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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 analyse 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 560–2800 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-successional 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.

Key words: herbaceous vegetation; overstorey–understorey interaction; arrested succession; Black Forest; Dischma valley; central Alps; dynamic vegetation model.

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Author Contribution T.T., R.S.S. and H.B. designed the study; T.T. and R.S.S. developed the submodel; T.T. conducted the simulation experiments; K.K-P. contributed data; T.T., H.B., K.K-P. and R.S.S. wrote the paper.

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INTRODUCTION

Biotic interactions are increasingly recognized as key mechanisms that influence vegetation dynamics at larger scales (for example, Nieto-Lugilde and others 2015). In forests, the study of biotic interactions has mostly focused on competition between woody species (Bugmann 2001; Gilliam 2007) and plant–animal interactions (for example, Kupferschmid and others 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 and others 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 and others 2006; Royo and Carson 2006; Li and others 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 and others 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 15–20 years, the effect of the herbaceous layer on tree regeneration is usually considered to be strongest (Balandier and others 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 (for example, George and Bazzaz 1999a, b). Thus, although 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 (for example, Ott and others 1997; Frehner and others 2005). At the landscape scale, disturbances are central for structuring spatial heterogeneity and driving ecosystem dynamics (Turner and others 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 and others 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 generalization of overstorey–understorey interactions. 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 (for example, of climate, biotic interactions, disturbances and land-use change).

Despite repeated pleas to include a herbaceous layer in dynamic models of forest growth (for example, Maguire and Forman 1983; Weisberg and others 2003; McKenzie and others 2009), there are only a few process-based forest models that have put this into practice (for example, Kellomäki and Väisänen 1991). Dynamic global vegetation models (DGVMs) generally include herbaceous and shrubby components (for example, LPJ-GUESS, Smith and others 2001; SEIB-DGVM, Sato and others 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 (for example, Hickler and others 2012). To our knowledge, no process-based forest model has been used specifically to investigate the two-way interactions between the overstorey and understorey layers. 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 and others 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 and others 2004; Henne and others 2013), North America (Schumacher and others 2006) and New Zealand (Thrippleton and others 2014). Landscapes are represented in LandClim in the form of raster grids ($25 \times 25 \text{ m}^2$) with specific environmental conditions for each grid cell (i.e., aspect, slope, soil and climate). Within each grid cell, stand-scale processes are simulated, that is 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 (for example, 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 and others 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 Understorey

Due to the high species diversity in the understorey, we chose to represent it as plant functional types (PFTs), i.e., species groups based on similar architecture and ecological strategies (for example, Weisberg and Bugmann 2003; Balandier and others 2006). We focus on four groups of herbaceous PFTs (listed according to increasing shade tolerance, compare online 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) (compare section ‘Model evaluation’ and online Appendix A1). Details on the parameterization of the understorey PFTs are provided in online Appendix A1.

Each understorey 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, understorey PFTs can be assumed to be present all the time, i.e. from the point of view of the model that they are perennial, even though from a botanical point of view that 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 and others 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 understorey 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 (equation 1) that was derived by fitting a linear model to empirical data (compare

online Appendix A3). Second, herbaceous vegetation cover ($\text{cover}_{\text{Herb}}$) was considered as an additional, down-weighting factor in the calculation of the grid cell LAI for each cohort (equation 2), to account for the patchiness of the herbaceous vegetation at scales of a few metres (George and Bazzaz 2003). The percentage of ground cover by each PFT was calculated using allometric equations from different empirical studies (compare online Appendix A4).

$$\text{LAI}_{\text{Herb}} = 0.7442 \cdot \text{Biomass}_{\text{Herb}} \quad (1)$$

$$\text{LAI}_{\text{Herb,cohort}} = \text{LAI}_{\text{Herb}} \cdot \text{cover}_{\text{Herb}} \quad (2)$$

