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PATUMOD: a compartment model of vegetation dynamics in wooded pastures

François Gillet [a,1]*, Olivier Besson [b], Jean-Michel Gobat [a]

[a] *Department of Plant Ecology, University of Neuchâtel, Institute of Botany, rue Emile-Argand 11, CH-2007 Neuchatel, Switzerland*

[b] *University of Neuchâtel, Institute of Mathematics, rue Emile-Argand 11, CH-2007 Neuchatel, Switzerland*

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Abstract

A system of wooded pasture can be described by seven biological state variables (trees, shrubs, underwood grasslands, fallows, eutrophic meadows, oligrotrophic lawns and cattle) linked by a network of dynamic interactions, which are controlled by altitude and human activities. PATUMOD is a spatially implicit compartment model designed to simulate vegetation dynamics in such silvopastoral ecosystems at community level and according to an equilibrium paradigm. Computer simulations show that the state variables generally end up on a steady-state (one-point attractor), independent on their initial values but strongly dependent on cattle load. At a given altitude, to each value of the stock density is corresponding a stable equilibrium characterised by a given relative cover of each vegetation component. If the initial values are very far of the attractor, a long succession of intermediate stages is required before leading to the steady-state. A remarkable exception to this rule can occur at low altitude, with a repellor between switching trajectories towards two attractors, corresponding to a threshold between scarcely and densely wooded pastures. PATUMOD can be applied to simulate different management scenarios, which include changing global stock density and cutting trees or shrubs. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Community dynamics; Silvopastoral ecosystems; Simulation scenarios; Stability; Steady-state; Sustainability; Phytocoenosis; Vegetation succession

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1. Introduction

1.1. Dynamic modelling of plant communities

Many of the themes and problems recognised by plant ecologists during the first decades of the 20th century are still important research objectives in the modern field of vegetation dynamics (Glenn-Lewin et al., 1992). Vegetation ecologists have accumulated precise observations, performed field experiments and developed various theories about plant succession and regeneration dynamics.

Vegetation science is concerned with plant communities, which are traditionally described by

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* Corresponding author. Tel.: +41-32-718-2317.

E-mail address: francois.gillet@unine.ch (F. Gillet).

[1] URL: http://www.unine.ch/bota/levp/fg.html(the STELLA model PATUMOD is downloadable from this page).

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their physiognomy or their species composition. Agronomists use frequently taxonomic aggregates of species (e.g. grasses, forbs or legumes) to describe plant successions in grasslands. Many other textural descriptors of plant communities have been used as well, mostly based on life forms, growth forms (Barkman, 1988), life strategies (Grime, 1977; Tilman, 1988) or other functional groups (Steffen, 1996). Many authors have tried to explain plant species assemblages by historical, evolutionary and ecological factors (see Zobel, 1992 or van der Valk, 1992 for a review).

Since the mid-1970s two major conceptual trends have dominated research in vegetation dynamics (Glenn-Lewin et al., 1992): (1) a shift away from holistic explanations of successional phenomena (Clements, 1916; Margalef, 1968; Odum, 1969) towards reductionist and mechanistic approaches emphasising proximate causes of vegetation change; (2) a shift away from equilibrium towards non-equilibrium paradigms (Pickett and White, 1985). Following these trends, deductive predicting was replaced by inductive forecasting and succession was viewed as a population process, emphasising life histories and competitive interactions of the component species within fluctuating environment conditions, rather than emergent properties of communities (Peet and Christensen, 1980; Pickett et al., 1987). The role of disturbances and other stochastic processes was often put forward to explain divergent successional patterns (Glenn-Lewin, 1980; Pickett and White, 1985).

Concerning quantitative prediction, an application of this reductionist paradigm was to focus on population dynamics by use of individual-based models (DeAngelis and Gross, 1992; Judson, 1994). Indeed, *i*-state configuration approach (Metz and Diekmann, 1986) is very interesting to model processes concerning spatio-temporal behaviour of one or several isolated populations, especially if the number of individuals is low and the local interactions are strong. But the extrapolation of this method to a whole community is a serious problem, for two main reasons, one technical and the other theoretical. The first one, also the easiest one, is that the number of individuals to consider to achieve a computer simulation can be easily prohibitive, even if this limitation is less and less decisive as far as computers become more powerful. The second reason is more fundamental: the reductionist approach—or at least its rhetoric—ignores the evidence of simplicities in complex systems (Cohen and Stewart, 1994) and the reality of high-level organisations, as a consequence of the fundamental hierarchical structure of ecological systems (Allen and Starr, 1982; O'Neill et al., 1987; Waltho and Kolasa, 1994; Earn and Rohani, 1999).

Roughly speaking, we can reduce the variety of dynamical, process-oriented models developed in the field of plant ecology in a simple dichotomy: (1) population models, which seek to predict individual or population dynamics of one or several species within a community; (2) ecosystem models, using integrated measurements of community structure and function, such as overall standing crop, energy or material turnover. Surprisingly, very few mechanistic quantitative models have been developed to simulate the dynamics of whole plant communities, considered as states; even in this case, succession stages are reduced to dominant species (Bledsoe and Van Dyne, 1971; Cooper and Huffaker, 1997; Hahn et al., 1999). The main reason is perhaps the lack of theoretical knowledge of the processes involved at this level of organisation, which is only described by statistical tools and phenomenological approaches (van Hulst, 1992).

However, the old debate between the organismic (Clements, 1916) and the individualistic (Gleason, 1939) conception of the community is not yet ended, even if occulted by the success of evolutionary and molecular biology. As van Hulst (1992) argue, population dynamics and community dynamics occur on different time and space scales, and a description or model that is satisfactory at one scale level may be quite inappropriate at another level. Plant communities can therefore be considered as fuzzy but discrete entities evolving in a different state space than individual organisms, cells or molecules. Different levels of spatio-temporal organisation of plant communities should even be considered (Gillet et al., 1991;

Gillet and Gallandat, 1996a). Some vegetation ecologists proposed a qualitative formulation for describing and comparing successions or zonations of community-types in small landscape units, using system and structuralism concepts (Gillet et al., 1991; de Foucault, 1993). A theoretical model of the plant community, derived from Forrester's system dynamics, was proposed by Pignatti (1996). But no precise mathematical formulation of such models was proposed until now.

Vegetation dynamics have temporal and spatial aspects and can be observed and modelled at different spatio-temporal scales (van der Maarel, 1993). Over a small scale (short term and fine-grained pattern), periodic or aperiodic fluctuations may occur inside a given plant community (regeneration cycles, gap processes). Over a large scale (long term and coarse-grained pattern), the community can remain constant or be involved into a succession process. Within the scope of dynamic modelling of ecosystems, spatially implicit models do not consider the influence of spatial heterogeneity inside the system (compartments models), whereas spatially explicit models do (Poiani and Johnson, 1993; Sklar et al., 1994; Ellison and Bedford, 1995), either in a continuous (transport models, using partial differential equations) or in a discrete way (cell-grid models, cellular automata). Many models of forest dynamics have been developed, based on tree regeneration and growth in canopy gaps (Shugart, 1984; Hill et al., 1994; Liu and Ashton, 1995; Chave, 1999); these spatially explicit models only consider populations of tree species.

The present paper is an attempt to model vegetation change (secondary allogenic successions) in silvopastoral ecosystems by means of a spatially implicit system approach combining holistic entities and mechanistic processes at the community level.

1.2. The vegetation of wooded pastures

Wooded pastures are traditional silvopastoral ecosystems, with high biodiversity, adapted to multiple use (Etienne, 1996; Gillet and Gallandat, 1996b). They must not be confounded with agroforestry systems, where all trees are planted and grasses are sown; in typical wooded pastures, the regeneration of both grassland and woodland is natural. They are structurally complex and heterogeneous at a wide range of temporal and spatial scales. Most silvopastoral ecosystems in Europe suffered a dramatic decline during this century, due to concentration of agricultural management, involving local intensification or extensification. Nevertheless, in certain regions like Jura Mountains in Switzerland, they are still the most abundant type of man-made landscape. The conservation of such a landscape requires precise knowledge about vegetation dynamics.

In absence of pastoral activities, wooded pastures evolve towards climacic forest ecosystems (secondary progressive succession); if grazing pressure is too high (intensive use), tree regeneration is impossible and they evolve towards more simple grassland ecosystems (secondary retrogressive succession). Between these two extreme conditions, the vegetation of a wooded pasture is composed of a complex and various assemblage of trees, shrubs, grasses, forbs and mosses, forming shifting mosaics driven by the alternation of plant facilitation and competition (Olff et al., 1999). We have analysed this vegetation at three integration levels, which correspond to three spatio-temporal scales (Gillet and Gallandat, 1996a): (1) the level of the synusiae (elementary communities of plants competing into the same layer and sharing a similar environment), (2) the level of the phytocoenoses (complex communities of herb, shrub and tree synusiae) and (3) the level of the landscape (assemblages of different phytocoenoses inside a pastoral management unit).

Four main phytocoenoses types were defined by structural criteria. Unwooded pastures (type 1000) are characterised by tree and shrub covers below 1%, high forage production but low diversity. In scarcely wooded pastures (type 2000), the tree cover is ranging between 1 and 20%; most of the trees are sparse; forage production and diversity are high. In densely wooded pastures (type 3000), the tree cover is between 20 and 50–70%; most of the trees are clumped; forage production is low, while diversity is high. Grazed and ungrazed forests (type 4000) are characterised by a tree cover above 50–70% and by both low forage production and diversity.

1.3. The phytocoenotic system

We applied a system approach to model the organisation of the phytocoenoses of wooded pastures and to simulate their evolution. A general qualitative model was first developed to synthesise knowledge and hypotheses elaborated from many observations and analyses.

A phytocoenosis of wooded pasture can be considered as a concrete system, which is composed of synusiae, linked together by a network of spatial and temporal relationships. The structure of this network, together with the environmental context, is supposed to cause the dynamic behaviour of the system (maintenance or evolution towards a more stable composition, resistance to environmental change and disturbances).

Some relations between the components of a phytocoenotic system can be defined as transformations when one can distinguish an initial and a final component (de Foucault, 1993). The transformation can be spontaneous (e.g. layering) or initiated by the action of a transformation operator, as an environmental stress (e.g. shading, grazing) or disturbance (e.g. clearing). Other interrelations between components can be considered, like the determinant influence of a component on the survival of another component (e.g. an underwood herbaceous synusia being dependent on a tree synusia) or on the development of another component (e.g. a shrub synusia conditioning the regeneration of trees).

