Zoological Studies
a SpringerOpen Journal

RESEARCH ARTICLE Open Access

Diversity decrease of ant (Formicidae, Hymenoptera) after a forest disturbance: different responses among functional guilds

Tae-Sung Kwon[1], Cheol Min Lee[2*] and Joo Han Sung[2]

Abstract

Background: Disturbance is one of the main causes for determining diversity of natural communities. A 3-year (2003 to 2005) monitoring of ant communities at a Long-Term Ecological Research (LTER) site in South Korea revealed a drop of ant diversity due to a forest disturbance which was evidenced by decrease of leaf area index (LAI) associated with the dropping of tree branches. In order to determine the process of the decrease in diversity, we compared the annual change of functional ant guilds, which are composed of forest ground foragers (FGF), forest vegetation foragers (FVF), soil and litter dwellers (SLD), and open-land foragers (OF).

Results: Four functional guilds of ants responded differently to the forest disturbance; FGF and SLD decreased, but OF and FVF increased. Species richness decreased, due to the decrease in SLD, and species evenness decreased mainly due to a sudden increase in an OF species, *Formica japonica*. Based on these findings, a mechanism is proposed for the decrease in ant diversity after the forest disturbance.

Conclusions: Ant communities responded significantly to even a slight forest disturbance of branch dropping with decrease in diversity and change in functional guild structures.

Keywords: Ant; Richness; Diversity; Abundance; Disturbance; Community; Functional guild

Background

Disturbance is a factor strongly influencing many ecosystems, and variations in disturbance regime can affect the ecosystem and community structure and functioning (Sousa 1984; Hobbs and Huenneke 1992). In tropical rainforests and coral reefs, disturbance decreases the dominance of few abundant species in stable ecosystems, and it gives a chance for the coexistence of various subordinate species, resulting in the highest diversity occurring in the intermediate disturbance (Connell 1978). Most communities exist in a state of nonequilibrium, which results in a stable level of diversity by prevention of competitive displacement (Huston 1979). Nonequilibrium states are created by various types of disturbance (Connell 1978; Hobbs and Huenneke 1992). Forest gaps formed by disturbance give a chance for pioneer (disturbance tolerant) species, which might be replaced by forest-specialist (disturbance intolerant) species in climax forest (Bouget and Duelli 2004). Global climate change has increased the intensity and frequency of various disturbances, such as insect outbreaks, strong winds, huge typhoons, heavy rainfalls, landslides, and mega forest fires (IPCC 2007; Choi and Choi 2011). Increase in extreme disturbance events has the potential to drastically affect the natural structure of ecological communities.

Ants are abundant and diverse across a range of terrestrial habitats, are easily collected, and have a wide season of activity (Agosti et al. 2000). Ants play important roles as predators, herbivores, scavengers, and seed dispersers in forest ecosystems (Hölldobler and Wilson 1990; de Bruyn 1999). Moreover, ants play ecological roles in maintaining soil condition and quality, increasing forest productivity and keeping agroecosystems ventilated (Hölldobler and Wilson 1990; de Bruyn 1999; Agosti et al. 2000). Ants respond quickly to forest disturbances of various types, e.g., livestock grazing (Nash et al. 2004), tree cutting (Zettler et al. 2004), fire (Andersen 1991), mining and farming (Majer 1983), and forest management (Maeto and

* Correspondence: leecheolmin77@gmail.com
[2]Division of Forest Ecology, Korea Forest Research Institute, 57 Hoegi-ro, Dongdaemun-gu, Seoul 130-712, Republic of Korea
Full list of author information is available at the end of the article

Sato 2004; Arnan et al. 2009). Hence, ants have been recognized as good bioindicators for the impacts of various disturbances such as mining, fire, pesticides, and logging (Andrew et al. 2000; Maeto and Sato 2004; Kwon et al. 2005).

Monitoring of ant communities was annually conducted for 3 years beginning in 2003 at the Long-Term Ecological Research (LTER) site in Gwangneung forest, mid-western South Korea. Ant diversity decreased significantly in 2004, compared to that in 2003 and 2005, which was caused by a forest disturbance. In ant species inhabiting forest, there are disturbance-tolerant species and disturbance-intolerant species. After a disturbance, the former will increase, whereas the latter will decrease. Such change will change the diversity and structure of ant communities. The present study was aimed to find the process of the decrease in ant diversity by analyzing ant functional guilds. Four functional guilds (two disturbance-tolerant and two disturbance-intolerant guilds) were devised for Korean ants, according to the main foraging habitats of ants (Kwon et al. 2012; Lee and Kwon 2013). These guilds can be useful for analyzing the characteristics of ant communities in northern Asia such as north China and Japan as evidenced by the present study.

Methods

Study site

This study was carried out at the LTER site (37.44 N and 127.08 E) in the Gwangneung forest, mid-western South Korea. This forest was selected as the grave forest of the seventh King, Saejo in the Joseon Dynasty in 1468, and it has been rigidly protected by the Korean government since then (Korea National Arboretum 2008). This forest (2,240 ha) has been used as an experimental forest for forestry research by the Korea Forest Research Institute since 1929. Therefore, the Gwangneung forest comprises old natural forest (1,200 ha, hardwood and pine) and plantation of diverse tree species (1,040 ha, 52 tree species) (Korea Forest Research Institute 2003a, 2012a). The wood biomass (310 m^3) of this forest was more than three times that of the national average in South Korea. The deciduous forest is in climax state and is composed of 130 tree species, with dominant species of *Quercus serrata* and *Carpinus laxiflora* (Lee et al. 1990). In South Korea, old natural deciduous forests (>100 years) rarely remain in areas such as the Gwangneung forest and Mt. Jeonbongsan due to the nationwide forest destruction of logging for firewood, the Korean war, and development. The average annual temperature and rainfall in the Gwangneung forest are 11.3°C and 1,625 mm, respectively (Lim et al. 2010). Although this forest is located on the outskirts of Seoul, its biodiversity is one of the highest in South Korea, and endangered species live there, such as *Dryocopus javensis richardsi* and *Callipogon relictus*. In 2010, the old natural deciduous forest (755 ha) was determined as a core area of biosphere conservation of the United Nations Educational, Scientific and Cultural Organization (UNESCO) (http://www.unesco.org/mabdb/br/brdir/directory/biores.asp?code=ROK+04&mode=all, accessed in 18 June 2010). Details on the Korean climate, vegetation, and topography are shown in Kwon et al. (2010, 2011c).

