



Succession of *Lasius* s. str. ant species (Hymenoptera: Formicidae) in moist pine forests – reassessment after taxonomic revisions of the subgenus¹

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Abstract: Czechowski et al. (1995) described the structure and structuring of ant assemblages along a successional gradient of moist pine forests (Peucedano-Pinetum and Leucobryo-Pinetum) in Poland. That paper did not take into account two systematic revisions where two common and abundant *Lasius* s. str. species, namely, *L. niger* (L.) and *L. alienus* (Först.), were split into two and three species respectively (Seifert 1991, 1992). In the light of the revised taxonomy and the present work, the former *L. niger*, in fact, included two sibling species: *L. platythorax* Seifert and *L. niger*, and the former *L. alienus* appeared to be *L. psammophilus* Seifert. In the present paper, the occurrence and abundances (nest densities) of these *Lasius* s. str. species in the successional habitats of the moist pine forests are reassessed according to the present taxonomic knowledge. The pioneer nature of *L. platythorax* in forest habitats is stressed.

Key words: *Lasius niger*, *Lasius platythorax*, *Lasius alienus*, *Lasius psammophilus*, assemblages, succession, pine forests, Poland

INTRODUCTION

The taxonomic status of *Lasius niger* and *L. alienus*, common members of the ant subgenus *Lasius* s. str., did not raise doubt for more than two centuries and one and a half centuries respectively after the two species were described. It was rather recently that revisions (Seifert 1991 and 1992 respectively) demonstrated that both were actually collective species, with the former containing two [*L. niger* (Linnaeus, 1758) and *L. platythorax* Seifert, 1991], and the latter three [*L. alienus* (Förster, 1850), *L. paralienus* Seifert, 1992 and *L. psammophilus* Seifert, 1992] sibling species that are quite clearly distinguishable morphologically and also differ in their ecological requirements (Seifert 1991, 1992, 1996; see also Czechowski et al. 2002). As for the latter criterion, an especially noticeable difference occurs between *L. niger* and *L. platythorax*, the first being a species of open habitats nesting in mineral soil, and the second a forest species nesting in organic substrate, mainly in wood. The ecological differentiation of the *L. alienus*-complex is more subtle; all the species are xerophilous, and the differences among them are mostly related to a type of soil substratum and the closure of the grass layer (see the above references for details).

It is obvious that the revisions brought about the depreciation of all earlier faunistic and ecological (including zooecological) data regarding the ‘old’ *L. niger* and *L. alienus* or at least made those data uncertain. The above applies also to data published for some years after Seifert’s papers, as the revisions were not immediately applied. Thus only a few papers – except for the two mentioned below (and a few unpublished dissertations) – had adopted the

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names of these rather common species until 1999 (Disney 1994, Prince 1996, Glaser 1998, Boer 1999, Markó 1999).

Consequently, old data should be re-examined and verified to the extent possible. So far three such reassessments have been published. The first two are devoted to specimens kept in the collection of the Museum and Institute of Zoology PAS in Warsaw (Radchenko et al. 1999a, b). The third paper reassesses Gallé's (1991) quantitative results concerning *Lasius* s. str. species found in his study on the structure and succession of ant assemblages in a sand dune habitat in Finland (Czechowski et al. 2005). The present paper brings the same in relation to *Lasius* s. str. in the study of Czechowski et al. (1995) on the composition and structuring of ant communities in the course of secondary succession of Polish moist pine forest. Some questions are also posed here about differences among *Lasius* s. str. species concerning the changes in their occurrence and abundance shown during the successional process.

STUDY AREAS, MATERIAL AND METHODS

The moist pine forest is a forest community commonly occurring on poor sandy soils with a low level of ground water. The pine (*Pinus sylvestris* L.) is the species building the tree stand, and it is accompanied mainly by birch (*Betula verrucosa* Ehrh.), rowan (*Sorbus aucuparia* L.), oak (*Quercus robur* L.), juniper (*Juniperus communis* L.), and occasionally by spruce [*Picea excelsa* (Lam.) Lk.], fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.). Within its range the moist pine forest occurs in two vicarious forms: subcontinental (Peucedano-Pinetum) in Eastern and North-Eastern Poland and farther on in Eastern Europe, and suboceanic (Leucobryo-Pinetum) in Western and partly Southern Poland and in Eastern Germany (for details see Matuszkiewicz W. 1981, Matuszkiewicz J. M. 1987).

