Succession in ant communities (Hymenoptera: Formicidae) in deciduous forest clear-cuts – an Eastern European case study

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Abstract. Clear-cutting, the main method of harvesting in many forests in the world, causes a series of dramatic environmental changes to the forest habitat and removes habitat resources for arboreal and epigeal species. It results in considerable changes in the composition of both plant and animal communities. Ants have many critical roles in the maintenance and functioning of forest ecosystems. Therefore, the response of ants to clear-cutting and the time it takes for an ant community to recover after clear-cutting are important indicators of the effect of this harvesting technique on the forest ecosystem. We investigated ground-dwelling ant communities during secondary succession of deciduous forests in Transylvania, Romania. Using space-for-time substitution, we explored a chronosequence from clear-cuts to mature forests (>120 years). The object was to determine if cutting has measurable effects on ant community structure, and if ant species richness differs between successional stages. We recorded a total of 24 species of ants, 11 characteristic of forests and seven of open landscape. Ant species richness was higher in clear-cuts compared to closed-canopy and old stands. Number of ant individuals was highest in young age classes and lowest in closed-canopy age classes. There was no drastic change in species richness during the succession, however differences in community composition at different stages were recorded. Open landscape species are able to rapidly colonize following disturbance but disappear when the forest sites mature and many forest ant species are capable of surviving clear cutting.

INTRODUCTION

Temperate deciduous forests provide important habitats for a wide range of invertebrate species associated with coarse woody debris, large deciduous trees and dead wood (Niemelä, 1997). Despite being widespread, temperate deciduous forests are among the most human-disturbed forests in the world, being exploited intensively for timber and biomass (Röhrig & Ulrich, 1991). Habitat disturbances such as fire (Paquine & Coderre, 1997), forest fragmentation (Carvalho & Vasconcelos, 1999), logging and, in particular, clear-cutting (Punttila et al., 1991; Niemelä, 1997) can cause a decline or loss of forest inhabiting vertebrate and invertebrate species.

Clear-cutting is the main method of harvesting in many forest regions in the world, especially in North America and Europe (reviewed in Paillet et al., 2010). This results in habitat loss for arboreal species (MacKay et al., 1991), reduces leaf litter (Ash, 1995) and causes environmental changes such as increased insolation of the soil and expo-

sure to wind, leading to reduced quality or even complete loss of habitats for forest floor dwelling species (Kaila et al., 1997; Andersson et al., 2012). Thus, direct sunlight and wind as well as loss of connectivity between mature forest stands due to clear-cutting are known to affect ground beetle assemblages (Niemelä et al., 1993; Koivula et al., 2002); whereas high rainfall and compaction of the forest floor through the use of heavy machinery leads to a significantly lower abundance of oribatid mites in clear-cut areas (Marra & Edmonds, 1998; Lindo & Visser, 2004). Arboreal food resources of relevance to arthropods such as ants are also significantly reduced, due to the loss of trees as foraging areas (Sorvari & Hakkarainen, 2009).

Ants are important components of forest ecosystems, because they are generalist predators. Furthermore, ants play an important role in belowground processes by altering the physical and chemical environment and through their effects on plants, microorganisms and other soil organisms (Hölldobler & Wilson, 1990; Frouz & Jilkova, 2008). They

are important seed dispersers and can influence the carbon and nutrient cycles in soils (Folgarait, 1998; Del Toro et al., 2012).

Ant communities are affected by clear-cutting of forests, in particular through: changes in microhabitat availability, such as dead wood, rotten logs and empty acorns (Czechowski et al., 2002; Seifert, 2007); reduction in food resources due to the loss of forest vegetation, such as aphids tended for honeydew or arthropods collected from trees (Punttila et al., 2004; Johansson & Gibb, 2012); increased aggression between neighbouring colonies (in the case of red wood ants), due to loss of visual orientation cues (Sorvari & Hakkarainen, 2004). Effects of clear-cutting of coniferous forests on ants have been studied at different levels: population (Zettler et al., 2004; Sorvari & Hakkarainen, 2005, 2007, 2009; Żmihorski, 2010, 2011), community (Punttila et al., 1994; Czechowski et al., 1995; Markó, 1999; Palladini et al., 2007) and behaviour of individuals (Sorvari & Hakkarainen, 2004; Sorvari et al., 2008). Results from these studies show that red wood ants are particularly negatively affected ways that are briefly discussed in the following section.

