Analyzing the Fine-Scale Dynamics of Two Dominant Species in a *Polytrichum—Myrtillus* Pine Forest.
I. A Homogeneous Markov Chain and Cyclicity Indices

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Abstract—Long-term direct observations in a *Polytrichum—Myrtillus* pine forest are used to construct and verify a homogeneous Markov chain model of fine-scale dynamics of two dominant species (*Vaccinium myrtillus* and *V. vitis-idaea*) at the late stages of succession. The sampling design featured a large sample size (2000 quadrats) on permanent transects, re-examinations with an interval of 5 years, and the use of species rooted frequency. The discrete Markov chain used to model the process under consideration consists of four states: an absence of both species from the quadrat, the presence of one species of the two, and the joint presence of both species. The time step of the model coincides with the interval between the observations. The data of two successive examinations are used to calibrate the model, and the data of one additional examination are used to verify the model. All possible transitions between states, as well as the absence of transitions from each specific state, were revealed in quadrats within one time interval, and this resulted in a complete *digraph* (directed graph) of transitions. The main results of the model obtained from the formulas of finite Markov chain theory included steady-state square distribution, cyclicity characteristics, and the mean durations of stages in the fine-scale dynamics. The distribution among quadrats expected for the steady-state (stable) outcome of succession was the following: 30% of quadrats were occupied by *V. myrtillus* alone, 11% by *V. vitis-idaea* alone, 18% by both species, and 41% were "empty." This demonstrates the possibility of stable coexistence of *V. myrtillus* and *V. vitis-idaea* at the latest stages of succession with a clear predominance of *V. myrtillus*, yet without competitive exclusion. The quantitative characteristics of cyclicity and the durations of stages in fine-scale dynamics enabled us to estimate the total duration of secondary postfire succession (until the attainment of a state distribution that differed from the steady-state one by less than 5%) at about 45 years. Of the four specific states, the average time of persistence was the smallest (8 years) for quadrats with *V. vitis-idaea* alone, while the "empty" ones persisted for the longest time (18 years). Comparison of the real square distribution and the forecast of the dynamics for one model time step (5 years) showed that the measure of difference was 5.4%. This illustrates the efficiency of the (time-)*homogeneous* Markov chain as a short-term forecast tool, but the question of validity of the homogeneity hypothesis in the longer term is left open.

INTRODUCTION

An understanding of the mechanisms that underlie plant community dynamics and stability is impossible without a description of the processes at a fine scale, with the census site size being comparable to the size of an individual[1] and not exceeding several square decimeters. The duration of microsite retention by different species, the speed at which representatives of a species move within a community, and substitution for individuals of different species determine the general characteristics of communities, such as species diversity, patch diversity, and succession status (Maslov, 2001). The dynamics of relationships between dominant species with a similar life form and similar ecology is of particular interest in this regard, since fine-scale dynamics is one of the mechanisms that underlie ecological niche separation in this case (Maarel and Sykes, 1993).

The two dominant species, bilberry *Vaccinium myrtillus* and lingonberry *V. vitis-idaea* (Makipaa, 1999), are the most common for boreal forests and are characterized by close ecological optima; they were chosen as model species for the analysis of fine-scale dynamics in the present study. The joint ecological and syntaxonomical distribution of these two species

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[1] Here and below, only aerial counting units (ramets) are considered.

is very wide, with the included communities ranging from forest raised bogs to pine forests on rock outcrops (Rysin, 2009). *V. myrtillus* and *V. vitis-idaea* form an inseparable pair at different levels of spatial heterogeneity, from small intracenotic mosaics to geographical zones, since the species jointly diagnose the class of *Vaccinio-Piceetea* boreal forests in the Braun-Blanquet classification system (Maslov, 1990, p. 95). These species are usually combined into a single "*V. myrtillus—V. vitis-idaea*" group upon the diagnostics of forest type on the community level (Fedorchuk et al., 2002).

Markov models are widely used in the studies of forest community successions (Knyazkov et al., 1992; Vinogradov and Shitov, 1994; Logofet and Lesnaya, 2000), as described in a recent review (Logofet, 2010). The use of Markov models at the structural level below community is significantly less common (Hobbs, 1984; Samoylov and Tarkhova, 1985; Wootton, 2001; Hill et al., 2004; Baasch et al., 2010). The goal of the present study was to analyze the fine-scale dynamics of two dominant species with similar ecological features by the Markov model (the first (time-)*homogeneous* version) with *V. myrtillus* and *V. vitis-idaea* as an example and to perform a quantitative assessment of the steady-state distribution of status probability, mean duration of the stages, and cyclicity indices.