The field studies were carried out in 1988 and 1989 in moist pine forests within three large forest complexes in Poland: Puszcza Białowieska (Białowieża Primeval Forest; Podlasie Lowland), Puszcza Biała (Biała Forest; Mazovian Lowland) and Bory Tucholskie (Tuchola Forests; Pomeranian Lake District) (see Fig. 1 in Czechowski et al. 1995). The former two forest complexes supported moist pine forests of the subcontinental form (in its subboreal and Sarmatian varieties respectively), while the third supported the Pomeranian-Silesian variety of the suboceanic form. Within each complex, ants were studied in plots representing four successional stages of moist pine forest: (I) plantation (4–7 years old), (II) young coppice (12 years old), (III) maturing tree stand (\approx 50 years old), and (IV) mature tree stand ($>$ 80 years old). For details concerning the study objects and plots, sampling methods and material obtained see Czechowski et al. (1995).

The present paper concentrates on the occurrence and nest densities of the *Lasius* s. str. species obtained during those studies by the biocoenometric method, and now reassessed in the light of current taxonomy of the subgenus and presented against data on entire local ant assemblages inhabiting moist pine forests. A total of 199 retained *Lasius* s. str. nest samples (out of 245 originally collected) have been re-determined. Despite of the loss of some samples, the retained material was sufficiently representative of all the study objects, plots and stages.

RESULTS

In general, three species of the subgenus *Lasius* s. str. have been revealed in the materials from the moist pine forest successional gradients in the three forest complexes: *L. platythorax* and *L. niger* (formerly reported as the collective species *L. niger*) and *L. psammophilus* (superseding the 'old' species *L. alienus*). Both members of the *L. niger/platythorax*-complex co-occurred only in the habitats studied in Puszcza Białowieska (Table 1); in Puszcza Biała and Bory Tucholskie, only *L. platythorax* was present (Tables 2 & 3). *L. psammophilus*, the only recorded

representative of the *L. alienus*-complex, was present only in Bory Tucholskie, where it occurred only at the young coppice stage as a subdominant species of the local ant community (Table 3).

Table 1. Approximate nest densities (number of nests per 1 ha) and proportions (%; in brackets) of particular ant species in the successional sequence of the moist pine forest in Puszcza Białowiecka (I – plantation, II – young coppice, III – maturing tree stand, IV – mature tree stand; + – minute density or proportion). (According to Czechowski et al. 1995 and Czechowski 1998, after re-determination of the *Lasius* s. str. species).

No.	Species	Successional stage			
		I	II	III	IV
1	<i>Myrmica ruginodis</i> Nyl.	150 (3.5)	50 (0.7)	1650 (52.3)	2830 (65.2)
2	<i>Myrmica scabrinodis</i> Nyl.	50 (1.2)	50 (0.7)	-	30 (0.7)
3	<i>Myrmica sabuleti</i> Mein.	-	-	-	70 (1.6)
4	<i>Myrmica lobicornis</i> Nyl.	-	100 (1.4)	50 (1.6)	30 (0.7)
5	<i>Myrmica schencki</i> Viereck	50 (1.2)	200 (2.8)	-	30 (0.7)
6	<i>Leptothorax acervorum</i> (F.)	30 (0.7)	50 (0.7)	1000 (31.7)	710 (16.4)
7	<i>Leptothorax muscorum</i> (Nyl.)	-	50 (0.7)	-	140 (3.2)
8	<i>Tetramorium caespitum</i> (L.)	2700 (63.1)	4750 (65.5)	-	30 (0.7)
9	<i>Strongylognathus testaceus</i> (Schenck)	-	50 (0.7)	-	-
10	<i>Formica (Formica) rufa</i> L.	0.5 (+)	-	1 (+)	+ (+)
11	<i>Formica (Formica) polyctena</i> Först.	1.5 (+)	-	1 (+)	-
12	<i>Formica (Formica) truncorum</i> F.	-	-	-	+ (+)
13	<i>Formica (Serviformica) fusca</i> L.	80 (1.9)	200 (2.8)	40 (1.3)	50 (1.2)
14	<i>Formica (Raptiformica) sanguinea</i> Latr.	5 (+)	-	-	-
15	<i>Camponotus (Camponotus) herculeanus</i> (L.)	10 (0.2)	-	-	-
16	<i>Lasius (Lasius) niger</i> (L.)	220 (5.1)	450 (6.2)	-	10 (0.2)
17	<i>Lasius (Lasius) platythorax</i> Seifert	930 (21.8)	1250 (17.2)	250 (7.9)	160 (3.7)
18	<i>Lasius (Cautolasius) flavus</i> (F.)	50 (1.2)	50 (0.7)	50 (1.6)	70 (1.6)
19	<i>Lasius (Chtonolasius) umbratus</i> (Nyl.)	-	-	100 (3.2)	170 (3.9)
20	<i>Lasius (Dendrolasius) fuliginosus</i> (Latr.)	-	-	10 (0.3)	10 (0.2)
Total density (per ha)		ca. 4280	ca. 7250	ca. 3150	ca. 4340