Some transformations and interrelations correspond, directly or not, to dynamic processes, i.e., changes through time. Both spatial and temporal relationships can be symbolised by arrows in qualitative diagrams, which describe the structure and the organisation of the phytocoenoses (Gillet et al., 1991).

The comparison of the qualitative diagrams of different concrete phytocoenoses allows to reveal homologies in their structure, independently of the diversity of their taxonomical components, and thus to define generalised qualitative models (de Foucault, 1993). In such models, the components are abstract categories of synusiae, called homoecies, defined by their structural and functional characteristics, which determine their role in the networks of relationships.

The fallows form a relatively heterogeneous group of tall grass and forb synusiae sharing common characteristics: the height is greater than 30 cm and the grazing pressure is very low. The species richness is important and the forage yield is variable.

The herbaceous underwoods are conditioned by the presence of a phanerophytic canopy. The height is usually lower than 30 cm. The species richness and the forage yield are low.

The oligotrophic lawns are conditioned by a middle or important grazing, but come under a low fertilising. The height is lower than 20 cm (short grass). The forage yield is low but the species richness high. They can be acidophilous or neutrophilous (calcicolous).

The mesotrophic and eutrophic grazed meadows are conditioned both by a high degree of grazing and a sufficient nutrient richness. The height is maintained lower than 20 cm by grazing. The species richness is variable and the forage yield is important.

The comparison of six phytocoenoses studied in detail in the framework of the PATUBOIS research programme (Gallandat et al., 1995a; Gillet et al., 1998) has shown that a system of wooded pasture (Fig. 1) can be divided into two subsystems: a forest subsystem with trees, shrubs and underwood and a pasture subsystem with eutrophic meadows and oligotrophic lawns. When grazing pressure or tree cover are very high, one subsystem tends to be exclusive and the opposition becomes less important; however, a typical balanced wooded pasture is characterised by the stable coexistence of these two subsystems. The spatial and temporal relationships within each subsystem are generally stronger than those between the components belonging to different subsystems. Very few components ensure the connection between the two subsystems, which are forb ungrazed synusiae (fallows). A series determined by grazing and fertilising intensity can generally be observed inside the pasture subsystem, involving lawns, meadows and temporary fallows, which entertain bilateral spatio-temporal relationships. Tree regeneration depends essentially upon a heliophilous high shrub synusia, which develops itself from a fallow or an undergrowth shrub synusia, after a clearing-cut.

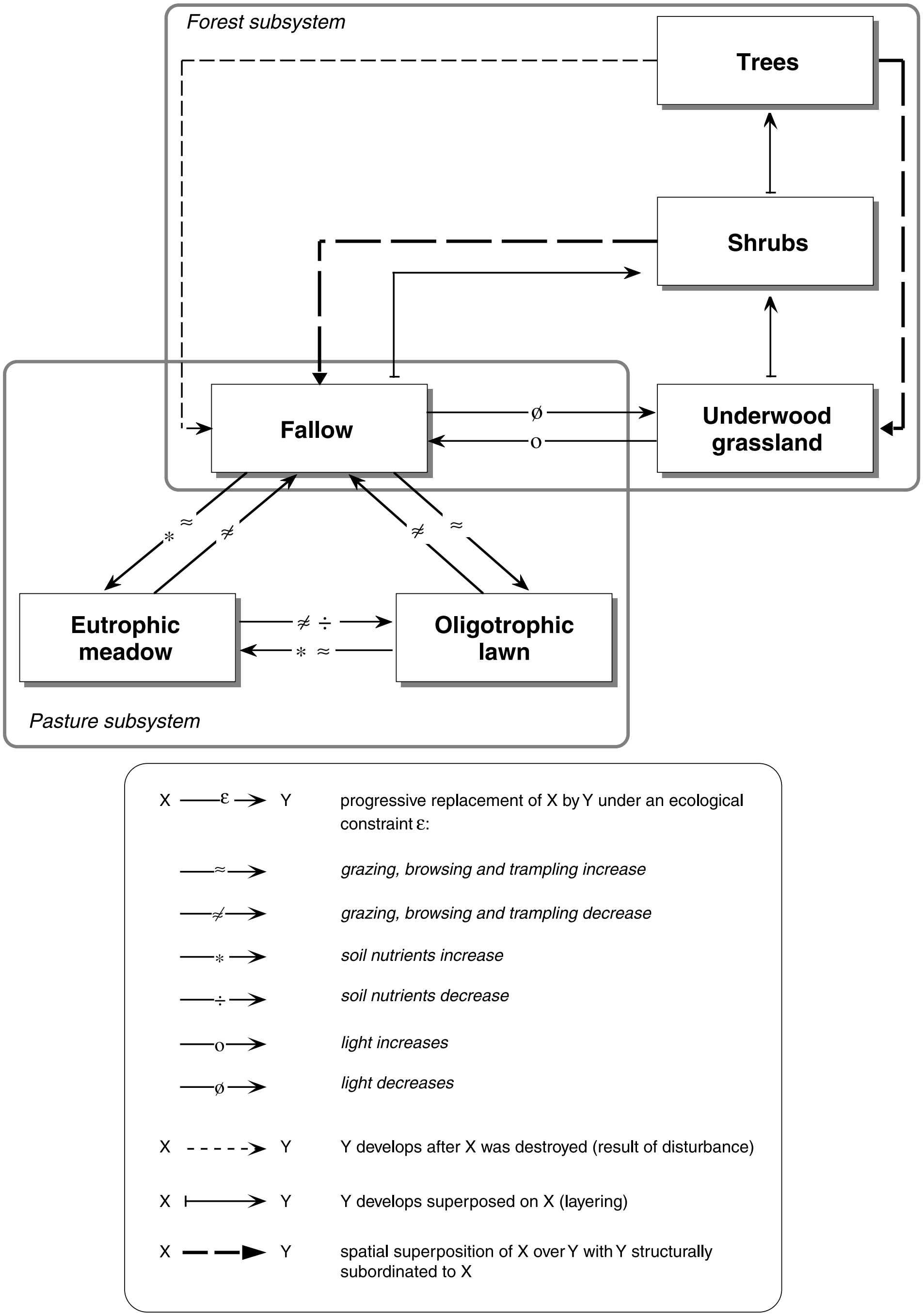

Fig. 1. Qualitative model of a phytocoenotic system of wooded pasture (after Gillet and Gallandat, 1996b, modified).

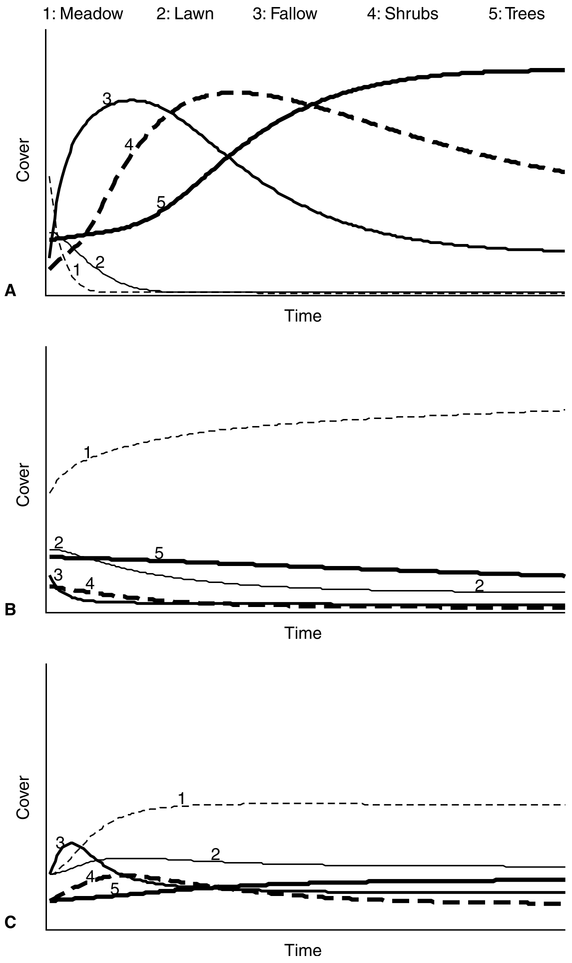

Fig. 2. Three reference behaviour patterns used to build and to calibrate the quantitative dynamic model. (A) Stock density = 0; (B) stock density = carrying capacity; (C) stock density close to the steady-state.

2. Objectives and expected behaviour of the model

2.1. Objectives

Our goal is to develop a dynamic model, called PATUMOD, to simulate and predict the evolution of the vegetation of a phytocoenosis of wooded pasture under the influence of abiotic (altitude) and land use (stock density) conditions.

In this spatially implicit model, we consider that the phytocoenosis has no spatial dimension but is located inside an elementary pastoral management unit, which is the smallest enclosed patch into which a cattle herd can pasture freely. This pastoral unit can be the whole range—under continuous grazing management—, or a paddock—under rotational grazing management. Two structural levels are thus considered: local variables apply to the phytocoenosis level and global variables to the pastoral unit or landscape level.

Our purpose is both strategic and tactical.

1. The model is a new attempt to apply a deterministic approach to vegetation dynamics at the community level, following the system dynamics paradigm and using non-linear differential equations (compartment model). This strategic purpose concerns the evaluation of a set of sustainable hypotheses applied to plant succession inside a phytocoenosis of wooded pasture. To reach this fundamental purpose, our model has to be as general as possible and focus on the essential features of the processes at this level of organisation.
2. But this model is also expected to provide accurate predictions of the dynamical trends of the vegetation, starting from a given initial composition and controlled by constant or changing driving variables. This tactical purpose concerns the potential applications of the model within the scope of silvopastoral management (sustainability assessment).

2.2. Reference behaviour patterns

A reference behaviour pattern is a graph over time of some variables which best characterise the phenomena we are trying to understand. To achieve its purpose, our model must realise three typical behaviours (Fig. 2).

A. It is assumed that when the stock density is null, we must observe a quick transition to a stable climax forest stage, whose duration depends only on initial conditions and altitude. The first steps of this process concern the herb layer: replacement of meadows by lawns, replacement of meadows and lawns by fallows. In a second step, shrub cover increases dramatically. In the last step, trees and their understory increase since fallows and shrubs decrease.

B. When the pasture pressure is very high, i.e. when the stock density is equal to the carrying capacity, the simulations must first show a progressive decrease of lawns, which are replaced by meadows. The following step is the decrease of the shrubs, the last step being the slow disappearing of the trees, which cannot regenerate. The long-term effects of a huge over-grazing are not to be taken into account in this model, since we consider that (1) the carrying capacity might not be overshoot and (2) the total area covered by herbaceous homoecies cannot decrease.

