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Article

Modeling community succession and assembly: A novel method for network evolution

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Abstract

The process of modeling community succession and assembly is in some sense a method for network evolution, as done by Barabasi and Albert (1999). It is also one of the methods to create a sample network from the statistic network I proposed earlier. I think that the mechanism of network evolution supposed by Barabasi and Albert is most likely applicable to the natural phenomena with emergency property. For natural phenomena without emergency property, the present study indicated that a scale-free network may be produced through a new mechanism, i.e., whether the connection of a taxon *x* occurs, dependent on the type and property of taxon *y* (in particular, the degree of its direct correlation with *x*) to be connected but not necessarily the existing number of connections of taxon *y*, as proposed in present study.

Keywords community succession; assembly; network evolution; mechanism; modeling.

1 Introduction

Understanding the mechanism of community succession is the focus of ecologists (Hraber and Milne, 1997; Zhang, 2012b). It is also one of the central questions in food web theory (May, 1973; Case, 1990; Pimm, 1991; Cohen et al., 1993). A community is a self-organizing system, generated from repeating species invasions, selection, adaptation and optimization. So far, some mechanisms governing community succession and assembly have been confirmed. For example, a community can have multiple distinct steady distributions or alternative steady states. They represent different species assemblages occurring at possible similar conditions. History of community succession determines which steady state will occur (Hraber and Milne, 1997).

In a sense, the process of modeling community succession and assembly is a method for network evolution, as done by Barabasi and Albert (1999). Degree distribution and connection structure of networks is one of the focuses in network analysis (Dunne et al., 2002; Ibrahim et al., 2011; Kuang and Zhang, 2011; Paris and Bazzoni, 2011; Tacutu et al., 2011; Zhang, 2011; Zhang and Zhan, 2011). However, the research on network evolution or network dynamics is still seldom due to lack of relevant knowledge. For this reason, the present study tried to propose a novel mechanism for network evolution, and provided a new method for modeling community succession and assembly.

2 Method

Suppose there are totally *v* taxa (species, or subspecies, etc.) in a community. Given a correlation matrix,

$r=(r_{ij})_{v\times v}$, in which the elements are between-taxa correlation coefficients (Jaccard coefficients, or other correlation measures, etc.) that reflect between-taxa dynamic relationships in the community succession, $r_{ij}=r_{ji}$, $-1\leq r_{ij}\leq 1$; and an attribute vector, $a=(a_i)_v$, in which 0 means detrital/neutral taxon, 1 means herbivorous/grazing taxon, 2 means predatory/carnivorous taxon, and 3 means parasitoid/parasite taxon.

Some assumptions are made in this method: (1) once a taxon invaded the community, it will establish the community and will not disappear again; (2) all taxa in the pool will finally invaded and established the community; (3) the first taxon, i.e., pioneer taxon is a detrital/neutral or herbivorous/grazing taxon, and each time a randomly chosen taxon invades the community; (4) the taxon invaded tends to connect (interact with) each of existing taxa at a probability proportional to its direct correlation with the taxon to be connected, the connected (interactive) taxa probabilistically follow a similar (connection value 1) or inverse (connection value -1) trend in the changes of population size during the community succession; however, an isolated taxon is featured with its distinct and independent population dynamics. The network evolution method for modeling community succession and assembly is described bellow.

(1) Generate v ordered taxa by producing v random numbers that represent v taxa. If the first taxon is not a detrital/neutral taxon or herbivorous/grazing taxon, repeat the procedure to produce the first taxon, i.e., pioneer taxon. The Java algorithm is

```
c=0;
for(j=1;j<=v;j++) w[j]=j;
do {
cs=(int)((v-c)*Math.random()+1);
if ((a[w[cs]]!=1) & (a[w[cs]]!=0) & (c==0)) continue;
x[c+1]=w[cs];
if (cs<(v-c))
for(j=cs+1;j<=v-c;j++) w[j-1]=w[j];
c++; }
while (c<=(v-1));
```

The resultant ordered series of invasion taxa is $x(i)$, $i=1,2,\ldots,v$.

