



Modelling succession from pasture to forest in time and space

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Abstract: A set of coupled logistic growth equations is used to simulate the temporal replacement of vegetation (species or groups). Simulation results approximately reproduce two time series of 415 to 585 years obtained from field investigations in the Swiss National Park (SNP). Although the shape and the fit of the simulated curves are convincing, the assumption that all species must be present at the beginning of the simulation and also the absence of movement in space are not realistic. To overcome this, the model is extended to include space and is used for simulating the succession in an abandoned pasture of the SNP. As long as only vegetation change in all individual quadrats is simulated separately, vegetation boundaries remain unchanged over the simulated period of 400 years. When species are allowed to move between quadrats, the spatial pattern changes over the simulated time, and field data can be taken as boundary conditions to realistically simulate change. It is concluded that spatial dynamics must be taken into account to model long-term succession.

Nomenclature: Hess et al. (1976).

Abbreviation: SNP - Swiss National Park.

Introduction

Succession

Filed data of succession over long time periods are rare (Foster and Tilman 2000). For the investigation of long-term change, the chrono-sequence approach sometimes offers the only alternative to excessively long observation time. In a chrono-sequence, trends observed in plots from different locations are averaged. It is therefore also known as space-for-time substitution (Pickett 1989). The approach involves several well-known risks. The most obvious is that the ecological conditions in two different plots are often close, but never identical. Despite many potential pitfalls in the interpretation of results, the fact that rates of change in succession as well as the direction are directly related to the initial conditions has been shown in various investigations (Myster and Pickett 1994), a prerequisite of space-for-time substitution. The data I analyse here are of this type. We took relevés from 59 plots, where the earliest observations started in 1917 until present with time intervals of 5 years. Using space-for-time substitution we obtained succession series of up to 585 years (Wildi and Schütz 2000). Such a series cannot be verified in practice or even observed directly. Therefore, I was seeking a model that would explain past

observations and the actual state of the system and predict its future dynamics.

Models

It is relatively easy to find mathematical functions that reconstruct short-term dynamics. When field data from permanent plots are inspected, simple temporal patterns can be detected, such as linear increase, linear decrease, constancy or undirected fluctuation of the parameters (Huisman et al. 1993, Schütz et al. 1998). A straightforward method to describe transitions in multi-state systems is based on a Markov-process (Horn 1976, Usher 1981, 1992, Orłóci et al. 1993, Balzter 2000). It merely assumes that the components involved change type according to a set of probabilities, the transition coefficients. Time series data alone do not yield a unique Markov model (Orłóci et al. 1993), but including some straightforward assumptions, like the existence of a mass-effect, the transition matrix is easily approximated from permanent plot data. Markov models work in many cases, but they reach their limits when the systems properties and hence the transition probabilities change. This is the case when species vanish, and even more, when new species enter the system. In my data, a linear Markov process successfully simulates changes within the range of up to one half-

change (Hill and Gauch 1980), but then it approaches a stationary stage and no further development occurs.

A classical way of simulating succession is by the use of gap models (Botkin et al. 1972, Shugart and West 1977, Shugart 1984, Bugmann 2001). In these, the life cycle of individuals (trees) is simulated and different competition behaviour causes species performance to change. Stand development in a great number of model plots is averaged. More advanced versions use a distribution based model of populations, deterministically computing height classes (Lischke and Zierl 2002). As our community starts out as grassland, a gap-model would have to deal with plants of vastly different sizes. Another problem is the invasion of new species (Price et al. 2001): all species need to be present in all plots from the start, if only with minimal cover values. Although this may not be realistic, it suggests that the introduction of movement of species is crucial in long-term changes (Solomon and Kirilenko 1997). I therefore also use spatial information, assuming that 'time and space are related, in that forcing functions for vegetation change over large areas tend to be the same as those causing change over long time periods' (Glenn-Lewin and van der Maarel 1992).

Reductionist view

Our time series data conform to the often described, bell-shaped model of succession (Whittaker 1953, Gauch and Whittaker 1972, Austin 1990). What I intend to present in the sequel is not a global explanation of a large number of processes, but rather a reductionist view. The type of succession intended is deterministic, its trajectory pointing towards a stationary stage. Van Hulst (1992) has shown that different, simple dynamic models easily simulate such a process involving species replacement. However, even in more trivial cases, they involve a considerable number of parameters, which have to be fitted. Van Hulst warns that this may lead to a kind of 'phenomenological curve fitting'. I do not intend to avoid this, but rather follow his suggestion 'to construct a predictive model by attempting to emulate in a more formal manner the intuition-based predictions of the expert'.

