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Spatial succession modeling of biological communities: a multi-model approach

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Abstract Strong spatial correlation may exist in the spatial succession of biological communities, and the spatial succession can be mathematically described. It was confirmed by our study on spatial succession of both plant and arthropod communities along a linear transect of natural grassland. Both auto-correlation and cross-correlation analyses revealed that the succession of plant and arthropod communities exhibited a significant spatial correlation, and the spatial correlation for plant community succession was stronger than arthropod community succession. Theoretically it should be reasonable to infer a site's community composition from the last site in the linear transect. An artificial neural network for state space modeling (ANNSSM) was developed in present study. An algorithm (i.e., Importance Detection Method (IDM)) for determining the relative importance of input variables was proposed. The relative importance for plant families Gramineae, Compositae and Leguminosae, and arthropod orders Homoptera, Diptera and Orthoptera, were detected and analyzed using IDM. ANNSSM performed better than multivariate linear regression and ordinary differential equation, while ordinary differential equation exhibited the worst performance in the simulation and prediction of spatial succession of biological communities. A state transition probability model (STPM) was proposed to simulate the state transition process of biological communities. STPM performed better than multinomial logistic regression in the state transition modeling. We suggested a novel multi-model framework, i.e., the joint use of ANNSSM and STPM, to predict the spatial succession of biological communities. In this framework, ANNSSM and STPM can be separately used to simulate the continuous and discrete dynamics.

Keywords Plant and arthropod communities · Spatial succession · Modeling · Artificial neural network · State transition probability model · Multinomial logistic regression · Ordinary differential equation · Multivariate linear regression

Introduction

Plants account for 15% of global species and arthropods account for more than 60% of global species and nearly 80% of animal species (McGavin 2000). On a temperate grassland, both plants (20,000 kg/ha) and arthropods (1,000 kg/ha) hold a large amount of biomass (Pimentel et al.

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1992; Chen and Ma 2001). Both plants and arthropods are dominant organisms in most ecosystems and they always determine the structures and functions of ecosystems (Wilson 1987). Plant and arthropod communities are much different but they always interact to maintain an ecosystem (Altieri and Letourneau 1984; Andow 1991; Altieri 1994, 1995; Schultz and Wieland 1997; Dong et al. 2005; Jia et al. 2006).

Community succession has been widely studied for a long time. Many studies put their focus on the temporal succession of a community at a given site (Bork et al. 1997; Jackson and Bartolome 2002; Jasinski and Payette 2005). The spatial succession of biological community is a recent topic. Community composition will affect biomass (Grime 1998; Lavorel and Garnier 2002; Chapin 2003), and may thus cause the changes in community structure and function. Modeling the community succession is so important for understanding the dynamics and mechanisms of community succession and for detecting the determinant variables of community succession. Some models, for instance, the state and transition model, were used to describe the temporal dynamics of community composition. Overall the spatial succession of communities is usually described by simple models like multivariate linear regression. Actually the spatial succession of biological communities is always determined by various biological and environmental variables. Moreover, complex relationships can be found between these variables. The relationships are generally nonlinear and could not be easily described by traditional models (Schultz and Wieland 1997; Pastor-Barcenas et al. 2005).

Artificial neural networks (ANNs) are recognized as the adaptive and universal function approximators for nonlinear ecological relationships (Acharya et al. 2006; Nour et al. 2006; Zhang and Barrion 2006; Zhang 2007a, b; Zhang et al. 2007, 2008a, b; Zhang and Zhang 2008). They have the advantages of more automated model synthesis and analytical input-output models (Tan et al. 2006). A lot of studies on theories and applications of ANNs in ecology and environmental sciences were conducted in the past 10 years. Concerning the dynamic modeling of environmental processes, ANNs were used for modeling short and middle long-term concentration levels (Viotti et al. 2002), subsurface process (Almasri and Kaluarachchi 2005), sediment transfer (Abrahart and White 2001), subsurface drain outflow and nitrate–nitrogen concentration in tile effluent and surface ozone (Sharma et al. 2003; Pastor-Barcenas et al. 2005), flow and phosphorus concentration (Nour et al. 2006), dioxide dispersion (Nagendra and Khare 2006), and the growth of Chinese cabbage and food intake dynamics of holometabolous insect (Zhang et al. 2007, 2008a). In the areas of invertebrate and plant researches, ANNs are always used to make simulation and prediction. They were used to explain the observed structure of functional feeding groups of aquatic macro-invertebrates (Jørgensen et al. 2002). The Self-Organizing Map (SOM) was used to determine pest species assemblages for global regions, which classified the high dimensional data into two-dimensional space such that geographical areas that had similar pest species assemblages were organized as neighbours on a map or grid (Worner and Gevrey 2006). BP and RBF ANNs were used to simulate and predict species richness of rice arthropods (Zhang and Barrion 2006). ANNs were also used to recognize spatial distribution of invertebrates (Cereghino et al. 2001; Zhang et al. 2008b), and make vegetation classification and discrimination (Marchant and Onyango 2003; Filippi and Jensen 2006). In addition to the applications above, ANNs have been widely used in other studies, for example, to explain observed changes in species composition and abundance with neural network (Jaarsma et al. 2007); to construct transfer functions that implement organism-environment relationships for paleoecological uses (Racca et al. 2007), and to classify community assemblages (Zhang 2007a, b; Tison et al. 2007).

Empirical models regained popularity in recent years due to the complexity and nonlinearity of ecosystems (Tan et al. 2006). Various conventional models, mostly empirical models, have been used to compare simulation performances between ANNs and these models. ANNs were proved to be superior to linear models, generalized additive models, and classification and regression trees (Moisen and Frescino 2002). They outperformed logistic regression, multiple discriminant model and multiple regression in predicting community composition (Olden et al. 2006) and the number of salmonids (McKenna 2005). They can also provide a feasible alternative to more classical spatial statistical techniques (Pearson et al. 2002).

The need for better techniques, tools and practices to analyze ecological systems within an integrated framework has never been so great (Shanmuganathan et al. 2006). Multi-model approach conditioned on data should thus be preferred. In present study we proposed a neural network model and a state transition probability model. Using the sampling data investigated in the natural grassland, various models were compared in order to present a novel framework for modeling spatial succession of community composition. A hypothesis on the predictability of spatial succession of community composition was tested using various methods.

Materials and methods

Field investigation and data pre-processing

Field sampling

Field sampling was conducted on the natural grassland in Guangdong, China. In total 50 plots, each with the size of 1 × 1 m and the between-plot distance of 2-m, were investigated along a linear transect on the grassland (Fig. 1). Plant species and their abundance (i.e., cover-degree (%)), and the abundance of arthropod orders were recorded and measured for each plot.

Data pre-processing

In total 17 plant families were found on the grassland, of which Gramineae (64.8%), Compositae (22.1%) and Leguminosae (9.3%) were the dominant plant families. Excepting for the three families above, the remaining plant families made up only 3.8% of total abundance. The families, Gramineae, Compositae and Leguminosae, were thus determined to be representative components of plant community.

Most of the arthropods were insects, of which the orders Homoptera (37.9%), Diptera (21.1%) and Orthoptera (14.4%) were the dominant orders. As a consequence, the three orders were determined to be representative components of arthropod community.

