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Reaction of ant communities to degradation of forest habitats in the Karkonosze Mountains

Abstract. The studies were conducted along the gradient of degraded forest habitats of the Mumlawski Wierch in the western part of the Karkonosze Mts. Comparisons were performed between well preserved forests, damaged tree stands and a regenerating spruce forest. Ant communities in degraded habitats tended to become more alike to the ant communities of open areas (a mountain pasture of the Hala Izerska). The observed changes consisted in: a) an increase in the number of species, density and frequency of nests, b) a greater society size, c) a larger body size of individuals of dominating species, d) a decrease in turnover of society biomass, i.e. ecologically longer lifetime of ants. The recorded changes were the effect not only of improvement of life conditions for ants but also of the age of habitats.

INTRODUCTION

Many ant species do not leave man-transformed habitats, such as urbanized areas, drained peatlands, intensively fertilized meadows, derelict industrial lands. None the less ants react to habitat changes by mobilizing habitat-modifying behavioral defensive reactions and altering certain parameters of their societies and populations. Studies conducted so far have revealed that at early stages of habitat transformations there have been recorded changes in the number of ant species, density of their nests and the size of ant societies. All these have been accompanied by a more rapid development of larvae, decrease in an average weight of mature individual and increase in society biomass turnover, evidencing a decreased survival rate of ants (PETAL 1977, 1978, 1980, 1991, KRZYSZTOFIK 1991). In the effect of these changes the contribution of ants to total predation pressure of transformed habitats diminishes.

Ecological effects of forest decline are one of the main issues in studies on anthropogenic transformations of Karkonosze landscapes. The research on ant reactions to degradation of forest habitats comes within the scope of these studies. The aim of the present work was to determine how transformations of plant communities affect societies and populations of various ant species.

STUDY AREA

The studies were carried out in 1992 on the south-western slope of the Mumlawski Wierch in the western part of Karkonosze as well as on a mountain pasture of the Hala Izerska. Habitats on the Mumlawski Wierch were situated in the upper forest zone of Sudeten spruce-trees, *Piceetum hercynicum* (MATUSZKIEWICZ 1967).

The study area exemplified typical transformations of spruce ecosystems in Karkonosze. Industrial effluents windblown from over the territory of Germany, Czech and southern Poland have caused a strip decline of trees on the slope since the mid-seventies. For the last 20 years new forest plantings and spontaneous renewal of a spruce forest have created several habitats characterized by a various degree of transformation of forest vegetation. There occur habitats with the preserved tree stand, habitats where the tree stand was totally devastated and the herb layer was noted for a vehement development of grasses and decline of coniferous forest plants as well as habitats of the renewed spruce forest (WASIŁOWSKA 1992, FABISZEWSKI et al. 1992).

According to WASIŁOWSKA 1992, in habitats of the died out forest, a natural transformation of plants communities proceeds. It was reflected in the values of coefficient of coverage with species dominating in the two communities, namely, with *Calamagrostis villosa* (CHAIX) GMEL. dominating in the grassy community and *Vaccinium myrtillus* L. – in the forest community (Table 1).

Table 1. Values of coefficient of coverage with dominating species in different habitats (acc. WASIŁOWSKA 1992)

Species \ Habitat	Dead forest	New forest plantings and self-sown wood	15 years old young forest with vast glades	Live forest
	(1)	(2)	(3)	(6)
<i>Calamagrostis villosa</i>	3973	1893	1465	1180
<i>Vaccinium myrtillus</i>	110	822	1337	1647

According to a preliminary analysis the study site ranked among areas of low dust level, a distinctly acid rain water and an average inflow of nitrogen and sulphur compounds (STACHURSKI et al. 1992). Pollutant deposition was uneven, its higher values being noted on the forest edge except for nitrogen compound fall, which was greater on open areas (KMIEĆ et al. 1992).

Soil in most of the examined habitats was of podzolic or podzolic-peatype of a shallow, skeleton profile and high acidity (pH in H₂O = 3.6–4.0) (SKIBA, DREWNİK 1992). It was marked for a restrained rate of organic substance degradation, a property likely to affect immobilization of nutrients and restrict their accessibility to plants (PIETR et al. 1992).

