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Ant communities (Hymenoptera: Formicidae) of Flemish (north Belgium) wet heathlands, a declining habitat in Europe

DIRK MAES[1,*], HANS VAN DYCK[2], WOUTER VANREUSEL[2] and JOERI CORTENS[2]

[1]Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium
[2]University of Antwerp, Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium

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Abstract. During a survey of 23 wet heathland sites in Flanders (north Belgium) in 1999 and 2000, using both manual nest searching and pitfall traps as sampling techniques, we found 28 ant species. One species (*Myrmica lonae*) was new to the Belgian fauna and several rare species were encountered. Three ecological groups could be distinguished based on soil preference: the first group of species was characteristic of sandy soil, the second contained species that were more numerous on peat soil (with *Sphagnum* spp.), and the third group of species had no soil preference. Ant nest numbers increased strongly between 1999 and 2000, especially on the plots that were inundated during the winter of 1999–2000, but the number of ant species did not differ significantly between years. Ant nest density showed an optimum at a Purple Moor-grass (*Molinia caerulea*) cover of about 45%; the number of species did not show such an optimum. Pitfall traps yielded more species than manual nest searching; in particular temporary social parasites, species with a large foraging range and winged females from the surrounding habitats were missed by the latter technique. Finally, we give some recommendations for the conservation of, and suitable management measures for, ants on wet heathland.

INTRODUCTION

Despite the widely recognised conservation importance of wet heathlands, detailed information on the distribution and abundance of typical heathland and other species, particularly invertebrates, is scarce. Ants are among those poorly investigated invertebrates even though they play an important ecological role in many ecosystems and are increasingly used in a management and restoration context (Bisevac & Majer, 1999; York, 2000). They have a major influence on soil development (especially on sites where earthworms are absent) and nutrient cycling, they often represent the largest biomass in various biotopes; and, are important predators of other arthropods (Hölldobler & Wilson, 1990; Seifert, 1996; Alonso & Agosti, 2000). Many heathland ant species are endangered in the few NW-European countries where their conservation status has been assessed (Falk, 1991 - Great Britain; Seifert, 1998 - Germany). Dry *Calluna* heathlands have been sampled rather extensively for ants (e.g. Brian, 1964; Mabelis, 1976; Assing, 1989), but studies dealing with wet *Erica* heathlands are rare. Furthermore, little is known about the effects of habitat degradation on ant species composition and ant nest density and few studies have examined between-year variation in the presence of species and their nest densities in the same site (Elmes et al., 1998).

North Atlantic wet heathland dominated by *Erica tetralix* is a semi-natural, declining habitat in Europe (Habitat 31.11 in the EU Habitat Directive 92/43/EEC). It is restricted to a relatively narrow coastal zone with an oceanic climate from SW-Norway to Portugal (Gimmingham, 1972). The decline of heathland area in several European countries (estimated at up to 80% - Gimmingham, 1981; Webb, 1989; Riecken et al., 1994) has mainly been caused by afforestation and changes in agricultural practices (Webb & Haskins, 1980; Rebane & Wynde, 1997). This in turn has lead to severe fragmentation and isolation of the remaining heathland sites and hampers the conservation of many, especially sedentary, heathland species (Webb & Hopkins, 1984; Webb, 1989; Webb & Thomas, 1994). In Belgium, wet heathlands are restricted to the Campine region of NE Flanders (north Belgium) and to the "Hautes Fagnes" region in Wallonia (south Belgium). Wet heathland is one of the most threatened habitats in Flanders because it has declined strongly in both distribution area (85% decline - Allemeersch et al., 1988) and in quality (71% decline, based on the former and present "completeness" of the habitat using indicator values of typical wet heathland plants - Van Landuyt, 2002) and because its current area is very restricted (about 1800 ha) and fragmented. The high values of nitrogen deposition in Flanders (north Belgium) - on average 30–50 kg/ha/year with peaks of more than 90 kg/ha/year in some regions, Vanongeval et al. (1998) - cause a serious threat for the conservation and the management of heathland remnants. The nitrogen input via atmospheric deposition is now higher than what can be fixed by the heathland vegetation (5–20 kg/ha/year - Geypens et al., 1994; Van Gijseghem et al., 2000). This nitrogen surplus, together with a lowering of the water table and lack of management measures have transformed many heathland sites into a dense and high vegetation dominated by the Purple Moor-grass *Molinia caerulea*

* Corresponding author. Phone: +32.2.558.18.37; fax: +32.2.558.18.05; e-mail: dirk.maes@instnat.be