The study site is located in the old deciduous forest and is composed of 180 plant species including 15 tree species in an area of 1 ha (Korea Forest Research Institute 2003b, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012b). The dominant tree species were *Q. serrata*, *Euonymus oxyphyllus*, and *C. laxiflora*. The understory vegetation of shrub and herb layer was well developed and in 2003 was mainly composed of *Ainsliaea acerifolia* (16% of coverage), *E. oxyphyllus* (10%), *A. pseudosieboldianum* (9%), *Callicarpa japonica* (8%), *Disporum smilacinum* (8%), and *Oplismenus undulatifolius* (6%). Annual production of plant biomass is 266 tons/ha, and soils are brown forest soils composed of granitic gneiss, with effective soil depth of 20 to 30 cm. The soil pH was 4.9 in A layer and 5.09 in B layer. The ground was all covered by litter composed of dropped leaves and branches.

Survey and ant identification

Ants were surveyed in 2003 to 2005. The survey was carried out using pitfall traps one time per year in July to August in 2003 and 2004, and May to June in 2005 (Table 1). The traps had been set in the field for 11 or 14 days. The temperature for the sampling periods ranged from 13.4°C to 35.6°C with average of 23.8°C (24.1°C in 2003, 26.8°C in 2004, and 20.5°C in 2005) (Korea Meteorological Administration 2013). Precipitation during the sampling period was 200 mm in 2003,

Table 1 Weather conditions during ant surveys from 2003 to 2005

Factor	Year		
	2003	2004	2005
Period	22 July to 1 August	29 July to 11 August	3 June to 16 June
Duration (days)	11	14	14
Temperature	24.1 ± 1.9 a (18.9 to 32.3)	26.8 ± 0.9 b (20.4 to 35.6)	20.5 ± 1.6 c (13.4 to 31.9)
Degree days	154.6	235.4	146.8
Rainy days	8	3	6
Rainfall (mm)	199.4	8	32.4

The weather data was obtained from the nearest weather station (Dongducheon, 17 km from the study site, http://www.kma.go.kr/). Degree days were calculated with 10°C threshold because ants rarely begin foraging <10°C (Hölldobler and Wilson 1990). Daily averages (with SE) of temperature were significantly different between years (ANOVA, $F_{2,36} = 63.8$, $P << 0.0001$), and the different letters following the values indicate significant difference ($P < 0.05$) between years according to the Fisher LSD multiple comparison test.

8 mm in 2004, and 32 mm in 2005. The LTER site (1 ha) was divided into 100 plots (10 m × 10 m), using plastic pipes. Three pitfall traps were set along a transect of 2-m intervals, in the center of each plot. A total of 300 traps were set up each year, but 300, 267, and 283 traps were returned for analysis in 2003, 2004, and 2005, respectively. The unreturned traps were usually disturbed by boars. The pitfall traps were plastic cups (diameter 95 mm, depth 68 mm) and were one third filled with polyethylene glycol, a nonattracting and nonevaporating preservative (Bestelmeyer et al. 2000).

The ant specimens were identified using taxonomic keys (Imai 2006; JAID 2010; Terayama and Kuboda 2009). The ants were identified to the level of species. All specimens were deposited in the forest ecology laboratory of the Korea Forest Research Institute (KFRI). According to their main foraging habitat, Kwon et al. (2012) devised five Korean ant functional guilds as follows: forest ground forager (FGF), forest vegetation and ground forager (FVGF), forest vegetation forager (FVF), soil and litter forager, and grassland forager. This guild system has been devised from previous field studies in seven metropolitan cities which included forest sites and open-land sites (T-SK, unpublished data), ant survey for 14 years in soils of eight forest sampling sites in four locations (T-SK, unpublished data), ant survey from ground to crown in pine forests (Kwon et al. 2005), and nationwide ant survey (Kwon et al. 2012). We unified FGF and FGVF as FGF, because these functional guilds cannot be clearly bifurcated, due to the lack of direct empirical evidence, and we changed the term of soil and litter forager to soil and litter dweller (SLD). Soil and litter forager is confusing with forest ground forager, because the forest ground is covered with litter and soil. SLD ants live and forage within litter and soil, and they usually prey on small soil invertebrates (Kwon et al. 2012). The term of grassland forager was changed to open-land forager (OF), because these ants do not restrictively forage in grassland, but prefer foraging over open land, such as grasslands, forest gaps, and forest edges, compared to dark forest interior. In Korea, the OF ants are *Formica japonica*, *Camponotus japonicus*, and *Tetramorium tsushimae* (Kwon et al. 2011b; Kwon et al. 2012; Lee and Kwon 2013). In Kwon's classification, *Lasius japonicus* was FVF, but this species is OF rather than FVF, because the species foraged more frequently in forest gaps than in forests, in five places (T-SK, unpublished data). FGF ants mainly forage over ground of forests, as well as vegetation, whereas FVF ants prefer foraging over vegetations (understory and crown) of forest rather than over forest ground. From this regard, *Pristomyrmex pungens* is FGF, rather than FVF, because this species is abundantly collected by both pitfall traps and sweeping (T-SK, unpublished data). The functional guilds for each species are represented in Table 2.

