

## MODELLING SECONDARY SUCCESSION ON OLD FIELDS USING MARKOV CHAIN AND AN OVERVIEW OF MATHEMATICAL MODELLING OF SUCCESSIONAL PROCESS

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### Abstract

In search for models of succession a number of mathematical and statistical models have been tried by various ecologists and range workers including, descriptive, based on ordinary or partial differential equations, cellular automata, fractals and stoichiometric models as well as ordination techniques and matrix models including Markov chains. This paper examines the old-field succession using Markov chain stochastic model to describe, predict and simulate the vegetation dynamics of the abandoned fields at Malir-Landhi area, southern Sind, Pakistan.

Recorded data over 4-years period from permanent plots (patches) permitted an estimation of transition probabilities using the frequency of plots in various states that moved to other states over a period of one year at various sampling times. Average transition matrix using four years data was employed for the sake of accuracy in the estimation of probabilities. The paper discusses the Markov properties and its features, studies and exemplifies the test of first order Markov chain. The results indicate that the secondary succession under study conform to first-order Markovian process since the observed field data was found to fit closely to the first-order transition process. Transition matrix successfully exposed the nature and mechanism of succession and provided insights into the process of secondary succession. Succession was found to be almost unidirectional. Stability of the system was also checked which disclosed relatively greater stability at the later stage of succession pointing it to be the disclimax of the area. Though not all assumptions of Markovian process were held by the data it appears that the transition matrices provide useful descriptive devices even when the system is not absolutely Markovian. The succession was related to second law of thermodynamics and entropy. The entropy of the successional ecosystem changed with the onward march of the succession. The overall system Entropy of the successional ecosystem was moderately high.

**Key words:** Secondary succession, Markov chain, Modeling, Ordination, Entropy.

### Introduction

Biotic communities are not static but constantly under the state of flux. Syndynamics or succession is one the most important community process that can play a significant role in vegetation preservation, recovery and restoration (Bazzaz, 1975; Miles *et al.*, 1987; Peng *et al.*, 2004; Tucker & Anand, 2004; Hang, 2005; Walker & del Moral, 2003, 2009; Pickett *et al.*, 2009; Hanson, 2011). Secondary succession which follows a major perturbation such as fire, flood, clearcutting of a forest or abandonment of a cultivated field, etc. is much more rapid than primary succession (Anderson, 1987; Burrows, 1990; Ricklefs & Miller, 2000). Succession is currently not viewed as a deterministic process that eventually leads to a unique stable climax community (Connell & Slatyer, 1977).

The earliest models of succession such as those of Drury & Nisbet (1973) recognizing the importance of environmental gradients that influence the differential growth and survival rates of species), Grime (1974, 1979) (Competitors-Stress-tolerators-Ruderals) and Connell & Slatyer (1977) (Facilitation-Tolerance and Inhibition models) were dioristic models, *i.e.*, they were descriptive or verbal.

The first mathematical models developed were simulation or computer models (e.g., Leak, 1970; Botkin *et al.*, 1972a, Shugart *et al.*, 1973; Shugart & West, 1980; Pickett *et al.*, 1987; Favier *et al.*, 2004). Botkin *et al.*, (1972b) developed a gap model JABOWA that was founded on tree establishment, growth and mortality.

Pacala *et al.*, (1996) constructed a spatially structured stand level model (SORTIE) incorporating seed dispersal, recruitment, growth and mortality. In essence it was based

on an earlier model FOREST developed by Ek & Monsurd (1974). The gap model of mangrove forest dynamics (FORMAN) developed by Chen & Twilley (1998) that incorporates the influence of salinity on mangrove tree growth. These models were basically designed to have predictive value for a specific succession or sere. Acevedo *et al.*, (1996) employed transition and gap model to forest dynamics.

Various ordination models have also been employed by many ecologists to analyse and examine successional sequences (Shaukat, 1985; Shaukat & Uddin, 1989; Shaukat *et al.*, 1981, 2014; Odland & del Moral, 2002; Tucker & Anand, 2003; Prach *et al.*, 2007; Marler & del Moral, 2013; Prach *et al.*, 2013; Chang *et al.*, 2014; Dini-Andreote *et al.*, 2016).

Succession can be modelled by means of ordinary differential equations (Shigesada *et al.*, 1984; Yang *et al.*, 2010; Hastings & Gross, 2012; Marino *et al.*, 2014) or partial differential equations; Holmes *et al.*, 1994; Hastings & Gross, 2012). Based on population dynamics model, van Hulst (1979 a-b) used logistic equations (sigmoidal equation) of population growth:

Using ordinary differential equations Shigesada *et al.*, (1984) modelled a system of N competing species. Under this system, they used the intrinsic growth rate, within-species competition, between-species competition, and the species resilience ( $\sigma$ ) (or the degree to which they are capable of resisting competition). Marino *et al.*, (2014) used a modified Lotka-Volterra equation.

Brennan & Reneke (1984) used diffusion process in conjunction with continuous parameter Markov chain. Blatt *et al.*, (2001) included herbivore effect in Lotka-Volterra equations to model succession. Leps & Prach (1981) used

discrete logistic equations to model secondary succession with considerable success. Marleau *et al.*, (2011) presented a primary succession model based on ecological stoichiometry that permitted integration of major biotic processes with other aspects including biogeochemical cycles. Hodgeweg (1988) applied cellular automata as a paradigm for ecological modelling and provided a model for succession based on cellular automata. Cellular automata models have also been employed by a number of workers (Silvertown, 1992; Colasanti & Grime, 1993; Ermentrout & Edelstein-Kechet, 1993; Halley *et al.*, 1994; Baltzer *et al.*, 1998; Atkinson *et al.*, 1998; Caswell & Etter, 1999; Soares-Filho *et al.*, 2002; Almeida *et al.*, 2003; Walther *et al.*, 2003; and Sloot *et al.*, 2004). Almeida *et al.*, (2003) used stochastic cellular automata model for urban land use dynamics. Ecological applications dealing with time-series such as successional data often require the use of nonlinear techniques. Cellular automata models provide potentially useful approach that could decipher linear as well as nonlinear dynamics of ecological succession and consequently lead to applications in conservation and management issues.

