



LandS: Vegetation modeling based on Ellenberg's ecological indicator values



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ABSTRACT

We present LandS, a new version of the Gras Model. The Gras Model was designed to simulate grassland development at local scales based on Ecological Indicator Values (EIVs) for different grassland management practices. In LandS, we complemented the existing set of EIVs with a second set representing several environmental factors: light, moisture, temperature, soil pH and nitrogen, also known as Ellenberg's EIVs. These new EIVs make the model more versatile and applicable to a wide range of sites across Central Europe. For example, it can be used on sites with dry or moist, acidic or calcareous soils in grassland or forest environments. We have also improved the implementation of the model by introducing version control and moving species and site-specific variables to data input files, so that species sets can be easily swapped for application in new study sites. We demonstrate the use and behavior of the model in two simulation experiments exploring interactions mediated by Ellenberg's EIVs, using input files to apply the model to different landscapes. We also provide detailed guidance on species selection and calibration, and discuss model limitations.

- LandS is an improved version of the GraS Model for simulating vegetation development at the local scale.
- It includes Ellenberg-like indicator values for environmental variables for inverse prediction of species occurrence and composition.
- The model is now flexible enough to be used for study sites throughout Central Europe, using data input files for species initialization.

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Specifications Table

Subject area:	Environmental Science
More specific subject area:	Ecological landscape modeling
Name of your method:	LandS Model (Landscape Succession Model)
Name and reference of original method:	Previous Model Versions: GraS Model and WoodS Model GraS Model: Siehoff, S., Lennartz, G., Heilburg, I. C., Roß-Nickoll, M., Ratte, H. T., & Preuss, T. G. (2011). Process-based modeling of grassland dynamics built on ecological indicator values for land use. <i>Ecological Modelling</i> , 222(23), 3854–3868. https://doi.org/10.1016/j.ecolmodel.2011.10.003 WoodS Model: Hudjetz, S., Lennartz, G., Krämer, K., Roß-Nickoll, M., Gergs, A., & Preuss, T. G. (2014). Modeling Wood Encroachment in Abandoned Grasslands in the Eifel National Park – Model Description and Testing. <i>PLOS ONE</i> , 9(12), e113827. https://doi.org/10.1371/journal.pone.0113827
Resource availability:	Executable version of the model with a user guide and initialization files is available at https://github.com/gaiac-eco/LandS

Method details

Background

Ecosystems are threatened by a variety of anthropogenic activities, such as urbanization, agricultural practice and resource extraction, as well as climate change. These threats have led to habitat destruction, fragmentation and overexploitation of remaining areas and declines in biodiversity. It is therefore essential to gain a better understanding of how to effectively protect or restore these ecosystems. Ecological models can support conservation and restoration decisions and actions by providing insights into the complex interactions between species and their environment [1]. For example, models can be used to predict the effects of different land use scenarios on the distribution and abundance of species, and to identify areas of greatest conservation concern. Models can also help assess the effectiveness of different options, such as the design of conservation areas or the selection of restoration sites. In this way, models can help managers and policy-makers make informed decisions about how to effectively protect and conserve natural and semi-natural ecosystems [2].

The LandS model (Landscape Succession Model, former GraS Model [3] and WoodS Model [4]) is an example of such a decision support model that has been successfully developed and applied for conservation [2]. It simulates vegetation development at a local scale, such as in a national park or protected area, and combines herbaceous vegetation [3] with early shrub and tree encroachment [4]. A key feature of the model is the combination of local vegetation data with the dynamic simulation of growth for each species based on Ecological Indicator Values (EIVs).

EIVs are based on the general principle that vegetation is closely linked to the environment in which it occurs, and that plant species can therefore be used as indicators of the environmental conditions. This plant sociological principle has been described under various names: phyto-indicators, bio-indicators, ecological indicator values, or Ellenberg indicator values after the most prominent example of EIVs [5–9]. For EIVs, the indication of various environmental factors is typically described on an ordinal scale. This scale is determined empirically by observing the presence or absence of a species. Thus, the term EIVs is used here for any ordinal scale that describes the environmental preferences of a plant species with respect to specific environmental conditions. It is important to note, however, that this preference or optimum represented by the EIVs is not a physiological optimum, but rather refers to the realized niche in which a species is found under competition. Ellenberg et al. [6] provide a typical example: Plants at the dry end of the moisture scale may have their physiological growth optimum in well-saturated soils and are therefore not xerophilic per se. Competition with other less drought-tolerant species pushes them to the dry end of their growth range.

To model vegetation, EIVs are used inversely. Instead of inferring environmental variables from the presence and absence of species, environmental variables are used to predict species occurrence. The first version of the model (GraS model) included EIVs representing different grassland management practices, i.e. EIVs for cutting, grazing, and trampling according to Briemle et al. [10]. It was developed for the Eifel National Park to simulate future landscape management scenarios. The original set of EIVs focused on the response of species to management, as management practices were among the most influential factors in the landscape studied. However, nature conservation interest is not limited to managed grasslands, as natural and semi-natural landscapes also play an important role in conservation.

Therefore, in our new version of the model (LandS model), we complement the existing set of EIVs with a second set representing important environmental gradients: Ellenberg's EIVs for light, moisture, temperature, soil pH, and nitrogen [6,11,12]. While Ellenberg's EIVs are a widely used tool by ecologists when interpreting vegetation data and species distributions in Europe [5,9], they are rarely used in ecological modeling. This is despite the potential of these kinds of EIVs to integrate a wide range of environmental factors, when the exact mechanisms and influence of these variables on species distributions are still unknown [13]. The rationale of Ellenberg's EIV is similar to that of Species Distribution Models (SDM), which are based on the correlation between environmental variables and the presence or absence of species [14]. Like SDMs, observed correlations are inversely used to predict the occurrence of species under new conditions.

We also improved the structural consistency and transparency of the model. We moved all site-specific variables, such as plant species and species groups with all their parameters, into data input files for initialization. This makes the model easily applicable to other study areas by swapping sets of species without changing the source code. In addition, we put the model in a version control environment and implemented automated model testing to ensure consistency between model versions and to track changes during future model development.

Finally, we demonstrate the model's behavior in two test scenarios. Because the model is complex and the idea of using EIVs in a simulation is novel, it is important to be clear at the outset about the types of scenarios and predictions for which the LandS model was designed. Running the model for realistic landscapes will produce predictions that are often difficult to test because data for future scenarios may not exist. We therefore adopted the approach of Carter et al. [15], who first applied their model, designed to predict tiger range in a Nepalese national park, to an artificial landscape where the driving environmental variable followed a simple gradient. Accordingly, by inference alone, they were able to predict that home ranges should be smaller and tiger densities should be higher when prey densities were high.

Similarly, we designed the two test scenarios in which the setting was simple enough that the model outcome could be predicted by simple inference. In one scenario, we show that the model correctly predicts the dominance of certain species in certain habitat types. In the other scenario, we show that the model can be calibrated to mimic observed community compositions on specific habitat types, i.e. fertilized vs. unfertilized, and that the model is able to correctly predict the gradual transition between the two community compositions when the habitat type is changed from fertilized to unfertilized.

Despite the improvements we have made, LandS is of course not without limitations, particularly with respect to the geographic limitations of the EIVs for plant species described in the literature, the environmental gradients represented by the EIVs, and the extent of the study area that can be simulated with the model. These are outlined in the Discussion.

Method

Model description

This model description follows the ODD (Overview, Design concepts, and Details) protocol [16]. Earlier versions of the model were published separately, focusing on different aspects of the landscape: herbaceous vegetation and early woody encroachment. While herbaceous vegetation is a mandatory element of the model, wood encroachment is optional. As the model extension in this publication has been developed for herbaceous vegetation only, the description for the woody encroachment part only provides an overview. For more information on woody vegetation, see Hudjetz et al. [4].

Following Supplement S3 of Grimm et al. [16], we provide a “nested ODD”, where the submodel representing herbaceous vegetation is described by an ODD description of its own. In addition, we follow Supplement S4 of Grimm et al. [16] on “ODD of modified models” by using different font colors to distinguish elements of the model that are new or from the two earlier versions. See Supplement 1 for the colored ODD document.

Note that the ODD was specifically designed to be read in a hierarchical order, i.e. to get an overview first before going into details. We therefore recommend reading the Overview part of the ODD first (ODD 1–ODD 3), and also the Design Concepts part (ODD 4), as they introduce the overall structure and, in particular, the rationale of the model, which to our knowledge is the first (with its precursors) to use indicator values, or concepts from plant sociology, in a simulation model. After that, we recommend reading about the stylized test applications (Section ‘Two exemplary model applications for demonstration’) first, as it will facilitate understanding the details of the model, its initial settings, and calibration, if one knows the overall purpose of all this.

The original Delphi code implementing the model has been overhauled. It is now strictly object-orientated. All objects and processes described in the text correspond to objects and methods in the source code. The executable version of the model is available at <https://github.com/gaiac-eco/LandS>.

ODD 1. Purpose and patterns

Purpose. The main purpose of this model is to illustrate and predict vegetation succession in semi-natural landscapes for small-scale applications, such as a national park. Therefore, the model simulates the dynamics of the vegetation in a landscape mosaic and includes competition among herbaceous species as well as early wood encroachment. To make the model applicable to different landscapes, the modeled plant species from the data input files require calibration in a pre-configuration process. The model can be used to develop different management scenarios for situations where the landscape has changed or where changes are imminent. Examples include intended/planned changes in land management in protected areas, or action plans following severe storms that have created windthrow areas in forests. Ultimately, the model is intended as a decision support system (DSS) for stakeholders involved in the management of these landscapes.

Patterns. In evaluating the model, we distinguish between two types of vegetation patterns: equilibrium vegetation communities and intermediate state vegetation communities. Equilibrium patterns are observable in reality and can be derived from field data, expert knowledge, or the literature. Intermediate vegetation communities occur after a change in environmental conditions, such as abandonment. These communities transition between equilibria, are usually short-lived, and are not necessarily realistically simulated. We thus focus on the final outcome of succession, rather than on all the details of the transient dynamics, which are known to be often idiosyncratic anyway. If time series of vegetation data are available, the transition stage can also be evaluated.

ODD 2. Entities, state variables and scales

The model contains the following entities: the landscape representing the global environment, grid cells, and two types of plant entities for the herbaceous and woody vegetation. The entities and their state variables are listed in Table 1.

The *landscape* component contains the spatiotemporal information of the model, and deals with the simulation, i.e. iterations over years and time steps. The usual cell size is 10 m × 10 m, but it can be adjusted if necessary. The total size of the simulated area can be large, but it depends on the given study site. The maximal size simulated so far was about 1500 ha, i.e. 150,000 cells of

Table 1

Model components. Simulation settings, state variables, and parameters of the model.

Model component	Symbol	Default/Initialization value	Unit
Landscape (global environment)			
Number of cells		10 x 10	–
Cell size	A	100	m ²
Number simulation years	y	10	a
Time steps per year	t	365/52	d/w
Cell			
X-Y-coordinates		0,0	–
Type of cell, to be modeled or not to be modeled		Yes/No	–
Site Ecological Indicator Value for light, temperature, moisture, reaction, nutrients	site EIV _{L/T/M/R/N}	∈ [1, ..., 9] ¹	[–]
Utilization intensity for cutting, grazing, trampling	I _{C/G/TR}	Scenario specific ¹ ; ∈ [0, ..., 100]	–
Available space	AS	–	m ²
Vegetation type	VT	Study site/landscape specific; depending on observations	–
Herbaceous vegetation with grass and forb species (Study site/landscape specific)			
Species ecological indicator value for cutting, grazing, trampling	species EIV _{C/G/TR}	∈ [1, ..., 9] ²	–
Species ecological indicator value for light, temperature, moisture, reaction, nutrients	species EIV _{L/T/M/R/N}	∈ [1, ..., 9] ²	–
Maximum growth rate	g _{max}	∈ [0, ..., 10] ¹	a ⁻¹
Factor for self-regulation	F _S	∈ [0, ..., 15,000] ¹	–
Cover	c	For initialization depending on observations; later simulated	m ²
Woody vegetation with bush and tree species (Study site/landscape specific), optional and not used in the current model setup.			

¹ See the corresponding initialization section for further instructions on selection or calibration.² According to Ellenberg et al. [6], Dierschke [17], and Briemle et al. [10] within a maximal change of +/- 0.2.

100 m² over a simulation period of 100 years, calculated in daily time steps. The landscape uses closed boundaries that represent the spatially explicit landscape derived from observations and mapping. In the landscape grid, modeled cells are typically embedded in an environment of unmodeled cells, which are assumed to be stable landscape elements that are not affected by succession. The general idea is that in order to produce recognizable maps and scenarios, it is helpful to include surrounding structures, such as roads or forest areas, that shape the landscape but are either not involved in the short-term succession or are only indirectly involved (e.g., forest areas can still serve as a seed source). These surrounding structures also act as a buffer around the modeled area, so the model is not dependent on periodic boundary conditions.