C. From diachronic comparisons of aerial photographs, we have observed that the vegetation pattern of some wooded pastures did not change with time (Gallandat et al., 1995a). We can deduce from this observation that if environmental conditions are constant and compatible with the coexistence of both forest and pasture subsystems, the composition of the vegetation might tend to a steady-state.

3. Methods

The qualitative nature of the model presented in the introduction (Fig. 1) does not allow predictions of the global dynamic behaviour of the system, but it can be useful as a step in the elaboration of a quantitative model. For this elaboration, we use STELLA software (Peterson and Richmond, 1996) to transform our generalised qualitative model of wooded pasture into a quantitative compartment model. STELLA is a famous simulation development environment, whose modularity and user-friendly graphical interface allow to manage easily very complex models (Costanza et al., 1998; Costanza and Gottlieb, 1998). Among many ecological applications, it was used to model population dynamics in woody rangelands (Whisenant, 1991) and was the central modelling framework of the General Ecosystem Model, designed to simulate a variety of ecosystem types using a fixed model structure (Fitz et al., 1996).

3.1. Building structure

The construction of a model with STELLA is an iterative process (Richmond and Peterson, 1997). After having defined the purpose, stated the assumptions and developed a system diagram, the first step is to flesh out the map of our hypotheses by building the structure of the STELLA diagram, i.e. defining state variables, flows, parameters, auxiliary variables, and linking these building blocks with connectors. After that, we have to make this map computable, i.e. to specify the associated algebra and include numbers.

3.2. Calibration and tests

The calibration is the most tricky and time-consuming step of the modelling process. Precise data, like time series or experimental results, were not available to estimate the key parameters of the equations, so that the optimisation process was mainly intuitive and empirical, using a trial-and-error recursive method (Fig. 3).

After the first definition of equations and parameters, robustness tests were applied to eliminate trivial errors, until the model exhibit realistic outputs according to the two first reference behaviour patterns A and B (cattle density null or very high). Sensitivity tests were used to search the most sensitive parameters and to adjust their values.

Known equilibrium situations were used as initial conditions to adjust more precisely the parameters, up to obtain realistic steady-state reference behaviour patterns C (steady-state tests).

Knowing initial conditions and predictable evolution of six concrete phytocoenoses, chosen in different situations, parameters and flow rates were finally adjusted so that the simulation output fit with the dynamic behaviour expected for each of them (behaviour tests).

Concerning simulation algorithm, Euler and 4th-order Runge-Kutta methods were used to perform calculations, with time step dt set to 0.5 year.

3.3. Steady-state analysis

Once the model PATUMOD is calibrated, some conditions of equilibrium were investigated using series of simulations. Due to the model complexity, it is very difficult to use analytical methods for this purpose and we have foregone describing any equilibrium condition.

Two different ways can be used to perform a steady-state analysis: (i) solve the highly non-linear system of algebraic equations derived from the differential equations; (ii) solve the system of differential equations and use the values corresponding to a stationary solution. In both cases numerical methods have to be used in view of the high non-linearity of the equations. In case (i), fixed point or Newton–Raphson methods are in common use and require heavy computations. We preferred strategy (ii) since in this case the simple explicit Euler or Runge–Kutta scheme can be used. Moreover this method allows the study of the time evolution of the system. Notice the steady-state obtained using any numerical method is the same for all (conditionally) stable algorithm.

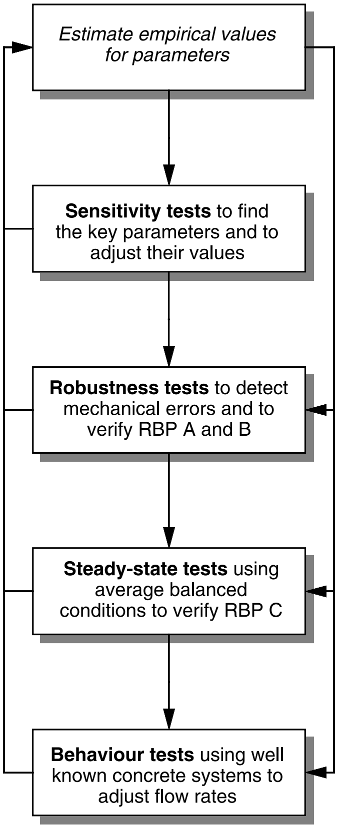

Fig. 3. The optimization process applied to calibrate the model. RBP, reference behaviour pattern.

The pastoral values of the homoecies, depending on the species composition and determining the forage yield, were set to their observed mean values. The pastoral value of the pastoral unit was also considered as a constant (21). For each of three chosen values of altitude (middle value: 1000 m a.s.l.; extreme values: 600 and 1600 m a.s.l.), a series of values for the global stock density was considered, ranging from 0 to a maximum value, obtained when the local stock density was reaching the carrying capacity. For each value of the global stock density, the initial values of the homoecies were adjusted to their final values up to obtain no change in these values at a precision of 0.1% and during a last simulation run of 1000 years. The phytocoenotic system was thus considered to be in steady-state; the values of state variables and other characteristic local variables were recorded. The type of phytocoenosis was deduced from the tree cover and from the proportions of herbaceous homoecies (c.f. Section 1).

3.4. Sensitivity analysis

To illustrate the effects of changing the main control parameter of the model, we applied successively different values of the global stock density to an initially balanced system at a middle altitude of 1000 m a.s.l.

3.5. Stability analysis

Stability analyses were used to assess the stability and the resilience of the system, starting from a steady-state and simulating the effects of a disturbance affecting a particular state variable.

The effect of a sudden reduction of the tree cover was studied by applying different values of the trees' clearing rate (harvesting intensity ranging from 0 to 1), starting from two balanced situations at 1000 and at 600 m a.s.l. In each case, simulation runs allowed to know if the system recovered its initial equilibrium after disturbance, evolved towards a new steady-state, or entered into a periodic or chaotic regime.

3.6. Scenario analysis

The calibrated model was thereafter applied to different management scenarios. For this purpose, we added several control features to PATUMOD: cutting-out shrubs or trees with varying beginning, intensity and period; modifying stock density. The user interface was developed in order to manipulate easily the model, using sliders and high-level authoring tools.

4. Results

4.1. Model structure and assumptions

The STELLA diagram of PATUMOD (Appendix A) is subdivided into four sectors: trees, shrubs, herbs and cattle. The system is composed of (1) seven state variables or compartments (rectangles), which accumulate (the six homoecies and the local stock density), (2) several flow variables (small circles with 'pipes'), connected to one or two state variables and containing differential equations, (3) many constants, or parameters, and instantaneous auxiliary variables (large circles). Sources and sinks (clouds) are connected to non-conserved flows and indicate model boundary. A lot of connectors (arrows) establish logic links between these components.

The stock density (cattle load) is expressed in ABU days per hectare and per year. One adult bovine unit (ABU) is equivalent to a dairy cow; other types of animals correspond to a fraction of an adult bovine unit, in proportion to their forage consumption (e.g. in Switzerland, 0.8 for a suckler cow, 0.7 for a steer, 0.6 for a 2–3-year-old heifer, 0.4 for 1–2-year-old growing steer or heifer, 0.25 for a calve less than 1-year-old). The global stock density (GSD) of a pastoral unit is calculated from the amount of ABU in the herd H, the effective grazing duration GD in the patch (in days per year) and its area PA (in hectares):

$$\mathrm{GSD} = \frac{\mathrm{H} \times \mathrm{GD}}{\mathrm{PA}} \text{ (ABU day/ha/year)} \qquad (1)$$

The pastoral value, which ranges theoretically from 0 to 100, is a synthetic empirical measurement of the forage availability of the patch, based on productivity, digestibility and attractiveness of each grassland species, summarised into a single quality index (Daget and Poissonet, 1971). The global pastoral value of the pastoral unit is calculated from the vegetation map (Gallandat et al., 1995b). A regression analysis has shown that a good estimation of the annual forage production P could be obtained from pastoral value PV and altitude A:

$$\mathrm{P} = \frac{115\,000 \times \mathrm{PV}}{\mathrm{A}} \text{ (kg dry matter/ha/year)} \qquad (2)$$

This forage production determines the maximum stocking rate or global carrying capacity of the pastoral unit GCC (Gallandat et al., 1995b). The calculation is based on an estimate forage consumption of 18 kg dry matter per ABU and per day:

$$\mathrm{GCC} = \frac{\mathrm{P}}{18} \text{ (ABU day/ha/year)} \qquad (3)$$

The global utilization rate of the pastoral unit GU is calculated as the ratio between the global stock density GSD and the global carrying capacity GCC:

$$\mathrm{GU} = \frac{\mathrm{GSD}}{\mathrm{GCC}} \text{ (no dimension)} \qquad (4)$$

It is assumed that the utilization rate must always be lower or equal to 1 (100%).

Global stock density, pastoral value, carrying capacity and utilization rate of the pastoral unit are considered as constants and are not affected by vegetation changes inside the phytocoenosis. By contrast, at the phytocoenosis level, the local stock density (LSD) is a state variable, while local pastoral value (LPV), carrying capacity LCC and utilization rate LU are instantaneous variables.

At initial conditions, the local stock density of the phytocoenosis LSD is equal to the global stock density of the pastoral unit GSD multiplied by the ratio between the local and the global pastoral value:

$$\mathrm{LSD} = \mathrm{GSD}\,\frac{\mathrm{LPV}}{\mathrm{GPV}}\ (\mathrm{ABU\ day/ha\ per\ year}) \qquad (5)$$

This relation expresses the hypothesis that cattle concentrates in phytocoenoses where pastoral value is high in comparison with the value of the pastoral unit. The phytocoenosis will have an attractive or repulsive effect according to its relative forage availability.

The local pastoral value of the phytocoenosis depends on the changing relative cover and on the pastoral value, supposed constant, of the different herbaceous homoecies. Changes of the pastoral value of the phytocoenosis LPV determine directly those of its carrying capacity LCC. During the dynamic process, the local stock density LSD adjusts itself so that the utilization rate of the phytocoenosis LU tends to be equal to this of the whole pastoral unit GU.

To simulate non-linear effects of altitude and local stock density on vegetation dynamics, two converters are used in the equations of the flows, called respectively altitude effect and grazing pressure. Their values range between 0 and 1 (arbitrary units).

The equation converting altitude A into altitude effect AE is a sigmoid function using two parameters (b and c):

$$\mathrm{AE} = \frac{\exp(b(\mathrm{A} - c))}{1 + \exp(b(\mathrm{A} - c))}\ (\text{no dimension}) \qquad (6)$$

These parameters are calibrated so that the altitude effect is close to 1 when altitude is below 600 m a.s.l., close to 0 when altitude is above 1600 m, and 0.6 when altitude is 1000 m. This altitude effect increases the development of shrubs, trees and the transformation of lawns into fallows.