(2) Based on ordered taxa $x(i)$, $i=1,2,\ldots,v$, let the taxon invade the community one by one. The first taxon invading the community is the pioneer taxon. In the k-th invasion, randomly produce a value p, and

$$\begin{aligned}
&d_{x(k),\,x(i)}= d_{x(i),\,x(k)}=1,\ \text{if } r_{x(k),\,x(i)}>0 \text{ and } r_{x(k),\,x(i)}>p;\\
&d_{x(k),\,x(i)}= d_{x(i),\,x(k)}=-1,\ \text{if } r_{x(k),\,x(i)}<0 \text{ and } |r_{x(k),\,x(i)}|>p;\\
&d_{x(k),\,x(i)}= d_{x(i),\,x(k)}=0,\ \text{if } |r_{x(k),\,x(i)}|<p;\\
&\qquad i=1,2,\ldots k-1.
\end{aligned}$$

where $D=(d_{ij})$ is the adjacency matrix. If $d_{x(k),\,x(i)}= d_{x(i),\,x(k)}=1$, then there is a positive connection (positive interaction) between the taxa $x(k)$ and $x(i)$; if $d_{x(k),\,x(i)}= d_{x(i),\,x(k)}=-1$, then there is a negative connection (negative interaction) between the taxa $x(k)$ and $x(i)$. The taxon $x(k)$ is an isolated taxon, if $d_{x(k),\,x(i)}= d_{x(i),\,x(k)}=0$, for $i=1,2,\ldots k-1$.

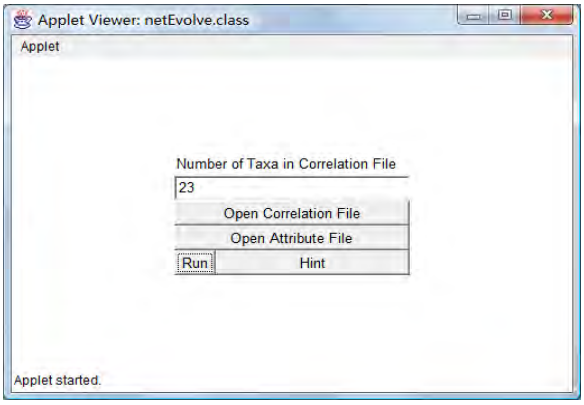
Finally, record all pairs of connected taxa and isolated taxa based on the adjacency matrix.

After the k-th invasion, there are in total k taxa in the community, i.e., $x(i)$, $i=1,2,\ldots,k$.

(3) If all taxa have invaded the community, terminate procedure; or else return to (2).