Methods

Investigation area and data

The Swiss National Park (SNP) was created in 1914 to conserve and protect an area of subalpine and alpine habitats from adverse human impacts. In 1917, Braun-Blanquet and colleagues established permanent plots in the area to investigate vegetation recovery processes following the removal of domestic cattle and sheep (Braun-

Blanquet et al. 1931). Stüssi (1970) continued these long-term observations and established some additional plots after 1940. Most of the resulting data were never published. There are approximately 150 well-documented time series, many spanning 50 years and some almost 90 years. The collection of vegetation information, usually done at 5-year intervals, has continued to this day. The two time series derived from this using space-for-time substitution (Wildi and Schütz 2000) are shown in Figure 1. They stretch over a time-span of 415 and 585 years respectively.

The spatially explicit data used to test the model describe the state of a meadow at 1900 m a.s.l., Alp Stabelchod (Figure 2). Until 1914, this was a pasture surrounded by *Pinus mugo* forest, and the vegetation found there is a result of cattle grazing, clear-cutting, and related management activities. Some of the plots used to derive the time series shown in figure 1 are located inside this meadow, others in remote, but ecologically similar locations. For documenting today's state, the vegetation has been surveyed in a regular grid. Using the time series data, the state of 1917 was taken as the outset (Braun-Blanquet et al. 1931, Achermann 2000). The vegetation types distinguished in this map carry the names of the dominant species (i.e., *Aconitum*, *Trisetum*, etc.).

The temporal model

In order to avoid excessive complexity of the model, the species are grouped into six guilds, i.e., assemblages of species (Wildi and Schütz 2000). These are the state variables. The basic process considered is thus colonization of plots and subsequent species interactions. The plots follow the research grid established in the SNP. Plot size is 20 m x 20 m, the number of plots within the un-forested area of Alp Stabelchod is 286 (Achermann 2000). For simplicity, it is assumed that there is no overlap of species guilds in space, occurring in the grassland vegetation. The model plot is eventually overgrown by one or several species guilds, so that the total cover will reach 100% and the "open soil" 0%.

The objective then is to quantify overgrowth including replacement. In the original time series from the permanent plots it can be observed that overgrowth always starts slowly (Wildi and Schütz 2000). With increased cover of the guilds, the spread accelerates. When approaching 100%, overgrowth slows down. This finding is illustrated graphically in Figure 3. A function that has this behaviour is the logistic growth equation which, in case of only one guild, has the general form of