Examinations of ant communities were made along the north-western slope of the Mumlawski Wierch from its foot to the top, enclosing all the characteristic habitats,

namely habitats differing image of phytosociological succession as well as an old living forest and a glade:

- 1) dead forest above habitat 2;
- 2) new forest plantings on the foot of the slope;
- 3) young spruce tree forest, ca 15 years old, at the level of habitat 2, light-penetrated, enclosing large areas grown with lush grassy vegetation;
- 4) woodland glade in live forest (5), above habitat 3;
- 5) live forest at the level of habitats 1, 2, 3;
- 6) live forest right below the top of the Mumlawski Wierch.

Ants communities of forest and deforested habitats of the Mumlawski Wierch were compared to ants of a typically montane grassy habitat of the Hala Izerska (habitat 7).

METHODS

Spatial distribution of ant-hills, the size of societies and their age structure and the size of individuals have been examined. The methods employed were described in earlier papers (PEŁAL 1972, PEŁAL, PISARSKI 1993).

The examinations were made in the latter part of June 1992, i.e. in the mid-period of ant seasonal activity. Examinations of species composition and spatial distribution of ant-hills were carried out along 10 m long and 1 m wide transects. In each habitat 10–36 samples were taken. The size of societies was estimated by means of digging out ant nests and extracting all the specimens: imagines, pupae and larvae of various size classes. A total of 3–11 samples of this kind was taken from each habitat.

Dry mass of larvae, pupae one-year old and older imagines was measured in order to estimate society mass and production. Calculation of production was the basis for determining turnover of society biomass and consumption.

RESULTS

Characteristic of ant communities (Table 2)

A total of 11 ant species was recorded in all the examined habitats, each habitat being populated by 1–8 species. Live forests were the poorest in species due to their dimness and shadow, which did not offer propitious conditions for ants to settle (habitat populated by 1 and 2 ant species at nest density of $0.10 \times 10 \text{ m}^{-2}$ and 10% frequency). The greatest number – 5 ant species – were found, in the woodland glade (habitats 4), their nest density amounting to $3.3 \times 10 \text{ m}^{-2}$ and frequency reaching 100%.

In the deforested habitats there was observed succession of ant communities related to the age of plant community transformation. Density and frequency of nests were the lowest in the dead forest (habitat 1) and greater in the new forest plantings (habitat 2) as well as on the open areas of a young spruce forest (habitat 3). Besides

species recorded to occur in other habitats, also typical forest species were found in the latter habitat (*Leptothorax acervorum*, *Formica sanguinea*, *Camponotus herculeanus*).

Table 2. Ants of the forest habitats on the north-western slope of the Mumlowski Wierch (1 – dead forest above 2; 2 – new forest plantings, foot of the slope; 3 – young spruce forest, ca 15 years, above 1 and 2; 4 – woodland glade; 5 – live forest at the level of 1, 2 and 3; 6 – live forest below the top; 7 – the Hala Izerska)

Parameter	Habitat	Successional gradient			Not degraded habitats			
		1	2	3	4	5	6	7
Number of species		5	5	8	5	1	2	4
Density of ant-hills ($N \times 10 \text{ m}^{-2}$)		0.85±0.23	1.7±0.22	1.75±0.31	3.33±0.21	0.10±0.10	0.10±0.07	1.97±0.28
Frequency of ant-hills (%)		55	90	80	100	10	10	78
Contribution of species: dominance (%)/frequency (%)								
<i>Manica rubida</i> LATR.		—	—	—	30/83	—	—	—
<i>Myrmica ruginodis</i> NYL.		17.6/20	44.1/55	40/50	10/33	—	50/5	52.3/64
<i>Myrmica jacobsoni</i> KUTT.		11.8/10	20.6/35	17.1/30	5.1/17	—	50/5	35/33
<i>Myrmica rugulosa</i> NYL.		—	—	11.4/20	—	—	—	—
<i>Myrmica scabrinodis</i> NYL.		—	—	—	—	—	—	8.6/17
<i>Leptothorax acervorum</i> F.		—	—	5.7/10	—	—	—	—
<i>Lasius niger</i> L.		35.3/25	5.9/10	—	—	—	—	—
<i>Formica fusca</i> L.		11.8/10	—	11.4/10	15/50	—	—	—
<i>Formica lemni</i> BONDR.		17.6/15	23.5/30	5.7/10	39.9/100	—	—	4.1/5
<i>Formica sanguinea</i> LATR.		—	5.9/10	2.8/5	—	—	—	—
<i>Camponotus herculeanus</i> L.		—	—	5.7/5	—	100/5	—	—
Diversity of species (H')		1.52	1.32	1.76	1.39	0	0.69	1.05
Evenness (J)		0.94	0.84	0.94	0.87		1.0	0.76