Leaf area index

Leaf area index (LAI), which is highly associated with canopy openness, was measured using a digital camera (Nikon Coolpix 4500, Tokyo, Japan) with a fisheye lens (FC-E8, Nikon), which was set horizontally about 1 m above the ground. Photos of the canopy from the ground at 23 plots were analyzed using Hemiview software (Delta-T Devices Ltd. 1999). The photo sites were fixed. The LAI measurements were conducted every year in July. LAI was estimated by the following equation: $LAI = \log_e(G)/-K(\theta)$, where G is the gap fraction, and $K(\theta)$ is the extinction coefficient at θ (azimuth).

Cause of the forest disturbance

The temporary decrease in ant diversity in 2004 (see the 'Results' section) was due to a forest disturbance (as indicated by a LAI decrease). To find the cause for this forest disturbance, we first examined the route and damage area of typhoon Maemi, which struck the Korean peninsula on September 11, 2003 (Seo 2004). Second, to identify the impacts of heavy rain and strong wind, heavy rainfall (>100 mm) and strong wind speed (meters per second) were analyzed for 5 years beginning 2001 (Korea Meteorological Administration 2001, 2002, 2003, 2004, 2005). Data from Dongducheon weather station (about 17 km from the study site) were used for the analysis. Massive dropping of tree branches (*Quercus* spp.) which was caused by nut weevil (*Mechoris ursulus*) was intermittently observed in the Gwangneung forest (T-SK, personal observation). To evaluate *M. ursulus* occurrence, the nationwide damage level of *M. ursulus* was compared between 5 years, beginning in 2001. We used the data from the annual monitoring report for forest insect pests and diseases from 2001 to 2003 (Korea Forest Research Institute 2001, 2002, 2003c) and unpublished data from 2004 to 2005, which was provided by Dr. SH Go and Dr. WI Choi of the Insect Pest Division at KFRI. These pest data were obtained from the nationwide monitoring of forest insect pests which, since 1968, has been conducted monthly in May to September at 80 sites by the KFRI. However, Gwangneung forest is not a monitoring site for forest insect and disease pests.

Data analysis

Raw data and log-transformed data of abundance (number of individuals per trap), species richness (number of species per trap), and LAI were significantly different with normal distribution (Shapiro-Wilk test, $P < 0.05$). Hence, nonparametric Kruskal-Wallis ANOVA was used to test the difference between 3 years. The difference between 2 years was tested by Mann-Whitney U test with

Table 2 Ants collected in pitfall traps from 2003 to 2005 at the study site

	Year			Friedman ANOVA		Change	Guild
	2003	2004	2005	$F_{2,\ 847}$	*P*		
Species							
Camponotus japonicus	0.01 ± 0.01 a	0 ± 0 a	0.31 ± 0.04 b	57.09	0.000	Increased	OF
Formica japonica	0.83 ± 0.13 a	6.40 ± 0.74 b	9.98 ± 1.13 c	124.13	0.000	Increased	OF
Lasius japonicus	0.28 ± 0.12 a	0.10 ± 0.03 a	5.41 ± 2.22 b	39.29	0.000	Increased	OF
Aphaenogaster japonica	2.73 ± 0.16 a	1.46 ± 0.11 b	2.12 ± 0.14 c	22.69	0.000	Decreased	FGF
Camponotus atrox	0.05 ± 0.02 a	0.13 ± 0.03 b	0.12 ± 0.02 b	5.32	0.005	Increased	FGF
Lasius spathepus	0 ± 0 a	0.01 ± 0.01 b	0 ± 0 a	4.42	0.012		FGF
Nylanderia flavipes	0.43 ± 0.07 a	0.02 ± 0.01 b	0.18 ± 0.04 c	23.18	0.000	Decreased	FGF
Pachycondyla chinensis	0.08 ± 0.02 a	0.05 ± 0.02 a	0.004 ± 0.004 b	6.21	0.002	Decreased	FGF
Pachycondyla javana	0.36 ± 0.05 a	0.64 ± 0.08 b	0.34 ± 0.05 a	7.98	0.0004		FGF
Pheidole fervida	2.33 ± 0.27 a	0.11 ± 0.03 b	0.89 ± 0.13 c	109.03	0.000	Decreased	FGF
Pristomyrmex pungens	0.07 ± 0.03 a	0 ± 0 b	0.01 ± 0.01 b	5.32	0.005	Decreased	FGF
Temnothorax nassonovi	0.06 ± 0.02 a	0 ± 0 a	0.48 ± 0.05 b	80.36	0.000	Increased	FGF
Camponotus kiusuensis	0.01 ± 0.005 a	0.02 ± 0.01 b	0.11 ± 0.03 b	9.23	0.0001	Increased	FVF
Camponotus nipponensis	0.003 ± 0.003	0.004 ± 0.004	0.01 ± 0.01	0.81	0.446		FVF
Camponotus tokioensis	0 ± 0	0 ± 0	0.004 ± 0.004	1.00	0.368		FVF
Crematogaster teranishi	0.01 ± 0.005	0 ± 0	0 ± 0	1.84	0.160		FVF
Crematogaster matsumurai	0.003 ± 0.003 a	0.004 ± 0.004 a	0.09 ± 0.03 b	13.36	0.000	Increased	FVF
Dolichoderus sibiricus	0 ± 0	0 ± 0	0.004 ± 0.004	1.00	0.368		FVF
Cryptone sauteri	0.03 ± 0.01 a	0 ± 0 b	0.01 ± 0.01 b	4.88	0.008	Decreased	SLD
Hypoponera sauteri	0.003 ± 0.003	0 ± 0	0 ± 0	0.92	0.400		SLD
Myrmecina nipponica	0.11 ± 0.02 a	0.01 ± 0.01 b	0.07 ± 0.02 a	10.12	0.000	Decreased	SLD
Ponera japonica	0.19 ± 0.03 a	0.01 ± 0.01 b	0.06 ± 0.02 c	25.66	0.000	Decreased	SLD
Strumigenys lewisi	0.18 ± 0.03 a	0 ± 0 b	0.01 ± 0.005 b	40.83	0.000	Decreased	SLD
Vollenhovia emeryi	0.56 ± 0.07 a	0.01 ± 0.01 b	0.13 ± 0.02 c	57.58	0.000	Decreased	SLD
Species richness	21	15	21				
Abundance	8.34 ± 2.20 a	8.99 ± 2.33 a	20.34 ± 2.27 b	8.87	0.000		
Species evenness (*J'*)	0.65	0.32	0.50				