$$dX/dt = X \cdot r \cdot (100\% - X)/K$$

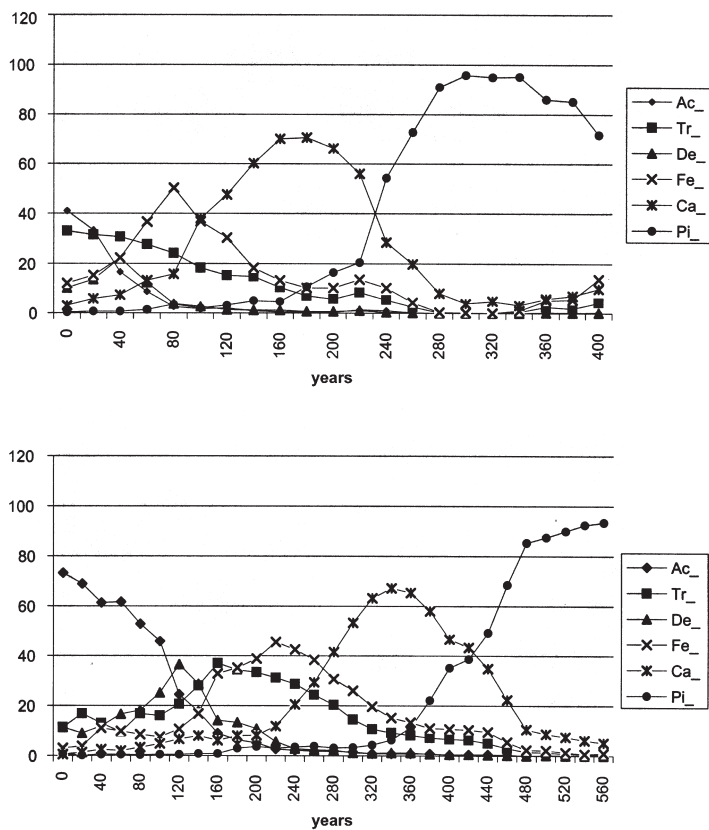


Figure 1. 415-year time series (above), 585-year time series (below) derived from field data. Ac: *Aconitum* guild, Tr: *Trisetum*, De: *Deschampsia*, Fe: *Festuca*, Ca: *Carex*, Pi: *Pinus*. The 6 genus names identify guilds of species.



Figure 2. The initial state of the vegetation of Alp Stabelchod, i.e., the state in the year 1917 approximated from relevés from this year (Braun-Blanquet et al. 1931). The gray scale accords with the six types distinguished in the following order: *Aconitum* (light), *Trisetum*, *Deschampsia*, *Festuca*, *Carex*, *Pinus* (dark).

(Wissel 1989). Here, r is the growth rate of guild X and K is the carrying capacity, i.e., 100%. As X is also measured in percent, the space not yet occupied is $100\% - X$. Colonization stops when X reaches 100%. The growth is regulated by X itself, as a result of intra-specific competition. It must be noted that logistic growth requires all guilds X_i to be present at the beginning of any simulation run.

Competition comes into play because of two assumptions. First, the gain of guild X_i in cover is lost by any other guild of lower competition power (or by open ground). In order to keep the cover percentages balanced, dX_i/dt will always occur in the model twice, i.e., once as a gain and once as a loss. Second, $100\% - X_i$ is the available space only for the best competing guild i . If there is another, even better competing guild X_j , then the space reduces to $100\% - X_i - X_j$. As will be seen in the description of the model, the mechanism has to make provision for many more competing guilds, six in the present case. Based on previous findings (Wildi and Schütz 2000) the following order of competition power has been established:

Pinus (1) → *Carex* (2) → *Festuca* (3) → *Trisetum* (4) → *Deschampsia* (5) → *Aconitum* (6)

The logistic growth equation for *Carex* (X_2), which is out-competed by *Pinus* (X_1) is given by

$$dX_2 / dt = X_2 \cdot r_2 \cdot \frac{100\% - X_1 - X_2}{K} - (dX_1 / dt) \frac{X_2}{\sum_{i=2}^6 X_i}$$

It can be seen that *Carex* loses a proportion of the space gained by *Pinus*. For *Festuca* (X_3), there is additional loss to *Carex*:

$$dX_3 / dt = X_3 \cdot r_3 \cdot \frac{100\% - X_1 - X_2 - X_3}{K} - (dX_1 / dt + dX_2 / dt) \frac{X_3}{\sum_{i=3}^6 X_i}$$

The third important factor in this pasture is recurrent disturbance. Here, it is trampling by grazing deer (Schloeth 1972, Krüsi et al. 1998). I assume that it affects all the plants equally within a plot. The intensity will of course vary depending on animal density. Trampling is a very fast process, instantly generating open space. This causes a loss t_i for guild i which is simply proportional to the state X_i . Re-colonization c_i is also relatively fast. I assume that it happens instantly, i.e., within the relative short time span of one year. It is proportional to the exponential growth of each guild. Direct competition as happens in species replacement is not assumed. Trampling and re-colonization are balanced within the year:

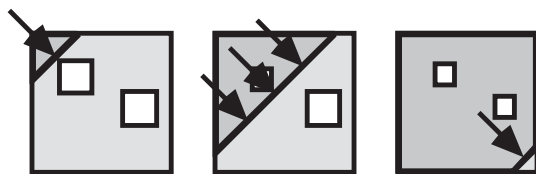


Figure 3. Overgrowth of a plot by a new guild. The white squares indicate patches inappropriate for growth causing the growth to slow down towards the end of the process.

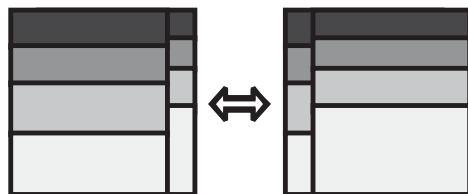


Figure 4. Diffusion takes place by mutual exchange of vegetation between adjacent plots.

$$\sum_{i=1}^6 t_i = \sum_{i=1}^6 c_i$$

This assumes that growth is fast enough to colonize any gap that has occurred within one year. Furthermore, trampling leads to a yearly change of the system provided that the growth rates r_i vary among guilds.

