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Disassembly or assembly of an ant community in a temperate forest

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ABSTRACT

Because the occurrence of living organisms is limited by competition, it is normal for organisms to follow the assembly rule in which similar species do not co-occur. In order to test whether ants within a forest follow the assembly rule, ant data surveyed for 10 years in an old temperate forest were analyzed. In most cases, co-occurrence among ant species was not different to random co-occurrence, and less co-occurrence was found only in some years, indicating ephemeral influence of competition. This finding was confirmed in the correlation analysis using data of abundance. Therefore, ants living together in a small area within a forest did not follow the assembly rule.

Introduction

One of the most fundamental questions in ecology is whether communities of living organisms are determined by the assembly rule (Gotelli and McCabe 2002). The assembly rule is a principle that species with similar niches do not coexist in the same space due to their competition. The assembly rule was first proposed by Diamond (1975) on birds. As statistical tools were developed in order to test null hypothesis of the assembly rule (Gotelli and Entsminger 2001; Stone and Roberts 1990), studies verifying the assembly rule were reported in various organism groups (Lester et al 2009; Ribas and Schoereder 2002; Sanders et al 2007). From a meta-analysis using occurrence data of various taxonomic groups, Gotelli and McCabe (2002) assessed that the assembly rule is general rather than exception.

Since competition is crucial for determining the assembly of ants (Hölldobler and Willson 1990), it was expected that the assembly rule would occur generally when analyzing the co-occurrence of ants, but some results followed the assembly rule and some did not (Lester et al 2009; Ribas and Schoereder 2002; Sanders et al 2007). This study was carried out to test whether the assembly rule is applicable for ant species living within a small area of a forest. Analysis was carried out using the ant data examined over 10 years from 2002 to 2012 in a small area (1 ha) of an old forest in South Korea (Kwon et al 2014). During the survey period, the ant community underwent a large change due to a disturbance of the forest (Kwon et al 2014), and we attempted to find whether such environmental changes influenced the assembly rule.

Materials and methods

Survey of ants

The ant survey was carried out at the Long Term Ecological Research site in the Gwangneung forest (GN LTER site). The GN LTER site is located in the forest and is mainly composed of > 100 years old trees such as *Carpinus laxiflora* and *Quercus serrata*, and thus has well-developed shrub and herbaceous layers, and the soil surface is covered with a litter layer. Details on the GN LTER site are introduced by Kwon et al (2014). The area is 1 ha and is divided into 100 plots that are 100 m^2, in which plastic pipes are placed in the corners. In 2002, one pitfall trap was installed in the center of each plot (100 in total), and from 2003 to 2012, three pitfall traps were installed at 2 m intervals diagonally in the center of the plots (300 in total). Plastic cups (diameter 9.5 cm, depth 6.5 cm) were used for the pitfall traps. The pitfall traps were installed on August 2nd and returned on August 20th in 2002. In 2003, they were installed on July 23rd and returned on August 1st. In 2004, they were installed on July 23rd and returned on August 11th. After 2005, they were installed in late May and then returned 10–15 days later. Ant surveys were conducted for 7 years during the study period (Table 1). According to the analysis of Kwon et al (2014), there was almost no

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Table 1. Occurrence of ant species in the Gwangneung LTER site from 2007 to 2012.*

Species	Year						
	2002	2003	2004	2005	2007	2008	2012
Aphaenogater japonica	75.7	99.0	84.8	97.0	88.9	87.9	89.6
Camponotus atrox	5.7	6.0	21.2	22.0	6.1	10.1	18.8
Camponotus japonicus	1.4	3.0		44.0	23.2	22.2	64.6
Camponotus kiusuensis	4.3	2.0	6.1	14.0	10.1	11.1	12.5
Camponotus nipponensis		1.0	1.0	3.0	2.0	1.0	6.3
Camponotus sp. 1				1.0			1.0
Crematogaster matsumurai	1.4	1.0	1.0	17.0	4.0	3.0	7.3
Crematogaster teranishi		2.0			3.0		9.4
Cryptone sauteri	1.4	9.0		3.0	3.0	1.0	10.4
Dolichoderus sibiricus				1.0	1.0	1.0	1.0
Formica japonica	48.6	58.0	89.9	91.0	77.8	80.8	75.0
Hypoponera sauteri		1.0			1.0		1.0
Lasius spathepus			4.0				1.0
Lasius spp. (jap.+al.)	5.7	24.0	15.2	58.0	63.6	55.6	57.3
Myrmecina nipponica	1.4	26.0	2.0	16.0	3.0	6.1	17.7
Nylanderia flavipes	2.9	36.0	4.0	26.0	25.3	28.3	59.4
Pachycondyla chinensis	2.9	12.0	9.1	1.0	2.0	2.0	8.3
Pachycondyla javana	31.4	45.0	50.5	33.0	31.3	24.2	31.3
Pheidole fervida	32.9	85.0	17.2	62.0	30.3	52.5	71.9
Ponera japonica		37.0	2.0	14.0			
Ponera scabra					8.1	4.0	11.5
Pristomyrmex pungens		7.0		2.0	4.0	2.0	1.0
Stenamma owstoni					4.0	2.0	7.3
Strumigenys lewisi	4.3	38.0		2.0	1.0	6.1	3.1
Temnothorax nassonovi		12.0		64.0	59.6	40.4	43.8
Temnotothorax sp. 3							1.0
Temnotothorax sp. 4							1.0
Vollenhovia emeryi	1.4	57.0	2.0	27.0	9.1	5.1	10.4
No. of species	15	21	15	21	23	21	27