Sensitivity Analysis for Herbaceous Growth Parameters

The herbaceous growth parameters (maximum growth rate ‘ R_{max} ’ and maximum biomass ‘ K_{max} ’) are decisive for determining the outcome of competition with trees, but their values are subject to considerable uncertainty (compare online Appendix 1). Thus, these parameters were studied in more detail using a sensitivity analysis. Parameters were varied within ranges informed by empirical measurements (compare online Appendix A3). Maximum biomass was varied from 16 to 800 g m⁻² (i.e., 0.16–8 t ha⁻¹), and maximum growth rate varied from 0.01 to 1 y⁻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 greater than 1000 mm (Bogenrieder and Rasbach 1982; Schumacher and others 2004) and were selected because together they represent a large elevation range from 560 m to above 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 to 2012 (DWD, Deutscher Wetterdienst; <https://werdis.dwd.de/>, July 2014). Details on the topographic and soil input maps for Feldberg are given in online Appendix A2. Information regarding the climate and soil data for the Dischma landscape can be found in Schumacher and others (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 and others (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) (compare online 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-year rotation period and (3) windthrow disturbances with a rotation period of 400 years (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-year chronosequence by Jules and others (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 and others 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 and others (2008): stage 1—an understorey peak (mostly grasses and shrubs) within the first 25 years; stage 2—a gradual decline towards a minimum cover around year 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 and others (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 years after disturbance (for details compare Priewasser 2013; Kramer and others 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 *R*, version 3.1.2 (R Development Core Team 2014).

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_{\max} (maximum growth rate) influenced the results only when it was greater than 0.2 y^{-1} , whereas the parameter K_{\max} (maximum biomass) had a strong effect throughout the investigated parameter range. Very high K_{\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).

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).

Landscape Simulations: Spatial Patterns

Understorey vegetation followed clear elevational trends in both landscapes (Figure 3). Elevations below 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 below 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 10–20 showed a dominance of *Rubus* and fern at lower elevations and forbs and grasses at higher elevations (Figure 3I).

Understorey Impact on Forest Dynamics

At low elevations, the presence of understorey vegetation delayed forest succession by several