MATERIALS AND METHODS

Objects. Field studies were conducted at the scientific forest reserve no. 67 in the north of the Dmitrov raion of the Moscow oblast (Maslov, 2009). A permanent sample plot of 50 × 40 m in size was marked in a *Polytrichum—Myrtillus* pine forest. The community occupied a closed saucer-shaped depression in the upper part of a gentle slope; the microrelief was very pronounced. The tree stand consisted of Scots pine (*Pinus sylvestris*) with some birches (*Betula pendula*) and small Norway spruces (*Picea abies*) (in the undergrowth). The ground layer was dominated by *Polytrichum commune*, *Pleurozium schreberi*, and *Sphagnum fallax*. Two dwarf shrub species, *Vaccinium myrtillus* and *V. vitis-idaea*, were the absolute dominants of the herb and shrub layer, with other plant species represented by single individuals (Maslov, 1990, p. 33). The beginning of secondary succession dated back to 1923, when an even-aged pine stand emerged at the site of a massive windfall. The pine stand was affected by a middle-severity ground fire in 1954.

Sample design and data. Field and ground layer observations were performed on permanent transects constituted by quadrats (size 0.2 × 0.2 m) adjacent to each other (Fig. 1); the total number of quadrats on the sample plot was 2000. Only the presence or absence (rooted presence) of each species was recorded for each site, and aerial shoots of *V. myrtillus* and *V. vitis-idaea* served as the counting units

(Smirnova, 1976). The presence of fallen logs (tree trunks and large branches) on the soil surface was recorded separately. A presence—absence dot map of species distribution inside the plot was constructed for each species. The observation of rooted presence or absence of a species on small quadrats has an advantage over any other parameters in the research on successions, since the "rooted" presence of species does not undergo virtually any changes during the vegetation season and shows only weak dependence on fluctuations associated with the most drastic phytomass changes in most species (Maslov, 1990, p. 16). The fine-scale dynamics of lower layers in a *Polytrichum—Myrtillus* pine forest was studied over 25 years, with repeated observations on transects every five years. The total number of observations with species distribution maps for the different years was six. *V. myrtillus* and *V. vitis-idaea* distribution maps for 1985 and 1990 were used to construct the transition matrix in the present study, and observational data from 1995 were used to verify the quality of the short-term forecast based on the model constructed.

Markov chain as a model of the process under observation. The ideology of Markov models does not require knowledge of the causal mechanisms of the process being studied. However, such a model "can help to pinpoint areas where such insight would be valuable, and hence acts both as a guide and a stimulus to further research" (Jeffers, 1978, p. 92). If the presence of *V. myrtillus* on the site is indicated with the letter V and that of *V. vitis-idaea* is indicated with the letter W, as done during the field observations, then the two-species system on each plot can only be in one of the four states at every time point: (1) ∅—both species are absent, (2) V—*V. myrtillus* is present, (3) W—*V. vitis-idaea* is present, and (4) VW—both species are present. The states defined above are naturally identified with the states of the chain, and finite probability distributions of chain states, $\mathbf{x}(t)$, at the observation time t serve as the model state variables.

Markov property postulate means that the probability distribution for the transitions from any state S ($S = \varnothing$, V, W, VW) to all other states is determined entirely by the current state and does not depend on the path the chain has attained this state within the chain. A priori biological concepts do not rule out any type of transitions between the four abovementioned states in nature, and (given that the Markov property postulate is applicable and assigning numbers 1 to 4 to the states for simplicity) the transition scheme can therefore be displayed as a *complete directed graph* (Fig. 2). Formally, if the distribution of transition probabilities is represented by a stochastic row-vector $[p_{S\varnothing}, p_{SV}, p_{SW}, p_{S,VW}]$ and the probabilities of the states themselves at the current time point t are represented by a stochastic column-vector $\mathbf{x}(t) = [x_\varnothing, x_V, x_W, x_{VW}]^T$, an elementary
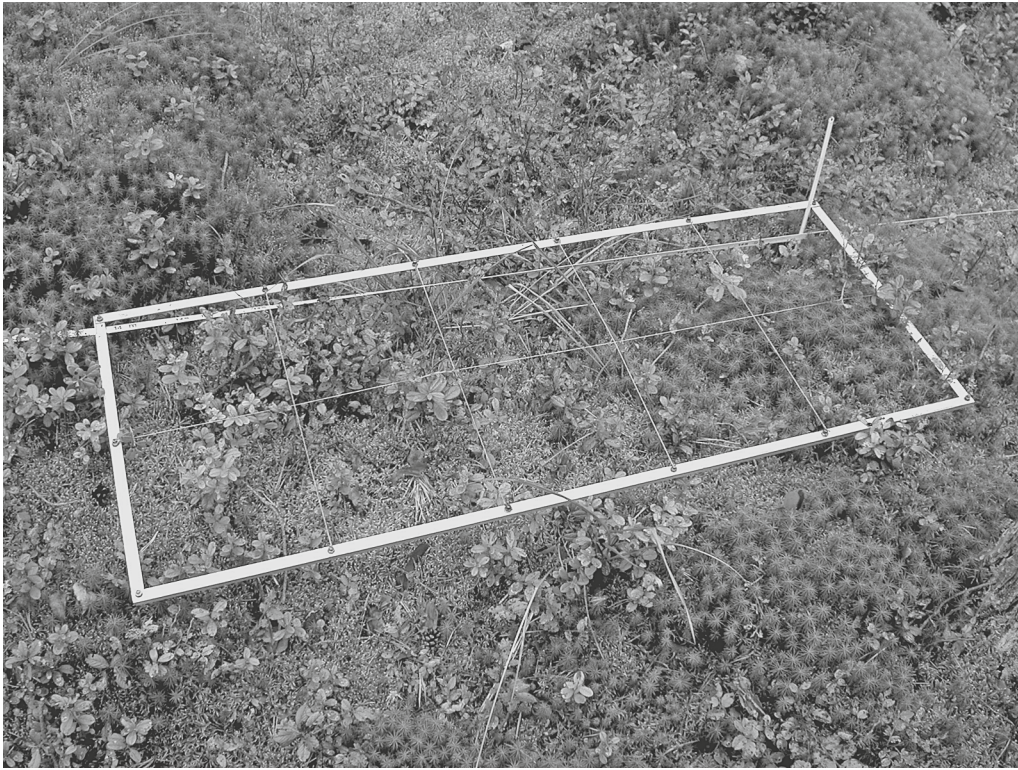
Fig. 1. Sample frame on the permanent transect and field layer patterns in a *Polytrichum−Myrtillus* pine forest.

