

1 Final published version:

2 Balzter, H. (2000): Markov chain models for vegetation dynamics. *Ecological Modelling* 126, 139-154.

3 4 Markov Chain Models for Vegetation Dynamics

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21 22 23 Abstract

24
25 A theoretical implementation of Markov chain models of vegetation dynamics is
26 presented. An overview of 22 applications of Markov chain models is presented, using
27 data from four sources examining different grassland communities with varying
28 sampling techniques, data types and vegetation parameters. For microdata, individual
29 transitions have been observed, and several statistical tests of model assumptions are

performed. The goodness of fit of the model predictions is assessed both for micro- and macrodata using the mean square error, Spearman's rank correlation coefficient and Wilcoxon's signed-rank test. It is concluded that the performance of the model varies between data sets, microdata generate a lower mean square error than aggregated macrodata, and time steps of one year are preferable to three months. The rank order of dominant species is found to be the most reliable prediction achievable with the models proposed.

Keywords

Markov chains; Grassland; Prediction; Transition matrix models; Goodness of fit; Point-quadrat method

1 Introduction

Predicting vegetation dynamics is no easy task, and some authors even doubt its feasibility (Collins and Adams, 1983). A wide range of models have been developed for application to vegetation data. These include deterministic and stochastic models for time-series and spatio-temporal data. Markov chains are stochastic processes, and can be parameterised by empirically estimating transition probabilities between discrete states in the observed system. Their usefulness in forest communities in New England and Wisconsin has been demonstrated as early as 1976 by Horn. In forests, transitions

between saplings and mature trees are usually examined. Based on Horn's approach other forest models were developed (Miles et al., 1985; Acevedo, 1981; Acevedo et al., 1995). Post-fire succession in *Quercus* forests in France was modelled with Markov chains by (Rego et al., 1993). Good predictions were also achieved by Runkle (1981). Other authors, however, report a low validity of predictions in hardwood forests derived from Markov chains (Barden, 1980; Binkley, 1980) and relate it to violations of the underlying assumptions. The rapid development of new remote sensing techniques in combination with improved GIS technology will potentially offer a wide range of applications of Markov chains (see Hall et al., 1988).

Grassland is characterised by a variety of interacting factors, like inter- and intraspecific competition, herbivory, weather and soil properties. Because of the large amount of potentially important factors and their interactions influencing grassland dynamics, it is very difficult to construct deterministic models. Approaches to the simulation of grassland dynamics include the rule-based spatially-explicit model of two species by Winkler and Klotz (1997), the use of artificial neural networks (Tan and Smeins, 1996), and the gap model by Coffin and Lauenroth (1990). Despite the complexity of the subject, stochastic models may empirically describe and predict changes in species composition and abundance, saving costs and labour by avoiding measurements of a large number of factors. Few authors have tried to apply Markov chains to grassland (Cooke, 1981; Usher, 1987) and heathland (Hobbs and Legg, 1983; Lippe et al., 1985).

The aim of this paper is to assess the applicability of Markov chain models to predict vegetation changes using several different data sets, both from the scientific literature and own observations. It is anticipated that the results and the insights in model behaviour will also be useful for large-scale landscape ecosystem models by using Markov chains as submodels.

2 Markov chains

The Russian mathematician Andrei Andreyevich Markov (1856-1922) developed the theory of Markov chains in his paper 'Extension of the Limit Theorems of Probability Theory to a Sum of Variables Connected in a Chain' (Markov, 1907). A Markov chain is defined as a stochastic process fulfilling the Markov property (Eq.3) with a discrete state space and a discrete or continuous parameter space. In this paper, the parameter space represents time, and is considered to be discrete. Accordingly, a Markov chain represents a system of elements making transitions from one state to another over time. The order of the chain gives the number of time steps in the past influencing the probability distribution of the present state, and can be greater than one.

The conditional probabilities $P(X_t = j | X_s = i) = p_{ij}(s, t)$ are called transition probabilities of order $r = t - s$ from state i to state j for all indices $0 \leq s < t$, with $1 \leq i, j \leq k$.

They are denoted as the transition matrix P . For k states P has the form

98

$$99 \quad P = \begin{bmatrix} p_{11} & p_{12} & \cdots & p_{1k} \\ p_{21} & p_{22} & \cdots & p_{2k} \\ \cdots & \cdots & \cdots & \cdots \\ p_{k1} & p_{k2} & \cdots & p_{kk} \end{bmatrix} \quad (1)$$

100

101 At time 0 the initial distribution of states is $P(X_0 = i) = p_i(0) \quad \forall i \in \{1, \dots, k\}$

102 The state probabilities $p_i(t)$ at time t are estimated from the relative frequencies of the k
 103 states, resulting in the vector

104

$$105 \quad \underline{p}(t) = (p_1(t), p_2(t), \dots, p_k(t)) \quad (2)$$

106

107 Denoting the ν -th observed state with i_ν , a stochastic chain fulfilling Eq. 3 is a first-
 108 order Markov chain:

109

$$110 \quad \begin{aligned} &P(X_{t+1} = i_{\nu+1} | X_t = i_\nu, X_{t-1} = i_{\nu-1}, \dots, X_0 = i_0) = P(X_{t+1} = i_{\nu+1} | X_t = i_\nu) \\ &\forall \nu \geq 2, \forall i_0, i_1, \dots, i_{\nu+1} \in \{1, \dots, k\} \end{aligned} \quad (3)$$

111

112 Predictions of future state probabilities can be calculated by solving the matrix equation:

113

$$114 \quad \underline{p}(t) = \underline{p}(t-1) \cdot P \quad (4)$$

115

116 With increasing time steps, a Markov chain may approach a constant state probability
 117 vector, which is called limiting distribution.

$$p(\infty) = \lim_{t \rightarrow \infty} p(t) = \lim_{t \rightarrow \infty} p(0) \cdot P^t \quad (5)$$

A state i is called an 'absorbing state' if the state cannot be left again once it is entered, i.e. $p_{ii}=1$. A Markov chain is time-homogeneous, if the transition probabilities are constant over time (Binkley, 1980; Usher, 1981).

For several special cases where assumptions are violated, modifications of Markov chain models have to be made. Transition probabilities are modelled as linearly dependent on ecological factors by some authors (Usher, 1987; Baker, 1989). If the time intervals between observations are not equal, specific estimation techniques are available (Frydman, 1992; 1995a; 1995b).

3 Material and methods

3.1 Model implementation

Vegetation consists of several plant populations interacting with each other and site-specific ecological factors (Odum, 1991). Changing ecological factors do not only influence the performance of plant species but may in return be modified by the species themselves, e.g. through nitrogen accumulation by *Rhizobium* bacteria. Each plant species occupies a certain physical space, both above and below the ground. Imagining

an abstract multidimensional space, bounded by available resources plant species again occupy a certain space, the ecological niche (Pratt, 1995). Each dimension of this resource space represents an ecological factor like N, P, K, pH, irradiation, land-use etc. Limitations in resource availability delineate a subspace which includes the actually consumable resources. Within this subspace one plant species has a better ability to occupy a certain segment than other species, which in due course have to evade into remaining segments or become locally extinguished. They may later colonise the site again either by immigration or from the seed bank in the soil.

Here, for modelling vegetation dynamics with Markov chains plant species are regarded as states of the chain. A transition from one state to another is equivalent to the replacement of one species in a segment of the subspace of available resources by another species. A species replacement occurs stochastically with a given probability. The analysis of the transition probabilities alone may give insights into the abilities of species to replace each other. However, predictions of future species proportions are based on the following assumptions, if not stated otherwise:

- time-homogeneity
- spatial independence
- absence of colonisation by new species
- first-order Markov dependence

Statistical analyses were carried out using SPSS 6.1.3 and 7.5.2, and EXCEL 97. Graphs were produced with CA-Cricket Graph III. If not stated otherwise α is assumed to be 5%

in hypothesis testing. Parameter estimation and calculation of predictions were performed using the windows program Markov Chain Simulator 1.0 (MCS) which was written in DELPHI 2.0 by the author. It encompasses a translated FORTRAN algorithm published by Lee et al. (1970). MCS was verified using sample data from Lee et al. (1970). The program is capable of reading macro- and microdata from ASCII files, interactively testing some model assumptions and predicting and saving reports to an output file in ASCII format. An SPSS 6.1.3 syntax file is automatically created, which calculates Spearman's R, Wilcoxon's signed-rank test and the mean square error (mse) and gives a histogram of the deviations of predictions from observations. MCS is freeware and can be ordered from the author.