The ants were collected from the Long-Term Ecological Research (LTER) site in Gwangneung forest, mid-western Korea. Abundance (number of individuals per trap) is provided by mean with SE. Different letters following values denote significant difference between groups in the Mann-Whitney *U* test. Change in abundance was determined by the difference between 2003 and 2004 or 2003 and 2005. Guilds were defined as follows: FGF, forest ground forager; SLD, soil and litter dweller; OF, open-land forager; FVF, forest vegetation forager. Definition of the guilds is shown in the text.

Bonferroni's inequality correction, because multiple comparison test was not available in this ANOVA. Rarefaction curves of species richness were evaluated on the basis of samples (EstimateS, Colwell 2005) and individuals (EcoSim, Gotelli and Entsminger 2001). Species evenness was calculated using the species evenness index (J') (Pielou 1969). Morisita's similarity index C_λ (Morisita 1959) was utilized to compare the similarity of ant community between years. This index was calculated by following equation:

$$C_\lambda = \frac{2\sum_i n_{i\mathrm{A}}\ \ n_{i\mathrm{B}}}{(\lambda_\mathrm{A}+\lambda_\mathrm{B})\sum_i n_{i\mathrm{A}}\ \ \sum_i n_{i\mathrm{B}}},$$

where $n_{i\mathrm{A}}$ and $n_{i\mathrm{B}}$ represent the abundance of species i in samples A and B, respectively.

$$\lambda_\mathrm{A} = \frac{\sum n_{i\mathrm{A}}\left(n_{i\mathrm{A}^{-1}}\right)}{\sum_i n_{i\mathrm{A}}\left(\sum n_{i\mathrm{A}^{-1}}\right)}$$

The χ^2 test was used to compare the difference in functional structure (number of species and number of individuals) between 2 years on a 4 × 2 contingency table. Statistical analyses were performed using STATISTICA version 8.0 (StatSoft Inc. 2004).

Results

LAI, which is highly associated with canopy thickness, was compared annually. The LAI was 4.9 ± 0.30 (SE) in 2003, 3.1 ± 0.19 in 2004, and 3.2 ± 0.20 in 2005. The LAI was significantly different between years (Figure 1; Kruskal-Wallis test, $\chi^2 = 15.42$, $df = 2$, $P < 0.0004$). In the Mann-Whitney *U* test, the LAI in 2003 was significantly different from those in 2004 and 2005 (2003 vs. 2004: $U = 65$, $Z = 4.3828$, $P < 0.000012$; 2003 vs. 2005: $U = 77$, $Z = 4.1192$, $P < 0.000038$), but the LAI in 2004 was not significantly different from that in 2005 (2004 vs. 2005: $U = 259$, $Z = -0.1208$, $P = 0.904$). In 2003, only one tree was dead at the study site (T-SK, unpublished data), and therefore, thinned crown layer, rather than gap formations, might be related to the decrease of LAI. Strong wind, heavy rain, and a national outbreak of *M. ursulus* that can lead to heavy dropping of branches occurred in 2003 (Figure 2).

In the ant survey for 3 years since, 11,301 ants belonging to 24 species were collected. The abundance (number of individuals per trap) of each ant species is annually compared in Table 2. The number of ant species collected in 2003 and 2005 was 21, whereas that in 2004 was 15. However, the abundance increased more than two times in 2005, compared with 2003 and 2004. The annual change of abundance greatly varied among ant species. Many silvicolous species significantly showed a common pattern of decreasing temporally in 2004: *Aphaenogaster japonica* (FGF), *Nylanderia flavipes* (FGF), *Pheidole fervida* (FGF), *Myrmecina nipponica* (SLD), *Ponera japonica* (SLD), and *Vollenhovia emeryi* (SLD). Three other silvicolous species decreased significantly after 2003: *P. pungens* (FGF), *Cryptone sauteri* (SLD), and *Strumigenys lewisi* (SLD). On the other hand, three open-land-preferring species gradually increased (*F. japonica*), or lagged-increased in 2005 (*C. japonicus* and *L. japonicus*). In addition, some silvicolous species increased after 2003: *Camponotus atrox* (FGF), *Temnothorax nassonovi* (FGF), *Camponotus kiusuensis* (FVF), and *Crematogaster matsumurai* (FVF). Besides, *Pachycondyla chinensis* (FGF) decreased in 2005, and two FGF species (*Lasius spathepus* and *Pachycondyla javana*) increased temporally in 2004. Thus, population change after forest disturbance was different among functional guilds: all OF and FVF species showing significant annual change increased after 2003, whereas all SLD species decreased. In FGF species, however, the response was bifurcated: five species decreased, and four species increased. As a result of the reduction in ant numbers, the species richness of ants temporally decreased in 2004, and afterward recovered in 2005, to some extent (Table 2). The abundance increased more than twofold in 2005, compared to 2003 and 2004 ($P < 0.05$). As results of different abundance change of ant species to a forest disturbance, post-disturbance ant communities in 2004 and 2005 were more similar, compared with the pre-disturbance ant community in 2003, despite more similar species composition between 2003 and 2005 (Table 3).

