

RESEARCH ARTICLE

Integrating models across temporal and spatial scales to simulate landscape patterns and dynamics in mountain pasture-woodlands

Rebecca S. Snell · Alexander Peringer · Harald Bugmann

Received: 8 February 2016 / Accepted: 31 March 2017
© Springer Science+Business Media Dordrecht 2017

Abstract

Context Pasture-woodlands are semi-natural landscapes that result from the combined influences of climate, management, and intrinsic vegetation dynamics. These landscapes are sensitive to future changes in land use and climate, but our ability to predict the impact on ecosystem service provisioning is limited due to the disparate scales in time and space that govern their dynamics.

Objectives To develop a process-based model to simulate pasture-woodland landscapes and the provisioning of ecosystem services (i.e., livestock forage, woody biomass and landscape heterogeneity).

Methods We modified a dynamic forest landscape model to simulate pasture-woodland landscapes in Switzerland. This involved including an annual herbaceous layer, selective grazing from cattle, and interactions between grazing and tree recruitment.

Results were evaluated within a particular pasture, and then the model was used to simulate regional vegetation patterns and livestock suitability for a ~198,000 ha landscape in the Jura Vaudois region.

Results The proportion of vegetation cover types at the pasture level (i.e., open, semi-open and closed forests) was well represented, but the spatial distribution of trees was only broadly similar. The entire Jura Vaudois region was simulated to be highly suitable for livestock, with only a small proportion being unsuitable due to steep slopes and high tree cover. High and low elevation pastures were equally suitable for

Electronic supplementary material The online version of this article (doi:[10.1007/s10980-017-0511-1](https://doi.org/10.1007/s10980-017-0511-1)) contains supplementary material, which is available to authorized users.

R. S. Snell (✉) · H. Bugmann
Forest Ecology, Department of Environmental Sciences,
Institute of Terrestrial Ecosystems, ETH Zürich,
8092 Zurich, Switzerland
e-mail: snell@ohio.edu

A. Peringer
Ecole Polytechnique Fédérale de Lausanne EPFL, School
of Architecture, Civil and Environmental Engineering
ENAC, Laboratory of Ecological Systems ECOS, Station
2, 1015 Lausanne, Switzerland

A. Peringer
WSL Swiss Federal Institute for Forest, Snow and
Landscape Research, Site Lausanne, Switzerland

A. Peringer
Department of Landscape and Vegetation Ecology,
University of Kassel, Kassel, Germany

Present Address:
R. S. Snell
Department of Environmental and Plant Biology, Ohio
University, Athens, OH, USA

livestock, as lower forage production at higher elevations was compensated by reduced tree cover.

Conclusions The modified model is valuable for assessing landscape to regional patterns in vegetation and livestock, and offers a platform to evaluate how climate and management impact ecosystem services.

Keywords Livestock · Dynamic vegetation model · Jura · LandClim · Switzerland · WoodPam

Introduction

Understanding the causes of landscape patterns is crucial for our ability to predict how landscapes will respond to future climate and land use change. Landscape patterns can be caused by variability in abiotic factors, biotic interactions, natural disturbance regimes, as well as both current and historical land use (e.g., de Vries et al. 2012; Agnoletti et al. 2015). However, the importance of these processes in each landscape and across different spatial and temporal scales is unclear (e.g., McGill 2010; Pias et al. 2014; Bourgeron et al. 2015). This is particularly true for pasture-woodland landscapes, which are dynamically shaped by feedbacks between abiotic features, biotic interactions and management. Over the last 40 years, many European pasture-woodlands have experienced woody encroachment (Gehrig-Fasel et al. 2007; Garbarino et al. 2014). Preserving these landscapes requires an in-depth understanding of the various processes that form and maintain these heterogeneous systems, so as to develop appropriate land management regimes.

Pasture woodlands are composed of a mosaic of vegetation types, from open pastureland, to semi-open woodlands and closed forest patches. In the Swiss Jura mountains, these highly heterogeneous landscape patterns are created and maintained by interactions between livestock grazing (i.e., without livestock, the entire landscape would be closed forest) and natural tree regeneration (Buttler et al. 2009). Grazing by cattle suppresses tree seedling establishment, but cattle are selective about where they graze within the pasture. For example, forage production, tree and shrub cover, slope, rocks and human-made structures were found to influence the frequency of patch occupancy by cattle (Kohler et al. 2006; Meisser

et al. 2014). The resulting spatial heterogeneity in grazing pressure has strong impacts for the likelihood of tree establishment and thus the emerging landscape pattern.

The forest-grassland mosaic patterns that emerges within a pasture and beyond, is highly sensitive to changes in management (i.e., grazing pressure; Gillet 2008), climate (Peringer et al. 2013) and successional dynamics. For example, recent climate changes were found to reduce plant growth at low elevations while increasing plant growth at higher elevations (Jolly et al. 2005). Climate change will also impact species-specific tree growth and establishment rates (e.g., Chang et al. 2015). However, the consequences of changing grazing pressure and tree population dynamics (i.e., changes to establishment, mortality and species composition) may take decades or centuries to become apparent (Cailleret et al. 2014; Speed et al. 2014). Thus, an integrative framework is required that combines these processes across temporal and spatial scales to understand their relative importance as a basis for predicting future changes to landscape patterns.

Dynamic, process-based models are able to integrate processes across spatial and temporal scales and simulate emerging properties of landscape dynamics based on local factors and interactions. They are also able to simulate novel environmental conditions, such as climate change or alternative management regimes. Furthermore, they account for transient changes through time, such as forest succession or lags caused by dispersal limitations or biotic interactions (Snell et al. 2014).

To date, pasture modelling has focused on grass dynamics without considering interactions with woody vegetation and cattle (e.g., Jouven et al. 2006; Trnka et al. 2006; Castellaro et al. 2012), while simulations of woody encroachment in semi-natural grasslands focused on tree dynamics and ignored herbaceous plants and grazing by livestock (e.g., Mairotta et al. 2014). Models that include grazing, pasture management and interactions between woody and non-woody plants are typically developed for very fine spatial grains and small spatial extents (e.g., cell size of 1–5 m² and total extent of 2 ha; Lohmann et al. 2012; Komac et al. 2013), which do not reflect the typical size of pasture management units (i.e., >50 ha). In addition, these models represent all woody vegetation as one generic shrub plant

functional type. Representing woody plants at the species level is especially important to capture species-specific responses to climate change (e.g., Broadmeadow and Jackson 2000; Basler and Körner 2012) and different tolerances to grazing and competition (Vandenbergh et al. 2008). This limits the ability of these models as tools for decision-making in landscape management.

The spatially explicit ecosystem model WoodPaM has been developed to simulate pasture-woodland dynamics at spatial extents of 25–125 ha (Gillet 2008; Peringer et al. 2013). The model also simulates grassland and woody plant successional dynamics as influenced by the selective foraging behaviour of cattle, and species-specific responses to grazing and abiotic conditions. However, model parameters are specifically calibrated to operate under a particular range of climatic and edaphic conditions. Therefore, it is not possible to apply WoodPaM across larger landscapes that encompass various climatic, topographic and soil conditions, such as mountain valleys.

Thus, the goal of this paper was to integrate the grazer-plant dynamics from WoodPaM into a vegetation landscape model that can be applied at regional scales and across heterogeneous environmental conditions. We chose to build upon the existing dynamic, forest landscape model LandClim, as it contains process-based representations of forest succession driven by competition and environmental factors (i.e., tree establishment, growth, competition, reproduction and mortality are simulated at the species level), natural disturbances and forest management (Schumacher et al. 2004). To our knowledge, LandClim is also the only forest landscape model that includes both woody and herbaceous vegetation (Thriplleton et al. 2016). LandClim has been used to simulate forest dynamics and productivity across Central Europe (Schumacher and Bugmann 2006; Henne et al. 2011; Temperli et al. 2012), and thus the new pasture module was designed to be broadly applicable for pasture-woodland landscapes in this region as well. We aimed to develop a model that integrates the relevant details from the pasture level (i.e., the scale at which management decisions are made, 10's to 100's of ha) towards applications at the landscape level (i.e., the scale at which implications of land use and land cover change are observed, 1000's of ha). Although the spatial pattern within an individual

pasture is important in reality, in the context of upscaling it crucial to capture the ecosystem services provided by these landscapes, including livestock suitability, biodiversity and the aesthetic appeal (i.e., the heterogeneity of vegetation cover types).

Methods

We decided to integrate selected processes from WoodPaM into LandClim, as LandClim already had a process-based representation of plant growth and dynamics, and can be applied across a wide range of environmental conditions without being calibrated. The calculations for determining selective grazing by herbivores is based on WoodPaM equations, however some simplifications were necessary due to the differences between models. We describe the set of equations for determining spatially explicit grazing pressure, which is then used to determine the impact of grazing on tree regeneration. Below, we provide a brief description of LandClim and WoodPaM before describing the updated pasture module in LandClim.