Due to the continuous transition of climatic and soil conditions and the continuous percolation of organisms in a space, we hypothesize that biological community succession along a linear transect will likely exhibit a strong linear or nonlinear spatial correlation and may be mathematically described. Linear spatial correlation was analyzed in present study using SPSS (SPSS 15.0 for Windows 2006).

Artificial neural network

Model description

In present study, an artificial neural network (ANNSSM) was developed to generate a mapping on a space, $F{:}R^m \rightarrow R^m$. Given an input (for plot s), $\boldsymbol{x}(s) \in R^m$, and its output (for plot $s + \triangleleft s$, where $\triangleleft s = 1$ in general), $\boldsymbol{x}(s + \triangleleft s) \in R^m$, there is a mapping $\boldsymbol{g}$ such that: $\boldsymbol{x}(s + \triangleleft s) = \boldsymbol{g}(\boldsymbol{x}(s))$. A mapping $\boldsymbol{f} \in F = \{\boldsymbol{f}|\boldsymbol{f}{:}R^m \rightarrow R^m\}$, i.e., the optimal approximation onto $\boldsymbol{g}$, could be obtained by training the neural network. The neural network obtained is a mathematical function and may approximate $\boldsymbol{g}(\boldsymbol{x})$ such that: $|\boldsymbol{f}(\boldsymbol{x}) - \boldsymbol{g}(\boldsymbol{x})| < \varepsilon$, $\boldsymbol{x} \in R^m$, where $\boldsymbol{x} = (x_1, x_2, \ldots, x_m)^T$, and $\varepsilon > 0$ is a constant. A $2m$-layer neural network was developed to model the spatial succession of plant and arthropod communities (Fig. 2). In this neural network, each of the layers 1,2,...,m, contains a certain number of neurons. Transfer functions for the layers 1,2,...,m, are logarithmic sigmoid transfer functions:

$$\log\mathrm{sig}\,(x) = 1\big/(1 + \exp(-x)) \tag{1}$$

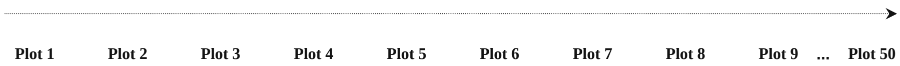


Fig. 1 Linear transect on the grassland

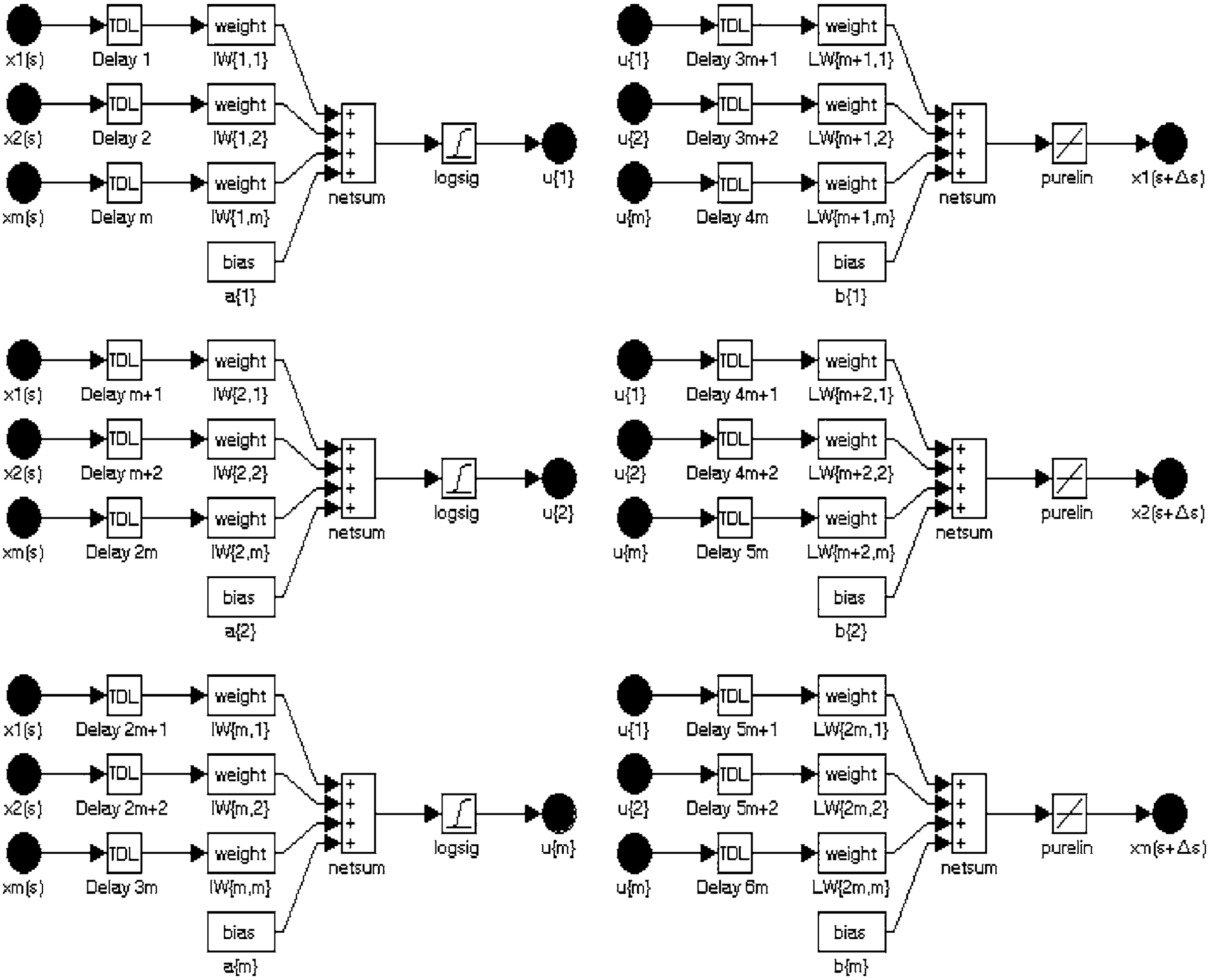


Fig. 2 Architecture of the artificial neural network ANNSSM

and for layers $m+1, m+2,...,2m$, are linear transfer functions: purelin$(x) = x$. Bias is used to each layer. The initialization of network, weights and bias for each layer i $(i = 1, 2, ..., 2m)$ is performed by a function (Hagan et al. 1996; Mathworks 2002; Fecit 2003). Gradient function calculates the Jaccobian of network's errors with respect to its vector of weight and bias values. Network is trained by Levenberg-Marquardt backpropagation algorithm. Desired performance function is mean squared error performance function (mse). Each of the layers 1,2,...,m, receives the same inputs from sample space and yields outputs for the layers $m+1$, $m+2$,...,$2m$. For each layer the net input functions calculates the layer's net input by its weighted inputs and biases. Mathematically, the output of j-th output node is:

$$f_j(\boldsymbol{x}) = x_j(s + \lhd s) = \sum\nolimits_{k=1}{}^{m} \omega_{jk} u_k(\cdot) + b_j,$$

$$u_k(\cdot) = 1\Big/\left(1+\exp\left(-\left(\sum\nolimits_{l=1}{}^{m} \omega'_{kl} x_l(s) + a_k\right)\right)\right),$$

$$j = 1, 2, \ldots, m \tag{2}$$

where $\boldsymbol{x}(s) = (x_1(s), x_2(s),...,x_m(s))^{\mathrm{T}}$ is the input, $\boldsymbol{x}(s+\lhd s) = (x_1(s+\lhd s), x_2(s+\lhd s),...,x_m(s+\lhd s))^{\mathrm{T}}$ is the output, $\boldsymbol{\omega}_j = (\omega_{j1}, \omega_{j2},...,\omega_{jm})^{\mathrm{T}}$ and $\omega'_k = (\omega'_{k1}, \omega'_{k2},...,\omega'_{km})^{\mathrm{T}}$ are the weight vectors for output nodes j, $j = 1, 2, ..., m$, and input nodes k, $k = 1,2,...,m$.