The grazing pressure GP is an auxiliary instantaneous variable depending directly only on the local stock density LSD, according to an exponential function:

$$\mathrm{GP} = 1 - \exp(d \times \mathrm{LSD})\ (\text{no dimension}) \qquad (7)$$

The grazing pressure plays a key role in the model: it controls directly six flows, concerning meadows, lawns, fallows, shrubs (effect of browsing on their extension and regression) and trees (effect on their development only).

The herbaceous vegetation is divided into four interconnected compartments, without any flow connected to sources, sinks or other homoecies, so that the sum of them is constant and adjusted to 1 (100%) from the beginning of each simulation. Changes in herbaceous vegetation depend on grazing pressure, altitude effect and percentage cover of trees and shrubs. It is assumed that temporal transformations between lawns and meadows are not blocked by edaphic or topographic heterogeneity, the phytocoenosis being considered as spatially homogeneous.

The local pastoral value is calculated at each time step dt from the composition of the herbaceous vegetation. Changes in this pastoral value modify the carrying capacity and the utilization rate of the phytocoenosis, which influences changes in local stock density and grazing pressure, which itself modifies the composition of the herb layer. This process includes some of the main feedback loops of the model (see diagram, Appendix A).

Two herbaceous homoecies, fallows and underwoods, influence positively the development of shrubs, which is restrained by grazing pressure, altitude effect and tree cover. Tree regeneration depends itself on shrub cover, grazing pressure and altitude effect. A feedback connection between the tree compartment and its inflow ensures that the latter is null when the percentage cover is reaching 100%. The same regulation is applied to the shrub compartment.

A diversity index (Shannon entropy) is also calculated at each time step, depending mainly on the differences in relative cover of all homoecies. While it is not comparable to the real species or community diversity of the vegetation, it is assumed that its variations reflect those of biodiversity indices.

The equations of PATUMOD are given, according to their order of execution, in Appendix B.

4.2. Steady-state analysis

Results for a middle altitude of 1000 m a.s.l. are given in Figs. 4–7 and Appendix C. The relationship between the global stock density of the pas-

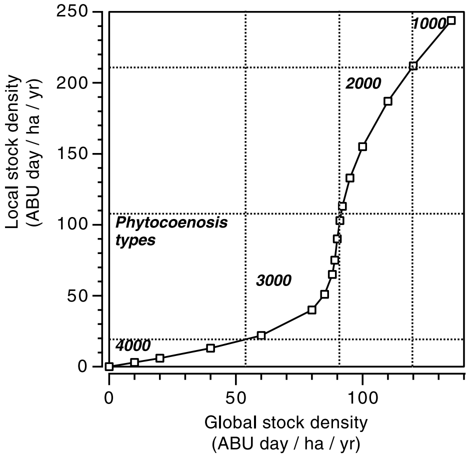

Fig. 4. Balanced values of the local stock density of the phytocoenotic system at 1000 m a.s.l., for different values of the global stock density.

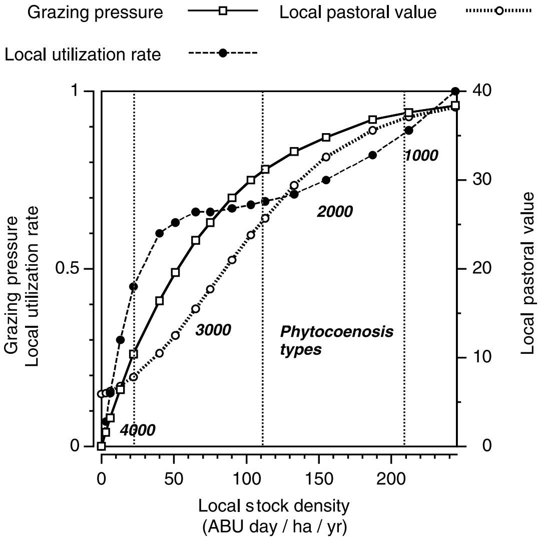

Fig. 5. Balanced values of the grazing pressure, the utilization rate and the pastoral value of the phytocoenotic system at 1000 m a.s.l., for different values of the local stock density.

toral unit and the local stock density of the phytocoenosis in balanced ecosystems is expressed by a S-shaped curve (Fig. 4). Scarcely (type 2000) and densely (type 3000) wooded pastures can survive only if the global stock density is ranging between ca. 50 and 120 ABU day/ha/year. The range of the global stock density decreases from type 4000 (forests) to 1000 (unwooded pastures). The inflexion point of the curve corresponds approximately to the boundary between types 2000 and 3000, at ca. GSD = 90 ABU day/ha/year. Near this point—one of the two only balanced states where global and local stock densities are equal—a little difference in the global stock den-

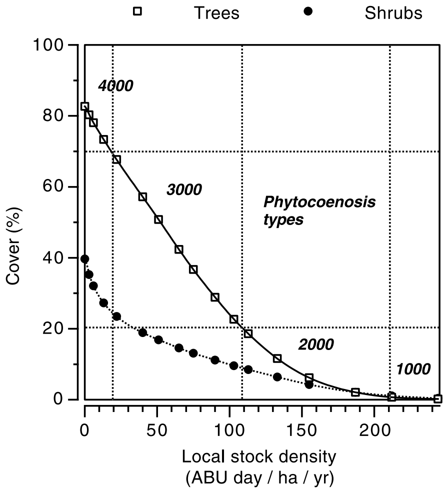

Fig. 6. Balanced values of the tree cover and the shrub cover within the phytocoenotic system at 1000 m a.s.l., for different values of the local stock density, with interpolated curves.

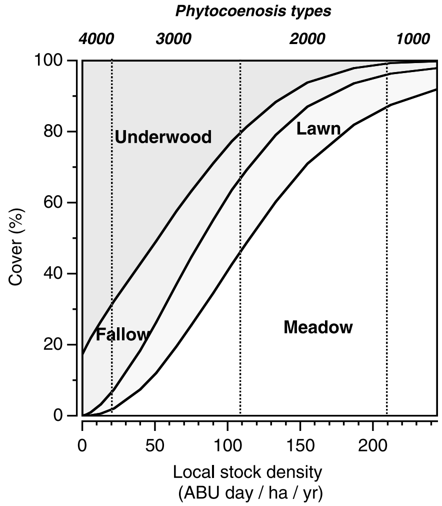

Fig. 7. Balanced values of the relative covers of the components of the herb layer within the phytocoenotic system at 1000 m a.s.l., for different values of the local stock density.

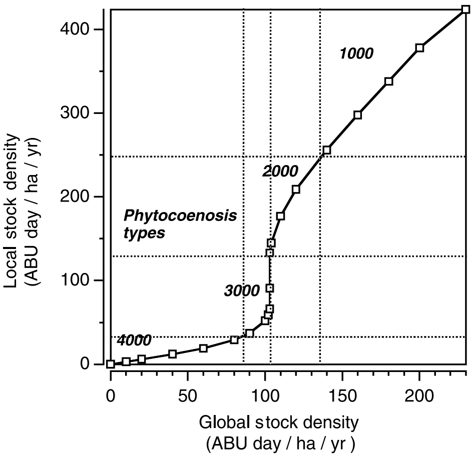

Fig. 8. Balanced values of the local stock density of the phytocoenotic system at 600 m a.s.l., for different values of the global stock density.

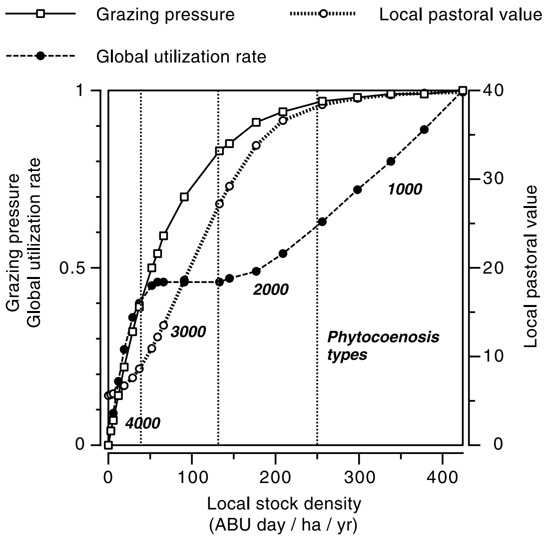

Fig. 9. Balanced values of the grazing pressure, the utilization rate and the pastoral value of the phytocoenotic system at 600 m a.s.l., for different values of the local stock density.

sity entails a great increment in the local stock density. If we plot the utilization rate of the phytocoenosis versus its stock density (Fig. 5), this situation appears to correspond to a plateau, where the slope is the lowest. At this point, the grazing pressure is at about 70% of its maximum value. At each combination of the environmental parameters (global stock density and pastoral value) corresponds a single point attractor in the phase space for the seven state variables. When the system is in steady-state, the tree cover, the shrub cover (Fig. 6) and the composition of the herb layer (Fig. 7) can be deduced from the local stock density. Considering the phase plane of the two state variables local stock density and tree cover (Fig. 6), we can easily fit a curve through the simulated point attractors (by an interpolation method), which contains all possible points of stable equilibrium, up to 244 ABU day/ha/year, the maximum sustainable stock density at this altitude.

When altitude is set to 600 m a.s.l. (Figs. 8–10 and Appendix C), some differences appear. The maximum sustainable stock density of the phytocoenosis is now reaching 424 ABU day/ha/year. The survival domain of typical wooded pastures is between ca. 90 and 130 ABU day/ha/year for the global stock density (Fig. 8). The critical value for the transition between type 2000 and 3000 is about 103 ABU day/ha/year. A very interesting feature concerns the possibility to obtain three equilibria for a same global stock density close to this value, depending on the initial proportions of homoecies. In this region of the phase space (Fig.

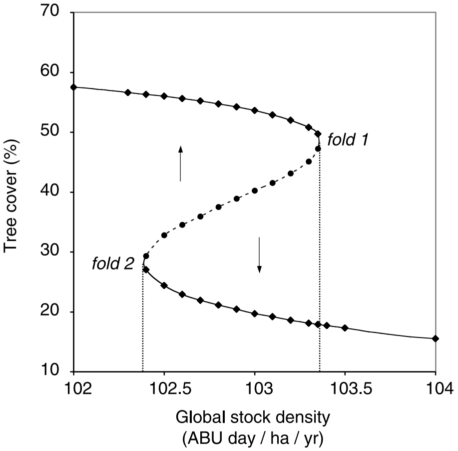

Fig. 10. Bifurcation diagram of the tree cover within the phytocoenotic system at 600 m a.s.l., for different values of the global stock density, characterized by twofold bifurcations. The solid lines indicate stable equilibria, whereas the dashed line represents an unstable equilibrium.

