

Article

A generalized network evolution model and self-organization theory on community assembly

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Abstract

Community assembly is the process that species grow and interact to establish a community. In present study, a generalized, rule-based network evolution model, CommAssembly, for community assembly was proposed. The model is based on difference equations with different number of species in different stages of evolution. It consists of pioneer rule, invasion and growth rule, extinction rule, connection (flow) rule and termination rule, etc. Species invades, grows in, or quits the community following specific rules. In addition, I proposed the self-organization theory on community assembly. In this theory, I think that community assembly is a self-organization process. In terms of the model proposed, the practical community can spontaneously adjust its $A(t)$, and guarantee itself to evolve in a natural way. Temporal dynamics and species composition of community depend on species composition of species pool, between-species interactions, intrinsic growth of species, environmental capacity (resource availability), and the probability, strength and history of invasions, etc. The invasion, establishment, growth, and extinction of species follow a series of rules. Community assembly can be best described and modeled with self-organization approaches. The model provides the basis to build self-organization models of community assembly.

Keywords community assembly; network evolution; differential equation; difference equation; rules; self-organization theory.

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1 Introduction

Community assembly is the process that species growth and interact to establish a community (Zhang, 2014c). It stresses the change of community over a single phase (Warren et al., 2003). Community assembly may likely lead to a diverse and stable community. Community assembly might be constrained by local (abiotic characteristics of habitat) or regional (composition of species pool, habitat isolation) factors (Bossuyt et al., 2005). Theory and knowledge on community assembly provides basic rules for species assembly (Chase, 2003; Zhang, 2011, 2012a, 2012b, 2012c, 2014a, 2014b). Community assembly rule was firstly proposed by

Diamond in 1975. He pointed out that community assembly is the process that species in the regional species bank join the local community through the multiple-layer filtering of the environment and biological interactions (Diamond, 1975; Wang et al., 2014). Wilson and Roxburgh (1994) thought that the rules for plant community assembly are a series of potential rules restricting the presence or increase of species. Up till now, a lot of rules have been proposed, among which the most accepted rule is species co-occurrence hypothesis proposed by Diamond (1975). Fukami (2010) defined the mechanism of community assembly as a construction and conservation process of local community through sequential arrival of species from the external species bank and increase/extinction of species in the community. Community assembly acknowledges that the community tends to be stable over the time, and acknowledges the role of interspecific interactions, in particular competition. So far, ecological niche theory and neutral theory are two well-known interpretations of the mechanism for community assembly. Methods used in community assembly include establishing research plots, indoor simulation, etc. Some methods of community succession can be used in community assembly research also.

Some researchers have built the predation structures of some communities (Dunne et al., 2002). These models include cascade model (Cohen and Newman, 1985; Zhang et al., 2014), habitat model (Williams and Martinez, 2000), and the model for energy flows and functional groups (Fath et al., 2007). In addition, Zhang (2012c) presented a simple probabilistic network model.

In present study, a generalized, rule-based network evolution model for community assembly will be proposed. The model is based on difference equations with different number of species in different stages of evolution. It consists of pioneer rule, invasion and growth rule, extinction rule, connection (flow) rule and termination rule, etc. In addition, I will propose the self-organization theory on community assembly, based on modeling results and previous knowledge.

2 Model: CommAssembly

Suppose there are totally m species (i.e., m nodes in the network) in the species pool of a community being assembled. The nonlinear differential equation of dynamics of the n -species ($n \leq m$) community is

$$dx/dt=f(x, t)$$

where $x=(x_1, x_2, \dots, x_n)$, $f(x, t)=(f_1(x, t), f_2(x, t), \dots, f_n(x, t))$. Suppose $f(x, t)$ is second-order differentiable, then in a short time interval, the nonlinear equation can be approximated with a linear differential equation

$$dx/dt=A(t)x$$

where $x=(x_1, x_2, \dots, x_n)$, $A(t)=(a_{ij}(t))_{n \times n}$, $a_{ij}(t)=\partial f_i(x, t)/\partial x_j(t)$, $i, j=1, 2, \dots, n$. The linear differential equation can be transformed to a difference equation

$$\Delta x = A(t)x \Delta t$$

$$\text{i.e.,} \quad \Delta x_i = (a_{i1}(t)x_1 + a_{i2}(t)x_2 + \dots + a_{in}(t)x_n) \Delta t \quad i=1, 2, \dots, n$$