Sorvari & Hakkarainen (2009) show that food limitation may have an effect on the ability of wood ants to regulate nest temperatures. Logging enhanced the encapsulation reaction in gynes ("an unspecific, constitutive, cellular response that acts as defence for insects against multicellular pathogens such as nematodes, fungi, and parasitoids" – Gillespie et al., 1997), but decreased that of workers (Sorvari et al., 2008). In general, clear-cutting and deforestation affect red wood ants negatively as the area occupied by *Formica* species decreases following clear-cutting (Sorvari & Hakkarainen, 2005, 2007; Żmihorski, 2010, 2011). The effects of clear-cutting of deciduous forest on ant communities, where wood ants (i.e. *Formica* s. str.) are often absent or less dominant (Szujecki et al., 1978; Lynch, 1981; Dekoninck et al., 2008; Babik et al., 2009), are much less understood. In deciduous forests, dominant ant species often belong to the subfamily Myrmicinae, with *Myrmica ruginodis* being one of the most common species (Dekoninck et al., 2008). Whereas successional pathways in plant communities resulting from clear-cutting of deciduous forests are rather well studied and understood (Elliott & Swank, 1994; Decocq et al., 2004), ground-dwelling ant species may show different patterns of recovery after disturbance (Osborn et al., 1999; Bestelmeyer & Wiens, 2001; Dahms et al., 2005; Dauber & Simmering, 2006; Englisch et al., 2005; Azcarate & Peco, 2012; Német et al., 2016).

The novelty of our study resides in assessing for the first time an ant community's response to deciduous forest clear-cutting in Europe. In order to elucidate the immediate effect of clear-cutting on ant communities and the trajectory of community recovery with regrowth of the forest, we explored a chronosequence, from clear-cuts to mature forests (>120 years). The simultaneous availability of forest sites of different age classes allowed us to use the "space-for time substitution" (SFT) approach (Pickett, 1989) as a surrogate for a long-term study on ant succession. Specifically, we hypothesized that clear-cutting would have measurable effects on ant community structure, including a decrease in ant abundance and loss of forest species from the first stages, followed by a recovery of both ant abundance and forest species richness along the chronosequence towards the climax stage. Furthermore, we tested whether ant species richness differs between successional stages.

MATERIAL AND METHODS

Study region and study sites

The sites studied were at two locations in Transylvania: in the vicinity of Cluj-Napoca (Cluj County) and of Dumbrăveni (Sibiu County). The sites are at between 450–550 m a.s.l., and almost all of the sites were on north-facing slopes ranging from 12 to 32 degrees (data retrieved from the Forestry authorities at Cluj-Napoca and Dumbrăveni) (Table 1).

We selected a total of 16 sites. In addition to forest habitats nearby grasslands were also sampled, as they were considered sources of ants in the case of newly opened habitats such as young clearcuts. Knowing the location of nearby grassland and its ant species pool, we can assess which species could potentially colonize these sites apart from the remnants of the forest ant community. In the case of Dumbrăveni, seven deciduous forest sites of different age classes were chosen (D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest). Two grasslands were also sampled (M1 and M2 were not regularly grazed by domestic livestock, but used to produce hay). In the vicinity of Cluj-Napoca five forest sites of different age classes were sampled (C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest) and one grassland (P – used for grazing livestock). Data regarding the age of the sites was provided by the Dumbrăveni and Cluj-Napoca Forestry Agencies. For all the sites soil pH was measured in the field using a Nahita soil pH device (a metallic electrode was inserted to depth of 30 cm in the soil and the pH measured based on the moisture content, organic matter content and other characteristics). Within the quadrat where the ants were sampled, three replicates were randomly taken per site and the average value is given in Table 1. Based on our vegetation survey

Table 1. Site parameters (size, slope, altitude, and soil pH) of the different aged sites at Dumbrăveni and Cluj-Napoca (Dumbrăveni: D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest; Cluj-Napoca: C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest; for pH values – three samples were taken and the average value is given).

Sites	Dumbrăveni							Cluj-Napoca				
	D1	D2	D15	D35	D55	D75	D120	C1	C5	C10	C60	C120
Slope (degrees)	20	32	24	24	28	27	20	12	12	13	14	20
Size (ha)	2	1	4.3	2	4.4	4.2	4.5	2	1.5	2.2	7.6	14.3
Altitude (m)	470	450	380	400	420	430	480	450	450	400	420	400
pH	4.08	5.9	5.48	5.52	5.62	5.54	5.96	4.56	4.38	4.2	4.96	5.74