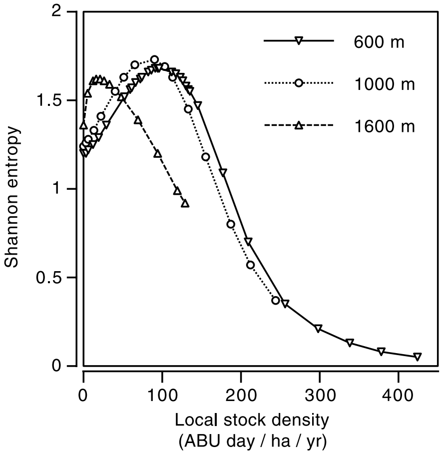

Fig. 11. Balanced values of the Shannon entropy of the phytocoenotic system at 600, 1000 and 1600 m a.s.l., for different values of the local stock density.

9), the local utilization rate is constant while the variation in grazing pressure and local pastoral value is strong. The middle equilibrium requires a precise adjustment of the initial values of homoecies in the particular situation where the local variables pastoral value and stock density are close to the global values: this equilibrium is unstable and evolves at very long term—after several thousand years—towards one of the two others. This point in the phase space can be interpreted as a repellor. It has other interesting properties: it corresponds precisely to the maximum value of the Shannon entropy and to the inflexion point in the sigmoid curve representing local pastoral value versus local stock density (Fig. 9) as well.

A bifurcation analysis, according to the geometric approach presented by Rinaldi and Scheffer (2000), shows that the system has two alternative stable equilibria (attractors) for $102.3 < \mathrm{GSD} < 103.4$, separated by an unstable equilibrium (repellor). The bifurcation diagram (Fig. 10) representing the tree cover (state variable) with respect to the global stock density (control parameter) is characterized by two fold bifurcations, which explain catastrophic shifts of equilibria at this low altitude. Close to each fold bifurcation or to the saddle line separating the two basins of attraction, the system evolves very slowly.

At 1600 m a.s.l., the tree cover cannot exceed 40%, so that only three phytocoenosis types can be obtained. The transition between densely and scarcely wooded pastures occurs for a global stock density ca. 25 ABU day/ha/year. The survival domain of these wooded pastures is between 0 and 80 ABU day/ha/year for the global stock density. The cover of oligotrophic lawns is more important than at lower altitudes, even in unwooded pastures. These features are consistent with our observations in real systems near this high altitude.

Whatever the altitude may be, the Shannon entropy shows an unimodal relation to the local stock density at equilibrium (Fig. 11). The optimum values are about 100 ABU day/ha/year at 600 m a.s.l., 90 ABU day/ha/year at 1000 m a.s.l. or 30 ABU day/ha/year at 1600 m a.s.l. They correspond to densely wooded pastures at 600 and 1000 m a.s.l. or to scarcely wooded pastures at 1600 m a.s.l. These results are also consistent with comparative statistics about biodiversity performed in real silvopastoral ecosystems (Gallandat et al., 1995a).

4.3. Sensitivity analysis

When the initial conditions are far from that of the steady-state, the system tends to evolve towards a stable equilibrium, after a more or less complicated and long trajectory. The attractor is nearly always a single point, even if sometimes difficult to reach.

Starting from a balanced phytocoenosis—a densely wooded pasture at 1000 m a.s.l. with a global stock density of 90 ABU day/ha/year and a global pastoral value of 21—, we have analysed the consequences of changing the global stock density at each simulation (Fig. 12). When the coordinates of the initial point in the phase plane (tree cover and local stock density) are outside an attractor line, the system evolves towards a new configuration, which is a point on the attractor line. The process can take more than thousand years, but at each global stock density is corresponding a single attractor point. The attractor line is confounded with the curve fitting the steady-state points (see Fig. 6).

4.4. Stability analysis

To assess the stability and the resilience of the system, we have started with the same densely wooded pasture in steady-state at 1000 m a.s.l., and we have disturbed it by affecting once only the tree cover 10 years after the beginning of each simulation of 3000 years. In the phase plane (Fig. 13), we can observe that for each value of the clearing rate between 20 and 100%, the system evolves rapidly towards a transient attractor line, and then follows more slowly this line to recover at long term the same attractor point.

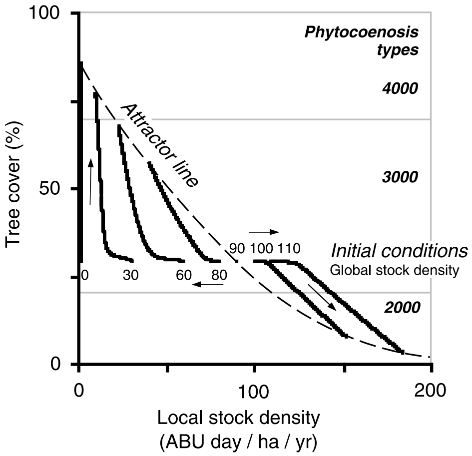

Fig. 12. Sensitivity runs starting from different values of the global stock density and from a same initial composition of the phytocoenotic system (densely wooded pasture at 1000 m a.s.l.).

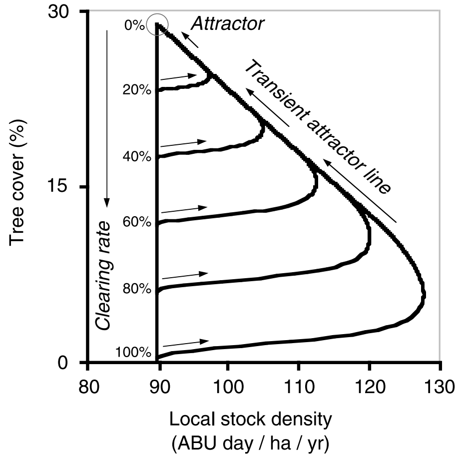

Fig. 13. Stability analysis of the response of tree cover and local stock density at different intensities of disturbance affecting a balanced phytocoenotic system (densely wooded pasture at 1000 m a.s.l.).

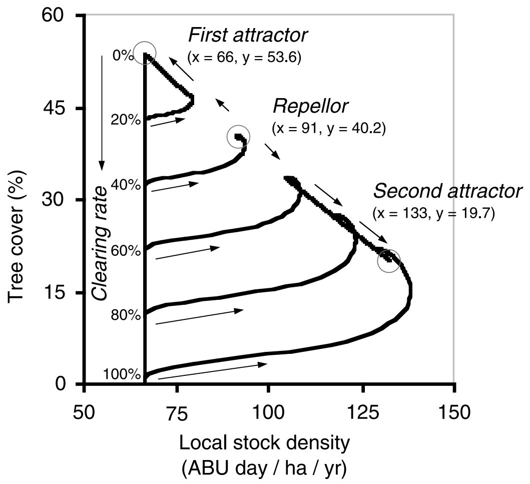

Fig. 14. Stability analysis of the response of tree cover and local stock density at different intensities of disturbance affecting a balanced phytocoenotic system (densely wooded pasture at 600 m a.s.l.).

A remarkable exception to this general behaviour can be observed when the model is set up with an altitude of 600 m a.s.l., a global pastoral value of 21 and a global stock density of 103 ABU day/ha/year (Fig. 14). In this case, the stability analysis reveals two attractor points, instead of one. The first attractor is corresponding to the initial configuration of the steady-state (densely wooded pasture with more than 50% tree cover), the second one to a scarcely wooded pasture, with about 20% tree cover. The two basins of attraction are separated by a boundary, which includes the repellor identified in the steady-state analysis (at about 40% tree cover). A simulation starting with a tree cover near 32% leads to this unstable equilibrium, the variation of the tree cover not exceeding 0.01% during 5000 years. When the initial disturbance is leading close to this critical boundary, the system evolves first rapidly towards a ‘pseudo-attractor’, localised on the transient attractor line, then seems to stabilise at this point for about hundred years, before beginning a long divergent trajectory towards one of the two attractors.

4.5. Scenario analysis

Different management scenarios can be applied to test their effectiveness, having regard to expected objectives.

As an example, let us consider the problem of finding a sustainable management for a scarcely wooded pasture located at 1100 m a.s.l. (Fig. 15). During the 30 first years, the stock density of the pastoral unit is maintained at 50 ABU day/ha/year and 10% of the trees are harvested every 20 years. The system is far from the steady-state: rapidly, eutrophic meadows are replaced by fallows, involving the development of shrubs. To prevent this negative evolution without changing the stock density, the owner decides to cut 80% of the shrubs every 5 years from the 30th year. This intervention entails a relative stabilising of the system, but with a herb layer still dominated by fallows. From the 60th year, it is decided to increase the period (10 years) and to decrease the rate (40%) of shrub cutting, while increasing the global stock density up to 85 ABU day/ha/year. These new conditions reverse the process, but tree regeneration is not ensured anymore. Finally, from the 90th year, the stock density is adjusted to 80 ABU day/ha/year and all human direct interventions on shrubs and trees are stopped. Then we obtain the desired conditions for a long-term sustainable management of this wooded pasture: steady-state at a high level of biodiversity and pastoral value, with only few human interventions.

5. Discussion

5.1. Comparison with other models

Recently, several models of silvopastoral ecosystems have been developed, which can be compared with PATUMOD.

ALWAYS (Bergez and Msika, 1996; Bergez et al., 1999) is an object-oriented model which describes the biophysical functioning of a silvopastoral system, considering the interactions processes between five components (tree, sward, sheep, soil and climate) at a plot and daily scale. The biotic components of this model are simpler than in PATUMOD, but the global functioning of the ecosystem is more explicit. Its specifications are designed for intensive agroforestry (artificial and simplified ecosystems), while PATUMOD is adapted to extensive management of seminatural established pasture woodlands.