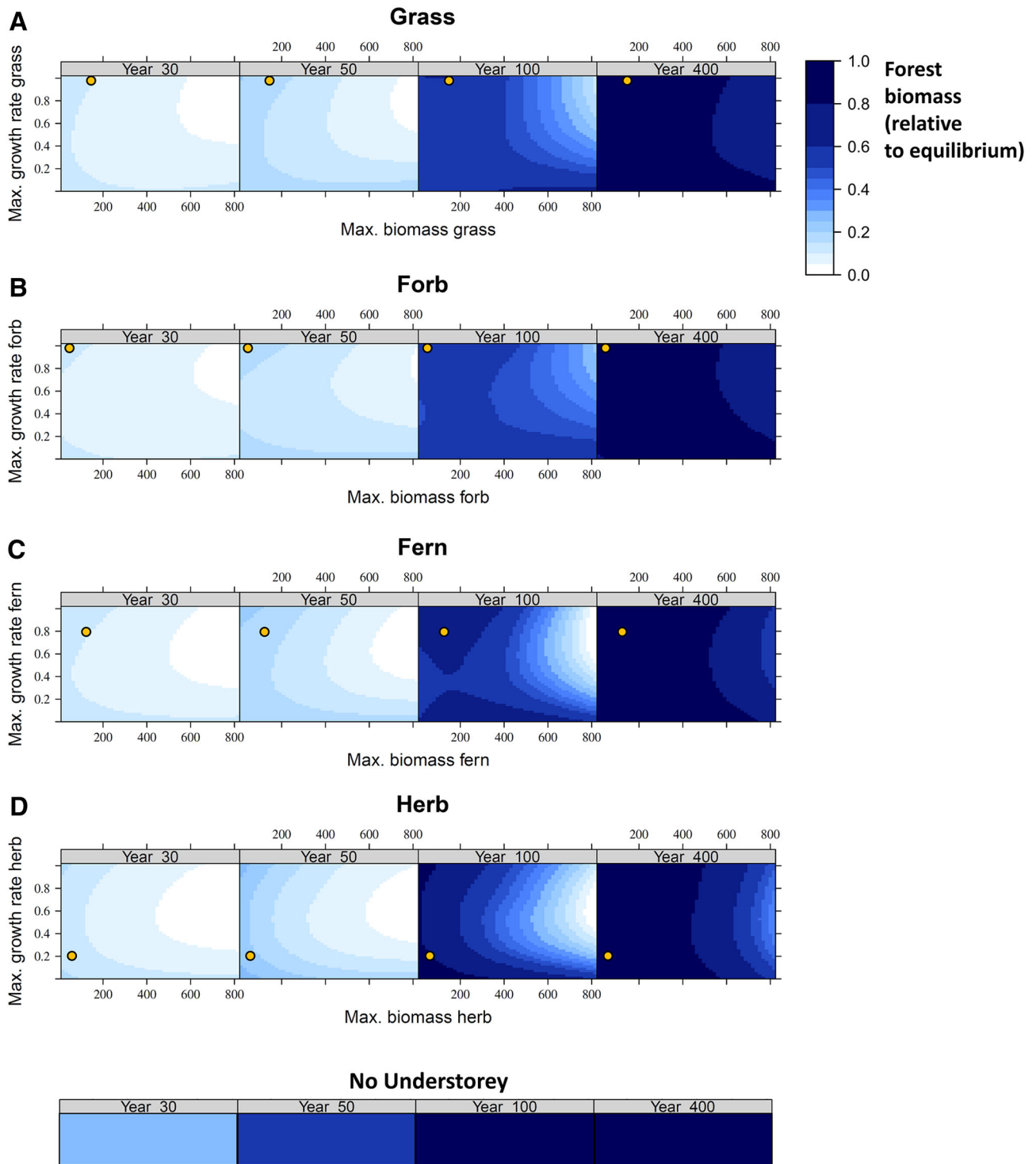


Fig. 1. Sensitivity analysis of the herbaceous growth parameters ‘maximum biomass’ (g m^{-2}) and ‘maximum growth rate’ (y^{-1}) for the four simulated plant functional types. The impact of the herbaceous layer on forest biomass development (expressed as biomass relative to equilibrium biomass, that is, 400 t/ha) is shown. *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) (Color figure online)