Density and frequency of ant-hills in the two older deforested habitats did not statistically differ from the values estimated for the ant community on the Hala Izerska. In all the examined habitats (except the for live forests 5 and 6) the same species dominated, namely, *Myrmica ruginodis* and *M. jacobsoni*.

Diversity of ant species in the deforested habitats, the woodland glade and on the Hala Izerska was much alike (Shannon-Wiener's $H' = 1.05$ – 1.76), yet differed significantly from the values estimated for the forest habitats ($H' = 0$ and $H' = 0.69$, respectively).

The size of society (Table 3)

The dominants in the deforested habitats and on the Hala Izerska (*Myrmica ruginodis*, *M. jacobsoni*) were not noted to reveal any statistically significant differences in their society sizes in one and the same habitat. However, society sizes differed significantly when particular habitats were compared.

Also age structure of societies of these species varied in different habitats. Differentiation of the number of larvae, pupae and one-year old and older worker ants in the examined habitats amounted to Friedman's $\chi^2 = 5.1$; $p = 0.19$ for *M. ruginodis* and $\chi^2 = 6.0$; $p = 0.07$ for *M. jacobsoni*. It pointed to differentiation of the examined habitats in regard to living requirements of ants.

Table 3. The size and composition of ant societies (for denotations of habitats see Table 2)

Species	Habitat	1	2	3	7
	Stage				
<i>M. ruginodis</i>	larvae	154.0 ± 38.2	238.8 ± 47.3	220.3 ± 15.4	105.2 ± 51.3
	pupae	63.3 ± 15.6	11.9 ± 3.9	45.3 ± 36.2	79.7 ± 6.2
	young imagines	42.7 ± 21.4	148.0 ± 32.1	216.3 ± 84.6	108.2 ± 56.4
	old imagines	34.3 ± 5.9	140.8 ± 43.5	213.0 ± 23.1	108.2 ± 50.4
	Total	294.3 ± 43.8	539.5 ± 101.9	694.9 ± 274.1	401.3 ± 177.7
<i>M. jacobsoni</i>	larvae	—	243.7 ± 42.0	357.7 ± 59.3	317.6 ± 72.2
	pupae	—	9.2 ± 3.8	70.0 ± 39.3	107.4 ± 48.6
	young imagines	—	123.5 ± 4.9	523.7 ± 12.8	218.2 ± 71.3
	old imagines	—	95.2 ± 34.4	169.7 ± 66.6	225.8 ± 82.1
	Total	—	471.6 ± 70.5	1121.1 ± 166.2	869.0 ± 197.7
<i>M. scabrinodis</i>	larvae	—	—	—	237.0 ± 106.8
	pupae	—	—	—	70.0 ± 17.0
	young imagines	—	—	—	123.2 ± 25.1
	old imagines	—	—	—	300.0 ± 77.2
	Total	—	—	—	730.2 ± 176.0

In the young spruce forest (habitat 3) at the furthest stage of phytosociological transformations, societies of dominants (*Myrmica ruginodis*, *M. jacobsoni*) were the largest and were marked for a more advanced development of young generation than in the other deforested habitats. Pupae and young, one-year old worker ants were more abundant in these societies, which proved that also in the previous year these habitats offered better conditions for ant development. As compared to the habitats discussed above, societies of dominants on the Hala Izerska found there better living conditions, as attested by a greater abundance of pupae and one-year old worker ants.