Table 2. Approximate nest densities (number of nests per 1 ha) and proportions (%; in brackets) of particular ant species in the successional sequence of the moist pine forest in Puszcza Biała (for explanations see Table 1). (According to Czechowski 1995, after re-determination of the *Lasius* s. str. species).

* – Earlier (among others in Czechowski et al. 1995) regarded as a junior synonym of *S. westwoodi* Westw. (see Czechowski et al. 2002).

No.	Species	Successional stage			
		I	II	III	IV
1	<i>Myrmica ruginodis</i> Nyl.	100 (17.6)	1050 (38.9)	300 (20.2)	1070 (37.4)
2	<i>Myrmica scabrinodis</i> Nyl.	-	150 (5.6)	50 (3.4)	30 (1.1)
3	<i>Myrmica sabuleti</i> Mein.	50 (8.8)	350 (13.0)	-	100 (3.5)
4	<i>Myrmica lobicornis</i> Nyl.	-	200 (7.4)	250 (16.9)	130 (4.5)
5	<i>Myrmica schencki</i> Viereck	-	250 (9.3)	-	30 (1.1)
6	<i>Stenamma debile</i> (Först.)*	-	50 (1.8)	-	-
7	<i>Leptothorax acervorum</i> (F.)	-	-	500 (33.7)	140 (50.3)
8	<i>Tetramorium caespitum</i> (L.)	-	500 (18.5)	-	-
9	<i>Formica (Formica) rufa</i> L.	1 (0.2)	0.5 (+)	0.5 (+)	+ (+)
10	<i>Formica (Formica) polyctena</i> Först.	1.5 (0.3)	0.5 (+)	2 (0.1)	0.5 (+)
11	<i>Formica (Formica) truncorum</i> F.	1 (0.2)	+ (+)	+ (+)	-
12	<i>Formica (Formica) pratensis</i> Retz.	0.5 (0.1)	0.5 (+)	+ (+)	+ (+)
13	<i>Formica (Serviformica) fusca</i> L.	10 (1.8)	-	80 (5.4)	20 (0.7)
14	<i>Formica (Raptiformica) sanguinea</i> Latr.	4 (0.7)	1 (+)	+ (+)	+ (+)
15	<i>Lasius (Lasius) platythorax</i> Seifert	350 (61.6)	50 (1.8)	-	-
16	<i>Lasius (Cautolasius) flavus</i> (F.)	50 (8.8)	50 (1.8)	300 (20.2)	30 (1.1)
17	<i>Lasius (Chtonolasius) umbratus</i> (Nyl.)	-	50 (1.8)	-	-
18	<i>Lasius (Dendrolasius) fuliginosus</i> (Latr.)	-	-	-	10 (0.3)
Total density (per ha)		ca. 570	ca. 2700	ca. 1480	ca. 2860

Table 3. Approximate nest densities (number of nests x 1 ha⁻¹) and proportions (%; in brackets) of particular ant species in the successional sequence of the moist pine forest in Bory Tucholskie (for explanations see Table 1). (According to Czechowski et al. 1995, after re-determination of the *Lasius* s. str. species).