*Occurrence means proportion (%) of occurred plots.

difference in the ant community depending on the survey period (May–June vs. July–August), and it was found that most ant species inhabiting the survey area could be collected by using 300 pitfall traps (Kwon et al 2014). One third of the pitfall trap was filled with polyethylene glycol (automobile antifreeze, SK energy, Seoul, South Korea) for preservation fluid. The collected ants were identified using the identification key of Kwon et al (2012).

Data analysis

In this study, it was analyzed based on plot-occurrence. Because most ants live within boundary of a few meters in the forest (Doncaster 1981; Ichinose 1986, 1987), foraging areas of ants may not be overlapped between plots because the distance of nearest plots is 10 m. In this study, co-occurrence refers to two species being collected in the same plot. The number of individuals per species collected in each plot was converted to binary data of presence (1) and absence (0) to analyze co-occurrence. Null hypothesis of co-occurrence (i.e., random co-occurrence) was tested using the software EcoSym version 7.71 (Gotelli and Entsminger 2001).

The C-Score estimates checkerboard score of distribution (Stone and Roberts 1990). This index calculates the average number of checkerboard units (CU) using the following formula:

$$CU = (r_i - S)(r_j - S), \quad (1)$$

where S is the number of shared plots (plots containing both species), and r_i and r_j are the numbers of plots in which i and j species occur. An option of fixed rows and fixed columns was used for the estimation. This program calculates the co-occurrence through 5000 simulations under the presumption that species are distributed randomly, and the statistical significance is calculated by comparing this with the observed value. This analysis was recognized as a robust method (good type 1 error property; Gotelli 2000) and it is widely used for co-occurrence analysis. Co-occurrence analysis was carried out for all species and for dominant species that occurred in > 30% of the total plots. In order to identify species interaction (competition), correlation analysis was carried out using the number of individuals of ant species collected in each trap. If interspecific competition affects occurrence, then significant negative correlation will occur between species. Correlation analysis was conducted for species collected in > 20% of traps from the total traps. Statistica version 8.0 (Statsoft, Inc., Tulsa, OK, USA) was used for correlation analysis.

Results

A total of 28 species of ants had been collected at the GN LTER site (Table 1). Results from the analysis of co-occurrence are shown in Table 2. In the case of all species, contrary to the expectations, there was no difference between observed co-occurrence and random co-occurrence in most years except 2004 and 2008 when observed scores were significantly higher than simulated scores (Table 2, Figures 1–6). In the case of dominant species, observed score was not different than random co-occurrence in most years except in 2005 and 2008. The observed score was higher than the simulated score in 2008, whereas it was lower in 2005. In the interspecific correlation analysis, significant correlation was found only 16 times among the 55 interspecific correlations. Among the cases of the significant correlation, most were positive correlations and only three were negative correlations (Table 3).

Discussion

Co-occurrence of ant species in the present study was not different to random co-occurrence in most years except 2 years (2004 and 2008) when ant species co-occurred less compared with the random co-occurrence. Therefore, occurrence of ants was not influenced by competition in most years except these two years (2004 and 2008). High value of the C-Score (checkerboardedness) indicates low co-occurrence between species (Stone and Roberts 1990). In 2004, the number of ant species decreased due to forest

Table 2. C-score values to estimate co-occurrence of ant species in the Gwangneung LTER site from 2007 to 2012.*

Groups	Year	C-score values		*p*	
		Observed scores	Mean of simulated scores	Obs. < Exp.	Obs. > Exp.
All ants	2002	29.36	28.47	0.902	0.996
	2003	122.13	121.77	0.672	0.340
	2004	64.33	60.33	0.991	0.009
	2005	134.63	133.07	0.946	0.054
	2007	77.11	76.05	0.536	0.465
	2008	78.18	75.94	0.971	0.030
	2012	87.29	87.10	0.578	0.422
Dominant ants	2002	218.11	217.02	0.680	0.342
	2003	303.82	307.64	0.723	0.284
	2004	127.00	133.16	0.151	1.000
	2005	316.00	320.86	0.007	0.994
	2007	353.87	350.42	0.787	0.216
	2008	281.53	264.44	1.000	0.000
	2012	354.54	355.12	0.440	0.564

*C-scores of all ant species and dominant species were estimated using the software Ecosym version 7.71 (Gotelli and Entsminger 2001). All *p*-values are presented for one-tailed tests, with probabilities of the observed values being larger or smaller than the expected randomized matrices.
Exp = expected; Obv = observed.