest succession (defined as time between start of simulation and time when mean canopy cover of 10% was reached) and browsing pressure for the four study landscapes (colour indicates point density, i.e. number of simulations, with dark grey indicating highest density). Side figures show the distribution of delays for all simulations per site. Note that 95% of all (i.e. non-arrested) simulations showed a delay of ≤ 100 years.
Figure S2.4 Change in forest biomass growth rate for each study landscape, quantified as difference in forest growth rate relative to the respective reference simulations (i.e. forest growing under same abiotic conditions).
Table S2.1: Summaries of logistic regression models for the probability of arrested succession, using standardized variables (model estimates show the log of odds). Note that the study landscapes Dischma and Jura were excluded from the analysis since they had too few cases of arrested succession.

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<td>0.77</td>
<td>-4.73</td>
</tr>
<tr>
<td>Elevation</td>
<td>-2.09</td>
<td>0.25</td>
<td>-2.97</td>
</tr>
<tr>
<td>NS</td>
<td>-1.32</td>
<td>0.19</td>
<td>-1.09</td>
</tr>
<tr>
<td>EW</td>
<td>-0.59</td>
<td>0.17</td>
<td>-0.60</td>
</tr>
<tr>
<td>BucketSize</td>
<td>-2.52</td>
<td>0.28</td>
<td>-1.36</td>
</tr>
<tr>
<td>Max.Underst.Biom</td>
<td>3.12</td>
<td>0.38</td>
<td>1.90</td>
</tr>
<tr>
<td>Browsing</td>
<td>0.95</td>
<td>0.40</td>
<td>0.79</td>
</tr>
<tr>
<td>Management</td>
<td>0.14</td>
<td>0.35</td>
<td>0.22</td>
</tr>
<tr>
<td>Windthrow</td>
<td>-0.37</td>
<td>0.36</td>
<td>0.38</td>
</tr>
<tr>
<td>Max.Underst.Biom × Browsing</td>
<td>0.94</td>
<td>0.33</td>
<td>0.32</td>
</tr>
<tr>
<td>Max.Underst.Biom × Windthrow</td>
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<td>0.31</td>
<td>0.02</td>
</tr>
<tr>
<td>Max.Underst.Biom × Management</td>
<td>0.30</td>
<td>0.29</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Null deviance: 871.24 on 2499 degrees of freedom
Residual deviance: 286.47 on 2488 degrees of freedom
Null deviance: 2060.79 on 2499 degrees of freedom
Residual deviance: 852.67 on 2488 degrees of freedom

The study landscapes Dischma and Jura were excluded from the analysis since they had too few cases of arrested succession.
Table S2.2a Summaries of linear models for forest biomass growth rates, using standardized variables (model estimate shows $\beta$, the standardized slope of the linear models).

<table>
<thead>
<tr>
<th>Variables</th>
<th><strong>Dischma</strong></th>
<th></th>
<th></th>
<th></th>
<th><strong>Feldberg</strong></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>Std. Error</td>
<td>t value</td>
<td>Pr(&gt;</td>
<td>t</td>
<td>)</td>
<td>Estimate</td>
<td>Std. Error</td>
</tr>
<tr>
<td>(Intercept)</td>
<td>0.00</td>
<td>0.02</td>
<td>0.01</td>
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<td>0.01</td>
<td>0.03</td>
<td>0.98</td>
</tr>
<tr>
<td>Max. Underst. Biom</td>
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<td>0.02</td>
<td>-13.70</td>
<td>0.00</td>
<td>-0.37</td>
<td>0.01</td>
<td>-36.13</td>
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<tr>
<td>Browsing</td>
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<td>0.02</td>
<td>-9.71</td>
<td>0.00</td>
<td>-0.24</td>
<td>0.01</td>
<td>-23.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Windthrow</td>
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<td>0.02</td>
<td>-9.56</td>
<td>0.00</td>
<td>-0.15</td>
<td>0.01</td>
<td>-14.08</td>
<td>0.00</td>
</tr>
<tr>
<td>Harvest</td>
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<td>0.02</td>
<td>-10.64</td>
<td>0.00</td>
<td>-0.19</td>
<td>0.01</td>
<td>-18.51</td>
<td>0.00</td>
</tr>
<tr>
<td>Max. Underst. Biom × Browsing</td>
<td>0.00</td>
<td>0.02</td>
<td>-0.21</td>
<td>0.84</td>
<td>-0.03</td>
<td>0.01</td>
<td>-3.43</td>
<td>0.00</td>
</tr>
<tr>
<td>Max. Underst. Biom × Harvest</td>
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<td>0.02</td>
<td>-2.21</td>
<td>0.03</td>
<td>-0.04</td>
<td>0.01</td>
<td>-4.04</td>
<td>0.00</td>
</tr>
<tr>
<td>Max. Underst. Biom × Windthrow</td>
<td>0.01</td>
<td>0.02</td>
<td>0.49</td>
<td>0.62</td>
<td>0.01</td>
<td>0.01</td>
<td>0.64</td>
<td>0.52</td>
</tr>
</tbody>
</table>