Another approach to modelling succession is by means of fractal analysis. Excellent reviews are presented by Kenkel & Walker (1996) and Milne (1997) on the application of fractals in ecological and landscape research as well as ecosystem dynamics. Hastings *et al.*, (1982) and Mandelbrot (1983) showed how fractal exponents might be integrated into diffusion processes for normalizing increments in space and time. It was pointed out that  $D$  can be used as a fractal dimension (DI) in different point patterns including regular, random, random clumped pattern and aggregated clumped point patterns serving as index of succession in circumstances where simple patch-extinction models are reasonable. Li (2000) described patch patterns and patch dynamics using fractal analysis. Alados *et al.*, (2003) characterized an ecological succession using fractal geometry and demonstrated a drastic change in the fractal dimensions that disclosed a change in the vegetation structure, accurately indicating last successional vegetation stages. Saravia *et al.*, (2012) examined multifractal spatial patterns and diversity to elucidate ecological succession. Basically the fractal analysis methods help to disclose spatial and temporal complexity that involve purposeful manipulation of the scale of observation to explore how phenomena change steadily and predictably, with the change in scale.

Another widely used approach is the application of the so-called matrix models. Among the matrix models, Markovian models are more appealing and have received comparatively greater attention because they are more tractable form of stochastic mathematical models that may be employed in successional studies (Horn, 1975a,b; Usher, 1979, 1981; van Hulst, 1979b; 1980; Runkle, 1981; Lippe *et al.*, 1985; Facelli & Pickett, 1990; Isagi & Nakagoshi, 1990 - missing; Orloci *et al.*, 1993; Rego *et al.*, 1993; Aaviksoo, 1995; Osho, 1996; Baltzer, 2000; Logofet & Lesgnaya, 2000, Korotkov *et al.*, 2001; Benabdellah *et al.*, 2003; Logofet, 2003; Yin *et al.*, 2009). Markov models regard the landscape as an infinitely large area with a set of patches or points in space. A list of plant describes the occupancy of a plant species at each point while in another class of the model the list may comprise

of multiple coexisting species at each patch (or plot), the latter are often categorized as patch occupancy models (Hill *et al.*, 2004). Although time-varying models with non-homogeneous Markov process have been analysed (Hill *et al.*, 2002) as non-linear dynamics, the results are not encouraging (Hill *et al.*, 2004). Whereas models with time-invariant transition probabilities are homogeneous Markov chains seem to provide better results.

Old-field dynamics can be usefully described in terms of a finite number of states and the transition probabilities between these states. The Markov models are based on the idea that succession is an orderly process (as originally suggested by Clements) and therefore probabilities of transition from one succession stage to another can be estimated assuming that they remain constant throughout the time period and do not depend on past history of vegetation.

Here we focus on time invariant transition probabilities that furnish homogeneous finite-state Markov process to analyse the successional sequence associated with old-fields in southern Sind. The current paper investigates the possibility of modelling secondary succession of vegetation using the stationary Markov process to test certain hypothesis of interest. Markov models provide a unifying concept with regards to multiple approaches to succession. The Markov chains have been applied to ecological succession by a number of workers (see above for references). Appropriate Markovian models could be used to test a number of hypotheses pertaining to the process of succession analogous to the Markovian assumptions. It has been advocated by Hill *et al.*, (2004) that although Markovian models are effective tool for exploring ecological succession properties but they have not been gainfully employed to unravel various properties at population and community level in a successional ecosystem.

There are several approaches to modelling of succession as pointed out above. However, often the dominating role of historical and spatial factors in syndynamics creates difficulties in the development of reasonably satisfactory models.

Exposing successional trends in energy and matter exchange across the ecosystem-atmosphere boundary layer is a necessarily required aspect in ecological research although no general theory in this respect exists as yet that describes the observed patterns. Attempt has been made to evaluate whether the principle of maximum entropy could provide a reasonable solution (Harte, 2011; Banavar *et al.*, 2010). For this purpose pre- and post-entropy of the successional ecosystem has been computed, in addition to the overall system entropy.

## Materials and Methods

Markovian models have usually been successful in predicting successional changes when the states of the system are clearly defined (Usher, 1975, 1979, 1992). Similar to other transition models, Markov models are stochastic since at any point in time transition from one particular state to the next may or may not take place. The principal assumption of Markov models is that when a system is in a particular state then there exists a fixed

probability that it would move to some new state (or remain in the same state) at the next point in time. The number of prior states that are mandatory to determine the future behaviour of the model is known as the order of the Markov chain. When the future behaviour of the system depends solely on the present state then the model is said to be the first order Markov chain. Moreover, any change in the system does not depend on the initial conditions. Neither of these assumptions is usually true in both primary or secondary succession (Facelli & Pickett, 1990).

If a plant or animal assemblage, in a specific area, is examined at times  $t_1$  and  $t_2$  with an appropriate time

Collection K → Collection L → Collection M → Collection N

where collections K, L, M and N in the context of succession represent concrete communities at various stages of a particular sere.

Although the process of succession is continuous, for the sake of convenience and description, different stages can be distinguished with each other and usually a few key-species are selected to recognize each of the seral stage of a particular succession (Usher, 1979; Shaikat, 1985). In many of the Markov chain model application to ecological succession the workers use sampling points (often on a grid) where replacement of one species by another is recorded (Horn, 1975a; Lippe *et al.*, 1985). Alternatively, in other class of models multiple coexisting species in permanent plots are recorded. The latter models are referred to as patch occupancy models. The present study employs the latter approach.