Forest landscape model LandClim

LandClim is a stochastic forest landscape model designed to simulate long-term forest dynamics and the impact of climate, topography, disturbances (i.e. fire, wind, bark beetles) and management on a wide range of ecosystem goods and services (e.g., Schumacher and Bugmann 2006; Temperli et al. 2012; Elkin et al. 2013). The model is spatially explicit and represents the landscape using a grid of 25 m × 25 m cells. Within each cell, vegetation dynamics are represented using a simplified forest gap model where different cohorts represent trees of the same species and age (Schumacher et al. 2004). Processes such as establishment, growth, mortality and competition for light and water are modelled explicitly as being driven by temperature, precipitation, soil properties and topography. Establishment and mortality are stochastic processes. Establishment probabilities are based on species specific requirements for available light, temperature and drought. Mortality can be either due to increased stress (i.e., due to poor growing conditions) or approaching the maximum age of a tree. Thus, the environment influences the probability of an event but the event itself is determined by a uniform

random number generator. Spatially explicit processes such as seed dispersal, disturbances and forest management connect individual grid cells and are simulated on a decadal scale. Herbaceous plants and overstorey-understorey interactions have also recently been included in LandClim (Thriplleton et al. 2016; and see section Herbaceous understory below). The model has been used to simulate a variety of forest types and forest processes in Central Europe, in both unmanaged and managed stands (e.g., Schumacher et al. 2006; Temperli et al. 2012; Elkin et al. 2013), producing results that were consistent with empirical data. Additional details about LandClim can be found in Schumacher et al. (2004). LandClim version 1.6 was used for this study.

Pasture-woodland model WoodPaM

WoodPaM is a deterministic model that was developed to investigate the processes underlying pasture-woodland mosaic dynamics, using an annual time step and a grid of 25 m × 25 m cells. In the model, pasture-woodland dynamics emerge from herbivore-vegetation interactions that include the impacts of grazing, trampling and dunging on both grassland communities and tree seedlings (Gillet 2008). Grassland communities are represented by four successional stages that differ in forage quality and safe site provisioning for tree establishment (oligotrophic lawns, meadows, fallows, and understory herbs). Tree populations are divided into four stages (3-year old seedlings of height <40 cm, saplings of height 40–150 cm, small trees of height 150–500 cm and large trees with heights >500 cm). In the model, tree growth, competition and mortality are sensitive to climatic and soil conditions. Using the four height classes to simulate forest dynamics leads to simple patterns of stand structure and forest succession. WoodPaM further simulates shrubs, which along with tall forbs offer safe sites from grazing and facilitate tree seedling establishment (Olff et al. 1999; Smit et al. 2015). Resource selection functions for habitat use by cattle and the resulting browsing damage to seedlings were derived from a large body of field data (Kohler et al. 2006; Smit et al. 2006; Vandenberghe et al. 2007). Additional details about WoodPaM can be found in Gillet (2008) and Peringer et al. (2013).

Upscaling of WoodPaM processes to the LandClim framework

Herbaceous vegetation

As LandClim was developed as a forest landscape model, it did not initially include a representation of herbaceous vegetation. However, recent work by Thriplleton et al. (2016) has integrated herbaceous Plant Functional Types (PFT) into the LandClim model. Herbaceous vegetation is represented as one cohort per grid cell, and the biomass of the herbaceous layer is limited by the same growth-reducing functions as for trees (Schumacher et al. 2004). For the pasture module, we group all non-woody vegetation into one general herbaceous PFT that we refer to as “grass”, although it is intended to encompass other species groups such as meadow sedges, forbs and herbs as well. The grass PFT has a new annual growth form and can reach its maximum biomass (K) each year provided light, water and temperature are not limiting. Maximum herbaceous biomass was determined from the literature (Table 1). If one or multiple factors are limiting, grass biomass (B) is reduced by the most limiting factor. Data from the unfertilized, non-irrigated grassland field sites in Oensingen [C. Ammann, *unpublished data*, site description found in Ammann et al. (2007)] and from long-term MeteoSwiss observations about climate and hay harvest (*data not shown*) were used to evaluate the relationship between annual grass growth and the growth reducing functions. Additional information about herbaceous modelling in LandClim can be found in Thriplleton et al. (2016).

Cattle submodel

To describe resource selection by cattle in the landscape, we adapted and abstracted the approach used in WoodPaM (Gillet 2008). Whereas WoodPaM includes the impacts of cattle via grazing, trampling and dunging, we chose to focus on grazing as this is the most important mechanism through which cattle influence the plant community (Rook et al. 2004), and browsing damage to tree seedlings is related to grazing intensity (Mayer et al. 2005, 2006; Marquardt et al. 2009).

Table 1 New LandClim parameters specifically related to herbaceous growth and the grazing modules

Parameter	Description	Value	Equation	Source
K	Maximum grass biomass	4 t/ha	–	Duparc et al. (2013) and Finger et al. (2013)
sl_{max}	Maximum slope	40°	2	Gillet (2008)
fc	Forage consumption per day per cow	15 kg	3	Gillet et al. (2002)
gt	Grazing tolerance			
	<i>Abies alba</i>	0.25	7	Gillet (2008)
	<i>Acer pseudoplatanus</i>	1.0		
	<i>Fagus sylvatica</i>	0.75		
	<i>Picea abies</i>	2.0		
	<i>Pinus sylvestris</i>	0.5		
	<i>Populus nigra</i>	0.5		
	<i>Sorbus aucuparia</i>	1.0		
k	Grazing tolerance rank			Gillet (2008)
	<i>Abies alba</i>	6	8	
	<i>Acer pseudoplatanus</i>	3		
	<i>Fagus sylvatica</i>	4		
	<i>Picea abies</i>	1		
	<i>Pinus sylvestris</i>	5		
	<i>Populus nigra</i>	5		
	<i>Sorbus aucuparia</i>	3		

First, global stocking density [GSD ($\text{day}^{-1} \text{ ha}^{-1} \text{ year}^{-1}$)] is calculated for the pasture (Eq. 1).

$$GSD = \frac{ABU \cdot gd}{\sum_{i=1}^n area_i} \quad (1)$$

where ABU is an input to the model, i.e. the number of adult bovine units (one ABU equals one adult dairy cow), gd is the grazing duration per year [days], and $area$ is the total area of the pasture [ha]. Based on GSD, local stocking density [LSD ($\text{day}^{-1} \text{ ha}^{-1} \text{ year}^{-1}$)] is calculated every year for each grid cell (i) within the pasture based on the attractiveness of the grid cell (Eq. 2). LSD represents the cattle pressure within an individual grid cell and assumes that cattle are selective about their location within the pasture. Cattle prefer open areas (Meisser et al. 2014) and avoid densely wooded areas. We use a simplified version of the LSD calculation in WoodPaM (Gillet 2008), that disregards watering points as attractors and rocky outcrops as repellants for cattle.

$$LSD_i = GSD \left(\left(1 - \frac{\min(sl_i, sl_{max})}{sl_{max}} \right) \cdot (1 - Tc_i)^2 \cdot (1 - VO_i)^2 \cdot \frac{LCC_i}{GCC} \right)^{sp} \quad (2)$$

where sl_i is the slope of the grid cell [degrees], sl_{max} is the maximum slope (Table 1), Tc_i is the tree cover within the grid cell [0–1, with 1 being 100% cover], and VO_i is the vegetation openness [0–1]. Vegetation openness calculates tree cover of the neighbourhood, using a 3×3 block of cells centered at cell i . Tree cover was estimated using a power-sigmoid function (Shimano 1997), which uses diameter at breast height (DBH) to estimate crown area for deciduous and coniferous trees. Thus, crown area for each tree in the grid cell is calculated and then summed up. The ratio of total crown area to grid cell area indicates the tree cover.

Local carrying capacity (LCC_i) [$ABU \text{ day}^{-1} \text{ ha}^{-1}$] represents the maximum stocking density allowed in a single grid cell, based on the grass biomass produced (B_i) and the daily forage consumption (fc) of one adult cow [kg per ABU ; Table 1].

$$LCC_i = \frac{B_i}{fc \cdot area_i} \quad (3)$$

Global carrying capacity (GCC) [$ABU \text{ day}^{-1} \text{ ha}^{-1}$] is the maximum stocking density at the entire pasture level,

$$GCC = \frac{\sum_{i=1}^n B_i}{fc \cdot \sum_{i=1}^n area_i} \quad (4)$$

The ratio of LCC to GCC (in Eq. 2) is an indication if the local cell is producing more or less forage than average, and thus is more or less attractive to cattle.

Equation 2 is a non-linear function with the exponent sp , which represents the strength of selectivity in cattle foraging behaviour as a function of forage availability (Eq. 5). This means that cattle are more selective when forage production at the pasture level is high and less selective as forage production goes down. The mathematical formulation and coefficients are optimized based on work by Kohler et al. (2006) and Meisser et al. (2014), who observed that cattle preference was strongest when forage production was high.

$$sp = 0.65 \cdot e^{-\frac{1.3 \cdot GSD}{GCC}} \quad (5)$$

Global utilization (GU) is stocking density divided by carrying capacity. GU is used as a measure of livestock suitability. Livestock are unable to leave the pasture and never die. Thus, if the stocking density is much larger than the carrying capacity (i.e., GU > 1), livestock don't have enough to eat and the pasture is considered to be unsuitable at that specific stocking density. GU values around 0.6 are typical in low-intensity pasture-woodlands that are managed to simultaneously serve multiple goals (i.e., cost-efficient land use and the provisioning of habitats for biodiversity conservation) (Rosenthal et al. 2012).

$$GU = \frac{GSD}{GCC} \quad (6)$$

Effect of grazing on tree regeneration

Browsing on tree seedlings and saplings can be lethal, but once they reach a height of 1.5 meters they escape from cattle grazing (Buttler et al. 2009). In LandClim, cohorts establish once every 10 years at a height of ~1.4 meters tall, and thus the impact of cattle grazing can be modelled as a reduction of establishment success and density of new cohorts (and not mortality of established cohorts). Establishment probabilities are calculated each year based on environmental conditions (i.e., available light, temperature, drought index). LandClim tracks the number of years within a decade that were favorable for establishment,

and this is one of the factors used to determine establishment densities (Schumacher et al. 2004). To include the impact of grazing on tree establishment, we used the cell-specific local stocking density (Eq. 2) for annual tree establishment probability,

$$GI_{est} = \min\left(\frac{LSD_i}{LCC_i}, 1.0\right)^{gt} \quad (7)$$

where gt is the species-specific grazing tolerance (Fig. 1a; Table 1). This equation produces a value between 1 and 0, which is used in conjunction with a uniformly distributed random number generator to determine if establishment occurs in a given year or not. An additional constraint was added, that there needed to be a minimum of five years *in a row* that are favourable for tree establishment for a cohort of that particular species to actually establish.