3.2 Vegetation data

To ensure the use of a wide variety of vegetation data from different sites, climatic and soil conditions, three published data sets were taken from the literature and one from an own experiment. To ensure sufficiently precise parameter estimation only a subset of plant species is modelled. The criterion for species to be included is in having at least 5% percentage phytomass, percentage cover or proportion of specimen at one or more observation times. For percentage phytomass and proportion of specimen, which add to 100%, the other species are added up to a state 'others', while for percentage cover the other species are excluded from analysis and percentage cover values are normalised.

Linden

Five kilometres south of Giessen, Germany, is the experimental station Linden-Leihgestern owned by the Justus-Liebig-University. The average yearly temperature is 9.1°C and the sum of precipitation per year 587 mm. The site has a southern exposition and is relatively dry. 6 m x 8 m plots were sown in April 1982 with 15 g/m² seeds. Seed mixture A is a readily available mixture of grasses/herbs/legumes in proportions of 70/20/10, containing seven annual herbs, while seed mixture C is a specially prepared mixture of drought resistant species in proportions of 90/6.7/3.3 (Lüft, unpublished). Plot LINDEN1 had 0 cuts per year, plot LINDEN2 had 1 cut, plot LINDEN3 had 2 cuts and plot LINDEN4 had 4 cuts. Percentage phytomass was estimated each June. Seed mixture B is not examined by Lüft (unpublished), but is known to behave similar to A.

Heiliges Meer

Runge (1985) studies the vegetation dynamics of sites that were allocated to the fen nature reserve 'Heiliges Meer' near Hopsten in Northwest Germany in 1963 and 1976. He uses permanent quadrats to observe changes in percentage cover. Runge points out that the smallest quadrats are only sized 1 m², but are nevertheless representative for the surrounding vegetation.

Quadrat HEILIG1 is initially a wet ryegrass/white clover community (*Lolio-Cynosuretum lotetosum uliginosi*) on peat. There are alder woods in 20 m

distance. Runge (1985) describes a time series of 21 years with time steps of 3 years for HEILIG1. Since 1963 no more cattle grazing is taking place on the site. In 1964 and 1966 the site was covered with dead plant material which was penetrated only by a few species like sorrel, *Rumex acetosa*. Over the years the vegetation makes the transition to forest, dominated by alder (*Alnus glutinosa*), reaching a height of 1.50 m in 1967, 8 m in 1979 and 10 m in 1984. The increasing shade causes extinction of typical grassland species while the shade-tolerant tufted hair grass, *Deschampsia cespitosa*, reaches high percentage cover. Later a dense lawn of Yorkshire fog (*Holcus lanatus*) establishes itself. Runge (1985) shows with another example that 17 years after cultivation has been given up shrubs or trees are not necessarily present in this type of plant community.

Quadrat HEILIG2 is classified by Runge (1985) as a dry ryegrass/white clover community (*Lolio-cynosuretum typicum*), which developed on a brownfield given up in 1963 and consequently used for horse and sheep grazing. The soil is bleached sand and poor in nutrients. The quadrat is sized 1 m² and located in a fenced area which was excluded from grazing between 1974 and 1980. Runge (1985) observes a transition to the association *Agrostietum tenuis*.

The third quadrat HEILIG3 is sized 4 m² and located on bleached sand rich in organic material. This ryegrass/white clover community was subject to cattle grazing till 1965, followed by horse and sheep grazing from 1965 till 1976, and excluded from grazing from 1976 onwards. Since 1965 no fertilizer has been applied. Runge (1985) observes diminishing proportions of character species of the grassland communities *Molinio-*

232 *Arrhenatheretea* and increasing populations of *Festuca rubra* (creeping fescue),
233 *Dactylis glomerata* (cock's-foot) and *H. lanatus*. Runge reports on a thick layer of dead
234 plant material in 1982, causing decreasing percentage cover of *H. lanatus* and *F. rubra*.

235

236 **Zagreb**

237

238 Ilijanic et al. (1985) report on vegetation dynamics in three plots sized 9 m² with
239 different soil moisture conditions in the Botanical Garden of Zagreb between 1964 and
240 1974. The mean daily temperature is 11.6°C and the sum of precipitation 925 mm per
241 year. The plots are initially free of vegetation, and succession is directed towards
242 grassland by two cuts per year. 30 cm wide strips separate the plots from each other.
243 There are hedges in the south and in the west, and the so-called 'systematic field' in the
244 north and east, which consists of many small plots where a great variety of species are
245 grown. Plot ZAGREB1 was irrigated with 576 mm/a from March to November,
246 ZAGREB2 with 276 mm/a and ZAGREB3 received no additional water. Numbers of
247 specimen of plant species were counted, the blades of grasses, the number of rooted
248 parts of creeping plants, and the rosettes of plants without stems above-ground (Ilijanic et
249 al., 1985).

250

251 **Giessen**

252

253 Own data were sampled on a meadow in Giessen, Germany, by the point-quadrat
254 method (Goodall, 1952). The meadow is sized 616 m² and regularly mown about ten

times a year apart from an area in its centre. The point-quadrat frame holds three pins one metre above the vegetation. Sampling is performed by lowering each pin through a guide channel to the ground and then counting the number of contacts of the pin to each plant species. The frame was moved along ten parallel transects, and samples were taken at 12 frame positions on each transect. Methodological issues are described in Balzter et al. (1995).

From the point-quadrat data, percentage phytomass is estimated by linear regression of the parameter *percentage of sward (PS)* on species-specific dry phytomass proportions (*PM*) obtained by cutting six 30 cm x 30 cm plots. Regression lines are fitted for herbs and grasses separately, and three outliers are removed for herbs. The slopes of the lines are used as calibration factors. For herbs the resulting equation is $PM = 1.44 * PS$ with a coefficient of determination $r^2=0.72$ and for grasses $PM = 0.77 * PS$ with $r^2=0.98$. These factors correct the bias caused by pin diameter, which causes overestimation of grasses and underestimation of herbs due to the shapes of the leaves (Goodall, 1952).

In the analysis the three *Poa* species *P. pratensis* (smooth meadow-grass), *P. trivialis* (rough meadow-grass) and *P. annua* (annual meadow-grass) are aggregated to *Poa spp.*, because of uncertainties in species determination in the field by the three observers when the area was freshly mown. The mown and unmown area of the meadow showed different vegetation types and are treated separately. Both seasonal and yearly predictions are calculated from macro- and microdata. An overview of the eight different model applications to the Giessen data and their abbreviations is given in Table 1.

3.3 Macrodata

Macrodata are relative frequencies of states $p_i(t)$. Individual transition paths of a single object are not recorded (Lee et al., 1970). In this study, normalised percentage cover, proportion of specimen and percentage phytomass are used as state probabilities. Plant species are defined as the states of the Markov chain, a definition which is related to the concept of succession proposed by Pickett (1982). Estimation of the transition probabilities is carried out with the maximum likelihood estimator p_* , which is equal to the minimum χ^2 and the least squares estimator:

$$p_* = (X_*' \Sigma_*^{-1} X_*)^{-1} X_*' \Sigma_*^{-1} y_* \quad (6)$$

Given observations at T times and k possible states, p_* is a $(k(k-1))$ column vector, X_* is a $(T(k-1), k(k-1))$ block diagonal matrix with $k-1$ identical submatrices on the main diagonal, Σ_*^{-1} is the inverse of the covariance matrix with $T(k-1)$ rows and $T(k-1)$ columns, and y_* is a $(T(k-1))$ column vector (Lee et al., 1970).

This estimator is subject to the constraints that $0 \leq p_{ij} \leq 1$. In practice, to hold the constraints an iterative quadratic programming procedure (Lee et al., 1970) is used to find the absolute or a local maximum of the likelihood function. If it does not provide a single solution, a linear programming procedure and the minimum absolute deviations estimator is used instead (Lee et al., 1970).

Predictions are obtained by repeatedly multiplying the vectors of state probabilities with the estimated transition matrix. The goodness of fit of the Markov chain is then assessed by comparing predictions with observations on the frequencies of states at times $2, \dots, T$ using Spearman's rank correlation coefficient, Wilcoxon's signed-rank test and the mean square error.