ANNSSM was developed using Matlab (Mathworks 2002). Simulation performance of the neural network was represented by Pearson correlation coefficient, statistic significance, and regression coefficient for the linear relationship between the simulated and observed abundances.

Determination of relative importance of input variables

In order to approach the interpretability of neural network, it is necessary to identify the relative importance of input variables. Based on Eqs. 1, 2 and Fig. 2, the total importance of input variable i, i.e., community composition i, may be calculated by the following formula:

$$\begin{aligned} V_i &= \sum\nolimits_{k=1}^{m} \sum\nolimits_{j=1}^{m} \mathrm{LW}\{k+m,\ j\}/(1 \\ &\quad + \exp(-\mathrm{IW}\{j, i\})) \\ &= \sum\nolimits_{j=1}^{m} \omega_{ij}/(1+\exp(-\omega'_{ji}))\ i = 1, 2, \ldots, m. \end{aligned} \tag{3}$$

However, the relative importance of input variable i to output variable k may be obtained by the following formula:

$$V_{ki} = \sum\nolimits_{j=1}^{m} \mathrm{LW}\{k+m, j\}\big/(1+\exp(-\mathrm{IW}\{j, i\}))\quad k, i = 1, 2, \ldots, m. \tag{4}$$

The larger importance value represents the greater importance of the input variable. As a comparison, we used connection weight method (Olden et al. 2004) to test our importance detection method above (abbreviated as IDM).

Multivariate linear regression

The multivariate linear regression (He 2001; Mathworks 2002) was used for modeling spatial succession of biological communities:

$$\boldsymbol{x}(s+\triangle s) = a + \boldsymbol{b}^{\mathrm{T}}\boldsymbol{x}(s) \tag{5}$$

where a: constant; $\boldsymbol{b} = (b_1, b_2, \ldots, b_m)^{\mathrm{T}}$: parametric vector.

Ordinary differential equation

The nonlinear ordinary differential equation is an excellent tool to model community succession (Zhang et al. 2007):

$$d\boldsymbol{x}(s)\big/ds = \boldsymbol{f}(\boldsymbol{x}(s), s) \tag{6}$$

where $\boldsymbol{x}(s) = (x_1(s), x_2(s), \ldots, x_m(s))^{\mathrm{T}}$: state vector of community composition for plot s. However, it is hard to develop a precise nonlinear ordinary differential equation for community succession. Thus the following linear form of model (6) was used:

$$d\boldsymbol{x}(s)\big/ds = A\boldsymbol{x}(s) \tag{7}$$

where A: the system matrix with constant elements. Model (7) requires less information on the mechanism of community succession. The difference equation for the model (7) is as the following:

$$\boldsymbol{x}(s+\triangle s) = \boldsymbol{x}(s) + A\boldsymbol{x}(s)\triangle s \tag{8}$$

State transition probability model

The state transition probability was used to describe the discrete process of community succession, i.e., between-state transitions. In state transition probability model (STPM), the abundance in a plot was classified into q states:

$$\boldsymbol{x}(s+\triangle s) = P * \boldsymbol{x}(s) \tag{9}$$

where $P = (p_{ij})_{q\times q}$ is the transition probability matrix, p_{ij} is the transition probability from state i to state j, $\sum_{j=1}^{q} p_{ij} = 1$. The operator "*" in Eq. 9 was defined based on the following rules: Suppose that $\boldsymbol{y}(s) = (0, 0, \ldots 1_h, \ldots, 0)^{\mathrm{T}}$ is the state vector in which the k-th state is the state of plot s, then the k-th row of matrix P may be extracted as $(p_{k1}, p_{k2}, \ldots, p_{kq})$. A random value r, $r \in [0,1]$, is generated and the following rules should be followed:

$$\boldsymbol{x}(s+\triangle s) = (1, 0, \ldots 0, \ldots, 0)^{\mathrm{T}}$$

$$r < p_{k1}$$

$$\boldsymbol{x}(s+\triangle s) = \left(0, 0, \ldots 1_j, \ldots, 0\right)^{\mathrm{T}}$$

$$\sum\nolimits_{l=2}^{j-1} p_{kl} < r < \sum\nolimits_{l=2}^{j} p_{kl}, \quad j = 2, 3, \ldots, q$$

Multinomial logistic regression

Multinomial logistic regression (SPSS 15.0 for Windows 2006) was used to simulate the state of the $(p+1)$-th plot from the state of p-th plot.

Randomization procedure

A randomization procedure was used to produce the mean and the confidence interval in neural network modeling (Zhang 2007c). A large number of randomizations will generate a family of data from which the mean and the confidence interval of the modeling results of ANNSSM can be calculated. In the STPM modeling, a simple randomization procedure was conducted to achieve a better fitness on observed states, in which the simulation with the least fitting error was finally used.

Data description

(A) Training data. In the modeling of spatial succession, in total 50 plots were used to train ANNSSM, ordinary differential equation, and multivariate linear regression model.

In STPM modeling, four states were defined for plant families Gramineae, Compositae and Leguminosae, and for arthropod orders Homoptera, Diptera and Orthoptera, in view of the amplitude of their abundance, as indicated in Table 1.

(B) Cross validation. The first n plots were used to train models; predict the $(p+1)$-th plot from the p-th plot $(p > n)$ using the trained model. Comparisons between the predicted and observed were made, and Pearson correlation coefficient (r) and statistic significance were calculated to validate models.

(C) In ANNSSM modeling, plots were submitted to neural network in two ways, i.e., their natural orders in the linear transect, and randomized orders of plots.

Results

Both linear auto- and cross-correlation analyses showed that there was not any succession periodicity along the linear transect for both plant and arthropod communities. The spatial succession of natural communities in the linear transect were not independent stochastic processes (i.e., white noise).

The linear regression analysis revealed that both linear auto- and cross-correlation of spatial succession of plant (Auto-correlation = 0.36–0.022* Spatial-Lag, $r = 0.82$, $df = 14$, $p = 0.0001$; Cross-correlation = 0.29–0.017*Spatial-Lag, $r = 0.89$, $df = 14$, $p < 0.0001$) and arthropod communities (Auto-correlation = 0.02–0.013*Spatial-Lag, $r = 0.69$, $df = 14$, $p = 0.0029$; Cross-correlation = 0.15–0.006*Spatial-Lag, $r = 0.74$, $df = 14$, $p = 0.001$) was negatively related to the spatial lag (Table 2). Overall the spatial correlation for one-step lag was statistically significant. Thus, the biota in a plot was greatly determined by the biota in the last plot of transect. Succession of plant community produced a stronger spatial correlation than that of arthropod community. Theoretically, it is possible, by using mathematical models, to infer a plot's biota ($\boldsymbol{x}(s + \triangle s)$) from the last plot's biota ($\boldsymbol{x}(s)$) in the transect.