(quantitative data retrieved from vegetation quadrats), the forest sites at Dumbrăveni are dominated by the following plant associations*: Carpino – Fagetum, Querco petraeae – Carpinetum, Corylo avellanae – Carpinetum, Tillio tementosae – Carpinetum betuli* and *Fragario-Rubetum idaei.* At Cluj-Napoca similar plant associations occurred at the sites: *Querco robori – Carpinetum, Corylo avellanae – Carpinetum, Tillio tementosae – Carpinetum betuli* and *Fragario-Rubetum idaei.* The dominant plant associations in the grasslands at Dumbrăveni were: *Anthoxantho – Agrostieteum capillaries, Rumici acetosellae – Agrostietum capillaries, Cirsio – Convolvuletum arvensis* and at Cluj-Napoca: *Anthoxantho – Agrostieteum capillaries* and *Lolio – Plantaginetum majoris.*

Ant sampling and identification

The ants were collected using pitfall traps over three 10 day periods (in May, July and September) in 2011, at both locations. Altogether 16 pitfall traps (175 ml plastic cups) were used arranged in a 4 × 4 grid, with 5 m between neighbouring traps within a 225 m² randomly selected plot, at each site. The traps were filled with killing and preserving agent (glycol : water, 2 : 1 solution). 672 of a total of 720 pitfall traps were retrieved (93.33% retrieval due to accidental destruction by wild animals).

All individuals were identified to species level using the keys of Czechowski et al. (2002) and Seifert (2007). Specimens are kept in the private collection of Ioan Tăuşan. For statistical analyses only worker ants were considered. Habitat preferences of each ant species were assigned according to Czechowski et al. (2012) (Table 2): FOR – forest species, OPEN – open habitat species, UBIQ – ubiquitous species – which are found in any type of habitat including anthropogenic ones; F/O – species occuring in both forest and open habitats.

Data analyses

Secondary succession of ants was studied using the "space-for time substitution" (SFT) approach (Pickett, 1998). We tested comparability of sites within the chronosequence for each location separately using Kruskal Wallis tests for the site parameters; altitude, slope and soil pH. The parameters were not significantly different in terms of altitude (Dumbrăveni: p = 0.79, χ^2 = 0.06, Cluj-Napoca; p = 0.16, χ^2 = 1.84), slope (Dumbrăveni: p = 0.17, χ^2 = 1.8, Cluj-Napoca; p = 0.4 χ^2 = 2.13), or pH (Dumbrăveni: p = 0.22, χ^2 = 1.47, Cluj-Napoca; p = 0.07, χ^2 = 3.15), thus enhancing the comparability of the sites within the SFT approach.

Species richness and Shannon-Wiener index were calculated and an estimator, Chao2 (for species incidence) was determined using the "Species" package from R. Expected cumulative species curves for the observed species number were calculated for each site using EstimateS 9 software (Colwell, 2005). In each plot, pitfall traps were considered samples. The age of the plot as a predictor of species richness (number of species, Shannon-Wiener index, number of forest ant species) was tested using a generalised linear model (GLM, Poisson regression).

NMDS ordination based on pitfall traps (ant species represented by at least 5 individuals were taken into account) was carried out for all of sites. Differences in species composition between forest stages, at each location, were tested using a perMANOVA (5000 permutations). All statistical analyses (except the cumulative species curves) were done using R software (R Core Team 2013).

Table 2. Pitfall trap data of ant species caught at Dumbrăveni and Cluj-Napoca (habitat requirements according to Czechowski et al. (2012): FOR – forest species, OPEN – open habitat species, UBIQ – ubiquitous species – which are found in any type of habitat including anthropogenic ones; F/O – species occuring in both forest and open habitats; Dumbrăveni: D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest; M1, M2 – grasslands; Cluj-Napoca: C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest; P – grassland).