Without loss of generality, let $\Delta t = 1$, we have

$$\Delta x_i = a_{i1}(t)x_1 + a_{i2}(t)x_2 + \dots + a_{in}(t)x_n \quad i=1, 2, \dots, n$$

The rule for population dynamics is thus

$$x_i(t+1) = a_{i1}(t)x_1(t) + a_{i2}(t)x_2(t) + \dots + a_{i,i-1}(t)x_{i-1}(t) + (1+a_{ii}(t))x_i(t) + a_{i,i+1}(t)x_{i+1}(t) + \dots + a_{in}(t)x_n(t)$$

$$i=1, 2, \dots, n$$
(1)

The coefficients, $a_{ij}(t)$, $i, j=1, 2, \dots, n$; $i \neq j$, are correlated with various ecological interactions between species (e.g., competition, mutualism, predation, etc.). If both $a_{ij}(t)=0$ and $a_{ji}(t)=0$, the species i and j do not have niche overlap. The coefficients, $a_{ii}(t)$, $i=1, 2, \dots, n$, are correlated with intrinsic growth and resource availability of each species, etc.

Assign each species with an invasion probability $p_i(t)$, $i=1, 2, \dots, m$, and an invasion strength (population size) $c_i(t)$, $i=1, 2, \dots, m$.

(1) Pioneer rule. Let $t=1$; randomly choose a species, i , with the invasion strength $c_i(t)$, and let it establish in the community. Let $x_i(t)=c_i(t)$. As described in rule (1), The species will grow to the next time step, following the rule $x_i(t+1) = (1+a_{ii}(t))x_i(t)$.

(2) Invasion and growth rule. $t=2$; For each species in the species pool, randomly choose a species at its invasion probability from the species pool, in exception of i . If no species is chosen, $x_i(t+1) = (1+a_{ii}(t))x_i(t)$; otherwise, if the species j is chosen and established, let $x_j(t)=c_j(t)$, and we have the rule

$$x_i(t+1) = (1+a_{ii}(t))x_i(t) + a_{ij}(t)x_j(t)$$

$$x_j(t+1) = (1+a_{jj}(t))x_j(t) + a_{ji}(t)x_i(t)$$
(2)

The same species, for example, species j , established in earlier time, can invade the community again. In this case, let

$$x_j(t) \leftarrow x_j(t) + c_j(t)$$

Once an invasion occurs, the population changes according to the equation group (2). If the population tends to zero, as described in the following extinction rule, the establishment of the species is not successful. Thus species establishment is naturally included in the model.

Two or more species can be chosen and established simultaneously. In this case, several species and equations should be added in equation group (2), following the form of equation group (1).

(3) Extinction rule. Following the rule (1), repeatedly use invasion and growth rule. Suppose until certain time steps are conducted, the rule is the equation group (1), and a species, k (without loss of generality, suppose $k < i$), is removed from community because its population size becomes zero. Then the rule (1) becomes

$$x_i(t+1) = a_{i1}(t)x_1(t) + a_{i2}(t)x_2(t) + \dots + a_{i,k-1}(t)x_{k-1}(t) + a_{i,k+1}(t)x_{k+1}(t) + \dots + a_{i,i-1}(t)x_{i-1}(t) +$$

$$(1+a_{ii}(t))x_i(t) + a_{i,i+1}(t)x_{i+1}(t) + \dots + a_{in}(t)x_n(t)$$

$$i=1, 2, \dots, k-1, k+1, \dots, n$$
(3)

Two or more species can be removed simultaneously. In this case, several species and equations should be removed from equation group (1).