Table 1 Definition of four states in the STPM modeling

Description of states		Occassionally occurred	Commonly occurred	Relatively abundant	Considerably abundant
Definition of states		1	2	3	4
Plants	Gramineae	$< 40\%$	40–80%	80–120%	$\geq 120\%$
	Compositae	$< 30\%$	30–60%	60–90%	$\geq 90\%$
	Leguminosae	$< 15\%$	15–30%	30–45%	$\geq 45\%$
Arthropods	Homoptera	< 5	5–15	15–25	≥ 25
	Diptera	< 3	3–6	6–9	≥ 9
	Orthoptera	< 2	2–4	4–6	≥ 6

Table 2 Auto-correlation and cross-correlation of spatial succession of community composition

Spatial-Lag	Plant	Composition	Arthropod	Composition
	Averaged auto-corr.	Averaged cross-corr.	Averaged auto-corr.	Averaged cross-corr.
1	0.479*	0.330*	0.330*	0.118
2	0.346*	0.284*	0.243	0.178
3	0.357*	0.247	0.256	0.166
4	0.252	0.206	0.120	0.108
5	0.251	0.235	0.090	0.099
6	0.143	0.264	0.147	0.123
7	0.124	0.124	0.023	0.115
8	0.110	0.119	0.067	0.059
9	0.044	0.101	0.047	0.069
10	0.069	0.063	0.032	0.077
11	0.091	0.075	0.020	0.048
12	0.098	0.120	0.081	0.092
13	0.108	0.101	0.065	0.033
14	0.074	0.088	0.060	0.062
15	0.118	0.059	0.090	0.075
16	0.092	0.068	0.087	0.083

*$p = 95\%$ significance level

Neural network modeling

Modeling performance

If plots were submitted to neural network in their natural orders, the ANNSSM would perfectly perform (Fig. 3). Simulation on both plant (Gramineae: $r = 0.90$, $df = 47$, $F = 198.05$, $p < 0.0001$; Compositae: $r = 0.96$, $df = 47$, $F = 490.22$, $p < 0.0001$; Leguminosae: $r = 0.95$, $df = 47$, $F = 477.87$, $p < 0.0001$) and arthropod (Homoptera: $r = 0.45$, $df = 47$, $F = 14.40$, $p < 0.0001$; Diptera: $r = 1$, $df = 47$, $F = 1085.90$, $p < 0.0001$; Orthoptera: $r = 0.95$, $df = 47$, $F = 566.00$, $p < 0.0001$) communities exhibited an excellent goodness-of-fit (Table 3). Conversely, ANNSSM yielded a dissatisfied simulation when plots were submitted in randomized orders (Gramineae: $r = 0$, $df = 47$, $F = 0.0006$, $p = 0.98$; Compositae: $r = 0.22$, $df = 47$, $F = 2.38$, $p = 0.13$; Leguminosae: $r = 0.09$, $df = 47$, $F = 0.40$, $p = 0.53$; Homoptera: $r = 0.02$, $df = 47$, $F = 0.03$, $p = 0.86$; Diptera: $r = 0$, $df = 47$, $F = 0.0006$, $p = 0.98$; Orthoptera: $r = 0.03$, $df = 47$, $F = 0.03$, $p = 0.86$). However, there were 71.43%, 71.43%, 85.71%, 87.76%, 83.67% and 87.76% of observed plots falling inside the 95% confidence intervals of the simulated values of the six taxa, which exhibited a reliable performance for statistical prediction (Fig. 4).

Plots were submitted to ANNSSM in their natural orders for predicting the plots 41 to 50 from plots 1 to 39 (Fig. 5). The results showed that the prediction performance for both plant (Gramineae: $r = 0.43$, $df = 8$, $F = 1.79$, $p = 0.22$; Compositae: $r = 0.45$, $df = 8$, $F = 2.04$, $p = 0.19$; Leguminosae: $r = 0.25$, $df = 8$, $F = 0.54$, $p = 0.48$) and arthropod communities (Homoptera: $r = 0.03$, $df = 8$, $F = 0.01$, $p = 0.93$; $r = 0$, $df = 8$, $F = \mathrm{NaN}$, $p = \mathrm{NaN}$; $r = 0.46$, $df = 8$, $F = 2.19$, $p = 0.18$) was reliable (Table 3 and Fig. 5). The worse simulation performance for arthropod community succession was attributed to the weaker spatial correlation compared to plant community.

Simulation performance was improved as the increase of training epochs (Fig. 6). Thus the training epochs could be set as a larger number, e.g., 200,000, or 3,000,000, etc., in order to yield the better simulation.

Relative importance of input variables

Based on Eqs. 3, 4, the relative importance of every taxon in community was calculated, as indicated in Table 4. The overall tendency of relative importance of six taxa for IDM and connection weight method were similar. However, IDM is more reasonable than connection weight method in view of the structure of ANNSSM (Eq. 2).

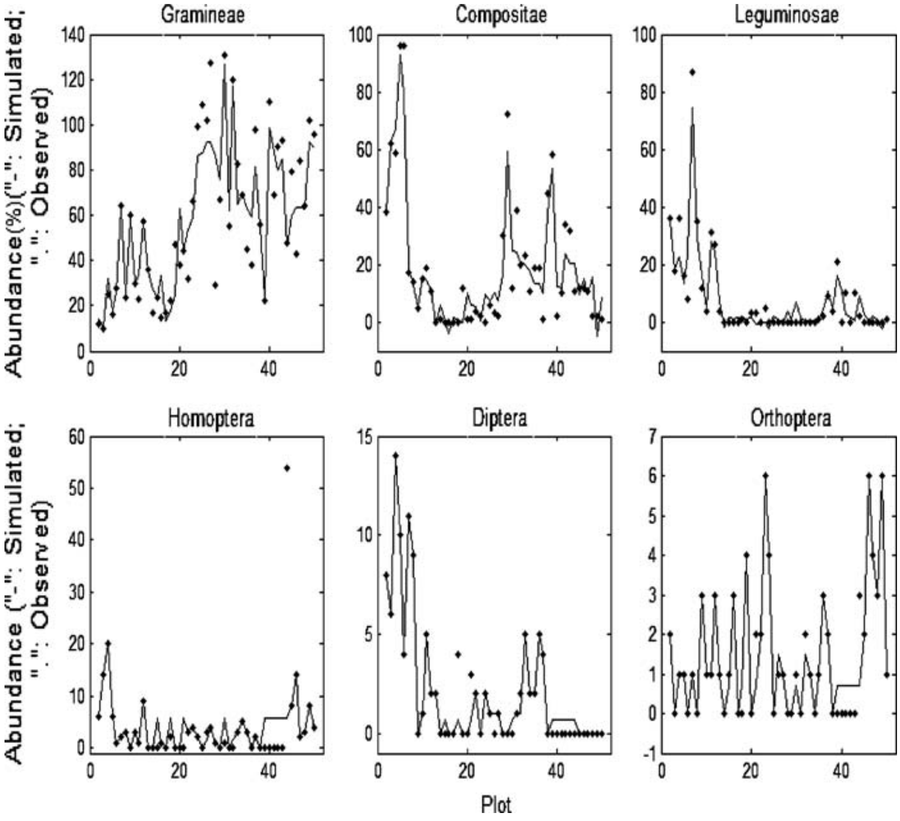


Fig. 3 Simulation performance of community succession using the neural network, ANNSSM. Plots were submitted to ANNSSM in their natural orders in the linear transect

Different ways of plots submission (i.e., randomized and natural orders) to ANNSSM would produce the relative importance with little changes. For instance, Homoptera was the most important taxon under plots submission with natural orders, but Diptera was the most important under plots submission with randomized orders (Table 4).