Res. std. error: 0.9265 on 2992 degrees of freedom
Adjusted R-squared: 0.1416

Res. std. error: 0.8598 on 6894 degrees of freedom
Adjusted R-squared: 0.2608
| Variables                        | Estimate | Std. Error | t value | Pr(>|t|) |
|---------------------------------|----------|------------|---------|---------|
| (Intercept)                     | 0.00     | 0.01       | -0.02   | 0.98    |
| Max. Underst. Biom              | -0.46    | 0.01       | -52.65  | 0.00    |
| Browsing                        | -0.29    | 0.01       | -33.49  | 0.00    |
| Windthrow                       | -0.21    | 0.01       | -23.40  | 0.00    |
| Harvest                         | -0.22    | 0.01       | -25.40  | 0.00    |
| Max. Underst. Biom × Browsing   | -0.07    | 0.01       | -8.03   | 0.00    |
| Max. Underst. Biom × Harvest    | -0.08    | 0.01       | -8.99   | 0.00    |
| Max. Underst. Biom × Windthrow  | 0.00     | 0.01       | -0.44   | 0.66    |

Res. std. error: 0.7722 on 7700 degrees of freedom
Adjusted R-squared: 0.4038

Table S2.2b: Summaries of linear models for forest biomass growth rates, using standardized variables. (Model estimate shows β, the standardized slope of the linear models.)
Appendix References


Synthesis

The objective of this PhD thesis was to investigate how resource competition between the herbaceous understorey and trees alter forest dynamics at large spatial (i.e., landscapes ≥ 1000 ha) and temporal (i.e., ≥ 100 years) scales under changing climate and disturbance conditions. By focusing on changes in forest structure and composition (Chapter I and II) and evaluating their potential to delay and arrest succession (Chapter I and III), I elucidated the role of this important vegetation interaction, which is often neglected in studies of long-term forest dynamics.

My thesis focused on resource competition for light and water as the main modes of interaction between herbs and trees. As a first step, I included herbaceous vegetation in the forest landscape model LandClim, and investigated how competition for light influences the long-term dynamics of two mesic forest landscapes in Central Europe (Chapter I). Then, I focused on the implications of competition for water by the herbaceous understorey under present and future climate change. For this, I extended the water balance module of LandClim to explicitly simulate competition for water between herbs, saplings and adult trees, and applied the new model to a drought-prone, inner-alpine valley in the Valais, Switzerland (Chapter II). Lastly, I identified the conditions that are most likely to result in herbaceous understorey arresting succession, as this is arguably the most extreme impact of herbaceous competition on forest dynamics. Here, I systematically explored the effects of herbaceous competition, bioclimatic and disturbance conditions on successional dynamics in a trans-Alpine gradient (Chapter III).

The synthesis will first evaluate the main results and briefly discuss how each chapter contributes to an improved understanding of understorey impacts on temperate forest dynamics. This summary is followed by a critical evaluation of the limitations and recommendations for future research. As a final step, I discuss how my PhD thesis contributes to an ongoing paradigm shift about the functional role of the herbaceous understorey in forest dynamics.
General evaluation of the results

In this PhD thesis, I demonstrated how the herbaceous understorey can alter forest dynamics across a range of environmental conditions and thereby shape the dynamics of forest landscapes in the long term. Under mesic environmental conditions, the herbaceous understorey can substantially delay succession within the first 100 years, and may have an even longer-lasting effect on the composition of overstorey trees (Chapter I). When an herbaceous understorey was present, the results showed a shift towards more shade-tolerant species (e.g. Abies, Fagus) at the expense of light-demanding species (e.g. Betula, Salix), which agrees with patterns from empirical studies (e.g., George and Bazzaz, 1999a; Den Ouden, 2000). Chapter I thus provided support for the long-standing claim that the filtering effect of understorey vegetation not only alters species composition of the advance regeneration layer, but also of overstorey dominants in the long-term (George and Bazzaz, 1999a).