The size of individuals (Table 4)

The dominating species *Myrmica ruginodis* and *M. jacobsoni* did not differ in respect to the mass of pupae, adult workers (one-year old and older) and queens in the same habitat. However, differences were recorded in the mass of individuals of the same species in different habitats. It concerned mainly one-year old and older worker ants, whose mass was smaller in habitats at the earlier stage of phytosociological transformations (1 and 2) than in the young spruce forest (3) and on the Hala Izerska (7). The mass of pupae was less diversified (statistically significant in the

habitat 1 and 2, 2 and 7, 3 and 7 in the case of *M. ruginodis*, and in the habitat 2 and 3 in the case of *M. jacobsoni*). The size of mature individuals formed an increasing series in the habitats:

$$1 < 2 > 7 < 3.$$

The recorded pattern indicated that ants found better living conditions and more food in the deforested habitat at an advanced stage of succession and in the woodless natural habitat than in habitats at an earlier stage of phytosociological transformations.

Table 4. Dry mass (mg/individual) of pupae and adults of dominating ant species in the degraded forest habitats on the slope of the Mumlawski Wierch and on the Hala Izerska (for denotations of habitat see Table 2)

Species	Stage	Habitat			
		1	2	3	7
<i>M. ruginodis</i>	worker pupae	0.43 ± 0.00	0.48 ± 0.02	–	0.35 ± 0.12
	sexual pupae	–	1.27 ± 0.14	1.08 ± 0.08	0.80 ± 0.06
	young worker imagines	0.86 ± 0.07	0.88 ± 0.01	1.16 ± 0.03	1.07 ± 0.03
	old worker imagines	0.89 ± 0.09	0.90 ± 0.05	1.15 ± 0.04	1.06 ± 0.06
	old queens	–	1.14 ± 0.96	–	–
<i>M. jacobsoni</i>	worker pupae	–	0.42 ± 0.03	–	0.44 ± 0.05
	sexual pupae	–	1.49 ± 0.00	0.95 ± 0.10	0.85 ± 0.03
	young worker imagines	–	0.89 ± 0.01	1.03 ± 0.11	1.02 ± 0.07
	old worker imagines	–	0.89 ± 0.04	1.08 ± 0.08	1.03 ± 0.04
	old queens	–	1.80 ± 0.10	1.57 ± 0.73	–

Ant society development index (Table 5)

Mean biomass of ant societies as well as ant production formed an increasing series paralleling the progressing stage of phytosociological transformations. However, the estimated values were lower for the Hala Izerska than for the open woodland glades of a young spruce forest, namely,

$$1 < 2 < 7 < 3.$$

Turnover of society biomass revealed a contrary tendency, i.e.

$$3 < 7 < 2 < 1.$$

The acquired data proved that better conditions for society development and lower mortality rate were characteristic of more stabilized habitats on Hala Izerska and in a young spruce forest as compared to habitats at earlier stages of phytosociological succession. A several times higher consumption recorded in the former habitats was also indicative of a more profuse food (mainly of small invertebrates) found there.

Table 5. Production, turnover of biomass and consumption of societies of *Myrmica* spp. in the degraded forest habitats on the Mumlawski Wierch and on the Hala Izerska (for denotations of habitats see Table 2). (Consumption calculated on the basis of $P/C = 0.026$ index (PĘTAL 1977))

Value	Habitat	1	2	3	7
Production (P) (mg d.wt.)		74.8 ± 24.8	145.8 ± 1.6	242.4 ± 78.6	167.7 ± 36.6
Society mass (B) (mg d.wt.)		125.7 ± 39.5	382.8 ± 64.5	848.4 ± 168.2	503.2 ± 104.2
P/B		0.59	0.38	0.28	0.33
Consumption (C) till mid-vegetation season:					
mg d.wt. per society		2876.9	5607.7	9307.7	6450.0
mg d.wt. × m ⁻²)		71.92	616.85	1116.92	1219.05

CONCLUSIONS

Changes in ant communities as observed in the degraded forest of Karkonosze should be related to formation of open, insolated areas, always preferred by ants, as well as to succession of grassy vegetation.

These areas are most likely populated by species occurring on woodland glades and nearby mountain pastures. Along with progressing habitat changes and plant succession the number of ant species as well as density and frequency of their nests increased, assuming values approximate to those recorded on the Hala Izerska.