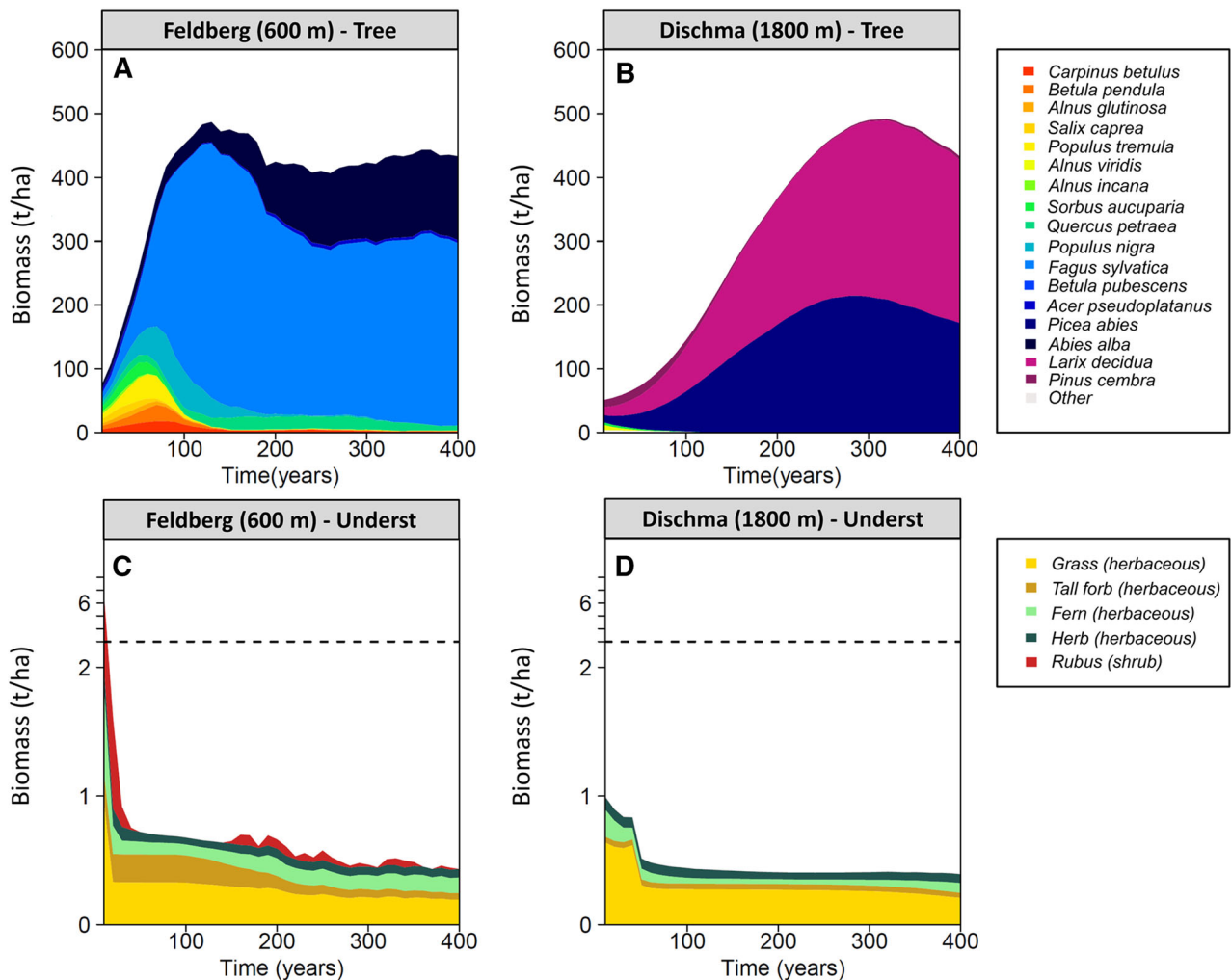


Fig. 2. Succession of tree species and understorey in the study landscapes (A, C) Feldberg at 600 m a.s.l. and (B, D) Dischma at 1800 m a.s.l. For clarity, the y-axis was rescaled by a factor of 10 above the horizontal dashed line

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). 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 (compare online Appendix A5).

Effects of Windthrow

The occurrence of large windthrow disturbances strongly increased average herbaceous biomass across the landscape (up to 56%; Figure 6).