formula of probability theory determines probability of the state S at the next moment:

$$x_S(t + \Delta t) = x_\varnothing p_{S\varnothing} + x_V p_{SV} + x_W p_{SW} + x_{VW} p_{S,VW},$$
$$S = \varnothing, V, W, VW. \quad (1)$$

Generally speaking, the nonzero elements p_{ij} of the transition matrix $\mathbf{P} = [p_{ij}]$ that characterize the probabilities of the transition from state j to state i in one step $\Delta t = 1$ ($i, j = 1, ..., 4$) and reflect the relative rate of species replacement at the sites depend on the time t, but this dependence is neglected and the hypothesis of (time) *homogeneity* of the chain is accepted.

If the hypothesis is true, the set of all four equations (1) assumes the following vector-matrix form (with the *digraph* in Fig. 2 taken into account):

$$\mathbf{x}(t + \Delta t) = \begin{vmatrix} p_{11} & p_{12} & p_{13} & p_{14} \\ p_{21} & p_{22} & p_{23} & p_{24} \\ p_{31} & p_{32} & p_{33} & p_{34} \\ p_{41} & p_{42} & p_{43} & p_{44} \end{vmatrix} \mathbf{x}(t), \quad (2)$$
$$t = 1985, 1990, \ldots,$$

where the numbers p_{ij} do not vary with time and the sum of each column is 1 according to the probabilistic meaning of the numbers (such matrices are called *stochastic*; Gantmakher, 1967, p. 381). The quantitative values of p_{ij} are inferred from the results of transition

matrix *calibration* based on expert assessment or observational data (see below).

The calibrated transition matrix enables the calculation of model process characteristics, such as the *steady-state probability distribution* of chain states ($\mathbf{x}^* = [x_1^*, x_2^*, x_3^*, x_4^*]^T$), that is, a positive and normalized (by the condition $x_1^* + x_2^* + x_3^* + x_4^* = 1$ or 100%) solution of the equation

$$\mathbf{x}^* = \mathbf{P}\mathbf{x}^*, \quad (3)$$

as well as the average *first-passage times* (t_{ij}) for the transition from the state j to the state i expressed as a number of chain steps.

The first-passage times, together with the average duration M_j of each state j, represent the temporal characteristics of the random process expressed as the number of steps. Since the magnitude of the time step is known, these characteristics can also be expressed in chronological units (years). The mathematical details of the corresponding computations are presented in Appendix A.

Calibration method. The character of the available data, namely, the availability of repeated observational data on permanent transects and a large sample size (N = 2000), enables unambiguous and reliable calculation of all model parameters, which is a rare possibility for ecology. Sixteen transition probabilities p_{ij} from equation (2), or, more precisely, 12 transition proba-
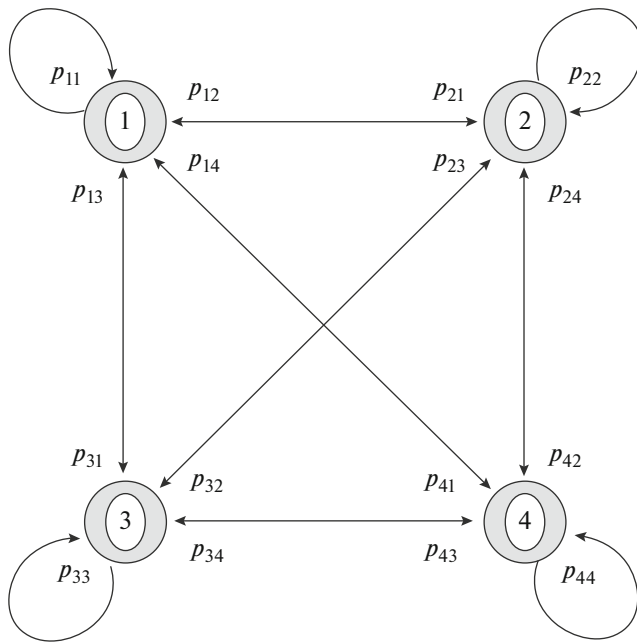
Fig. 2. Complete graph of transitions between four states of the sample quadrat in one time step $\Delta t = 5$ years and the corresponding elements of the 4×4 transition matrix $\mathbf{P} = [p_{ij}]$. Quadrat states: 1—both species are absent, 2—*Vaccinium myrtillus*, 3—*V. vitis-idaea*, 4—both species are present.