The following codes are the main Java codes of network evolution, netEvolve (Fig. 1; see http://www.iaees.org/publications/software/index.asp), for modeling community succession and assembly:

```
c=0;
for(j=1;j<=v;j++) w[j]=j;
do {
cs=(int)((v-c)*Math.random()+1);
if ((a[w[cs]]!=1) & (a[w[cs]]!=0) & (c==0)) continue;
x[c+1]=w[cs];
if (cs<(v-c))
for(j=cs+1;j<=v-c;j++) w[j-1]=w[j];
c++; }
while (c<=(v-1));
for(k=1;k<=v;k++) {
if (k==1) {
output.editt1.appendText("Invasion "+k+"\n");
output.editt1.appendText("Pioneer taxon: "+String.valueOf(x[k])+"\n");
continue; }
for(i=1;i<=k-1;i++) {
tem=Math.random();
if ((r[x[k]][x[i]]>0) & (r[x[k]][x[i]]>tem)) d[x[k]][x[i]]=d[x[i]][x[k]]=1;
if ((r[x[k]][x[i]]<0) & (Math.abs(r[x[k]][x[i]])>tem)) d[x[k]][x[i]]=d[x[i]][x[k]]=-1; }
c=0;
for(i=1;i<=v-1;i++)
for(j=i+1;j<=v;j++)
if (Math.abs(d[i][j])==1) c++;
output.editt1.appendText("\nInvasion "+k);
output.editt1.appendText("\nInvasion taxon: "+x[k]);
output.editt1.appendText("\nAll taxa in community: ");
for(i=1;i<=k;i++) output.editt1.appendText(String.valueOf(x[i])+"    ");
output.editt1.appendText("\n"+"Total connections: "+String.valueOf(c)+"\n");
output.editt1.appendText("Taxon      "+"to Taxon"+"       Connection\n");
for(i=1;i<=v-1;i++)
for(j=i+1;j<=v;j++)
if (Math.abs(d[i][j])==1) output.editt1.appendText(String.valueOf(i)+"            "+String.valueOf(j)+"            “+d[i][j]+
"\n");
for(i=1;i<=k;i++) {
cs=0;
for(j=1;j<=v;j++)
if (d[x[i]][j]==0) cs++;
if (cs==v)
output.editt1.appendText(String.valueOf(x[i])+"            "+String.valueOf(cols[i])+"            4"+"\n"); }
}
```



Number of Taxa in Correlation File
23

Fig. 1 The Java program, netEvolve

3 Results

I used a set of data that recorded in a rice field of Guangzhou, China, on September 2006. In total of 54 samples were surveyed and 23 arthropod families were found in the rice field: Culicidae, Chironomidae, Tipulidae, Ceratopogonidae, Ephydridae, Chloropidae, Aphididae, Delphacidae, Jassidae, Miridae, Veliidae, Theridium, Tetragnathidae, Linyphiidae, Erigohidae, Staphylinidae, Coccinellidae, Ceraphronidae, Encyrtidae, Braconidae, Pteromalidae, Eulophidae, Elasmidae. These families were labeled with IDs 1 to 23.

According to the diet habits of major species recorded in corresponding families, I assigned attribute values to 23 families as follows

0 0 0 0 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3 3 3 3 3

In a sense, the correlation coefficient achieved from spatial sampling may represent that achieved from temporal sampling. Using the data I calculated and obtained the matrix of between-taxa net linear correlation coefficients, as indicated in Table 1.