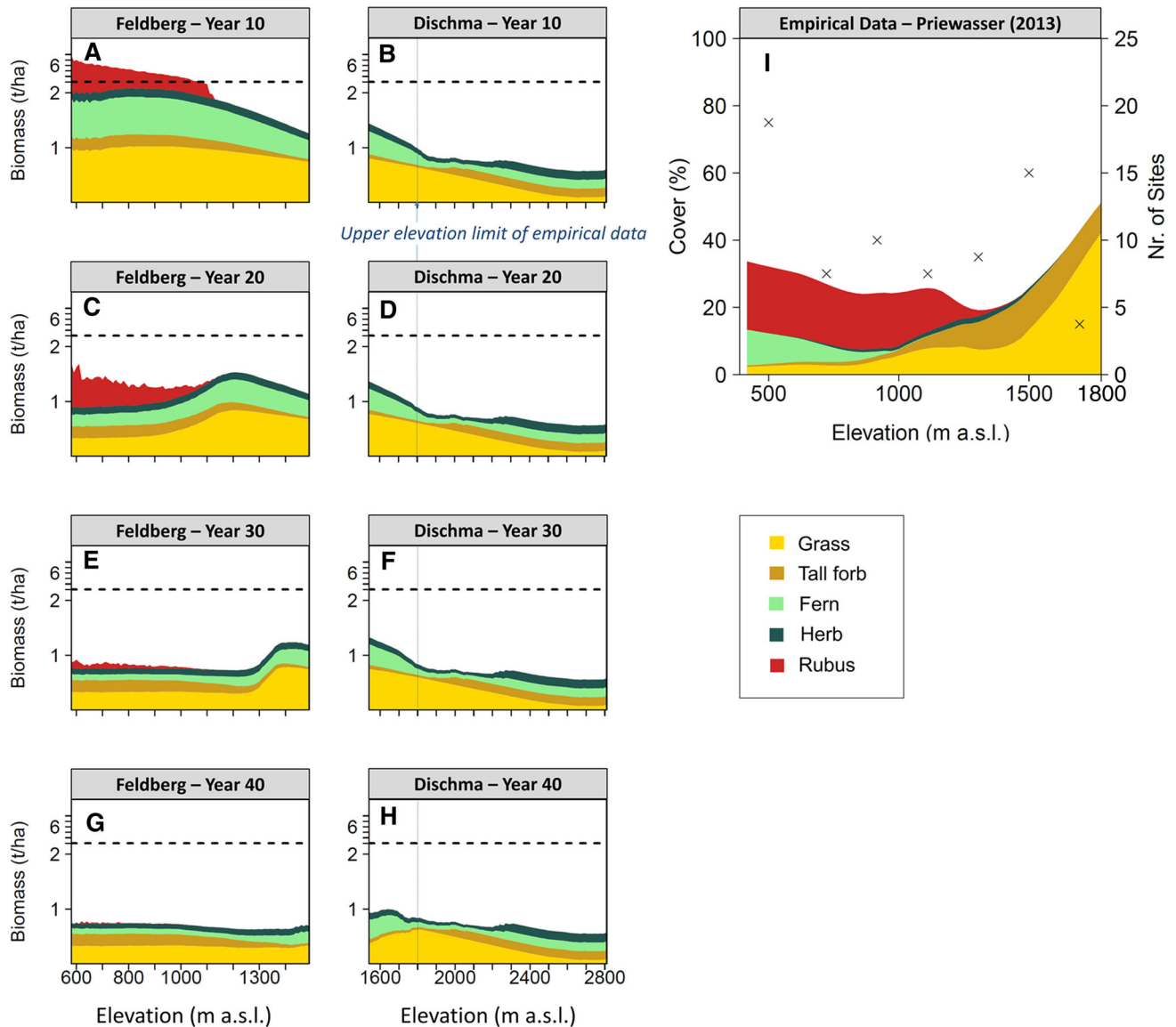


Fig. 3. Distribution of understorey plant functional types along an elevation gradient for Feldberg and Dischma. For clarity, the y-axis was rescaled by a factor of 10 above the *horizontal dashed line*. Cross marks in panel **I** show the number of study sites within each 200-m elevation belt. Sites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

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’).