Each *cell* is embedded in the landscape grid and characterized by its *X/Y coordinates*. Cells are divided into two *types*: cells to be modeled and cells not to be modeled. A modeled cell is further characterized by its environmental factors (i.e., light, temperature, soil moisture, reaction (soil pH), soil nutrients, and land use intensity of cutting, grazing, and trampling), which are determined by the study site and potential scenarios, see Section ‘[Initialization](#)’ ‘[Site parameterization – site EIVs](#)’ for a description on how to obtain values for these factors. These environmental factors are integrated either as *site-specific Ecological Indicator Values* (site EIVs) or as *Utilization Intensity* (I), see Section ‘[Basic Principles](#)’ for an in-depth explanation of the concept of EIVs. In each cell, the growth of the vegetation entities is modeled (Fig. 1). The whole community within a cell cannot occupy more than 100% of the area. Therefore, the *available area*, i.e. the area not yet covered by vegetation, in a cell is defined as a state variable. Each cell is further characterized by the state variable *vegetation type*, which represents the plant community in a cell. The vegetation type is used to initialize the vegetation entities. It is also a summarizing endpoint for convenient visualization and comparison with field surveys.

The model contains two types of plant entities, *herbaceous species* (i.e., grass and forb species) and *woody species* (i.e., tree and bush species). In the model, we use a hybrid approach for them: an individual-based model (IBM) for woody species and a compartment model with difference equations for the herbaceous species. While woody species are further divided into two types according to their life form (bushes and trees), grass and forb species are modeled equally at the population level in a cell. Therefore, each cell can contain only one compartment of each herbaceous species, but more than one woody individual, depending on the cell size and the size/age of the individuals.

Herbaceous vegetation. Herbaceous plants are modeled as compartments in a cell, with the state variable *cover* representing the abundance of each species. In general, each herbaceous entity is characterized by species-specific, static state variables for its preference or tolerance to various environmental factors, i.e. species-specific Ecological Indicator Values (*species EIVs*). These values are derived from the phytosociological literature; see Section [Initialization](#) ‘[Species parameterization – grouping and species-specific EIVs](#)’ on how and where to obtain these values. Other state variables are calibrated during the preliminary model setup, i.e. a *maximum growth rate* and a *self-regulation factor* (F_S).

Because of the compartmental model, the herbaceous layer is modeled as a homogeneous entity in each cell. This does not allow for fine-scale heterogeneity, which is important for plant coexistence [18]. Therefore, FS is used to substitute for microsites that are unfavorable for the dominant species. The factor makes room for more inferior species by limiting the species to a maximum cover

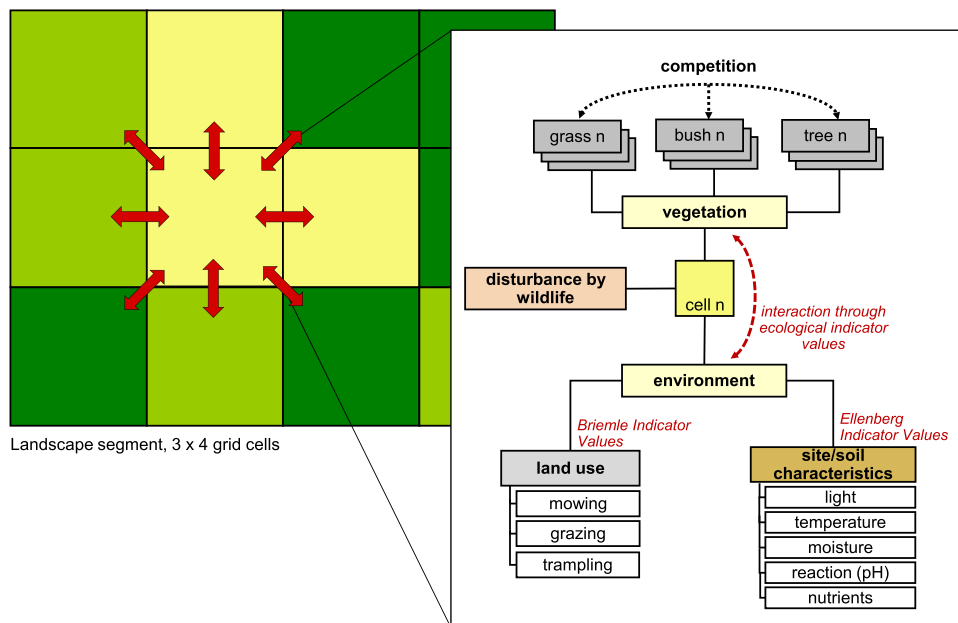


Fig. 1. General model concept.

and preventing the best-adapted species from taking over all the space. Plants with a low F_S value are reduced in growth at a lower cover than species with a high F_S -value.

While it is possible to model all existing species in the herbaceous layer, this could lead to overparameterization and hinder model calibration and output. In these cases, a set of representatives can be selected. Representatives are either a single plant species or a plant group consisting of species with similar ecological characteristics. For further details about the choice and parameterization of representatives, see ‘Species parameterization’.

Woody vegetation. Optional and not used in the current model setup.

Scale. Time in the model is run in years, with the time steps in a year set to either one-day or one-week. Thus, the user can specify the number of years, e.g., 10 or 100 years, and run a simulation with either 52 or 365 time steps per simulation. In a simulation, most of the processes will occur at every time step (e.g., growth), while some will occur only at certain times of the year, such as certain events in the life cycle of trees. The timing of such annual events is chosen to be close to reality (e.g., seed dispersal in summer). However, species-specific variability is not integrated. Furthermore, vegetation development is not seasonal or growing season dependent, i.e. there is no vegetation dieback in winter.

ODD 3. Process overview and scheduling

Landscape development is modeled by nesting processes at two spatial scales: the year and daily or weekly time steps within the year. All cells are recalculated from the upper left to the lower right at each time step. To account for interactions between neighboring cells, the relevant variables are stored and continuously updated throughout the cell cycle. Processes based on these neighbor interactions, which ultimately update the state variables, are then executed in separate cell cycles. The processes are scheduled as shown in Fig. 2.

Herbaceous vegetation. For the forbs and grasses, we considered processes of vegetative growth, mortality and interspecies competition within a cell, and vegetative growth from adjacent, neighboring cells. In each time step, the following processes for the herbaceous layer are executed in the given order. They are divided into two cell cycles. The process names correspond to those of the submodels that implement them, which are described in detail in Section ODD 7.

First cell cycle:

- Update visualization, i.e. vegetation type by a decision tree using the cover of all entities (not in every time step, only twice a year)
- Update of the cover of all herbaceous compartments (entities) in a cell by the dynamic growth and competition model, consisting of:
 - Mortality, which updates the cover of all compartments and the available space in the cell by the increased amount.
 - Potential growth in a cell, which updates the potential growth of each entity.
 - Potential growth to adjacent cells, which determines the target cell and the amount of potential ingrowth to the target cell, and updates the potential growth in the current cell by the reduced amount.
 - Realized growth (competition model), which uses the available space and the potential growth of all entities (in a cell and of its neighbors from the previous time step) to update the cover of each entity.

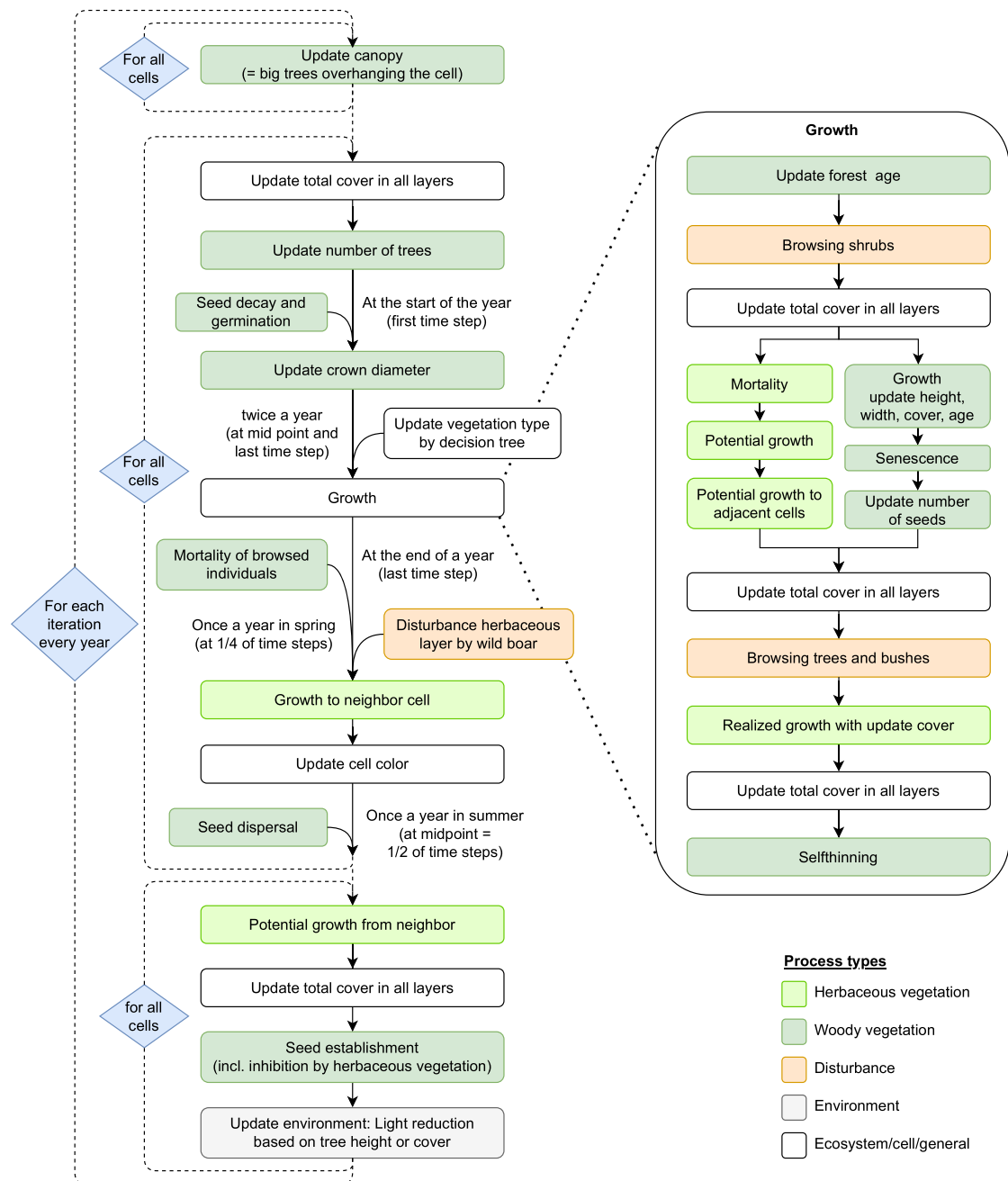


Fig. 2. Processes and scheduling. Process names correspond to those of the submodels described in detail in [Section ODD7](#).

- Update the storage variable of the amount of potential growth to neighboring cells in a temporary array for the next time step.

In a second cell cycle, the sum of potential growth from neighbors in each cell is updated.

Woody vegetation. Optional and not used in the current model setup.

ODD 4. Design concepts

Basic principles.

Grid-based approach. The model consists of two vegetation submodels that are embedded in a raster-based landscape. This raster-based approach allows the initialization with spatially explicit input data of the actual landscape, integrating the initial vegetation composition and the resulting neighborhood interactions, which are crucial for the course of the succession in a given landscape

[12,19–22]. Moreover, the approach allows the simulation of various management regimes on distinct areas of the modeled landscape. Further, we chose a detailed spatial scale for the grid cells to avoid artifacts, which might result from a wider grid [23].

Ecological indicator values. In our approach, the interaction of plant species with their environment is based on the plant sociological concept of Ecological Indicator Values (EIVs) often referred to as Ellenberg indicator values, which is one of the most prominent examples of EIVs [5,9]. EIVs are ordinal scales of environmental gradients such as light intensity, soil moisture, or nutrient availability that have been defined based on large, empirical datasets. The values do not represent physiological requirements, but rather the ecological preferences of plant species along these gradients. Thus, these values not only integrate the relationship of plants to environmental factors, but also capture to some extent distributional and competitive relationships. They are referred to here as 'species EIVs'. The actual growth, and hence cover, of a species then depends on how well the species EIVs match the corresponding environmental factors, the 'site EIVs'. Spatially explicit changes in site EIVs are used to simulate management or disturbance scenarios.