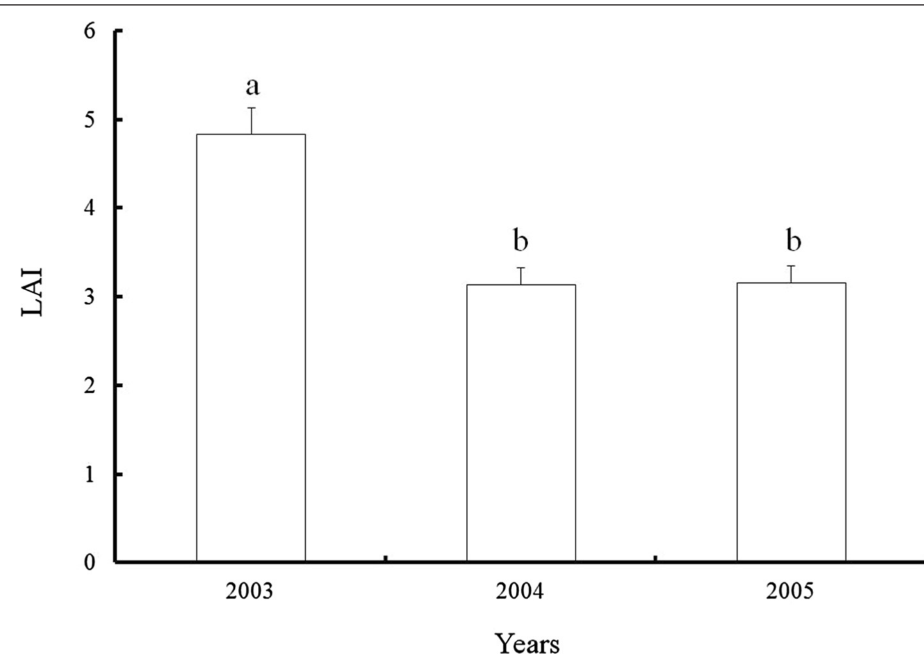

Figure 1 Leaf area index (LAI, $n = 23$) from 2003 to 2005 at the LTER site in Gwangneung forest. Error bars indicate one standard error. Different letters above error bars denote a significant difference (Mann-Whitney *U* test with Bonferroni's inequality correction for multiple comparisons, $P < 0.02$) between years.

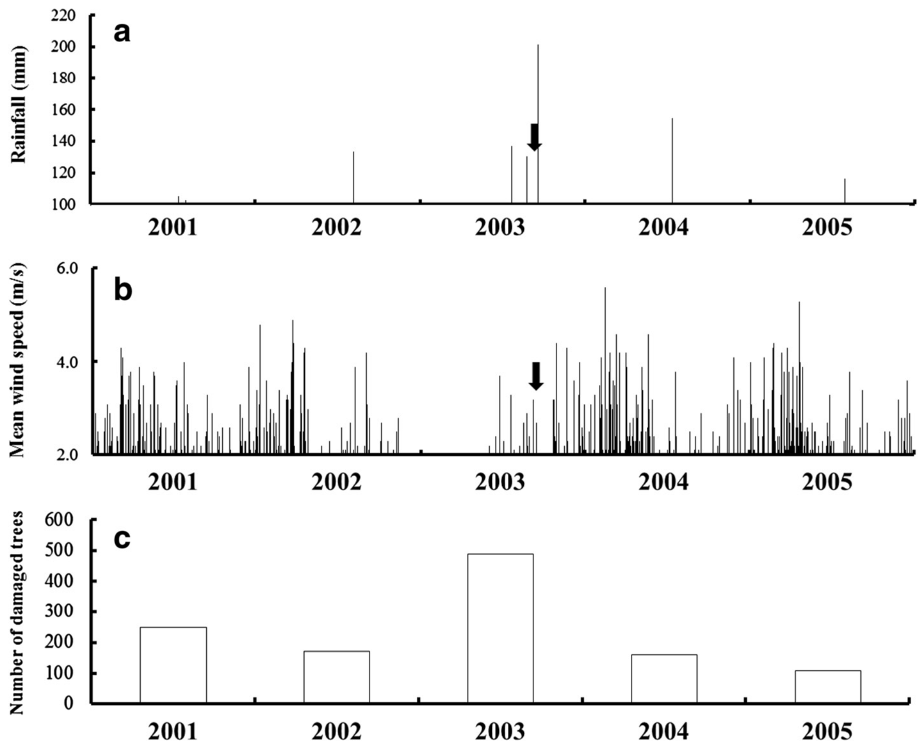

Figure 2 Factors that can lead to heavy dropping of branches. **(a)** Heavy rains (>100 mm in a day), **(b)** strong winds (>2.0 m/s), and **(c)** insect pest (*Mechoris ursulus*) damage from 2001 to 2005. Arrows indicate the period of the big typhoon 'Maemi' in September 2003.

Rarefaction curves of species richness clearly showed reduced richness in 2004 (Figure 3a, b). Sample-based richness was not different between 2003 and 2005, but individual-based richness was higher in 2003 than in 2005. However, species richness per trap was significantly different between years ($P < 0.01$), being highest in 2005 and lowest in 2004. Thus, species richness recovered in 2005, with more than double increase of ant numbers, as noted above (Table 2 and Figure 3), which might increase competition among ants in 2005. Species evenness (J') was 0.65 in 2003, but decreased to 0.32 in 2004, and then recovered to 0.50 in 2005. Despite the great increase in *F. japonica* (Table 2), species evenness recovered in 2005, which was due to the recovery of dominant FGF species such as *A. japonica* and *P. fervida* and the increase in another OF species, *L. japonicus*.

Table 3 Similarity among ant communities in 2003, 2004, and 2005

Year	2003	2004	2005
2003	-	14	19
2004	0.35	-	14
2005	0.40	0.85	-

Similarity was evaluated using Morisita's similarity index. Values in the lower left-hand part indicate similarity between years; and those in the upper right-hand part indicate the number of common species between years.