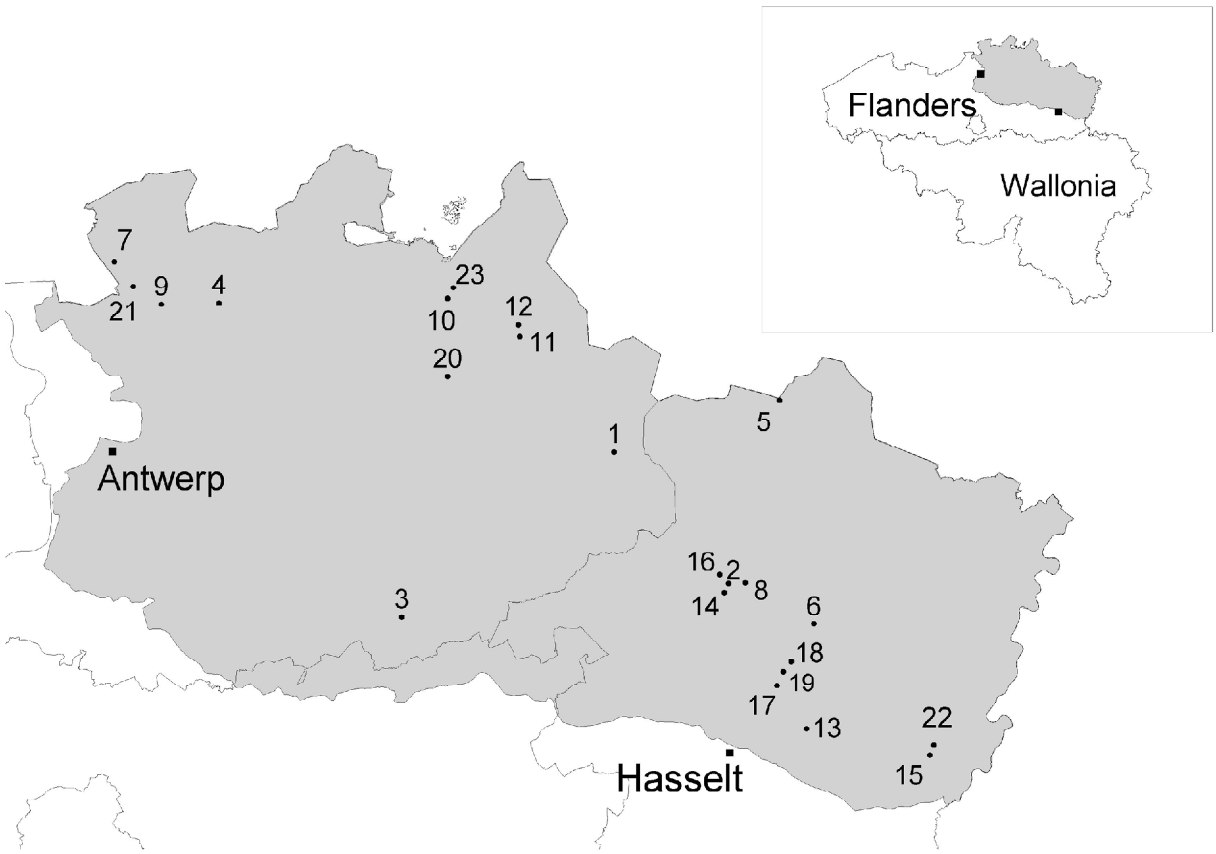

Fig. 1. Location of the sampled sites in Belgium. The Campine region is shaded in gray both on the small map of Belgium and on the detailed map with the sampled sites. Site numbers correspond with those in Table 1.

(Berendse & Aerts, 1984; Berendse et al., 1987; Aerts & Berendse, 1988; Aerts et al., 1990). The decline in habitat area and habitat quality of wet heathlands has led to a high number of typical wet heathland species being listed as threatened, e.g. the carabid beetle *Carabus clathratus* (Desender et al., 1995), the dolichopodid fly *Dolichopus atratus* (Pollet, 2000), the butterfly *Plebeius argus* (Maes & Van Dyck, 2001) and the dragonfly *Somatochlora arctica* (De Knijf & Anselin, 1996).

In this article, we deal with 1) the description of ant communities on wet heathlands in Flanders, 2) fluctuations in ant nest numbers and species between two sampling years, 3) the effects of *Molinia caerulea* cover (as a measure of habitat degradation) on ant diversity and nest density, and 4) methodological differences between manual nest searching and pitfall trap sampling and their suitability for ant surveys.

MATERIAL AND METHODS

Study areas and sampling methods

We selected 23 wet heathland (*Ericion tetralicis*, Schaminée et al., 1995) sites (Fig. 1) using the "Biological Valuation Map" (a database with biotopes covering the whole of Flanders, De Blust et al., 1994). The extent of wet heathland in the sampled sites was derived from the Biological Valuation Map and additional GPS measurements (Table 1). Ant nests were searched manually in 60 plots of 100 m^2 (10 m × 10 m) during July and August 1999 and 2000 (Table 1) by inspecting all possible nest sites (grass tussocks, sphagnum moss, soil, dead wood, etc. - Elmes et al., 1998). Depending on the variation in vegetation structure, we spent 4–6 man-hours searching in each plot. For each ant nest we collected at least five workers in small Eppendorf tubes. In large sites we usually sampled more than one plot. Additionally, in 9 sites, eighteen plots (two per site) were sampled by means of pitfall traps (diameter = 9 cm) between 30 March 2000 and 15 March 2001. In and around each plot, six pitfall traps, filled with a 4% formaldehyde solution, were placed at a distance of about 10 m from each other and were emptied at fortnightly intervals (Parr & Chown, 2001). In the laboratory, ants were sorted out and classified using Klein et al. (1998) and Wardlaw et al. (1998 for the *Myrmica* spp. and Seifert (1996) and Van Boven & Mabelis (1986) for the other species. In all plots, we determined the soil type (peat, i.e. with *Sphagnum* mosses, vs. sand) and we measured % vegetation cover in four subplots of 2 m × 2 m using the Londo scale (Schaminée et al., 1995). The best represented plant species in the plots were *Molinia caerulea* (present in 98% of the plots, mean coverage 42.3%), *Erica tetralix* (92%, 25.4%), *Calluna vulgaris* (75%, 11.3%), *Gentiana pneumonanthe* (57%, 0.6%) and *Scirpus cespitosus* subsp. *germanicus* (34%, 3.7%).