The spatial model

The following notation is used:

$$x_{i,x,y,t} \mid i = 1, \dots, 6; x = 1, \dots, 25; y = 1, \dots, 30; t = 1, \dots, 400$$

Here, i stands for guild, x and y are the spatial co-ordinates and t is time in years. The model space is a grid of plots of dimension 25 by 30. Not only the pasture, but also the adjacent forest stands fit into this rectangle. The spread of any particular guild happens by spatial exchange. A portion of the content of any plot is transferred yearly to the neighbouring plots as shown in Figure 4. The gains, g , and losses, l , are balanced:

$$x_{i,x,y,t+1} = x_{i,x,y,t} + g_{i,x,y,t} - l_{i,x,y,t}$$

$$g_{i,x,y,t} = d(x_{i,x-1,y,t} + x_{i,x+1,y,t} + x_{i,x,y-1,t} + x_{i,x,y+1,t})$$

$$l_{i,x,y,t} = 4d(l_{i,x,y,t})$$

This means that any plot receives a portion of the vegetation from each neighbouring plot. Simultaneously, it loses the same amount from its own vegetation to these same neighbouring plots. The speed of the exchange is given by the exchange factor, d . This is assumed constant, even though spatial processes may be faster where more animals circulate. Having no measurements of exchange at hand, I keep it at the very low level of $d=0.001$.

Along the edges of the system, outside the meadow, the exchange is mirrored. All these plots are covered by *Pinus mugo* forest, the final state of the succession so far.

Results

The comparison of Figures 1 and 5 shows that, with a suitable choice of parameter values, the temporal model can reproduce the basic pattern of the time series. In the model, output fluctuations are absent. The results shown in Figure 5 were obtained only after carefully adjusting the initial conditions (the state variables) and estimating the growth rates of the guilds by trial and error. Both are shown in Table 1. The initial states of the model are within the range of the values observed in the field (Wildi and Schütz 2000). It must be noted that the observed initial cover values are themselves subjected to random fluctuation whereas in the deterministic model, a fixed value is needed. Sensitivity tests showed that the time of

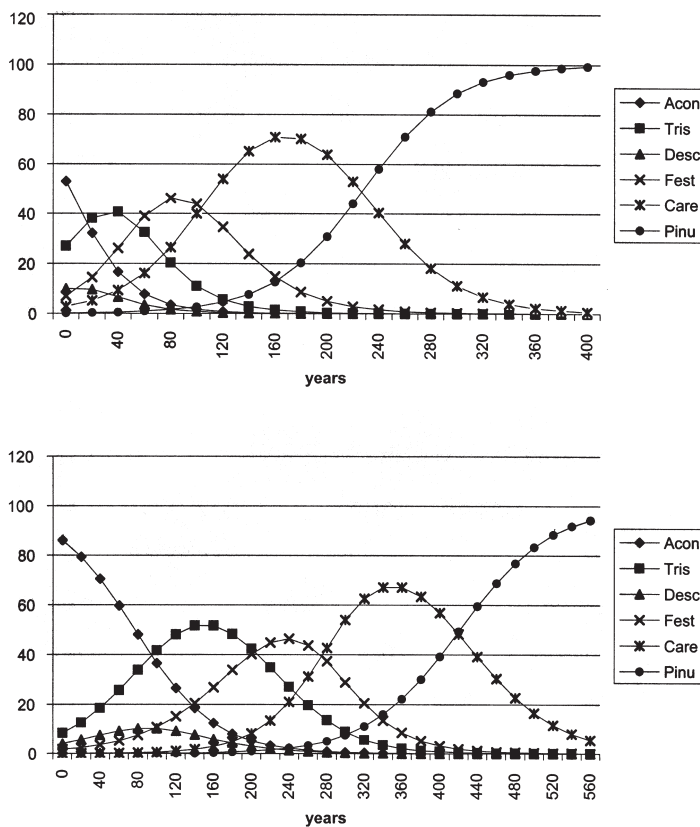


Figure 5. Temporal simulation of the time series. 415-year time series (above), 585-year time series (below). Acon: *Aconitum* guild, Tris: *Trisetum*, Desc: *Deschampsia*, Fest: *Festuca*, Care: *Carex*, Pinu: *Pinus*.