The current study focuses on secondary succession of old-fields in Southern Sind, Pakistan. For this purpose in all 100 plots (6 X 6 m) were permanently marked with metallic stakes in Landhi (near Karachi) area in 2000, where the cultivation was abandoned by the farmers during June 1999-January 2000. The total area of the fields surveyed was about 40 ha. The species composition and structure of the area was typical of abandoned fields in Southern Sind. To apply discrete Markov chain, we must break down the successional sequence into a series of discrete states ( $S_1, S_2, S_3, \dots, S_k$ ). Thus in this study the dynamics of patches of coexisting plant species rather than the individual plants are under investigation. In each plot vegetation was surveyed using a Braun-Blanquet cover scale (Mueller-Dombois & Ellenberg, 1974).

With respect to changes in vegetation, five more or less mutually exclusive states ( $k=5$ ) that could easily be distinguished were identified ( $S_1$ , earliest stage (mostly annual herbs, e.g., *Chenopodium album*, *C. murale*, *Argemonemexicana*, *Rhynchosia mininma*, *Tephrosia strigosa*, *Corchorus trilocularis*, *Euphorbia geniculata*, *E. thymifolia*), and a number of annual grasses (*Cenchrus biflorus*, *Eragrostis ciliaris*, *Eleusine indica* and *Brachiaria racemosa*),  $S_2$  = admixture of annuals and perennial herbs including *Pluchea lanceolata*, *Zaleya pentandra*, *Tribulus terrestris*, *Fagonia indica*, *Launaea procumbens*,  $S_3$  = perennial grasses (e.g., *Chrysopogon aucheri*, *Cymbopogon jawancusa*, *Desmostach*

interval, the observed data will show that the collection has changed, i.e., the composition of the collection (assemblage) would be altered. This can be represented as:

Collection X → Collection Y

The term 'collection' here does not imply clearly recognizable community of species or a change from one seral stage to another rather it is used in a 'loose sense' as a set individuals of species. When a similar piece of land is observed at a number of occasions, a sequence of communities can be disclosed:

*abipinnata*, *Dicanthium annulatum*, *Eleusine compressa*, *Cenchrus setigerus* and perennial herbs such as *Sida* spp., *Withania somnifera*, *Launaea procumbens*, *Pluchea lanceolata* and *Solanum surattense*;  $S_4$  = assemblages mostly constituted by shrubs or undershrubs (e.g., *Abutilon indicum*, *A. glaucum*, *Salsola inermis*, *Senna holosericea*), and  $S_5$  = shrubs (often tall) or small trees (e.g., *Capparis decidua*, *Calotropis procera*, *Salvadora persica*, *Prosopis juliflora*).

Occasionally, a species present in one state (patch) may also occur in another state but the overall composition of the patch and its dominant species remain conspicuous and can easily be recognized and categorized accordingly. Note that in this study 'vegetation states' were defined in terms of the dominance of particular set of species in each of the patch (plot) following the practice of Waggoner & Stephens (1970), Lippe *et al.*, (1985) and Rego *et al.*, (1993). Thus the categorization of the states is not problematic. According to Lippe *et al.*, (1985) one practical difficulty is the "measurement of real rather than inferred transition probabilities". Each plot was categorized into one of the state in the survey of 2000 based on its dominant species. The transition probabilities  $P_{ij}$  of transition from state  $S_i$  to state  $S_j$  have to be estimated. When repeated observations on the permanent plots are available, estimation of  $P_{ij}$  is a straightforward matter but without repeated observations, the estimation of transition probabilities is a complex procedure (cf. Usher, 1981). Transition probabilities represent functions of the natural rates of succession. Resampling of the permanent plots was performed after a period of one-year in the late summer (Sept. to Oct) for a period of four years (2001-2004) the plots were revisited and the vegetation examined and categorized into the appropriate states. The true transition matrix P can be estimated by converting transition frequencies to estimated probabilities from an observed sequence of successional states. Thus the transition probabilities calculated in this study are fairly close to real values. The non-negative row entries summing up to 1. The transition matrix provides an average picture of dynamics for the study period. The first step in the development of a Markov model is to construct a tally matrix that summarizes the number of times each state is followed by the rest of the states. Let  $m_{ij}$  be the observed number of transitions (i.e., transition

frequencies) from state  $i$  to state  $j$  in one-step transition. The transition probability  $p_{ij}$  can be estimated by dividing each row by its total that gives the maximum likelihood estimate of  $p_{ij}$ :

$$\hat{P}_{ij} = m_{ij} / \sum_j m_{ij} \geq 0 \dots \dots \dots$$
  

$$i=1, \dots, k; j=1, \dots, k \quad 0 \leq p_{ij} \leq 1 \quad (i,j = 1, 2, 3, \dots, k), \sum_j p_{ij} = 1.$$
 Usually one has to obtain a pooled time series i.e., macro-data on state frequencies as  $m_i(t)$  which means that the frequency of state  $i$  at time  $t$ . The estimator of transition probability is shown to be consistent, asymptotically unbiased and asymptotically normally distributed (Kelton & Kelton, 1984). The resulting transition matrix  $P$  is:

$$P = \begin{pmatrix} P_{11} & P_{12} & P_{13} & \dots & P_{1k} \\ P_{21} & P_{22} & P_{23} & \dots & P_{2k} \\ P_{k1} & P_{k2} & P_{k3} & \dots & P_{kk} \\ P_{31} & P_{32} & P_{33} & \dots & P_{3k} \end{pmatrix}$$

$P$  is a square matrix of transition probabilities, i.e., probability of moving from each state to all other states during one time step. The syndynamics are modeled by setting the probability distribution of the patch (plot) state at time  $t + 1$ , conditioned on its state at time  $t$  (the time interval was set at 1-year). In this case, the transition probabilities solely depend on the preceding state and are not dependent on any previous transitions. This implies that the *first-order* Markov model was employed that is a system in which probability distribution over next state is assumed to be dependent only on the current state, though higher order Markovian processes are possible and can be utilized to build-up models in ecology.