Table 1 Partial (pure) linear correlation coefficients between arthropod taxa

1	0.51	-0.22	0.14	-0.16	-0.02	0.1	0.06	0.19	-0.23	0.04	-0.1	0.05	0.39	0.06	0.02	-0.24	0.01	-0.2	0.24	-0.1	-0.2	0.43
0.51	1	0.56	-0.31	0	0.23	0.02	0.3	0.02	0.11	-0.11	-0.05	-0.02	-0.19	-0.1	0.02	0.2	0.2	0.26	-0.22	0.12	-0.04	-0.29
-0.22	0.56	1	0.68	-0.19	-0.07	0.25	-0.03	-0.08	-0.26	-0.14	0.01	0.13	-0.16	-0.12	-0.27	-0.19	-0.34	-0.18	0.18	0.31	0.35	0.04
0.14	-0.31	0.68	1	0.27	-0.06	-0.32	-0.13	0.03	0.23	0.09	0.16	-0.18	0.2	0.25	0.59	0.25	0.55	0.04	-0.28	-0.49	-0.35	-0.01
-0.16	0	-0.19	0.27	1	0.28	0.2	0.42	0.1	-0.2	-0.21	-0.15	0.57	-0.23	-0.18	0.02	-0.11	0.02	0.15	-0.11	0.23	0.08	-0.01
-0.02	0.23	-0.07	-0.06	0.28	1	0.02	-0.32	-0.1	0.25	0.05	0.26	-0.24	0	0.12	0.01	0.36	-0.14	-0.27	0.16	-0.19	0.05	0.01
0.1	0.02	0.25	-0.32	0.2	0.02	1	-0.27	-0.04	0.15	0.17	0.23	-0.16	0.2	0.44	0.15	0.02	0.04	0.08	-0.1	-0.33	0.03	0
0.06	0.3	-0.03	-0.13	0.42	-0.32	-0.27	1	-0.06	0.3	0.41	0.39	-0.14	0.33	0.32	-0.12	-0.01	-0.14	-0.16	0.24	-0.16	-0.12	0.27
0.19	0.02	-0.08	0.03	0.1	-0.1	-0.04	-0.06	1	0.01	-0.05	0.06	-0.04	-0.11	-0.04	-0.05	0.06	-0.04	-0.04	-0.05	0.01	0.1	-0.12
-0.23	0.11	-0.26	0.23	-0.2	0.25	0.15	0.3	0.01	1	-0.17	-0.05	0.19	0.06	0.01	0.06	-0.1	0.36	0.09	-0.16	0.11	0.32	-0.04
0.04	-0.11	-0.14	0.09	-0.21	0.05	0.17	0.41	-0.05	-0.17	1	0.23	-0.15	-0.26	-0.16	0.07	0.17	0.21	-0.14	-0.03	0.08	0.23	-0.26
-0.1	-0.05	0.01	0.16	-0.15	0.26	0.23	0.39	0.06	-0.05	0.23	1	0.49	0.05	-0.02	0.05	-0.11	0.13	0.38	-0.18	-0.03	-0.22	0.09
0.05	-0.02	0.13	-0.18	0.57	-0.24	-0.16	-0.14	-0.04	0.19	-0.15	0.49	1	0.02	0.04	0.05	0.1	-0.17	-0.28	0.2	-0.16	0.04	-0.08
0.39	-0.19	-0.16	0.2	-0.23	0	0.2	0.33	-0.11	0.06	-0.26	0.05	0.02	1	-0.32	-0.13	0	-0.2	-0.01	0.07	0.26	0.49	-0.33
0.06	-0.1	-0.12	0.25	-0.18	0.12	0.44	0.32	-0.04	0.01	-0.16	-0.02	0.04	-0.32	1	-0.33	-0.08	-0.21	-0.1	0.01	0.53	0.09	-0.18
0.02	0.02	-0.27	0.59	0.02	0.01	0.15	-0.12	-0.05	0.06	0.07	0.05	0.05	-0.13	-0.33	1	-0.21	-0.51	-0.09	0.32	0.6	0.29	-0.01
-0.24	0.2	-0.19	0.25	-0.11	0.36	0.02	-0.01	0.06	-0.1	0.17	-0.11	0.1	0	-0.08	-0.21	1	-0.22	0.01	0.42	0.15	0.02	0.15
0.01	0.2	-0.34	0.55	0.02	-0.14	0.04	-0.14	-0.04	0.36	0.21	0.13	-0.17	-0.2	-0.21	-0.51	-0.22	1	-0.17	0.42	0.3	0.14	0.01
-0.2	0.26	-0.18	0.04	0.15	-0.27	0.08	-0.16	-0.04	0.09	-0.14	0.38	-0.28	-0.01	-0.1	-0.09	0.01	-0.17	1	0.19	0.01	0.04	0.03
0.24	-0.22	0.18	-0.28	-0.11	0.16	-0.1	0.24	-0.05	-0.16	-0.03	-0.18	0.2	0.07	0.01	0.32	0.42	0.42	0.19	1	-0.14	-0.1	-0.18
-0.1	0.12	0.31	-0.49	0.23	-0.19	-0.33	-0.16	0.01	0.11	0.08	-0.03	-0.16	0.26	0.53	0.6	0.15	0.3	0.01	-0.14	1	-0.28	0.11
-0.2	-0.04	0.35	-0.35	0.08	0.05	0.03	-0.12	0.1	0.32	0.23	-0.22	0.04	0.49	0.09	0.29	0.02	0.14	0.04	-0.1	-0.28	1	0.22
0.43	-0.29	0.04	-0.01	-0.01	0.01	0	0.27	-0.12	-0.04	-0.26	0.09	-0.08	-0.33	-0.18	-0.01	0.15	0.01	0.03	-0.18	0.11	0.22	1

Using the method above, the process of community succession and assembly is simulated as the follows, where connection values 1 and -1 denote positive and negative connection between two taxa respectively, and 4 means isolated taxon.