3.4 Microdata

Microdata were only available for the Giessen test site. For microdata, transition paths of single objects, in this case point-quadrats, over time are known. The mown area has 306, the unmown area 54 objects. Each point-quadrat is characterised by a vector of the numbers of contacts of each species to the pin. The state space is defined by clustering the point-quadrats according to their species composition (SPSS 7.5.2, Quick Cluster); three clusters form the state space of the mown and two of the unmown area. The resulting transitions take place between plant communities, and correspond to the concept of succession proposed by Knapp (1971). Predictions are calculated for cluster frequencies, and the species-specific percentage phytomass is estimated by weighting the predicted cluster frequencies with the mean phytomass per cluster. The maximum likelihood estimator for microdata is obtained from the counted transition frequencies n_{ij} from cluster i to j :

$$p_{ij} = \frac{n_{ij}}{\sum_j n_{ij}} \geq 0 \quad (7)$$

324

325 For microdata the likelihood ratio test from Anderson and Goodman (1957; cit. in Usher,
 326 1987; see also Guttorp, 1995) for independence and identical distribution is applied. The
 327 null hypothesis states independence, i.e. multinomial distribution of state probabilities,
 328 and is accepted if the test statistic in Eq. 8 does not exceed the corresponding χ^2 value
 329 with $(k-1)^2$ degrees of freedom. Strictly speaking, the rejection of the null hypothesis is a
 330 prerequisite for assuming a Markov chain.

331

$$\chi_{iid}^2 = 2 \sum_{i=1}^k \sum_{j=1}^k n_{ij} \ln \frac{p_{ij}}{p_j}, \quad df=(k-1)^2 \quad (8)$$

333

334 with

$$p_j = \frac{\sum_{i=1}^k n_{ij}}{\sum_{i=1}^k \sum_{j=1}^k n_{ij}}$$

336

337 Time-homogeneity of the Markov chain is tested using another likelihood ratio test by
 338 Anderson and Goodman (1957; cited in Usher, 1987). The test statistic in Eq. 9 is
 339 obtained from the time-dependent transition probabilities $p_{ij}(t)$, and the time-independent
 340 transition probabilities p_{ij} . If it exceeds the corresponding χ^2 value, the null hypothesis
 341 of time-homogeneity is rejected and tests for the order of the chain have to be
 342 performed.

343

$$344 \quad \chi^2_{stat} = 2 \sum_{i=1}^k \sum_{j=1}^k \sum_{t=1}^T n_{ij}(t) \ln \frac{p_{ij}(t)}{p_{ij}}, \quad df=k(k-1)(T-1) \quad (9)$$

345

346 Testing the order of the chain is possible for microdata using hierarchical χ^2 tests
 347 (Guttorp, 1995). Given T observed times, one can iteratively test for all $r < T-1$ whether
 348 the Markov chain is of r -th order. If the test statistic shown in Eq. 10 exceeds the
 349 corresponding χ^2 value, the null hypothesis of the chain being of r -th order is rejected.
 350 Note that this procedure is problematic because the probability of falsely rejecting the
 351 true order of the chain cannot be controlled (Guttorp, 1995).

352

$$353 \quad \chi^2_{order} = \sum_{a_1, \dots, a_T} \frac{(n(a_1, \dots, a_T) - n(a_1, \dots, a_{T-1})p(a_1, \dots, a_{T-1}; a_T))^2}{n(a_1, \dots, a_{T-1})p(a_1, \dots, a_{T-1}; a_T)}, \quad df=(k-1)k^r(k^{T-r-1}-1) \quad (10)$$

354

355 where $p(a_1, \dots, a_{T-1}; a_T) = \frac{n(a_{T-r}, \dots, a_{T-1}, a_T)}{n(a_{T-r}, \dots, a_{T-1})}$ is the estimator of the probability to change

356 to state a_T after sequence a_{T-r}, \dots, a_{T-1} ;

357 a_i is the i -th state from $\{1, \dots, k\}$ and

358 $n(a_1, \dots, a_{T-1})$ is the number of observations of sequence a_1, \dots, a_{T-1} .

359

360 According to the results of these likelihood ratio tests an appropriate Markov chain
 361 model is selected. However, acceptance of the null hypothesis in the test for
 362 independence and identical distribution is not regarded as sufficient evidence against a

Markov chain, because it tests only T and $T-1$. It rather indicates that the interpretation has to be undertaken with greater care.

The results of testing the assumptions for the microdata of the Giessen test site are given in Table 1. Time-inhomogeneity and higher (r -th) order of the Markov chains are taken into account by periodically applying different mean normalised transition matrices with period $n_p=r$. These transition matrices are obtained by averaging and normalisation from the $T-1$ time-dependent transition matrices.

The goodness of fit of the Markov chain is assessed in the same way as for macrodata.

4 Results

The results presented in detail concentrate on a few examples that were selected to illustrate the methodology. The same analyses were carried out for all described data sets, and a comparison of the goodness of fit shows the variation of suitability of Markov chain models across different examples of vegetation dynamics. Full details of the applications of Markov models to all data sets are given in Balzter (1998).

4.1 Predictions of vegetation dynamics

LINDEN2

Plot LINDEN2 is mown once a year and was sown with seed mixture A. Figure 1 shows the observed changes in vegetation composition and the corresponding predictions from the Markov chain. Predictions are based on the percentage phytomass observations from 1982. The goodness of fit of the model can be assessed by comparing observations with predictions from 1983 till 1986. Predicted changes in percentage phytomass are smaller than observed, for instance the higher percentage phytomass of birdsfoot-trefoil, *Lotus spp.*, in 1984 and 1986 is smoothed by the model (Figure 1). The predictions from 1987 till 1991 show the expected development of the plant community beyond the observed time frame. The predicted trend is that the community will be dominated by *Achillea millefolium* (milfoil), *Sanguisorba minor* (salad burnet), *Lotus spp.* and *Festuca rubra/ovina*. Beyond 1986 the Markov chain is approaching its limiting distribution and the vegetation is predicted to be in equilibrium.

HEILIG3

HEILIG3 is used to illustrate Runge's (1985) data set. The decrease of *H. lanatus* and *F. rubra* in 1982 reported by Runge (1985) is shown in Figure 2. Mainly *A. millefolium* and *R. acetosa* were able to penetrate this layer (Runge, 1985). Until 1984 no forest established itself in the quadrat. Figure 2 shows that in 1980 the relative percentage cover of *F. rubra* increases strongly. The observed dynamics in HEILIG3 do not show any tendency towards a stable equilibrium. Accordingly, the Markov chain performs

poorly, and its predictions deviate considerably from the observations. The smoothing effect of the Markov chain (Figure 2) is likely to inhibit a good model fit to the highly changing vegetation data. The observed increase in *F. rubra* in 1980, for example, is also visible in the predictions, although it is predicted smaller than observed. The dominance of *A. millefolium* in 1982 is not detected by the Markov chain. Unexpected phenomena like the thick layer of dead plant material in 1982 which cause high rates of change supposedly limit the usefulness of Markov chain models to vegetation dynamics. Even if the Markov chain seems to be close to equilibrium of *Agrostis capillaris* (common bent-grass) and *F. rubra* in 1989, the true limiting distribution approaches a two-species mixture of creeping thistle, *Cirsium arvense* (64%) and lesser stitchwort, *Stellaria graminea* (36%) after more than 300 time steps. Predictions on this time scale are of course not interpretable given a data set over nine years.

The mown area in Giessen

The models with time steps of three months (MOMAC4 and MOMIC4) show poor model fits and are not presented in detail. The models for the mown area in Giessen using yearly time steps are shown together with the observed changes in percentage phytomass in Figure 3. The observed changes include a decrease in *Lolium perenne* (perennial rye-grass) and *Trifolium repens* (white clover), whereas the species *Ranunculus repens* (creeping buttercup) and *Glechoma hederacea* (ground ivy) increase. The dominant species *Poa spp.* reaches high percentage phytomass in 1996 but decreases again thereafter. The macrodata model MOMACY predicts a further increase

in *G. hederacea* and *R. repens*, and a continuous decline in *Poa spp.* (Figure 3). The limiting distribution of MOMACY consists of 16% *Poa* grasses, 48% *G. hederacea*, 26% *R. repens*, 5% *T. repens* and some species with low percentage phytomass. Despite the fact that the predictions of MOMACY differ from MOMAC4, the rank order of the four dominant species is identical in the first predicted year 1998. The predictions of MOMICY are shown in Figure 3 (bottom). The plant community shows no predicted trend, but is subject to periodic changes caused by the periodic use of three different transition matrices. This periodicity could either be a real cyclic phenomenon of the plant community or an artefact caused solely by a single event.