If there are  $k$  possible states then  $X(t) \in \{1,2,3, \dots, k\}$ , then  

$$P_{ij} = P\{x(t+1) = i \mid x(t) = j\} \quad i, j = \dots, \dots, k$$

$P_{ij}$  is a row stochastic i.e., each row adds up to 1). Let  $X(t)$  be a  $k$ -valued probability vector (i.e.,  $x_i \geq 0, \sum_i x_i = 1$ ) whose elements give the probability that an object is in state  $i$  then;

$$X(t + 1) = P X(t)$$

where  $P$  is the maximum likelihood estimate of the transition probability matrix. The matrix  $P$  is successively multiplied by a  $1 \times k$  state vector  $X(t)$  which contains the

$$\chi^2 = -2 \ln(\lambda) = -2 \sum_i \sum_j m_{ij} \ln(p_{ij} / P_j) \quad i=1, \dots, k; j=1, \dots, k$$

where  $m_{ij}$  is the frequency with which that transition from state  $i$  to state  $j$  has been observed (matrix  $M$ ) and  $p_{ij}$  is the transition probability from state  $i$  to state  $j$  ( $i,j=1,2,3, \dots, k$ ) and  $P_j$  is the marginal probability of column  $j$  ( $P_j = \sum_i m_{ij} / \sum_i \sum_j m_{ij}; i=1, \dots, k; j=1, \dots, k$ ). The approximate  $\chi^2$  is asymptotically distributed with  $(k-1)^2$  degrees of freedom (Usher, 1979). Generally the probability matrix ( $P$ ) described above is called an upward transition matrix. The downward transition probability matrix ( $Q$ ) is determined by dividing each

relative abundances of each vegetation type or patch ( $1, \dots, k$ ) that eventually translate to a steady state vector  $X_{stable}$  after a large number of iterations under the given set of environmental conditions including occasional mild grazing. The state vector is independent of the initial conditions provided that  $P$  is a stochastic matrix. This property can be represented as.

$$X_{stable} = P * X_{stable}$$

In the context of ecological succession  $X_{stable}$  can be interpreted as the species composition of the climax community of the area. This vector can be calculated directly as the right eigenvector of  $P$  and the corresponding eigenvalue is the largest eigenvalue of the matrix  $P$  that equals 1, thereby indicating that there is no net change to the sum of state vector. There are a number of assumptions inherent in the Markov models as pointed out above: 1) It is assumed that transitions within the system are temporarily stationary. This is seldom valid in ecological investigations because climate, the extent of disturbance and anthropogenic activity in the area vary to a large extent; also processes such as density-dependence operate in the biota. To build up models for non-stationary systems, several transition matrices may be required with each matrix being appropriate for a specific set of environmental conditions. 2) Local neighbourhood processes are disregarded, i.e., local spatial stationarity is assumed. This implies that the patches of one type do not affect the transition rates of the neighbourhood patches. Neighbourhood effects usually play an important role in shaping the structure and pattern of vegetation (Bergelson, 1993; Khan & Shaukat, 1997; Hubbell *et al.*, 2001; 3) The state of the system at time  $t+1$  solely depends on the system at time  $t$  and therefore disregards the past-history. Nonetheless, this assumption is relaxed when higher order Markov models are employed (Orloci *et al.*, 1993). A chi-square ( $\chi^2$ ) test for independence in a matrix of transition probabilities developed by Anderson & Goodman (1957) was employed. In this case the null hypothesis implies that the successive steps are independent of each other (i.e., randomness of the process) while the alternative hypothesis postulates that they are not independent and may constitute a first order Markov chain (Harbough & Bonham-Carter, 1970). The asymptotically equivalent test statistic for the likelihood test statistic is given by.

element of the transition frequency matrix ( $M$ ) by the corresponding column total:

$$q_{ij} = m_{ij} / \sum_i m_{ij} \geq 0 \quad i=1 \text{ to } k, j=1 \text{ to } k$$

$$0 \leq q_{ij} \leq 1 \quad (i,j = 1, 2, 3, \dots, k).$$

According to Hill *et al.*, (2004) Markovian model has been used to disclose useful information at two ecological levels: i) Species level properties and ii) Community level properties.

**Species (or group of species at state) level properties**

**Turnover rates:** The turnover rate here implies the rate at which plot (assemblage) change states and therefore provides a useful measure of rate of change of the successional process. The turnover rate of the *i*th assemblage (state) equals the probability that a plot in state *i* will change during the interval *t* to *t*+1, this is found as:

$$T_i = (1 - p_{ii})$$

whereas, the expected value of the turnover rate is obtained as:

$$E(\text{turnover time}) = \tau_i = 1 / T_i$$

**Replacement:** The process of replacement takes place when a species (or a group of ecologically similar species) that occupies a plot at time *t* is occupied by a different species (or a group of species) at time *t*+1. According to Sebbens (1986) this occurs when a more competitive species (or a group of spp) from a neighbouring area replace(s) a less competitive species. The Replacement probability is assessed as:

$$P(\text{replacement of species/state } j) = 1 - p_{ii} - p_{ki} \quad j=1, \dots, k-1$$

On the contrary, one can look at replacement by a species (or a group of species). Focus on *i*th row species (group) that replaces the other species with probability *p<sub>ij</sub>*; the mean for these probabilities is given as:

$$P(\text{replacement by species/state } i) = 1 / (k-2) * \sum_{p_{ij} \neq i, \dots, k}$$

In this formulation *p<sub>ii</sub>* and *p<sub>ki</sub>* are ignored as they do not represent replacement but stand for colonization and persistence respectively.