In most of the examined habitats the same species dominated, namely, *Myrmica ruginodis* and *M. jacobsoni*. The mass of adult worker ants, the size of societies and their production tended to increase along with advancing stage of phytosociological habitat changes. On the other hand, turnover of society biomass decreased, which was indicative of a higher survival rate of ants. The recorded data attest to the fact that habitats at advanced stages of phytosociological transformations offer better conditions for ant development. Ants may find there not only better conditions for nesting but also greater food resources as evidenced by a several times greater consumption. This, in turn, points to an increasing contribution of ants to trophic network and nutrient cycling in habitat as well as evidences capabilities of ants in regulating abundance of other invertebrates.

Abundant populations of ants and good condition of ant societies in the deforested habitats were also determined by the age of these habitats. Significance of time factor lies in the fact that only after several years a proper size of ant societies may be attained and ants become capable of expansion (UCHMAŃSKI, PĘTAL 1982).

A noteworthy fact is that an opposite tendency of changes, i.e. a decrease in the number of species and density indices, dwindling society size and production, diminishing size of individuals and an increase in biomass turnover, was observed in a series of habitats under augmenting effect of such factors as intensive organic and mineral fertilization (PĘTAL 1974, 1976), industrial and transport pollution (PĘTAL 1980, KRZYSZTOFIAK 1991), peatland drainage (PĘTAL 1991).

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STRESZCZENIE

Reakcja zespołów mrówek na degradację środowisk leśnych w Karkonoszach

Badania prowadzono w degradujących się środowiskach leśnych w zachodniej części Karkonoszy. Badane środowiska charakteryzują się różnym stopniem przekształcenia roślinności leśnej – od dobrze zachowanych drzewostanów, poprzez drzewostany zniszczone z ustępującymi gatunkami borowymi w runie i gwałtownie rozwijającą się roślinnością trawiastą, po odnowione świerczyny. Wraz ze zmianami sukcesyjnymi roślinności występują zmiany w zespołach mrówek, które u podobniają się do zespołu terenów

otwartych – Hali Izerskiej. Zmiany te polegają na: a) wzroście liczby gatunków oraz zagęszczenia i frekwencji gniazd, b) wzroście wielkości społeczeństw, c) wzroście wielkości dorosłych osobników gatunków dominujących oraz d) spadku rotacji biomasy społeczeństw, t.j. wydłużeniu ekologicznej długości życia mrówek. Zmiany te są związane nie tylko z poprawą warunków życia mrówek, ale i z wiekiem środowisk.

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Ways to reproductive success of wood ant queens¹

Abstract. The notion of "reproductive success" in queens of the *Formica rufa* group is discussed in the context of the life strategy and evolutionary success of these species. A queen is successful whenever she manages to produce her own family, regardless of the fact whether this occurs in a nest of *Serviformica* ants, in an orphaned colony of her own or related species of wood ants or within a conspecific polygynous society.

Ecological evolution of species is best expressed by their tendency to more and more complete control of the environment (ALLEY et al. 1949). Wood ants of the *Formica rufa* group are an example of animals whose success in this field has been spectacular. New societies of these ants are founded through temporary social parasitism of queens in other colonies. Most myrmecologists share the opinion that the effectiveness of this particular way is very low. Young (mixed) colonies established in this way are recorded extremely seldom. At the same time, however, wood ants are very common and their abundance and biotic pressure exerted on the habitat ensure their position as dominants not only within multispecific competitive communities (SAVOLAINEN, VEPSÄLÄINEN 1988, PISARSKI, VEPSÄLÄINEN 1989) but in entire forest zoocoenoses as well. In order to explain this (apparent) contradiction it is essential to consider an analysis of the biological features which characterize the species under discussion together with an analysis of their geographical and habitat distribution.

Ants of the *F. rufa* group inhabit forests, mainly coniferous ones, in the northern Palaearctic. Thus, they have evolved in permanent, stable and trophically rich habitats. (The food basis of these ants consists of aphid honeydew – a constant and inexhaustible source of the so-called energetistic food). Wood ants owe their position in the competitive hierarchy to the high abundance of their societies (millions of individuals), to the high level of social organization (efficient exchange of information, division of labour), to the type of nest construction which guarantees not only safety

¹ An extended version of a lecture presented at the First European Congress of IUSSI "Biology and Evolution of Social Insects", Leuven, 1991.