Generic process-based plant models for the analysis of landscape change

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Abstract: The analysis of landscape change impacts on community composition and dynamics is difficult for species rich plant communities, because of their high complexity. One approach to deal with this challenge are generic process-based models. In these models, the species are described by a common set of parameters and functional responses. Thus, they allow both the integration of knowledge on key processes, and a common description for several ecological patterns. An important aspect of these models are trade-offs in the species' physiological and life-history traits, which prevent 'super-species' that dominate under all environmental conditions.

We compare process-based models with two other model types that have been applied to similar ends – statistical habitat models, and phenomenological population models. These process-based models come at the price of an increased number of parameters for an individual species. However, a description of the interactions between species, which has proven difficult to incorporate in statistical habitat models, or requiring excessively many parameters in phenomenological population models, can be included easily. Finally, processed-based models produce a rich set of patterns on several organizational levels that can be compared to empirical observations, and thus be used for model calibration and validation.

The approach is illustrated with a case study of Southern African plant communities. The investigated semi-arid landscapes are characterized by high stochastic fluctuations in population sizes. These fluctuations may in the short term mask the effects of environmental or land use change, and models allow to assess likely long-term consequences. Questions pertinent to the management of these landscapes include the effect of grazing on the diversity of the plant communities and the impact of climate change.

Keywords: Landscape change; modelling; generic; process-based models; species richness

1 INTRODUCTION

The analysis of the effects of landscape change on species rich plant communities has received increased interests over the last years. Drivers of landscape change are climate change or changes in management practices.

In pasture landscapes, for example, some traditional management systems have become economically unsustainable [Kleyer et al., 2002]. Consequently, management alternatives are being sought that are both economically feasible and acceptable in their effect on the plant and animal communities (see for example, the MOSAIK project, [Kleyer et al., 2002]).

Common challenges to the assessment of the effect of landscape change are long time scales and transient dynamics, the need to assess a multitude of management options, and high species diversity.

In the following, we will first compare three model approaches for the assessment of landscape change on plant communities. We then exemplify the approach of generic, process-based models in more detail for a Southern African succulent plant community, where the impact of spatial and temporal variation in water availability as well as that of different grazing regimes on species richness is investigated. In the last two sections we discuss the opportunities and challenges of the process-based modelling approach, and draw conclusions.

2 MODEL APPROACHES

In this section we present three approaches to assess the likely impact of landscape change, in the order of increased structural complexity: statistical habitat models, phenomenological population models, and generic, process-based ('mechanistic') models.

2.1 Statistical habitat models

Statistical habitat models quantify the habitat requirements of species based on presence/absence records or density estimates of the species, and information on the environmental conditions at the investigated sites. Frequently used statistical methods are generalized linear models, generalized additive models or classification trees [Austin, 2002].

When landscape change can be related to changes in the environmental variables used in the construction of the habitat models, changes in the spatial distribution of suitable habitat as a consequence of landscape change can be predicted. Usually, separate models are developed for different species, and the community response is assessed as the sum of the individual species' responses.

Advantages. An important advantage of statistical habitat models is that, given available empirical data, they are quickly to develop, and that there are tools to quantify uncertainty in the predictions (though they are based on certain model assumptions that need not be fulfilled).

Problems. The models do not explicitly incorporate the dynamics of the system and assume usually that the observed patterns of species occurrences reflect an (quasi-)equilibrium state, given the values of the explanatory variables. Temporal dynamics can only be captured in a phenomenological way by explicitly incorporating a time variable such as time since last disturbance.

It is usually difficult to develop models for large sets of species, because many species are rare, such that there are few presence records to construct the statistical models from. As a rule of thumb, there should be a minimum of ten occurrences per explanatory variable used in a logistic regression model. Otherwise, there will be high uncertainty in model parameters and predictions.

In addition, models assume that the occurrences of different species do not interfere with each other.