**Persistence:** Persistence takes place when a species (or a group of species at time *t* remains in a plot at time *t*+1. This is determined as follows;

$$P(\text{persistence of species/state } i) = p_{ii} \\ P(\text{total persistence species/state } i) = \sum_i p_{ii} \quad i=1, \dots, k$$

**Community properties**

**Entropy:** The extent and nature of ordering of seres (states) can be examined following the concept of entropy. In the present context entropy is defined as the uncertainty in the composition of the system. Perhaps the earliest use of entropy in ecology is in the use of Shannon-Wiener index that measures informational entropy of a system. In a succession having Markovian property, it is pertinent to ask what is the type of repetition (or cyclicality). Secondary succession belongs to the category of cyclic (asymmetric) succession. From the *P* matrix where the row total is unity, *E<sup>post</sup>* i.e., entropy after successional progression for each state can be calculated using the following expression:

$$E^{post} = -\sum_j p_{ij} \log_2 p_{ij} \quad j=1, \dots, k$$

The second matrix (*Q*) where *q<sub>ij</sub>* represents the probability that the given transition is preceded by any other transition. The column total of *q<sub>ij</sub>* matrix sums to unity. *E<sup>pre</sup>* i.e., entropy before the development of seres (states), can be calculated as:

$$E^{pre} = -\sum_j q_{ij} \log_2 q_{ij} \quad j=1, \dots, k$$

The normalized entropies can be obtained as:

$$R^{post} = E^{post} / E_{max} \\ R^{pre} = E^{pre} / E_{max}$$

where *E<sub>max</sub>*(maximum entropy) = - log<sub>2</sub> [ 1/(*k*-1) ]

The entropy of the entire successional system *E<sup>synt</sup>* can also be calculated as follows:

$$E^{synt} = -\sum_i \sum_j t_{ij} \log_2 t_{ij} \quad i=1, \dots, k \quad j=1, \dots, k \\ t_{ij} = m_{ij} / T \\ T = \sum_i \sum_j m_{ij} \quad i=1, \dots, k \quad j=1, \dots, k$$

**Results**

**The vegetation:** The recorded data from the permanent plots disclosed that the vegetation succession proceeded rapidly after the commencement of the observations in 2000, it attained almost a stable state after 4-years of vegetation progression. Community replacement was a progressive, orderly and directional process. In the beginning when observations were taken, about 8 to 14 months following abandonment of cultivation (*S<sub>1</sub>* patches), the area was mostly occupied by annual forbs such as *Chenopodium album*, *C. murale*, *Argemone mexicana*, *Rhynchosia minima*, *Tephrosia strigosa*, and *Corchorus trilocularis*, and annual grasses like *Sporobolus coromandelianus*, *Dactyloctenium aegyptium* and *Aristida adscensionis*. Also there were almost bare ground patches that contained only one or a few annual plant species. Following two-years of abandonment (*S<sub>2</sub>* patches) could be recognized easily with the dominance of perennial herbs (e.g. *Pluchea lanceolata*, *Zaleya pentandra*, *Tribulus terrestris*, *Fagonia indica*, *Launaea procumbens* and perennial grasses including *Dicanthium annulatum*, *Chloris barbata*, *Dactyloctenium scidicum*, *Chrysopogon aucheri*. Other patch types, particularly *S<sub>3</sub>*, *S<sub>4</sub>* and *S<sub>5</sub>* were rare in the first sampling (2000). Whenever they were seen, they appeared around the periphery, near the hedges of the individual old-fields and represented older vegetation compared to vegetation element common after one or 2-year of abandonment. They were included in the respective categories as per their particular dominant species. *Chenopodium album* was relatively the abundant species in the first year which in many countries including Pakistan appears as a dominant element in the initial stage of secondary succession presumably because of its high dispersal ability and allelopathic potential (Shaukat, 1985; Holzner & Numata, 2013). After the first year two noteworthy changes occurred: a rapid decline in the annual species and an increase in perennial species both dicotyledonous species and perennial grasses. Apparently, perennial grasses mentioned above are more adapted to grazing and other disturbances and they usually reproduce by vegetative mode as well as through seeding; therefore, they persist for longer duration and even prevail in the disclimax communities. The perennial herbs, small shrubs or under shrubs dominated during 2002 to 2003 (for two years) and

subsequently (2004) shrubs such as *Abutilon indicum*, *A. glaucum* and *Prosopis juliflora* attained dominance. *Prosopis juliflora*, an exotic species from South America that can be seen invading different patches and suppressing the other herbaceous perennials and shrubs owing to its allelopathic nature (Khan & Shaukat, 2006; Siddiqui *et al.*, 2009). Besides, this species is fairly drought and salinity tolerant and invades saline and disturbed soils with low moisture regimes replacing the native shrub species (Khan & Shaukat, 2006). Thus when it invades an area, particularly a disturbed area it rapidly achieves dominance and attains the position of disclimax. Any burning or cutting in such areas also favours its growth and the species quickly achieves the dominant status after any major perturbation.

**PCA ordination:** To examine the vegetation changes over the sampling period (2000-2004) a principal component analysis (PCA) of the covariance matrix of transformed cover estimate data (Braun-Blanquet scale) was performed for all the states (patches) and for species recorded in at least 5 plots (Fig. 1). The first component explained 43.74% of the total variance while the second component accounted for 37.20% of the variance. It is apparent from the PCA ordination that the years of sampling, corresponding to the duration of the secondary succession occurred sequentially in the ordination plane, from the left to right of the configuration (Fig. 1). The ordination also disclosed that the species composition of the assemblages of first year of succession differed greatly from those for the rest of the year (the composition of the states is given earlier).