Under dry conditions, water competition by the herbaceous understorey had an even stronger impact on forest dynamics and altered tree species composition and forest structure profoundly (Chapter II). In particular, herbaceous competition reduced tree regeneration and shifted species composition towards more drought-tolerant species (e.g., Quercus), which is also consistent with empirical findings (Morris et al., 1993; Nambiar and Sands, 1993; Galiano et al., 2013). The effect of understory competition was relatively moderate under present climatic conditions and occurred mostly at drought-prone landscape positions (i.e., south-facing slopes at low elevations). However, the impact of overstorey-understorey interactions increased substantially under future climate change in the study landscape Valais. First, climate change caused an upward shift of elevations affected by water limitations exacerbated by herbaceous competition (i.e., from 800 to 1100 m). Second, the increasing frequency and intensity of drought events caused large-scale overstorey mortality, which intensified competition for water between the herbaceous vegetation and tree regeneration. At the driest parts of the landscape, no tree regeneration occurred and the vegetation shifted to a grass-dominated state. Although the limited time scale of Chapter II (100 years) did not allow for an unambiguous conclusion whether this state was in fact stable in the long term, this question was resolved in the following Chapter III, where I considered much longer time scales (1000 years).

Identifying the conditions that allow herbaceous vegetation to form a stable state was addressed in detail in Chapter III, where I systematically explored the effect of overstorey-understorey interactions on forest succession. This chapter extended the research question of Chapter I, i.e., quantifying the degree to which forest succession is delayed or potentially arrested by herbaceous competition, and addressed the unanswered question of Chapter II, whether the open herbaceous state that formed at the driest landscape conditions actually was a stable state. In contrast to the previous chapters, I explored the question about arrested succession within a much larger bioclimatic space (i.e., using four study landscape representing a trans-Alpine gradient) at a centennial time scale and accounted for the interactions with browsing and overstorey disturbances (windthrow and timber harvest). The results confirmed my conclusions from Chapter I, showing that herbaceous competition is
unlikely to arrest forest succession under mesic conditions, and indicating that the lack of tree regeneration at dry landscape positions in the Valais (Chapter II) was in fact arrested succession and stable on the long term. The systematic analysis revealed that herbaceous vegetation has an increasing probability of arresting succession under dry conditions and in combination with intensified browsing as well as overstorey disturbances. In particular, herbaceous competition together with browsing was identified as the main factors causing tree regeneration failure, as suggested by various empirical studies (e.g., Horsley and Marquis, 1983; Horsley et al., 2003). By conducting my investigations at much larger spatio-temporal scales than addressed in empirical studies, Chapter III provides support that herbaceous vegetation may be able to form a stable state that arrests forest succession in temperate regions. Thus my research represents an important step towards resolving this long-standing controversy.

Model limitations and recommendations for future developments

A central challenge of my thesis was developing a process-based representation of herbaceous understorey and its impact on resource competition, in a way that balances complexity and parsimony (cf. Gustafson, 2013). Since computational load at the landscape scale limits the degree of detail at which processes can be represented (He, 2008), I merged mechanistic and phenomenological approaches to arrive at an adequate level of detail that was applicable for the landscape scale. However, these simplified assumptions inevitably neglected processes and interactions that may require consideration in future research, depending on the research question. Below, I outline the aspects I consider to be most important, discuss how they may affect the results, and under which conditions they should be taken into account.

Mechanical inhibition

Mechanical inhibition (i.e., physical damage to tree regeneration by accumulation of understorey litter, or shedding of leaves and fronds) has been identified as an important factor that can reduce tree regeneration (Royo and Carson, 2006). This is particularly the case for fern (Dolling, 1996; Humphrey and Swaine, 1997) or dense grass understoreys (Lieffers et al., 1993) that inhibit tree regeneration by the accumulation of slowly decaying litter mats. Mechanical inhibition by grasses is considered to be especially important in high-elevation mountain forests (Ott et al., 1997; Kupferschmid and Bugmann, 2005). As outlined in the discussion of Chapters I and III, the absence of mechanical inhibition in the model most likely underestimated the effect of understorey vegetation on forest succession at higher elevations.