Where the interaction of species plays a key role in determining the presence or relative abundance of the species, the predictions from models neglecting competitive effects may be misleading.

Finally, it would often be useful to have a prospective assessment of management alternatives. However, extrapolating from correlational models to new situations is problematic.

2.2 Phenomenological population models

Dynamic population models address the issue of transient dynamics initiated by landscape change. This is true for phenomenological as well as process-based models. Phenomenological models here refers to those models that do not attempt to incorporate the mechanism underlying the observed phenomena, but focus on capturing key aspects of the observed dynamics. The value of model parameters are usually assigned by fitting the model to observed data. Matrix models or models of the Lotka-Volterra type belong to this class.

Advantages. There exist a lot of experience with phenomenological models, and they tend to be structurally fairly simple. Therefore, they can be implemented and analyzed reasonably quickly. These models do not need many parameters for an individual species.

Problems. Parameterization of the models poses a key problem. Estimation of competition parameters is difficult. In addition, the number of required competition parameters quickly grows as the number of modelled species increases. If only pairwise interactions are included, the number increases quadratically in the number of species. Usually, it is not feasible to collect data for many species, so a few species representing different functional groups are selected. Also, it is necessary to have information on changes of the parameter values under the different landscape change scenarios. One option is to model how the values of the parameters change with altered land use, i.e. to develop a model of the relationships of species model parameters with the land use characteristics. One example of such an approach, where the parameters in a matrix population model of a soil mite species are related to different levels of temperature and soil contamination, is given by Stamou et al. [2004].

2.3 Process-based models

In process-based models, species are described by morphological, physiological and/or life-history traits, and the model explicitly describes how resource uptake (e.g. water, nutrients, light) translates into population growth. An example of this approach is Tilman's ALLOCATE model of grassland plant communities, where plants compete for nutrients and light, and depending on their allocation strategy for photosynthates (roots, stem, leaves) face trade-offs that lead to different relative competitiveness under varying resource levels [Tilman, 1988].

Advantages. Process-based models in general need more parameters to characterize a single species than phenomenological models. However, because the interactions between species are the outcome of the modelled processes (water and nutrient uptake, light interception), additional parameters that describe the interactions are not necessary. The number of model parameters therefore increases only linearly with the number of model species.

Physiological and life-history traits determine how plant species respond to landscape change. By modelling the link between species traits and population dynamics, process-based models allow to investigate the effect of landscape change on a range of species for which the relevant traits are known. This way, they tie in the database projects on species traits with the understanding of landscape change effects. Modelling of the processes helps to identify key parameters that have to be estimated. In addition, this can help to identify traits that can easily be measured (with low time and money investment), or that can be reliably related to the traits that are directly relevant on the process level, but that are difficult to observe or quantify. This approach has been successfully applied in modelling the dispersal of plant species. Based on mechanistic models, a minimum set of plant and seed characteristics could be established, that together with information on the wind distribution allow to predict the distribution of primary dispersal distances [Tackenberg, 2003].

Process-based models produce patterns at several hierarchical levels. This can be used in model parameterization and validation [Grimm et al., 1996].

Problems. Process-based models aim at a controlled increase in complexity, i.e. to strike a balance between generality and specificity. However, the increased complexity in the model structure comes at a cost.

Often, these models put a high demand on computing resources. Therefore, it may not be possible to explicitly model large stretches of the landscape, but rather only smaller patches. In order to scale to the whole landscape, model simplifications have to be carried out. Yet, such aggregated descriptions also increase clarity and understanding of the model behavior.

Although many species traits that are represented in the model can be measured in principle in the field, they may not be available for the majority of the species. In addition, complex model structure allows for a rich set of dynamics, leading to substantial uncertainty in model predictions.

Finally, process-based models pose a greater challenge to the software development than the other approaches discussed. Dissemination and reuse of models or model components between research projects is difficult.

In the following section we present an extended example of a process-based plant model.