Invasion 1
Pioneer taxon: 8

Invasion 2
Invasion taxon: 18
All taxa in community: 8 18

```
Total connections: 0
Taxon    to Taxon    Connection
8          8            4
18           18           4

Invasion 3
Invasion taxon: 6
All taxa in community: 8   18   6
Total connections: 0
Taxon    to Taxon    Connection
8          8            4
18           18           4
6          6            4

Invasion 4
Invasion taxon: 5
All taxa in community: 8   18   6   5
Total connections: 1
Taxon    to Taxon    Connection
5          8            1
18           18           4
6          6            4

Invasion 5
Invasion taxon: 10
All taxa in community: 8   18   6   5   10
Total connections: 2
Taxon    to Taxon    Connection
5          8            1
8          10            1
18           18           4
6          6            4

Invasion 6
Invasion taxon: 23
All taxa in community: 8   18   6   5   10   23
Total connections: 3
Taxon    to Taxon    Connection
5          8            1
8          10            1
8          23            1
18           18           4
6          6            4

Invasion 7
Invasion taxon: 19
All taxa in community: 8   18   6   5   10   23   19
Total connections: 4
Taxon    to Taxon    Connection
5          8            1
5          19            1
8          10            1
8          23            1
18           18           4
6          6            4

Invasion 8
Invasion taxon: 3
```

```
All taxa in community: 8   18   6   5   10   23   19   3
Total connections: 4
Taxon     to Taxon      Connection
5            8              1
5            19              1
8            10              1
8            23              1
18            18              4
6            6              4
3            3              4

Invasion 9
Invasion taxon: 4
All taxa in community: 8   18   6   5   10   23   19   3   4
Total connections: 6
Taxon     to Taxon      Connection
3            4              1
4            18              1
5            8              1
5            19              1
8            10              1
8            23              1
6            6              4

Invasion 10
Invasion taxon: 11
All taxa in community: 8   18   6   5   10   23   19   3   4   11
Total connections: 7
Taxon     to Taxon      Connection
3            4              1
4            18              1
5            8              1
5            19              1
8            10              1
8            23              1
10            11              -1
6            6              4
```

(Results for invasions 11 through 21 are omitted here)

```
Invasion 22
Invasion taxon: 2
All taxa in community: 8   18   6   5   10   23   19   3   4   11   21   17   7   15   14   1   9   20   13   16   12   2
Total connections: 39
Taxon     to Taxon      Connection
1            7              1
1            14              1
1            20              1
2            3              1
2            8              1
2            20              -1
2            21              1
2            23              -1
3            4              1
3            20              1
4            7              -1
4            13              -1
4            18              1
```

```
4          20          -1
4          21          -1
5          8           1
5          19          1
6          12          1
6          13          -1
6          20          1
7          8           -1
7          14          1
8          10          1
8          21          -1
8          23          1
9          17          1
10         11          -1
11         17          1
12         13          1
13         21          -1
14         23          -1
15         19          -1
15         21          1
16         17          -1
16         18          -1
17         18          -1
18         20          1
18         21          1
20         21          -1

Invasion 23
Invasion taxon: 22
All taxa in community: 8    18    6    5    10    23    19    3    4    11    21    17    7    15    14    1    9    20    13    16    12    2    22
Total connections: 41
Taxon      to Taxon      Connection
1          7           1
1          14          1
1          20          1
2          3           1
2          8           1
2          20          -1
2          21          1
2          23          -1
3          4           1
3          20          1
4          7           -1
4          13          -1
4          18          1
4          20          -1
4          21          -1
4          22          -1
5          8           1
5          19          1
6          12          1
6          13          -1
6          20          1
7          8           -1
7          14          1
8          10          1
8          21          -1
8          23          1
```