Coupling of compartment and individual-based modeling for plants. In a landscape, different scales of vegetation need to be considered. In the case of grasses and forbs, clonal growth and size make it difficult to distinguish individuals in the field. Therefore, grasses and forbs are perceived more as the sum of these plants, whereas bushes and trees can be distinguished as single individuals in the landscape. To account for the activity of these plants at these different scales, we choose different modeling approaches for the vegetation layers: an IBM for woody species and a compartment model with difference equation for the grass and forbs. This type of hybrid approach is considered a powerful tool for environmental modeling [24,25]. For example, the model of native beech forests, BEFORE [26] uses cover to describe seedlings and young trees up to 3 m, and individuals to describe canopy and sub-canopy trees.

Vegetation types. We use the plant sociological concept of plant communities to categorize vegetation patterns that correspond to different combinations of environmental factors [17]. In the model, these plant communities are referred to as vegetation types. Species composition and abundance (cover) can be used to describe and distinguish vegetation types. A distinction is usually made between differential and companion species. Differential species are characterized by their relative abundance and consistent occurrence in a given plant community. Companion species, on the other hand, are species that occur in a plant community but do not play a constant or dominant role. This concept allows aggregating the simulated cover of the plant species, the primary model output, into the vegetation type corresponding to that species composition. For this reason, the model is equipped with a decision tree that derives a vegetation type based on the simulated cover for each cell. This model output can then be linked to a GIS to visualize detailed raster maps, which is a precondition for the application by stakeholders who want to apply the model to existing landscapes [27].

Initialization and calibration. The initialization and calibration of the herbaceous vegetation are based on two general ecological concepts, the dynamic equilibrium of plant communities [28] and space-for-time substitutions [29]. Plant communities in equilibrium in the sense of Braun-Blanquet [30] include both climax communities and permanent communities (=Dauergesellschaften) that have not reached their climax state but are stable in composition. The space-for-time concept is used to determine the long-term effects of varying environmental conditions on vegetation types by using spatially different sites in the given landscape with varying conditions to substitute for the temporal observations of vegetation succession. For the pre-configuration, the equilibrium vegetation patterns under different environmental conditions of the studied landscape are used to calibrate two species-specific state variables (g_{\max} and F_S). The more vegetation types, and therefore combinations of environmental factors, used in the calibration, the better the plant behavior will reflect different real-world scenarios.

Emergence. The main outputs of the model are vegetation type maps of the landscape that are based on a decision tree that evaluates the key outcomes of the simulation: the herbaceous plant cover, and the number, age and cover of trees and bushes. These key outcomes emerge from the competition within and between the different vegetation layers in a cell, the life cycle processes of trees and bushes, the disturbance by wildlife, and the effects of the environmental conditions.

Herbaceous vegetation. The competitive vigor of herbaceous species emerges from their growth rate in relation to that of the other herbaceous species in the community of a cell, and depends directly on the environmental conditions. The cover of species over the simulation time results from their initial cover, their growth under competition, and the ingrowth from adjacent cells (neighborhood interactions). Spatial and temporal vegetation dynamics then emerge from the cover of single species.

Woody vegetation. Optional and not used in the current model setup.

Adaptation. Herbaceous vegetation. Species have three behaviors that indirectly represent adaptation to their own state and that of their environment: the potential to grow into neighboring cells, the reduction of their growth under unfavorable environmental conditions, and a growth limit. Growth into neighboring cells is modeled as direct objective-seeking: if an entity's cover is above a threshold, it has the potential to grow into an adjacent cell (see Objectives and Stochasticity). Growth reduction under unfavorable conditions is modeled as indirect objective-seeking: if a species EIV is not equal to the corresponding site EIV in a cell its growth factor is reduced (see 'Sensing' below and 'Calculation of growth rate' in the Submodel section). The growth limit is also modeled as indirect objective-seeking. The species have two calibrated parameters, g_{\max} and F_S , which modify the growth rate. The values of the parameters are estimated for each species through an iterative calibration process (see 'Species parameterization' for a detailed description). The objective measures during calibration in the pre-configuration process are species assemblages with specific species cover that have been obtained at the study site. These vegetation assemblages differ between environmental conditions, e.g. the specific species cover of a meadow differs from the species cover of a pasture. If the simulated cover for a species during the pre-configuration process is not similar to the objective measure, the g_{\max} and F_S parameters are adjusted.

Woody vegetation. Optional and not used in the current model setup.

Objectives. Herbaceous vegetation. The objective measure of the adaptive behavior ‘growth into neighboring cells’ is the cover of the species. If the cover exceeds the threshold of 1%, a stochastic process is applied to decide whether the entity grows into a neighboring cell or not, and if so, which of the eight neighboring cells is chosen.

Woody vegetation. Optional and not used in the current model setup.

Sensing. Herbaceous vegetation. Plant entities can sense the site conditions (i.e., light, temperature, moisture, reaction, and nutrients) and the management regimes (i.e., different types of land use) in their cell. They do this by comparing their own species’ EIV with the corresponding site EIV of the cell. The comparison is made in separate control functions that result in a factor that modifies the growth of the species. For site conditions, Ellenberg’s species EIVs indicate the realized niche for a plant species. The further the species deviates from the optimal values, the more its growth is reduced. Species with a lower Briemle species EIVs are more sensitive to a certain form of land use and are more heavily restricted in their growth.

Woody vegetation. Optional and not used in the current model setup.

Interaction. The model includes interactions within and between the different vegetation layers. All plants compete directly or indirectly for space. Herbaceous species compete directly for space within their layer, while woody species, once germinated, grow and use the space indirectly in the herbaceous layer. Large trees can also interact directly with the environment by changing the light conditions.

Herbaceous vegetation. Due to interspecific competition, species cannot always realize their full potential growth but have to share the available space with other species. The share of the available area that each species gets is calculated according to the species’ potential growth, which is calculated dynamically based on the species’ current growth rate. The species with the highest potential growth will achieve the biggest share of the available area and will outcompete the other species over time. This approach is similar to the concept of “lottery competition” [31].

When trees and bushes are available, certain species in the herbaceous layer can inhibit species-specifically the growth of woody seeds by reducing the number of woody seeds available in a cell.

Woody vegetation. Optional and not used in the current model setup.

Stochasticity. To take natural variation into account, several processes are calculated stochastically:

Herbaceous vegetation. Since the raster-based approach can only distinguish between the different covers of species in different cells, and no information about distribution within a cell is given, the spatial dispersal of plants is modeled stochastically. At each time step, it is randomly chosen whether a plant grows into an adjacent cell. The probability (p) of spread to neighboring cells is implemented as a linear function of species’ cover (c), so that the higher the cover, the greater the probability of dispersal to other cells ($p = c / \text{cell size}$). It is randomly chosen, into which one of the adjacent cells the species spreads, as well as the percentage of growth that is transferred to the adjacent cell.

Woody vegetation. Optional and not used in the current model setup.

Disturbance by wildlife. Used for *woody vegetation*, therefore not relevant for the current model setup.

Observation. The primary output of a simulation is the cover of each species in each cell. For visualization, the cover of the dominant plants and differential species is used in a decision tree to derive the vegetation type corresponding to the species composition of a cell. These vegetation types can then be used to illustrate the simulation results in detailed raster-maps. The representation as a raster map with the cells as vegetation types resembles the results of a biotope mapping as it is done in reality in nature conservation and thus enables the comparison and transfer of the simulation results. The user can either view the output in the graphical user interface (GUI) or export it to text or CSV files for further analysis or upload to a GIS.

The GUI provides the user with an interactive copy of the simulated landscape, allowing navigation through the simulated years and individual cells. The vegetation type in each cell is indicated by a different color. Different observation tabs provide the user with different information, either based on a selected cell or for the entire simulated area (landscape level). For each cell, the user can toggle between a graph showing the development of each species cover over the simulated time or a pie chart view showing the species cover for a single simulation year. In addition, the user can view cell-defining environmental properties, such as the site EIVs, as well as simple summaries, such as the number of trees and bushes in a cell. For the entire simulated area, the user can also view graphs over time and pie charts, similar to the cell evaluation, but now for the species cover of all cells. These views are particularly useful for calibration and when simulating a homogeneous area. At the landscape level, the user is also provided with a pie chart showing the percentage of vegetation types present.

ODD 5. Initialization

Each landscape contains specific vegetation communities. While the basic concept of the model is generic and applicable to many landscapes, the model requires landscape-specific (= case-specific) initialization data that define the entities of a simulated landscape, i.e. the species of the herbaceous vegetation and the associated vegetation types. This means that the model must be pre-configured and calibrated for a specific landscape before simulations can be run. While the initialization uses data input files, which can be changed, the core concept of the model depends on using the same species list for a given study area with all its sites. Species competition and species adaptation to different environmental conditions will handle the site-specific variations within the study area. This means, for example, that in previous applications in the Eifel National Park in Germany [3], meadows, pastures, and abandoned grasslands were all modeled with the same initialization data for species.

Table 2

Overview of the elements for the initialization.

Element	Source	Type
Vegetation types and initial plant cover	Field data, literature on plant communities and vegetation classification (see ‘ Vegetation types for initialization and evaluation ’).	Global tables
Herbaceous species	Field data, expert knowledge, and species EIVs as suggested by Ellenberg et al. [6], Dierschke [17], and Briemle et al. [10]; guidance for calibration (see ‘Species parameterization’).	Global table
Woody species	Optional and not used in the current model setup.	Global table
Vegetation type map	Field data, status quo of the landscape, with cell-specific attribution of number of woody species, when applicable.	Cell-specific grid map
Site EIVs map	Observations, soil map, digital terrain models (DTM), and expert knowledge; guidance for site EIVs (see ‘Site parameterization’).	Cell-specific grid map
Land use map (present and historic)	Observations, aerial photographs, historical maps and interviews with farmers and land users; guidance for site-specific EIVs (see ‘Site parameterization’).	Cell-specific grid map
Decision tree for vegetation types (for output)	Developed based on the available species and possible vegetation types of the current landscape (see ‘ Vegetation types for initialization and evaluation ’).	Global table

Table 3

Global parameters specified in the GUI for the initialization.

Global parameters in the GUI	Symbol	Default/Initialization value
Slope for the control functions of each $EIV_{L/T/M/R/N}$	$slope_{L/T/M/R/N}$	$\in [0, \dots, 2]$
Slope for the control functions of each $EIV_{L/T/M/R/N}$ for species with indifferent EIVs	$slope_{red,L/T/M/R/N}$	$\in [0, \dots, 1]$
Optimum for the control functions of each $EIV_{L/T/M/R/N}$ for species with indifferent EIVs	$Opt_{red,L/T/M/R/N}$	$\in [0, \dots, 1]$
Weights for environmental factors (light, temperature, moisture, reaction, nutrients, cutting, grazing, trampling)	$w_{L/T/M/R/N/C/G/TR}$	$\in [1, \dots, 20]$

Initialization after pre-configuration. For initialization the model uses imported settings from initialization files, to allow case-specific initialization of different landscapes, and global parameters specified by the user in the GUI. These initialization files can be divided into two types of data: Tables with global settings that define the available plant species and their state variables, and raster-maps with cell-specific settings that define the state variables of the cells (Table 2). The tables with global initialization values are the result of the pre-configuration (see the next subsections for a detailed description of the general pre-configuration approach) and are generic for simulations within a landscape, while the cell-specific raster-maps are case-specific and partially exchangeable depending on the simulated scenario. For small test simulations, the cell-specific initialization files can be replaced with user input in the GUI to create a homogeneous cell grid.

The GUI allows the user to specify various settings, turn on/off mechanisms, and set the values for global parameters during a simulation. Some of the global parameters (Table 3) modulate the herbaceous vegetation growth model by changing the environmental control functions of the site conditions and weights to balance the effect of all factors. Depending on the landscape studied, each environmental control function of a site condition (light, temperature, soil moisture, reaction, and nutrients) can be adjusted by changing its slope for species with regular EIVs. In addition, the control function can be fitted with a slope and an alternative optimum for species with an indifferent EIV (see the ‘[Dynamic Growth Model](#)’ section in the Herbaceous Vegetation submodel for more details). Fitting these values is part of the pre-configuration.

Landscape and Cells. The landscape grid is created as a blank slate and then initialized with cell-specific information from raster maps or GUI input fields. Scenarios are later simulated by spatially explicit changes in environmental conditions or management for a cell or area or cells. It also includes global parameters such as calibrated slope and optimum values for the control functions or weights for each environmental factor.

Herbaceous vegetation. The entities are initialized with the status quo cover. However, this spatially explicit initialization of herbaceous entities is simplified, because vegetation maps typically consist of mapped vegetation types with a list of plants in each vegetation type. Accordingly, each cell is assigned a vegetation type for which a specific cover per plant species has been defined and provided in the imported global tables.

For simulating secondary succession, such as the development of established plant communities following a change in land use, this approach of starting with the status quo vegetation cover has proven useful. However, to simulate primary succession, i.e. the development of vegetation following disturbance or construction activities that result in larger areas with raw soil conditions, a soil seed bank can be mimicked by initializing all available species in the landscape with a low initial cover, e.g. 0.1%.