3 EXAMPLE: MODELLING A SEMI-ARID SUCCULENT PLANT COMMUNITY

The arid winter-rainfall region of the western Richtersveld (South Africa) harbors an unusually high plant species richness, with species densities approaching 40 perennials per 100 m^2 [Jurgens et al., 1999]. Although a wealth of processes have been invoked to explain biodiversity in plant communities, the relative importance of different factors remains poorly understood.

3.1 Model description

The model calculates plant water uptake and transpiration, carbon assimilation and respiration on a daily basis. The water and carbon cycles are coupled via the plant's water use efficiency. Immature plants allocate carbon to the compartments roots, succulent tissue, and leaves. Once plants have reached their size at maturity, all net carbon gain is invested in seeds. In times of drought, plants rely on water stored in succulent tissue for transpiration. If the carbon balance is negative, the plant suffers from increased mortality. At the level of the population, the key processes are germination, sur-

vival of individuals and seeds in the seed bank, and seed production. They are calculated on an annual basis. The germination rate and the seed survival rate are constant in the model. However, plant survival and seed production depend on environmental conditions, in particular rainfall and potential evapotranspiration.

The strategy types, i.e. 'species', differ only in the values of five parameters that define (a) biomass allocation to roots, leaves, and storage (effectively two parameters, as the sum of the fractions has to sum to 1), (b) size at maturity, and (c) germination rate and date. Allocation to the three compartments roots, leaves, and storage is assumed to be independent of total plant biomass. The key environmental state variable is soil water content. Soil water content increases through rainfall, and decreases through plant water uptake, drainage and evaporation. The soil is characterized by soil depth, saturation water content, and water content at permanent wilting point. An overview of the main model processes is shown in Figure 1.

The model takes as environmental input sequences of daily rainfall and potential evapotranspiration. With few exceptions, parameters in the plant model can be measured in the field. Parameter values were based on the literature and represent typical values for plants of semi-arid regions, or values chosen in similar process-based models of plant communities. The values of three parameters relating to drought mortality and water storage were selected such that some viable plant strategy types were possible under the most arid scenarios investigated.

The process-based model of plant growth and survival is combined with a spatially explicit individual-based population model. The simulated area is subdivided into square sites, with a side length of 25 cm. The maximum number of plants per cell is six, however, the roots and leaves of plants can extend over several cells.

The population processes (seed production, dispersal, germination) operate on annual time steps. Seeds are dispersed according to a log-normal dispersal kernel. Competition during germination is modelled as lottery competition.

Plant growth and survival are calculated in daily time steps. Established plants compete for water in areas where roots overlap. Shading effects are not taken into account. The state of individual plants is given by their age (i.e. cohort assignment), mass, amount of water in succulent tissue, and the time
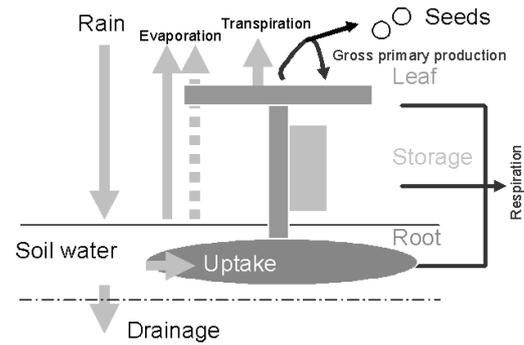

Figure 1: Overview of the key model processes. Light grey arrows indicate water fluxes, black arrows represent carbon fluxes.

period over which the growth rate has been negative.

3.2 Simulated environmental change scenarios

An area of 10 times 10 m, corresponding to the dimensions of long-term observation sites established in the Richtersveld, was simulated. Starting from a situation with no established plants and a seed bank containing equal seed densities of all model species, the population dynamics were simulated for a period of 200 years. Within this time frame, the community dynamics reached an equilibrium state. The model species pool consisted of 36 species, comprised of 12 different allocation strategies and 3 sizes at maturity.