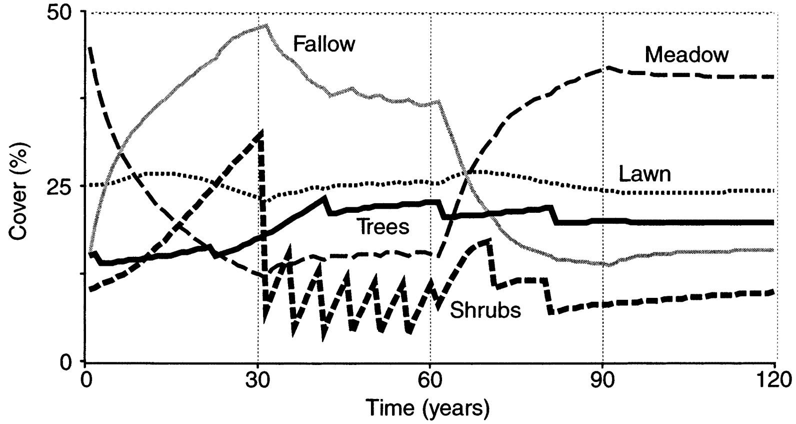

Fig. 15. Scenario analysis of the management of a scarcely wooded pasture at 1100 m a.s.l. (explanations in text).

FORGRA (Jorritsma et al., 1999) is an example of a dynamic simulation model of forest development in relation to ungulate grazing, which is an illustration of system analysis. The main state variables are dominant species; the parameterisation concerns 12 tree and shrub species, six herba-ceous species and four ungulate species. This plot-based model provides insight in the influence of selective browsing and grazing by wild or domestic ungulates upon tree regeneration in lowland forest-heathland ecosystems on poor sandy soils. The structural aspects of plant communities, quite important in more diverse wooded pastures, are ignored in this model based on the interactions between few plant and herbivore populations.

Frame-based modelling is a method of simulating rangeland production systems in the long term proposed by Hahn et al. (1999). Frames correspond to distinct states of the system (e.g. grasslands with scattered mature trees). Independent models are developed for each frame, which simulate the key processes identified within that frame, depending on rainfall, stocking density and animal condition. Rules are established for switching frames. Even if it can be considered as an interesting way to manage both long-term changes and short-term processes, this frame-based model cannot be used to understand vegetation dynamics at community level.

5.2. Ecological implications

PATUMOD has addressed at least one of our main objectives: to prove the sustainability of our set of hypotheses based on a dynamic scheme at the community level. The exploration of the model has shown that these assumptions could lead to realistic features, even if these features cannot be considered as a true validation. It is generally assumed that validation of long-term predictions of ecological models is rather impossible.

But the heuristic interest of PATUMOD is to bring sound explanations of some features observed in real systems. For example, the limit between scarcely and densely wooded pastures was defined empirically—about 20% tree cover—from physiognomic and phytosociological data (Gallandat et al., 1995a); model simulations show that this limit corresponds precisely to a dynamic threshold, characterised by a high sensitivity to small variations in stock density, especially at low altitude. At 600 m a.s.l., the model predicts that a densely wooded pasture has no stable equilibrium between 30 and 50% tree cover. PATUMOD revealed also that wooded pastures with a high Shannon entropy, and therefore a high biodiversity, were more unstable: in these conditions, the steady-state was difficult to reach and required a precise adjustment of the stock density. These important results might be confirmed by experimental studies.

Van Hulst (1992) has shown that the general pattern of successional species replacement can be faithfully reproduced by a variety of simple models, even if based on very restrictive, reductionist and unrealistic assumptions. According to this author, ‘some progress can be achieved in succession modelling once mathematical models of sufficient sophistication are being used’, in order ‘to avoid both the Scylla of phenomenological curve fitting and the Charybdis of a mechanistic particularism’. If we agree with this opinion, we are also convinced that sound models of vegetation dynamics cannot be only based upon a reductionist approach, which simply ignore the community-level phenomena.

The system approach has been recently criticised by many population ecologists, who do not recognise any utility to such basic concepts as system, equilibrium, emergence and hierarchy. Yet, former ecologists have played an important role in the elaboration of these concepts, which have been successfully applied in many sciences. The modelling process cannot be reduced to a reductionist point of view; moreover, it can help us to understand how complex (low-level) systems can generate simple (high-level) structures and behaviour, or how simple systems can generate complex and unpredictable patterns, reducing the field of poor stochastic explanations.

5.3. Management implications

PATUMOD model can be used to predict the dynamical trends of a concrete phytocoenosis at short term and to determine the attractor at long term. This prognostic is quite crucial for management purposes.

Careful planning is needed to meet the needs of trees, forage and livestock. Sustainability is the essence of successful silvopastoral practices. It entails long-term production of goods and services with a minimum of resource depletion and environmental deterioration.

In this scope, PATUMOD has proved to be a useful tool by its prediction abilities and scenario analyses (Gallandat and Gillet, 1999).

5.4. Model limitations

This model does not take into account the spatial heterogeneity inside the phytocoenosis (microtopography, soil mosaic, vegetation pattern), which can limit the connectivity between synusiae and the possibilities of temporal transformations.

Considering homoecies as building blocks is a severe simplification. A more precise simulation of vegetational change within and between homoecies requires to consider processes at synusia level; future developments of PATUMOD could concern dynamics of plant functional types and keystone species, exploring potential connections between population and community dynamics (Verweij, 1995; Olff et al., 1999).

The assumed invariance of the environmental parameters (global stock density and carrying capacity) neglects the influence of local dynamics on the environment of the system and can lead to unrealistic long-term predictions.

A lot of misunderstood processes do influence vegetation dynamics in wooded pastures, which are not taken into account in this model (effect of slope, aspect, high altitude, selective behaviour of cattle, etc.).

PATUMOD focuses on the vegetation and the ecological space, but two other points of view are interesting to consider in silvopastoral systems: the point of view of the animal and that of the human actors (Hubert, 1991). The integration of ecological and economic dynamics requires considering different spatiotemporal scales (Costanza et al., 1993). The use of spatial modelling environments (Maxwell and Costanza, 1997), multi-agent simulations (Bousquet et al., 1998; Bakam and Bousquet, 1999; Mechoud et al., 1999) and multimodelling methods (Lee and Fishwick, 1996; Maxwell, 1999) could be complementary means to find an issue out of the limitations of the current models.

Thus, to resolve the limitations of PATUMOD, we are planning (1) to develop spatially explicit grid-based models at different levels of organisation (synusia, phytocoenosis, landscape), (2) to get more precise data for calibration and validation, from field experiments and observations, (3) to integrate models at different space and time scales into multimodels.

Acknowledgements

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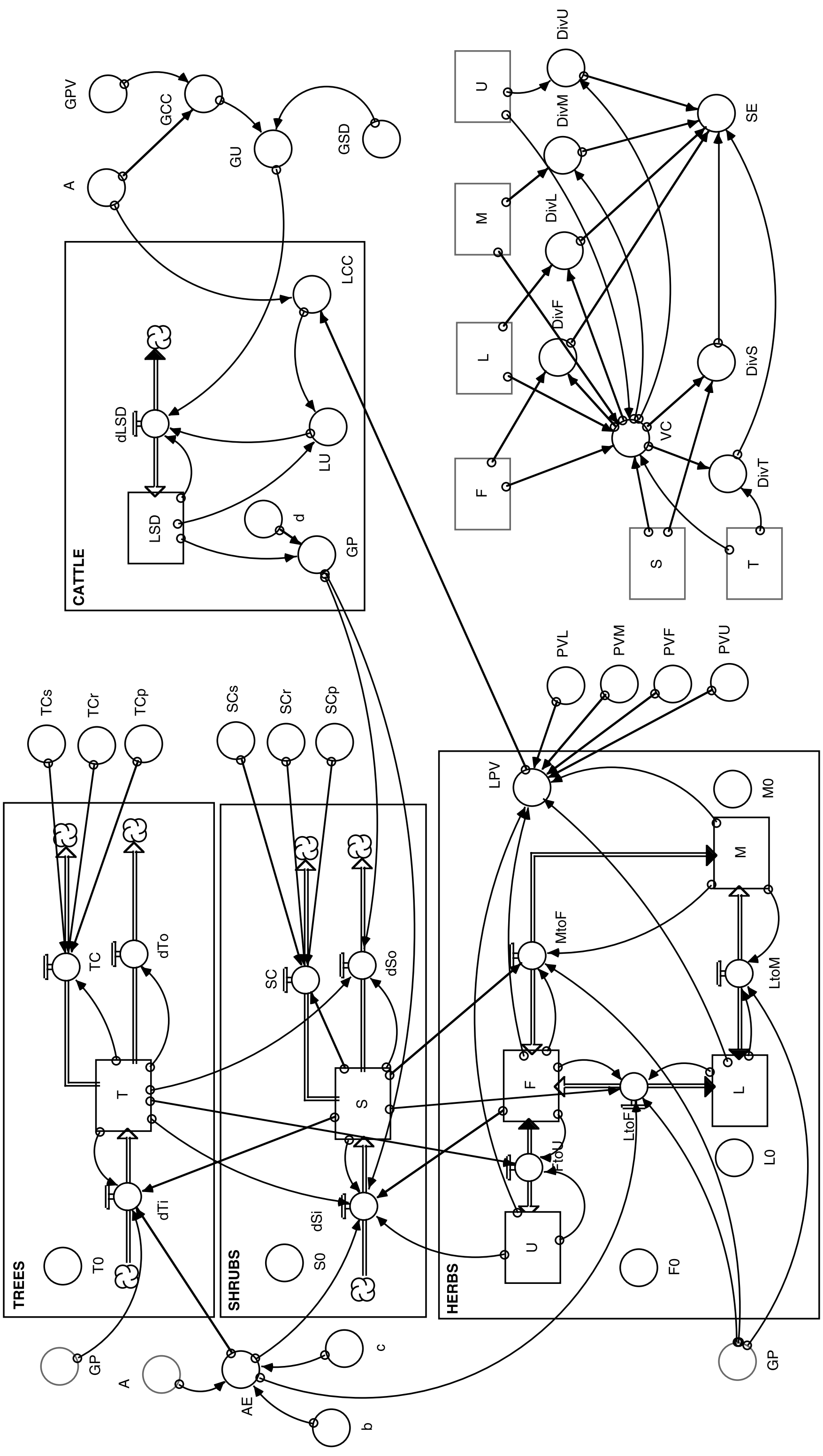
Appendix A

STELLA diagram of PATUMOD. For an explanation of the flow variables, see equations in Appendix B.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Appendix A.