According to the results of IDM method, Gramineae was the most important taxon for predicting Compositae; Compositae was the most important taxon for predicting itself, and

Table 3 Simulation performance of the neural network, ANNSSM, on spatial succession of biological communities

	Gramineae	Compositae	Leguminosae	Homoptera	Diptera	Orthoptera
ANNSSM simu.	Simu. = 14.17 + 0.76*Obs.	Simu. = 2.88 + 0.84*Obs.	Simu. = 1.35 + 0.82*Obs.			
Nat. orders				Simu. = 2.99 + 0.23*Obs.	Simu. = 0.09 + 0.96*Obs.	Simu. = 0.11 + 0.92*Obs.
ANNSSM. simu.	Simu. = 58.36– 0.001*Obs.	Simu. = 20.86– 0.09*Obs.	Simu. = 7.78– 0.03*Obs.			
Rand. orders				Simu. = 3.93– 0.005*Obs.	Simu. = 2.16 + 0.002*Obs.	Simu. = 1.50– 0.01*Obs.
ANNSSM	Predi. = 20.96 + 0.57*Obs.	Predi. = 6.41 + 0 0.38*Obs.	Predi. = 7.07– 0.75*Obs.			
Predi.				Predi. = 2.78– 0.007*Obs.	Predi. = 1.86 + 0*Obs.	Predi. = 0.26 + 0.50*Obs.

Simu. Simulated, *Obs.* Observed, *Predi.* predicted

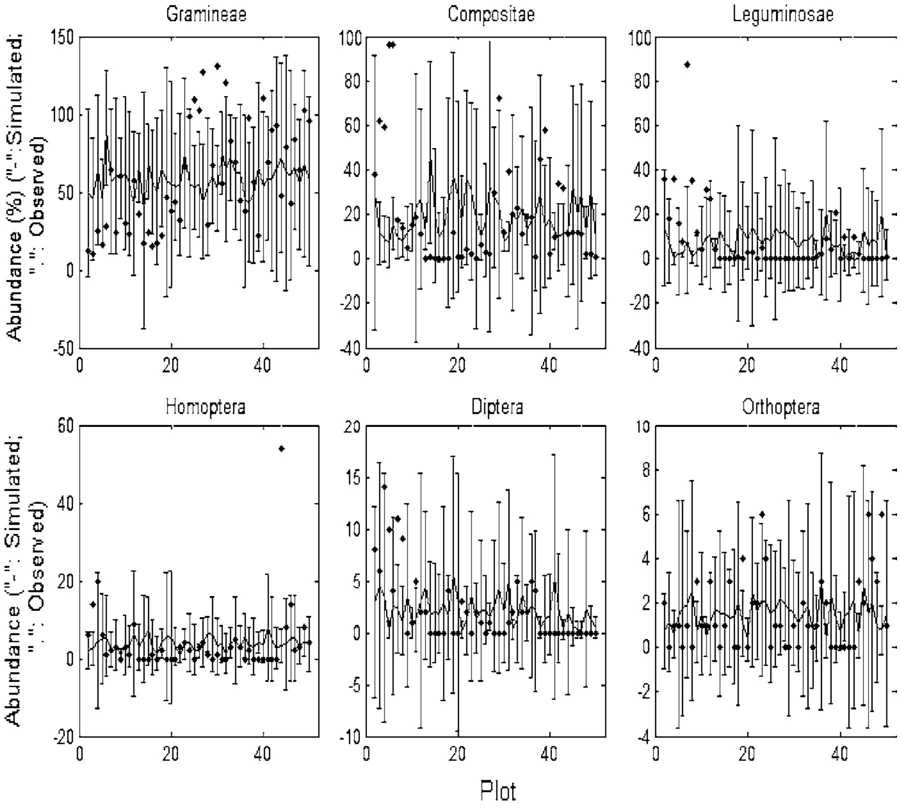


Fig. 4 Simulation performance of community succession using ANNSSM. *Plots* were submitted to ANNSSM in randomized orders. 95% confidence intervals from five randomizations of plots orders were indicated

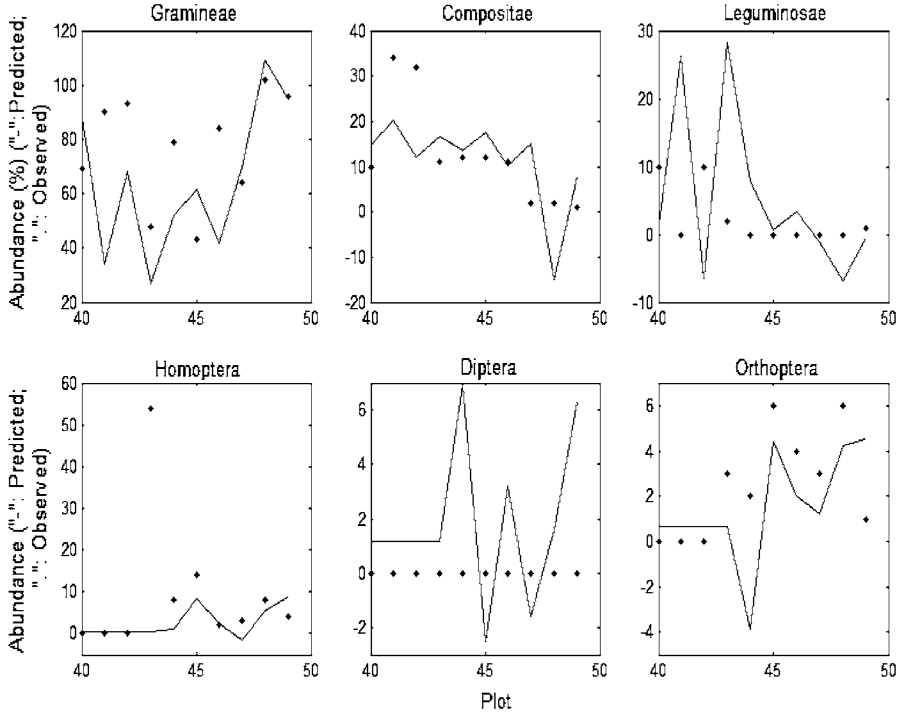


Fig. 5 Cross validation of community succession modeling using ANNSSM. *Plots 1–39* were used to train the model and submitted in natural orders, and *plots 41–50* were predicted from *plots 40–49* using the trained model