Analyses

We determined ecological groups based on densities per plot using a Two Way Indicator Species Analysis (TWINSPAN - Hill, 1979), using the ant data obtained from manual nest searching; if plots were sampled in both years, ant nest numbers were averaged across years; only plots with at least three ant

TABLE 1. Plot code and plot area of the investigated sites. M1999, M2000: manual searching in 1999/2000: number of ant nes (between brackets the number of species); P2000 = pitfall traps in 2000: number of individuals (between brackets the number species).

Site	Plot	Area (in m^2)	M1999	M2000	P2000
1. Buitengoor-Meergoor	BUI-1-1	5126	11 (2)	–	–
	MEE-1-1	4497	5 (2)	–	–
	MEE-1-2	4497	1 (1)	–	–
	MEE-3-1	1348	8 (4)	–	–
2. Fonteintje	ZWB-2-1	52944	15 (5)	–	134 (12)
	ZWB-2-2	52944	12 (6)	–	–
	ZWB-2-3	52944	–	64 (5)	–
3. Goor	GOO-1-1	1437	1 (1)	–	–
4. Groot Schietveld	GRS-1-1	7382	11 (4)	–	–
	GRS-4-1	11503	10 (1)	21 (2)	–
	GRS-5-1	2410	9 (1)	11 (2)	–
	GRS-8-1	1015	9 (5)	16 (3)	–
5. Hageven	HAG-1-1	1192	15 (4)	33 (8)	–
	HAG-15-1	816	–	18 (6)	264 (14)
	HAG-2-1	1244	10 (4)	–	–
	HAG-3-1	10574	–	19 (6)	–
	HAG-5-1	6791	19 (6)	–	190 (10)
	HAG-5-2	6791	10 (4)	–	–
	HAG-8-1	2838	19 (5)	19 (6)	–
	HAG-8-2	2838	16 (3)	–	–
6. Houthalen-Helchteren	HHH-1-1	12466	16 (6)	9 (4)	103 (12)
	HHH-3-1	2568	–	20 (5)	445 (17)
7. Kalmthoutse hei	KAL-2-1	2985	12 (2)	–	–
	KAL-3-1	10975	7 (2)	–	–
	KAL-4-1	8735	–	63 (6)	1172 (12)
8. Katershoeve	ZWB-4-1	5843	23 (5)	27 (6)	–
9. Klein schietveld	KLS-1-1	22357	–	39 (7)	–
10. Koeiven	KOE-1	14104	–	44 (5)	336 (11)
11. Korhaan	KOR-1	2274	3 (3)	–	–
12. Liereman	LIE-1-1	10288	21 (6)	–	–
	LIE-1-2	6889	12 (2)	29 (1)	–
	LIE-2-1	41563	12 (4)	–	143 (9)
	LIE-2-2	41563	–	43 (4)	–
	LIE-3-1	19593	–	29 (5)	106 (7)
13. Maten	MAT-1-1	8550	9 (3)	–	–
	MAT-2-1	692	1 (1)	–	–
14. Mathiashoeve	ZWB-1-1	17514	19 (5)	37 (7)	–
	ZWB-5-1	8634	–	50 (4)	291 (12)
	ZWB-5-2	8634	–	12 (4)	–
15. Neerharenheide	NEE-1-1	6742	13 (4)	–	–
16. Panoramaduinen	ZWB-3-1	29919	22 (5)	25 (6)	–
	ZWB-3-2	29919	36 (6)	38 (6)	266 (8)
	ZWB-6-1	2338	–	33 (6)	415 (13)
17. Slangebeekbron	SLA-2-1	547	8 (4)	–	–
18. Tenhaagdoornheide	TEN-1-1	1152	6 (3)	–	–
19. Teut	TEU-1-1	47729	6 (4)	20 (5)	117 (11)
	TEU-2-1	6250	24 (3)	–	–

TABLE 1 (continued).

Site	Plot	Area (in m^2)	M1999	M2000	P2000
	TEU-3-1	3973	20 (6)	–	85 (10)
	TEU-3-2	3973	–	12 (2)	–
20. Tielenhei	TIE-1-1	1212	3 (2)	–	–
21. Withoefse heide	WIT-1-1	25932	18 (7)	17 (6)	138 (11)
	WIT-1-2	25932	17 (5)	17 (5)	–
	WIT-1-3	25932	–	2 (1)	–
	WIT-1-4	25932	–	5 (3)	–
22. Ziepbeek	ZIE-1-1	20228	10 (4)	28 (5)	150 (6)
	ZIE-2-1	8833	29 (3)	50 (3)	–
	ZIE-3-1	10570	36 (3)	–	141 (7)
	ZIE-4-1	2274	28 (4)	–	–
23. Zwart water	ZWW-1-1	26869	11 (4)	–	333 (13)
	ZWW-1-2	26869	–	22 (4)	–
Number of plots	60		44	32	18

nests (n = 53) and species present in at least five plots (n = 11) were used in the analysis. Differences in overall and specific ant nest densities and in species richness between 1999 and 2000 were tested using a paired t-test. The relationships between ant diversity and nest densities (averaged across years) on the one hand and % *Molinia caerulea* cover on the other was examined by a polynomial regression of the second order. Numbers of species found by manual nest searching and pitfall trap sampling were compared only for the twelve plots that were investigated by both techniques in 2000.