Table 1. Initial values in the times series data, initial state variables (percentage cover of 6 guilds) and growth rates used in the models.

Series	415 yr			585 yr		
	state, %		growth rate	state, %		growth rate
	field data	model		field data	model	
<i>Aconitum</i>	41.1	53.0	0.050	73.1	86.0	0.018
<i>Trisetum</i>	33.0	27.0	0.045	11.4	8.4	0.022
<i>Deschampsia</i>	10.3	10.0	0.045	11.3	4.0	0.022
<i>Festuca</i>	12.1	7.0	0.045	3.0	1.6	0.020
<i>Carex</i>	3.1	2.8	0.035	0.6	0.03	0.026
<i>Pinus</i>	0.3	0.2	0.030	0.6	0.01	0.022

emergence of late successional guilds depends on the initial states. In other words, the initial state of the guilds determines the speed of succession. This is not a realistic feature. Even worse: to allow growth to occur, all species guilds have to be present in the model (i.e., within all pixels) from the very beginning of the simulation.

Interestingly, the estimated growth rates that were compatible with a realistic model behaviour do not differ much among guilds. The model is not too sensitive to the growth rates (Table 1). The two time series differ in growth rates. In the 415-year model, they are by a factor of 2 larger than in the 585-year model, and they are not

proportional. Using identical rates for all guilds reproduces the temporal pattern shown in Figure 1 as well. If all are set to 0.045 (Table 1), succession will last about 400 years, if values of 0.022 are taken, this will be about 600 years.

Including spatial extent in the model poses serious problems. The initial condition of the meadow, i.e., the state in the year 1917, is not known precisely. Only the discrete states can be inferred from the present state and the temporal model (Figure 6, upper left). The spatial system could of course be fine-tuned using the simulated states from the temporal model. This would be highly un-

Table 2. Six discrete vegetation states used as initial conditions of the six state variables (guilds) in spatial modelling, cover-%.

Guild	state 1	state 2	state 3	state 4	state 5	state 6	Σ
<i>Aconitum</i>	50.00	17.50	17.50	10.00	5.00	0.00	100.00
<i>Trisetum</i>	10.00	35.00	35.00	15.00	5.00	0.00	100.00
<i>Deschampsia</i>	7.00	15.00	35.00	35.00	6.00	2.00	100.00
<i>Festuca</i>	2.00	3.00	30.00	42.00	20.00	3.00	100.00
<i>Carex</i>	1.00	1.00	10.00	15.00	65.00	8.00	100.00
<i>Pinus</i>	0.00	0.00	1.00	1.00	8.00	90.00	100.00

**Figure 6.** Vegetation map of Alp Stabelchod. The gray scale (light to dark) conforms with the six guilds distinguished (*Aconitum* (light), *Trisetum*, *Deschampsia*, *Festuca*, *Carex*, *Pinus* (dark)). The surrounding is *Pinus mugo* forest. Upper left: Initial stage based on field data. Upper right: 400yr of spatial process. Lower left: Succession after 200yr temporal process. Lower right: Succession after 200yr spatial and temporal process.

realistic as the initial parameters of all 268 plots would have to be precisely set. Instead, I use mean values for all guilds to define the composition of the plots. These are shown in Table 2. As a result, at the beginning of the simulation the system consists of a limited number of discrete states, whereas in reality, the vegetation forms a continuum.

The domination of the meadow by subsequent successional guilds and finally by *Pinus* forests lasts about 500 years in individual simulations using the temporal model. In this case, the edges of the individual plots dominated by different “guilds” are not moving in space as observed in the survey data (Wildi and Schütz 2000). As a result, the pattern of edges remains unchanged over the entire simulation time. This can be seen, e.g., in the state shown in Figure 6, lower left. There, the boundaries from the initial state are still visible. Only the states of the pixels have changed.

The effect of spatial exchange among pixels can be tested in isolation. Assuming the extremely low rate of exchange of $d=0.001$, the state of the system after 400 years is shown in Figure 6, upper right. The overall composition is almost the same as at the beginning. But patches of similar composition have become more homogeneous compared to the initial state. Along the forest edges, *Pinus mugo* has invaded the first row of plots. Other types have spread as well. The *Aconitum*-stage has increased in surface. After all, the spatial process does not reflect ordinary succession.