(4) Connection rule (flow rule). At each time step, for species i and j ($i \neq j$)

if $a_{ij}(t) \neq 0$, or $a_{ji}(t) \neq 0$, there is a connection (interaction) between species i and j

if $a_{ij}(t) \neq 0$ and $a_{ji}(t) = 0$, there is a connection from species j to i , and $a_{ij}(t)$ is the flow coefficient (connection weight)

if $a_{ij}(t) = 0$ and $a_{ji}(t) \neq 0$, there is a connection from species i to j ; $a_{ji}(t)$ is the flow coefficient (connection weight)

if $a_{ij}(t) \neq 0$ and $a_{ji}(t) \neq 0$, there is a loop between species i and j ; $a_{ij}(t)$ and $a_{ji}(t)$ are the flow coefficients (connection weights)

if $a_{ij}(t) = 0$ and $a_{ji}(t) = 0$, there is not a connection between species i and j

In addition

if $a_{ij}(t) = 0$ and $a_{ji}(t) = 0$, $j = 1, 2, \dots, n$; $i \neq j$, species i is a isolated (redundant) species

(5) Termination rule. Repeat the steps (2) to (4), until the community tends to be stable, i.e.,

$$x_i(t+1) = x_i(t) \quad i \in S \quad (4)$$

where S is the set of species occurred in the community, or until a certain number of iterations is achieved.

3 Application Example

3.1 Model simplification and computational codes

For present example, I simplify above model for convenient demonstration as follows

In the equation group (1), if $x_i(t+1) \geq K_i(t+1)$, let $x_i(t+1) = K_i(t+1)$, $i = 1, 2, \dots, n$, where $K_i(t)$ is environmental capacity of species i at time t , and further, let $K_i(t) = K_i$, $i = 1, 2, \dots, m$;

Let $A(t) = A$, where A is a constant matrix;

Let $p_i(t) = p_i$, $i = 1, 2, \dots, m$;

Let $c_i(t) = c_i$, $i = 1, 2, \dots, m$.

K_i , A , p_i , and c_i , are generated with random numbers. The simplified model and data generation method are included in the following Matlab codes

```
%Reference: Zhang WJ. 2015. A generalized network evolution model and self-organization theory on community assembly. Selforganizology, 2(3): 55-64
```

```
m=30; % Set the number of species in species pool
```

```
tmax=1000; % Maximum number of iterations
```

```
% Generate the coefficient matrix A
```

```
a=rand(m);
```

```
growfac=0.05;
```

```
interactfac=0.1;
```

```
nointeractfac=0.3;
```

```
neginteractfac=0.8;
```

```
for i=1:m; for j=1:m;
```

```

if (i==j) a(i,j)=a(i,j)*growfac; continue; end
if (a(i,j)<nointeractfac) a(i,j)=0;
else if (a(i,j)<neginteractfac) a(i,j)=-a(i,j)*interactfac; end; end;
end; end
K=500+rand(1,m)*500;      % Set the environmental capacity, Ki(t), for each species; for simplified model only
p=ones(1,m)*rand()*0.1;  % Set the invasion probability, pi(t), for each species
c=ones(1,m)*rand()*5;    % Set the invasion strength, ci(t), for each species
x=zeros(1,m);
id=zeros(1,m);
t=1;
idx=round(rand()*m+0.5);
id(idx)=1;
x0=zeros(1,m);
x(idx)=c(idx);
while (t<tmax)
x0=x;
for i=1:m;
if (id(i)==0) x(i)=0; continue; end
s(i)=0;
for j=1:m;
if (id(j)==0) continue; end
s(i)=s(i)+a(i,j)*x(j);
end;
x(i)=s(i)+x(i);
end;
w=zeros(1,m); v=zeros(1,m);
nn=0;
fprintf(['t=' num2str(t) '\nSpecies list and population size\n'])
for i=1:m
if (id(i)==0) continue; end
if (x(i)>=K(i)) x(i)=K(i); end          % For simplified model only
if (x(i)<=0) id(i)=0; continue; else id(i)=1; end
nn=nn+1;
v(nn)=i;
w(nn)=x(i);
fprintf(['num2str(i) '(x(' num2str(i) ')=' num2str(round(x(i)*100)/100) ') ']);
end
fprintf(['\nTotal number of species=' num2str(sum(id)) '\nConnection and connection weight (flow coefficient)\n']);
for i=1:nn
for j=1:nn
if (i==j) continue; end
if (a(v(i),v(j))~=0) fprintf(['num2str(v(i)) ' ' num2str(v(j)) ' ' num2str(round(a(v(i),v(j))*1000)/1000) '\n']); end;
end; end
iso=zeros(1,m);
for k=1:nn