Herbaceous entities of the same species only differ in their state variable ‘cover’ at initialization. This depends on the cell and its vegetation type in which they were created. Entities of different species will also differ based on the remaining state variables defined in the imported global tables. EIVs are based on literature values. Species with similar ecological preferences and occurrences may also be similar at initialization.

Woody vegetation. Optional and not used in the current model setup.

Disturbance by wildlife. Used for woody vegetation, therefore not relevant for the current model setup.

Table 4
Landscapes with existing preliminary model setups.

Landscape and site location	Special features	Source
Mesophilic, extensively used grassland; Eifel National Park, Germany	Based on land use, Briemle EIVs	Siehoff et al. [3]
Windthrow areas in spruce forests; Hochsauerland district, Germany	Based on land use and environmental conditions, Briemle's EIVs and Ellenberg's EIVs	Not published

Table 5
Different types of initialization tables depend on the vegetation type.

Table	Description
Vegetation type	Contains all vegetation types of the landscape and whether a type is simulated or not, e.g. roads or field paths are structural elements and are not dynamically simulated. It is required as attribute table for the raster-based vegetation type map.
Initialization cover	Contains all simulated vegetation types with the respective initialization cover for each relevant plant entity
Decision tree	Contains dominating and districting entities with thresholds to derive the vegetation type from the simulated cover of the plant assemblage

Pre-configuration.

Necessary data obtained from a pre-configuration. The pre-configuration includes the following mandatory elements: vegetation types, herbaceous layer entities, and environmental conditions. The main sources for the pre-configuration are local vegetation relevés from different sites of the study area, covering the different environmental conditions and combinations. They are supplemented by expert knowledge, literature, or historical data (Table 2). The quality and completeness of the vegetation data available from the study area can greatly influence the quality of the pre-configured model, it is important to cover the range of environmental conditions. Detailed instructions for the pre-configuration and the estimation of site-specific EIVs are provided below.

Herbaceous vegetation. For vegetation distribution, the cover of each modeled species must be specified for each vegetation type. A cell is then assigned a vegetation type and the corresponding cover for all its entities. The initial vegetation distribution in the simulated landscape can influence the simulation outcome. Species that would be favored by a certain set of environmental conditions, but do not exist in that part of the landscape, might migrate from other parts of the landscape and thus affect vegetation dynamics.

Environmental conditions. Site and soil conditions are defined similarly to Ellenberg's species EIVs on a 9-point scale. Land use is applied with relative values between 0 and 100 for cutting, grazing, and trampling, i.e., all set to 0 for no disturbance.

Woody vegetation. Optional and not used in the current model setup.

General approach for the pre-configuration and calibration of the model. The pre-configuration of the model and the parameter calibration of the chosen entities have a great influence on the model output. Therefore, we describe here the general approach and patterns followed for calibration. These are required for each new landscape to be simulated. Existing model configurations are listed in Table 4.

Vegetation types for initialization and evaluation. Vegetation types, a concept from phytosociology (see 'Basic principles'), are important for the aggregation of information on species composition and abundance at a higher landscape scale. They play two roles in the model. First, they manage the initialization of plant entities, and second, they aggregate the simulated cover of all plants into a single endpoint for visualization. Therefore, we initialize the model with three different global tables: one general, one for the initialization process, and one for the evaluation process (Table 5). Each of these tables must be adapted to the specifics of a new landscape during the pre-configuration.

Set of vegetation types. Using field data from a given study area and expert knowledge is the best way to determine the vegetation types of a landscape in the pre-configuration process. First, an analysis of vegetation relevés (or vegetation inventories) and vegetation maps can be used to determine which vegetation types are most prevalent in the study area. In addition, it is important to determine which vegetation types are in a stable state of equilibrium under the current environmental conditions and which vegetation types may be in an active successional process between equilibrium states. These equilibrium states will be the reference for the calibration of species competition parameters (see 'Initialization'). It is also necessary to analyze which environmental factors, such as light availability in forests, soil moisture in arid areas, or soil nutrients in nutrient poor areas, etc., or some combination of thereof, are responsible for the observed patterns in the current landscape. This can then be used to calibrate the weights for site EIVs in the model, and thus the influence, that individual environmental factors have in modifying the growth function of species in a simulation (see 'Calculation of growth rate' in the submodel section).

Initialization cover. Simulations typically begin with the vegetation status quo at a study site. However, the real landscape is simplified in that each vegetation type is assumed to have a particular species composition and cover. It is therefore necessary to specify the initial cover of each herbaceous entity for a given vegetation type. This initial cover is also derived from the relevés, e.g. as an average of the mapped plots of a vegetation type. However, it is important to use only plots that represent mostly pure equilibrium states of a vegetation type for the calculation to exclude edge effects due to vegetation plots that are in a transition between states.

Decision tree. One of the last steps in the pre-configuration is usually the creation of the decision tree. The decision tree is based on the dominant and differential species that are used in the current simulation and their cover in a cell. The model executes queries using logical conditions such as "IF species 1 > 50% AND/OR species 2 < 5%". Once a logical condition is satisfied, the corresponding vegetation type is assigned to a cell. It is therefore important to make the conditions specific enough and to allocate them in an ecologically meaningful order, e.g. starting with the dominant species with a high cover, followed by a combination of species with

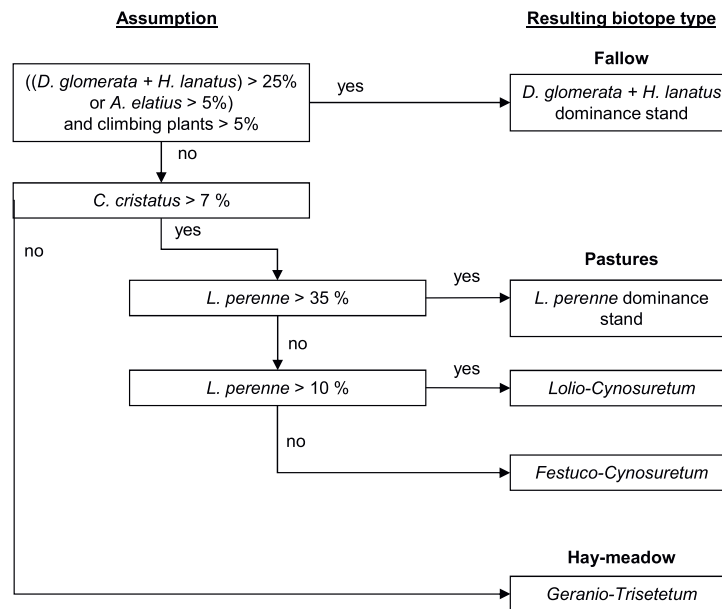


Fig. 3. An example decision tree for deriving vegetation types from species composition, the name of species is referring to their simulated cover, first published by Siehoff et al. [3].

Table 6

Land use scenarios with their corresponding utilization intensity were first published by Siehoff et al. [3].

Description of the land use form	Utilization intensity (cutting – grazing – trampling)
Hay-meadow	75 – 1 – 1
Mown pasture (very extensive)	75 – 20 – 10
Extensive pasture	0 – 35 – 20
Intensive pasture	0 – 50 – 50
Sheep pen	0 – 85 – 85 or 0 – 80 – 80
Fallow	0 – 1 – 1

a high cover and differential species that indicate certain conditions. An example decision tree for the Eifel National Park with the dominant grasses *Arrhenatherum elatius*, *Cynosurus cristatus*, *Dactylis glomerata*, *Holcus lanatus*, *Festuca rubra* agg. and *Lolium perenne*, and the climbing plants as differential species is shown in Fig. 3.

Site parameterization – site EIVs. In our approach, species interaction with the environment relies on EIVs (see ‘Basic principles’). This means that a species depends on how well its species EIVs match the corresponding environmental factors, the *site EIVs*. For this interaction to work, it is necessary to provide corresponding scales for site EIVs. Unlike species EIVs (see ‘Species parameterization’), site EIVs are not generally available. In the past, there have been some attempts to generate site EIVs for different plant communities, e.g. Böcker et al. [32]. However, there are not many sources available for easy reference. Therefore, we provide general guidance on how to obtain site EIVs.

Briemle site EIVs. The Briemle species EIVs describe the tolerance of species to three types of land use (utilization): cutting, grazing, and trampling [10]. They have been developed mainly for grasslands. The scale ranges from less tolerant (1) to very tolerant (9). For the corresponding site EIVs, Siehoff et al. [3] developed a relative intensity scale and defined different land use scenarios (Table 6).

Ellenberg site EIVs. The original Ellenberg species EIVs describe the optimum of species in their realized niche [17]. Therefore, we use a different approach than for the Briemle site EIVs and introduce Ellenberg site EIVs as 9-point scales analogous to the original species scales. There are two ways to determine the values at a given site: (1) calculation of average species EIVs based on all mapped species of a vegetation type, and (2) theoretical estimation from other sources such as soil maps with parameters such as elevation, slope, and soil parameters. Both approaches have their advantages and disadvantages (Table 7). The calculation of site EIV from average species EIVs is a common practice in the analysis of vegetation data and is well described [5,17]. Site EIVs derived from a detailed vegetation mapping can indicate very small-scale changes in local conditions. Theoretical estimation of site EIVs requires expert knowledge of phytogeography and is more general because national soil maps are often provided at larger scales and fine-scale maps are not available everywhere. Nevertheless, these soil maps can provide valuable information where meaningful vegetation mapping is not available, such as after a recent disturbance.

Site EIVs based on vegetation mapping. If detailed vegetation data are available, average site EIVs can be calculated based on the species lists for each vegetation type. This is based on the assumption that the presence of all species in an area reflects the

Table 7

Advantages and disadvantages of the possible methods for the derivation of Ellenberg site EIVs.

	Calculation of average EIVs based on vegetation mapping and species lists	Theoretical estimation of site EIVs, based on soil maps
Advantage	<ul style="list-style-type: none"> • Fine-scale • Easy to obtain • The principle is well described in the literature • Applicable without further expertise 	<ul style="list-style-type: none"> • Often widely available • Future scenarios use the same logic as current scenarios to derive values
Disadvantage	<ul style="list-style-type: none"> • Not available for future scenarios (only over time for space) • Not available after recent disturbances when the vegetation is destroyed/absent, such as fires, floods, or raw soil conditions • The same sources are used for species EIV selection 	<ul style="list-style-type: none"> • National or federal state-specific standards for soil maps and the available parameters • Requires expert knowledge of phytogeography to determine how soil and site characteristics affect the vegetation

environmental conditions more reliably than a single species. [5]. Areas are therefore defined and distinguished by the similarity of their species composition. Since the species composition also determines the vegetation type, this is similar to the concept of vegetation types (see ‘Basic principles’). Therefore, the calculation must be performed separately for each vegetation type with its characteristic species community.

There are several ways to calculate these site EIVs from vegetation data. Either the median or a weighted mean of an EIV can be calculated over all species present. For the weighted mean, there is also a choice between qualitative and quantitative weighting (using presence/absence or abundance data). For a comprehensive analysis and discussion of considerations and pitfalls when calculating weighted average or median EIVs, see Diekmann et al. [5]. Technically, there is no difference in the model depending on which calculation is chosen. It is therefore important that the chosen approach is appropriate for the quality of the available data.

Site EIVs based on soil map information. The availability of digital soil maps and the information they provide varies across Germany [33]. Here, we provide a compilation of parameters that can be used to estimate site EIVs (Table 8) based on information from German soil maps from North Rhine-Westphalia (NRW) [34]. We have focused on estimating EIVs for open and semi-open landscapes up to high montane altitudes. As a result, not all of the environmental factors, in particular the L- and T-values, are fully available here. Another problem was that the soil maps provide some parameters aggregated in classes. Therefore, it is not always possible to refer to each value on the 9-point scale, and some values are given as proxies for a group.

Site EIV for light (L-Value). Ellenberg’s light availability scale for plants ranges from deep shade (1) to partial shade (5) to full light (9) [6]. To determine the site value from the soil map information, the size of the site, its aspect, and slope can be used (L-Value, Table 8). For an open or semi-open landscape, the L-Values should be 6 or higher. This is because the shaded condition is only temporally. On small sites, the surrounding area may affect the light availability, e.g. due to tree shading. To account for these peripheral effects of the surroundings, we distinguish between small sites (< 5000 m²) and large sites (≥ 5000 m²) for the L-Value estimation. Small sites generally have a lower value than larger sites with the same parameters. In addition to the site size, aspect, and slope are used to estimate the L-Value. A southern aspect with a moderate slope gradient is beneficial for a high L-Value, while a northern aspect with a steep slope results in a lower L-Value.

For completeness, it should be noted that for a site to be classified as half-shaded or less (1–5), there must be sufficient cover. This may be due to other vegetation, such as a forest, or to special features, such as at the base of a north-facing cliff. A meaningful classification then requires further information to determine the L-Values, such as stem density and forest type.