The four different models predict different vegetation dynamics. Stability (MOMAC4) is contrasted by a slow increase in *G. hederacea* (MOMACY). Seasonal changes are exhibited by MOMIC4, which does not show a trend over the years. MOMACY is considered to be the most reliable model.

The unmown area in Giessen

Vegetation dynamics in the unmown area intermediately exhibits a rise of *Poa spp.* which is followed by a subsequent decline (Figure 4 top). *Medicago x varia*, a hybrid of sickle medick (*Medicago falcata*) and alfalfa (*Medicago sativa*), makes up most of the phytomass in 1993 but then rapidly loses weight in the plant community. The ruderal species *C. arvensis* and *Urtica dioica* (stinging nettle) increase their percentage phytomass. In 1996 *G. hederacea* invades the unmown area, and reaches a high

proportion of the phytomass in 1997. Note that there is also a slow increase in the proportion of the species category 'others' (Figure 4 top). The models using time steps of three months are not discussed in detail, as their model fit is very poor. The macrodata model UNMACY (Figure 4 centre) shows the smoothing effect of the Markov chain compared to the observations. For instance, the observed sudden increase in *G. hederacea* in 1997 is comparatively very small in the predictions, but lasts longer into the future. In the model, *G. hederacea* eventually drives out all other species after several hundred time steps and reaches 100% phytomass in the limiting distribution. This is caused by the unitary transition probability from *G. hederacea* to itself. *G. hederacea* is an absorbing state of the Markov chain. The predictions of the microdata model UNMICY are presented in Figure 4 (bottom). They immediately reach a limiting distribution with dominance of *Poa spp.* and *M. x varia*.

4.2 Goodness of fit

The goodness of fit of the different Markov models for all used vegetation data sets is used to assess their applicability for predicting vegetation dynamics of grassland communities. The scatterplots of predicted versus observed values give a first impression of the variability of goodness of fit (Figure 5). LINDEN2 shows a relatively good model fit compared to HEILIG3. For the mown area of the Giessen test site MOMACY and MOMICY show better model fits than MOMAC4 and MOMIC4, while UNMACY is the only satisfying model for the unmown area (Figure 5). MOMAC4 and UNMAC4 show inhomogeneity of the scatterplots. From the pairs of predictions and

corresponding observations some statistics of the goodness of fit can be calculated.
 Table 2 presents the mean square error (mse), Spearman's rank correlation coefficient
 and the significance probability of Wilcoxon's signed-rank test. While the mse measures
 the squared differences between predictions and observations, Spearman's R ranks the
 values first and compares the rank orders. If R is close to one then the rank orders of
 predicted and observed values correspond closely, and the model may at least be used to
 predict a rank order of dominant plant species. Uncertainty of predicted values is
 quantified by the mse. For instance, the 95% confidence interval calculated from twice
 the root mean square error for a percentage phytomass of 30% would be approximately
 $CI_{95}=[10\%; 50\%]$, assuming $mse=0.01$. Table 2 shows that a ranking of values (R) gives
 better results than metric predictions (mse). A graphical overview of the goodness of fit
 of all models is given in Figure 6. LINDEN5, HEILIG3 and UNMAC4 exhibit
 particularly poor model fits, while the predictions of LINDEN3, HEILIG2 and
 MOMICY correspond well to the observations. The mse of HEILIG3 is almost tenfold
 compared to HEILIG2.

The Wilcoxon test results in agreement of predictions with observations for all Markov
 models except ZAGREB3, UNMAC4 and UNMIC4 (Table 2). R and mse of all models
 are in comparable ranges. However, seasonal changes cause poor model fits, when time
 steps of three months are used. The unmown area in Giessen shows generally poorer
 model fits than the mown area, which is probably caused by the comparatively high rates
 of change in the unmown plant community.

For the Giessen test site a comparison of the goodness of fit of Markov models using time steps of one year instead of three months and by using microdata instead of macrodata was carried out. Except when comparing UNMICY to UNMACY, models with microdata produce a smaller mse than models with macrodata (Table 3). A further reduction of mse is generally achieved by using time steps of one year rather than three months. Just UNMICY has a slightly greater mse than the corresponding model UNMIC4, but as UNMIC4's predictions differ significantly from the observations (Wilcoxon $P < 0.05$), UNMICY is still preferable.

5 Discussion

Markov chain models have the advantage of aggregating very complex information in the transition matrix, so that even ecosystems can be examined for which the underlying processes are not fully understood. The applicability of Markov chain models to vegetation dynamics of grassland communities is, however, limited by often occurring unexpected disturbances or other events that change ecological factors drastically. Events like an unusually cold winter could have the effect that the assumption of time-homogeneous transition probabilities is violated. Such unexpected large shifts in species composition were found in this study as well, confirming Binkley's (1980) findings. Possible improvements could be the explicit modelling of changing weather using a Hidden Markov model (Zucchini and Guttorp, 1991). This approach models transitions between weather states as a Markov chain and uses transition matrices conditional on the

particular weather state to predict the stochastic process of interest. If disturbing events during data sampling are known, another option would be to estimate separate transition matrices for time periods in which the assumption of time-homogeneity seems to be better justified. If spatial autocorrelation is present in the data, a spatial model is more appropriate. A generalisation of a Markov chain to a spatio-temporal Markov chain (STMC), which is a type of cellular automaton model, is presented by Balzter et al. (1998). One major drawback of this model is the rapidly increasing number of parameters that need to be estimated, and this requires a very large spatial data set.

The mse found in the models examined in this paper is considered to be too high to allow metric predictions of species composition in grassland. The metric variables are valuable as input to the chain, but interpreting the predictions must be undertaken with care. It is recommended to look at ranks of dominant species rather than predicting species proportions in the community. The correlation of the ranks is measured by Spearman's R. It is important to check whether the predicted ranks deviate significantly from the observed ranks with Wilcoxon's signed-rank test, too. Although R is satisfactory, Wilcoxon's P may still discover a poor model fit, if the majority of ranked predictions is all higher or all lower than the observations (Figure 6). R is more robust than Pearson's r, as the assumption of bivariate normal distribution is rarely true for grassland communities, because usually only a few species have high proportions but many have low proportions of the vegetation. This phenomenon was called 'law of constants' in vegetation science by Raunkiaer (1934; cit. in Collins and Glenn, 1991).

545 Cooke (1981) concludes that the validity of Markov chain predictions in grassland is
 546 species-specific.

547

548 The predictions of the Markov chains are smoothed in comparison to the observations.
 549 High rates of change in the plant community are particularly hard to model with Markov
 550 chains because of this smoothing effect, and they cause a greater mse. Such high rates of
 551 change are commonly observed in grassland communities (Dodd et al., 1995). Seasonal
 552 variation causes the model to perform particularly poorly, when transitions are
 553 influenced by the annual weather cycle (MOMAC4, MOMIC4, UNMAC4, UNMIC4).

554

555 Different data sets produce a different goodness of fit of the Markov chains. For
 556 instance, the Linden plots with seed mixture A (LINDEN1 to LINDEN4) generally has a
 557 lower mse and a greater R than seed mixture C (LINDEN5 to LINDEN8, Figure
 558 6). There is no clear relationship between the goodness of fit and

- 559 • the modelled parameter (percentage phytomass, relative percentage cover, percentage
 560 of specimen)
- 561 • the sampling site (Linden, Heiliges Meer, Zagreb, Giessen)
- 562 • the number of states in the model (two to 18, Table 2)
- 563 • the number of observed time steps (five to 15, Table 2).

564

565 The use of microdata instead of macrodata is likely to reduce the mse. Microdata are not
 566 often available, though, and most vegetation records contain some kind of macrodata.

Microdata also have the advantage that some statistical tests can be performed before running the model, although these need careful interpretation of what is actually tested.

Regardless of the data type used, the first step is to define the state space of the chain. In case of microdata obtained by the point-quadrat method, the multivariate observations need to be classified before defining the state space. This approach models transitions between vegetation types rather than between species. On the contrary, macrodata models may be defined using single species as states. A decision has to be made, which species to include in the model, because the number of parameters to be estimated increases exponentially with the number of states. On the one hand, the more parameters are necessary, the less precise the estimation becomes. On the other hand, omission of important species may cause poor predictions. Some authors use only two states in their vegetation Markov model (Usher, 1987), but others use more than ten (Miles et al., 1985; Hobbs and Legg, 1983) or even 400 in a model of amino acid substitution (Gonnet et al., 1994). To increase the precision of parameter estimation, the data set should extend over a time period as long as possible.