Finally, the spatial and temporal processes are run simultaneously. This accelerates the simulation of succession and the meadow is already covered by *Pinus mugo* after 360 years (not shown here). In Figure 6, lower right, the state after 200 years is presented. It can now be seen that the vegetation boundaries have moved and differ from the initial state. The diffusion process causes *Pinus* to invade the meadow from the edges to the centre.

Discussion

The model shown above describes secondary succession (Van Andel et al. 1993). The initial state of the system is assumed to be the result of disturbance or, in extreme cases, of fertilization, irrigation and grazing after logging. It is known that in previous centuries, almost all forests in the SNP have been logged, some for timber export and some for extraction of charcoal for iron melting. From the originally dominating species, *Pinus mugo*, *Pinus cembra* and *Larix decidua*, the first is nowadays dominating in the area. It is a pioneer species as trees are concerned. This indicates that the vegetation of the entire

area is still undergoing a long-term recovery process under which the dominance pattern is subjected to slow, but distinct change. The initial stage of the succession considered here, the *Aconitum* dominated, highly fertilized resting places of cattle, are a result of trampling and over-fertilization. This phase can no longer be observed nowadays. The first phase of regeneration must therefore have been invasion, mainly of tall herb species coming from lower elevation sites, like *Aconitum compactum*, *Rumex alpinus* or *Chenopodium bonus-henricus*. This is modelled here as an event of “instantaneous replacement”, i.e., replacement of open soil within one season. As I start here with already closed vegetation, overgrowth plays a role only in case of trampling damage by browsing deer. In terms of the life strategies of Grime (1979), the initial stage is formed by ruderals.

The competition implemented in the model consists of simple replacement events. Guilds of species suppress others of lower competitive power while spreading over a plot. This involves a fairly high level of abstraction, about the same as in an ordinary Markov chain where random events determine the change of the system (Usher 1992, Balzter 2000).

In the temporal model, the complex temporal pattern of guilds is a result of their initial quantities. Although these quantities conform to the field records (Wildi and Schütz 2000), the presence of a strong competitor in an early phase would speed up the succession drastically. Yet, there has no case been observed in which, as an example, the *Pinus* guild directly followed the *Aconitum* guild. Furthermore, it must be noted that the modelled succession follows just one pathway. This is not surprising, as the environmental conditions as well as the rules of competition are kept constant during simulation time. Achermann et al. (2000) showed, that different successional patterns can in fact be found in the area. From many other investigations, alternative pathways can generally be expected (Cattalino et al. 1979, Peet 1992, Van Andel et al. 1993, McCook 1994). The present model would yield these, e.g., under altered disturbance regimes.

Returning to the terminology of Grime (1979), ruderals are followed by competitors, and later on, by stress tolerant species (the *Pinus* guild). As shown by Achermann (2000), the phosphorous content decreases continuously in time. But nutrient content does not seem to be the main factor in succession. Species in highly fertilized patches can survive for more than a hundred years, even if the nutrients have been exported. If deer invade into the system, the nutrients are removed by grazing (Achermann 2000). Animals play an important role in later stages of succession as well. The establishment of *Pinus montana* seed-

lings is fostered by disturbance of deer (Krüsi et al. 1998). At this time, the phosphorous content is almost stable.

The second model used here focuses on spatial outcomes. Without considering space, the first model requires all species to be present in the system from the very first moment. This is highly unrealistic. Moving edges can be observed in many records of permanent plots (Achermann et al. 2000), especially along forest boundaries (Matlack 1994). In many cases, considerable increase in the number of species has been observed (Camenisch and Schütz 2000, p. 179). Over long time periods, the movement of species in space seems to be the most important factor of change. The lack of explicit spatial processes has also been identified as the most serious shortcoming in gap modelling. Price et al. (2001) argue that the assumption that seeds of all species are uniformly available over space leads to wrong estimates in species diversity. Just as in the present case, they conclude that the interactions between herbivores and (forest) plants are a big unknown.