Site EIV for temperature (T-Value). Ellenberg’s temperature scale for plants ranges from plants as cold indicators (1) to extreme heat indicators (9). In Ellenberg et al. [6], the authors made a first attempt to assign elevation classes and mean annual temperature to the T-Values. Consistent with this, we use the elevation from the soil maps as a parameter for estimating the T-value. Values 8–9 should only be used for warm, lowland sites with and require further information. Similar to the L-Values aspect and hillslope could be used here. To use T-Values below 4, a further adaptation to alpine and subalpine conditions is required.

Site EIV for soil moisture (M-Value). Ellenberg’s soil moisture scale for plants ranges from plants as very dry indicators (1) to wet indicators (9) to underwater plants (12). Since the LandS model is designed for terrestrial habitats, the original scale was truncated at 9, to exclude the values dedicated to aquatic plants. German soil maps from North Rhine-Westphalia provide a parameter called “ecological moisture class” [34]. It uses the soil properties usable field capacity in the effective root zone, waterlogging level, and groundwater level to assess the soil moisture. We use this parameter to estimate the M-Value. Other valuable sources could be the slightly different ecological moisture assessments according to Bechler & Toth [35] or Hauße et al. [36].

Site EIV for soil reaction (R-Value). Ellenberg’s soil reaction scale for plants ranges from plants as strong acid indicators (1) to alkaline and calcareous soil indicators (9). The soil reaction EIV can be measured by the pH, for example, and is one of the better measurable Ellenberg EIVs [17]. We used Cation Exchange Capacity (CEC) classes from soil maps to estimate the R-Value. Low CEC values result in low R-Values and vice versa. With more detailed parameter classes, some of the combined categories could be further developed.

Site EIV for soil nutrient/nitrogen (N-Value). Ellenberg’s soil nutrient scale for plants ranges from indicators of nutrient-poor sites (1) to indicators of excessively nutrient-rich sites (9). We use soil type, texture, and topsoil thickness from soil maps to estimate how well the soil provides nutrients to plants and derive the N-Value from this estimate. Some soils, such as podzols, regosols, plaggens, syrosemes, or rankers, are naturally low in nutrients. For other soil types, texture plays an important role, as coarser textures such as gravel and sand have lower nutrient retention [37,38]. Finally, for very fine-grained soils (clays, class 3–1), the thickness of the soil layer can be used to further segment the N-value.

Table 8

Overview of how soil map information is used to derive site EIVs. The parameters provided refer to the information available in the German soil map of NRW, BK50 [34,39].

Parameter	Values						
<u>L-Value</u>							
I) Small sites; open area < 5000 m ²	1–5		6	6.5	7	7.5	8–9
Aspect	Used for a covered area of any size, e.g. woodlands. Requires further information.		WSW to ESE	Any not specified	WSW to ESE	SE to SW	not defined
Hillslope			> 20°	< 5° not specified	5° - 20°	> 5°	not defined
II) Large sites; open area ≥ 5000 m ²	1 – 6			6.5	7.5	8	9
Aspect Hillslope	Used for a covered area of any size, e.g. woodlands. Requires further information.			WSW to ESE > 20°	WSW to ESE 5° - 20°	Any < 5° not specified	SE to SW > 5°
<u>T-Value</u>							
	1–3	4	4.5	5	6	7	8–9
Altitude [m]	> 1500	1500–800	800–650	650–450	450–300	< 300	exceptional warm sites, consider aspect
<u>M-Value</u>							
	1–2 (1.5)	3		4–6 (5)		7	8–9 (8.5)
Ecological moisture classes	very dry	dry	moderately dry - slightly moist			moist	wet
<u>R-Value</u>							
	1–2 (2)	3	4	5–6 (5.5)	7–8 (7.5)		9
Classes for cation exchange capacity (CEC) [mol ⁺ /m ²]	< 40	40–80	80–160	160–320	320–640		> 640
<u>N-Value</u>							
	1–3 (2)	3	3–4 (3.5)	4–6 (5)	6–7 (6.5)		8–9 (8.5)
Soil type	P, Q, E, O, N	R, Z	B, L, K, S, SG, G, GN	B, L, K, S, SG, G, GN	B, L, K, S, SG, G, GN		B, L, K, S, SG, G, GN
Soil textural classes (of the top layer)	any	any	4, 5, 6, 7, 8, 9	3	2, 3		1, 2, 3
Thickness of the top soil layer	any	any	any	< 60 cm	60–200 cm		> 200 cm

Soil type abbreviations: P = podzol; Q = regosol; E = plaggen; O = syrosem; N = ranker; R = rendzina; Z = pararendzina; B = brown earth; L = para-brown earth; K = colluvisol; S = pseudogley; SG = stagnogley; G = gley; GN = wet gley. Soil texture classes: 1 = loamy clay; 2 = clayey loam; 3 = clayey silt; 4 = sandy loam; 5 = very loamy sand; 6 = sandy silt; 7 = loamy sand; 8 = sandy; 9 = low on fine-grained soil.

Adjusting and adapting site EIVs. Estimating site EIVs from soil map information may not accurately capture all environmental conditions. Depending on local conditions or the scenario being considered, it may be necessary to modify the values that were estimated above. For example, when simulating used grassland, the effect of fertilization or airborne nitrogen deposition must be considered and the N-value may need to be increased. Small-scale landscape patterns may also require adjustments. For example, it may be necessary to increase the F-Value at the foot of a slope or in depressions; similarly drainage could be accounted for by decreasing the F-Value. This can be done, for example, by using observations or information from a DTM so that the final EIV map reflects the environmental conditions as accurately as possible. In addition, different climate scenarios can be simulated by adjusting the T-Value.

Species parameterization – grouping and species-specific EIVs. Based on the previous analysis of vegetation types, a set of representative species and ecological plant groups can be defined to represent the habitat-specific species composition. First, the species EIVs for site condition and land use are calculated based on literature values, and then the maximum growth rate g_{\max} and the self-regulation factor (F_S) are calibrated for all species. The calibration follows vegetation patterns that have been identified as being in the equilibrium state (see previous section).

Set of representative species. Since modeling of all existing herbaceous species could result in over-parameterization and could make model calibration impossible, a set of representative species can be selected. First, it is important to select the most abundant species that dominate the competition in the study area, as single species. These are often grass species among a few other species, depending on the landscape. It is also useful to select a few characteristic species that are not dominant but are characteristic of certain equilibrium states. Beyond these single species, the remaining species can be grouped into plant groups of species with similar ecological behavior. These groups usually need to be adapted to the set of environmental factors that drive the specific landscape. For example, when studying managed grasslands, traits that integrate a response to mechanical disturbance by cutting or grazing [10] may be useful. However, in wetlands, for example, other factors such as different moisture or nutrient groups may be more appropriate.

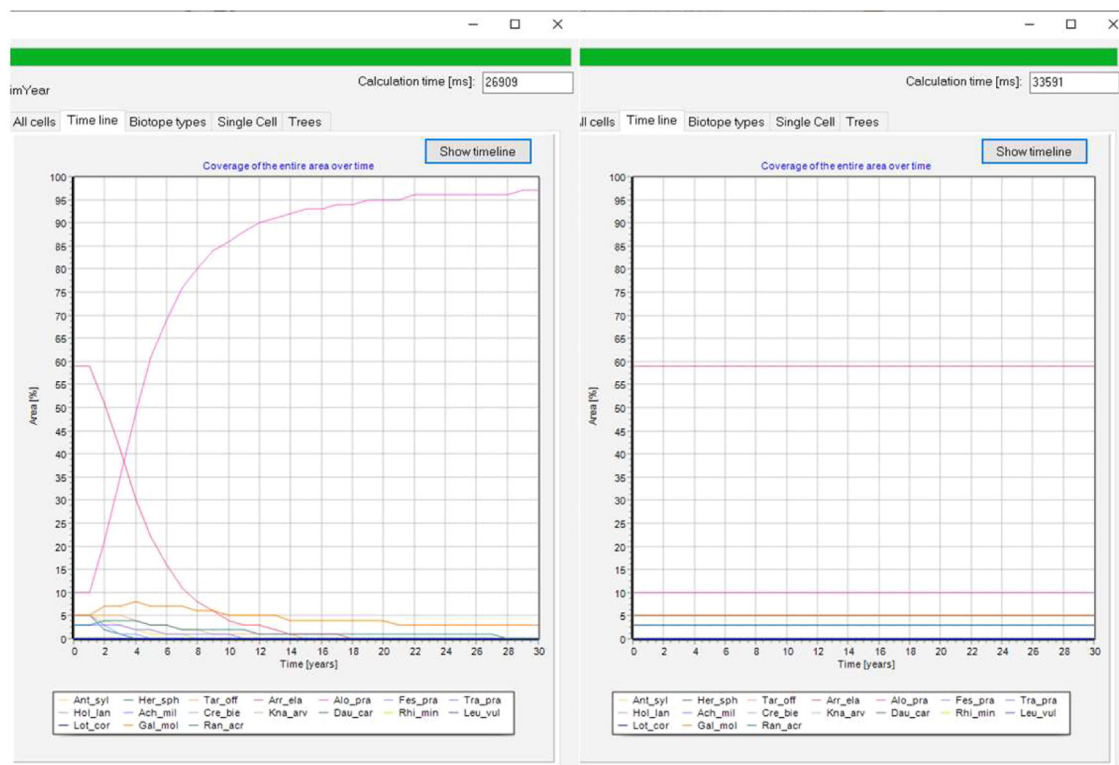


Fig. 4. Screenshots showing parts of the output GUI of two different simulation runs: at the start of the calibration process (left) and after calibration (right) with the dynamic equilibrium of the examined community.

Species EIVs. Values for the different species can be found in the literature. Ellenberg's EIVs for light, temperature, moisture, soil reaction (pH), and nutrients are published for Germany in Ellenberg et al. [6,11] and Ellenberg & Leuschner [12]. Ellenberg-type EIVs are also available for other European countries and on a European scale [40]. A European map with recommendations for areas where these Ellenberg-type values can be applied is also provided by Tichý et al. [40]. Briemle's EIVs for cutting, grazing, and trampling are published in Dierschke & Briemle [41]. EIVs of species groups can be represented either by a group indicator species and its literature values, or by an average of all species in the group and their literature values. If an average of all species in a group is calculated, it may be necessary to introduce a threshold for the degree of occurrence to exclude randomly occurring species. Calibration results can be enhanced during the pre-configuration process by adjusting the EIVs of some species to the simulated geographic area according to the obtained data at the study site and expert knowledge as suggested by Ellenberg et al. [6], Dierschke [17], and Briemle et al. [10], within a maximum change of ± 0.2 .

Calibrating the g_{\max} and F_S parameters. The iterative calibration process involves adjusting the parameters g_{\max} and F_S for each plant species to visually match the simulated cover with the predefined cover of different calibration scenarios. These calibration scenarios are usually vegetation types in the equilibrium state under the influence of different environmental factors, and sometimes short-term developments from one vegetation type to another after a change in environmental conditions. The procedure starts by simulating a single scenario and adjusting the parameters until the simulated vegetation composition matches the observed reference values (Fig. 4).

Subsequent scenarios are calibrated in the same way, but with a backward check to ensure that previously calibrated scenarios are still accurate. The parameters need to be fine-tuned, especially for species that are present in multiple calibration scenarios, to prevent the species cover from evolving too far from reality. Before calibration, it is helpful to categorize species based on the patterns of dominance and abundance observed in the scenarios (Table 9). Species with high cover tend to be dominant and thus have high F_S values. Species with low abundance often have a low g_{\max} and are therefore less competitive in the community in a variety of scenarios. Once a few scenarios have been calibrated, this should become easier. If the calibration or backward checks are difficult, it may be necessary to change the weighting of the environmental factors (see below) to better represent the dominant environmental gradients of the simulated sites. The calibrated g_{\max} and F_S values of all species are then used for all simulations of the given landscape.

Weighting of environmental factors. The weights of the environmental factors are important to regulate the impact that a factor has on the growth of species (see 'Dynamic growth model'). While it is possible and sometimes necessary to tweak the weighting values during the pre-configuration process, the weights should depict the important gradients at the studied site. For example, modeling grasslands along a moisture gradient may benefit from a higher weight for moisture, or modeling a forested landscape may make

Table 9
Categorization of observable patterns to derive exemplary start values for calibration.

Observable pattern	Calibration values
Dominant species	$F_s = 1000$
Less dominant species	$F_s = 500$
Least dominant species	$F_s = 100$
Species with a high abundance	$g_{\max} = 5.0$
Species with a medium abundance	$g_{\max} = 4.5$
Species with a low abundance	$g_{\max} = 3.5$

light availability more important and thus more heavily weighted, while other factors such as soil pH, if constant in these landscapes, are less heavily weighted because they do not play a strong role in differentiating the vegetation. Observations and data analyses of the observed species with their species EIVs at different sampling sites within the landscape can help evaluate the importance of different factors.