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

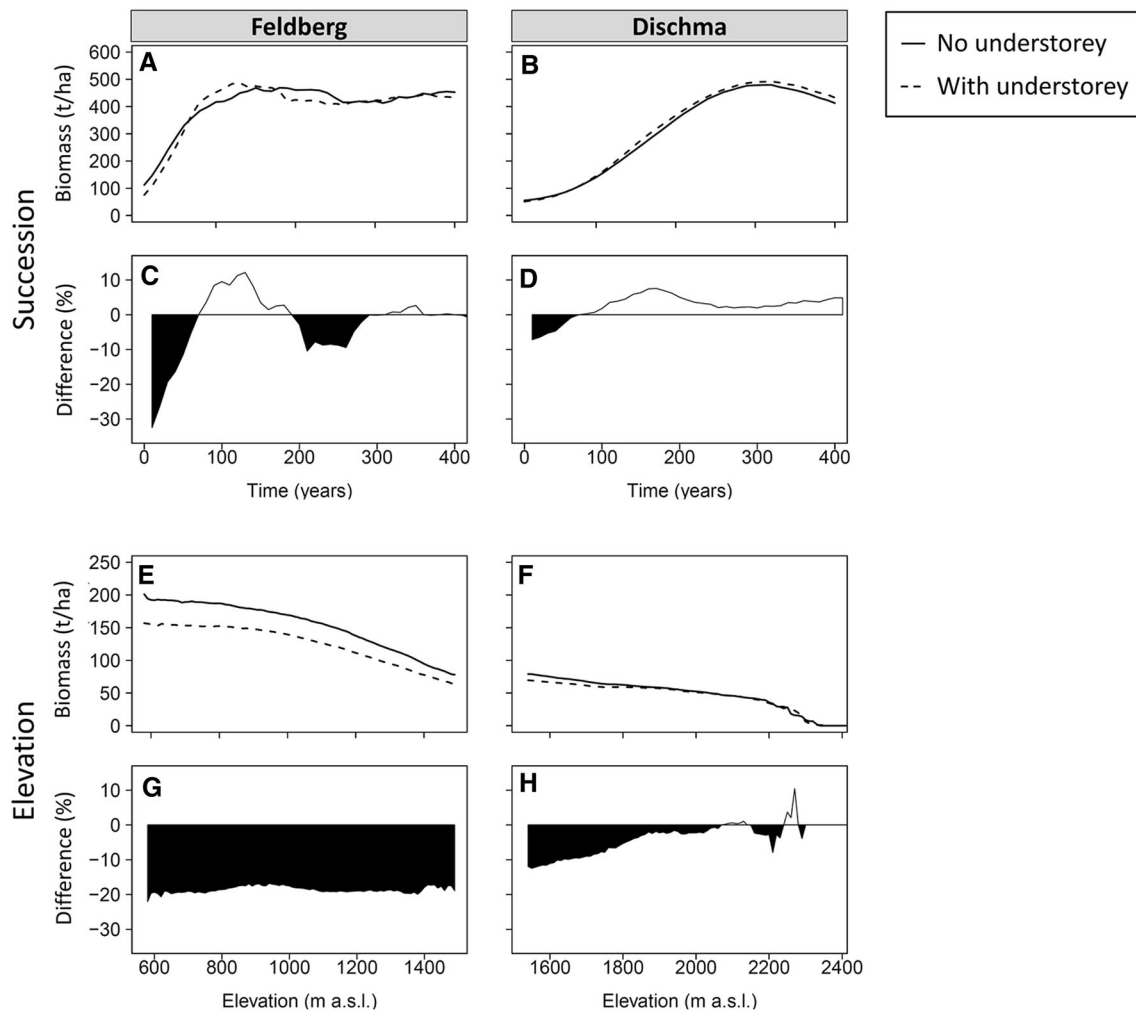


Fig. 4. Effect of understorey vegetation on forest biomass development with time (A–D) for Feldberg at 600 m and Dischma at 1800 m, and across the elevational gradient at year 30 (E–H). In both cases, the top panels (A, B, E, F) illustrate the absolute biomass values and the bottom panels (C, D, G, H) show the percent difference between the *two lines* (with and without understorey)

suggested by Horsley 1993; DenOuden 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 DenOuden (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 (1999a, b), 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 (for example, Lieffers and others 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