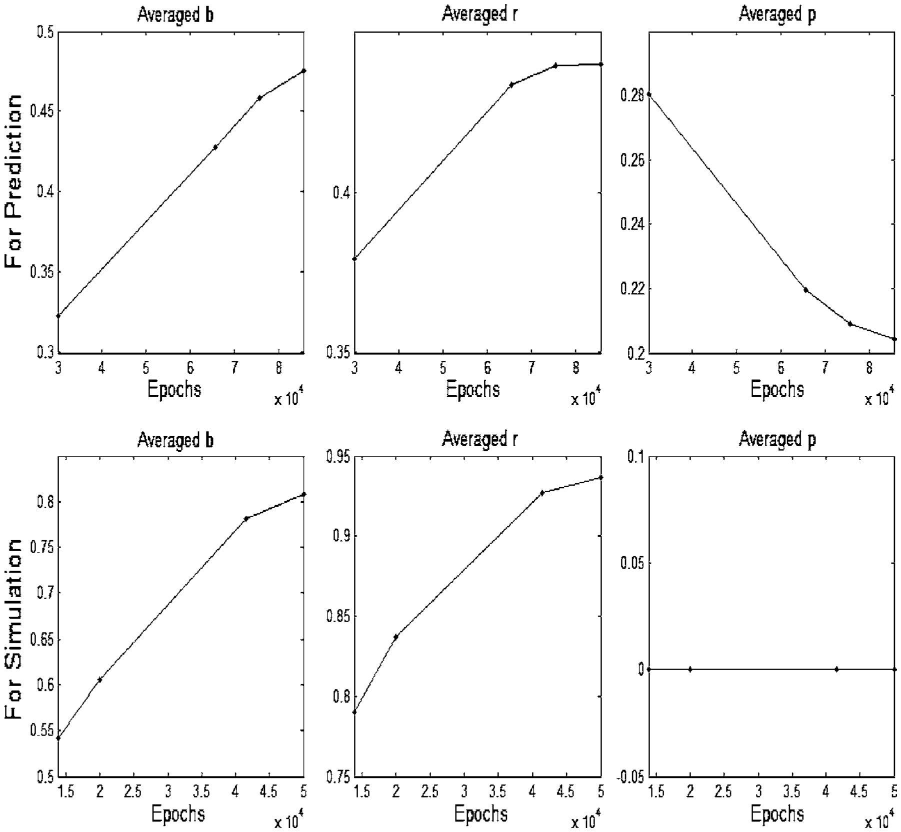


Fig. 6 The changes of modeling performance as the increase of training epochs. b: regression coefficient for simulated-observed relationship; r: correlation coefficient; p: significance level

Leguminosae was the most important taxon for predicting Gramineae. In the prediction of Compositae, Gramineae would be the most important taxon, seconded by Compositae (Table 4).

In the prediction of spatial succession of arthropod community, each arthropod order was mostly determined by itself (Table 4).

From the results in Table 4, it was concluded that complex relationships existed between plant families, while the relationships between arthropod orders were relatively simple. These results coincided with the spatial correlation (Table 2), and partially verified the reasonability of IDM.

Multivariate linear regression modeling

Multivariate linear regression exhibited a better performance in the simulation of spatial succession of plant (Gramineae: $r = 0.94$, $df = 47$, $F = 706.17$, $p < 0.0001$; Compositae: $r = 0.92$, $df = 47$, $F = 543.99$, $p < 0.0001$; Leguminosae: $r = 0.91$, $df = 47$, $F = 496.09$, $p < 0.0001$) and arthropod communities (Homoptera: $r = 1$, $df = 47$, $F = 5{,}700$, $p < 0.0001$; Diptera: $r = 0.96$, $df = 47$, $F = 537.86$, $p < 0.0001$; Orthoptera: $r = 1$, $df = 47$, $F = 2{,}331$, $p < 0.0001$; Fig. 7 and Table 5). Overall, its simulation performance was not better than ANNSSM in view of the regression coefficients for the simulated-observed relationships (regression coefficient should approximate to 1.0; see Tables 3 and 5). Our conclusion is similar to the conclusions given by Moisen and Frescino (2002) and Olden et al. (2006) that multivariate regression performed worse than neural network model.

Predictive performance of multivariate linear regression for both plant (Gramineae: $r = 0.28$, $df = 8$, $F = 0.68$, $p = 0.43$; Compositae: $r = 0.50$, $df = 8$, $F = 2.68$, $p = 0.14$; Leguminosae: $r = 0.01$, $df = 8$, $F = 0.0004$, $p = 0.98$) and arthropod (Homoptera: $r = 0.06$, $df = 8$, $F = 0.03$, $p = 0.87$; Diptera: $r =$ NaN, $df = 8$, $F =$ NaN, $p =$ NaN; Orthoptera: $r = 0.35$, $df = 8$, $F = 1.12$, $p =$

Table 4 Relative importance of community taxa computed from ANNSSM

Methods	Importance types	Submission ways	Taxa	Gramineae	Compositae	Leguminosae	Homoptera	Diptera	Orthoptera
IDM	Relative importance	Natural orders	Gramineae	122.453	168.813	$5.11{*}10^{-14}$			
			Compositae	−15.930	31.742	$-8.96 * 10^{-15}$			
			Leguminosae	30.301	0.262	$1.97{*}10^{-14}$			
		Randomized orders	Gramineae	25.925	100.017	0.671			
			Compositae	15.639	48.484	0.406			
			Leguminosae	5.630	13.263	0.150			
	Total importance	Natural orders		136.825	200.817	$6.18{*}10^{-14}$			
		Randomized orders		47.195	161.764	1.226			
	Relative importance	Natural orders	Homoptera				20.117	9.614	−0.652
			Diptera				12.864	20.390	−0.165
			Orthoptera				−1.319	−4.909	0.061
		Randomized orders	Homoptera				−23.865	17.309	$1.46{*}10^{-16}$
			Diptera				7.592	5.709	$2.56{*}10^{-17}$
			Orthoptera				−1.170	3.928	$3.53{*}10^{-18}$
	Total importance	Natural orders					31.662	25.095	−0.756
		Randomized orders					−17.443	26.946	$1.75{*}10^{-16}$
Connection Weight Method	Relative importance	Natural orders	Gramineae	595.070	3,328.200	−8, 671.727			
			Compositae	−903.977	1,488.101	−2, 071.149			
			Leguminosae	849.098	−721.418	437.814			
		Randomized orders	Gramineae	−167.398	650.629	−970.657			
			Compositae	−54.599	293.494	−365.040			
			Leguminosae	−3.288	75.790	−53.492			
	Total importance	Natural orders		540.191	4,094.884	−10, 305.062			
		Randomized orders		−225.284	1,019.913	−1, 389.189			
	Relative importance	Natural orders	Homoptera				696.520	186.037	−1, 120.735
			Diptera				−228.909	623.630	−567.074
			Orthoptera				156.658	−187.021	80.321
		Randomized orders	Homoptera				−665.108	269.997	1,322.525
			Diptera				136.672	63.071	−801.591
			Orthoptera				−78.077	114.171	−100.582
	Total importance	Natural orders					624.269	622.646	−1, 607.488
		Randomized orders					−606.514	447.239	420.351