As LandClim is intended to simulate processes important in mountain forests, I recommend an implementation of mechanical inhibition as an interference mechanism by the herbaceous understorey in the model. It may be possible to build on the fuel pool of the current fire submodel, which tracks tree litter decomposition based on temperature and precipitation
(Schumacher et al., 2006). An additional ‘herb-litter’ pool could be implemented in the fuel submodel without much effort (which may also be a required step for connecting herbaceous vegetation to fire disturbances; see below). Data from litter decomposition experiments (e.g., Frouz et al., 2011) could inform the parameterization of the herb litter pool and its decay rates. Biomass within the herbaceous litter pool could then be used as a proxy for determining the degree of mechanical inhibition on tree regeneration, as described in the conceptual model by Lieffers et al. (1993).

The water balance model

The considerable uncertainty in estimates of soil water holding capacity and tree rooting depth has been identified as a key issue for modelling drought impacts on forests (Cáceres et al., 2015). As discussed in Chapter II, an overestimation of soil water holding capacity (WHC) for parts of the study landscape Valais may have resulted in an underestimation of drought. Due to the mostly unknown rooting depth (e.g., Joffre and Rambal, 1993; Rigling et al., 2002) and lack of soil data at the landscape scale (Henne et al., 2011), this issue is however difficult to resolve. The Master Thesis of Marc Folini (2015) evaluated the water balance model of LandClim by comparing its results to measurements from the FLUXNET database (Baldocchi et al., 2001), and concluded that the evaluation was difficult at some sites due to a lack of detailed soil information (i.e., depth and texture of each soil layer). Incorporating better estimates of rooting depth and soil characteristics at the landscape scale could thus considerably improve model reliability. A number of approaches have been developed to tackle this challenge, from statistical modelling of soil properties at the landscape scale (e.g., Nussbaum et al., 2016) to estimating rooting depths at the catchment scale using process-based models (e.g., Schymanski et al., 2008). Most mechanistic approaches with this focus require substantial parameterisation and computation effort in their own right, which probably renders their use in a forest landscape model framework infeasible. However, such mechanistic models may for instance be used in a meta-model approach (cf. Urban et al., 1999), i.e. to represent selective behaviour of the original model (e.g., estimates of rooting depth) as a statistical construct in a forest landscape model.

For the development of the two-layer soil model, I used the approach of dynamic global vegetation models (DGVMs) to represent water competition between trees and herbs in separate soil layers (e.g., Gerten et al., 2004). My original idea was to explicitly simulate percolation and root zone competition (as in Gerten et al., 2004), but this did not work out. In a pilot version of the two-layer water balance model that included an explicit consideration of percolation (based on Haxeltine and Prentice, 1996), I found the model results to be quite sensitive to percolation between the soil layers, which strongly depended on depth and texture of each layer. Given the high degree of uncertainty in soil characteristics (depth, texture) at the landscape level (Henne et al., 2011), I had to conclude that a mechanistic representation of percolation and rooting depth was not feasible in LandClim, and thus I chose a simplified approach. Other studies applying the DGVM approach to simulate water balance at the landscape scale have encountered similar scale-dependent problems (e.g., Tang et al., 2015), although considerable improvements have been made to represent processes at the regional
scale (e.g., Manusch et al., 2014). The simplified assumption of unconstrained infiltration and percolation in my approach may however be problematic in areas characterized by strongly pulsed precipitation events (such as the Ticino in southern Switzerland, Reineking et al., 2010). Due to the monthly resolution of the water balance model, which implicitly assumes a uniform distribution of precipitation across the month, the soil water content may be overestimated relative to real conditions where a significant proportion of precipitation may be lost due to surface runoff. This problem could theoretically be solved by increasing the temporal resolution to a daily time step and implementing water fluxes within the soil at a higher level of mechanistic detail. However, before implementing more details and a higher temporal resolution in LandClim, I would recommend a systematic exploration of the costs and benefit of different levels of mechanistic detail in a theoretical experiment, to prioritize feasible development targets.