In conclusion, Markov chains are a framework for estimated replacement rates (or transition probabilities) between plant populations. They can contribute to the numerical analysis and understanding of species replacements in a pathway of succession. The mechanistic richness which is often observed in a succession (Pickett et al., 1987) is summarised in the transition matrix. The existence of a limiting distribution of a Markov chain implies a successional pathway with directional change and termination.

Fluctuations in the plant community are smoothed by the Markov chain predictions, and the remaining successional trend can be regarded as the expected dominance order of the plant species. It has been shown that Markov chain models are sensitive to changes in the frequency and regularity of disturbances, like cutting and grazing. Information about land use practices are therefore essential for interpretation of the model predictions. Despite the complex nature of grassland dynamics, it is possible to get good predictions under certain circumstances with an appropriate model. The predictions achievable with Markov chains are ranks of dominant species rather than metric variables. There is still more potential for development of simple but sophisticated models of grassland dynamics. But the information from Markov chain models surely is valuable for conservation, landscape planning and ecology.

Acknowledgements

This project was funded by a grant from the Federal State of Hessen. I would like to thank Prof Wolfgang Köhler and Paul Braun from Justus-Liebig-University (JLU) Giessen, Germany, for their supportive supervision of my work. Paul Braun also took part in vegetation sampling together with Marcus Hoffmann. My colleagues Gabriel Schachtel, Elisabeth Schmidt and Antje Herrmann (JLU) provided very helpful discussions. Angelika Hoffmann and Jörg von Prondzinski played an important role in determination of plant species. Thanks to Peter North (ITE) for checking the manuscript.

References

- Acevedo, M.F., 1981. On Horn's Markovian model of forest dynamics with particular reference to tropical forests. *Theor. Pop. Biol.* 19: 230-250.
- Acevedo, M.F., Urban, D.L. and Aflan, M., 1995. Transition and gap models in forest dynamics. *Ecol. Appl.* 5: 1040-1055.
- Baker, W., 1989. A review of models of landscape change. *Landsc. Ecol.* 2: 111-133.
- Balzter, H., 1998. Modellierung der Vegetationsdynamik verschiedener Pflanzengemeinschaften des Grünlandes mit Markov-Ketten. *Boden und Landschaft* 23, Justus-Liebig-Universität, Giessen, 152 pp.
- Balzter, H., Braun, P. and Köhler, W., 1995. Detection of spatial discontinuities in vegetation data by a moving window algorithm. In: W. Gaul and D. Pfeifer (Editors), *From Data to Knowledge: Theoretical and Practical Aspects of Classification, Data Analysis and Knowledge Organization*, Springer, Berlin, pp. 243-252.
- Balzter, H., Braun, P.W. and Köhler, W., 1998. Cellular automata models for vegetation dynamics. *Ecol. Model.* 107: 113-125.
- Barden, L.S., 1980. Tree replacements in a cove hardwood forest of the Southern Appalachians. *OIKOS* 35: 16-19.
- Binkley, C.S., 1980. Is succession in hardwood forests a stationary Markov process? *Forest Sci.* 26: 566-570.
- Coffin, D. P. and Lauenroth, W. K., 1990. A gap dynamics simulation-model of succession in a semiarid grassland, *Ecol. Model.* 49: 229-266.

636 Collins, S.L. and Adams, D.E., 1983. Succession in grasslands: thirty-two years of
637 change in a Central Oklahoma tallgrass prairie. *Vegetatio* 51: 181-190.

638 Collins, S.L. and Glenn, S.M., 1991. Importance of spatial and temporal dynamics in
639 species regional abundance and distribution. *Ecology* 72: 654-664.

640 Cooke, D., 1981. A Markov chain model of plant succession. In: R.W. Hiorns and D.
641 Cooke (Editors), *The Mathematical Theory of the Dynamics of Biological Populations*
642 II, Academic Press, London, pp. 231-247.

643 Dodd, M., Silvertown, J., McConway, K., Potts, J. and Crawley, M., 1995. Community
644 stability: a 60-year record of trends and outbreaks in the occurrence of species in the
645 park grass experiment. *J. Ecol.* 83: 277-285.

646 Frydman, H., 1992. A nonparametric estimation procedure for a periodically observed
647 three-state Markov process, with application to AIDS. *Statistical Methodology* 54: 853-
648 866.

649 Frydman, H., 1995a. Nonparametric estimation of a Markov 'illness-death' process from
650 interval-censored observations, with application to diabetes survival data. *Biometrika*
651 82: 773-789.

652 Frydman, H., 1995b. Semiparametric estimation in a three-state duration-dependent
653 Markov model from interval-censored observations with application to AIDS data.
654 *Biometrics* 51: 502-511.

655 Gonnet, G.H., Cohen, M.A. and Benner, S.A., 1994. Analysis of amino acid substitution
656 during divergent evolution: the 400 by 400 depeptide substitution matrix. *Biochem.*
657 *Biophys. Res. Commun.* 199: 489-496.

658 Goodall, D.W., 1952. Some considerations in the use of point quadrats for the analysis
 659 of vegetation. *Aust. J. Scient. Res. B* 5: 1-41.
 660 Guttorp, P., 1995. *Stochastic Modeling of Scientific Data*. Chapman and Hall, London,
 661 372 pp.
 662 Hall, F.G., Strebel, D.E. and Sellers, P.J., 1988. Vegetation, atmosphere, climate and
 663 remote sensing. *Landsc. Ecol.* 2: 3-22.
 664 Heller, W.-D., Lindenberger, H., Nuske, M. and Schriever, K.-H., 1978. *Stochastische*
 665 *Systeme*. De Gruyter, Berlin.
 666 Hobbs, R.J. and Legg, C.J., 1983. Markov models and initial floristic composition in
 667 heathland vegetation dynamics. *Vegetatio* 56: 31-43.
 668 Horn, H.S., 1976. Succession. In: R.M. May (Editor), *Theoretical Ecology. Principles*
 669 *and Applications*, Saunders, Philadelphia, pp. 187-204.
 670 Ilijanic, L., Topic, J. and Segulja, N., 1985. Meadow-succession experiment on the
 671 permanent plots in botanical garden in Zagreb. In: K.-F. Schreiber (Editor), *Sukzession*
 672 *auf Grünlandbrachen*, Schöningh, Paderborn, pp. 69-80.
 673 Knapp, R., 1971. *Einführung in die Pflanzensoziologie*. Ulmer, Stuttgart.
 674 Lee, T.C., Judge, G.G. and Zellner, A., 1970. *Estimating the Parameters of the Markov*
 675 *Probability Model from Aggregate Time Series Data*. North-Holland Publishing
 676 Company, Amsterdam, 261 pp.
 677 Lippe, E., De Smidt, J.T. and Glenn-Lewin, D.C., 1985. Markov models and succession:
 678 a test from a heathland in the Netherlands. *J. Ecol.* 73: 775-791.

679 Markov, A., 1907. Extension of the limit theorems of probability theory to a sum of
 680 variables connected in a chain. The Notes of the Imperial Academy of Sciences of St.
 681 Petersburg, VIII Series, Physio-Mathematical College XXII, No. 9.
 682 Miles, J., French, D.D., Zhen-Bang, X. and Ling-Zhi, C., 1985. Transition matrix
 683 models of succession in a stand of mixed broadleaved-*Pinus koraiensis* forest in
 684 Changbaishan, Kirin province, North-east China. J. Environ. Manage. 20: 357-375.
 685 Odum, E.P., 1991. Prinzipien der Ökologie: Lebensräume, Stoffkreisläufe,
 686 Wachstumsgrenzen. Spektrum der Wissenschaft, Heidelberg, 305 pp.
 687 Pickett, S.T.A., 1982. Population pattern through twenty years of oldfield succession.
 688 Vegetatio 49: 45-59.
 689 Pickett, S.T.A., Collins, S.L. and Armesto, J.J., 1987. Models, mechanisms and
 690 pathways of succession. Bot. Rev. 53: 335-371.
 691 Pratt, C.R., 1995. Ecology. Springhouse, Springhouse, PA, 168 pp.
 692 Rego, F., Pereira, J. and Trabaud, L., 1993. Modeling Community Dynamics of a
 693 *Quercus-Coccifera* L garrigue in relation to fire using Markov chains. Ecol. Model. 66:
 694 251-260.
 695 Runge, F., 1985. 21-, 10- und 8-jährige Dauerquadratuntersuchungen in aufgelassenen
 696 Grünländereien. In: K.-F. Schreiber (Editor): Sukzession auf Grünlandbrachen.
 697 Schöningh, Paderborn, pp. 45-49.
 698 Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United
 699 States. Ecology 62: 1041-1051.
 700 Tan, S. S. and Smeins, F. E., 1996. Predicting grassland community changes with an
 701 artificial neural network model. Ecol. Model. 84: 91-97.