9	17	1
10	11	-1
11	17	1
12	13	1
13	21	-1
14	22	1
14	23	-1
15	19	-1
15	21	1
16	17	-1
16	18	-1
17	18	-1
18	20	1
18	21	1
20	21	-1

The pioneer taxon is Delphacidae. Degree distribution and network graph of the final network (community) are indicated in Table 2 and Fig. 2 respectively.

Table 2 Number of connections (degree) of taxa

Taxon	Degree	Taxon	Degree	Taxon	Degree	Taxon	Degree
4	7	7	4	3	3	19	2
20	7	13	4	23	3	12	2
21	7	14	4	15	2	11	2
8	6	17	4	16	2	22	2
18	5	1	3	10	2	9	1
2	5	6	3	5	2		

Taxa 1 through 23 denote Culicidae, Chironomidae, Tipulidae, Ceratopogonidae, Ephydridae, Chloropidae, Aphididae, Delphacidae, Jassidae, Miridae, Veliidae, Theridium, Tetragnathidae, Linyphiidae, Erigohidae, Staphylinidae, Coccinellidae, Ceraphronidae, Encyrtidae, Braconidae, Pteromalidae, Eulophidae, Elasmidae.

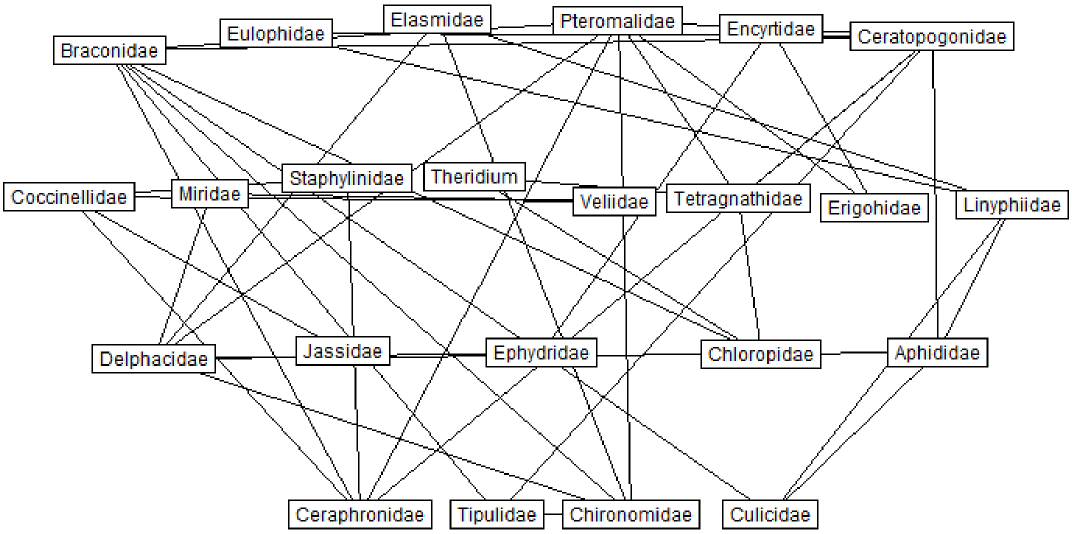


Fig. 2 Network of final community (Drawn by using the software of Zhang (2012a, b))

Using the algorithm for network type detection (Zhang and Zhan, 2011; Zhang, 2012b), degrees (number of connections of a taxon) of the final network (community) are power law distributed ($f(x)=x^{-3.404}$, $x\geq 3$), and the Kolmogorov-Smirnov test D value for power law distribution is 0.239 ($<1.63/14^{0.5}=0.436$). It is thus a scale-free complex network.