Appendix B. Model equations

{INITIALIZATION EQUATIONS}

$L0 = 14.8$	Initial cover of lawns (%)
$INIT\ L = L0/100$	Oligotrophic lawns (cover between 0 and 1)
$d = -0.013305$	
$GSD = 103$	Global stock density (ABU day/ha/year)
$PVF = 10$	Average pastoral value of the fallows
$F0 = 14.7$	Initial cover of fallows (%)
$INIT\ F = F0/100$	Fallows (cover between 0 and 1)
$PVL = 20$	Average pastoral value of the lawns
$PVM = 40$	Average pastoral value of the meadows
$M0 = 30.3$	Initial cover of meadows (%)
$INIT\ M = M0/100$	Eutrophic meadows (cover between 0 and 1)
$PVU = 5$	Average pastoral value of the underwood grasslands
$INIT\ U = 1 - (L + M + F)$	Underwood grasslands (cover between 0 and 1)
$LPV = PVF \times F + PVL \times L + PVM \times M + PVU \times U$	Local pastoral value
$GPV = 21$	Global pastoral value
$INIT\ LSD = GSD \times LPV/GPV$	Local stock density (ABU day/ha/year)
$GP = 1 - EXP(d \times LSD)$	Grazing pressure (reducer between 0 and 1)
$LtoM = 0.06 \times L \times GP - 0.05 \times M \times (1 - GP)$	
$S0 = 12.3$	Initial shrub cover (%)
$INIT\ S = S0/100$	Shrubs (cover between 0 and 1)
$b = -0.005$	
$A = 600$	Altitude (m)
$c = 1081.093$	
$AE = \exp(b \times (A - c))/(\exp(b \times (A - c)) + 1)$	Altitude effect (reducer between 0 and 1)
$LtoF = 0.5 \times L \times (1 - GP) \times (0.3 + S) \times AE - 0.1 \times F \times GP$	
$MtoF = 0.8 \times M \times (1 - GP) \times (0.3 + S) - 0.4 \times F \times (GP^2)$	
$T0 = 40.2$	Initial tree cover (%)
$INIT\ T = T0/100$	Trees (cover between 0 and 1)
$FtoU = F \times (T - U)$	
$dSi = 0.2 \times DELAY((F + 0.5 \times U) \times (1 - GP), 5) \times (1 - S) \times (1 - T) \times AE$	
$dSo = (0.1 + GP) \times (0.1 + T) \times S \times 0.2$	
$SCr = 0.8$	Shrub clearing rate (between 0 and 1)
$SCs = 200$	Shrub clearing start (year)
$SCp = 200$	Shrub clearing period (years)
$SC = PULSE(SCr \times S, SCs, SCp)$	
$dTi = DELAY(S \times (1 - GP), 10) \times (1 - T) \times 0.1 \times AE$	
$dTo = T \times 0.005$	
$TCr = 0.2$	Tree clearing rate (between 0 and 1)

$\mathrm{TCs} = 200$	Tree clearing start (year)
$\mathrm{TCp} = 200$	Tree clearing period (years)
$\mathrm{TC} = \mathrm{PULSE}(\mathrm{TCr} \times \mathrm{T}, \mathrm{TCs}, \mathrm{TCp})$	
$\mathrm{VC} = \mathrm{M} + \mathrm{L} + \mathrm{S} + \mathrm{F} + \mathrm{T} + \mathrm{U}$	Total vegetation cover
$\mathrm{DivF} = \mathrm{IF}(\mathrm{F} = 0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{F}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{F}/\mathrm{VC}))$	
$\mathrm{DivL} = \mathrm{IF}(\mathrm{L} = 0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{L}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{L}/\mathrm{VC}))$	
$\mathrm{DivM} = \mathrm{IF}(\mathrm{M} = 0)\mathrm{THEN}(0)$ $\mathrm{ELSE}(\mathrm{M}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{M}/\mathrm{VC}))$	
$\mathrm{LCC} = \mathrm{LPV} \times 115000/18/\mathrm{A}$	Local carrying capacity (ABU day/ha/year)
$\mathrm{GCC} = 115000 \times \mathrm{GPV}/18/\mathrm{A}$	Global carrying capacity (ABU day/ha/year)
$\mathrm{DivT} = \mathrm{IF}(\mathrm{T} = 0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{T}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{T}/\mathrm{VC}))$	
$\mathrm{DivS} = \mathrm{IF}(\mathrm{S} = 0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{S}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{S}/\mathrm{VC}))$	
$\mathrm{DivU} = \mathrm{IF}(\mathrm{U} = 0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{U}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{U}/\mathrm{VC}))$	
$\mathrm{SE} = -(\mathrm{DivT} + \mathrm{DivS} + \mathrm{DivF} + \mathrm{DivL} + \mathrm{DivM} + \mathrm{DivU})$	Shannon entropy (diversity index of the phytocoenosis)
$\mathrm{LU} = \mathrm{LSD}/\mathrm{LCC}$	Local utilization rate (between 0 and 1)
$\mathrm{GU} = \mathrm{GSD}/\mathrm{GCC}$	Global utilization rate (between 0 and 1)
$\mathrm{dLSD} = \mathrm{IF}(\mathrm{LU} < 1)\mathrm{THEN}(\mathrm{LSD} \times (\mathrm{GU} - \mathrm{LU}))$ $\mathrm{ELSE}(\mathrm{LSD} \times (1 - \mathrm{LU}))$	
{RUNTIME EQUATIONS}	
$\mathrm{L}(t) = \mathrm{L}(t - dt) + (-\mathrm{LtoM} - \mathrm{LtoF}) \times dt$	Oligotrophic lawns (cover between 0 and 1)
$\mathrm{F}(t) = \mathrm{F}(t - dt) + (\mathrm{LtoF} + \mathrm{MtoF} - \mathrm{FtoU}) \times dt$	Fallows (cover between 0 and 1)
$\mathrm{M}(t) = \mathrm{M}(t - dt) + (\mathrm{LtoM} - \mathrm{MtoF}) \times dt$	Eutrophic meadows (cover between 0 and 1)
$\mathrm{U}(t) = \mathrm{U}(t - dt) + (\mathrm{FtoU}) \times dt$	Underwood grasslands (cover between 0 and 1)
$\mathrm{LSD}(t) = \mathrm{LSD}(t - dt) + (\mathrm{dLSD}) \times dt$	Local stock density (ABU day/ha/year)
$\mathrm{S}(t) = \mathrm{S}(t - dt) + (\mathrm{dSi} - \mathrm{dSo} - \mathrm{SC}) \times dt$	Shrubs (cover between 0 and 1)
$\mathrm{T}(t) = \mathrm{T}(t - dt) + (\mathrm{dTi} - \mathrm{dTo} - \mathrm{TC}) \times dt$	Trees (cover between 0 and 1)
$\mathrm{LPV} = 1 \times \mathrm{PVF} \times \mathrm{F} + \mathrm{PVL} \times \mathrm{L} + \mathrm{PVM} \times \mathrm{M} + 1 \times \mathrm{PVU} \times \mathrm{U}$	Local pastoral value
$\mathrm{GP} = 1 - \mathrm{EXP}(d \times \mathrm{LSD})$	Grazing pressure (reducer between 0 and 1)
$\mathrm{LtoM} = 0.06 \times \mathrm{L} \times \mathrm{GP} - 0.05 \times \mathrm{M} \times (1 - \mathrm{GP})$	
$\mathrm{AE} = \exp(b \times (\mathrm{A} - c))/(\exp(b \times (\mathrm{A} - c)) + 1)$	Altitude effect (reducer between 0 and 1)
$\mathrm{LtoF} = 0.5 \times \mathrm{L} \times (1 - \mathrm{GP}) \times (0.3 + \mathrm{S}) \times \mathrm{AE} - 0.1 \times \mathrm{F} \times \mathrm{GP}$	
$\mathrm{MtoF} = 0.8 \times \mathrm{M} \times (1 - \mathrm{GP}) \times (0.3 + \mathrm{S}) - 0.4 \times \mathrm{F} \times (\mathrm{GP}^2)$	
$\mathrm{FtoU} = \mathrm{F} \times (\mathrm{T} - \mathrm{U})$	
$\mathrm{dSi} = 0.2 \times \mathrm{DELAY}((\mathrm{F} + 0.5 \times \mathrm{U}) \times (1 - \mathrm{GP}), 5) \times (1 - \mathrm{S}) \times (1 - \mathrm{T}) \times \mathrm{AE}$	
$\mathrm{dSo} = (0.1 + \mathrm{GP}) \times (0.1 + \mathrm{T}) \times \mathrm{S} \times 0.2$	
$\mathrm{SC} = \mathrm{PULSE}(\mathrm{SCr} \times \mathrm{S}, \mathrm{SCs}, \mathrm{SCp})$	

$\mathrm{dTi} = \mathrm{DELAY}(\mathrm{S} \times (1-\mathrm{GP}),10) \times (1-\mathrm{T}) \times 0.1 \times \mathrm{AE}$	
$\mathrm{dTo} = \mathrm{T} \times 0.005$	
$\mathrm{TC} = \mathrm{PULSE}(\mathrm{TCr} \times \mathrm{T},\mathrm{TCs},\mathrm{TCp})$	
$\mathrm{VC} = \mathrm{M}+\mathrm{L}+\mathrm{S}+\mathrm{F}+\mathrm{T}+\mathrm{U}$	Total vegetation cover
$\mathrm{DivF} = \mathrm{IF}(\mathrm{F}=0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{F}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{F}/\mathrm{VC}))$	
$\mathrm{DivL} = \mathrm{IF}(\mathrm{L}=0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{L}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{L}/\mathrm{VC}))$	
$\mathrm{DivM} = \mathrm{IF}(\mathrm{M}=0)\mathrm{THEN}(0)$ $\mathrm{ELSE}(\mathrm{M}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{M}/\mathrm{VC}))$	
$\mathrm{LCC} = \mathrm{LPV} \times 115000/18/\mathrm{A}$	Local carrying capacity (ABU day/ha/year)
$\mathrm{GCC} = 115000 \times \mathrm{GPV}/18/\mathrm{A}$	Global carrying capacity (ABU day/ha/year)
$\mathrm{DivT} = \mathrm{IF}(\mathrm{T}=0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{T}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{T}/\mathrm{VC}))$	
$\mathrm{DivS} = \mathrm{IF}(\mathrm{S}=0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{S}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{S}/\mathrm{VC}))$	
$\mathrm{DivU} = \mathrm{IF}(\mathrm{U}=0)\mathrm{THEN}(0)\mathrm{ELSE}(\mathrm{U}/\mathrm{VC} \times \mathrm{LOGN}(\mathrm{U}/\mathrm{VC}))$	
$\mathrm{SE} = -(\mathrm{DivT}+\mathrm{DivS}+\mathrm{DivF}+\mathrm{DivL}+\mathrm{DivM}+\mathrm{DivU})$	Shannon entropy (diversity index of the phytocoenosis)
$\mathrm{LU} = \mathrm{LSD}/\mathrm{LCC}$	Local utilization rate (between 0 and 1)
$\mathrm{GU} = \mathrm{GSD}/\mathrm{GCC}$	Global utilization rate (between 0 and 1)
$\mathrm{dLSD} = \mathrm{IF}(\mathrm{LU}<1)\mathrm{THEN}(\mathrm{LSD} \times (\mathrm{GU}-\mathrm{LU}))$ $\mathrm{ELSE}(\mathrm{LSD} \times (1-\mathrm{LU}))$	

Appendix C

Equilibrium conditions for different values of the altitude and of the global stock density (global pastoral value = 21). The lines in italic style correspond to unstable equilibria.