RESULTS

Ant diversity and communities

During the two years of sampling, we found 28 ant species (Table 2), representing 53% of all indigenous species in Flanders (Dekoninck & Vankerkhoven, 2001a). One species, *Myrmica lonae*, was new to the Belgian fauna.

Ant diversity tended to be positively correlated with site area (N = 47, Spearman R = 0.264, p = 0.07) but not with plant species richness (N = 52, Spearman R = –0.151, p = 0.29); ant diversity did not differ significantly between sandy and peat soils (3.89 (n = 35) vs. 4.18 (n = 25), Kruskall-Wallis H (1,60) = 0.324, p = 0.57).

The TWINSPAN distinguished three ecological groups of ants on wet heathlands in Flanders. A first group of species was more numerous in the plots on sandy soil (Kruskall-Wallis test H (1,50) = 5.846, p = 0.016): *Formica fusca*, *Lasius niger*, *Leptothorax acervorum*, *Myrmica sabuleti* and *Tetramorium caespitum*. A second group consisted of two species that were more abundant in the plots on peat soil (with *Sphagnum* spp.) (Kruskall-Wallis H (1,56) = 14.414, p < 0.001): *Formica transkaucasica* and *Myrmica scabrinodis*. The four remaining species did not show any preference for soil type (Kruskall-Wallis H (1,122) = 0.018, p = 0.89): *Lasius platythorax*, *Leptothorax muscorum*, *Myrmica ruginodis* and *M. rubra*.

Nest densities and between year fluctuations in nest densities

Overall nest density varied strongly among plots (1–64/100 m^2, Table 1) and was positively correlated with site area (N = 47, Spearman R = 0.488, p < 0.001). Nest density was significantly higher in plots on peat soil (5.8 nests/100m^2, n = 25) than in plots on sandy soil (4.0 nests/100 m^2, n = 35; Kruskall-Wallis: H (1,60) = 4.901, p = 0.027), although the % cover of the most frequently used nest substrate (*Molinia caerulea* tussocks) did not differ significantly between soil types (Kruskall-Wallis H (1,51) = 0.239, p = 0.62).

The mean number of ant nests per plot was significantly lower in 1999 than in 2000, but the mean number of species per plot was similar across both years (Table 3). When grouping species with different life strategies (*Lasius* spp. and *Formica* spp. with stable and long-living nests on the one hand and *Myrmica* spp. with transient nests on the other) the number of nests is only significantly different for the *Myrmica* spp. (Table 3). Considering the species separately, two species had significantly higher nest densities in 2000 compared with 1999: *Myrmica ruginodis* and *Myrmica scabrinodis* (Table 3). The difference between the abundance of ant nests between 1999 and 2000 can be explained by the fact that six of the sixteen investigated plots were inundated for several weeks during the winter of 1999–2000. These plots had to be re-colonised by ants in the following spring or ants had to survive inundation for several weeks. Analysing the inundated and non-inundated plots separately, showed that the number of ant nests was significantly higher in 2000 in the inundated plots (paired t-test, t = –4.259; p = 0.008) but not in the non-inundated plots (paired t-test, t = –0.847; p = 0.42). Furthermore, the number of nests increased particularly for species that occur in wetter and cooler microclimates (*Myrmica scabrinodis*, *M. ruginodis* and *Lasius platythorax*) whereas species of drier microclimates (*Lasius niger* and *Myrmica sabuleti*) tended to decrease (Table 3) suggesting that microclimatic changes in the inundated plots probably caused a shift towards the