```

```

temprow=0;
for j=1:nn
if (j==k) continue; end
if (a(v(k),v(j))==0) temprow=temprow+1; end
end;
tempcol=0;
for j=1:nn
if (j==k) continue; end
if (a(v(j),v(k))==0) tempcol=tempcol+1; end
end;
if ((temprow==nn-1) & (tempcol==nn-1)) iso(k)=1; end
end
for i=1:nn
if (iso(i)==1) fprintf([num2str(iso(i)) '(isolated species)\n']); end
end
fprintf('\n\n');
if (sum(x==x0)==m) break; end
if (x==K) break; end           % For simplified model only
t=t+1;
for i=1:m
if (rand()<p(i)) id(i)=1; x(i)=x(i)+c(i); end
end
end

```

The codes can be revised and improved for further specific uses.

3.2 A result set and analysis

Running the simplified model, a result set was obtained as follows

```

t=1
Species list and population size
17(x(17)=2.34)
Total number of species=1
Connection and connection weight (flow coefficient)
1(isolated species)

```

```

t=2
Species list and population size
17(x(17)=2.45)
Total number of species=1
Connection and connection weight (flow coefficient)
1(isolated species)

```

```

t=3

```

Species list and population size

17(x(17)=2.44) 26(x(26)=4.29)

Total number of species=2

Connection and connection weight (flow coefficient)

17 26 -0.059

26 17 0.828

t=4

Species list and population size

17(x(17)=2.31) 26(x(26)=6.29)

Total number of species=2

Connection and connection weight (flow coefficient)

17 26 -0.059

26 17 0.828

t=5

Species list and population size

5(x(5)=1.77) 16(x(16)=7.64) 17(x(17)=1.51) 26(x(26)=9.41)

Total number of species=4

Connection and connection weight (flow coefficient)

5 16 -0.05

5 17 -0.066

5 26 -0.034

16 5 -0.067

16 17 -0.078

16 26 0.892

17 5 -0.062

17 16 -0.058

17 26 -0.059

26 5 0.987

26 17 0.828

t=6

Species list and population size

5(x(5)=0.99) 16(x(16)=18.07) 21(x(21)=2.16) 26(x(26)=10.27)

Total number of species=4

Connection and connection weight (flow coefficient)

5 16 -0.05

5 26 -0.034

16 5 -0.067

16 21 0.842

16 26 0.892

26 5 0.987

26 21 -0.067

t=7

Species list and population size

16(x(16)=29.89) 21(x(21)=2.26) 26(x(26)=10.07)

Total number of species=3

Connection and connection weight (flow coefficient)

16 21 0.842

16 26 0.892

26 21 -0.067

t=8

Species list and population size

16(x(16)=42.14) 21(x(21)=2.37) 26(x(26)=10.12)

Total number of species=3

Connection and connection weight (flow coefficient)

16 21 0.842

16 26 0.892

26 21 -0.067

.....

t=26

Species list and population size

1(x(1)=873.51) 2(x(2)=654.96) 3(x(3)=958.25) 4(x(4)=891.13) 6(x(6)=640.55) 7(x(7)=953.75) 8(x(8)=555.54)
 9(x(9)=894.91) 11(x(11)=883.97) 12(x(12)=831.03) 13(x(13)=886.55) 15(x(15)=588.44) 16(x(16)=510.21)
 17(x(17)=916.82) 18(x(18)=736.6) 20(x(20)=544.53) 21(x(21)=557.56) 22(x(22)=583.99) 23(x(23)=986.26)
 25(x(25)=799.51) 27(x(27)=622.39) 30(x(30)=655.3)

Total number of species=22

Connection and connection weight (flow coefficient)

(318 connections. They are omitted for page limitation)

In this example, there are 30 species in species pool. In exception of species ID 5, 10, 14, 19, 24, 26, 28, and 29, in total of 22 species are finally established in the community. The number of species does not necessarily increase monotonously with the time. The changes of No. species and No. interactions are shown in Fig. 1.