ODD 6. Input data

The model does currently not include input data that is loaded during the simulation run.

ODD 7. Submodels

As the model contains mandatory and optional submodels for vegetation and disturbance elements, we use a nested ODD approach here to describe each submodel in detail if used.

Herbaceous vegetation. The model for the forb and grass layer was first developed by Siehoff et al. [3] and used as a submodel by Hudjetz et al. [4]. Here we extend the existing model with a second set of growth dependencies.

Purpose. The forb and grass layer submodel is the foundation of the landscape and thus the underlying component for all subsequent succession. The model simulates vegetation growth based on environmental conditions and disturbances.

Process overview and scheduling. The herbaceous submodel is embedded in each cell of the landscape grid to calculate species' cover. All cells are recalculated each time step from the upper left corner to the lower right one. At each time step within all cells, each plant behaves in the following order (for an overview see Fig. 2, green boxes represent processes of the herbaceous vegetation):

First, a certain part of the cover of each plant dies creating available space within the cell. Mortality is implemented to allow the processes of competition to take place even when the whole space is used up. Without mortality, the plants could not grow (and thus compete) as soon, as the whole area is covered. The plants are not able to push each other out, but gain competitive power only by their realized growth under competition with the other plants into available (uncovered) space.

The growth of the species is then calculated as a function of its cover, its sensitivity to the given environmental conditions and land use (using EIVs), its maximal growth rate, and its factor for self-regulation. A part of the species' growth is transferred to the adjacent cells, simulating vegetative spread; seed dispersal over larger distances is not taken into account. This ingrowth into neighboring cells results either in additional growth of an already existing species or in a new species immigrating into the cell. If the sum of potential growth and ingrowth from neighboring cells of all species exceeds the available space within the cell, the available area is divided according to the species' potential growth, and a new realized growth is calculated. The competition between the different species takes place only in this step when the potential growth is recalculated to realized growth. The competitive strength of each plant is derived from the dynamic growth model by the relative weighting of the potential growth of each species.

At the end of each time step, the cover of all species is updated. From the cover of the dominant plants, the vegetation type of the cell is derived, which can be plotted into raster-maps.

Herbaceous vegetation submodel. The simulation of herbaceous species is divided into four submodels: a constant mortality model, a dynamic growth model that calculates the potential growth of the species based on its growth rate, and the competition model. These submodels and the equations used (Table 10) are described in the following sections.

Mortality. A fixed arbitrary mortality rate of 200% per year for all species is assumed to create available space. To obtain the corresponding mortality for each growth cycle, the annual mortality is divided by time steps. At the beginning of each growth cycle, the cover of each entity is reduced accordingly.

Dynamic growth model

Calculation of growth rate. The growth rate of each plant species is calculated according to its current cover, its maximal growth rate, its factor for self-regulation, and the local environmental dependencies (Eq. 1).

The values for maximum growth rate and factor for self-regulation need to be calibrated on vegetation data from the area under study. More information about data and scenarios used for calibration is given in Section 'Species parameterization'.

The environmental dependencies on the EIVs are implemented as two different types of control functions: the site condition control function and the land use control function. These control functions are then weighted to represent the importance of each environmental factor to the simulated landscape and the study site. Finally, an overall environmental growth factor is calculated from

Table 10
Equations used in the herbaceous vegetation submodel.

Eq.#	Description	Function	Source
1	Mortality	$M = \text{cover} \times 200\% \text{ a}^{-1}$	Siehoff et al. [3]
2	Growth rate	$g = g_{\max} \times \frac{F_j - (\frac{F_j}{x_{50}}) \times 100}{F_j} \times f_{\text{total}}$	Siehoff et al. [3], this paper
3	Control function for land use X and species j	$f(x) = (1 - \frac{EIV_{sj}}{9}) \times \frac{100 - SV_x}{100} + \frac{EIV_{sj}}{9}$	Siehoff et al. [3]
4	Control function for site condition X and species j	$f(x) = \begin{cases} \text{normal EIV, } e^{-\text{slope}_x \frac{(SV_x - EIV_{sj})^2}{9}} \\ \text{indifferent EIV, } e^{-\text{slope}_x \frac{(SV_x - EIV_{sj})^2}{9}} - Opt_x \end{cases}$	This paper
5	Weighting of control functions	$W_x = (2 - f(x))^{0.5}$	This paper
6	Total environmental dependency function	$f_{\text{total}} = \frac{\sum (W_x \times f(x))}{\sum x - \sum W_x}$	This paper
7	Potential growth	$(\frac{dc}{dt})_{\text{pot}} = g \times c$	Siehoff et al. [3]
8	Realized growth	$(\frac{dc}{dt})_{\text{real}} = g \times c \times \frac{\text{available space}}{\sum (\frac{dc}{dt})_{\text{pot}}}$	Siehoff et al. [3]

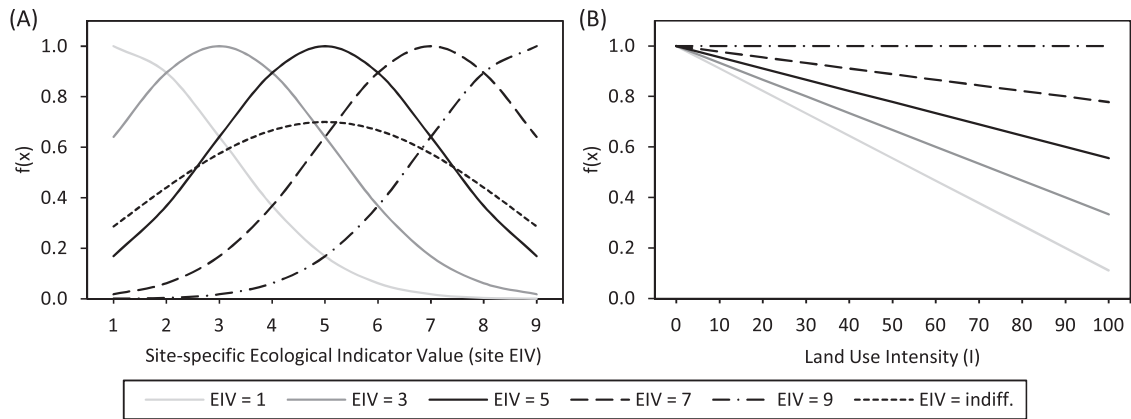


Fig. 5. Control functions for site conditions (A) and land use (B) at different species EIVs. (A) Control functions are calculated here for regular species EIVs with a slope of 1, and for indifferent species EIVs with a reduced slope of 0.3 and a reduced optimum of 0.6. (B) There are no indifferent species for the land use.

the weighted growth functions. How environmental factors influence growth rate has changed from the previous model version with the introduction of the second set of EIVs (see below). For a detailed description of how the species EIVs are obtained see ‘Species parameterization’.

Control function for site conditions. The control functions for site conditions are calculated as ecological tolerance functions (Eq. 4). The optimum value of 1 is reached when a species’ EIV is equal to the corresponding site EIV. Suboptimal conditions are indicated by values below 1 (see Fig. 5A). In addition, the slope regulates the width of the optimum curve, increasing or decreasing the sharpness of the ecological tolerance to an environmental condition. It therefore determines how strong the growth factor is reduced when species EIV and site EIV are not equal. In case an EIV is indifferent for a certain species, we modified the regular control function with the possibility to reduce the slope and the optimum. The reduced slope mimics the broader tolerance of the species. These modifications, as well as the regular slope, are specific to each EIV, but globally valid for all species.

Control function for land use. The control functions for the form of land use are calculated as linear sensitivity functions (Eq. 3). The degree of growth inhibition depends on the intensity of land use. The function $f(X)$ results in values between 0.1 and 1, decreasing the growth rate of species that are sensitive to the given land use (Fig. 5B). A value of 1 signifies that the species is not affected by the form of land use. *Total environmental dependence function and weights.* In an earlier version of the model, we calculated the environmental dependence by simply multiplying all the values of the environmental control functions. Typically, however, environmental dependencies are at suboptimal conditions, i.e., below values of 1. With three control functions, a typical value would be $0.7^3 \approx 0.34$, but introducing five more factors shifts the value in the example to 0.7^8 , resulting in a total value < 0.1 . This issue has previously been discussed in a forest gap model [42]. Therefore, we introduce here an alternative way to calculate the total environmental factor (Eq. 6). This approach uses the weighted means of the control functions (Eq. 5). It also introduces the possibility of weighting individual factors according to their ecological relevance to the current landscape and study site. These weights are global within the modeled environment and therefore the same for all species. They can be adjusted for different landscapes and are assessed during pre-configuration (see ‘Initialization’). When weighted equally, environmental factors play similar roles in the growth of species. When individual factors are weighted significantly higher, the growth curve shifts toward adaptation to those factors. This flexibility allows better calibration for a variety of landscapes with different dominating gradients.

Calculation of potential growth. The total potential growth of each species is the sum of potential growth within a cell and ingrowth from adjacent cells. Potential growth is calculated according to the species' growth rate and its cover (Eq. 7). This potential growth refers to the capability of a species to grow into an uncovered area. Since each cell is a homogeneous entity and no information about the distribution of species within one cell is given, potential growth is randomly split into the potential growth within the actual cell and to adjacent cells (see [Design concepts](#), 'Interaction'), where it is added to the total potential growth of the plant species.

Competition model - calculation of realized growth. Plant species interact by struggling for the available space. The share of available space that each species gets depends on its potential growth compared to the others. If the sum of the potential growth of all species exceeds the available area, the area is divided among the species according to their potential growth, i.e. the sum of growth within the cells and ingrowth from adjacent cells (Eq. 8).

This function simulates a 'simultaneous' growth of all species and their competition for space. The species with the highest potential growth will occupy the largest fraction of the available area, where potential growth is dynamically calculated as a function of cover, maximum growth rate, intraspecific competition, and sensitivity to the given environmental conditions '[Dynamic growth model](#)'.

This competition model acts in a way that the competitive vigor of a species does not only depend on its intrinsic strength, indicated by the parameters g_{\max} and F_S , but is strongly influenced by its tolerance of the prevailing environmental conditions as well as the applied form of land use. Two species with the same values for g_{\max} and F_S , but different EIVs will therefore behave differently according to the environmental factors.

Woody vegetation

Woody vegetation. Optional and not used in the current model setup.

Disturbance by wildlife

Disturbance by wildlife is used for *woody vegetation*. Therefore, it is not relevant to the current model setup.

Software improvements

Compared to the first version of the model [3], three major technical improvements have been implemented: version control, automated model testing, and variable landscape initialization. While the first two are primarily for the model development phase to ensure consistency and error prevention, the last one also has implications for the user in the application of the model.

As an important step in making model development traceable, we moved the model to the Git version control system. Changes to the model repository are now recorded in the form of commits, with comments and annotations. In the commits, we started using the keywords listed by Ayllón et al. [43] for maintaining model notebooks. Prior to the Git implementation, the extension with Ellenberg's EIVs described in this paper was implemented. The other software improvements were implemented using version control.

Another improvement to the model development phase was the implementation of automated model testing. Up to this point, the model had been developed in a straightforward manner for a specific landscape. The simulated results were manually checked for plausibility at the landscape level, with no automated test routines. We have now developed an automated routine to compare the model output at any time during development with the results of previous model runs. For these tests, we selected ecologically meaningful landscape scenarios from previous model runs to cover a wide range of settings. Model output for comparison included species cover and vegetation type information for all cells over the simulated time period. Differences were calculated for both image and text files. When the test script detected differences, we actively evaluated whether or not the code changes made were intended to affect the test scenario. In some cases, the changes in model behavior were intentional; in these cases, the valid test results were updated to reflect these model changes. This automated testing routine helped us track unexpected model behavior during the development process.

Finally, to allow a wide application of the model for different users, we made the landscape initialization variable. To do this, we have removed all hard-coded generic species specifications from the source code. Instead, processes are now completely dependent on initialization parameters. This was necessary for three main reasons: (1) it gives the model the flexibility to change vegetation entities based on landscape needs without changing the source code; (2) it allows transparency of all parameters and categorizations used by the model; and (3) it made the code cleaner and also increased the consistent application of the processes. For example, some processes, such as seed dispersal, were previously initialized only for the hardcoded entity names. Therefore, we changed the trigger for the processes to a Boolean parameter in global initialization tables so that the dependency for the respective entities could be initialized accordingly.