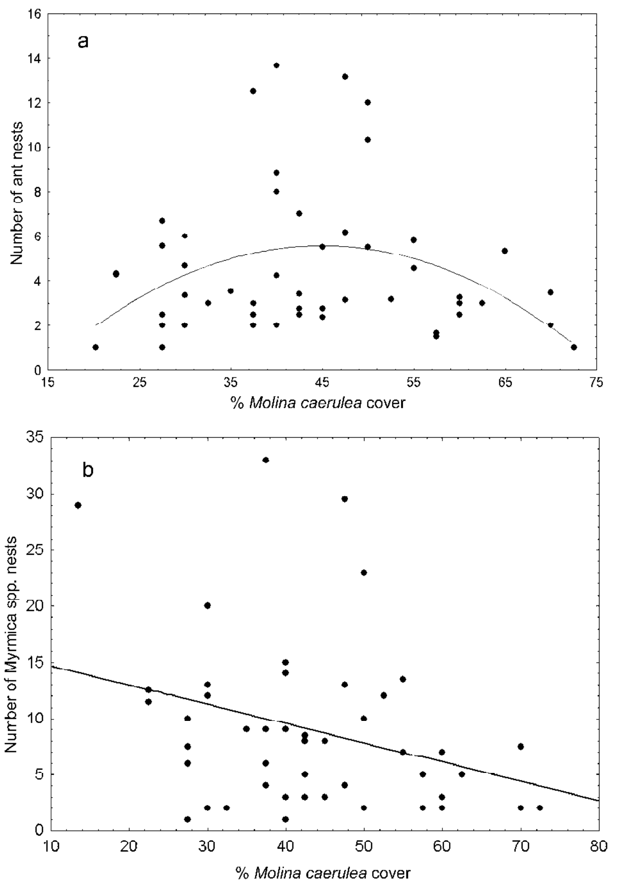

Fig. 2. a – number of ants nests as a function of percent *Molinia caerulea* cover. The line is a fit of a polynomial regression of the second order; b – number of *Myrmica* ant nests as a function of percent *Molinia caerulea* cover. The line is a fit of a simple regression.

part of the spectrum representing species that prefer wetter and colder conditions.

TABLE 3. Mean species and ant nest number and specific ant nest numbers in the 16 plots that were manually sampled in 1999 and in 2000 (between brackets the number of plots used in the analyses). Differences are tested by means of a paired t-test (t). ** = p < 0.01, * = p < 0.05, $^{n.s.}$ = not significant.

	1999	2000
No. of ant nests (16)	17.4	23.8**
No. of ant species (16)	4.3	4.5$^{n.s.}$
Species with stable nests (16)		
Lasius spp. and *Formica* spp.	8.9	11.4$^{n.s.}$
Species with transient nests (16)		
Myrmica spp.	7.6	11.7$^{n.s.}$
Formica fusca (5)	1.2	2.2$^{n.s.}$
Formica transkaucasica (5)	7	7.8$^{n.s.}$
Lasius niger (5)	3.2	2.6$^{n.s.}$
Lasius platythorax (13)	6.6	9.2$^{n.s.}$
Myrmica rubra (12)	1.7	1.8$^{n.s.}$
Myrmica ruginodis (10)	3.2	4.8*
Myrmica sabuleti (4)	2.5	1.8$^{n.s.}$
Myrmica scabrinodis (14)	4.3	7.9*

TABLE 2. Species list and number of nests (between brackets the number of plots in which the species was found) for all species that were found by manual nest searching in 1999 (MS1999, 44 plots) and in 2000 (MS2000, 32 plots) and the number of individuals per ant species in the pitfall traps (PF2000, 18 plots).

Species	MS1999	MS2000	PF2000
Formica cunicularia	2 (1)	3 (2)	7 (4)
Formica fusca	11 (6)	28 (9)	214 (4)
Formica pratensis	–	–	5 (5)
Formica rufa	–	–	2 (1)
Formica rufibarbis	1 (1)	–	23 (2)
Formica sanguinea	–	2 (1)	411 (9)
Formica transkaucasica	93 (14)	44 (7)	293 (11)
Lasius flavus	1 (1)	2 (1)	3 (1)
Lasius fuliginosus	–	–	15 (6)
Lasius meridionalis	–	–	17 (10)
Lasius mixtus	–	–	1 (1)
Lasius niger	34 (12)	24 (8)	444 (7)
Lasius platythorax	179 (33)	291 (25)	838 (17)
Lasius psammophilus	–	–	1 (1)
Lasius umbratus	–	–	49 (14)
Leptothorax acervorum	4 (4)	15 (5)	21 (6)
Leptothorax muscorum	2 (2)	3 (2)	21 (4)
Myrmica lonae	3 (1)	–	–
Myrmica rubra	47 (25)	88 (22)	242 (17)
Myrmica ruginodis	70 (25)	109 (23)	464 (18)
Myrmica sabuleti	24 (6)	26 (6)	823 (9)
Myrmica scabrinodis	125 (26)	203 (25)	555 (18)
Myrmica schencki	1 (1)	4 (3)	140 (8)
Stenamma debile	–	–	4 (3)
Strongylognathus testaceus	–	–	5 (2)
Tapinoma ambiguum	6 (2)	1 (1)	1 (1)
Tapinoma erraticum	1 (1)	2 (1)	12 (1)
Tetramorium caespitum	8 (3)	17 (4)	218 (5)
Number of nests/individuals	612	856	4829
Number of species	18	17	28

The effect of *Molinia caerulea* encroachment on ant diversity and nest density

The highest overall nest densities were found on plots with a *Molinia caerulea* cover between 38–50%. Overall nest density increased non-linearly with % *Molinia caerulea* cover. A linear regression did not show a significant relationship between the variables (R^2= 0.001, F(1,48) = 0.055, p = 0.81). However, addition of the second order term for % *Molinia caerulea* cover explained a significant proportion of the variation in the overall nest density (R^2 = 0.13, F(2,47) = 3.509, p = 0.038). Overall nest density reached an optimum at 40–45% *Molinia caerulea* cover (Fig. 2a). Species with stable and long-lived nests (*Lasius* spp. and *Formica* spp.) show no significant linear correlation between % *Molinia caerulea* cover and nest densities (R^2 = 0.02, F(1,45) = 0.932, p = 0.339); including the second order

TABLE 4. Number of plots that were both manually searched and sampled by means of pitfall traps in 2000 (total = 12) in which each ant species was found. MS = manual nest searching in 2000. PF (YC) = pitfall trap results of the complete yearly cycle (30 March 2000–15 March 2001); PF (JA) = pitfall trap results of July-August 2000; PF (FN) = fortnight pitfall trap period in which the manual nest searching took place.