SITES	D1	D2	D15	D35	D55	D70	D120	M1	M2	C1	C5	C10	C60	C120	P	Habitat
Species																
Myrmica ruginodis Nylander, 1846	55	41		13	120	12	152			102	5	2	6	4		FOR
Myrmica scabrinodis Nylander, 1846								3	1		27	1			4	F/O
Myrmica rubra (Linneaus, 1758)										12	274	7	90	40		UBIQ
Myrmica gallienii Bondroit, 1920											14					OPEN
Temnothorax crassispinus (Karawajew, 1926)	31	1		1	29	4	1			3			2	1		FOR
Myrmecina graminicola Latreille 1802	2	5	2		10											FOR
Stenamma debile (Förster, 1850)	4	5	2	2	8	5	5			2				1		FOR
Aphaenogaster subterranea (Latreille, 1798)	2				5											FOR
Tetramorium cf. *caespitum*					3			18	36						22	UBIQ
Formica fusca Linnaeus, 1758	1	2			5				81			1				F/O
Formica cinerea Mayr 1853	1							115	109		5					F/O
Formica cunicularia Latreille, 1798		5						53	106	1	17				21	OPEN
Formica sanguinea Latreille, 1798											3					F/O
Formica rufibarbis Fabricius, 1798				1				130	19		1				97	OPEN
Lasius niger (Linnaeus, 1758)								1499	3119						4486	OPEN
Lasius platythorax Seifert, 1991	32	18	5	1	2	4	6			1	5	3	5			FOR
Lasius emarginatus (Olivier, 1792)		1														F/O
Lasius fuliginosus (Latreille, 1798)					1	3										FOR
Lasius brunneus (Latreille, 1798)												2	5			FOR
Polyergus rufescens (Latreille, 1798)									19						1	OPEN
Camponotus vagus (Scopoli, 1763)										18	5					FOR
Camponotus piceus (Leach, 1825)									465							OPEN
Solenopsis fugax (Latreille, 1798)								1	1							OPEN
Tapinoma subboreale Seifert, 2012								4	51		5				1	OPEN
Total no. of individuals	128	78	11	17	183	28	164	1823	4007	140	405	16	108	46	4632	
Total no. of species	8	8	4	4	9	5	4	8	10	7	11	6	5	4	7	
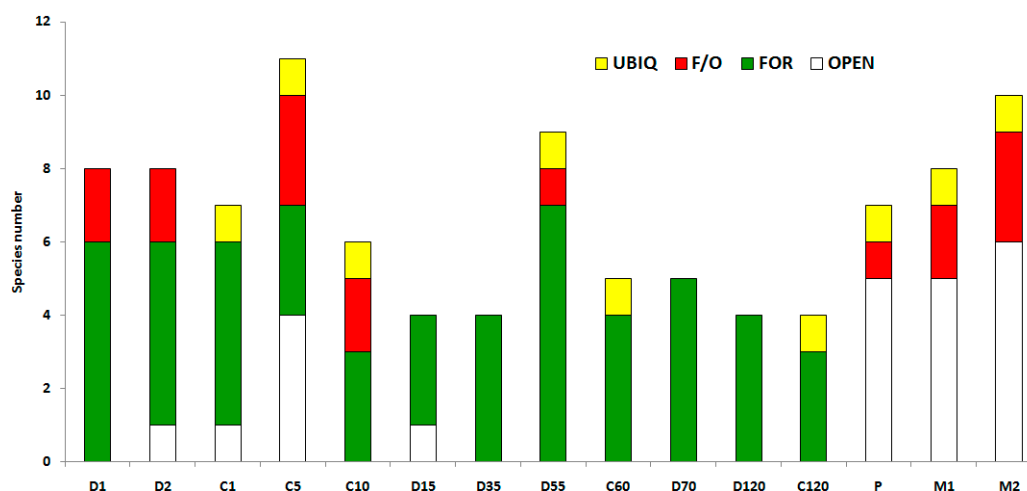
Fig. 1. Total number of ant species and their habitat preferences at different successional stages at Dumbrăveni and Cluj-Napoca (codes: habitat requirements FOR – forest species, OPEN – open habitat species, UBIQ – ubiquitous species – which are recorded in any type of habitat including anthropogenic ones ; F/O – species occuring in both forest and open habitats; Dumbrăveni: D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest*;* M1, M2 – grasslands; Cluj-Napoca: C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest; P – grassland).

RESULTS

Altogether we collected a total of 11,786 ant workers belonging to 24 species. However, the ant catches at forest sites (all age classes included), were relatively low, yielding only 1,324 individuals (12.88%) and 20 species. The total number of ants caught at the grassland sites was 10,462 belonging to 11 species. A complete list of the species is given in Table 2.

The most abundant species were *Myrmica ruginodis* at Dumbrăveni and *Myrmica rubra* at Cluj-Napoca (Table 2). Both these species were sampled at all the forest sites. Due to its habitat requirements (dry and semidry open habitats),

Lasius niger was abundant (Table 2) at all grassland sites. In addition, *Camponotus piceus*, was abundant at M1 and M2 (Table 2) and *Formica rufibarbis* occurred at P (Table 2).