In the network view, the nodes, connections and topological structure change during the network evolution. In some conditions, the topological structure of the network will gradually stabilize with the time. The mechanism of the present network evolution model is thoroughly different from previous ones (Barabasi and Albert, 1999; Zhang, 2012a, 2012c). In addition, the networks generated by my model are directed graphs rather than previous undirected graphs.

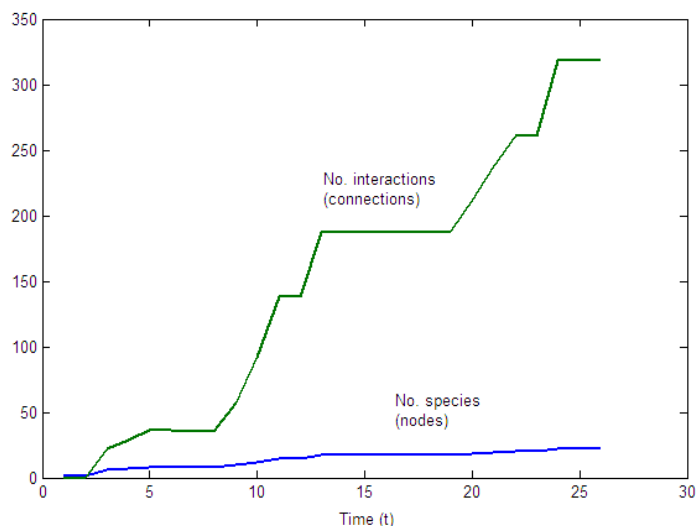


Fig. 1 The changes of No. species and No. interactions with the time.

4 Conclusions

A lot of conclusions can be drawn from a number of running of the simplified model. The following findings are only from various settings of constant A , K_i , p_i , and c_i . With the changes of $A(t)$, $K_i(t)$, $p_i(t)$, and $c_i(t)$, community dynamics and species composition are expected to yield more diverse patterns.

- (1) Effect of A . Set different sets of coefficients, $a_{ij}(t)$, $i, j=1, 2, \dots, n$; $i \neq j$, community assembly dynamics will change accordingly, depending on signs and absolute values of $a_{ij}(t)$, and if $a_{ij}(t)=0$ or not. If $a_{ij}(t)=0$ and $a_{ji}(t)=0$, $i, j=1, 2, \dots, n$; $i \neq j$, all species have not niche overlap, and the coefficients, $a_{ii}(t)$, $i=1, 2, \dots, n$, are thus pure growth rates. With different growth rates, community assembly dynamics are different. The greater growth rates lead to faster growth of species population.
- (2) Effect of p_i . The speed of community assembly increases with p_i . The species with small p_i are harder to invade the community.
- (3) Effect of c_i . The greater c_i facilitate the species to reach their environmental capacity fastly.
- (4) Effect of K_i . The smaller K_i lead to the community reaching its final state earlier.

5 Discussion: Self-organization Theory on Community Assembly

Using the present model to describe community assembly, the expected and natural dynamics may occur in certain conditions. In the field, however, community assembly is a natural process, in which the community always evolves in natural ways (e.g., it gradually evolves to a diverse and stable climax). Thus I think that community assembly is a self-organization process. In terms of the model above, the natural community can spontaneously adjust its $A(t)$, and guarantee itself to evolve in a natural way. Temporal dynamics and species composition of community are dependent on species composition in species pool, between-species interactions (in which both niche differentiation and ecological interactions are included), intrinsic growth of species (which includes both the reproduction potentiality and the adaptability of the species to the environment), environmental capacity (resource availability), and the probability, strength and history of invasions, etc. The invasion, establishment, growth, and extinction of species follow a series of rules. Community assembly can be well modeled. It can be best described and modeled with self-organization approaches (Zhang, 2012a). The present model provides the basis to build self-organization models of community assembly.

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