Plots were submitted in natural and randomized orders

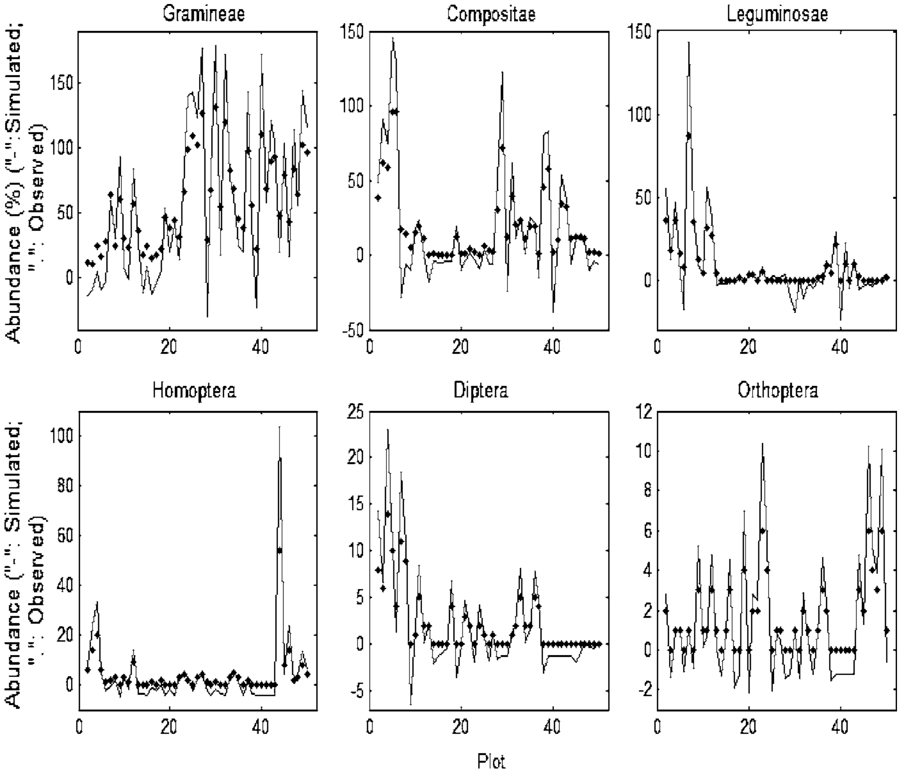


Fig. 7 Simulation performance of community succession using multivariate linear regression

0.32; Fig. 8 and Table 5) communities was inferior to ANNSSM (Table 3).

Ordinary differential equation modeling

For both simulation and prediction of plant community succession, the system matrix A in ordinary differential Eq. 7 and difference Eq. 8 was achieved as follows:

$$\begin{matrix} 0.1102 & 0.2827 & -0.0969 \\ -0.0309 & -0.2455 & 0.5654 \\ 0.0006 & 0.3203 & -0.779 \end{matrix}$$

and

$$\begin{matrix} 0.1329 & 0.2801 & -0.1057 \\ -0.0521 & -0.2423 & 0.5718 \\ 0.0137 & 0.3193 & -0.7843 \end{matrix}$$

However, the system matrix for both simulation and prediction of arthropod community succession was not available. The results indicated that linear ordinary differential equation would not reasonably model the plant community succession (Table 6; Fig. 9). Taken together, spatial succession for both plant and arthropod communities was not able to be described by linear ordinary

Table 5 Simulation and prediction performance of multivariate linear regression (MR)

	Gramineae	Compositae	Leguminosae	Homoptera	Diptera	Orthoptera
MR Simu.	Simu. = −42.06 + 1.73*Obs.	Simu. = −12.24 + 1.64*Obs.	Simu. = −4.69 + 1.59*Obs.	Simu. = −3.79 + 1.97*Obs.	Simu. = −1.37 + 1.63*Obs.	Simu. = −1.36 + 1.92*Obs.
MR Predi	Predi. = 78.55–0.16*Obs.	Predi. = 12.09 + 0.32*Obs.	Predi. = 2.88 + 0.007*Obs.	Predi. = 5.14–0.03*Obs.	Predi. = 3.53–inf*Obs.	Predi. = 1.23 + 0.03*Obs.

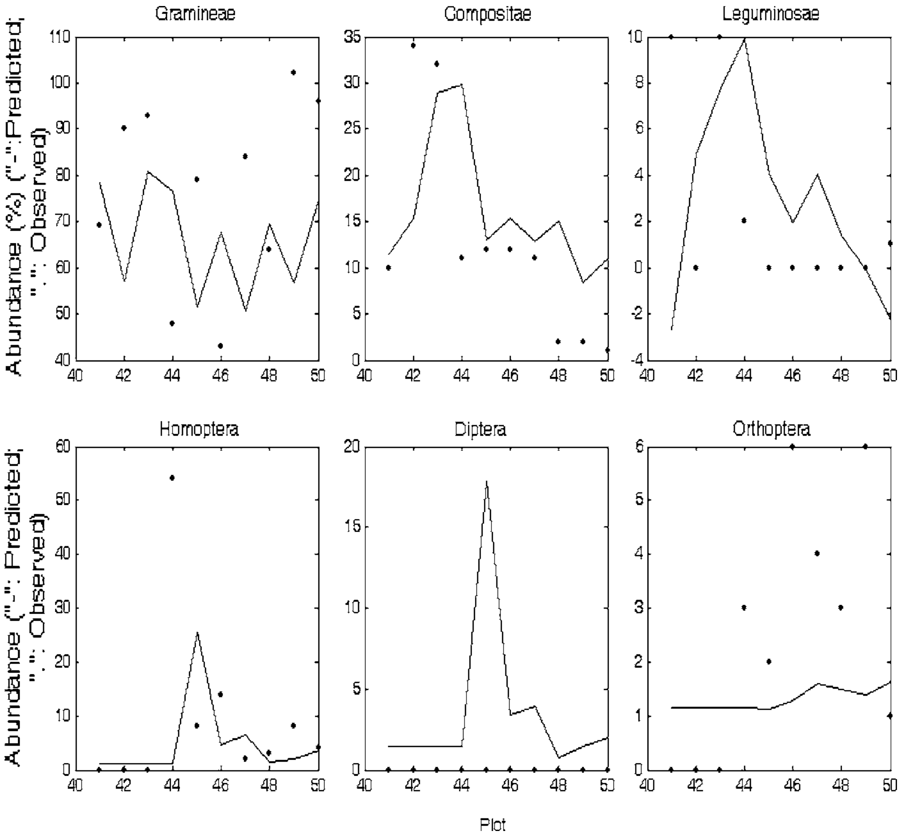


Fig. 8 Cross validation of community succession modeling using multivariate linear regression

differential equation. This conclusion supports the argumentation that neural network models were more effective in time series prediction than previous procedures based on dynamical system theory (Balaguer Ballester et al. 2002; Zhang et al. 2007).