After establishment of a cohort is determined, an appropriate number of stems in a cohort needs to be generated. This is determined by maximum sapling density, the available light on the forest floor, and growth potential based on environmental conditions of the previous 10 years. In pastures, the average GI (Eq. 7) over the decade is used to further reduce the stem number in a cohort,

$$SR = e^{-k \cdot GI_{avg}} \quad (8)$$

where k is a grazing tolerance rank (between 1 and 6, with 1 being the most tolerant to grazing; Table 1). SR produces a value between 0 and 1, and the number of stems in the cohort is reduced by this fraction (Fig. 1b). A sensitivity analysis for the pasture module was performed that tested a range of the input values for maximum grass biomass, grazing duration and number of livestock (Additional details and results from the sensitivity analysis can be found in Appendix 1).

Pasture simulations

We simulated a pasture in the Swiss Jura Mountains where WoodPaM had been extensively validated and tested (Peringer et al. 2013). The Pré aux Veaux pasture is located at 46°32'N, 6°12'E at an elevation of approximately 1300 m a.s.l. It has a mean annual temperature of 4.5 °C and mean annual precipitation sum of 1760 mm. The pasture has a size of 111 ha and

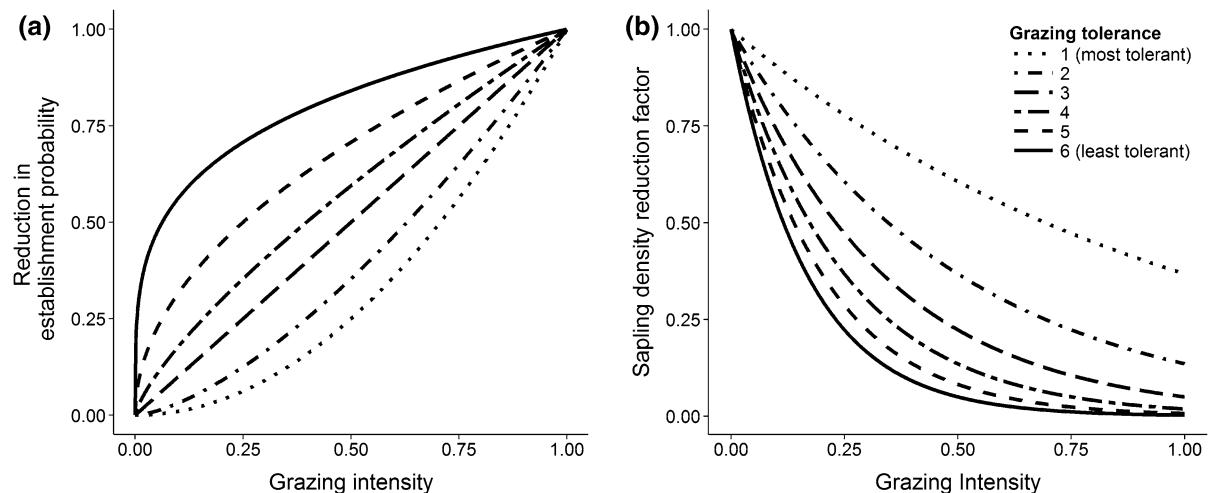


Fig. 1 Functions for how grazing intensity was used to reduce establishment success (a) and reduce sapling number within a cohort (b). The different lines illustrate the species specific grazing tolerances

a current grazing pressure of 78 adult cows for 124 days per year (i.e., GSD = 87, Eq. 1).

Pré aux Veaux was simulated using both WoodPaM and the modified LandClim model. Climate data (monthly temperature and precipitation) were available from 1901 to 2000 from a regionalization of weather station records (MPI-M 2006 and MPI-M 2009 processed by D. Schmatz, WSL, *unpublished report*). The climate data were randomly resampled with replacement to generate a 1000-year climate input for the models. Slope, aspect and elevation data were identical for both models and derived from a digital elevation model with 25 m resolution (from Swiss Federal Office of Topography, swisstopo.admin.ch, Appendix 2). WoodPaM does not require soil data, but instead uses the percent of rocky outcrops in each cell as a proxy for soil quality. Thus, the cover of rock outcrops was estimated for WoodPaM from topography (i.e., convexity, concavity, terrain steepness) and geology (i.e., presence of limestone). Additional details can be found in Peringer et al. (2013). LandClim uses ‘bucket size’, which represents the total amount of plant-available water (i.e., larger buckets hold more water) and reflects properties such as soil depth and soil texture. To be consistent, the percent rocky outcrop data from WoodPaM were transformed into LandClim bucket sizes using a linear transformation, assuming that a cell without any rocks corresponds to the largest bucket size (=20 cm of plant-available water), whereas the highest coverage by rocky outcrops corresponds to the smallest bucket

size (=6 cm). The 7 most common tree species found in the Jura mountains were included in all simulations (*Abies alba*, *Acer pseudoplatanus*, *Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, *Populus nigra*, and *Sorbus aucuparia*). Both models included short- and long-distance seed dispersal and did not consider external disturbances (i.e., wind, browsing by wild ungulates, forest management).

Both WoodPaM and LandClim simulations started from bare ground, with the current grazing pressure, and simulated 1000 years until the landscape properties had reached an equilibrium state (hypothetical, corresponding to twentieth-century climate and current land use). Due to the stochastic processes in LandClim (e.g., establishment and mortality), LandClim simulations were repeated 100 times each with a different seed for the random number generator.

Model evaluation for Pré aux Veaux

To evaluate the spatial patterns simulated by the models, observed landscape patterns obtained from an aerial photograph taken in 2000 (see Chételat et al. 2013 for image processing information) were visually compared to the deterministic simulation of tree cover by WoodPaM, and the probabilistic simulation of tree cover by LandClim. For the 100 LandClim simulations, we summed the number of simulations where tree cover was $\geq 20\%$ for each grid cell. This particular tree cover threshold was chosen as it corresponds to the densely wooded pasture classification described

below. We recognize that there are limitations to this comparison. Our simulations include current climate and current grazing pressure only, however observed landscape patterns are also a reflection of historical land use, past climate and natural disturbances (Chételat et al. 2013; Peringer et al. 2013). Our simulations will not recreate the exact landscape observed in the photograph, without including all of the historical events that shaped it. As this historical data is unknown, we are evaluating the ability of the models to approximate landscape patterns that are broadly similar, with regards to overall tree cover and the spatial distribution of vegetation.

In pasture woodlands, aesthetics is based on landscape heterogeneity (Plieninger et al. 2015). Thus, to evaluate how the models simulate this ecosystem service, we examined the percentage of open, semi-open and closed habitats in the pasture. Vegetation from the aerial photograph was categorized into one of four pasture cover types based on the classification scheme proposed by Gillet and Gallandat (1996), where ‘open landscapes’ have <1% tree cover, ‘sparsely wooded pastures’ have tree cover between 1 and 20%, ‘densely wooded pastures’ have 20–70% tree cover, and ‘forests’ have >70% tree cover. In WoodPaM and LandClim simulation results, tree cover for each grid cell was reclassified into one of the four cover types and the percentage in each category was determined. For LandClim, the mean value across all simulations was calculated for each category.

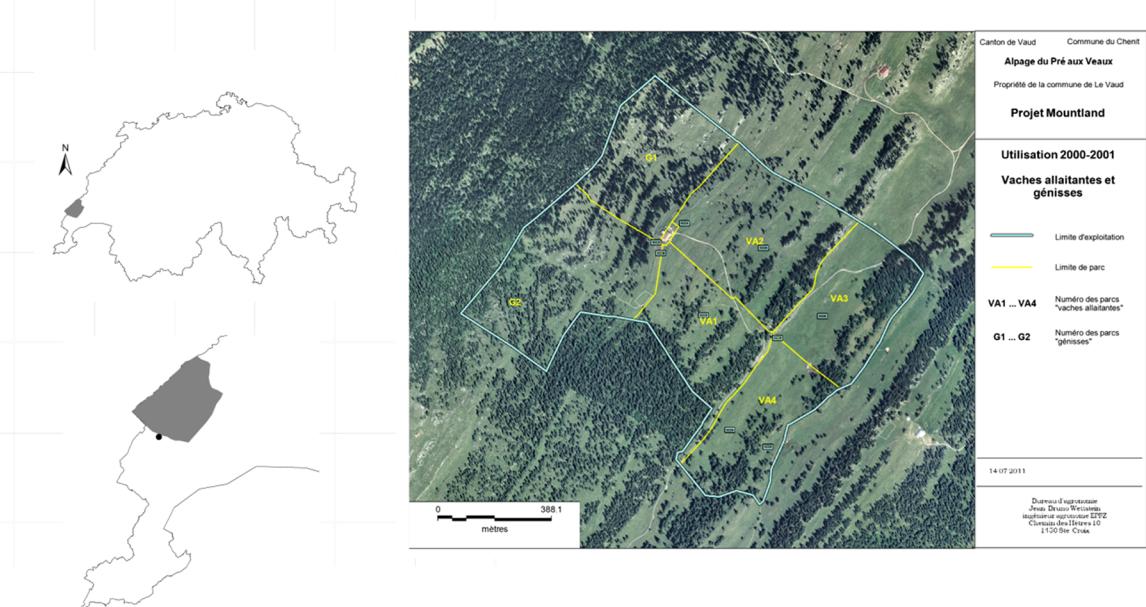
LandClim simulations also produce total above ground biomass as an output. However, there are no empirical measurements of woody biomass for this particular pasture. To produce an estimate of total above ground woody biomass, we used the aerial photograph that had been classified into the four cover types. We created a pasture where each grid cell was populated with data from LandClim reference simulations, that had a matching classification (i.e., a grid cell classified as a sparsely wooded pasture in the aerial photo would use a randomly chosen grid cell from a LandClim simulation that had a tree cover between 1 and 20%). Since the range of tree cover in some of the categories is quite large, particularly for the densely wooded pasture, this process was replicated 100 times. The mean above ground biomass for the entire pasture was compared to the mean total biomass from LandClim simulations under current grazing after 1000 years.