bilities and 4 probabilities p_{ij} of current state preservation for one step, serve as the parameters. The transition probabilities are inferred from the actual transition pattern, and the probabilities are estimated as the frequencies of the transition events that occurred.

The stochastic vectors $\mathbf{x}(t)$, $t = 1985$, 1990, of state probability distribution at the corresponding observation times are used in the calibration. The components of these vectors are calculated as frequencies, that is, by simply dividing the corresponding number by the sum of the components, which yields expressions in rational numbers. The use of species occurrence on the sites in field observations has the consequence of the number of transitions from one state to another always being a positive integer. Accordingly, the transition/retention probabilities in one time step (tradi-

tionally identified with the frequencies of the respective transition/conservation events) assume rational values in this study, as they are the quotients of two integers. The advantage of computations in rational numbers consists in the possibility of computing the calibration equality $\mathbf{x}(1990) = \mathbf{Px}(1985)$ as a *logical* equality, that is, with absolute accuracy (by means of symbolic algebra).

Model forecast. The Markov model can be used for forecasting purposes. Chain homogeneity (in time) implies constancy of the transition matrix over the time interval of the forecast, that is, the absence of noticeable changes in the key factors of the environment that determine the direction and rate of the process being simulated. The equality (2) at $t = 1985$ was used to calibrate the transition matrix, and the right side of this equality at the next step, that is, the vector $\mathbf{Px}(1990)$, therefore gives a short-term forecast of the system state in 1995. The hypothesis of homogeneity at one step can be verified by comparing this forecast with the results of observations in 1995.

RESULTS

Steady-state distribution of state probabilities. Data on the transitions between site states in 1985 and 1990 (in absolute values) are presented in Table 1. Sites with live and dead tree trunks and those with fallen logs (in each of the two observations) were excluded from the calculations in order to eliminate the influence of the spatial exclusion factor and the disturbance factor. As a result, the total sample size decreased from 2000 to 1747.

The absence of zero values in Table 1 confirms the assumption of the actual implementation of all theoretically possible transitions between states and conservation of current states. Moreover, it shows that the time step length and the number of sample sites were selected correctly, since all transitions were implemented in the community in 5 years, and this confirms the completeness of the digraph in Fig. 2. The probabilities of transitions and conservation of the states expressed in rational numbers as the frequencies of the corresponding events are presented in Appendix B,

Table 1. Data on transitions between quadrat states and on distributions of states in a *Polytrichum−Myrtillus* pine forest; V—*V. myrtillus*, W—*V. vitis-idaea*, ∅—none of the two species, N—total number of quadrats

1990	1985				
	∅	V	W	VW	N1990
∅	252	89	100	58	499
V	52	281	31	143	507
W	34	14	94	93	235
VW	12	67	53	374	506
N1985	350	451	278	668	1747

and the calibrated matrix up to the third decimal place takes on the form of

$$\mathbf{P} = \begin{vmatrix} 0.720 & 0.197 & 0.360 & 0.087 \\ 0.149 & 0.623 & 0.112 & 0.214 \\ 0.097 & 0.031 & 0.338 & 0.139 \\ 0.034 & 0.149 & 0.191 & 0.560 \end{vmatrix}. \qquad (4)$$

Accordingly, the *limit* or *equilibrium* probability vector (as a solution of equation (3)) is

$$\mathbf{x}^* = [0.410, 0.297, 0.112, 0.181]^T. \qquad (5)$$

In other words, the stationary (stable) result of succession (assuming the homogeneity in time) will be the following distribution of states: 29.7% of the sites were occupied by *V. myrtillus* only, 11.2% had *V. vitis-idaea* only, both species were present at 18.1% of sites, and neither *V. myrtillus* nor *V. vitis-idaea* were present at 41% of sites. All of this confirms the possibility of stable coexistence of *V. myrtillus* and *V. vitis-idaea* at the final stages of succession, with a clear predominance of *V. myrtillus* but without complete exclusion of one species by another.