Two exemplary model applications for demonstration

The model is designed to simulate the development of a vegetation community under a set of environmental conditions. Thus, both tolerance to environmental conditions and intrinsic competitive strength determine the ability of herbaceous plant species to grow. Environmental tolerance is represented by the species EIVs described in the phytosociological literature, while competitive

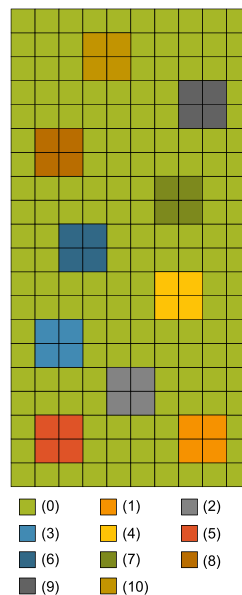


Fig. 6. Patchy test landscape. Different patch types: (0) surrounding open landscape; (1) dry, acidic and nutrient-poor grassland; (2) dry, calcareous and nutrient-poor grassland; (3) wet floodplain grassland; (4) acidic and nutrient-poor moorlands; (5) alkaline/calcareous and nutrient-poor moorlands; (6) woodland edge; (7) nonspecific woodland; (8) acidic and nutrient-poor woodland; (9) alkaline and nutrient-poor woodland; (10) alkaline and nutrient-rich woodland; for further information on patch types with site EIVs see Table 13.

strength is captured by two calibrated parameters, maximum growth rate (g_{\max}) and self-regulation factor (F_S), which account for fine-scale heterogeneity and simplify the remaining interspecific competition (for details on the design concept, see ODD). We designed two stylized model applications to demonstrate the model behavior for these two mechanics: a simulation of a landscape with patches of different environmental conditions (Test 1, ‘patchy landscape’) and the development of a grassland community under soil impoverishment by reducing the site EIV N-value (Test 2). An executable version of the model along with all initialization files, a start file for both tests and instructions on how to run the model is available online at (<https://github.com/gaiac-eco/LandS>). Both tests are designed to demonstrate how the model is used and that it produces meaningful results. For this purpose, we selected scenarios that are sufficiently simple that it is easy to predict the model’s output using reason alone.

Simulation of a patchy landscape with different environmental conditions (Test 1)

Preliminary model setup for Test 1

To test the part of growth based on environmental tolerance, we designed a patchy test landscape (Fig. 6) where ten different patches represent an ecologically viable combination of different environmental conditions (Table 11). Each patch type consisted of four cells, in a test plot of 10×20 cells, with each cell being 100 m^2 . The list of available herbaceous plants consisted of a wide range of ecologically diverse species and included one species that was typical for each type of patch (Table 12). For the simulation, the only difference between the species was their tolerance to the environment. All the other parameters of the plants were kept the same ($g_{\max} = 3.5$ and $F_S = 10,000$). Furthermore, the simulation was started with an equal cover of 1% for all species. Thus, growth differences depended only on the tolerance of a species to the environmental conditions of a cell. Our prediction was that in each patch only the most suitable plants would grow and eventually develop a high degree of cover.

Results for the ‘patchy landscape’ (Test 1)

The simulation of the patchy landscape showed that for all patches, the best adapted plant species eventually developed the highest cover (Fig. 7). For the surrounding cells with no particular environmental tendencies, *Lolium perenne* became the most dominant species, as expected, accompanied by a lower cover of *Bromus erectus*. One or two accompanying species were typical of all patch types and had a low abundance, mostly ranging between 5% and 15% cover. The accompanying species was mostly *L. perenne*, which is the species adapted to intermediate conditions and therefore plausible to have low growth in other patches representing environmental conditions at the more extreme end of the environmental gradients. However, its growth in woodland patches - where light availability was much worse for *L. perenne* - suggests that its presence in all patches may simply be due to the neighborhood interactions implemented. Each patch cell was adjacent to at least two surrounding cells with *L. perenne*, which ensured the continuous ingrowth from these neighboring cells. In woodland patches 7, 8 and 9, there was a small peak of *Poa nemoralis* next to the dominant species at the beginning, which makes sense as these patches are not ideal but somewhat suitable for this species. At the same time, the peak of *P. nemoralis* is missing in the last forest patch 10, because the difference in N values was too large in this plot. In patch

Table 11

Site parameterization: patchy experimental landscape with site-specific EIVs.

Patch number (#)	Site/Patch type description	Site EIVs				
		L	T	M	R	N
(0)	Surrounding: Grassland with no specific tendency towards moisture or nutrients	8	5	5	6	5
(1)	Dry grassland ^a , acidic and nutrient-poor	8	5	3	3	3
(2)	Dry grassland ^a , calcareous and nutrient-poor	8	5	3	8	3
(3)	Wet floodplain grassland ^a , nutrient-rich with no specific tendency towards soil pH	8	5	8	6	8
(4)	Moorlands ^a , wet, acidic and nutrient-poor	8	5	8	3	3
(5)	Moorlands ^a , wet, alkaline/calcareous and nutrient-poor	8	5	8	8	3
(6)	Woodland edge ^b , no specific tendency towards other factors	5	5	5	6	5
(7)	Woodland ^c , no specific tendency towards other factors	3	5	5	6	5
(8)	Woodland ^c , acidic and nutrient-poor	3	5	5	3	3
(9)	Woodland ^c , alkaline and nutrient-poor	3	5	5	8	3
(10)	Woodland ^c , alkaline and nutrient-rich	3	5	5	8	8

^a : open habitat in full light.^b : semi-shaded habitat.^c : fully shaded habitat; L: light value, T: temperature value, M: soil moisture value, R: reaction value (soil pH) and N: soil nutrient value.**Table 12**

Selected species with different species-specific EIVs for the patchy landscape, their ecological characteristics and the number (#) of the patch type where the species should, become dominant after some time. The EIVs are taken from plant sociological literature [12,44].

Species	Ecological characteristics	#	Species EIVs				
			L	T	M	R	N
<i>Lolium perenne</i>	Grass native to Europe and North Africa with medium site requirements, also widely distributed by anthropogenic seeding.	(0)	8	6	5	7	7
<i>Agrostis stricta</i>	Silicate and pioneer grassland characteristic species	(1)	9	7	2	2	1
<i>Bromus erectus</i>	Characteristic species of meager, calcareous, dry and semi-dry grasslands.	(2)	8	5	3	8	3
<i>Alopecurus geniculatus</i>	Characteristic species of floodplain grasslands, which are characterized by alternate periods of drought and flooding.	(3)	9	6	8	7	7
<i>Eriophorum angustifolium</i>	Acidophilic, characteristic species of acidic bogs.	(4)	8	x	9	4	2
<i>Carex davalliana</i>	Characteristic species of calcareous fen communities, representing alkaline or calcareous and low-nutrient wetland habitats.	(5)	9	4	9	8	2
<i>Poa nemoralis</i>	Half-shade plant, characteristic species of mixed deciduous woods, especially in open areas.	(6)	5	x	5	5	4
<i>Carex sylvatica</i>	Characteristic species of moderately dry to moderately moist central European broadleaf forests.	(7)	2	5	5	6	5
<i>Luzula luzuloides</i>	Acidophilic and characteristic species of the association of acidic red beech forests.	(8)	4	x	5	3	4
<i>Carex alba</i>	Distinctive species of lime-beech and pine forests on dry soils.	(9)	5	5	4	8	2
<i>Campanula trachelium</i>	Distinctive species of lime-beech forests on eutrophic and moderately dry to moderately moist soils.	(10)	4	x	6	8	8

L: light value, T: temperature value, M: soil moisture value, R: reaction value (soil pH), N: soil nutrient value and x: indifferent ecological behavior of this species.

9, *Carex alba* was the predominant species, with *Carex sylvatica* also strongly represented at the beginning, but declining in the long term, while *C. alba* increased steadily in cover.

In summary, Test 1 showed the successful establishment of the best-adapted species in each patch, as previously hypothesized. Semi-adapted species that grew alongside the best-adapted species declined and died out over time. Additionally, this simulation experiment showed the impact of the ingrowth mechanism from neighboring cells. Although this mechanism was not essential for this experiment, it is important for the general application of the model when the coexistence of communities leads to continuous competition along the edges, resulting in overlapping areas.

Simulation of a grassland community under soil impoverishment (Test 2)

Preliminary model setup Test 2

Our goal for Test 2 was to use an application example to demonstrate the functionality of a calibrated community under change. At the same time, it allowed us to examine the calibration process for two closely related communities. We designed two forms of a grassland community: One representing a fertilized lowland meadow and one representing an unfertilized lowland meadow (Table 14). These community forms were based on the plant community “Arrhenatheretum elatioris” (named after the characteristic dominant species *Arrhenatherum elatius* [12,44,45]). The fertilized meadow represents a nutrient-rich form of this community with a high proportion of stand-forming grasses. The unfertilized meadow is a less nutrient-rich form with a lower proportion of grasses

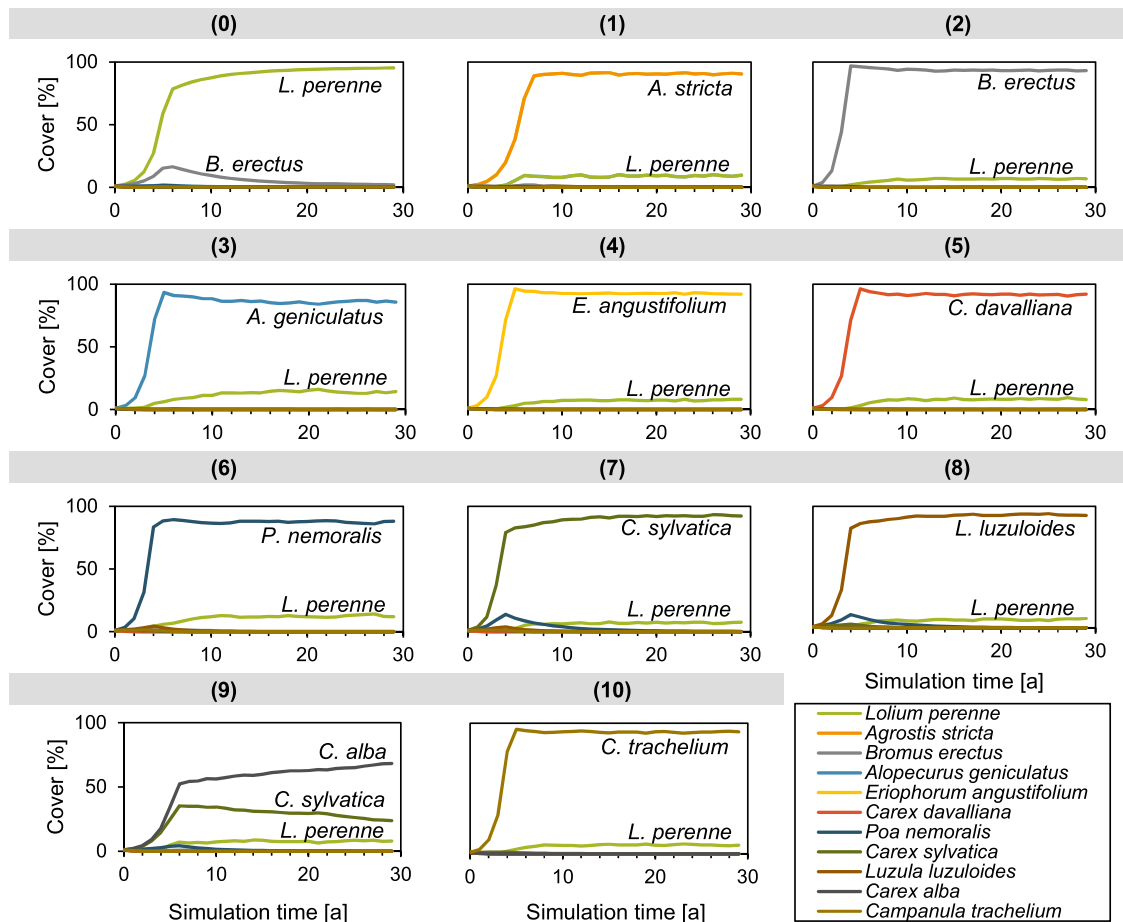


Fig. 7. Average species cover in each patch type (consisting of 4 cells) over time. Different patch types: (0) surrounding open landscape; (1) dry, acidic and nutrient-poor grassland; (2) dry, calcareous and nutrient-poor grassland; (3) wet floodplain grassland; (4) acidic and nutrient-poor moorlands; (5) alkaline/calcareous and nutrient-poor moorlands; (6) woodland edge; (7) nonspecific woodland; (8) acidic and nutrient-poor woodland; (9) alkaline and nutrient-poor woodland; (10) alkaline and nutrient-rich woodland; for further information on patch types with site EIVs see [Table 13](#) and for species characteristics see [Table 14](#).

and more flowering plants. In general, the species present could be divided into two groups: those present in only one of the two community forms and those that were present in both. The size of the test plot was 10×10 cells with each cell being 100 m^2 .

Each community form was calibrated to mimic the expected cover of the different species under the respective environmental conditions ([Table 13](#)). To mimic a general availability of species, those species that only occurred in one form were still initialized with a cover of 0.01% in the other form. During calibration, we changed the species parameters F_S and g_{\max} until the cover of all species in both communities remained constant at the predefined level over the calibration period of 30 years. In other words, we calibrated until the specified cover equilibrium was reached (see the ‘[Design Concepts](#)’ and ‘[Initialization](#)’ sections of the Model Description for a detailed description of the calibration process.).