Additional simulations were performed to evaluate the representation of forage production in the pasture. Forage production is an important ecosystem service as it determines the amount of livestock that can be supported in a pasture. Forage production also determines the degree of openness in the landscape under a certain stocking density, as tree cover is reduced under forage scarcity by increased browsing (and vice versa). Both LandClim and WoodPaM were initialized with current vegetation patterns based the aerial photograph. Then, they were run for 10 years using the climate data from 1990 to 1999. This was repeated 100 times for LandClim, each with a slightly different tree initialization file (as described above). Tree populations do not change significantly over this short time period, while the interaction between cow grazing and grass dynamics can lead to a stable pattern in WoodPaM. The total amount of forage produced in the pasture as well as its spatial patterns was compared between the models for the final simulation year, and with an empirically-based map of forage production by Jean-Bruno Wettstein (2011, *unpublished*, Fig. 4a).

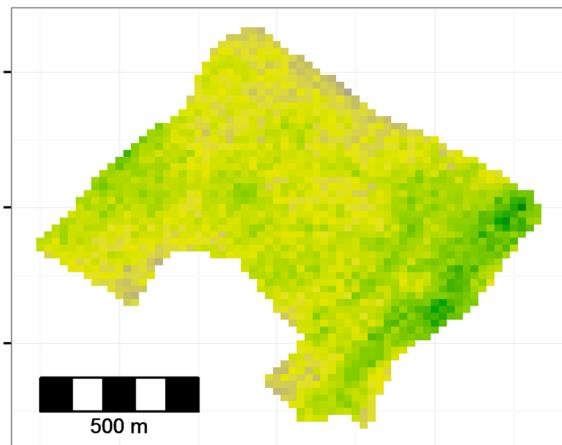
Regional simulations

To simulate the provisioning of ecosystem services from pasture woodlands across large landscapes, the entire Jura Vaudois region was simulated with the modified LandClim (the Pré aux Veaux is located just outside this larger area, Fig. 2a). This represents a total area of ~198,000 ha. The elevation ranges from 660 to 1680 m a.s.l. (Appendix 2), and has mean annual temperatures ranging from 8.6 to 3.0 °C and annual precipitation sums from 1168 to 2095 mm, respectively. Climate data (monthly temperature and precipitation) was available from 1930 to 2006 from a gridded data base (processed by D. Schmatz, WSL, *unpublished report*). Since the pasture module is spatially explicit, the entire landscape was divided into hypothetical, evenly spaced 1-ha pastures. Each pasture was given the same grazing pressure of 1 adult cow for 100 days, which represents an average livestock density for this region (Buttler et al. 2009). The spatial resolution of the model remains the same (25 m × 25 m), but each cattle is restricted to grazing within their 1 ha (i.e., 4 × 4 cell block). LandClim started from bare ground with the prescribed grazing pressure, and was run for 1000 years. The simulations were replicated 10 times and the final simulation year

(a) Pre aux Veaux pasture



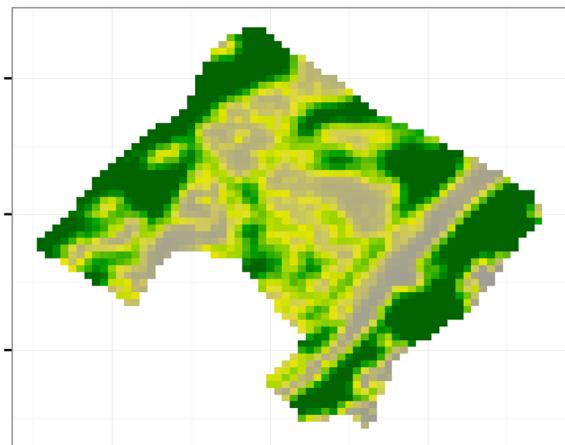
(b) LandClim



Percent of simulations with > 20% tree cover

0	25	50	75	100
---	----	----	----	-----

(c) WoodPaM



Tree cover (%)

0	25	50	75	100
---	----	----	----	-----

Fig. 2 **a** The Pré aux Veaux pasture (black dot) located in the Jura Vaudois region (grey area) of Switzerland. Model simulations of hypothetical equilibrium landscapes for 20th century climate and current land use (78 adult cows for 120 days) from **b** LandClim and **c** WoodPaM. Model simulations were run from bare ground and continued for 1000 years.

The final simulation year is shown. Due to stochastic processes in LandClim, the simulation was repeated 100 times. Illustrated here is the percent of replicated simulations where each grid cell had a minimum tree cover of 20%. WoodPaM is a deterministic model and thus was only run once. For WoodPaM, tree cover at the final year is shown

was selected to evaluate the ecosystem services. For each grid cell, we calculated the proportion of the simulations where tree cover was >20% (as above)

and the average grass biomass. For each 1-ha pasture, we also calculated the proportion of simulations where global utilization rates were >70% and >80% (Eq. 6).

To illustrate the impact of grazing on forested landscapes, we also simulated the Jura Vaudois region without grazing (i.e., potential natural vegetation). These simulations were also replicated 10 times and run for 1000 years. Species composition and total above ground biomass was compared between simulations with and without grazing.

Results

Pasture level

The equilibrium landscapes simulated by both models using twentieth century climate and current land use were in broad agreement with observed landscape patterns, based on the spatial distribution of tree cover (Fig. 2). Both models predicted reduced grazing and thus higher tree cover at the steep slopes along the southeast and northwest edges of the pasture (Appendix 2, Fig. A2 slope map of the pasture). Due to the stochastic processes in LandClim, the spatial patterns were more muted than those produced by WoodPaM (Fig. 2b, c), as for each grid cell it is possible to turn from forest to pasture (or vice versa) in repeated simulations, depending on several probabilities (e.g., mortality, seed dispersal, and establishment filters for grazing, temperature, drought, and light). However, the number of simulations where a certain grid cell was covered by trees in LandClim features the same pattern as WoodPaM (Fig. 2). Thus, the models agree that trees are most likely to establish along the northwestern and southeastern edges of the pasture, whereas the center is more likely to remain open.

Comparing the different pasture cover types, both models were able to qualitatively simulate the grass-land-forest ecotone (i.e., sparsely and densely wooded pastures), however WoodPaM simulated a comparatively high cover of closed forests, did not simulate any parts of the landscape as being fully open (i.e., 0% tree cover), and simulated most of the landscape as sparsely and densely wooded pasture (Fig. 3). LandClim produced proportions of vegetation cover that matched observed vegetation cover much better than WoodPaM (Fig. 3). LandClim simulated an appropriate proportion of densely wooded pastures and forests, and was able to simulate fully open parts of the landscape. The main difference was that LandClim under-estimated sparsely wooded pastures by 20%

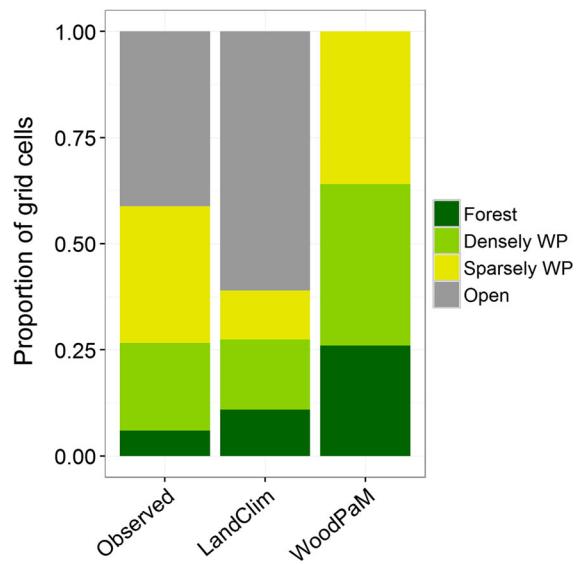


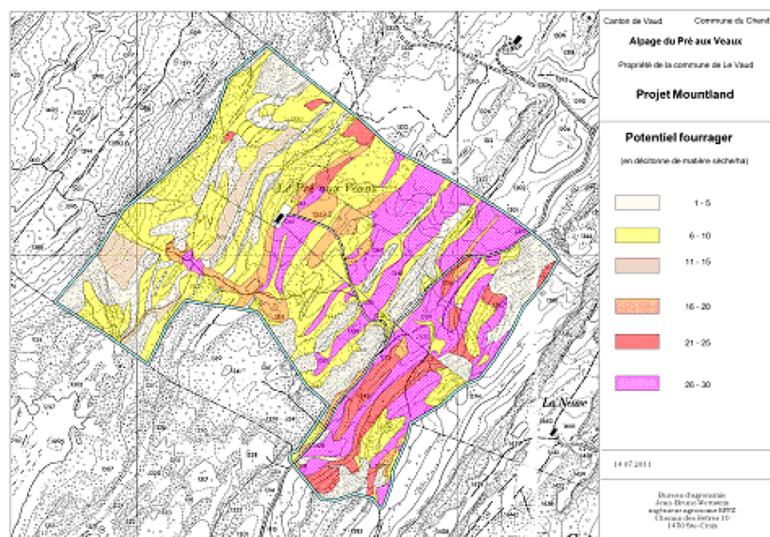
Fig. 3 Vegetation cover aggregated at the pasture level, using the phytocoenosis types (see Methods for a definition). Observed values are from the MOUNTLAND project (Peringer et al. 2013) based on the aerial photo in Fig. 2a. LandClim values are the mean of 100 simulations, standard deviation values are not shown (forest—2.9%, densely wooded pasture—2.0%, Sparsely wooded pasture—3.5%, Open—2.4%)

(only $12\% \pm 3.5\%$ of the landscape compared to 32% observed) and over-estimated open landscapes.