702 Usher, M.B., 1981. Modelling ecological succession, with particular reference to
703 Markovian models. *Vegetatio* 46: 11-18.

704 Usher, M.B., 1987. Modelling successional processes in ecosystems. In: A.J. Gray, M.J.
705 Crawley and P.J. Edwards (Editors), *Colonization, Succession and Stability*. Blackwell,
706 Oxford, pp. 31-56.

707 Winkler, E. and Klotz, S., 1997. Clonal plant species in a dry-grassland community: A
708 simulation study of long-term population dynamics. *Ecol. Model.* 96: 125-141.

709 Zucchini, W. and Guttorp, P., 1991. A hidden Markov model for space-time
710 precipitation. *Water Resour. Res.* 27: 1917-1923.

Tables

711

712 Table 1: Model applications to the meadow data from Giessen, with assumptions and results of
 713 the statistical tests. Each application is abbreviated as indicated in capitals (e.g. MOMAC4
 714 means mown, macrodata, 4 time steps per year). Note that for UNMICY the time-homogeneous,
 715 mean transition matrix is used despite the test results given in the table, because one of the row
 716 sums of the periodic matrices equals 0.

mown (MO) unmown (UN) area	macrodata (MAC)	microdata (MIC)
4 time steps per year 03/1994-09/1997 (4)	MOMAC4 UNMAC4 assumption of first-order, time-homogeneous Markov chains	MOMIC4 independence of transitions, fourth-order, time-inhomogeneity UNMIC4 independence of transitions, second-order, time-inhomogeneity
yearly time steps 06/1993-06/1997 (Y)	MOMACY UNMACY assumption of first-order, time-homogeneous Markov chains	MOMICY independence of transitions, third-order, time-inhomogeneity UNMICY independence of transitions, third-order, time-inhomogeneity

717

718

Table 2: Goodness of fit of the Markov models for all datasets. mse=mean square error, R=Spearman's rank correlation coefficient, n =number of pairs for calculation of R, P =significance probability of the Wilcoxon signed-rank test (marked with '*' if less than 0.05), pm%=percentage phytomass, pc%=percentage cover, ps%=percentage of specimen.

dataset	parameter	number of states	number of observed time steps	mse	R	n	P
LINDEN1	pm%	8	5	0.0084	0.92	32	0.350
LINDEN2		8	5	0.0050	0.91	32	0.627
LINDEN3		8	5	0.0027	0.97	32	0.360
LINDEN4		10	5	0.0048	0.91	40	0.270
LINDEN5		9	5	0.0204	0.75	36	0.300
LINDEN6		10	5	0.0133	0.69	40	0.119
LINDEN7		8	5	0.0141	0.81	32	0.112
LINDEN8		10	5	0.0030	0.90	40	0.192
HEILIG1	pc%	16	8	0.0034	0.87	119	0.657
HEILIG2		10	11	0.0018	0.91	110	0.859
HEILIG3		9	9	0.0161	0.81	80	0.095
ZAGREB1	ps%	14	11	0.0042	0.88	140	0.384
ZAGREB2		14	11	0.0068	0.70	140	0.677
ZAGREB3		18	11	0.0049	0.85	180	0.004*
MOMAC4	pm%	9	15	0.0056	-	126	0.841
MOMACY		7	5	0.0043	0.88	28	0.554
MOMIC4		3	15	0.0043	0.79	126	0.130
MOMICY		3	5	0.0020	0.87	28	0.909
UNMAC4		12	15	0.0361	-	168	<0.001*
UNMACY		8	5	0.0065	0.86	32	0.340
UNMIC4		2	15	0.0112	0.60	168	0.008*
UNMICY		2	5	0.0116	0.69	32	0.722

Table 3: Reduction of mean square error (mse) caused by using time steps of one year instead of three months and by using microdata instead of macrodata. Ratios < 1 actually reduce the mse and are shown in bold italic.

land use	time steps one year instead of three months	microdata instead of macrodata
mown	microdata: <i>0.47</i> macrodata: <i>0.77</i>	steps of one year: <i>0.47</i> steps of 3 months: <i>0.77</i>
unmown	microdata: 1.04 macrodata: <i>0.18</i>	steps of one year: 1.79 steps of 3 months: <i>0.31</i>

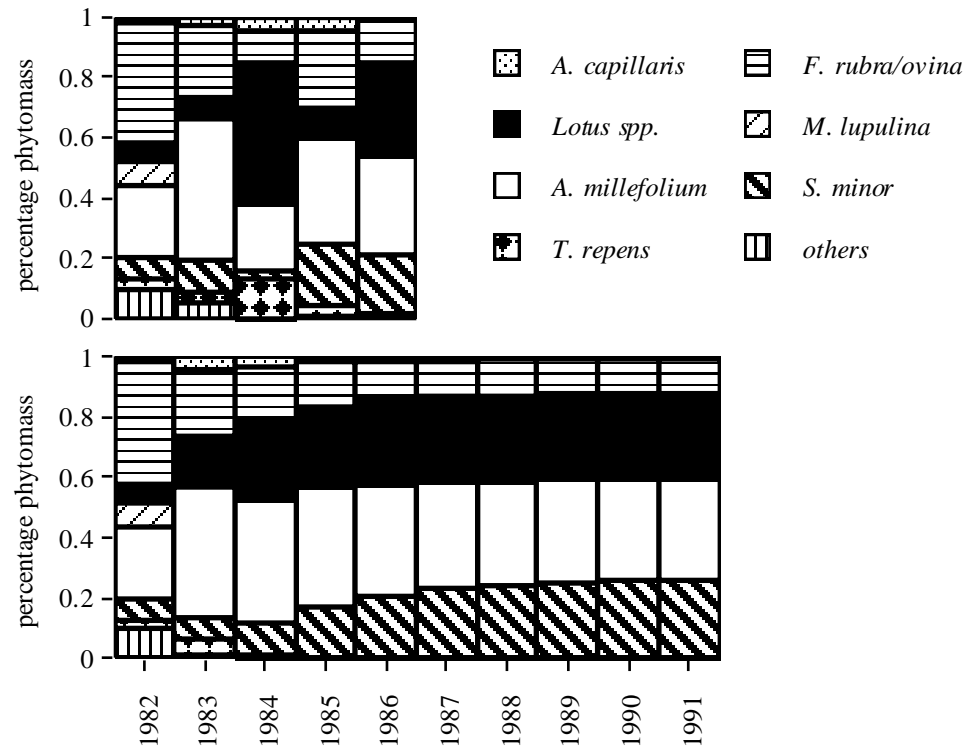


Figure 1

Balzter, H.