Contrary to expectations, richness of forest species (e.g. *Myrmica ruginodis, Temnothorax crassispinus, Myrmecina graminicola*) did not decline in the clear-cuts (D1, D2, C1 and C5) and species richness in general was higher than at the older forest sites (Fig. 1). The highest species richness was recorded at C5, where 11 species occurred, with four species of *Myrmica*: *M. ruginodis, M. rubra, M. scabrinodis* and *M. gallienii* (Table 2). At the latter sites, species richness ranged from 4 to 6, with the exception of
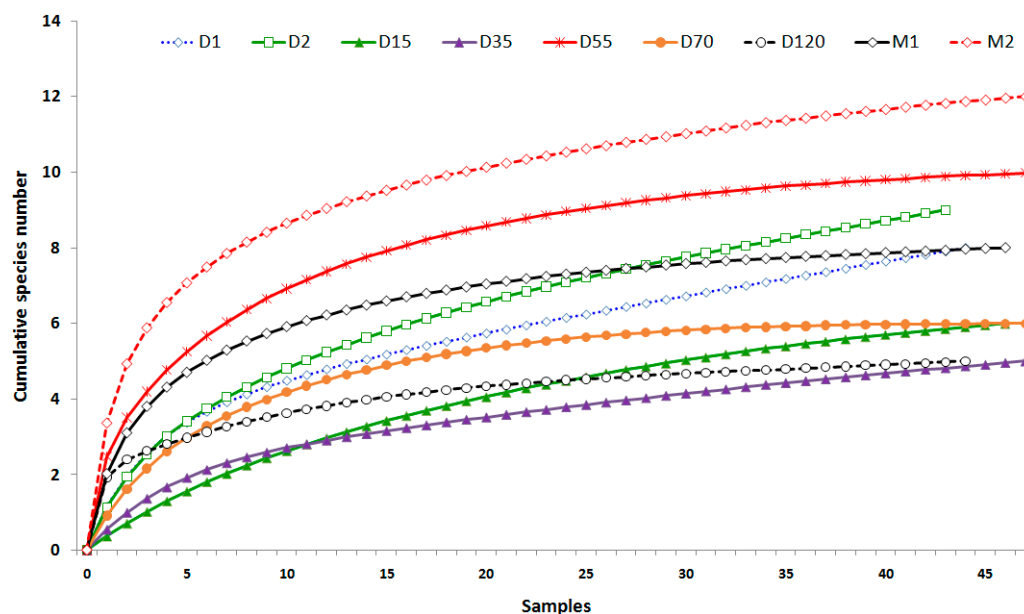
Fig. 2. The expected species accumulation curves of cumulative species numbers recorded for a given number of samples collected at Dumbrăveni (D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest*;* M1, M2 – grasslands).
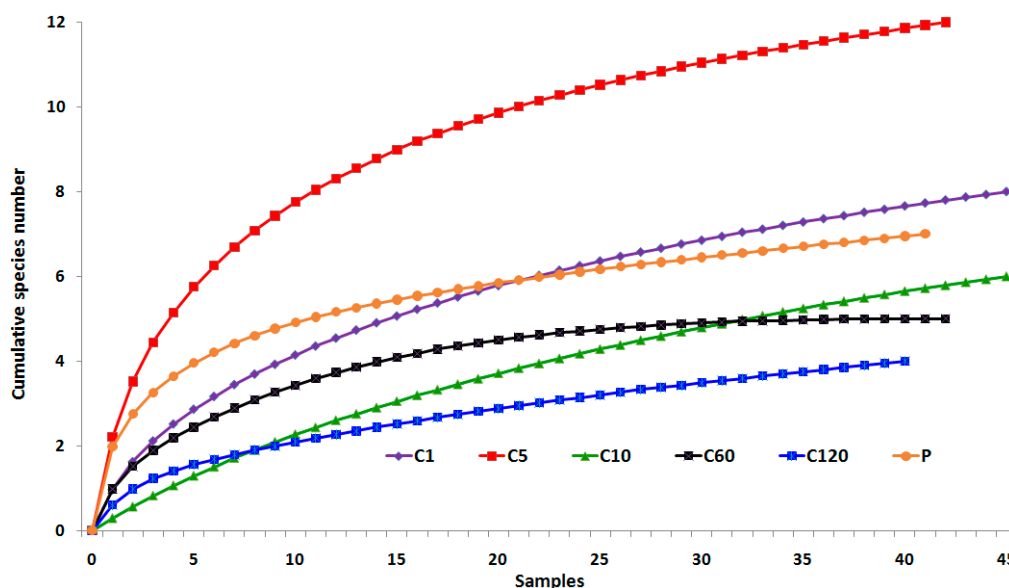
Fig. 3. The expected species accumulation curves of the cumulative species numbers recorded for a given number of samples collected at Cluj-Napoca (C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest, P – grassland).

D55, where 9 species were recorded (Fig. 1). In particular, the intermediate stages of succession (e.g. C10, D15) were characterized by low ant abundance and low diversity (Table 2). However, the age of the sites was an insignificant predictor of changes in the number of species during succession (GLM, p = 0.0849, z = –1.723). Thus, species richness showed little change as a result of succession.