One property of many models of vegetation change is the fact that species tend to disappear over long simulation periods. This is the case for most types of models, for the present as well as for Markov- and gap models. In my model, there is finally one guild of species left. This still holds fairly high species diversity. Species diversity there can be assumed to persist for several reasons, like spatial heterogeneity and disturbance. By accepting guilds as units of interest and not individual species, our models do not address diversity explicitly. It is as yet open question what would happen if the models would be extended to the species level. According to Gause's principle, a complete breakdown of diversity would be expected, a case never observed in the investigation area. To avoid this, inclusion of spatial processes in the models is indicated. The attempt used here, an undirected diffusion, needs to be extended to include varying site conditions, dispersal mechanisms and specifically the impact of animals.

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References

- Achermann, G. 2000. The influence of red deer (*Cervus elaphus* L.) upon a subalpine grassland ecosystem in the Swiss National Park. *Diss ETH No. 13479*. Swiss Federal Institute of Technology, Zürich. 93 pp.
- Achermann, G., M. Schütz, B.O. Krüsi and O. Wildi. 2000. Tall-herb communities in the Swiss National Park: Long-term development of the vegetation. *Nationalparkforschung in der Schweiz* 89: 67-88.
- Austin, M. P. 1990. Community theory and competition in vegetation. In: J.B. Grace and D. Tilman (eds.): *Perspectives on Plant Competition*; Academic Press, Inc.; San Diego. pp. 215-238.
- Balster, H. 2000. Markov chain models for vegetation dynamics. *Ecol. Model.* 126: 139-154.
- Botkin, D. B., J. F. Janak and J. R. Wallis. 1972. Rationale, limitations and assumptions of a northeastern forest growth simulator. *IBM Journal of Research and Development* 16: 101-116.
- Braun-Blanquet, J., S. Brunies, E. Campell, E. Frey, H. Jenny, Ch. Meylan and H. Pallmann. 1931. Vegetationsentwicklung im Schweiz. Nationalpark. Ergebnisse der Untersuchung von Dauerbeobachtungsflächen I. Dokumente zur Untersuchung des Schweiz. Nationalparks. *Jahresb. Nat. Ges. Graub.* 69: 3 – 82.
- Bugmann, H. 2001. A review of forest gap models. *Climate Change* 51: 259-305.
- Camenisch, M. and M. Schütz. 2000. Temporal and spatial variability of the vegetation in a four-year enclosure experiment in Val Trupchun (Swiss National Park). In: M. Schütz, B. O. Krüsi, and P. J. Edwards. (eds.), *Succession Research in the Swiss National Park. Nat. park-Forsch Schweiz* 89: 165-188.
- Cattalino P. J., I. R. Noble, R. O. Slatyer and S. R. Kessel. 1979. Predicting the multiple pathways of plant succession. *Environ. Manage.* 3: 41-50.
- Foster, B. L. and D. Tilman. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecol.* 146: 1-10.
- Gauch, G. H. and R. H. Whittaker. 1972. Coenocline simulation. *Ecology* 53: 446-541.
- Glenn-Lewin, D.C. and E. Van der Maarel. 1992. Patterns and processes of vegetation dynamics. In: D.C. Glenn-Lewin, R.K. Peet and T.T. Veblen (eds.), *Plant Succession: Theory and Prediction*. Chapman and Hall, London. pp. 11-59.
- Grime, J. P. 1979. *Plant Strategies and Vegetation Process*. Wiley, Chichester.
- Hess, H. E., E. Landolt and R. Hirzel. 1976. *Bestimmungsschlüssel zur Flora der Schweiz und angrenzender Gebiete*. Birkhäuser Verlag, Basel.
- Hill, H. E. and H. G. Gauch. 1980. Detrended correspondence analysis: an improved technique. *Vegetatio* 42: 47-58.
- Horn, H. S. 1976. Succession. In: R. M. May (ed.), *Theoretical Ecology: Principles and Applications*. Saunders, Philadelphia. pp. 187-204.
- Huisman, J., H. Olf and L. F. M. Fresco. 1993. A hierarchical set of models for species response analysis. *J. Veg. Sci.* 4: 37-46.
- Krüsi, B. O., M. Schütz, C. Bigler, H. Grämiger and G. Achermann. 1998. Huftiere und Vegetation im Schweizerischen Nationalpark von 1917 bis 1997. Teil 1: Einfluss auf die botanische Vielfalt der subalpinen Weiden; Teil 2: Einfluss auf das Wald-Freilandverhältnis. In: R. Cornelius. and R. Hofmann (eds.), *Extensive Haltung robuster Haustierrassen, Wildtiermanagement, Multi-Spezies-Projekte - Neue Wege in Naturschutz und Landschaftspflege?* Inst. Zoo-Wildtierforsch., Berlin, 62-74.
- Lischke, H. and B. Zierl. 2002. Feedback between structured vegetation and soil water in a changing climate: A simulation study. In: M. Beniston (ed.), *Climatic Change: Implications for the Hydrological Cycle and for Water Management*. Kluwer. pp. 349-377.
- Matlack, G. R. 1994. Vegetation dynamics of the forest edge – trends in space and successional time. *J. Ecol.* 82: 113-123.