Species	MS	PF(YC)	PF(JA)	PF(FN)
Formica cunicularia	–	3	3	2
Formica fusca	3	10	10	5
Formica pratensis	–	5	2	2
Formica rufibarbis	–	2	2	2
Formica sanguinea	1	6	5	4
Formica transkaucasica	4	8	4	4
Lasius flavus	–	1	–	–
Lasius fuliginosus	–	5	3	2
Lasius meridionalis	–	7	7	5
Lasius mixtus	–	1	–	–
Lasius niger	4	5	5	4
Lasius platythorax	10	11	11	10
Lasius psammophilus	–	1	1	–
Lasius umbratus	–	10	10	4
Leptothorax acervorum	3	4	3	–
Leptothorax muscorum	1	2	1	1
Myrmica rubra	11	11	10	5
Myrmica ruginodis	10	12	12	7
Myrmica sabuleti	3	7	5	4
Myrmica scabrinodis	11	12	12	6
Myrmica schencki	1	4	4	3
Stenamma debile	–	2	–	–
Strongylognathus testaceus	–	1	1	–
Tetramorium caespitum	4	4	4	3
No. of species	13	24	21	18
Average No. of species per plot	5.5	11.2	9.6	6.1

term of % *Molinia caerulea* cover did not improve the proportion of variation explained (R^2 = 0.02, F(1,44) = 0.472, p = 0.63). *Myrmica* spp., with transient nests, showed a significant negative linear correlation with % *Molinia caerulea* cover (R^2 = 0.09, F(1,45) = 4.626, p = 0.037, Fig. 2b). We found no significant (non-linear) relationship between ant diversity and % *Molinia caerulea* cover (R^2 = 0.05, F(2,47) = 1.306, p = 0.28).

Differences between manual nest searching and pitfall sampling

Pitfall traps resulted in a higher number of species than manual nest searching (Table 4). If only the pitfall trap results of the fortnightly period in which the manual searching took place were compared with the results of the manual searching, six species were caught exclusively by pitfall traps: *Formica cunicularia*, *F. pratensis*, *F. rufibarbis*, *Lasius fuliginosus*, *L. meridionalis* and *L. umbratus*. The first three species are not typical of wet heathlands and may only be present at very low nest densities, which may explain their absence in the manually searched plots. The latter three species are temporary social parasites on other *Lasius* spp. (Seifert, 1996) of which, almost exclusively, winged females were found; the absence of workers of the three *Lasius* spp. indicates that they do not necessarily nest in the sites in which the sexuals were found. Only one species was found by manual nest searching alone (*Leptothorax acervorum*).

The number of species per plot was significantly higher in the year-long catch from the pitfall traps (Table 4 - H(1,24) = 15.855; p < 0.001), and in the pitfall traps during July and August (the two months in which the manual searching took place) (H(1,24) = 15.883; p < 0.001) as compared with the manually searched plots. If the pitfall results of only the fortnightly period in which the manual searching took place, are used, the average number of species is no longer significantly higher in the pitfall traps (H(1,24) = 0.432; p = 0.51).

DISCUSSION

Ant diversity and communities

During this study, *Myrmica lonae* was observed for the first time in Belgium (Schoeters & Vankerkhoven, 2001). It also has only recently been found in the Netherlands (Elmes et al., 1994; Boer, 1999). According to Wardlaw et al. (1998) and Elmes et al. (1994), *M. lonae* occurs in wetter habitats (e.g. wet heathlands) than its sister species *M. sabuleti*, although Saaristo (1995) calls *M. lonae* a species of very hot and dry places in the SW-archipelago in Finland. In Central Europe, Seifert (2000) and Czechowski et al. (2002) found *M. lonae* nests mainly in xerothermal habitats (e.g. dry woods and sun exposed rocky slopes) and far less in open boggy habitats (mainly in the northern part of its distribution). We found three nests of *M. lonae* in the Liereman nature reserve in a plot with a *Molinia caerulea* cover of 60%; this corresponds better with the habitat description of Elmes et al. (1994; pers. comm.) and Seifert (2000) for the northern distribution range than with that of Saaristo (1995). Other typical heathland species found during our survey were:

Formica transkaucasica (a typical species of bogs and wet heathlands - Van Boven & Mabelis, 1986; Seifert, 1996) was only known previously from a limited number of sites in Flanders (Vankerkhoven, 1999; Dekoninck & Vankerkhoven, 2001b; Schoeters & Vankerkhoven, 2001); we found twelve additional sites;

Tapinoma ambiguum (an "inland heathland" species - Assing, 1989; Boer, 1999) was only known from two sites in Flanders (Dekoninck & Vankerkhoven, 2001b; Schoeters & Vankerkhoven, 2001) and was only recently found in Luxemburg (Baden, 1998); the species is very rare in Poland (Czechowski et al., 2002); we found the species in two additional sites;