The total species richness estimator Chao2 indicates that more species could be expected to occur in clear-cuts (14 species at D1 and 15 at D2, 12 at C1 and 16 at C5 – Table 3). This trend is also revealed by the species accumulation curves not reaching an asymptote, especially those for early successional sites (Figs 2 and 3), revealing that despite intensive sampling we did not collect all of the species. However, at mature sites (C60, D70 and D120) trapping estimated the maximum number of ant species (Figs 2 and 3).

Regarding Shannon diversity, our results indicated lower values for the mature sites (D120 and C120) due to the numerical dominance of *Myrmica ruginodis* and *Myrmica rubra* (Table 3) and there were also lower numbers of the other species. Yet, no significant differences in terms of diversity were recorded along the succession (GLM, p = 0.386, z = –0.886).

Ant community structure was very different at grassland compared to woodland sites (perMANOVA, 5000 permutations, p < 0.05, F = 10.98, Df = 14). However, the NMDS revealed that at least one clear-cut site (C5) shared several species, such as *Tetramorium* cf *caespitum* and *Formica cunicularia,* with the grasslands (Fig. 4). Yet, the overall analysis reveals that the forest sites cluster together by location and are characterized by a specific ant composition and the grasslands form a distinct group (Fig. 4).

Analyzing the habitat requirements we revealed that a shift in the ant community occurs ten years after clearcutting. Forest species such as *Myrmica ruginodis*, *Lasius platythorax*, *Temnothorax crassispinus* and *Stenamma debile* still occurred at clear-cuts (D1, D2, C1 and C5). However, *Myrmica ruginodis* was absent or was low in abundance at D15 and D35 and *Myrmica rubra* was low in abundance at C10. Open habitat species (*Tetramorium* cf. c*aespitum, Formica cunicularia* and *F. rufibarbis*) did not occur at sites that were clear cut 20 or more years previously (e.g. D35), only some ant species that prefer both forest and grassland habitats were sampled at mature sites (Fig. 1). Moreover, the number of forest ant species varied little (GLM, p = 0.802, z = –0.251) with the age of the site and only ubiquitous species (e.g. *Myrmica rubra*) survived throughout the succession (Fig. 1).

DISCUSSION

In the present study, we compared the composition of ant communities at sites of different ages in managed deciduous forests after clear cutting. In contrast to our expectations, which were partly based on studies of coniferous forests (Punttila et al., 1994; Czechowski et al., 1995;

Table 3. Estimates of species richness and diversity of ant species collected at Dumbrăveni and Cluj-Napoca (Dumbrăveni: D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest; M1, M2 – grasslands; Cluj-Napoca: C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest; P – grassland).

Sites	D1	D2	D15	D35	D55	D70	D120	M1	M2	C1	C5	C10	C60	C120	P
Shannon-Wiener	1.367	1.41	1.221	0.7902	1.206	1.466	0.329	0.7001	0.8707	0.9181	1.026	1.542	0.6709	0.5004	0.1716
Chao 2	14	15	6	7	10.5	6	5	8	13	12.5	16.5	8.25	5	5	8
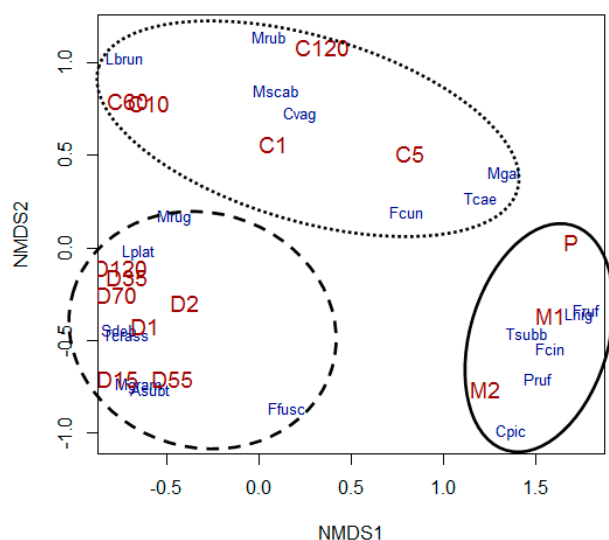
Fig. 4. Non-metric multidimensional ordination (Bray-Curtis index of similarity) based on pitfall trap data from Dumbrăveni (species represented by at least 5 individuals – Stress = 0.082; codes: Asubt – *Aphaenogaster subterranea*; Cvag – *Camponotus vagus*; Cpic – *C. piceus*; Ffusc – *Formica fusca*; Fcun – *F. cunicularia*; Fruf – *F. rufibarbis*; Fcin – *F. cinerea*; Lplat – *Lasius platythorax*; Lbrun – *L. brunneus*; Lnig – *L. niger*; Mgram – *Myrmecina graminicola*; Mrug – *Myrmica ruginodis*; Msca –*M. scabrinodis*; Mrub – *M. rubra*; Mgal – *M. gallienii*; Pruf – *Polyergus rufescens*; Sdeb – *Stenamma debile*; Tcae – *Tetramorium* cf *caespitum*; Tcrass – *Temnothorax crassispinus*; Tsubb – *Tapinoma subboreale*; D1 – one year after clear-cut; D2 – two years after clear-cut; D15 – 15 year-old forest; D35 – 35 year-old forest; D55 – 55 year-old forest; D70 – 70 year-old forest; D120 – 120 year-old forest*;* M1, M2 – grasslands; C1 – one year after clear-cut; C5 – five years after clear-cut; C10 – 10 year-old forest; C60 – 60 year-old forest; C120 – 120 year-old forest; P – grassland).