To also test if the model can predict the transition between the two community forms if key environmental variables are changed, we started simulations with the species composition of the fertilized meadow, but changed the environment to nutrient-poor conditions. We then predicted that the species composition of the fertilized meadow would change into the species composition of the nutrient-poor unfertilized meadow.

Results for the grassland community under soil impoverishment (Test 2)

The successful calibration of the considered community forms and the confirmation of the transition from one to the other after changing the environmental conditions are the main results of this simulation experiment. [Fig. 8A](#) and [B](#) show the successful calibration of the nutrient-rich and nutrient-poor forms of a lowland meadow after a calibration period of 30 years. For both communities it was possible to calibrate the equilibrium state towards the predefined cover for all species. Those species that were initialized at low cover for general availability (e.g. *Knautia arvensis* in the nutrient-rich form) disappeared completely after a few years in the forms to which they did not belong. The most abundant species, *Arrhenatherum elatius*, was calibrated to be stable at different cover levels in the fertilized and unfertilized meadow – 60% and 30%, respectively. In the calibration scenario, each cell contained a different

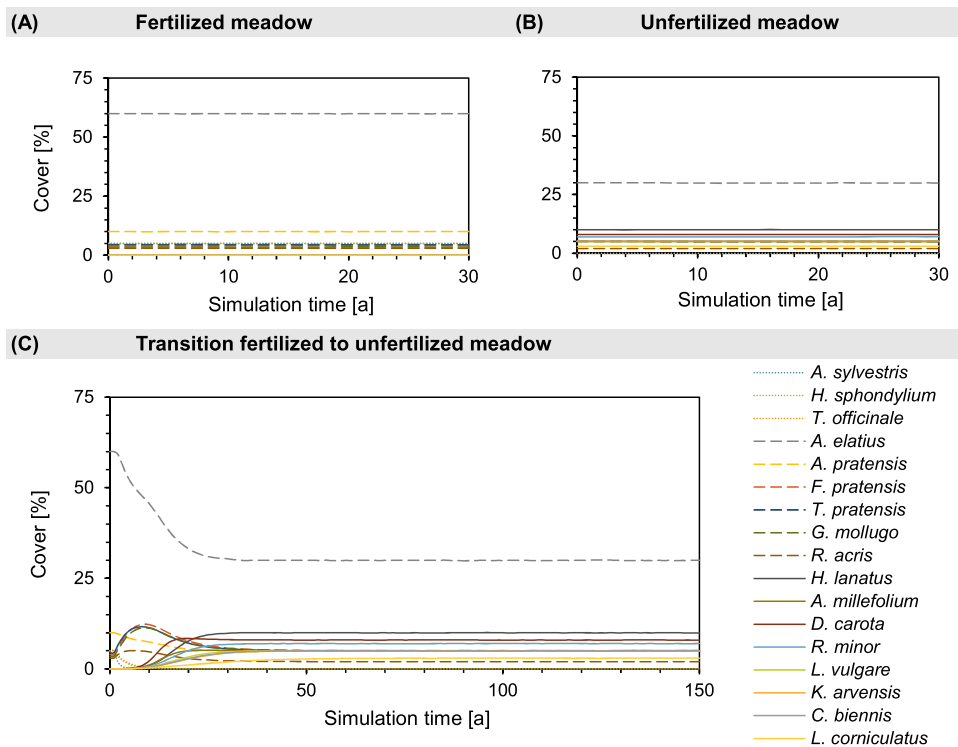


Fig. 8. Average species cover in the test plot. Calibrated equilibrium states of the grassland community in the fertilized (A) and unfertilized form (B) and the simulated transition from fertilized to unfertilized after the initial calibration (C).

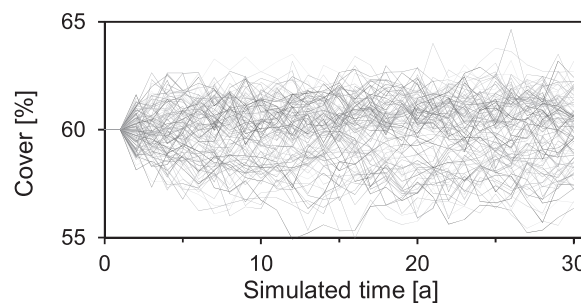


Fig. 9. Cover development of *Arrhenatherum elatius* in each of the 100 cells of the test plot for the fertilized meadow after the final calibration.

species cover and therefore a different community composition, while the average cover for each species in the test plot was stable. This is illustrated in Fig. 9 using *Arrhenatherum elatius* in the fertilized meadow as an example. While the average cover of *A. elatius* in this simulation plot was stable at 60%, the individual cells varied from 55% to 65%. This shows how each cell contains a dynamic equilibrium of varying species cover, which also reflects community diversity.

Most of the transition from fertilized to unfertilized meadow took about 25 years (Fig. 8, C). Some species, such as *Festuca pratensis* or *Galium mollugo*, initially developed a spike and increased their respective cover until competitive pressure from other species increased and the spiking species decreased to the expected level of the unfertilized community form. Only a few species, such as *Lotus corniculatus*, took longer to reach their equilibrium cover level and thus had little effect on the cover of the whole community. Both the initial spike and the longer transition period for some species may not necessarily reflect reality and could be artifacts. Therefore, the preliminary calibration of the model is usually based on empirical data of time-for-space substitution collected at the study site to confirm the main vegetation dynamics or to improve the simulation results by further calibration.

In addition, the current model only allows an instantaneous change of environmental conditions at the beginning of the simulation, i.e. for the transition simulation we changed the N-value from 8 to 5. It might be useful to implement the possibility of a gradual transition period with continuous changes in environmental conditions to simulate these transitions even more realistically in future model versions.

Table 13

Site EIVs for the patchy experimental landscape with (0) representing a nutrient-rich form of a lowland meadow and (2) a nutrient-poor form.

#	Site/Patch type description	Site EIVs							
		L	T	M	R	N	C	G	TR
(0)	Lowland meadow (fertilized)	8	5	5	6	8	75	1	1
(1)	Lowland meadow (unfertilized)	8	5	5	6	5	75	1	1

#: community form number; L: light value, T: temperature value, M: soil moisture value, R: reaction value (soil pH) and N: soil nutrient value.

Table 14

Exemplary species with different EIVs. Single species cover for each community form: (0) nutrient-rich, fertilized meadow with a total cover of 100.08% and (1) nutrient-poor, unfertilized meadow with a total cover of 100.03%.

Species	Cover [%]		Species EIVs								g_{\max}	F_s
	(0)	(1)	L	T	M	R	N	C	G	TR		
<i>Anthriscus sylvestris</i>	5	0.01	7	x	5	x	8	7	3	3	3.81	42
<i>Heracleum sphondylium</i>	5	0.01	7	5	2	x	8	7	3	3	5.94	64
<i>Taraxacum officinale</i>	5	0.01	5	x	5	x	8	8	7	7	6.361	63
<i>Arrhenatherum elatius</i>	60	30	8	5	5	7	7	6	3	3	5.336	201
<i>Alopecurus pratensis</i>	10	5	6	x	6	6	7	7	4	4	5.33	33
<i>Festuca pratensis</i>	4	5	8	x	6	x	6	6	4	6	4.255	105
<i>Tragopogon pratensis</i>	4.5	5	7	6	4	7	6	6	2	2	4.306	87
<i>Holcus lanatus</i>	0.01	10	7	6	6	x	5	6	4	4	4.52	106
<i>Achillea millefolium</i>	0.01	5	8	x	4	x	5	7	4	5	4.117	45
<i>Crepis biennis</i>	0.01	5	7	5	6	6	5	6	2	2	4.37	71
<i>Knautia arvensis</i>	0.01	5	7	6	4	x	4	5	3	2	4.95	72
<i>Daucus carota</i>	0.01	8	8	6	4	x	4	6	3	4	4.711	58
<i>Rhinanthus minor</i>	0.01	7	7	5	4	x	3	5	8	3	5.24	80
<i>Leucanthemum vulgare</i>	0.01	5	7	x	4	x	3	6	3	4	4.825	64
<i>Lotus corniculatus</i>	0.01	3	7	x	4	7	3	6	4	4	4.65	66
<i>Galium mollugo</i>	3.5	5	7	6	4	7	x	7	3	3	3.941	88
<i>Ranunculus acris</i>	3	2	7	x	6	x	x	6	5	6	4.314	32

L: light value, T: temperature value, M: soil moisture value, R: reaction value (soil pH), N: soil nutrient value and x: indifferent ecological behavior of this species.

Discussion and conclusions

Compared to its precursors, the model now includes important environmental factors such as light availability, temperature, soil moisture, soil pH, and soil nutrients. We believe that the inverse use of EIVs in the LandS model serves as a viable tool to simulate vegetation development using the vast amount of empirical information processed in EIVs. This can help provide more realistic predictions of species composition when simulating different landscapes to support conservation and restoration decisions.

Although validation is difficult for complex vegetation models due to unavailable data, our stylized tests showed that the LandS model simulated simple tasks as expected, which is important to build confidence in such a complex model. Species distributions evolved under different environmental conditions in a patchy landscape according to species EIVs. Furthermore, a set of calibrated species showed that the species composition of a fertilized meadow community evolved towards its unfertilized counterpart after environmental conditions were changed.

In our stylized scenarios, we followed the example of Carter et al. [15] who applied their tiger homerange model to a map of prey density in a national park in Nepal. It was impossible to “validate” their model regarding the distribution, shape, and size of homeranges because such data do not, and may never, exist. Still, to demonstrate that the model predictions of the response to prey density made sense, they applied the model to an artificial gradient of prey density. We tried to do the same approach here. This is partly because full validation, as physicists use the term, is rarely, if ever, possible in ecology. Moreover, in the ecological literature, validation is often confused with verification, which is usually calibration, i.e. the model is forced to mimic certain observations [46]. Even so, validation based on multiple data sets with continuous time series of different environmental conditions would be desirable and in principle possible, but was beyond the scope of this article.

A model executable with a user manual and initialization files for the stylized tests are available online at <https://github.com/gaiac-eco/LandS>. Several software improvements have made the development process more verifiable and the model application more flexible. The user can now freely change species and vegetation types in the initialization files to apply the model to different landscapes.

Several limitations must be considered when using the model for a study area/landscape. The most important limitation is the potential lack of species-specific EIVs that can be found in the literature. These species EIVs are primarily available at the national level, such as in Germany [12], the United Kingdom [47], the Czech Republic [48], or in a recent study for all of Europe [40], but are scarcely available outside of Europe. Furthermore, with the incorporation of the new set of Ellenberg EIVs, the model is not limited to managed grasslands, but can be applied to different landscapes. For example, the model can now be set up to simulate dry or wet grasslands. Conceptually, however, the model is limited to landscapes with environmental gradients represented by the EIVs. It has not

been tested in extreme environments, such as high alpine vegetation, coastal vegetation, or floodplain vegetation, which may depend on other factors, including erosion or flooding regimes that may not be well represented by the existing set of EIVs. In addition, while we have shown in Test 2 that the model can accurately represent species distributions under a wide range of environmental conditions; the model is designed to be used on a small scale for specific study areas to simulate species composition. In study areas, differences in site characteristics are usually limited, so the model was equipped with a global weighting of environmental factors. In those rare cases where there are too many different dominant environmental factors in a study area, it may be necessary to subdivide the study area and configure separate models with different weights. Finally, the model relies on constant competition among species to coexist, and may not adequately simulate rare species that occur only occasionally throughout the study area, or pioneer communities that rely on individual species adaptation to the harsh environment rather than community competition mechanisms.

Besides the limitations of the model discussed above, the biggest hurdle to its application is the process of calibration during the pre-configuration. When simulating not only species distribution, but also species composition, it is essential to obtain meaningful results. Since this step is done manually, it can be quite challenging. Therefore, other more automated approaches to calibration may be needed in the future to make the application of the model even more applicable and user-friendly.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used DeepL Writer in order to improve language and readability. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Quintana Rumohr: Conceptualization, Methodology, Software, Writing – original draft, Visualization, Validation. **Volker Grimm:** Writing – review & editing, Supervision. **Gottfried Lennartz:** Conceptualization, Validation, Funding acquisition, Supervision. **Andreas Schäffer:** Writing – review & editing, Supervision. **Andreas Toschki:** Conceptualization, Validation, Writing – review & editing. **Martina Roß-Nickoll:** Conceptualization, Writing – review & editing, Supervision. **Silvana Hudjetz:** Methodology, Conceptualization, Software, Supervision.

Data availability

We have shared the link to the data and the executable. We have no permission to share the source code.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.mex.2023.102486](https://doi.org/10.1016/j.mex.2023.102486).

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