**Transition matrix:** A transition matrix that comprises of probabilities that a system currently in a state will be in

some state *j* in a next time step (one year in this case). The calculated transition matrix based on 5 years data of the permanent plots and averaged over the years is as follows:

**Table 1. Transition probability matrix for the old-fields of Malir-Landhi area.**

| States | S1   | S2   | S3   | S4   | S5   |
|--------|------|------|------|------|------|
| S1     | 0.14 | 0.48 | 0.21 | 0.15 | 0.02 |
| S2     | 0.03 | 0.26 | 0.51 | 0.16 | 0.04 |
| S3     | 0.01 | 0.03 | 0.82 | 0.10 | 0.04 |
| S4     | 0.01 | 0.02 | 0.05 | 0.82 | 0.10 |
| S5     | 0    | 0.01 | 0.02 | 0.06 | 0.91 |

Table 1 shows that the high probabilities are generally located on the principal diagonal which is presumably because most of the patch (state) types (S<sub>2</sub>, S<sub>3</sub>, S<sub>4</sub> and S<sub>5</sub>) are predominately composed of perennial species and these species persist for more than a year. The highest transition probability (0.91) was for S<sub>5</sub> to S<sub>5</sub>.

A test was performed to determine if the transition probability matrix is a zero-order probability matrix. A zero-order transition probability matrix would mean that all the future states of the system are independent of the previous states. This also implies that all the rows are equal (here row sum is unity). As a consequence of this the replacement of any patch (species consortium) would be dependent on the species abundance of a given patch. The observed probabilities of the transition matrix do not fit this model ( $\chi^2 = 994.8$ ;  $df = 16$ ;  $p < 0.001$ ), in part this is owing to the fact that self-replacement probabilities (i.e., the diagonal probabilities), in general, are large. This shows that the replacement of species (patches) is not dependent on the proportional abundance of species that predominately constitute various patch types.

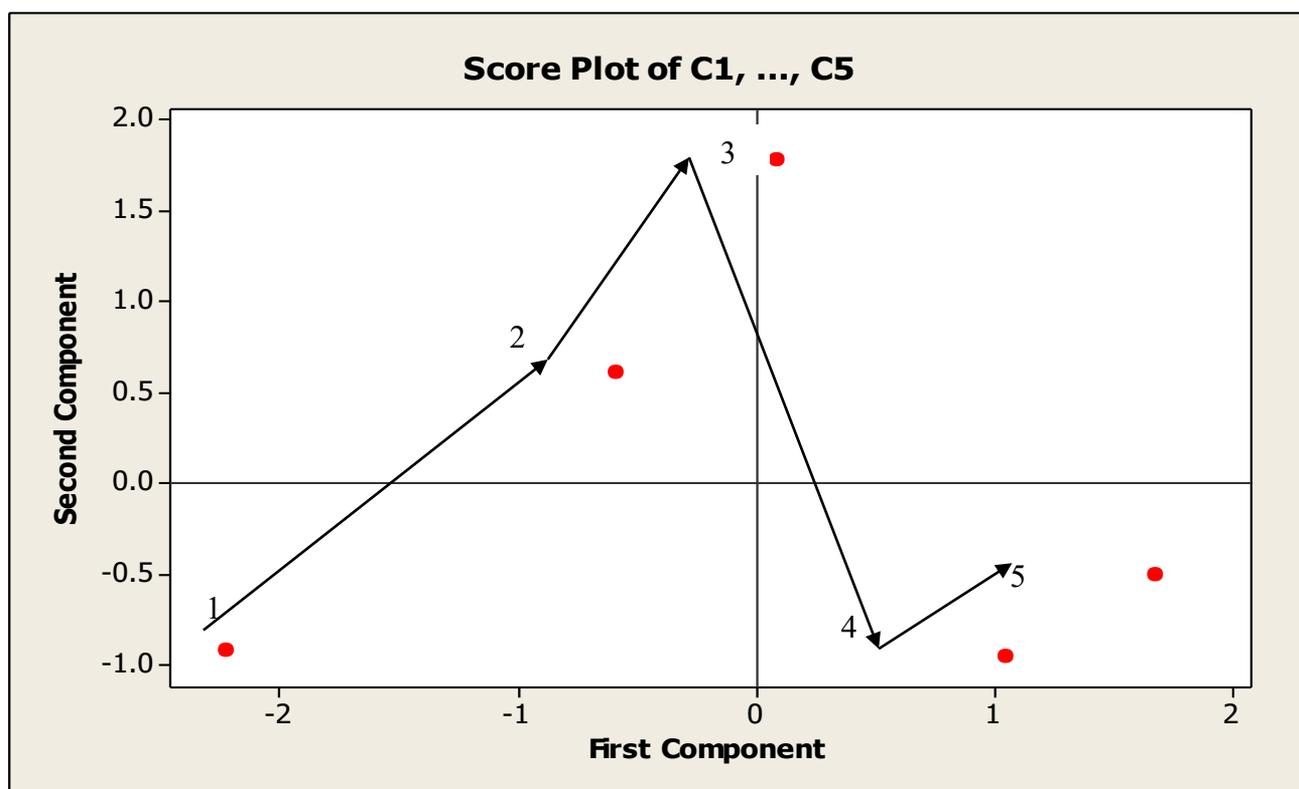


Fig. 1. Two-dimensional Principal Component Analysis (PCA ordination) of the secondary successional data. The numbers refer to successional stages.