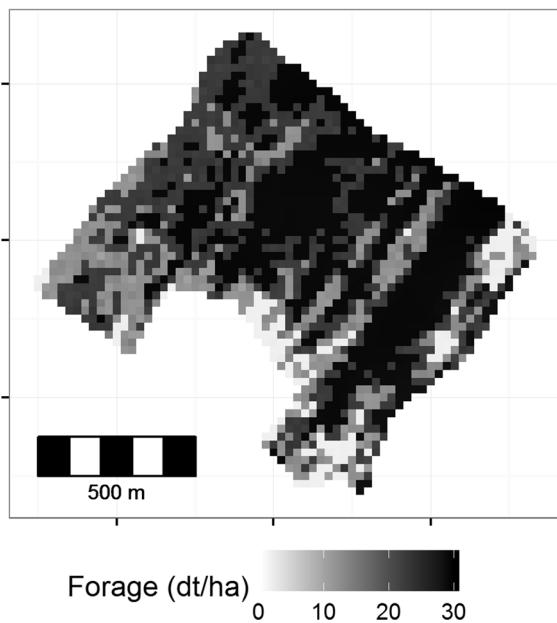
Simulated forage production for the pasture was slightly higher for WoodPaM (2.27 t/ha dry matter) than LandClim (mean = 2.2 t/ha of grass biomass ± 0.2 SD), and both estimates were higher than recent forage production estimates (1.7 t/ha in the year 2014; Gregory Egger, *unpublished data*). The spatial distribution of forage was quite similar between the models and the observations (Fig. 4), and matched the allocation of main forage areas on deep and productive soils in between the limestone ridges, as tree cover exerts a top-down control due to light competition (i.e., the most productive places are the open areas).

Total aboveground woody biomass simulated by LandClim under current grazing pressure had a mean value of 124.5 t/ha (± 17.2 SD). Based on observed vegetation cover, total above ground biomass was estimated to be 98.4 t/ha (± 28.6 SD). This over-estimation is likely due to the higher proportion of the pasture covered by closed forest in LandClim simulations (Fig. 3). LandClim also simulated almost a monoculture of trees, with *Picea abies* contributed 98% to the total woody biomass. The remaining 2%

(a) Pre aux Veaux pasture



(b) LandClim



(c) WoodPaM

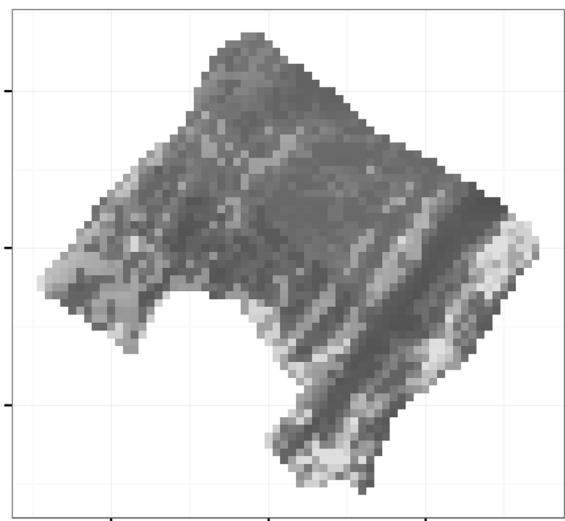


Fig. 4 a Observed forage production and simulated grass biomass from b LandClim and c WoodPaM. Note that forage production is shown in deciton per ha (dt/ha) for comparison with the observed forage production

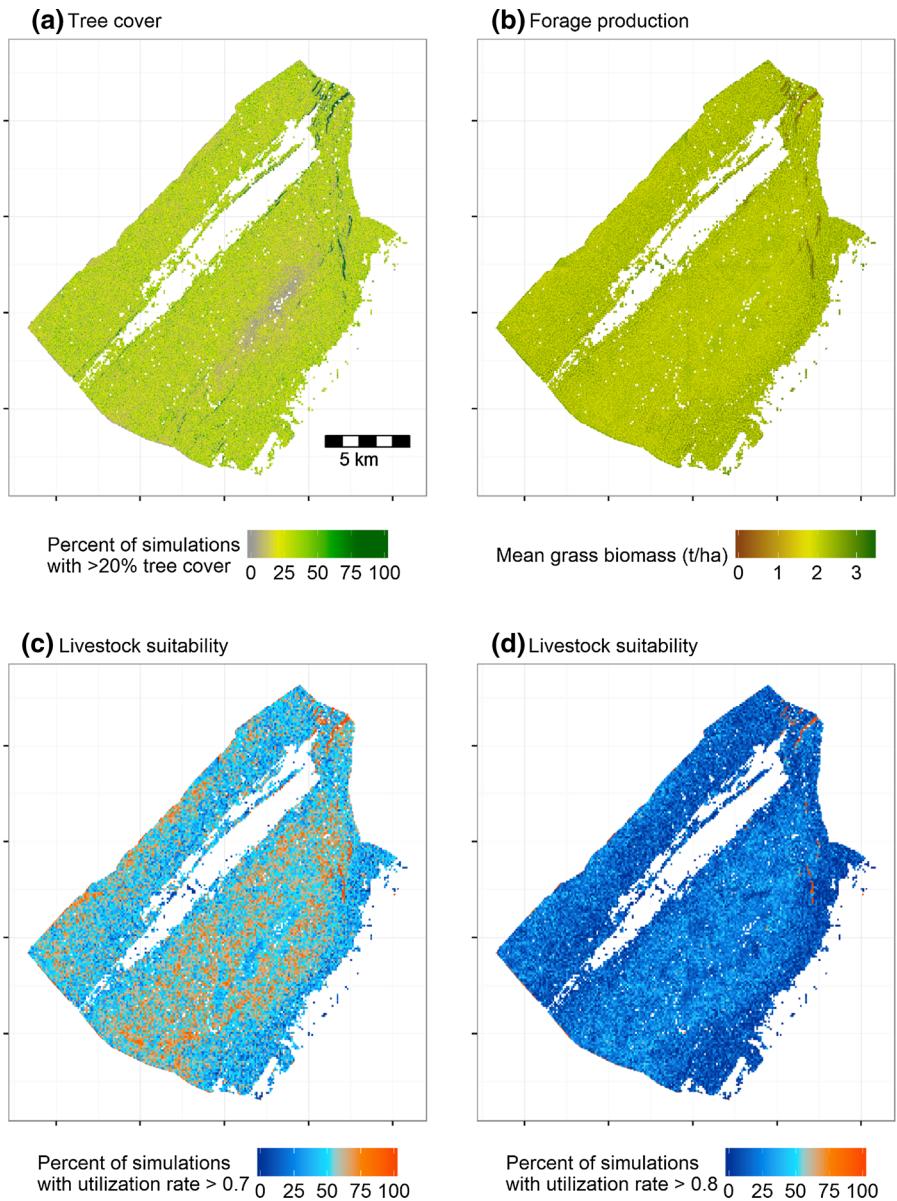
was composed of *Populus nigra*, *Fagus sylvatica* and *Abies alba*.

Regional level

Simulating a constant and even grazing pressure for the entire Jura Vaudois region resulted in a mostly open

landscape (Fig. 5a) and an average tree cover of just 15%. In fact, 71% of the area had $\leq 20\%$ tree cover, 28% had 20–50% tree cover, and only 1% had $\geq 50\%$ tree cover. The average global utilization rate (GU, calculated for each 1-ha pasture) was 0.72. Most of the region would be highly suitable for livestock grazing ($GU < 1.0$; Fig. 5c, d), with only 0.3% of the landscape

Fig. 5 Entire Jura region, assuming a constant and spatially uniform grazing pressure of 1 adult cow per ha across the entire landscape. Due to stochastic processes in LandClim, the simulations were repeated 10 times. **a** The percent of replicated simulations where each grid cell had a more than 20% tree cover, **b** mean grass production, **c** percent of simulations where a pasture had a global utilization rate ≥ 0.7 , and **d** ≥ 0.8