When the ant species were grouped into the four functional guilds, each guild showed different annual change of richness and abundance (Figure 4a,b). The species richness of all guilds decreased in 2004 and recovered in 2005. The richness of SLD decreased most (i.e., half that of the previous year). When the composition of the four functional guilds was compared using species richness, it was not significantly different between years (2003 vs. 2004 and 2004 vs. 2005: $\chi^2 = 0.42$, $df = 3$, $P = 0.94$; 2003 vs. 2005: $\chi^2 = 0.00$, $P = 1.00$). However, the functional composition using abundance was significantly different between years (2003 vs. 2004: $\chi^2 = 1815.34$, $df = 3$, $P = 0.00$; 2003 vs. 2005: $\chi^2 = 3056.24$, $P = 0.00$; 2004 vs. 2005: $\chi^2 = 69.74$, $P = 0.00$). The OF increased gradually along the years, whereas FVF decreased in 2004 and greatly increased in 2005. SLD decreased greatly in 2004 and recovered in 2005, but less than in 2003. FGF was most stable, with a slight decrease in 2004.

Discussion

A problem in our study is the single sampling in each year, which leads to the question of whether this snapshot sampling can be sufficient to represent ant assemblage in the study site. Our data in Additional file 1 confirms that one sampling with numerous traps (300 traps) collected most of the extant species. In the 2012

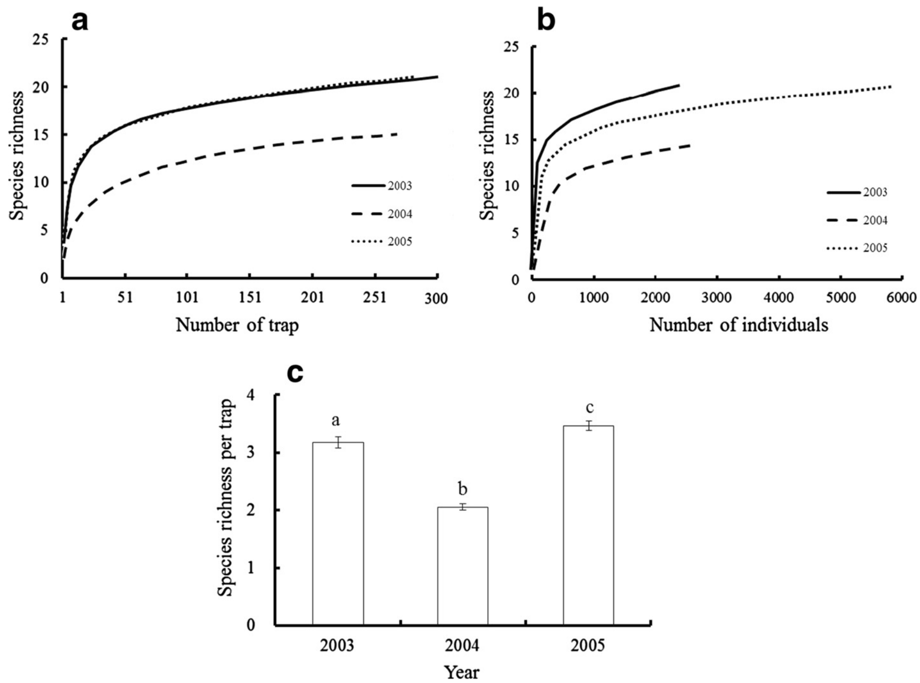

Figure 3 Pooled species richness (a, b) and average species richness per trap (c; mean with SE). The data were taken from the LTER site (1 ha) in Gwangneung forest, South Korea. Rarefaction curves of species richness along with samples **(a)** and number of individuals **(b)**. The former and latter curves were made using EstimateS (Colwell et al. 2004) and EcoSim (Gotelli and Entsminger 2001), respectively. In average species richness, different letters denote significant difference between groups (Mann-Whitney *U* test, $P < 0.05$).

study site, we collected ants in vegetation, litter, and soil with different collection methods, in which no further species were found. Therefore, the survey in 2003 and 2005 collected 88% of the total species in the study site. Furthermore, we found only an additional species in two other ant surveys in a pine forest and eight forests within the study area, Gwangneung forest (2,240 ha). These surveys had been conducted many times a year (monthly or biweekly). Therefore, our sampling design is likely sufficient to compare yearly variation of ant assemblages. Another problem is yearly different sampling seasons; the ants were collected in summer (July to August), in 2003 and 2004, but they were collected in late spring to early summer (May to June) in 2005. However, species composition and diversity in 2004 was most different among the 3 years (Tables 2 and 3). The species

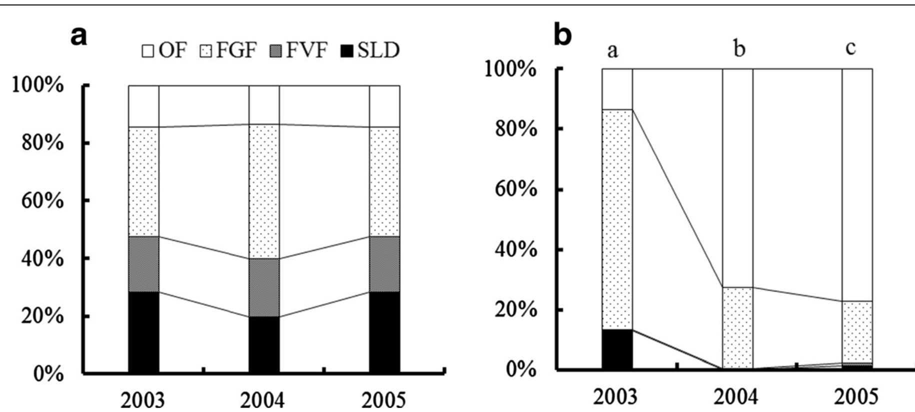

Figure 4 Composition of species richness (a) and abundance (b) in four functional guilds. Richness composition is not significantly different between years (χ^2 test, $df = 3$, $P > 0.05$), but abundance composition is significantly different between years ($P < 0.05$). Different letters above the bars indicate significant difference between years. Guilds were defined as follows: FGF, forest ground forager; SLD, soil and litter dweller; OF, open-land forager; FVF, forest vegetation forager. Definition for the guilds is shown in the text.

richness in 2004 decreased significantly, compared with those in 2003 and 2005, despite its most favorable weather conditions for the foraging of ants (i.e., lowest rainfall and highest temperature in 2004, Table 1). These findings indicate that the decrease in richness and diversity in 2004 were caused by other reasons rather than by weather conditions during the sampling seasons.