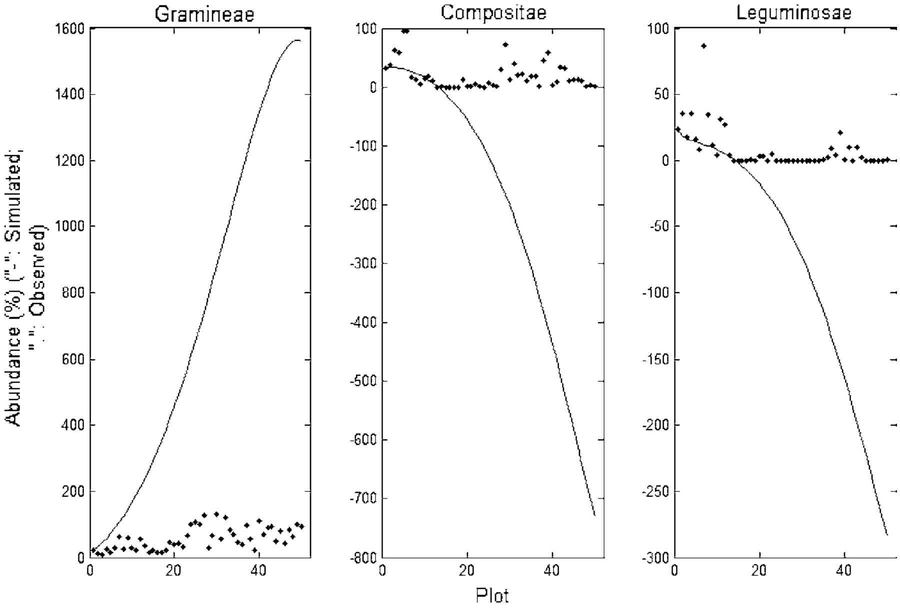
State transition probability modeling

Using state transition probability model proposed above and the definition of states in Table 1 (10,000 randomizations), the state changes for each taxon were simulated (The simulation was based on the single-step transition probability matrix constructed from all plots. The state of the first plot was the initial state for simulation) and predicted (Table 7). The correctly simulated percentage for Gramineae, Compositae, Leguminosae, Homoptera, Diptera, and Orthoptera were 62%, 88%, 94%, 94%, 84% and 74%, respectively, and correctly predicted percentage for the six taxa reached 70%, 100%, 100%, 80%, 100% and 80%, respectively. These results indicated that the state transition probability model was an efficient tool for modeling spatial succession of biological communities.

Table 6 Simulation performance of plant community succession using linear ordinary differential equation (ODE)

	Gramineae	Compositae	Leguminosae
ODE	Simu. = 242.9 + 8.79*Obs.	Simu. = −239.43 + 1.63*Obs.	Simu. = −94.39 + 2.16*Obs.
Simu.	$r = 0.57$, $df = 47$, $F = 22.25$, $p < 0.0001$	$r = 0.17$, $df = 47$, $F = 1.35$, $p = 0.25$	$r = 0.36$, $df = 47$, $F = 7.29$, $p = 0.01$
ODE	Predi. = 1,369.8 − 3.5*Obs.	Predi. = −935.8 + 5.4*Obs.	Predi. = −331.9 + 6.4*Obs.
Predi.	$r = 0$, $df = 8$, $F = 1$, $p < 0.0001$	$r = 0$, $df = 8$, $F = 8$, $p < 0.0001$	$r = 0$, $df = 8$, $F = 6$, $p < 0.0001$

Fig. 9 Simulation performance of plant community succession using linear ordinary differential equation



Multinomial logistic regression

The simulation performance of multinomial logistic regression was overall inferior to state transition probability model (Table 8). Using taxa assemblage to predict a single taxon would yield better results than using single taxon.

Both correlation analysis and modeling performance confirmed our previous hypothesis on spatial succession of community composition. From various comparisons on model performance, we proposed a novel multi-model framework, i.e., the joint use of ANNSSM and STPM, to predict the spatial succession of biological communities. In this framework, ANNSSM may be used to model the continuous dynamics, while STPM may be used to model the discrete process.

Discussion

Both ANNSSM and ordinary differential equation can simultaneously simulate multiple dependent variables. In contrary, multivariate linear regression and multinomial logistic regression will only simulate a single variable at the same time. ANNSSM, ordinary differential equation and multivariate linear regression can be used to describe continuous processes, while STPM and multinomial logistic regression may describe discrete processes. STPM includes randomization procedure and the prediction accuracy will be considerably improved. Moreover, STPM algorithm may simulate multiple dependent variables although it does not consider the between-variable relationships. According to the practical performances in interpretability and predictability of these models, our multi-model framework, the joint use of ANNSSM and STPM, should be an ideal model framed to jointly predict the spatial succession of biological communities. Using this framework, the discrete process may be described using STPM and the continuous dynamics can be simulated by using ANNSSM.

The power of data interpretation has long been the major concern for neural network models. Developing a systematic method for interpreting neural network models is the subject of recent researches (Kemp et al. 2007). Some methods to address neural network's data interpretation, like perturbation, neural interpretation diagram, sensitivity analysis, Garson's algorithm, inference rule extraction, randomization approach, etc., have been developed for practical uses (Scardi and Harding 1999; Bradshaw et al. 2002; Olden and Jackson 2002; Gevrey et al. 2006). The

Table 7 Prediction performance of community succession using state transition probability model

Plot ID	Gramineae		Compositae		Leguminosae		Homoptera		Diptera		Orthoptera	
Along transect	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.	Obs.	Pred.
40	3	3	1	1	1	1	1	1	1	1	1	1
41	2	2	1	1	1	1	1	1	1	1	1	1
42	3	3	2	2	1	1	1	1	1	1	1	1
43	3	3	2	2	1	1	1	2	1	1	1	1
44	2	2	1	1	1	1	4	3	1	1	2	2
45	2	2	1	1	1	1	2	2	1	1	2	2
46	2	3	1	1	1	1	2	2	1	1	4	4
47	3	3	1	1	1	1	1	1	1	1	3	3
48	2	3	1	1	1	1	1	1	1	1	2	1
49	3	3	1	1	1	1	2	2	1	1	4	3
50	3	2	1	1	1	1	1	1	1	1	1	1

The prediction was based on the single-step transition probability matrix constructed from the first 40 plots. The state of the 40-th plot was the initial state for prediction

Table 8 The percentages (%) correctly fitted with multinomial logistic regression

	Gramineae	Compositae	Leguminosae	Homoptera	Diptera	Orthoptera
$V_{1,2,3} \rightarrow V_i$	53.1	55.1	61.2	83.7	67.3	57.1
$V_i \rightarrow V_i$	49	46.9	59.2	83.7	61.2	57.1

$V_{1,2,3} \rightarrow V_i$ computing V_i ($i = 1$:Gramineae; $i = 2$:Compositae; $i = 3$:Leguminosae) from V_1(Gramineae), V_2 (Compositae), and V_3(Leguminosae); $V_i \rightarrow V_i$ computing V_i ($i = 1$:Gramineae; $i = 2$:Compositae; $i = 3$:Leguminosae) from the same V_i ($i = 1$:Gramineae; $i = 2$:Compositae; $i = 3$:Leguminosae)

most recent methods included connectivity weight method (Olden et al. 2004), HIPR (Kemp et al. 2007), et al., among which HIPR was an ANN architecture-independent method. The IDM presented in our study was improved from connectivity weight method, which was specifically used to the neural network ANNSSM. Our method indicated that the improved detection method for variable importance using specific neural network model should be conducted based on connectivity weight method in order to draw more reliable conclusions.

Data quality is an important aspect to train a neural network for stronger predictive power. Data quality can be improved by randomization procedure (Kilic et al. 2007; Tosh and Ruxton 2007), PCE (Zhang, to be published), et al. Moreover, the confidence interval of prediction may be obtained through randomization procedure, as indicated in present study. The predictive power could be further improved by limiting the complexity of the neural network, training neural network with noise, using weight decay, and limiting the training of the neural network (Ozesmi et al. 2006).

State transition models have been used as widely applicable, adaptive, heuristic, and empirical tools for understanding and managing ecosystems (Bork et al. 1997; Jackson and Bartolome 2002; Jasinski and Payette 2005; Herrick et al. 2006; Quétier et al. 2007). They can accommodate the possibility that different stable vegetation states were possible in a given location (Herrick et al. 2006; Quétier et al. 2007). Unlike interlinked models, our model (STPM), however, is a one-way-linked, transition probability based method that proposed to understand the spatial succession of biological communities. It is an adaptive statistic tool.

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