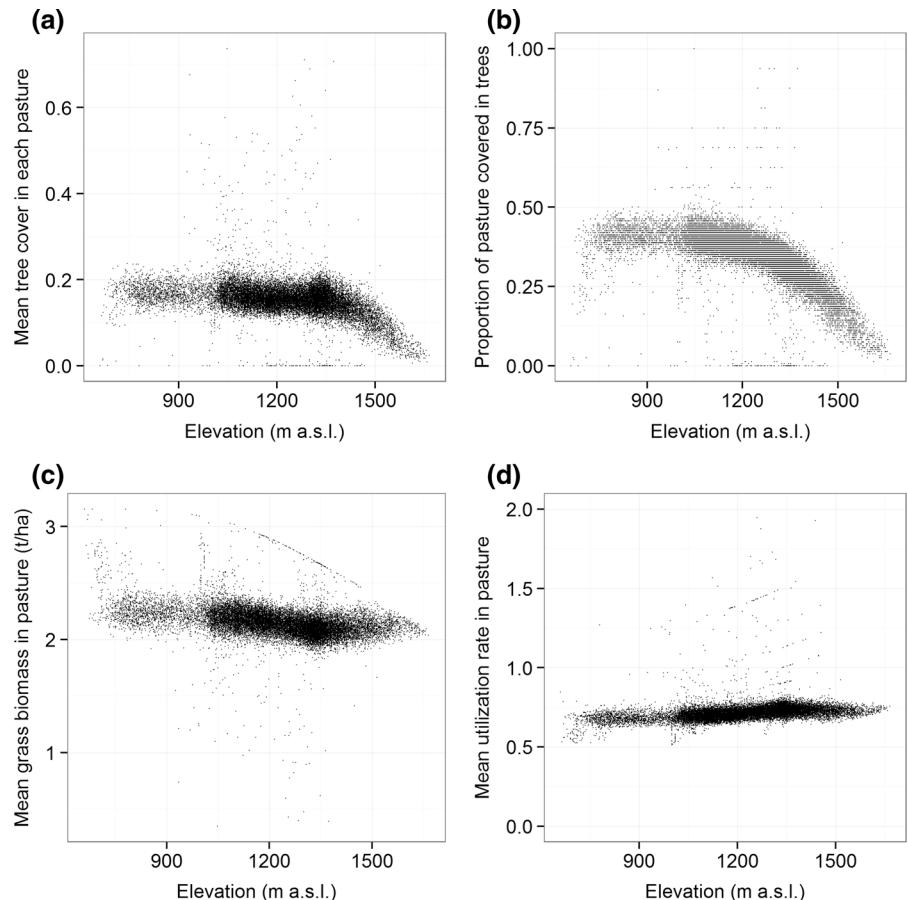


being unsuitable for pastures ($GU > 1.0$), and 0.08% of the landscape highly unsuitable ($GU > 1.5$). The most unsuitable pastures were generally those with the steepest slopes (Appendix 2 Fig. A3; Appendix 3 Fig. A4d) as cows avoid areas with very steep slopes; this lower grazing pressure resulted in higher tree establishment, and thus high tree cover (Fig. 5a; Appendix 3 Fig. A4a, b) and low grass biomass (Fig. 5b; Appendix 3 Fig. A4c).

Forage production across all elevations was fairly uniform (Figs. 5b, 6c), except in those areas with that

featured dense forest cover. Grass biomass (mean = 2.14 t/ha, SD = 1.3) rarely approached its potential maximum (4 t/ha). This was likely not due to climate limitations but rather due to light competition with trees, as temperature became limiting for grass growth only above 1200 m a.s.l. (Fig. 6c). Higher elevations showed only a small increase in utilization rates (Fig. 6d) because the reduction in grass growth was compensated by a reduction in tree cover (Figs. 5a, 6b) so the pasture as a whole still produced adequate forage for the stocking density.

Fig. 6 Relationships between elevation and tree cover, forage production and global utilization for the Jura Vaudois. Each point represents the mean value for each 1-ha pasture. Note, due to the scale of panel d, 8 points are not shown that have GU values >2



Without livestock grazing, LandClim simulated the Jura Vaudois region to be almost exclusively dominated by beech—fir forests, except at the highest elevations where *Picea abies* dominates (Fig. 7a). Under grazing, there is a strong species shift with spruce becoming the dominant species across all elevations (Fig. 7b). Other deciduous species (e.g., *Acer pseudoplatanus* and *Populus nigra*) are present only at very low biomass.

Discussion

Pasture-woodlands are unique landscapes resulting from the interaction between natural vegetation dynamics, livestock grazing, environmental constraints and management. We described a model that incorporates all these processes at a scale that is relevant for land management and regional planning. There are tradeoffs to our approach, which we discuss

in detail below. Specifically, we address the processes that influence the emergence of landscape patterns from pasture-scale processes, the relative importance of certain processes (particularly establishment) across spatial and temporal scales, and how the model can be used to estimate the provisioning of ecosystem goods and services under current and future climate change and land management.

Key factors and processes determining pasture- and regional-level patterns

Landscape patterns simulated by both LandClim and WoodPaM illustrate the strong impact of topography on the formation of vegetation patterns in mountain pasture-woodlands. Forests generally develop on steep slopes and rocky outcrops that are avoided by livestock, whereas flat, deep and productive soils are the main sources of forage, and intensive grazing keeps these areas open. The vegetation patterns

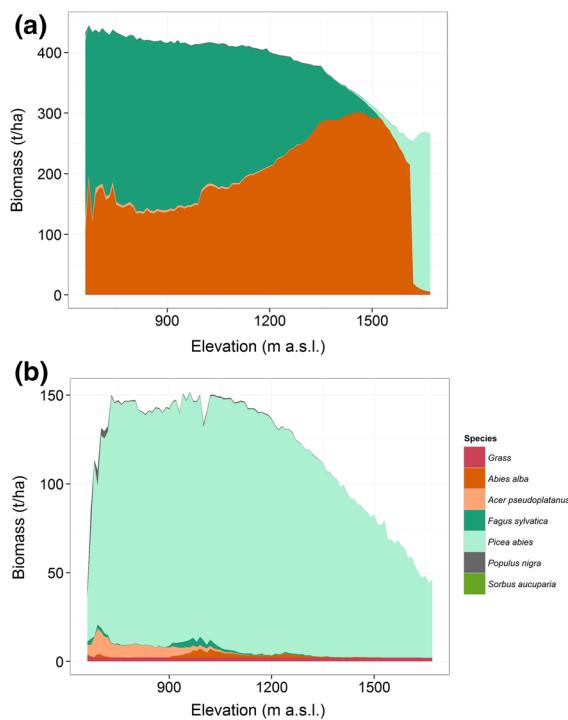


Fig. 7 Species biomass summarized by elevation, for the entire Jura Vaudois region. Simulation results **a** for potential natural vegetation (i.e., without grazing) and **b** with constant grazing pressure (1 ABU per 1 ha, for 100 days per year). The average of 10 simulations in LandClim is shown to account for stochastic differences, after 1000 simulation years under current climate. Note the difference in y-axis scales

produced by LandClim reflected the influence of topography, but the impact of stochastic processes (e.g., establishment and mortality) was prevalent, leading to a blurred pattern, in contrast to the results of the deterministic WoodPam model. Still, LandClim results indicate that for this pasture, a moderate level of grazing pressure in the absence of a strong environmental gradient implied that trees were able to establish in almost all grid cells in at least a fraction of the simulated landscape replicates. Even though the probability of tree establishment in particular locations differed considerably based on the underlying topography, in the replicated simulations almost every grid cell had at least one simulation where trees were present. This is a typical problem when comparing real landscape properties, which reflect a very specific course of past development, to simulation results from a stochastic landscape model that reflects multiple possible landscape trajectories.

Observed pasture-woodland patterns reflect legacy effects from historic forest clearing and pasture management (Chételat et al. 2013) as well as climate fluctuation and large disturbances (Peringer et al. 2013). These processes were not considered in our simulations but may explain the over-estimation of tree cover and the current locations of forest patches. Reconstructed data about historical management (McGrath et al. 2015), land use changes (Wu et al. 2015), or disturbances (Gannon and Martin 2014) can be used to simulate the specific path that led to current landscape structure. However, this type of data is rare. Although our simulations did not consider historical factors, LandClim was still able to simulate current ecosystem provisioning services (i.e., percent of the pasture that is open, semi-open and closed, forage production and livestock suitability), which is important for estimating responses to future changes in climate and management.

At the regional scale, simulation results showed that almost the entire Jura Vaudois would be highly suitable for pasture. As pasture-woodlands are the dominant land use in this region (Buttler et al. 2009), this is a confirmation that LandClim is appropriately representing the factors that determine pasture suitability. Interestingly, low- and high-elevation pastures were equally appropriate. On the one hand, temperature limitations caused lower forage production at higher elevations. On the other hand, due to interactions between climate, forage production, grazing intensity and tree establishment, in higher elevation pastures this was compensated by a reduction in tree cover (i.e., more open pastures leading to lower light competition for grasses). As the entire region is quite wet and the highest elevation is only ~1600 m a.s.l., the point where climatic limitations resulted in highly unsuitable grazing conditions was not reached in the simulations.

We acknowledge that the setup of the large-scale simulation experiment may not be entirely realistic, assuming a constant and equal livestock density that is uniformly distributed across ~200,000 ha. However, the aim of our simulation was not to make an accurate prediction of the current state of landscape properties across this region, but to illustrate the impact of elevation and environmental gradients on pasture suitability and landscape patterns. In reality, it is obvious that farmers would adjust their management to optimize livestock densities towards maximum

forage production (e.g., higher stocking densities at lower elevations).

Upscaling of establishment processes to large spatial and coarse temporal scales

One of the most important conceptual differences between LandClim and WoodPaM is the representation of tree establishment. To be computationally efficient for simulating larger spatial extents, in LandClim new tree cohorts are established only once a decade. The number of *suitable* years within the decade is tracked and determines the establishment probability as well as the number of trees established per cohort. The impact of livestock grazing adds an additional establishment filter to this stage, however this one filter aggregates a wide variety of separate processes (e.g., injury due to trampling (Lewis 1980), grazing-induced growth reductions (Vandenbergh et al. 2007) and mortality (Ameztegui and Coll 2015)).