The decrease in LAI clearly showed that the forest was disturbed between August 2003 and June 2004. There were three candidates of disturbance then: typhoon Maemi, heavy rain, and outbreak of nut weevil. Typhoon Maemi is one of the most destructive typhoon that struck Korea on September 11, 2003. According to the Dongducheon station weather data, rainfall was only 19 mm for 2 days (12 and 13 September) during the typhoon period. However, the maximum instantaneous wind speeds on September 12 (10.6 m/s) and 13 (15.5 m/s) were much stronger than those on the other days (Korea Meteorological Administration 2001, 2002, 2003, 2004, 2005). When rainfall and wind weather data were compared for 5 years, the heaviest rainfall of 202 mm occurred on 18 September 2003 (Figure 2a,b). Heavy rain of >200 mm occurred only once in the 5 years. When *M. ursulus* damage was compared for 5 years, the largest damage occurred in 2003 (Figure 2c). Massive dropping of tree branches (*Quercus* spp.) which was caused by *M. ursulus*, was intermittently observed in the Gwangneung forest (T-SK, personal observation). Female *M. ursulus* adults oviposit on acorns and cut-off branches (Park et al. 1998). These factors might compositely damage the forest.

Ant diversity generally decreases after a forest disturbance, such as clear cutting, forest fire, or wind falls (Andersen 1991; Dunn 2004; Touyama et al. 1997; Zettler et al. 2004), which is consistent with our findings. Forest disturbances sometimes seem to affect ant community structure more than ant diversity (Kalif et al. 2001; Maeto and Sato 2004; York 2000; Zettler et al. 2004). In this study, ant species richness seemed to recover in 2005. But post-disturbance ant fauna in 2005 was not similar to the pre-disturbance on in 2003 yet (Table 3, Figure 4b). According to the intermediate disturbance hypothesis (Connell 1978), the increase or decrease of ant diversity after a disturbance can be explained by strength and/or scale of disturbance. Strong (wide) and weak (narrow) disturbance will decrease and increase diversity, respectively. However, even the weak disturbance (i.e., branch dropping without tree kills) decreased ant diversity in the present study. It is expected that branch dropping leads to increase of OF and FVF with coexistence of FGF and SLD, which results in increased diversity. In reality, however, ant diversity decreased due to the richness decrease of forest-specialist ants (SLD) and the great abundance increase of disturbance-tolerant ants (OF). The different functional responses of ants to various disturbances such as land use, mining, and fire have been well established in Australia (Majer 1983; Andersen et al. 2002, 2009).

We found that *A. japonica* was the most susceptible species to forest disturbance. According to an ant survey at the Unduryeong experimental forest, *A. japonica* was abundant in a larch plantation but was not found after logging (Kwon et al. 2011b). Maeto and Sato (2004) reported that *A. japonica* is abundant in old growth forest and classified it as woodland specialist. The response of *P. fervida* to a forest disturbance is similar to the change in *A. japonica*. Ants of the genus *Pheidole* have been suggested to be useful indicators of disturbances in tropical forests (Kalif et al. 2001). In the present study, *P. fervida* was classified as FGF. FGF is comparable with the woodland specialist in Terayama's classification scheme (Terayama 1997). However, Terayama (1997) suggested that *P. fervida* is classified as a habitat generalist because it inhabits woodlands, parklands, and open lands. Terayama (1997) reported that *C. sauteri*, *S. lewisi*, and *P. japonica*, which were classified as SLD in the present study, are woodland specialists.

Formica japonica is a useful indicator because of its rapid increase in numbers after a forest disturbance. The open-land indicators (OF) in South Korea are *F. japonica*, *C. japonicus*, and *Tetramorium casepitum* (Kwon et al. 2011b). When these species were surveyed at seven metropolitan cities in South Korea, their abundance was consistently higher in open lands than in forests (T-SK unpublished data). In the present study, *L. japonicus* is determined as OF from FVF. Choi and Lee (1999) suggested eight species as urbanization indicators including these three species. Zettler et al. (2004) reported that after logging, ants of the genus *Camponotus* decrease. In the present study, *C. japonicus* responded slowly to the forest disturbance, compared with *F. japonica*. Terayama (1997) classified *C. japonicus* as an open-land specialist. In South Korea, *C. japonicus* occurs in forests and open lands and is expected to replace *C. atrox* inhabiting high mountains as global warming proceeds (Kwon et al. 2011a). Among the four open-land indicator species, *F. japonica* is the most reliable disturbance indicator, because this species quickly and invariably increases after most kinds of forest disturbances such as wind falls, fire, thinning, and logging (Lee et al. 2012; Kwon et al. 2013a, b).