Strongylognathus testaceus (a social parasite of *Tetramorium caespitum*, a common species of dry heathlands - seifert, 1996) was only known from two sites in Flanders (Vankerkhoven, 1999; Schoeters & Vankerkhoven, 2001);

Lasius meridionalis (a temporary social parasite of *L. psammophilus* - Seifert, 1996) was only recently added to the Belgian fauna (Dekoninck & Vankerkhoven, 2001; Schoeters & Vankerkhoven, 2001); Both *L. meridionalis* and *L. psammophilus* are rare species in Poland (Czechowski et al., 2002); we found winged females of *L. meridionalis* on nine sites and workers of *L. psammophilus* in only one site; since we only found winged females of *L. meridionalis*, we can not assume that *L. psammophilus* is present at all nine *L. meridionalis* sites as well.

Some species were absent from the wet heathlands in north Belgium (e.g. *Camponotus herculeanus*, *Formica lemani*, *Formica pressilabris*, *Myrmica lobicornis* and *Symbiomyrma karavajevi*) but are present in the same habitat type in the Hautes Fagnes in south Belgium (Bondroit, 1912; Van Boven, 1977). Some of these species are mountain species or boreal relics which may explain their absence in Flanders. Species richness on the studied Flemish wet heathlands is comparable with that in NW-Germany (Assing, 1989) but is lower than similar Central or Eastern European habitats. Seifert (1996) mentions four additional species for wet open habitats, such as wet heathlands, for Germany that do not occur in Belgium (Dekoninck & Vankerkhoven, 2001a): *Myrmica vandeli*, *M. gallienii*, *Formica uralensis* and *F. forsslundi*. However, due to a high amount of nitrogen deposition, the ant diversity in most NW-European nutrient-poor habitats (e.g. wet heathlands, bogs, species-rich grasslands) is decreasing more rapidly than less intensively cultivated areas in Eastern or Central Europe (Bobbink et al., 1998).

Plant diversity did not appear to be a useful surrogate for ant species richness (cf. Boomsma et al., 1987; Alonso, 2000). Gallé (1991) and New (2000) found the same for dunes in S-Finland and grasslands in Australia, respectively. We did find a positive correlation between area on the one hand and ant diversity and nest density on the other; if this correlation holds true for other small invertebrates (that can act as possible prey for ants), large sites may offer a larger food supply for ants and thus result in higher nest numbers. The higher species numbers in large sites may be explained by the greater variation in vegetation structure offering more possible nesting sites for a larger number of species. The correlation between both ant diversity and nest density on the one hand and area on the other, emphasizes the importance of large sites for the conservation of ants and, probably, also for other animal species.

In our classification, soil type (peat or sand) and, thus indirectly, moisture (as peat soils are wetter than sandy soils), was the main factor determining the three ecological groups. These groups correspond well with the species habitat preferences described in Brian (1964), Mabelis (1976), Assing (1989), Saaristo (1995) and Seifert (1996). In most ant studies on heathlands, moisture and vegetation structure are the most important factors separating ant communities (Brian, 1964; Boomsma & De Vries, 1980; Elmes & Wardlaw, 1982; Gallé, 1991). Given the limited extent of the studied region, macroclimatic differences are not very likely to have influenced ant distribution in the Campine region (an area of about 100 × 50 km); microclimatic data are not available for the different study sites.

Nest densities and between year fluctuations of nest densities

Nest density was higher on peat soils than on sandy soils and large sites had higher nest densities. The higher nest density on peat soil was caused by species like *Myrmica scabrinodis* and *Formica transkaucasica*. Since the studied sites on peat soil are significantly larger than those on sandy soil (Kruskall-Wallis $H(1,46) = 5.363$, $p = 0.021$), the higher mean nest densities on larger areas might be explained by soil type and not necessarily by area.

The number of ant species did not differ significantly between 1999 and 2000. However, the number of nests was significantly higher in 2000 than in 1999. Sampling itself was most probably not responsible for the differences in densities or species turn-over across the years (because the same people performed the manual searching), but could have caused ant colonies to move among nesting sites. Clearly more research is needed on this subject focusing on the repeated sampling of plots during the year, observations of the ants behaviour after sampling, etc. (Elmes et al., 1998). The generalized statement of Steiner & Schlick-Steiner (2002) that ant nests are very sedentary and that their densities do not vary much between years is not supported by our data. Differences across both years were only significant on the inundated plots where a much larger number of nests was found. As described by Boomsma & De Vries (1980) for *Lasius niger*, *Myrmica rubra* and *M. scabrinodis*, ants can survive inundations of 2–14 weeks using oxygen that is stored in and between roots and litter. The inundated plots had a more open structure and a wetter microclimate in the spring following inundation offering more suitable nesting sites for species of cooler and wetter habitats such as *Myrmica scabrinodis*, *M. ruginodis* and *Lasius platythorax*.