Conversely, vegetation dynamics simulated in WoodPaM focuses on the transitions between various categories of small trees (i.e., seedlings and saplings <1.5 m), with a separate consideration of the impacts due to grazing and trampling (Gillet 2008). As trees taller than 1.5 m are considered to have outgrown susceptibility to browsing damage, it is fair to say that LandClim starts to simulate tree population dynamics at the point when the livestock impact on trees is finished. So, how is it possible that LandClim can capture broad landscape patterns and the provisioning of ecosystem services? How important are the processes that impact the early life stages, and is it true that they can be collapsed into a few simple filters for tree establishment, which is a prerequisite for the approach to upscaling taken in this paper (cf. Bugmann et al. 2000)?

The hypothesis that biotic interactions are more important at fine spatial and temporal scales whereas environmental filtering is more important at large spatial scales is a fundamental assumption in community ecology that is supported by a wide range of evidence (e.g., McGill 2010; Belmaker et al. 2015). By including environmental variables to determine grazing preferences (i.e., forage production as influenced by climate and topography), we enhanced the LandClim model to perform well for simulating grazing effects on landscape patterns at large spatial extents. The trade-off is that its performance is only

broadly consistent with local data, but not highly accurate. We view the regional-scale applicability, however, as a clear benefit. The explicit consideration of climate and management means the model can simulate important differences between pastures, such as the un-even rates of land abandonment and woody encroachment (Garbarino et al. 2014; Vacquie et al. 2015), single farmers who utilize both summer and winter pastures, and the different climate change impact depending on elevation, topography and land cover (Rössler et al. 2012). Including these drivers will improve our ability to simulate future changes and will increase confidence in model predictions.

Managing pasture-woodlands for portfolios of ecosystem services

LandClim was able to simulate landscape heterogeneity, woody biomass, tree species composition as well as estimate forage production and livestock suitability at the scale of an individual pasture-woodland. These variables represent the most important ecosystem goods and services provided by these landscapes. LandClim was further able to capture current tree species composition in the Jura mountains, i.e. at much larger spatial scales. The three dominant tree species are *Picea abies* L. (spruce), *Acer pseudoplatanus* L. (maple), and *Fagus sylvatica* L. (beech), with spruce being most dominant (Buttler et al. 2009). This is in stark contrast to the expected species composition under unmanaged conditions (Frehner et al. 2005), where *Abies alba* (fir) and beech should be much more prominent. Hence, the dominance of spruce in both the real landscape and in the simulations is most likely due to its high grazing tolerance (Hjeljord et al. 2014). This view is corroborated by simulations without grazing, which indicate a much stronger dominance of beech and fir; the latter species is known to be particularly sensitive to browsing (e.g., Tinner et al. 2013), whereas the former is likely to have been reduced in abundance because conifer timber is commercially more attractive than beech wood.

The high biodiversity in pasture-woodlands is actually *maintained* by extensive land use (Buttler et al. 2009) as high landscape heterogeneity, including the many transitional zones and edges, supports a high diversity of species. While LandClim does simulate tree biodiversity, it does not consider biodiversity of the herbaceous layer or of any animal groups, which

may contain much higher species numbers than the tree layer itself (e.g., Hartel et al. 2014). However, simulated landscape metrics (e.g., tree cover and fraction of open land, landscape heterogeneity, number and length of edges, etc.) can be used to infer biodiversity in other guilds. For example, the optimal species richness in the herbaceous layer was found at ~30% tree cover (Gillet et al. 1999). Livestock species (i.e., cattle versus sheep or goats, Sanon et al. 2007; Hjeljord et al. 2014) or even different breeds of cattle (Rook et al. 2004) may also impact biodiversity. By modifying the grazer—grazing tolerance relationship, LandClim could be used to simulate how pasture management increases biodiversity both within a pasture and also over larger spatial extents.

The processes used to describe vegetation, climate and livestock dynamics in this paper, could also be applied to other pasture-woodland landscapes. Pastures outside of alpine regions tend to be located in more arid environments, although landscape patterns in Australia (e.g., Weinberg et al. 2011) and the Mediterranean (e.g., Pereira and da Fonseca 2003) are still largely driven by livestock pressure, with tree regeneration in particular being quite sensitive to grazing. Additional processes such as fire and soil nutrient cycling (Yates and Hobbs 1997) could also be included, if the modelling framework was to be extended into these regions.

Conclusion

In conclusion, we provide a novel tool that can serve to upscale the detailed grazing behavior of livestock and its interactions with vegetation from the pasture to the regional scale so as to evaluate the provisioning of ecosystem services that are important for pasture-woodland systems. We used general environmental variables, readily available at large spatial extents, to describe selective grazing by cattle, the interaction with vegetation and the formation of landscape patterns. In addition, the framework presented here in conjunction with climate change projections can be used to provide probabilistic estimates for the future provisioning of ecosystem services from these landscapes. Due to the explicit representation of pasture management, forest management, and natural forest dynamics as a function of climate, the modelling approach presented here offers a powerful tool to

simulate multiple external pressures on pasture-woodland systems, and test alternative management strategies to ensure the continuing provisioning of ecosystem services in the future.

Acknowledgements We gratefully acknowledge Christof Ammann (Agroscope), Jean-Bruno Wettstein (Bureau d'agronomie) and Gregory Egger (Environmental Consulting Klagenfurt) for providing data. This work was supported by the Competence Centre Environment and Sustainability (CCES) at ETH as part of the MOUNTLAND-II project.

References

- Agnoletti M, Tredici M, Santoro A (2015) Biocultural diversity and landscape patterns in three historical rural areas of Morocco, Cuba and Italy. *Biodivers Conserv* 24(13):3387–3404
- Ameztegui A, Coll L (2015) Herbivory and seedling establishment in Pyrenean forests: influence of micro- and mesohabitat factors on browsing pressure. *For Ecol Manag* 342:103–111
- Ammann C, Flechard CR, Leifeld J, Neftel A, Fuhrer J (2007) The carbon budget of newly established temperate grassland depends on management intensity. *Agric Ecosyst Environ* 121(1–2):5–20
- Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agric For Meteorol* 165:73–81
- Belmaker J, Zarnetske P, Tuanmu MN, Zonneveld S, Record S, Strecker A, Beaudrot L (2015) Empirical evidence for the scale dependence of biotic interactions. *Glob Ecol Biogeogr* 24(7):750–761
- Bourgeron PS, Humphries HC, Liptzin D, Seastedt TR (2015) The forest-alpine ecotone: a multi-scale approach to spatial and temporal dynamics of treeline change at Niwot Ridge. *Plant Ecol Divers* 8(5–6):763–779
- Broadmeadow MSJ, Jackson SB (2000) Growth responses of *Quercus petraea*, *Fraxinus excelsior* and *Pinus sylvestris* to elevated carbon dioxide, ozone and water supply. *New Phytol* 146(3):437–451
- Bugmann H, Lindner M, Lasch P, Flechsig M, Ebert B, Cramer W (2000) Scaling issues in forest succession modelling. *Clim Change* 44(3):265–289
- Buttler A, Kohler F, Gillet F (2009) The Swiss mountain wooded pastures: patterns and processes. In: Rigueiro-Rodrigues A, McAdam J, Mosquera-Losada MR (eds) Agroforestry in Europe, current status and future prospects. Springer, Dordrecht, pp 377–396
- Cailleret M, Heurich M, Bugmann H (2014) Reduction in browsing intensity may not compensate climate change effects on tree species composition in the Bavarian Forest National Park. *For Ecol Manag* 328:179–192
- Castellaro GG, Aguilar GC, Vera IR, Morales SL (2012) A simulation model of mesophytic perennial grasslands. *Chil J Agric Res* 72(3):388–396
- Chang X-Y, Chen B-M, Liu G, Zhou T, Jia X-R, Peng S-L (2015) Effects of climate change on plant population