Estimation of the duration of succession. The simple question of "How fast is equilibrium achieved?" is incorrect from a mathematical point of view. On the one hand, the mathematical meaning implies $\mathbf{x}^* = \lim_{t \to \infty} \mathbf{P}^t \mathbf{x}(0)$ for any initial distribution $\mathbf{x}(0)$, i.e., the number of steps t tends to infinity. On the other hand, common sense suggests that the required number of steps cannot be infinite if $\mathbf{x}(0)$ is already close to $\mathbf{x}^*$ and this number should be less than for $\mathbf{x}(0)$ that is farther from $\mathbf{x}^*$. Thus, the answer to the "simple question" needs an additional definition of the quantitative *measure of proximity* (or, simply, *distance*) between stochastic vectors (or finite probability distributions) and a corresponding reformulation of the question itself.

The distance $\Delta(\mathbf{x}, \mathbf{y})$ between two stochastic vectors $\mathbf{x}$ and $\mathbf{y}$ in demography is estimated according to Keyfitz (Keyfitz, 1968, p. 47) as the half sum of the differences of the same components of the vectors:

$$\Delta(\mathbf{x}, \mathbf{y}) = \frac{1}{2} \sum_{j=1}^{n} |x_j - y_j|, \qquad (6)$$

where n is the total dimension of the vectors. In this case, the distance values vary from zero for equal vectors to 1 for maximum difference between the vectors, such as $\mathbf{x} = [1, 0, ..., 0]$, $\mathbf{y} = [0, ..., 0, 1]$.

The distance between the initial vector $\mathbf{x}(1985)$ and the equilibrium $\mathbf{x}^*$ is $\Delta(\mathbf{x}(1985), \mathbf{x}^*) = 0.2485$, or about a quarter of the maximal possible distance, in the present study. Therefore, the correct form of the question is: "How many model steps should be made in order for the difference between the initial vector $\mathbf{x}(1985)$ and the equilibrium vector to become not higher than 0.1 or 10%?" It turned out that two steps would be sufficient already: $\Delta(\mathbf{P}^2\mathbf{x}(1985), \mathbf{x}^*) = 0.0732$, the next

Table 2. Mean first passage/return times expressed in years (approximate values), and men duration of the state before the transition

Initial state	Terminal state			
	∅	V	W	VW
∅	12	33	60	61
V	27	17	67	49
W	21	34	45	49
VW	31	29	56	28
Mean duration	18	13	8	11

step would enable a closeness value of 4%: $\Delta(\mathbf{P}^3\mathbf{x}(1985), \mathbf{x}^*) = 0.0432$, and the sixth step would ensure closeness within 1%: $\Delta(\mathbf{P}^6\mathbf{x}(1985), \mathbf{x}^*) = 0.0089$.

Thus, the results of using a homogeneous Markov chain show that the two-species *V. myrtillus*−*V. vitis-idaea* system was fairly close to a stable state at the moment when the sample plot was marked and the time of the secondary postfire succession (for the difference between the state of the system and the equilibrium state to become less than 5%) was 45 years: 30 years from the ground fire in 1954 to the beginning of calculations plus three five-year model steps.

Stage duration and process cyclicity. The average first-passage times for the transition into any state from any other state expressed in steps are given in Appendix B, and the approximate estimates in years (with the step length Δt of 5 years taken into account) are shown in Table 2. For example, 67 years on average are required to achieve the state W starting from V, and 34 years are required to achieve V starting from W.

The full set of these parameters reflects the *cyclical* nature of a random process, for which the conventional single value of *period* duration for deterministic oscillations does not make sense any longer. Thus, it takes a different number of years (12 to 45) for the different states to be repeated (see the diagonal cells of Table 2); an empty site reaches the W state in 60 years on average and the VW state in 61 years on average. However, this does not mean that the V species develops along with W within 1 year, since it takes 49 years on average for the VW state to develop from W.

The results for the average duration of the state before the transition are derived from the **M** vector (B4) according to a similar procedure; these results are shown in the bottom row of Table 2. The "empty" state of the sites is apparently preserved for the longest time intervals, which is probably due to the presence of deep hollows in the pine forest. These hollows are

periodically flooded with water and are therefore poorly adapted for the growth of dwarf shrubs. The modeling revealed a significant difference between the duration of site occupancy by *V. vitis-idaea* only (8 years) and by *V. myrtillus* only (13 years). These differences can be partially explained by the average age of aerial shoots that reportedly ranges from 3 to 5 years in *V. vitis-idaea* and from 5 to 8 years in *V. myrtillus* (see reviews by Balandina and Vakhrameeva, 1978, 1980). However, as the average duration of state retention by the respective site is only slightly longer than the average age of aerial shoots, we come to the conclusion that the species composition at the site usually changes as the aerial shoots die away (according to the model).

Model forecast. The short-term forecast based on the transition matrix (4) (more precisely, (B1)) yields a probability distribution for the states

$$\mathbf{x}(1995) = [0.3365, 0.3002, 0.1226, 0.2407]^T. \quad (7)$$

The measure Δ of the difference between the forecast (7) and the observed frequency distribution $\mathbf{n}(1995) = N1995/1747 = [0.2822, 0.3022, 0.1351, 0.2805]^T$ is

$$\Delta(\mathbf{x}(1995), \mathbf{n}(1995)) = 0.0543, \quad (8)$$

or 5.4%. Thus, estimate accuracy is significantly higher than the accuracy of similar forecasts obtained, for example, with the use of Markovian models of cyclic zoogenic succession of vegetation in small river floodplains, as the accuracy of the latter forecasts ranged from 9.6 to 25.5% (Logofet et al., 2016a, Tables 4 and 5).