Rainfall. With respect to water availability, we present results on the relevance of the following two factors: (a) Spatial heterogeneity of water availability through redistribution of precipitation, evaluated at three levels (no redistribution, moderate redistribution, strong redistribution). The total amount of precipitation was held constant (see Figure 2).
(b) Temporal heterogeneity of water availability through fluctuations in precipitation, evaluated at three levels (a standard scenario that corresponded to the model parameters of the Interactive South Africa Rain Atlas for the study region, an increased level of seasonality as well as a reduced level of seasonality). The mean annual rainfall was held constant at 70 mm by adjusting the mean daily probability of rainfall. In all scenarios, dew fall was simulated as a precipitation event with low magnitude (0.2 mm) and constant probability (see Figure 3).
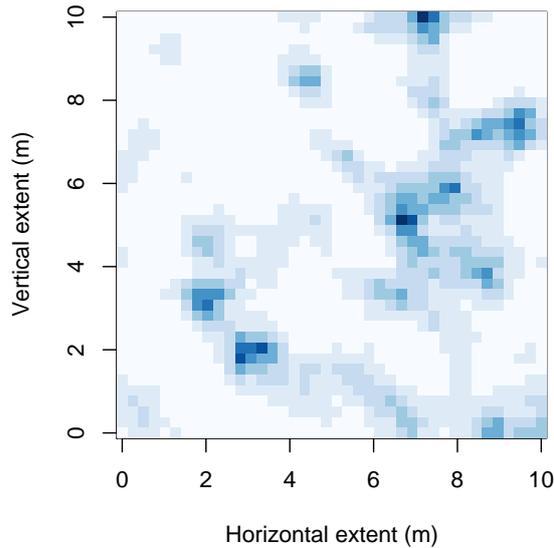
Figure 2: Water redistribution map for the most heterogeneous scenario. Darker colors correspond to increased water availability. The total amount of available water is identical in all redistribution scenarios.

Figure 3: Expected daily precipitation for three precipitation scenarios for the Richtersveld site, including dew.

Grazing. The expected proportion of a given plant to be grazed was held constant across species, i.e. no preferences of livestock for certain species were modelled. Grazing was applied spatially homogeneously in the model. The grazing intensity, i.e. the total amount of biomass removed annually, was constant over time, and two levels of intensity were simulated. A second aspect of the investigated grazing regimes are the frequencies, i.e. the number of times grazing occurred during a year. Three levels of grazing frequencies were simulated.

3.3 Results

Rainfall. The influence of rainfall variability and spatial water redistribution on species diversity is shown in Figure 4. Shannon diversity H was calculated as $H = -\sum_{i=1}^{N} p_i \ln p_i$, where p_i is the proportional abundance of species i, and the sum is over all N species. It is evident that water redistribution exhibits a strong positive effect on community diversity at the studied scale. The maximum diversity at a given level of temporal variability in rainfall is reached at the maximum level of heterogeneity. There is a positive effect of redistribution on diversity. The effect of spatial heterogeneity is to provide spots with increased water supply and thus improved growing conditions, allowing for a larger set of species to coexist. Temporal heterogeneity, on
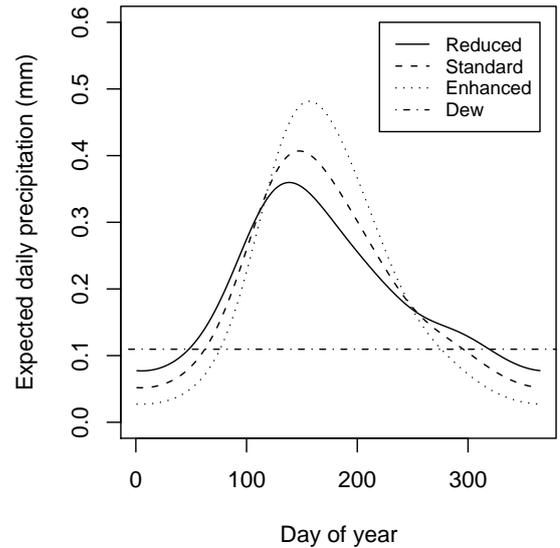
the other hand, does not have a positive influence on diversity in the studied form. The more aggregated the rainfall is in time, the longer the periods of unfavorable growing conditions. Since the plants in the system are 'living on the edge', the increased variability appears to increase the overall extinction risk to an extent that it outweighs the potentially positive effect of temporal niche differentiation.