No.	Species	Successional stage			
		I	II	III	IV
1	<i>Myrmica ruginodis</i> Nyl.	10 (7.8)	700 (20.0)	1300 (58.5)	1070 (47.8)
2	<i>Myrmica scabrinodis</i> Nyl.	5 (3.9)	-	150 (6.8)	130 (5.8)
3	<i>Myrmica sabuleti</i> Mein.	-	-	50 (2.3)	130 (5.8)
4	<i>Myrmica lobicornis</i> Nyl.	5 (3.9)	200 (5.7)	150 (6.8)	500 (22.3)
5	<i>Leptothorax acervorum</i> (F.)	45 (35.1)	100 (2.9)	500 (22.5)	330 (14.7)
6	<i>Tetramorium caespitum</i> (L.)	5 (3.9)	1300 (37.1)	-	-
7	<i>Formica (Formica) polyctena</i> Först.	-	-	0.5 (+)	-
8	<i>Formica (Formica) pratensis</i> Retz.	-	-	+(+)	+(+)
9	<i>Formica (Serviformica) fusca</i> L.	-	-	20 (0.9)	10 (0.5)
10	<i>Formica (Serviformica) cinerea</i> Mayr	35 (27.3)	-	-	-
11	<i>Formica (Raptiformica) sanguinea</i> Latr.	3.5 (2.7)	+(+)	-	-
12	<i>Lasius (Lasius) platythorax</i> Seifert	20 (15.6)	150 (4.3)	50 (2.3)	70 (3.1)
13	<i>Lasius (Lasius) psammophilus</i> Seifert	-	1050 (30.0)	-	-
Total density (per ha)		ca. 130	ca. 3500	ca. 2220	ca. 2240

In Puszcza Białowieska, where *L. platythorax* and *L. niger* occurred side by side, the former was much more abundant and it was found in all stages of the moist pine forest. An analysis of relative nest density taking into account the whole successional gradient revealed that *L. platythorax* constituted 79% and *L. niger* 21% of this two-species complex. In particular successional stages, the *platythorax/niger* ratios were as follows: 81% : 19% in the forest plantation, 74% : 26% in the young coppice, and 94% : 6% in the mature tree stand, with no *L. niger* recorded in the maturing tree stand. Similarly, in Bory Tucholskie *L. platythorax* occurred across the whole successional gradient of the moist pine forest. In Puszcza Biała, it was recorded only in the two early stages. Both *L. platythorax* nest densities and proportions in ant communities varied widely between the forest complexes, as well as locally, i.e. within succession series (Tables 1–3).

DISCUSSION

The state of whole ant assemblages of the moist pine forests and the course of their succession in three variants corresponding to the particular forest complexes were discussed in the original paper (Czechowski et al. 1995). Following reassessment of the data on the *Lasius* s. str. species in the present paper, those original considerations have retained general validity. The only issue that actually merits a comment is the transfer (of all or most) of the results formerly ascribed to *L. niger* to *L. platythorax*, the reasons being ecological rather than taxonomic. The ‘old’ *L. niger* (as a collective species) was considered to be a eurytope (ubiquist) with an unusually wide ecological flexibility and a great biological plasticity that manifested itself, among others, in the ‘species’ ability to nest both in mineral soil and organic substrate. Conversely (and opposed to the current ecological status of *L. niger*, a ground-nesting polytope of dry open habitats), *L. platythorax* is a forest polytope preferring fairly humid sites and it nests in organic substrate, particularly in rotten wood (Seifert 1991, 1992, 1996). The occurrence of *L. platythorax* in the succession series of moist pine forests studied was associated specifically with the presence of rotten wood in the study sites.

As Czechowski et al. (1995) found, “The course of succession [of the ant assemblage] leading to the final state [...] depended on very many factors, including the local habitat conditions, the composition of the myrmecofauna in the adjoining habitats, remnants of the [plant] community from the previous tree stand ...”. These “remnants” are, most importantly,

rotten stumps left over following a clear-cut of the previous stand and gradually disappearing as a result of decomposition during the growth of the new forest.

In the ant assemblages, *L. platythorax* was a major contributor to overall abundance only at the youngest stages of forest succession, i.e. plantations, being the first (ca. 62%), second (ca. 22%) and third (ca. 16%) species in respect of nest density in Puszcza Biała, Puszcza Białowieska and Bory Tucholskie respectively. At the same time, these high ranks of *L. platythorax* were, in practice, the most striking common feature of the ant communities in all the plantations studied. High shares of *L. platythorax* in the ant assemblages of the forest plantations were usually accompanied by relatively high abundance of the species at this stage of forest succession, which was most spectacular in Puszcza Biała and Puszcza Białowieska (Tables 1–3). All these findings point to a pioneer nature of the species, which, of course, is able to manifest itself in full only in the presence of an ample number of suitable nesting places. Puszcza Białowieska was a case in point as the local plantations were particularly abundant in stumps left over after logging and *L. platythorax* nest density at this stage (ca. 930/ha) reached the highest values compared to the plantations in the other two forest complexes studied. The pioneering nature of *L. platythorax* is well illustrated by its occurrence in a relatively early successional stage of sand dune habitats in Finland (a site sparsely overgrown with herb vegetation), where the species nested under or in decaying pieces of wood artificially introduced in the habitat (Czechowski et al. 2005).