- growth rate and community composition change. PLoS ONE 10(6):e0126228
- Chételat J, Kalbermatten M, Lannas KSM, Spiegelberger T, Wettstein J, Gillet F, Peringer A, Buttler A (2013) A contextual analysis of land-use and vegetation changes in two wooded pastures in the Swiss Jura mountains. *Ecol Soc* 18(1):39
- Duparc A, Redjadj C, Viard-Cretat F, Lavorel S, Austrheim G, Loison A (2013) Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands. *Appl Veg Sci* 16(2):305–316
- Elkin C, Gutiérrez AG, Leuzinger S, Manusch C, Temperli C, Rasche L, Bugmann H (2013) A 2 C warmer world is not safe for ecosystem services in the European Alps. *Glob Change Biol* 19(6):1827–1840
- Finger R, Gilgen AK, Prechsl UE, Buchmann N (2013) An economic assessment of drought effects on three grassland systems in Switzerland. *Reg Environ Change* 13(2):365–374
- Frehner M, Wasser B, Schwitter R (2005) Nachhaltigkeit und Erfolgskontrolle im Schutzwald. Wegleitung für Pflegemaßnahmen in Wäldern mit Schutzfunktion. Bundesamt für Umwelt Wald Landschaft (BUWAL), Bern
- Gannon BM, Martin PH (2014) Reconstructing hurricane disturbance in a tropical montane forest landscape in the Cordillera Central, Dominican Republic: implications for vegetation patterns and dynamics. *Arct Antarct Alp Res* 46(4):766–776
- Garbarino M, Sibona E, Lingua E, Motta R (2014) Decline of traditional landscape in a protected area of the southwestern Alps: the fate of enclosed pasture patches in the land mosaic shift. *J Mt Sci* 11(2):544–554
- Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: climate change or land abandonment? *J Veg Sci* 18(4):571–582
- Gillet F (2008) Modelling vegetation dynamics in heterogeneous pasture-woodland landscapes. *Ecol Model* 217(1–2):1–18
- Gillet F, Gallandat JD (1996) Integrated synusial phytosociology: some notes on new, multiscale approach to vegetation analysis. *J Veg Sci* 7(1):13–18
- Gillet F, Murisier B, Buttler A, Gallandat JD, Gobat JM (1999) Influence of tree cover on the diversity of herbaceous communities in subalpine wooded pastures. *Appl Veg Sci* 2(1):47–54
- Gillet F, Besson O, Gobat JM (2002) PATUMOD: a compartment model of vegetation dynamics in wooded pastures. *Ecol Model* 147(3):267–290
- Hartel T, Hanspach J, Abson DJ, Mathe O, Moga CI, Fischer J (2014) Bird communities in traditional wood-pastures with changing management in Eastern Europe. *Basic Appl Ecol* 15(5):385–395
- Henne PD, Elkin CM, Reineking B, Bugmann H, Tinner W (2011) Did soil development limit spruce (*Picea abies*) expansion in the Central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. *J Biogeogr* 38(5):933–949
- Hjeljord O, Histol T, Wam HK (2014) Forest pasturing of livestock in Norway: effects on spruce regeneration. *J For Res* 25(4):941–945
- Jolly WM, Dobbertin M, Zimmermann NE, Reichstein M (2005) Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps. *Geophys Res Lett* 32(18):4
- Jouven M, Carrere P, Baumont R (2006) Model predicting dynamics of biomass, structure and digestibility of herbage in managed permanent pastures. 1. Model description. *Grass Forage Sci* 61(2):112–124
- Kohler F, Gillet F, Reust S, Wagner HH, Gadallah F, Gobat JM, Buttler A (2006) Spatial and seasonal patterns of cattle habitat use in a mountain wooded pasture. *Landscape Ecol* 21(2):281–295
- Komac B, Kefi S, Nuche P, Escos J, Alados CL (2013) Modeling shrub encroachment in subalpine grasslands under different environmental and management scenarios. *J Environ Manag* 121:160–169
- Lewis CE (1980) Simulated cattle injury to planted slash pine—combinations of defoliation, browsing, and trampling. *J Range Manag* 33(5):340–345
- Lohmann D, Tietjen B, Blaum N, Joubert DF, Jeltsch F (2012) Shifting thresholds and changing degradation patterns: climate change effects on the simulated long-term response of a semi-arid savanna to grazing. *J Appl Ecol* 49(4):814–823
- Mairota P, Leronni V, Xi WM, Mladenoff DJ, Nagendra H (2014) Using spatial simulations of habitat modification for adaptive management of protected areas: mediterranean grassland modification by woody plant encroachment. *Environ Conserv* 41(2):144–156
- Marquardt S, Marquez A, Bouillot H, Beck SG, Mayer AC, Kreuzer M, Alzérreca H (2009) Intensity of browsing on trees and shrubs under experimental variation of cattle stocking densities in southern Bolivia. *For Ecol Manag* 258(7):1422–1428
- Mayer AC, Estermann BL, Stockli V, Kreuzer M (2005) Experimental determination of the effects of cattle stocking density and grazing period on forest regeneration on a subalpine wood pasture. *Anim Res* 54(3):153–171
- Mayer AC, Stockli V, Konold W, Kreuzer M (2006) Influence of cattle stocking rate on browsing of Norway spruce in subalpine wood pastures. *Agrofor Syst* 66(2):143–149
- McGill BJ (2010) Matters of scale. *Science* 328(5978):575–576
- McGrath MJ, Luyssaert S, Meyfroidt P, Kaplan JO, Bürgi M, Chen Y, Erb K, Gimmi U, McInerney D, Naudts K, Otto J (2015) Reconstructing European forest management from 1600 to 2010. *Biogeosciences* 12(14):4291–4316
- Meisser M, Deléglise C, Freléchoux F, Chassot A, Jeangros B, Mosimann E (2014) Foraging behaviour and occupation pattern of beef cows on a heterogeneous pasture in the Swiss Alps. *Czech J Anim Sci* 59(2):84–95
- Olff H, Vera FWM, Bokdam J, Bakker ES, Gleichman JM, Maeyer KD, Smit R (1999) Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. *Plant Biol* 1(2):127–137
- Pereira PM, da Fonseca MP (2003) Nature versus nurture: the making of the montado ecosystem. *Conserv Ecol* 7(3):7
- Peringer A, Siehoff S, Chételat J, Spiegelberger T, Buttler A, Gillet F (2013) Past and future landscape dynamics in pasture-woodlands of the Swiss Jura Mountains under climate change. *Ecol. Soc.* 18(3):11
- Pias B, Escribano-Avila G, Virgos E, Sanz-Perez V, Escudero A, Valladares F (2014) The colonization of abandoned land

- by Spanish juniper: linking biotic and abiotic factors at different spatial scales. *For Ecol Manag* 329:186–194
- Plieninger T, Hartel T, Martín-López B, Beaufoy G, Bergmeier E, Kirby K, Montero MJ, Moreno G, Oteros-Rozas E, Van Uytvanck J (2015) Wood-pastures of Europe: geographic coverage, social–ecological values, conservation management, and policy implications. *Biol Conserv* 190:70–79
- Rook AJ, Dumont B, Isselstein J, Osoro K, WallisDeVries MF, Parente G, Mills J (2004) Matching type of livestock to desired biodiversity outcomes in pastures—a review. *Biol Conserv* 119(2):137–150
- Rosenthal G, Schrautzer J, Eichberg C (2012) Low-intensity grazing with domestic herbivores: a tool for maintaining and restoring plant diversity in temperate Europe. *Tuxenia* 32:167–205
- Rössler O, Diekkrüger B, Löffler J (2012) Potential drought stress in a Swiss mountain catchment—Ensemble forecasting of high mountain soil moisture reveals a drastic decrease, despite major uncertainties. *Water Resour Res* 48:W04521
- Sanon HO, Kabore-Zoungrana C, Ledin I (2007) Behaviour of goats, sheep and cattle and their selection of browse species on natural pasture in a Sahelian area. *Small Rumin Res* 67(1):64–74
- Schumacher S, Bugmann H (2006) The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Glob Change Biol* 12(8):1435–1450
- Schumacher S, Bugmann H, Mladenoff DJ (2004) Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecol Model* 180(1):175–194
- Schumacher S, Reineking B, Sibold J, Bugmann H (2006) Modeling the impact of climate and vegetation on fire regimes in mountain landscapes. *Landscape Ecol* 21(4):539–554
- Shimano K (1997) Analysis of the relationship between DBH and crown projection area using a new model. *J For Res* 2(4):237–242
- Smit C, Gusberti M, Müller-Schärer H (2006) Safe for saplings; safe for seeds? *For Ecol Manag* 237(1–3):471–477
- Smit C, Ruifrok JL, van Klink R, Olliff H (2015) Rewilding with large herbivores: the importance of grazing refuges for sapling establishment and wood-pasture formation. *Biol Conserv* 182:134–142
- Snell RS, Huth A, Nabel JE, Boedhi G, Travis JM, Gravel D, Bugmann H, Gutiérrez AG, Hickler T, Higgins SI, Reineking B (2014) Using dynamic vegetation models to simulate plant range shifts. *Ecography* 37(12):1184–1197
- Speed JDM, Martinsen V, Mysterud A, Mulder J, Holand O, Austrheim G (2014) Long-term increase in aboveground Carbon stocks following exclusion of grazers and forest establishment in an Alpine ecosystem. *Ecosystems* 17(7):1138–1150
- Temperli C, Bugmann H, Elkin C (2012) Adaptive management for competing forest goods and services under climate change. *Ecol Appl* 22(8):2065–2077
- Thrippleton T, Bugmann H, Kramer-Priewasser K, Snell RS (2016) Herbaceous understory—an overlooked player in forest landscape dynamics? *Ecosystems* 19:1240–1254
- Tinner W, Colombaroli D, Heiri O, Henne PD, Steinacher M, Untenecker J, Vescovi E, Allen JR, Carraro G, Conedera M, Joos F (2013) The past ecology of *Abies alba* provides new perspectives on future responses of silver fir forests to global warming. *Ecol Monogr* 83(4):419–439
- Trnka M, Eitzinger J, Gruszcynski G, Buchgraber K, Resch R, Schaumberger A (2006) A simple statistical model for predicting herbage production from permanent grassland. *Grass Forage Sci* 61(3):253–271
- Vacquie LA, Houet T, Sohl TL, Reker R, Sayler KL (2015) Modelling regional land change scenarios to assess land abandonment and reforestation dynamics in the Pyrenees (France). *J Mt Sci* 12(4):905–920
- Vandenberge C, Frelechoux F, Moravie MA, Gadallah F, Buttler A (2007) Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures. *Plant Ecol* 188(2):253–264
- Vandenberge C, Frelechoux F, Buttler A (2008) The influence of competition from herbaceous vegetation and shade on simulated browsing tolerance of coniferous and deciduous saplings. *Oikos* 117(3):415–423
- Vries FT, Manning P, Tallowin JR, Mortimer SR, Pilgrim ES, Harrison KA, Hobbs PJ, Quirk H, Shipley B, Cornelissen JH, Kattge J (2012) Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol Lett* 15(11):1230–1239
- Weinberg A, Gibbons P, Briggs SV, Bonser SP (2011) The extent and pattern of Eucalyptus regeneration in an agricultural landscape. *Biol Conserv* 144(1):227–233
- Wu JG, Zhang Q, Li A, Liang CZ (2015) Historical landscape dynamics of Inner Mongolia: patterns, drivers, and impacts. *Landscape Ecol* 30(9):1579–1598
- Yates CJ, Hobbs RJ (1997) Temperate eucalypt woodlands: a review of their status, processes threatening their persistence and techniques for restoration. *Aust J Bot* 45(6):949–973