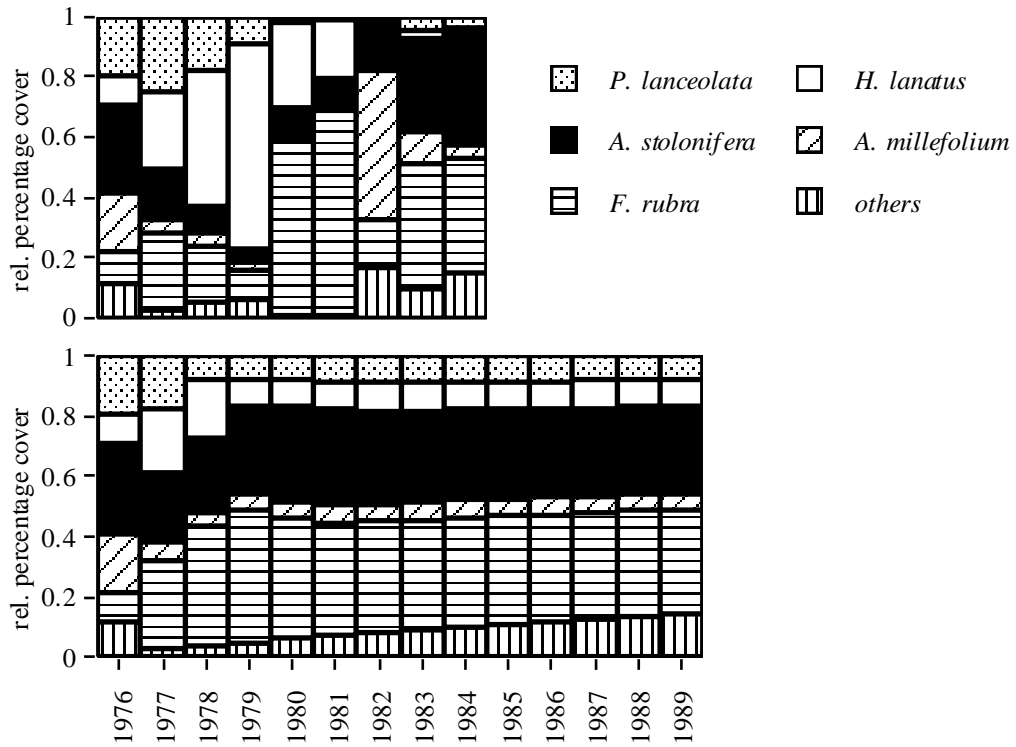


Figure 2

Balzter, H.

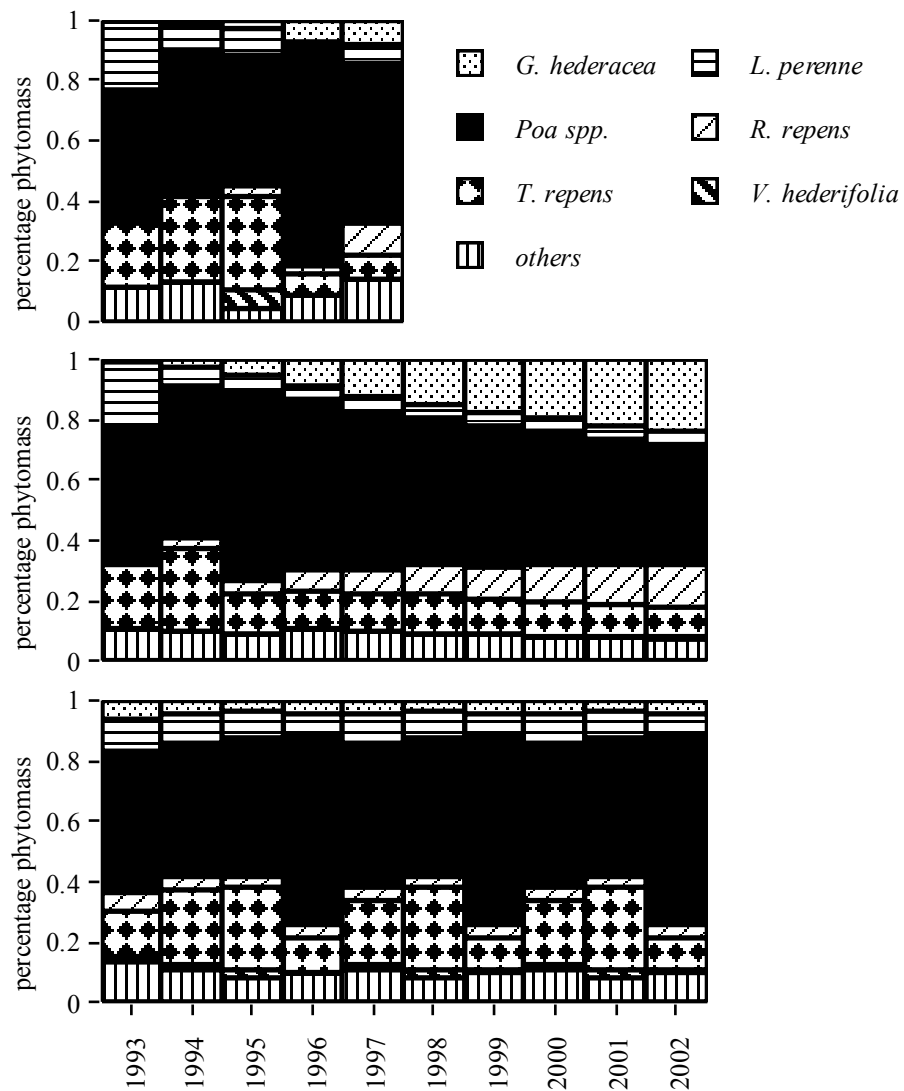


Figure 3

Balzter, H.

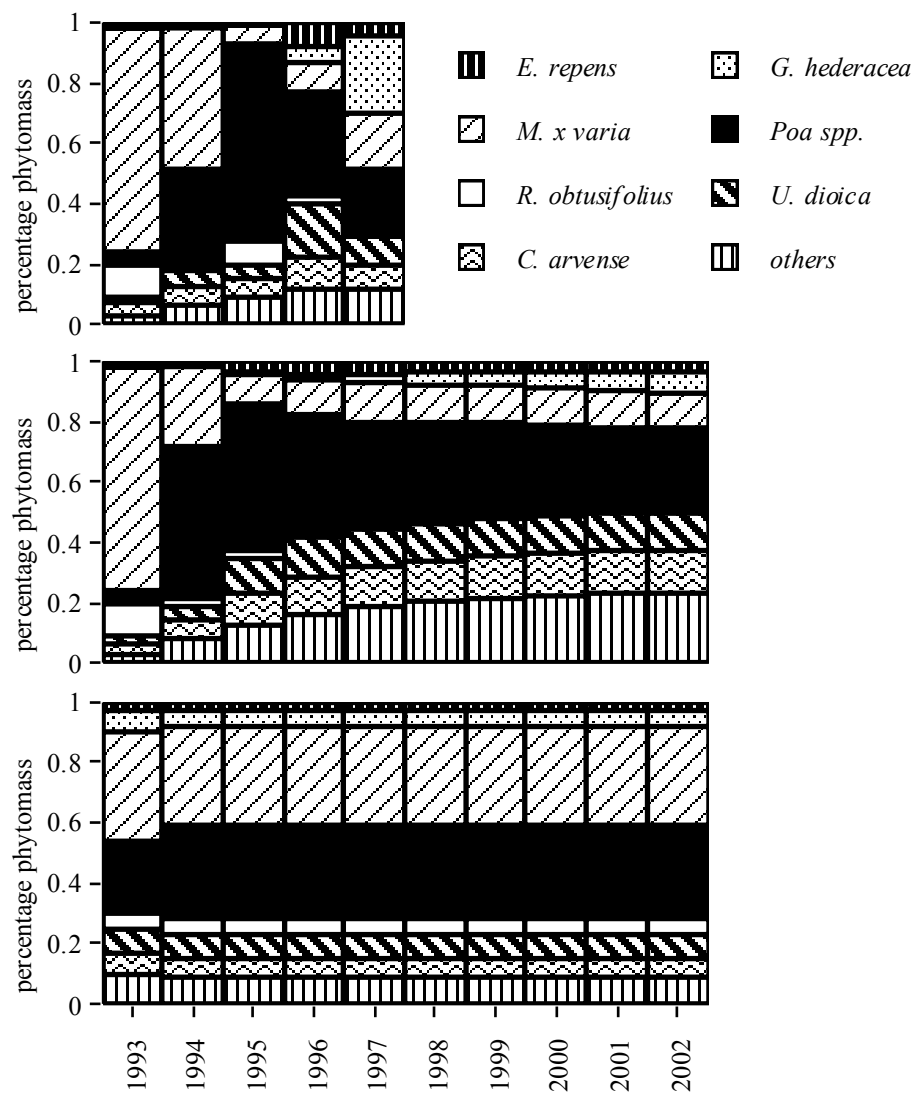


Figure 4

Balzter, H.