- McCook, L. J. 1994. Understanding ecological community succession: Causal models and theories, a review. *Vegetatio* 110: 115-147.
- Myster, R. W. and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr in 10 contrasting old fields. *Ecology* 75: 387-392.
- Orlóci, L., M. Anand and X. He. 1993. Markov chain: A realistic model for temporal coenoser? *Biom. Praxim.* 33: 7-26.
- Peet, R. K. 1992. Community structure and ecosystem function. In: D. C. Glenn-Lewin, R.K. Peet and T.T. Veblen (eds.), *Plant Succession*. Chapman and Hall. London. pp. 103-151.
- Pickett, T. A. 1989. Space-for-time substitution as an alternative to long-term studies. In: E. Likens (ed.), *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer, New York. pp. 110-135.
- Price, D. T., N. E. Zimmermann, M. J. L. van der Meer, P. Leadley, I. T. M. Jorritsma, J. Schaber, D. F. Clark, P. Lasch, S. McNulty, J. Wu and B. Smith. 2001. Regeneration in gap models: priority issues for studying forest responses to climate change. *Climatic Change* 51: 475-508.
- Schloeth, R. F. 1972. Die Entwicklung des Schalenwildbestandes im Schweizerischen Nationalpark von 1918 – 1971. *Schweiz. Zeitschr. Forstwes.* 123: 565-571.
- Schütz, M., B. O. Krüsi, G. Achermann, and H. Grämiger. 1998. Zeitreihenanalyse in der Vegetationskunde: Analyse und Interpretation von Einzelflächen am Beispiel von Daten aus dem Schweizerischen Nationalpark. *Bot. Helv.* 108: 105 –124.
- Shugart H. H. and D. C. West. 1977. Development of an Appalachian Deciduous Forest Succession Model ant its Application to Assessment of the Impact of Chesnut Blight. *J. Environ. Manage.* 5: 161-179.
- Shugart, H. H. 1984. *A Theory of forest Dynamics. The Ecological Implications of Forest Succession Models*. Springer-Verlag, N.Y.
- Solomon, A. M. and A. P. Kirilenko. 1997. Climate change and terrestrial biomass: What if trees do not migrate! *Global Ecol. Biogeog. Lett.* 6: 139-148.
- Stüssi, B. 1970. Naturbedingte Entwicklung subalpiner Weiderasen auf Alp La Schera im Schweizer Nationalpark während der Reservatsperiode 1939-1965. *Ergebnisse der wissenschaftlichen Untersuchungen im schweizerischen Nationalpark*. Bd XIII, 385 p.
- Usher, M. B. 1981. Modelling ecological succession, with particular reference to Markovian model. *Vegetatio* 46: 11-18.
- Usher, M. B. 1992. Statistical models of succession. In: D. C. Glenn-Lewin, R. K. Peet and T. Veblen (eds.), *Plant Succession: Theory and Prediction*. Chapman and Hall, London. pp. 215-248.
- Van Andel, J., J. P. Bakker, and A. P. Grootjans. 1993. Mechanisms of vegetation succession: a review of concepts and perspectives. *Acta Bot. Neerl.* 42: 413-433.
- Van Hulst, R. 1992. From population dynamics to community dynamics: modelling succession as a species replacement process. In: D. C. Glenn-Lewin, R. K. Peet and T. Veblen (eds.), *Plant Succession: Theory and Prediction*. Chapman and Hall, London. pp. 188-214.
- Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecol. Monog.* 23: 41-78.
- Wildi, O. and M. Schütz. 2000. Reconstruction of a long-term recovery process from pasture to forest. *Community Ecol.* 1: 25-32.
- Wissel, C. 1989. *Theoretische Ökologie*. Springer-Verlag, Berlin.