Altitude (m)	Global stock density (ABU day/ha/year)	Local stock density (ABU day/ha/year)	Grazing pressure	Local utilization rate	Local pastoral value	Shannon entropy	Meadow (%)	Lawn (%)	Fallow (%)	Underwood (%)	Shrubs (%)	Trees (%)	Phytocoenosis type
600	0	0	0.00	0.00	5.6	1.20	0.0	0.0	12.2	87.8	39.1	87.8	4000
600	10	3	0.04	0.04	5.7	1.20	0.0	0.2	13.7	86.1	34.9	86.1	4000
600	20	6	0.07	0.09	5.8	1.22	0.0	0.4	15.1	84.5	31.9	84.5	4000
600	40	12	0.14	0.18	6.2	1.25	0.3	1.1	17.3	81.3	27.6	81.3	4000
600	60	19	0.22	0.27	6.7	1.29	1.1	2.2	19.0	77.7	24.4	77.7	4000
600	80	29	0.32	0.36	7.6	1.36	2.9	4.2	20.1	72.8	21.5	72.8	4000
600	90	37	0.39	0.40	8.6	1.41	4.9	5.8	20.3	69.0	19.8	69.0	3000
600	100	52	0.50	0.45	10.9	1.52	10.3	8.9	19.5	61.3	17.3	61.3	3000
600	102	59	0.54	0.46	12.2	1.56	13.4	10.3	18.8	57.5	16.2	57.5	3000
600	102.3	61	0.55	0.46	12.5	1.57	14.2	10.6	18.6	56.6	16	56.6	3000
600	102.4	61	0.56	0.46	12.6	1.57	14.5	10.7	18.5	56.3	15.9	56.3	3000
600	102.5	62	0.56	0.46	12.7	1.58	14.8	10.8	18.4	56	15.8	56	3000
600	102.6	63	0.57	0.46	12.8	1.58	15.1	10.9	18.4	55.6	15.7	55.6	3000
600	102.7	64	0.57	0.46	13.0	1.58	15.5	11.1	18.2	55.2	15.6	55.2	3000
600	102.8	64	0.58	0.46	13.2	1.59	15.9	11.2	18.2	54.7	15.5	54.7	3000
600	102.9	65	0.58	0.46	13.3	1.59	16.4	11.4	18	54.2	15.4	54.2	3000

600	103	66	0.59	0.46	13.5	1.60	16.9	11.6	17.9	53.6	15.2	53.6	3000
600	103.1	68	0.59	0.46	13.8	1.60	17.5	11.8	17.8	52.9	15.1	52.9	3000
600	103.2	69	0.6	0.46	14.1	1.61	18.3	12.1	17.6	52	14.9	52	3000
600	103.3	72	0.61	0.46	14.6	1.62	19.5	12.4	17.3	50.8	14.6	50.8	3000
600	103.35	74	0.62	0.46	15.0	1.63	20.6	12.7	17	49.7	14.3	49.7	3000
600	*103.4*	*76*	*0.64*	*0.46*	*15.4*	*1.64*	*21.7*	*13.1*	*16.7*	*48.5*	*14*	*48.5*	*3000*
600	3.35	78	0.65	0.46	15.9	1.65	23	13.4	16.4	47.2	13.8	47.2	3000
600	103.3	82	0.66	0.46	16.7	1.66	25.2	13.8	15.9	45.1	13.4	45.1	3000
600	103.2	86	0.68	0.46	17.5	1.67	27.3	14.3	15.3	43.1	12.9	43.1	3000
600	103.1	89	0.69	0.46	18.1	1.67	29	14.6	14.9	41.5	12.6	41.5	3000
600	103	91	0.70	0.46	18.6	1.68	30.3	14.8	14.7	40.2	12.3	40.2	3000
600	102.9	94	0.71	0.46	19.1	1.68	31.8	15	14.3	38.9	12.1	38.9	3000
600	102.8	96	0.72	0.46	19.7	1.68	33.4	15.2	13.9	37.5	11.8	37.5	3000
600	102.7	99	0.73	0.46	20.3	1.68	35.2	15.4	13.5	35.9	11.4	35.9	3000
600	102.6	102	0.74	0.46	20.9	1.68	36.8	15.6	13.1	34.5	11.2	34.5	3000
600	102.5	105	0.75	0.46	21.5	1.68	38.7	15.7	12.8	32.8	10.8	32.8	3000
600	102.4	112	0.78	0.46	23.0	1.66	43	15.9	11.8	29.3	10.1	29.3	3000
600	*102.4*	*117*	*0.79*	*0.46*	*24.0*	*1.65*	*45.9*	*15.9*	*11.2*	*27*	*9.6*	*27*	*3000*
600	*102.5*	*123*	*0.8*	*0.46*	*25.1*	*1.63*	*49.2*	*15.9*	*10.5*	*24.4*	*9*	*24.4*	*3000*
600	*102.6*	*126*	*0.81*	*0.46*	*25.8*	*1.61*	*51.1*	*15.9*	*10.1*	*22.9*	*8.7*	*22.9*	*3000*
600	102.7	128	0.82	0.46	26.2	1.59	52.5	15.8	9.8	21.9	8.4	21.9	3000
600	102.8	130	0.82	0.46	26.6	1.58	53.6	15.7	9.6	21.1	8.2	21.1	3000
600	102.9	132	0.83	0.46	26.9	1.57	54.6	15.6	9.4	20.4	8.1	20.4	2000
600	103	133	0.83	0.46	27.2	1.56	55.5	15.6	9.2	19.7	7.9	19.7	2000
600	103.1	135	0.83	0.46	27.5	1.55	56.3	15.5	9	19.2	7.8	19.2	2000
600	103.2	136	0.84	0.46	27.7	1.54	57	15.5	8.9	18.6	7.6	18.6	2000
600	103.3	137	0.84	0.46	27.9	1.53	57.7	15.4	8.8	18.1	7.5	18.1	2000
600	103.35	138	0.84	0.46	28.0	1.52	58	15.4	8.7	17.9	7.5	17.9	2000
600	103.4	139	0.84	0.46	28.1	1.52	58.4	15.3	8.6	17.7	7.4	17.7	3000
600	103.5	140	0.84	0.46	28.3	1.51	59	15.2	8.5	17.3	7.3	17.3	2000
600	104	145	0.85	0.47	29.2	1.47	61.6	14.9	8.0	15.5	6.8	15.5	2000
600	110	177	0.91	0.49	33.8	1.09	76.5	12.0	5.1	6.4	3.9	6.4	2000
600	120	209	0.94	0.54	36.6	0.70	86.0	8.7	3.2	2.1	1.9	2.1	2000
600	140	256	0.97	0.63	38.4	0.35	93.0	5.0	1.7	0.3	0.5	0.3	1000
600	160	298	0.98	0.72	39.1	0.21	96.1	3.0	0.9	0.0	0.2	0.0	1000
600	180	338	0.99	0.80	39.5	0.13	97.7	1.8	0.5	0.0	0.0	0.0	1000
600	200	378	0.99	0.89	39.7	0.08	98.6	1.1	0.3	0.0	0.0	0.0	1000
600	230	424	1.00	1.00	39.8	0.05	99.2	0.6	0.2	0.0	0.0	0.0	1000
1000	0	0	0	0	5.9	1.24	0	0	17.3	82.7	39.7	82.7	4000
1000	10	3	0.04	0.07	6.0	1.26	0	0.4	19.3	80.3	35.3	80.3	4000
1000	20	6	0.08	0.15	6.2	1.28	0.1	0.9	20.9	78.1	32.1	78.1	4000
1000	40	13	0.16	0.3	6.8	1.33	0.6	2.6	23.4	73.4	27.3	73.4	4000
1000	60	22	0.26	0.45	7.8	1.41	2.1	5.3	24.9	67.7	23.5	67.7	3000
1000	80	40	0.41	0.6	10.5	1.55	7.4	11	24.4	57.2	18.9	57.2	3000
1000	85	51	0.49	0.63	12.5	1.63	12.1	14.2	22.9	50.8	16.9	50.8	3000
1000	88	65	0.58	0.66	15.5	1.70	19.6	17.5	20.5	42.4	14.6	42.4	3000
1000	89	75	0.63	0.66	17.7	1.73	25.5	19.2	18.6	36.7	13.1	36.7	3000
1000	90	90	0.7	0.67	21.0	1.73	34.5	20.6	16	28.9	11.2	28.9	3000
1000	91	103	0.75	0.68	23.8	1.69	42.7	20.9	13.7	22.7	9.6	22.7	3000
1000	92	113	0.78	0.69	25.7	1.63	48.7	20.5	12.2	18.6	8.5	18.6	2000
1000	95	133	0.83	0.71	29.4	1.45	60.3	18.8	9.3	11.6	6.4	11.6	2000
1000	100	155	0.87	0.75	32.6	1.18	71	16	6.8	6.2	4.3	6.2	2000
1000	110	187	0.92	0.82	35.6	0.80	81.9	11.7	4.3	2.1	2.1	2.1	2000
1000	120	212	0.94	0.89	37.1	0.57	87.5	8.8	3	0.7	1.1	0.7	1000
1000	135	244	0.96	1	38.2	0.37	91.9	6	1.9	0.2	0.4	0.2	1000
1600	0	0	0	0	8.1	1.36	37	43	63	0	0	37	3000
1600	10	5	0.06	0.12	10.0	1.54	30	33	55	15	0	30	3000
1600	20	12	0.14	0.14	12.2	1.61	23	25	46	29	2	23	3000
1600	30	21	0.24	0.36	14.5	1.62	16	19	39	40	5	16	2000
1600	40	33	0.35	0.48	17.1	1.59	11	14	32	47	10	11	2000
1600	60	69	0.6	0.72	24.1	1.39	3	6	20	45	32	3	2000
1600	80	119	0.79	0.95	31.2	0.99	1	1	10	28	61	1	1000
1600	90	129	0.82	1	32.3	0.92	0	1	9	25	66	0	1000

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