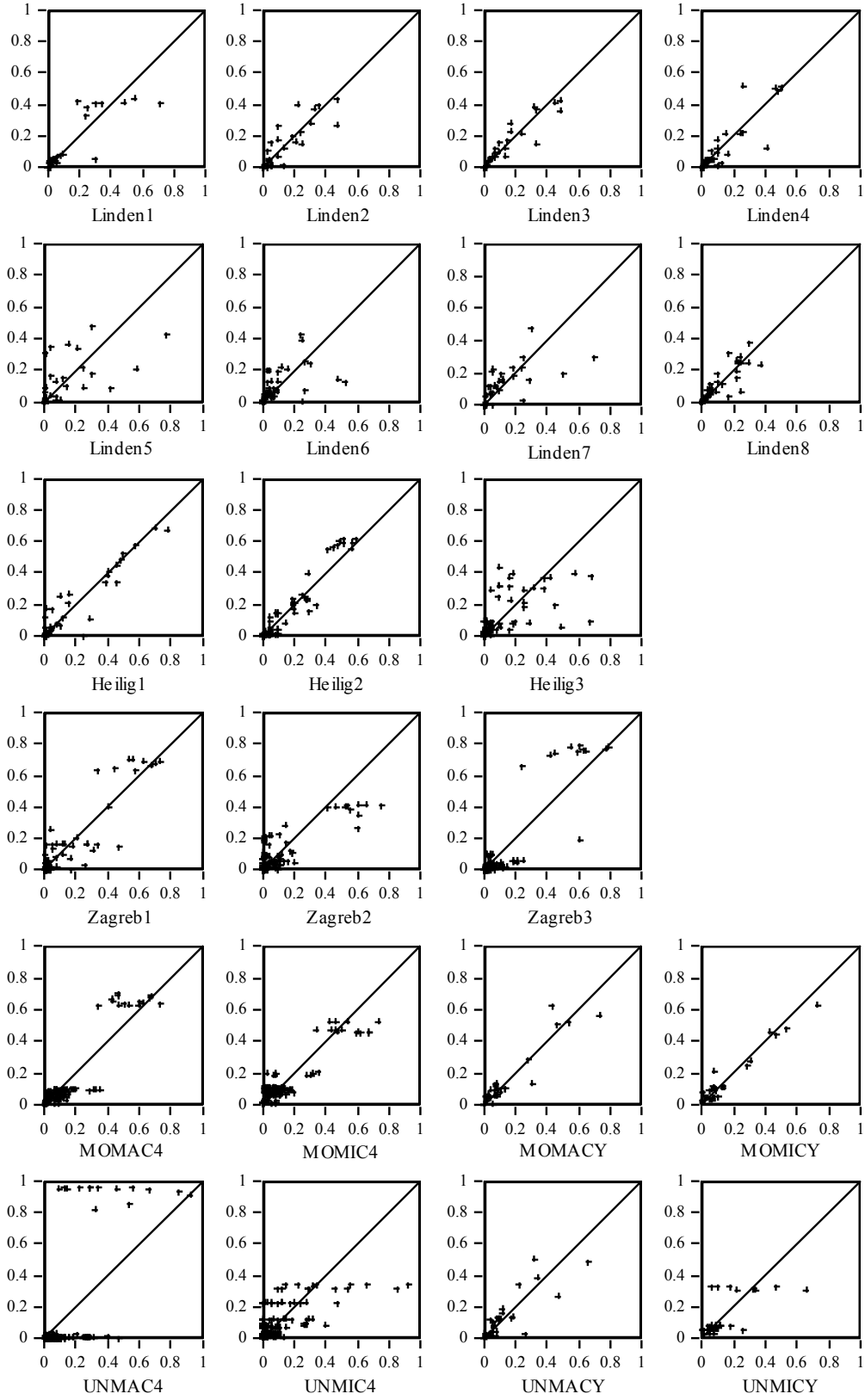


Figure 5

Balzter, H.

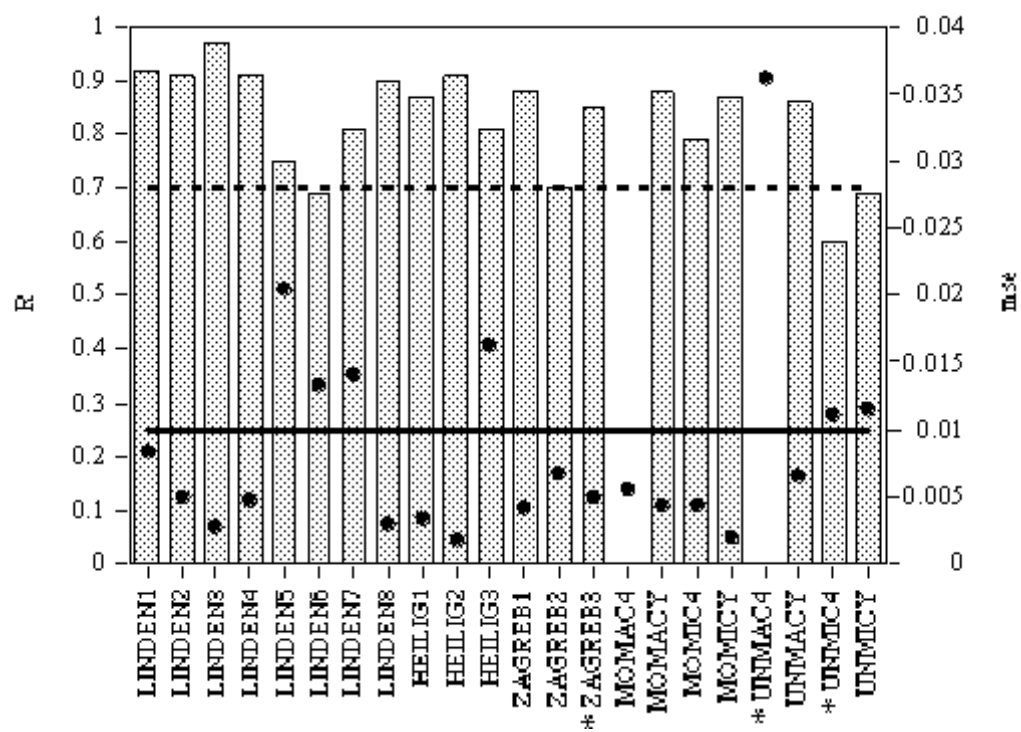


Figure 6

Balzter, H.

Figure captions

Figure 1: Changes in percentage phytomass of the plant species in plot LINDEN2.

Observations (top) and predictions based on 1982 (bottom). The species *Agrostis*

capillaris, *Festuca rubra/ovina*, *Medicago lupulina* (black medick), *Achillea*

millefolium, *Trifolium repens*, *Sanguisorba minor* and *Lotus spp.* are presented

separately. Species that never exceeded 5% phytomass are aggregated to the state

'others'.

Figure 2: Changes in relative percentage cover of the plant species in plot HEILIG3.

Observations (top) and predictions based on 1976 (bottom). The species *Plantago*

lanceolata (ribwort), *Holcus lanatus*, *Agrostis capillaris*, *Achillea millefolium* and

Festuca rubra are presented separately. *Trifolium repens*, *Dactylis glomerata*, *Rumex*

acetosa, *Cirsium arvense* and *Stellaria graminea* are modelled as separate states but

aggregated to the category 'others' for graphical presentation.

Figure 3: Changes in percentage phytomass of the plant species in the mown part of the

meadow in Giessen. Observations (top), predictions based on June 1993 for MOMACY

(centre) and for MOMICY (bottom). The species *Glechoma hederacea*, *Lolium perenne*,

Poa spp., *Ranunculus repens*, *Trifolium repens* and *Veronica hederifolia* (ivy speedwell)

are presented separately. Species that never exceeded 5% phytomass are aggregated to

the state 'others'. Predictions for MOMICY are obtained from predicted cluster

frequencies.

Figure 4: Changes in percentage phytomass of the plant species in the unmown part of the meadow in Giessen. Observations (top), predictions based on June 1993 for UNMACY (centre) and for UNMICY (bottom). The species *Glechoma hederacea*, *Medicago x varia*, *Poa spp.*, *Rumex obtusifolius* (broad-leaved dock), *Urtica dioica*, *Cirsium arvense* and *Elymus repens* (couch-grass) are presented separately. Species that never exceeded 5% phytomass are aggregated to the state 'others'. Predictions for UNMICY are obtained from predicted cluster frequencies.

Figure 5: Scatterplots of predicted vs. observed values for all modelled vegetation datasets.

Figure 6: Comparison of the goodness of fit of all Markov models assessed with Spearman's R and the mean square error (mse). '*' indicates models with significant deviation from the observations (Wilcoxon test, $P < 0.05$). Due to inhomogeneity R is not calculated for MOMAC4 and UNMAC4.