DISCUSSION

The values of M_j (A4) in general, and (B4) in particular, i.e., the mean expectations until the corresponding state changes in a two-species system of *V. myrtillus* and *V. vitis-idaea* system expressed in steps, and their approximate expressions in years (Table 2) allow assessment of the correspondence between the time step length chosen during the planning of observations and the rate of the processes monitored (if the homogeneity hypothesis is accepted). Values that range from 1.5 to 3.5 steps are indicative of the adequacy of the choice, but the completeness of the digraph of transitions (Fig. 2), i.e., the implementation of all possible transitions between the states of the sites within just one interval between observations, is the best evidence of an adequate choice.

Situations of this type are quite rare in ecological modeling. If matrix models are constructed for the dynamics of discrete-structured single-species populations (Caswell, 2001; Logofet and Belova, 2008, Logofet, 2013b; Logofet et al., 2016b), the *life cycle* graph for the individuals of the species in question can never be complete. Indeed, this graph reflects the process of development of the individuals directed from birth to death regardless of the choice of classification type (according to age, size and/or stage of development). Even though the graph may contain the so-called *regressive transitions* in the opposite direction (Logofet et al., 2012; Logofet, 2013a), which reflect various adaptive reactions of the organism (Horvitz and Schemske, 1995; Salguero-Gómez and Casper, 2010; Logofet et al. 2017), these reactions are observed at particular stages only and cannot provide completeness of the entire graph. Graphs of interspecies relations in multi-species communities (Svirezhev and Logofet, 1978; Logofet, 1993; Borelli et al., 2015) cannot be complete either, since they would otherwise include biologically incredible links (such as direct influence of a primary producent on a third-order consument). The completeness of the scheme of transitions between the stages is also ruled out in the case of vegetation succession models (Logofet, 2010), in this case by process directionality from the pioneer stages to the climax. Moreover, even in the case of cyclic (for example, zoogenic) successions (Logofet et al., 2016a), returns to individual stages are not sufficient for ensuring the completeness of the entire scheme of transitions.

Completeness of the transition digraph constructed in the present study (Fig. 1) implies the maximal number of 16 for the model parameters to be calculated upon the calibration of the 4 × 4 transition matrix. Notwithstanding the extreme laboriousness of the field experiment (with repeated observations at several thousand test plots), this does not cause technical difficulties in the calculations, but confers certain methodological advantages that will be essentially clarified after the hypothesis of Markov chain homogeneity in time is discussed. Indeed, six observations within 25 years enable a similar calibration of another four transition matrices $\mathbf{P}_1$, $\mathbf{P}_2$, $\mathbf{P}_3$, and $\mathbf{P}_4$ that will obviously differ from the calibrated matrix $\mathbf{P}_0 = \mathbf{P}(4)$, simply due to natural differences in the data. Formally, this implies the dependence of the matrix $\mathbf{P}$ on the time t in the basic model equation (2), i.e., *Markov chain inhomogeneity*, as in the situations observed in other projects that involved Markov models for successions (Logofet, 2010; Logofet et al., 2016a) or landscape dynamics (Vinogradov et al., 1989). However, the strength of this dependence, the putative correlation (or the absence thereof) between variability of the $\mathbf{P}_j$ matrices and some trend in the change of key environmental factors, and, finally, the procedure that would allow for the assessment of the quantitative characteristics of the process that generalize all 25 years of observations can only be addressed if the *averaged* matrix concept is introduced (this matrix will be referred to as $\mathbf{P}_{av}$).

Matrix averaging issus have not received adequate attention in ecological literature. Theoretical constructions (see Tuljapurkar, 1990; Caswell, 2001) simply postulate the existence of the average matrix, whereas the authors of practical works use the *arithme-*

tic mean (Logofet, 2013a) by default, without in-depth analysis of the meaning of averaging. Meanwhile, the conceptual meaning of averaging follows from the proposition that the average matrix should give exactly the same result on the entire observation segment as the *nonhomogeneous* (or, more generally, *nonautonomous*) model. In our case, the distribution of states in the year 2005 of the final (sixth) observation (i.e., the result of the successive transformation of the vector of the initial distribution $\mathbf{x}(1980)$ into the vector $\mathbf{x}(2010)$ by analogy with equation (2):

$$\mathbf{x}(2010) = \mathbf{P}_4 \cdot \mathbf{P}_3 \cdot \mathbf{P}_2 \cdot \mathbf{P}_1 \cdot \mathbf{P}_0 \cdot \mathbf{x}(1980) \qquad (9)$$

should constitute the modeling result for the entire segment(see Logofet et al., 2017, equation (6)). Therefore, the average matrix in the power of five should yield the products of matrices on the right-hand side of (9):

$$\mathbf{P}_{av}^5 = \mathbf{P}_4 \cdot \mathbf{P}_3 \cdot \mathbf{P}_2 \cdot \mathbf{P}_1 \cdot \mathbf{P}_0 \qquad (10)$$