Markó, 1999; Zettler et al., 2004; Sorvari Hakkarainen, 2005, 2007; Palladini et al., 2007; Sorvari et al., 2008; Żmihorski, 2010), we found that species composition changed throughout succession. The most abundant species collected at the sites studied were *Myrmica ruginodis* at Dumbrăveni and *Myrmica rubra* at Cluj-Napoca. The succession recorded for the ant communities in the chronosequence proved interesting in that contrary to expectation, many forest ant species survived clear cutting. A comparison with grassland sites in the vicinity revealed that ants of open grassland habitats occurred at clear cut sites shortly after the trees were harvested. Ant species richness was initially high in clear-cuts and then decreased with the time since the trees were felled, whereas at mature sites, only forest species prevailed. These findings are discussed in more detail.

Species richness and community composition recorded in the chronosequence

Altogether we identified 24 ant species: 21 species at Dumbrăveni and 18 at Cluj-Napoca. This was due probably to the sampling method, but pitfall trapping is still regarded as an accurate method for studying epigaeic ant communities (Ward et al., 2001; Corti et al., 2013; Wiezic et al., 2015). Compared to other studies, carried out at

forest and grassland habitats in Transylvania, the species number is similar. Markó (2008) report 29 species, whereas both Tăuşan & Markó (2009) and Német et al. (2012) report 19 species. Moreover, we did not collect any red wood ants (*Formica* s. str.), which do occur in deciduous forests (Dekoninck et al., 2008; Babik et al., 2009). However, the species found covered a wide spectrum of habitat preferences, ranging from disturbance tolerant, open habitat species (e.g. *Lasius niger*, *Myrmica rubra*, *Tetramorium* cf. *caespitum* and *Formica rufibarbis*), via species preferring cooler and moister semi-open habitats (e.g. *Myrmica scabrinodis*) and species preferring thermophilic habitats (e.g. *Aphaenogaster subterranea*), to typical forest species (e.g. *Myrmica ruginodis*, *Lasius platythorax*, *Temnothorax crassispinus*, *Stenamma debile* and *Myrmecina graminicola*) (Czechowski et al., 2012). Our results are largely in accord with those of previous studies on comparable European deciduous forests (Glaser, 2006; Dekoninck et al., 2008; Babik et al., 2009).

Despite differences in community composition at young sites and in mature forests (>100 years), more important forest species (including *Myrmica ruginodis*, *Lasius platythorax* or *Temnothorax crassispinus*) occurred throughout the succession. Both *M. ruginodis* and *L. platythorax* occurred mainly at the forest sites, and their presence in sun exposed clear-cuts might be explained by available microhabitats such as decaying wood but also patches of dense vegetation (Czechowski et al., 2012). Moreover, it is possible that the surrounding forests, both at D2 and C5, may have provided enough shading, whereas as at D1 and C1 the ant communities could have foraged in adjacent patches of forest. However, at the clear-cut sites, we recorded a lower abundance of this species than at the later succession sites, possibly due to a lower availability of suitable microhabitats. Other species, such as *Formica fusca*, *F. cinerea* and *Myrmecina graminicola*, were uncommon throughout the chronosequence. In addition, the high species richness at D1, DC2, CI and C5 included possible colonizers such as the open habitat species: *Myrmica rubra*, *Tetramorium* cf. *caespitum* and *Formica rufibarbis*. At both study areas, open habitat species of ants colonized the clear-cuts. *Formica cunicularia*, *F. rufibarbis*, *Myrmica scabrinodis* and *Tetramorium* cf. *caespitum* were recorded at D1 and D2. Only the latter species thrived throughout the succession. A possible explanation for this is its aggressiveness towards other ant species and mass worker recruitment (Seifert, 2007; Czechowski et al., 2012). This species is the most tolerant of all European *Myrmica*, is highly aggressive (Seifert, 2007; Czechowski et al., 2012) and occurs in many habitats. Besides being highly competitive, its populations are well established in Romanian deciduous forests (Markó et al., 2006; Czekes et al., 2012).