A mechanism to explain the decrease in ant diversity due to the forest disturbance is proposed based on the different changes of functional guilds (Figure 5). When a forest disturbance occurs, many tree branches drop to the ground, and the litter layer slightly increases. However, as the canopy opens and solar radiation increases on the ground, the temperature and wind increase. The increase in solar radiation, temperature, and wind, along

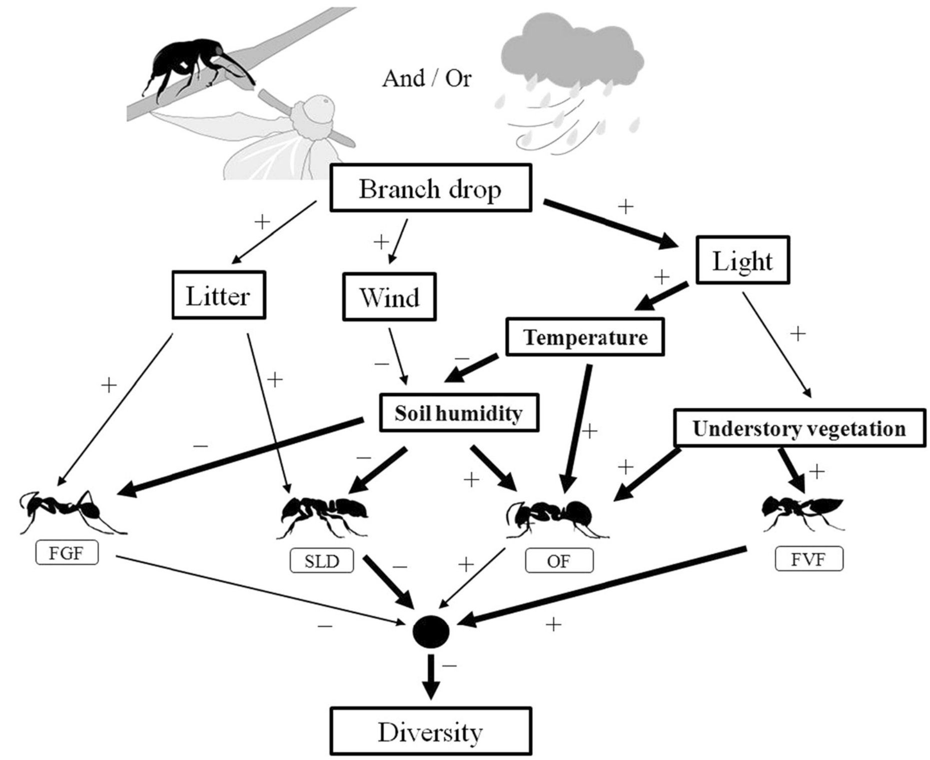

Figure 5 Proposed mechanism for the decrease in ant diversity at the LTER site in Gwangneung forest. Arrow size indicates intensity of the effect. Plus and minus signs indicate positive and negative effects, respectively. Korean ant functional guilds: FGF, forest ground forager; SLD, soil and litter dweller; OF, open-land forager; FVF, forest vegetation forager.

with the increase in canopy openness, may cause a decrease in soil humidity. SLD, which inhabit humid litter and soils, may be negatively affected by these environmental changes. These environmental changes may negatively affect FGF as well, which favors a humid ground environment. In contrast, this type of disturbance positively affects OF which favors dry soil conditions. The understory vegetation that develops with increasing solar radiation may positively affect FVF and OF. We found that OF preferring vegetation (i.e., *L. japonicus* and *C. japonicus*) and two FVF species increased after 1 year, indicating that the ants responded to the vegetation change with a time lag. Thus, when a forest is disturbed, FGF and SLD decrease, whereas OF and FVF increase. Hence, the decrease in ant diversity after a forest disturbance results from a combination of the opposite changes in the four functional guilds.

Conclusions

Although the cause for forest disturbance was not known, crown thinning (induced by disturbance) seemed to change ant community. This slight disturbance led to an increase in abundance of disturbance-tolerant species, but a decrease in that of disturbance-intolerant species; as a result, the disturbance decreased richness and changed functional structure of ant community. Ants in forests forage in soils, ground, and vegetation. Their main foraging layers and favorable environments for dwelling vary among species, so the vertical niche differentiation among ant species leads to the bifurcated responses (decrease or increase) of ant species to forest disturbance, which is deeply linked to environmental changes (i.e., increase of light intensity, wind, understory vegetation, decrease of soil humidity, etc.).

Additional file

Additional file 1: Ants collected in the study area (Gwangneung forest, 2,240 ha). In 2012, field experimental survey on ants inhabiting vegetation (by sweeping), litters (by the Winker method), and soils (soil extraction by the Tullgren method) was conducted in the study site (1 ha, Gwangneung LTER site of the Korea Forest Research Institute). In 2011, the ants were biweekly surveyed from April to October using pitfall traps at six sites in a pine forest (about 5 ha). In 2009, the ants were monthly surveyed from April to October using pitfall traps at eight sites in eight forests (four deciduous forests and four coniferous forests; within area of about 1,000 ha). O, occurrence. Asterisk denotes that the species occurred in May to August. Data of eight forests was published in Kwon et al. 2011a, and other data are unpublished.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions

T-SK designed the experiment for the present study, wrote the manuscript, and surveyed the ant fauna. CML analyzed the data and wrote the manuscript. JHS the analyzed data. All authors read and approved the final manuscript.

Acknowledgements

We thank Dr. J.H. Lim for providing his LAI data and Miss B.G. Gu for the picture of Figure 5. *Mechoris ursulus* damage data were kindly provided by Drs. W.I. Choi and S.H. Go at KFRI. This manuscript was significantly improved by a few of anonymous reviewers. This study was conducted under the support of the Korea Forest Research Institute (Project FE 0100-2009-01, Effect of climate change on forest ecosystem and adaptation of forest ecosystem).

Author details

[1]Division of Forest Insect Pests and Diseases, Korea Forest Research Institute, 57 Hoegi-ro, Dongdaemun-gu, Seoul 130-712, Republic of Korea. [2]Division of Forest Ecology, Korea Forest Research Institute, 57 Hoegi-ro, Dongdaemun-gu, Seoul 130-712, Republic of Korea.

Received: 24 December 2013 Accepted: 20 June 2014
Published: 15 July 2014

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doi:10.1186/s40555-014-0037-z
Cite this article as: Kwon *et al.*: **Diversity decrease of ant (Formicidae, Hymenoptera) after a forest disturbance: different responses among functional guilds.** *Zoological Studies* 2014 **53**:37.