**Nutrient competition**

The belowground competition I developed in *Chapter II* focused on soil water only. However, herbaceous understorey can also be a significant competitor for nutrients, in particular nitrogen (Nambiar and Zed, 1980; Balandier et al., 2006). This effect is most notable in areas of acid, podzolised soils (Den Ouden, 2000). In boreal forests in particular, understorey vegetation has been shown to rapidly sequester nitrogen and can contribute to nutrient leaching by soil acidification (e.g., as shown for ericaceous dwarf shrubs or grasses, Mallik, 1995; Hart and Chen, 2006; Matsushima and Chang, 2006). In contrast to most boreal forests, temperate ecosystems have been transformed from nitrogen-limited to a widespread (over-) saturated state (Posch et al., 2015), and thus eutrophication is a widespread problem in most regions of Europe, affecting temperate forests, heathlands and alpine grasslands (Bobbink et al., 2010). It is therefore not surprising that empirical studies in European temperate forests have found nutrient competition by understorey vegetation to be of minor importance compared to water competition (e.g., Provendier and Balandier, 2008; Giuggiola, 2016). Overall, I therefore consider nitrogen competition as a highly important process in most boreal forests, but posit that its significance has diminished strongly for central Europe over the past decades.

Compared to nitrogen, competition for other nutrients is usually less important in the context of herb-tree interactions (Nambiar and Sands, 1993), although some studies reported that understorey can reduce calcium and magnesium availability by variable amounts (Mohammed et al., 1998; Nilsen et al., 2001). Effects of herb-tree competition for plant available phosphorus were mostly reported to be relatively small in temperate forests (e.g., Horsley, 1993), but can be of high importance in tropical regions (e.g., Russell et al., 1998).

**Effect of browsing ungulates on the herbaceous understorey**

For the study of arrested succession, I assumed that the herbaceous understorey consisted entirely of an unpalatable grass plant functional type. Several studies have shown that browsing ungulates usually avoid specific herbaceous groups that are either low in nutritional
value, hard to digest or even toxic, such as many ferns (de la Cretaz and Kelty, 1999; Rooney and Waller, 2003). Selective herbivory has been shown to lead to the development of a simplified, ‘depauperated’ understorey, often dominated by a few unpalatable species (Royo and Carson, 2006; Rozman et al., 2015). Establishing a direct link between browsing and understorey vegetation in models such as LandClim would be an important step for future model development. An obstacle for this development are the complex interactions between browsing and understorey vegetation, which depend on food supply, feeding preference, ungulate density and the type of understorey species (Horsley et al., 2003; Weisberg and Bugmann, 2003; Royo et al., 2010). Although the majority of studies show that dense understorey vegetation and deer browsing act in combination to prevent tree regeneration (see review by Royo and Carson, 2006), the combined presence of understorey vegetation and browsing is not exclusively negative. Some studies have shown that moderate browsing can reduce the abundance of highly competitive understorey species and thereby favour tree regeneration (e.g., Nakashizuka, 1987). Thorny, unpalatable understorey shrubs can also protect saplings from browsing, thus facilitating tree regeneration (Morgan, 1991; Harmer et al., 2005; Van Uytvanck et al., 2008). Thus, there is ample scope and evidence for improving the representation of browsing in forest landscape models like LandClim.

However, due to the complex and highly species-specific responses, it is difficult to provide general recommendations how to incorporate these interactions. One aspect of particular concern is the influence of spatial heterogeneity in vegetation and environmental conditions that drives ungulate distribution and foraging behaviour at this scale (Weisberg and Bugmann, 2003; Côté et al., 2004). Vegetation also creates a feedback on ungulate population density in the long term, since ungulate populations are mostly limited by forage availability (Weisberg and Bugmann, 2003). Thus, a possible next step would involve integrating a simulation of ungulate population dynamics and browsing impacts into LandClim. Some dynamic vegetation models have already included these processes explicitly (e.g., FireBGCv2, Riggs et al., 2015; LANDIS-II, De Jager et al., 2017). Although such an approach would come with a considerable increase in computational demand and parameterisation effort (e.g., species-specific thresholds for growth reduction and mortality increase), I consider it a promising direction for addressing the issue of combined understorey and browsing impacts on forest dynamics. As a matter of fact, the recent incorporation of cow grazing in LandClim in the context of pasture-woodland systems (Snell et al., 2017), could lead the way towards a more general ungulate browsing module.