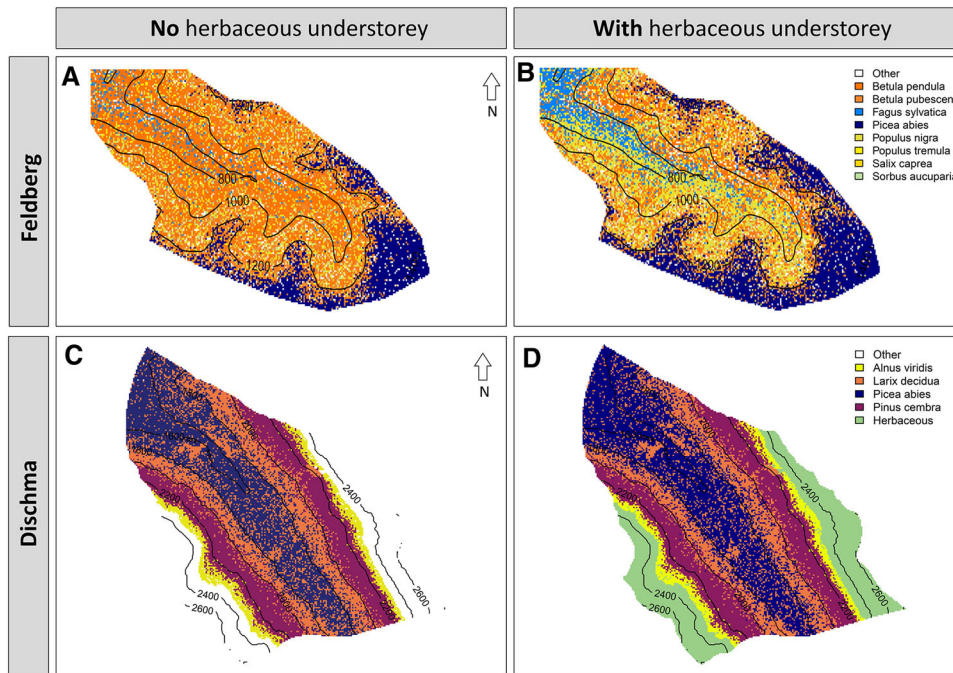


Fig. 5. Maps of dominant species for the Feldberg and Dischma landscapes at year 50 of the succession, excluding and including understorey vegetation

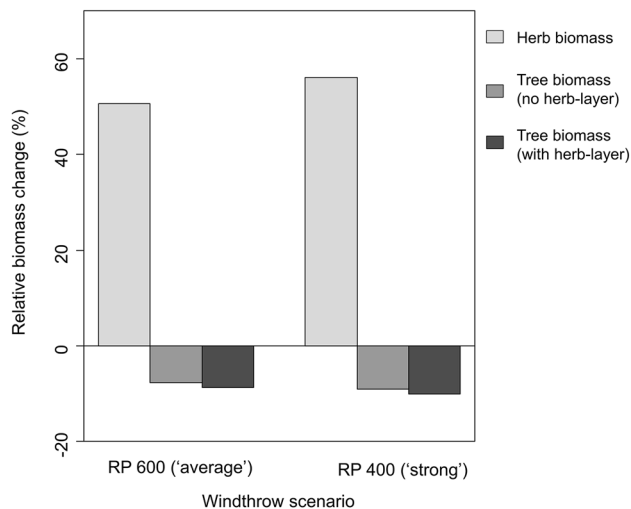


Fig. 6. Effects of simulating windthrow disturbances on the understorey and the tree layer (elevation band 600 m in the Feldberg landscape) for two different windthrow scenarios (rotation period of 600 years and 400 years, based on Schumacher 2004). The results indicate the percentage change compared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

of patience) compared to forests (compare Hiltbrunner and others 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 (for example, 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 and others 2004); (2) enhanced seed predation, but little quantitative knowledge is available on this (Royo and Carson 2008); (3) allelopathic effects (for example, Nilsson

and Wardle 2005), which are hard to study experimentally (Priewasser 2013); (4) mechanical inhibition of seedling germination and growth (for example, Dolling 1996) and (5) interactions with browsing animals (for example, 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 unaf-

affected by browsing and can subsequently form a dense understorey (for example, the ferns *Dennstaedtia punctilobula* and *Pteridium aquilinum*; de la Cretaz and Kelty 1999; DenOuden 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 dataset, the model produced an understorey biomass (herbaceous and *Rubus* PFTs) comparable to measurements from temperate and boreal regions (for example, 5.2 t/ha, Alaback 1982; 6.9 t/ha, Lieffers and others 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 and others 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 and others 2006). Some studies found longer-lasting delays (for example 20–30 years in boreal forests, Lieffers and others 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 (for example, Alaback 1982; Alaback 1984; Jules and others 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 and others 1993; Hart and Chen 2006). LandClim sim-

ulated the first two phases in good accordance with empirical observations, that is, 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 (that is, the re-appearance of the 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 (for example, 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 (compare online 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 (for example, Laurent and others 2004, see online 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 and others 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 and others (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 and others 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 (for example, Raich and others 1997; De Long and others 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 (for example, *Betula*, *Salix*). A number of studies report similar findings (for example, Koop and Hilgen 1987; George and Bazzaz 1999a), where establishment of light-demanding species, in particular *Betula*, was drastically reduced by the presence of a herbaceous understorey, whereas more shade-tolerant species (for example *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 and others 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 and others 1997; Dale and others 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 and others 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 (for example 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 (for example, Allen 2007), forest landscape models provide a particularly helpful tool to explore the implications of cross-scale interactions between disturbance regimes (Temperli and others 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 understorey, although there was no evidence for ‘arrested’ succession in the long term. Our results suggest that the strongest impact of understorey 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 understorey 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 understorey 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 understorey layer (for example, 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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