(ibid., equation (7)), and therefore the substantial meaning of $\mathbf{P}_{av}$ is that of the *geometric mean*. The problem of geometric averaging of nonnegative (in particular, stochastic) matrices does generally not have any exact solution, and this constitutes a methodical difficulty (Logofet, 2015; Logofet et al., 2017), but an *approximate* solution (ibid) comes to the rescue in this case. However, the particular case of the complete transition graph (Fig. 2) points at the possibility of finding an exact solution of the averaging problem, and this, as well as the issues discussed above, will be addressed in the second part of the present article.

CONCLUSIONS

The mathematical apparatus of finite homogeneous Markov chain theory has been successfully used for the example of secondary succession in the two-species dominant system of *V. myrtillus* and *V. vitis-idaea* after a ground fire in the *Polytrichum−Myrtillus* pine forest. The field experiment had the following distinctive features: a large sample size on permanent transects (2000 sites), several regular observations at 5-year intervals, and the recording of species occurrence on the sites. All possible transitions between the four states were implemented at the test plots during one interval between observations (5 years): (1) the absence of both species; (2) the presence of *V. myrtillus* only; (3) the presence of *V. vitis-idaea* only; (4) the presence of both species. The conservation of states was also observed. A complete digraph of transitions was formed, which is an extremely rare instance in ecology, and unambiguous calibration of the corresponding transition matrix was performed according to direct observations.

Formulas of the theory of finite homogeneous Markov chains have been used to obtain the main results of the model: stationary distribution of areas, cyclicity characteristics, and the average duration of the stages of fine-scale dynamics. The expected state distribution for the sites (the stable result of succession) was shown to be the following: 29.7% of sites were occupied by *V. myrtillus* only; 11.2% had *V. vitis-idaea* only; both species were found at 18.1% of the sites, and neither *V. myrtillus* nor *V. vitis-idaea* were found at 41% of the sites. This confirms the possibility of stable coexistence of *V. myrtillus* and *V. vitis-idaea* at the final stages of succession, with a clear predominance of *V. myrtillus* but without complete exclusion of one species by another.

Evaluation of the cyclicity characteristics and the average duration of the stages of fine-scale mosaic revealed a fact that was not apparent a priori: the two-species system of *V. myrtillus* and *V. vitis-idaea* was rather close to a stable state at the moment when the study area was marked, and the time of the secondary postfire succession (until the attainment of the state that differed from the equilibrium state by less than 5%) was approximately 45 years. Sites with *V. vitis-idaea* only had the shortest average lifetime (8 years) of the four types of sites described, and those devoid of both *V. myrtillus* and *V. vitis-idaea* had the longest average lifetime (18 years).

A model forecast of the dynamics for one step (5 years) ahead and comparison with the actual distribution of sites showed that the measure of difference was 5.4%, which is indicative of the efficiency of the short-term forecast for a homogeneous model. However, the question of the validity of the homogeneity hypothesis remained open. Verification of this issue, as well as the questions of transition matrix averaging over the entire 30-year period of observations, should form the subject of the second part of the study.

APPENDIX A

Stationary Probability Distribution and Average First-Passage Times

Since the transition graph is complete (Fig. 1), matrix $\mathbf{P}$ is positive, i.e., none of its 16 elements p_{ij} vanishes. In this case, the matrix is also *primitive*, and then there is a limit

$$\lim_{t \to \infty} \mathbf{P}^t = \mathbf{X}^*, \qquad (A1)$$

where $\mathbf{X}^*$ is a matrix composed of identical columns $\mathbf{x}^*$ (Kemeni and Snell, 1970, p. 94). The relation (A1) allows the calculation of $\mathbf{x}^*$ with any given accuracy if the matrix $\mathbf{P}$ is raised to a sufficiently large power of t.

On the other hand, the *irreducible* (Gantmakher, 1967, p. 352) matrix $\mathbf{P}$ has a positive eigenvector that corresponds to the dominant eigenvalue $\lambda_1 > 0$ or the Perron root of its characteristic polynomial, according to the classical Perron-Frobenius theorem for nonnegative matrices (ibid., p. 355). As the matrix $\mathbf{P}$ is stochastic, its $\lambda_1(\mathbf{P}) = 1$ and the corresponding stochastic Perron's vector $\mathbf{x}^*$ is uniquely determined by the equation (3). As shown in Appendix B, the elements p_{ij} of

the calibrated matrix $\mathbf{P} = [p_{ij}]$ are rational numbers, and hence the linear equation (3) is solvable in rational numbers, for example, using the symbolic algebra toolbox in the MATLAB environment (MathWorks, 2016).