**Stability:** The stability of the system needs to be evaluated. A simple measure is to employ the frequency matrix of states. One such stability measure is calculate the ratio of the sum of frequencies on the principal diagonal (i.e., the trace of the matrix) to the total sum of frequencies of the matrix (Rego *et al.*, 1993):

$$\text{Stability} = \sum f_{ii} / \sum f_{ij} \dots\dots\dots i=1, \dots S; j=1, \dots S$$

The transition matrix P, as pointed out earlier, can also be employed to simulate the equilibrium or the stable state of the system, i.e., the species composition that would be attained by the terminal community. Such equilibrium vector can either be computed by successive

multiplication of the transition matrix P by an arbitrary initial vector until stabilization or by calculating the first eigenvector (i.e., eigenvector corresponding to the largest eigenvalue). The ratio of the largest eigenvalue  $\lambda_1$  to the second largest eigenvalue  $\lambda_2$  i.e.,  $|\lambda_1| / |\lambda_2|$  provides the rate at which the system approaches towards stability because matrix P is stochastic  $\lambda_1$  is=1.

$$\rho = |\lambda_1| / |\lambda_2|$$

The ratio of the two largest eigenvalues for this study was found to be 1.175. For the purpose of comparison, the ratios of the eigenvalues  $|\lambda_1| / |\lambda_2|$  for various transition matrices of previous studies are given in Table 2.

**Table 2. The Ratio of the modulus of the first two largest eigenvalues  $|\lambda_1| / |\lambda_2|$  for transition matrices of animal or plant communities.**

| S. No. | Community                            | Reference                     | $ \lambda_1  /  \lambda_2 $ |
|--------|--------------------------------------|-------------------------------|-----------------------------|
| 1.     | Mixed hardwoods (New Jersey)         | Horn (1975a)                  | 1.57                        |
| 2.     | Mixed hardwoods (Connecticut)        | Waggoner & Stephens (1970)    | 1.34                        |
| 3.     | Termites in Ghana                    | Usher (1975)                  | 3.82                        |
| 4.     | Predator and prey mites on oranges   | Huffaker (1958)               | 5.60                        |
| 5.     | Heathland (Netherland)               | Lippe <i>et al.</i> , (1985)  | 1.58                        |
| 6.     | Oldfield succession (Karachi, Sindh) | Shaukat and Khan (this study) | 1.175                       |

Evidently, the ratio found in this study was the smallest of all those previously reported. It is also apparent from Table 2 that the eigenvalue ratios of the processes involving animals are larger than those of forest succession. It is not certain whether it truly represents the difference between animal and plant succession. For the current study the ecosystem mostly includes the early part of secondary succession that involves mostly herbaceous (or shrubby) vegetation. The stability of such vegetation is expected to be low as the constituent species prevailing in plots are mostly short-lived (exception being *Prosopis juliflora* a tall shrub to a small tree) and the vegetation could change relatively easily by even slight perturbation. Given the longevities of various species involved in the sere such a result for stability test is not unexpected. The community structure converges in the long run to the equilibrium.

**Turnover rates:** The turnover rates of state *i* into *j* and the corresponding turnover time are given in Table 3.

Turnover rates were high in the beginning of the vegetation dynamics (first two states) and then the rate declined dramatically (states 3 and 4) and finally it was very low in state 5. On the other hand, turnover time followed the inverse trend with a non-significant negative correlation ( $r = -0.7098$ ).

**Replacement:** Replacement of a species (patch) *j* for state 1-5 and the replacement by species (patch) *i* are given in Table 4.

Replacement of species (patch) *j* declined rapidly with the state (1 to 5). On the other hand, replacement by species (patch) *i* increased with the state. The two attributes were found negatively related ( $r = 0.835$ ) though non-significant (Table 5).

**Persistence**

$$\text{Total persistence of all states} = 2.95$$

Evidently the persistence of the species (states) increased rapidly with the onward march of the succession. The total persistence of all states (2.95) was also high though no such parameter values are available for comparison.

**Entropy:**  $E^{post}$  i.e., entropy after successional progression and  $E^{pre}$  i.e., entropy before the development of seres (states) and their normalized values are presented in Table 6.

**Table 3. Turnover rates (Ti) and the expected turnover time ( $\tau_i$ ) between states for the succession.**

| States        | 1     | 2     | 3     | 4     | 5      |
|---------------|-------|-------|-------|-------|--------|
| Turnover rate | 0.86  | 0.74  | 0.18  | 0.18  | 0.04   |
| Turnover time | 1.162 | 1.351 | 5.555 | 5.555 | 24.999 |

**Table 4. Replacement of a Species (patch) *j* with the and replacement by species (patch) *i*.**

| States         | 1     | 2     | 3     | 4     | 5     |
|----------------|-------|-------|-------|-------|-------|
| Replacement of | 0.84  | 0.70  | 0.14  | 0.08  | 0.09  |
| Replacement by | 0.387 | 0.450 | 1.851 | 1.851 | 3.703 |

**Table 5. Persistence of species (patch) is presented in Table 5 as follows.**

| States      | 1    | 2    | 3    | 4    | 5    |
|-------------|------|------|------|------|------|
| Persistence | 0.14 | 0.26 | 0.82 | 0.82 | 0.91 |

**Table 6. Pre and post- entropy of the successional system, their normalized values and the total entropy of the system.**

| States              | 1       | 2     | 3     | 4     | 5     |
|---------------------|---------|-------|-------|-------|-------|
| <b>Entropy type</b> |         |       |       |       |       |
| $E^{post}$          | 1.901   | 1.761 | 0.970 | 0.962 | 0.546 |
| $E^{pre}$           | 1.615   | 2.019 | 1.355 | 1.240 | 0.598 |
| $R^{post}$          | 0.950   | 0.880 | 0.485 | 0.481 | 0.273 |
| $R^{pre}$           | 0.807   | 1.009 | 0.677 | 0.620 | 0.299 |
| $E^{syst}$          | = 3.550 |       |       |       |       |

Both Pre- and Post-entropies and their normalized quanta declined steadily with the onward march of the chronosequence though post-entropy declined with a slightly lesser rate. However, the total entropy  $E^{\text{svst}}$  of the system was moderately high, which perhaps indicated that though the successional ecosystem under study reached its destined culminating stage (disclimax) it had sizable entropy component.