In light of these differences in community composition, we did not find any significant changes in species richness during the succession, both in species number and Shannon diversity. This implies that the effects of clear cutting may not be as severe as expected.

Patterns in the recovery of communities after clear-cutting. Time frame of recovery

The recovery of ant communities following clear-cutting depends on several factors. According to Cerda et al. (2013) the structure of ant communities is driven by "a complex network of interactions involving different abiotic and biotic factors". Environmental factors such as temperature, moisture (Kaspari et al., 2003, 2004; Sanders et al., 2007), habitat complexity and micro-structure diversity, such as litter characteristics and the vegetation (Armbrecht et al., 2004; Dekoninck et al., 2008), and soil attributes (Boulton et al., 2005, Dahms et al., 2005) are the most important determinants of variation in ant species richness. Dekoninck et al. (2008) show that even after 25 years of natural succession or reforestation, with or without management, typical forest ant communities are still absent. Moreover, studies in Finland show that certain ant species present in 120 year old forests, had not colonized clear-cuts after 10 years due to lack of food resources (Puntilla et al., 1991). Vepsäläinen et al. (2000) report that only a few ant communities at 35 year-old sites can be classified as forest communities. The composition of ant communities in old forest fragments (40–80 years) differ from those in 140 year or old forests (Puntilla et al., 1994) and this is particularly the case for *Formica* s. str. and *Serviformica* species (Puntilla, 1996). In our case, despite the fact that clear-cutting enabled open habitat species to colonize young sites, forest species (*Myrmica ruginodis*, *Temnothorax crassipinus* and *Lasius platythorax*) were present at almost every stage of succession.

After 60 years, almost exclusively only forest ant species prevailed. Ant communities in old deciduous forests are well represented by *Myrmica ruginodis*, *Stenamma debile* and *Temnothorax nylanderi* (Förster, 1850) (cf. Dekoninck et al., 2008). In our case, communities of ants at the forest sites at Dumbrăveni had a typical composition (see Table 2), with one exception: *Temnothorax nylanderi*. In Eastern Europe, this species is replaced by *T. crassispinus* (Czechoswki et al., 2002). At some sites, *Myrmica ruginodis* was less abundant than *Myrmica rubra* but otherwise the overall community composition included forest species (e.g. *Lasius platythorax*, *L. brunneus*, *Stenamma debile* and *Temnothorax crassispinus*) (Table 2).

Ant succession: Effects of tree "succession" or management

Ant species richness was higher at the young sites (e.g. D1, D2, C1, C5) compared to closed-canopy (e.g. C10, D15) or old sites (e.g. C120, D120), possibly due to the change in microclimatic conditions (e.g. light, moisture) that occurred after clear-cutting. Those patterns resemble those that are reported by Palladini et al. (2007) for coniferous forest succession. D15 and C10 were characterized by low ant abundance and species richness. A potential explanation is the major environmental changes in the understory, including increased shading, high relative humidity and lower wind speed (Aussenac, 2000). Moreover, according to the "closed canopy" conventional successional model,

severe disturbances to forests are followed by "establishment of a dense, even-aged cohort of pioneer tree species" (Donato et al., 2012). The growth of trees eventually leads to canopy closure, probably the most dramatic developmental stage in the life of a stand (Franklin et al., 2002). This stage effectively dominates sites by means of a single-layer canopy and simplified understory. The closed-canopy affects the diversity of many groups (Spies & Franklin, 1991; Franklin et al., 2002), including ants (Petal, 1980).

However, based on our results, forest ant species can survive clear-cutting. Thus ant diversity and the important processes performed by ants are little affected by this management and young forest is as important an habitat for ants as old growth forest or even more important, as it also includes early succession species. Similar results are reported by Palladini et al. (2007) for coniferous forest clearing and by Zettler et al. (2004) in deciduous forests clear-cuts. Moreover, Arnan et al. (2009) show that there are no differences in species richness despite different types of forest management.

CONCLUSIONS

Our results show that clear-cutting alters the composition of ground-dwelling ant communities in temperate deciduous forests. Changes in terms of composition were recorded throughout the succession. Nevertheless, the succession within deciduous forest stands indicates that typical forest ant species can survive clear cutting. Forest ant species were present throughout the succession and after 60 years the forest species prevailed. Despite a higher number of ant species in the clear-cuts, there was no clear shift in species richness during succession. It remains an open question whether other factors besides clear-cutting can affect ant communities. For example, forest management induced changes in interactions among ant communities are largely unknown and provide an interesting approach for future studies.

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