From the results of running the algorithm many times, it can be found that as the advance of community succession, both the number of taxa and the degree of association among taxa in the community increases, the number of isolated taxa without connection to other taxa decreases (Fig. 3). In the final community, most of the connections are positive connections (positive interactions). These trends are coincident with the general rules of community succession and assembly observed in the field.

Running the model repeatedly, I found that community succession and structure vary with the variation of pioneer taxon and invasion sequence, which is coincident to a common mechanism for community succession (Hraber and Milne, 1997).

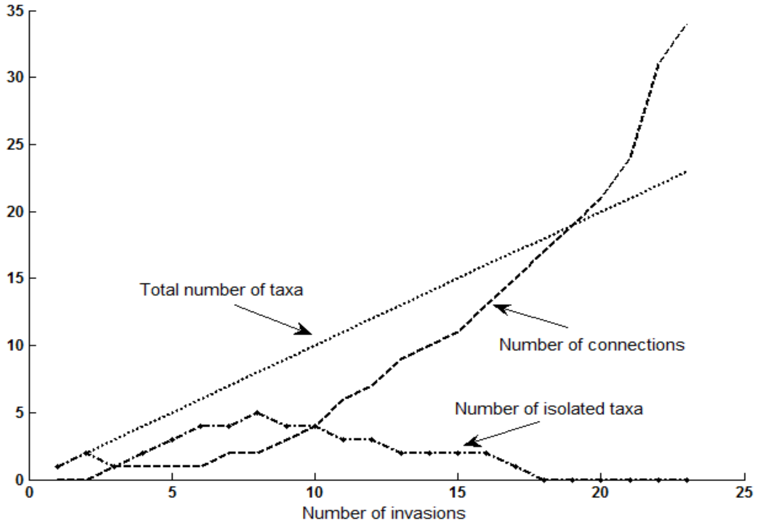


Fig. 3 Simulated succession of community

4 Discussion

The process of modeling community succession and assembly is also a method for network evolution, as done by Barabasi and Albert (1999). It is one of the methods to create a sample network from statistic network (Zhang, 2012c). I think that the mechanism of network evolution supposed by Barabasi and Albert (1999) is most likely applicable to the natural phenomena with emergency property. They supposed that new nodes to be added into network tend to connect to already better connected nodes (Barabasi and Albert, 1999). Different from their supposition, for natural phenomena without emergency property, the above results indicate that a scale-free network may be produced based on the mechanism proposed in present study, i.e., whether the connection of a taxon x occurs, dependent on the type and property of taxon y (in particular, the degree of its direct correlation with x) to be connected (y traverses all existing taxa in the community) but not necessarily the existing number of connections of taxon y. This mechanism is intensively reflected in the step (2) of the above algorithm.

The present study proved that community succession and structure will be distinct as the variation of pioneer taxon and invasion sequence. We may therefore obtain different succession patterns by repeatedly running the algorithm.

In present study, community succession and assembly is modeled as the evolution process of network. Connections are deterministic and networks are thus non-weighted networks. In a strict sense, however, different pairs of taxa are connected with different strengths (correlation coefficients). Therefore, two additional methods for network evolution can be used: (1) once a taxon invades the community, it becomes a node of the weighted network immediately. In the weighted network, all weights are correlation coefficients; (2) once a taxon invades the community, it becomes a node of the network if its correlation coefficient to any of the existing taxa in the community is statistically significant. The network is weighted network if its connections are weighted with the correlation coefficients, or else it is a non-weighted network.

Assumptions in present method are not always held in the nature, and should be improved in the future studies. For example, a taxon may invade the community but could likely not establish well or even disappear, i.e., it should experience a selection process. In addition, the population size, or abundance of each taxon is not considered in the method. These will be included in the future versions of the method.

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