## Discussion

While testing of ecological models it is necessary that the behaviour of the system under investigation should be well-understood. From this standpoint the abandoned field (old-field) vegetation offers an effective test data for several basic reasons. Considerable understanding has been achieved for this type of disturbed ecosystem. It is noteworthy that a large number of ecologists have focussed attention on the vegetation of abandoned fields in North America and Europe (Bazzaz, 1975; Shaukat, 1985; Benjamin *et al.*, 2005; Stolcova, 2002; Osbornova *et al.*, 2012; Prach *et al.*, 2013). However, Markovian models have been rarely utilized in such studies. Though the transition matrix modelling approach used here did not explicitly incorporate the environmental and interactive effects of species that occurred in the successional sequence, this was perhaps indirectly expressed by the response at the composite level of patches (plots) where processes such as allelopathy played a significant role in the replacement of species (cf. Osho, 1996, Fernandez *et al.*, 2013). In fact it has been demonstrated by Shaukat (1985) that allelopathy plays an important role in species replacement by way of inhibition of germination and growth during the old-field succession in London, Ontario, particularly at the initial stages of the sere.

Before making any predictions using the Markov chain model, we must assure that the stochastic model possesses Markovian property. Only by conforming to this we can be confident of accuracy and precision of prediction. To test whether the calculated transition matrix confirms to Markovian property, appropriate statistical test developed by (Anderson & Goodman, 1957 and Harbaugh & Bonham-Carter, 1970) was employed. This test yielded a significant value of chi-square which would mean that the successional process at hand was a non-independent sequence in character and therefore Markovian in its broader perspective and not merely random (*sensu stricto*, a sequence of statistically independent events). The significance of the  $\chi^2$  test also implies that the process is not stationary. The first of the inference is regarded as fairly robust (Usher, 1979) and leads to the generalization that the “*successional process is not independent in character*” which mathematically conforms to a first order Markov chain. For the second statement Usher (1979) suggested that on theoretical grounds a generalization could be drawn that “*most ecological succession are non-stationary processes*”.

Entropy and Boltzman's second law of thermodynamics are the fundamental themes of organization of ecosystems and succession. This direct linkage to thermodynamics and entropy was noticed in several pioneering works in the field of landscape ecology (see Cushman, 2017). Ecosystems are open systems that continuously exchange energy and entropy

with their external environment that leads to continuous evolution of the internal structure and function of the successional ecosystem. In accordance with the universal law of the maximal energy dispersal, an ecosystem evolves toward a stationary state in its surroundings by consuming free energy through diverse mechanisms. The results of this and several other studies are consistent with the hypothesis that the development of successional ecosystems leads to greater interactions and organization thereby moving towards lesser disorder (entropy) (Holdaway *et al.*, 2010). The pre-succession entropy declined to a lesser degree because perhaps the ecosystem before the abandonment of the field was more organized (organismic *sensu* Clements). Accordingly,  $E^{\text{pre}}$  declined at a lower rate than  $E^{\text{post}}$  after the completion of each stage (state) there was less disorder compared to that at the beginning of the seral stage. The decreasing law of entropy is a characteristic of an organized system (Chakrabarti & Ghosh, 2010). The extent of organization at any stage is quantified by the loss of entropy (or gain of information). EP (entropy production) changes owing to dynamic change from r- to K-selected dominance of communities through time. For example, using a mature ecosystem, a maximum in  $EP_{\text{mature}}$  could be tested for by manipulating conditions more or less favorable (e.g. through experimental water stress, reducing the incoming solar energy or removing certain species) and looking for the expected increase or decrease in ecosystem entropy production (Holdaway *et al.*, 2010). In long duration studies of succession, species could be limited only to r- or K-strategists to test for changes in  $dEP/dt$ . In a successional sequence, r-strategists attain dominance in the early stage of succession and are gradually replaced by K-selected species. In order to make detailed investigation of entropy change, the accuracy and comparability of the energy balance measurements improved methods are available (Holdaway *et al.*, 2010). The higher the ecological diversity, the lower the production of entropy per unit of biomass, because resources are better utilized and support the growth of the entire spectrum of ecosystem hierarchy. This fact is also borne out by the result of the present study.  $E^{\text{svst}}$  was moderately high which perhaps indicates that though the successional ecosystem under study reaches its destined culminating stage (disclimax) it has sizable entropy component as it is not a primary succession that is more organismic (*sensu* Clements) with less entropy (because of greater interactions between the constituent species), while in the secondary succession in the beginning the substratum retains a vast and diverse pool of propagules of species representative of different succession stages *i.e.*, most species of the chronosequence are present at the beginning (though possibly with little interaction with each other) (Egler, 1954) and different species take the role of dominance at different times, therefore the system contains moderate entropy when taken as whole. Instead, before abandoning the field simplified ecosystems with fewer species (such as agricultural monocultures) do not use available resources and co-products as effectively, resulting into a higher production of entropy per unit of time and biomass. Nonetheless, it has been noted that relationship between succession and entropy production depends on vegetation characteristics (Stoy *et al.*, 2014). It must be pointed out that Soil entropy also changes, in addition to vegetation alteration during succession, owing to the degree of soil weathering (residual soil) and soil structural development (fluxes) (Li, 2000).

## Conclusions

Lastly, it can easily be concluded that Markov models provide interesting insight into the process of secondary succession on abandoned fields and instead of focussing on individual dominant species of successive stages we can consider the vegetation patches (plots of vegetation at various stages of succession) and trace their dynamics. Ecological succession as suggested by this study and other workers seem to follow the second law of thermodynamic and the entropy appears to decrease as the secondary succession proceeds to termination (disclimax). Although not done here but perturbations including fire and grazing intensity can also be conveniently incorporated into the Markovian models.

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