**Interactions between fire and understory vegetation**

Fire is a key process causing vegetation shifts from woodland to grass- or shrub-dominated landscapes in many tropical and subtropical regions (Kramer et al. 2003, Scheffer et al. 2001, Holmgren et al. 2001, Acacio et al. 2009). In temperate and boreal regions of North America, severe fire disturbances contribute to the formation of a dense herbaceous understorey, which can substantially inhibit post-fire succession (Liefers et al., 1993; Hart and Chen, 2006; Royo and Carson, 2006). However, fire can favour either regeneration of herbs or trees, depending on the characteristics of the fire regime (Liefers et al., 1993). Riggs et al. (2015) developed a
landscape fire model approach and suggested that a high degree of mechanistic detail in the representation of fire and understorey vegetation is important to adequately capture the effect of herbs and shrubs on fire spread and intensity.

The effect of the herbaceous understorey on fire behaviour as simulated by LandClim was tested in the Bachelor thesis by Dominik May (2016). Since I have not explicitly included a feedback between herbaceous vegetation and fire in LandClim, herbaceous understorey contributes to the litter fuel compartment, but only indirectly affects fire spread due to the influence on the drought index. The results from Dominik May’s thesis showed only a minimal impact of grass vegetation on the fire regime, much lower than reported in empirical studies (e.g., Balch et al., 2013). Thus, future model development should explicitly link herbaceous biomass (as a surrogate for herbaceous ground cover) to fire spread (as for instance described conceptually in Allen, 2007). This step could be informed by empirical studies from North America that quantified the relationship between grass cover and the probability of burning (e.g., Just et al., 2016). In addition, a reconsideration of the contribution of herbaceous litter to the flammable fuel pool in LandClim would be necessary, as well as including differential effects of fire on different herbaceous PFTs (e.g., FireBGCv2, Keane et al., 2011). Despite the challenges inherent in this more mechanistic approach, implementing a link between understorey vegetation and fire could significantly improve the applicability of LandClim to fire-prone regions e.g. in North America, or for studying the transitions of currently non-fire-prone landscapes to novel wildfire regimes under climate change (e.g. in central Europe, Seidl et al., 2011).

**Seed dispersal**

The simulation setup across my thesis assumed global seed dispersal, i.e. that seeds of all tree species are present throughout the landscape at all times. I based this assumption on the results of He and Mladenoff (1999), who found that the effect of seed dispersal diminishes in the long-term (i.e., simulations exceeding 250 years). By doing so, I did not account for the possibly increasing importance of seed dispersal in landscapes shaped by large disturbances, particularly if they are fragmented. Empirical studies have shown that the removal of seed-bearing trees by stand-replacing disturbance contributes to tree regeneration failure and the formation of a stable herbaceous states (e.g., Payette and Delwaide, 2003; Acacio et al., 2007). By ignoring the effect of seed dispersal, it is possible that I underestimated the effect of overstorey disturbances on the probability of arrested succession in Chapter III. Still, the species set used in Chapter III includes highly effective wind-dispersed trees (e.g., Salix, Betula) that would likely be present throughout the landscape (e.g., Houle, 1992) even if seed dispersal was simulated explicitly. Furthermore, the large time scales considered in this study (1000 years) would likely have allowed trees with much slower dispersal rates to establish within the landscape. I nevertheless suggest that seed dispersal should be considered for studying the effect of large-scale, stand-replacing disturbances in future research, particularly if locally or temporally accurate projections are to be made.
Significance of results for ecological research

Forest dynamics can be profoundly influenced by vegetation interactions occurring during the early successional stage (Swanson et al., 2011). Competition between herbaceous vegetation and trees is considered as the most important vegetation interaction during this stage (Alaback, 1984; George and Bazzaz, 2003; Balandier et al., 2006), yet it is widely neglected in studies of forest dynamics (Royo and Carson, 2006). This discrepancy may reflect a traditional under-appreciation of the early successional stage and particularly the role of herbaceous vegetation from a forestry perspective (Gilliam, 2007; Swanson et al., 2011). My results underline that competition for light by the herbaceous understorey can significantly delay succession and alter the structure and composition of mesic forests (Chapter I). The results of Chapter II and III illustrate that neglecting herbaceous vegetation is even more critical under drought-prone conditions, particularly when taking climate change and disturbances into account. Thus, my thesis is not only an important step towards an improved representation of vegetation interactions in landscape models, but it also contributes to an ongoing paradigm shift towards an increasing recognition of the key role of herbaceous vegetation for forest dynamics, especially in view of future climate and disturbance regimes.