In the context of the above findings, the low nest density of *L. platythorax* at the plantation stage in Bory Tucholskie is puzzling, in comparison with both the more advanced stages of local forest succession and plantations in the other forest complexes (46.5-fold and 17.5-fold, respectively, lower than in Puszcza Białowieska and Puszcza Biała; Tables 1–3). Such big differences cannot be wholly ascribed to differences in numbers of rotten stumps available. Other factors must have been at play there, such as, perhaps, interspecific competition. The plantation in Bory Tucholskie (and no other stage anywhere) supported abundant *Formica cinerea* Mayr (Table 3), a highly aggressive and strongly competitive ant species (see Markó & Czechowski 2004, Czechowski & Markó 2005). Its competitive impact (perhaps even direct aggression) might have been the factor limiting the abundance of *L. platythorax* in this site. This is even more probable as all older successional stages in Bory Tucholskie, where *F. cinerea* was not recorded, supported (exceptionally) much higher densities of *L. platythorax* which were comparable to density figures obtained in corresponding stages of moist pine forest succession at other forest complexes (Tables 1–3).

The problem of *L. psammophilus*, the only member of the *L. alienus*-complex recorded during the studies, is also intriguing. The species occurred only in Bory Tucholskie, and only in the young coppice stage, but it was strikingly abundant there. The question arises why this evidently pioneer species of open sandy habitats (Czechowski et al. 2005) was lacking from the local forest plantation. Its absence from that early successional stage cannot be explained only by the presence of *Formica cinerea* as these two, though competitive, species are able to occur side by side (see Markó & Czechowski 2004).

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STRESZCZENIE

[Sukcesja gatunków mrówek *Lasius* s. str. (Hymenoptera: Formicidae) w borach świeżych – weryfikacja po rewizjach taksonomicznych podrodzaju]

W opracowaniu poświęconym kształtowaniu się zespołów mrówek w trakcie sukcesji wtórnej borów świeżych (Peucedano-Pinetum i Leucobryo-Pinetum) w Puszczy Białowieskiej, Puszczy Białej i Borach Tucholskich (Czechowski et al. 1995) nie uwzględniono poprzedzających je rewizji taksonomicznych podrodzaju *Lasius* s. str., rozbijających dotychczasowe, jak się okazało, gatunki zbiorcze *Lasius niger* (L.) i *L. alienus* (Först.) na, odpowiednio, dwa (Seifert 1991) i trzy (Seifert 1992) gatunki bliźniacze. Niniejsze opracowanie weryfikuje tamte wyniki w zakresie składu i liczebności (zagęszczeń gniazd) zgrupowań gatunków *Lasius* s. str. stosownie do aktualnego stanu taksonomii tego podrodzaju. Powtórne oznaczenie dawnych materiałów wykazało obecność we wszystkich badanych środowiskach łącznie trzech gatunków *Lasius* s. str.: *L. platythorax* Seifert i *L. niger* (w miejsce poprzednio wykazanego *L. niger*) oraz *L. psammophilus* Seifert (zamiast poprzednio wykazanego *L. alienus*). Oba gatunki z kompleksu *L. niger/platythorax* współwystępowały z sobą (przy dużej przewadze *L. platythorax*) tylko w ciągu sukcesyjnym boru świeżego w Puszczy Białowieskiej; w Puszczy Białej i Borach Tucholskich obecny był tylko *L.*

platythorax, leśny gatunek politopowy. Obecność *L. psammophilus* odnotowano tylko w stadium młodnika boru świeżego Borów Tucholskich. Szczegółowe wyniki (na tle składów całych zespołów mrówek) zawierają tabele 1–3. Na podkreślenie zasługuje ujawniony w badaniach pionierski charakter *L. platythorax*, przejawiający się jego licznym występowaniem we wczesnych stadiach sukcesyjnych borów świeżych, zwłaszcza tam, gdzie po wycięciu poprzedniego drzewostanu pozostało wiele próchniejących pniaków, stanowiących dogodne miejsca gniazdowania dla tego dendrofilnego gatunku.

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