Grazing. Grazing reduced the number of surviving species. Only the dominant species in the scenario without grazing were viable under grazing pressure. As expected, grazing intensity was overall more important than grazing frequency. However, the effect of grazing frequency changed under low and high grazing pressure. While a higher frequency had a marginally positive influence under low grazing pressure (Figure 5), it exerted a strong negative effect under high grazing pressure, where species only survived if grazing occurred infrequently.

4 CONCLUSIONS

We argue that generic, process-based plant simulation models, though no panacea, can be expected to become a key tool in the assessment of landscape change. These models are able to meet the challenges posed by the assessment of future landscape change – long time scales and transient dynamics, the need to assess a multitude of manage-
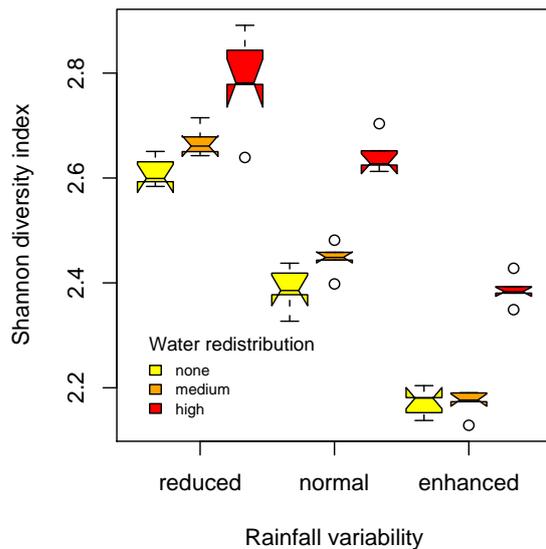
Figure 4: Notched boxplots showing the relative effect of rainfall variability and water redistribution on community diversity. Each boxplot represents 5 replications.

Figure 5: Effects of grazing frequency on community diversity at two levels of grazing intensity.

ment options, and high species diversity. They can be geared to specific environmental situations, thus allowing model results to be directly compared to specific patterns observed in the field. Additionally, key findings are likely to generalize to other ecosystems of similar environmental conditions, because of the models' generic structure.

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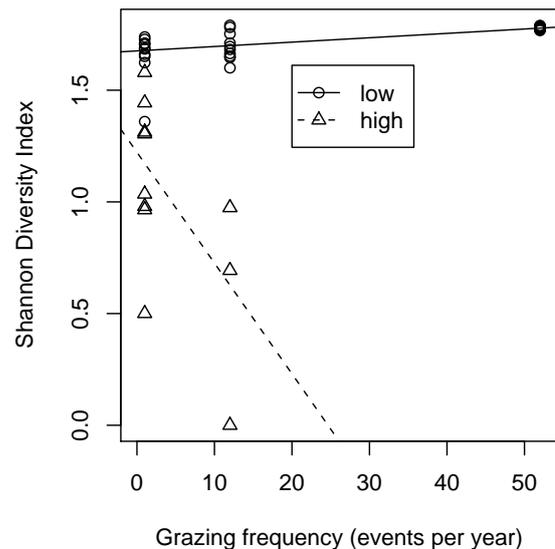Jurgens, N., I. H. Gotzmann, and R. M. Cowling. Remarkable medium-term dynamics of leaf succulent mesembryanthemaceae shrubs in the winter-rainfall desert of northwestern namaqualand, south africa. *Plant Ecology*, 142:87–96, 1999.

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