Considering herbaceous understorey in dynamic vegetation models

Dynamic vegetation models (DVM), in particular ‘forest gap models’, have frequently been used to study potential natural vegetation, thus focussing on a ‘quasi-equilibrium’ state that is assumed to be reached after several centuries (e.g., Bugmann, 2001; Hall and McGlone, 2006; Foster et al., 2017). However, forest landscape models (FLMs) were specifically developed to represent disturbance processes and non-equilibrium states (Perry and Enright, 2006; He, 2008). Thus, considering herbaceous vegetation and its interaction with trees should be of particular relevance for FLMs, given the importance of this interaction for post-disturbance dynamics.

To my knowledge, my thesis provides the first comprehensive analysis of the implications of herbaceous vegetation on temperate forest dynamics, using a landscape DVM. The results of my thesis demonstrate that herbaceous vegetation has the strongest impact on early successional stages (≤ 100 years), and decreases in importance towards later successional stages (>200 years) under mesic, undisturbed conditions (Chapter I). In this way, my thesis supports the robustness of previous DVM studies that did not include an herbaceous layer, provided that they focused on the late-successional stage (e.g., Henne et al., 2011; Schuler et al., 2016). However, Chapter II demonstrated that DVMs that do not consider herbaceous understorey likely underestimate the impacts of severe drought events, which are becoming an increasing concern for temperate forests under future climate change (IPCC, 2014). This has important implications for the range of stand- and landscape-scale models that have been used to project climate change impacts in temperate forests (e.g., Scheller et al., 2007; Elkin et al., 2013).
Therefore, I recommend that DVMs should be modified to include the herbaceous understorey if they focus on at least one of the following aspects: (1) early successional dynamics (cf. Chapter I), (2) climatic extreme events (cf. Chapter II), (3) the effects of browsing, or (4) overstorey disturbances (e.g., windthrow, fire, harvest, insect outbreaks), especially if these disturbances occur in combination with each other (cf. Chapter III). While mesic forest dynamics may be less affected, I emphasize that future studies focusing on forest dynamics in drought-prone landscapes should consider herbaceous vegetation (cf. Chapter III).

The representation of herbaceous understorey I developed in this thesis provides a relatively simple approach that could be incorporated into other DVMs, without much effort in terms of programming, computational load, or parameterisation. This is especially the case for the representation of light competition (Chapter I), which should be compatible to most DVMs built upon the forest gap model framework (i.e., representing establishment, growth and mortality of tree species at the individual or cohort level on small patches of land). Including herbaceous water competition in other DVMs may need further adjustments, to match the spatiotemporal scales used in their representation of the water balance.

Ultimately, incorporating herbaceous vegetation in landscape models is an important step towards a more holistic ecosystem representation at the landscape scale, which comprises not only forests but also managed or unmanaged grasslands. This aspect becomes more important as DVMs are increasingly used in transdisciplinary approaches to explore the trade-offs in ecosystem services and socio-economic feedback effects (e.g., Huber et al., 2013; Snell et al., 2017).

**Contributing to a paradigm shift: the importance of herbaceous understorey in forest dynamics**

Traditionally, herbaceous vegetation has been of little interest to forest ecologists, although this perspective has begun to change over the last decades (Gilliam, 2007). An increasing number of studies have emphasized the importance of herbaceous vegetation for biodiversity, and studied its response to overstorey structure and diversity (e.g., Barbier et al., 2008; Reusser et al., 2010). However, studies that focused on the interaction between herbs and trees have gained less attention, despite compelling empirical evidence (e.g., George and Bazzaz, 1999a) as summarized in comprehensive literature reviews (e.g., Hart and Chen, 2006; Royo and Carson, 2006). In my opinion, this is to a large degree an issue of human perception that often does not recognize (and thus not appreciate) processes taking place at very small spatial scales while revealing their effect at large temporal scales. Herbaceous vegetation typically has the largest effect on the earliest tree life stage, i.e. this process takes place at the spatial scale of a few centimetres. Empirical studies have shown that this process alters the structure and composition of the advance regeneration layer (e.g., George and Bazzaz, 1999b), but evidence for how this effect translates into overstorey composition has been lacking due to the large time scales involved. In this thesis, I used a modelling approach to upscale the observed process and demonstrated its importance at large spatio-temporal
scales. The thesis thus bridges the gap between a small-scale process and the large-scale implication, which is critically needed to demonstrate its ecological significance. Furthermore, in Chapters II and III I have shown that the importance of herbaceous understorey for forest dynamics is likely to increase under a future climate characterized by more frequent drought and disturbance events. Particularly in view of the current research focus on drought legacy effects in forest ecosystems (e.g., Anderegg et al., 2013), the results of Chapter II – emphasizing the key role of herbaceous vegetation – should be of high interest for the scientific community. I hope that the studies in this thesis will contribute to an increased appreciation of the functional role of herbaceous understorey and give the topic the much deserved impetus to gain a more recognized role in ecological research.