The effect of *Molinia caerulea* encroachment on ants

Molinia caerulea tussocks are by far the most frequently used nest substrates in the wet heathland sites we studied. However, sites with a very high *Molinia caerulea* cover are expected to have a cooler microclimate at ground surface level (Bobbink et al., 1998; Van Dyck, pers. obs.) which reduces the invertebrate diversity (Thomas et al., 1999) in general, and the potential number of sunlit, warm nesting sites for ants in particular (Elmes & Wardlaw, 1982; Thomas, 1995; Thomas et al., 1998). De Boer (1978) found a significantly higher number of ant nests in wet *Erica* heathland with a relative high *Molinia caerulea* cover (on average 30%) than in sites with lower *Molinia caerulea* densities (on average 13%). When vegetation cover of *Molinia caerulea* tussocks became too dense, De Boer (1978) observed negative effects on ant nest densities. Our results confirm that there is indeed an optimal % *Molinia caerulea* cover for nest density (about 40–45%); a further increase in the % *Molinia caerulea* however resulted in a lower number of nests. The higher nitrogen deposition in the last few decades (Bobbink et al., 1992; Vanongeval et al., 1998) has caused a very strong increase in *Molinia caerulea* cover in oligotrophic habitats such as wet and dry heathlands (Bobbink et al., 1998; Chambers et al., 1999). More research is needed to investigate the impact of degradation of wet heathlands on invertebrates and other faunal elements in general and on ant colony sizes in particular (cf. Elmes & Wardlaw, 1982; Bobbink et al, 1998).

Despite their important role in most ecosystems and their potential as bio-indicators (cf. York, 2000), invertebrates in general and ants in particular are seldom used in nature management and restoration evaluation. Most management and restoration measures in heathlands are based mainly on plant diversity (e.g. Smith et al., 1991; Jansen et al., 1996). Plants represent only a small fraction of the biodiversity present in ecosystems (Thomas, 1994). Differences in scale, habitat use and mobility call for specific management measures for invertebrates that are not met with by using only birds, mammals or plants as target species (Webb & Thomas, 1994). Much more research is needed to estimate the impact of management and restoration measures on ant communities on wet heathlands (e.g. long-term monitoring of different management practices, rate of colonisation on restored heathlands, influence of the neighbouring unmanaged habitats on rate of colonisation, etc.). Management measures (e.g. large-scale sod cutting and burning) can be very beneficial for the restoration of wet *Erica* heathland vegetation (Jansen et al., 1996), but can cause severe damage to ant communities and nesting sites. Gorssen (1999) found that sod cut and burned plots had a lower number of nests and species than unmanaged heathland plots. Brian et al. (1976) and De Boer (1978) did not find any differences in ant species composition and even found higher nest numbers after burning of dry heathland. The very high values of nitrogen deposition however, suggest that burning is at present no longer recommended because fast growing grasses such as the Purple Moor-grass, *Molinia caerulea*, will become dominant and reduce nest densities. Low intensity grazing and mowing also reduced the number of nests compared with unmanaged plots but seem to be less detrimental than burning and sod cutting (Mabelis, 1976; De Boer, 1978). Restoration of heathland sites on former mining grounds in Australia showed that 20 years after the rehabilitation of the mining grounds, the original ant assemblage structure still had not been achieved (Bisevac & Majer, 1999). Following York (2000), we recommend low-intensity and small-scaled management and restoration measures on degraded wet heathland sites to minimise the effects on the existing ant diversity and its associated (myrmecophilous) communities. Management measures are not only necessary in degraded wet heathland sites even high quality wet heathlands need regular small-scale management to maintain and/or create suitable nesting sites for ants and other invertebrates. Invertebrates can thus be used in a complementary way to other, more frequently used biota (e.g. plants, birds) in managing or restoring degraded sites (Thomas, 1994).

Differences between manual nest searching and pitfall sampling

Combining different trapping techniques (pitfall traps, manual searching, or litter extraction) gives the most complete information on ant species richness and densities (Andersen, 1997; Delabie et al., 2000; York, 2000; Parr & Chown, 2001). However, the information needed will determine which (combination of) sampling techniques is the most cost-effective one (Bestelmeyer et al., 2000). If only a species list of a relatively large number of wet heathland sites is needed, our data showed that three pitfall traps are sufficient (cf. Stein, 1965; Kabacik-Wasylik, 1970). On average 81% of the total species richness per site was caught in one of the three pitfall traps, while the additional pitfall traps only added 14% and 4% respectively to the total species richness per site. When sampling efforts must be to limited in time, pitfall traps can best be placed between mid July and mid August: 20 of the 28 species were caught during this period and the remaining eight species were only found in very small numbers (except for *Tapinoma erraticum* that was mainly caught in spring). Advantages of pitfalls are the possibility of sampling many sites simultaneously (Greenslade, 1973; Bestelmeyer et al., 2000; Parr & Chown, 2001) and the ability to find social parasites and ants with hidden nests (especially winged females during the mating season). Disadvantages of pitfall traps are the large number of individuals to be classified, the lack of information on nest densities and the fact that the numbers of individuals per ant species cannot be compared between species and sites due to different activity patterns and differences in catching ratio (i.e. the number of ants finally caught against the total number of trap contacts - Seifert, 1990; Bestelmeyer et al., 2000). Disadvantages of manual nest searching are its very time consuming nature (about 4–6 man-hours per 100 m^2), the disturbance caused to the nests, and the difficulty of finding social parasites (Bestelmeyer et al., 2000).

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