The average *first-passage* times t_{ij} are expressed as the number of steps and are the elements of the matrix

$$\mathbf{T} = \mathbf{D}\,(\mathbf{I} - \mathbf{Z} + \mathbf{Z}_{dg}\mathbf{E}), \qquad (A2)$$

where $\mathbf{D} = \mathrm{diag}\{d_{jj}\}$ is the diagonal matrix with the elements $d_{jj} = 1/x_j^*$ $(j = 1, ..., 4)$ on the diagonal, $\mathbf{I} = \mathrm{diag}\{1, 1, 1, 1\}$, $\mathbf{E}$ is the matrix with all elements equal to 1, $\mathbf{Z} = (\mathbf{I} - \mathbf{P} + \mathbf{X}^*)^{-1}$ is the *fundamental matrix* of the chain, and $\mathbf{Z}_{dg}$ is the diagonal matrix with elements of the principal diagonal of the matrix $\mathbf{Z}$ (Kemeni and Snell, 1970, pp. 101, 106). Like matrix $\mathbf{P}$ and vector $\mathbf{x}^*$, the matrices $\mathbf{X}^*$, $\mathbf{Z}$ and $\mathbf{D}$, and, consequently, $\mathbf{T}$ also can be computed in rational numbers.

There is a fundamental relationship between the mathematical expectation (M_j) of a random number of steps, after which the state j changes, and the corresponding diagonal element p_{jj} of the transition matrix, i.e., the probability of remaining in the state j in one step:

$$p_{jj} = 1 - 1/M_j, \quad j = 1, ..., 4 \qquad (A3)$$

$$\begin{bmatrix} -7/25 & 89/451 & 100/278 & 58/668 \\ 26/175 & -170/451 & 31/278 & 143/668 \\ 17/175 & 14/451 & -92/139 & 93/668 \\ 6/175 & 67/451 & 53/278 & -147/334 \end{bmatrix} \begin{bmatrix} 1\,079\,509\,025/2\,634\,986\,874 \\ 783\,519\,143/2\,634\,986\,874 \\ 147\,712\,103/1\,317\,493\,437 \\ 18\,328\,250/101\,345\,649 \end{bmatrix} == \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}. \qquad (B3)$$

Calculations of the matrix $\mathbf{T}$ by the formula (A2) and the vector $\mathbf{M} = [M_j]^{\mathrm{T}}$ (A4) can also be performed in rational numbers, but this has no practical sense. Two characters after the decimal point (in steps) are sufficient for the approximate estimation of these parameters in years.

$$\mathbf{T} \approx \begin{bmatrix} 2.44 & 5.48 & 4.24 & 6.28 \\ 6.61 & 3.36 & 6.75 & 5.71 \\ 12.00 & 13.31 & 8.92 & 11.12 \\ 12.19 & 9.84 & 9.80 & 5.53 \end{bmatrix},$$

$$\mathbf{M} \approx \begin{bmatrix} 3.57 \\ 2.65 \\ 1.51 \\ 2.27 \end{bmatrix}. \qquad (B4)$$

The forecast for one step yields the probability distribution of states

(Kemeni and Snell, 1970, p. 84), and therefore the average *duration of the state* before the change is

$$M_j = 1/(1 - p_{jj}), \quad j = 1, ..., 4. \qquad (A4)$$

APPENDIX B

Results of Transition Matrix Calibration

The calibrated matrix $\mathbf{P}$ in rational numbers assumes the form

$$\mathbf{P} = \begin{bmatrix} 126/175 & 89/451 & 100/278 & 58/668 \\ 26/175 & 281/451 & 31/278 & 143/668 \\ 17/175 & 14/451 & 94/278 & 93/668 \\ 6/175 & 67/451 & 53/278 & 374/668 \end{bmatrix}, \qquad (B1)$$

which obviously possesses the column-stochastic property and conforms to the verification equality (2) for $t = 1985$ with absolute accuracy (the sign of logical equality ==):

$$\begin{bmatrix} 499 \\ 507 \\ 235 \\ 506 \end{bmatrix} \Big/ 1747 == \mathbf{P} \begin{bmatrix} 350 \\ 451 \\ 278 \\ 668 \end{bmatrix} \Big/ 1747. \qquad (B2)$$

The solution $\mathbf{x}^*$ of the equation (3), or the equivalent $(\mathbf{P} - \mathbf{I})\mathbf{x}^* = 0$, is verified in a similar way:

$$\mathbf{x}(1995) = \mathbf{P} \begin{bmatrix} 499 \\ 507 \\ 235 \\ 506 \end{bmatrix} \Big/ 1747$$

$$= \begin{bmatrix} 153\,842\,227\,416/261\,726\,575 \\ 961\,027\,852\,437/1\,832\,086\,025 \\ 784\,569\,530\,683/3\,664\,172\,050 \\ 1\,540\,892\,151\,969/3\,664\,172\,050 \end{bmatrix} \Big/ 1747, \qquad (B5)$$

with a sum logically equal to 1 (regardless of the expression being lengthy).

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