In this respect, I would like to address an issue of personal concern, which I have only briefly touched upon in Chapter II, i.e. the prevailing perception of herbaceous understorey as deleterious ‘weeds’ in forest management. From a management perspective, the results presented in this thesis could be viewed as support for the widespread use of herbicides in many countries to improve forest growth, as often recommended in production forests (Wagner et al., 2006; Willoughby, 2008). Some studies even have come to the conclusion that the application of herbicides has only short-term effects on biodiversity and is thus compatible with conservation objectives (Wagner et al., 2004). I am highly sceptical about this perspective and argue on the contrary that changes to the herbaceous understorey affect forest structure and diversity on time scales exceeding human time horizons by far, as shown throughout my thesis.

In a similar manner, the results of my thesis could be (mis-)used to confirm prevailing paradigms about the negative effects of herbaceous vegetation, as implied in the negative connotation of the terms ‘delayed’ and ‘arrested’ succession. From a forestry perspective, it is obvious that a prolonged (or even stable) herbaceous state is undesirable and may be perceived as a ‘loss of capital’ (Swanson and Chapin, 2009). However, I would like to underline the ecological importance of open herbaceous states, which may play a key role for species diversity (including species which are obligate to this state, such as many butterflies and moths, Swanson et al., 2011). The stable herbaceous state as found in Chapter III should thus by no means be interpreted as ecologically ‘inferior’ or ‘undesirable’. On the contrary, the presence of open herbaceous vegetation alongside closed canopy forest enhances structural diversity and is thus important for biodiversity in a landscape context (Whittaker, 1972; Laurila-Pant et al., 2015).
Conclusion

This thesis has shown that herbaceous understorey can change forest dynamics on large spatio-temporal scales by altering forest structure and composition, as well as delaying or even arresting forest succession. Studies of long-term forest dynamics that neglect herbaceous vegetation (as frequently done in dynamic vegetation models, DVMs) may thus overlook an essential vegetation interaction that can lead to drastically different forest responses to changing climate and disturbance regimes.

While the effect of overstory-understorey interactions is relatively moderate in mesic forests, it increases considerably towards drier conditions. At very dry landscape positions (i.e. south-facing slopes, low elevations) herbaceous vegetation is able to exclude tree regeneration in the long term and hence arrest succession. The results from this thesis thus suggest that herbaceous vegetation can form a stable state in temperate forests, particularly when it occurs in combination with high ungulate browsing pressure.

Quantitative, dynamic models are an indispensable part of such research, because only they allow us to extend and upscale the analysis to spatial and temporal scales that are not accessible to observation, let alone experimentation. As shown in this thesis, DVMs should particularly take into account herbaceous vegetation when they focus on (1) early successional dynamics, (2) impacts of climatic extreme events, particularly drought, (3) the long-term effect of browsing, (4) effects of overstorey disturbances. The approach presented in this thesis provides a simple and flexible framework to represent herbaceous vegetation and its competition with trees for light and water. Furthermore, it is broadly applicable to other DVMs with a reasonable parameterisation effort. In particular landscape-scale DVMs with their focus on disturbance impacts on vegetation dynamics should consider including an herbaceous component. Ultimately, the results of this thesis show that landscape scale DVMs, such as LandClim, are suitable tools to investigate the effect of overstorey-understorey interactions on forest dynamics and to disentangle the complex interactions between vegetation, climate and disturbance regimes.
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