

Ant assemblages in successional stages of Scotch Broom stands (Hymenoptera: Formicidae; Spermatophyta)¹

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Abstract

Scotch Broom (*Cytisus scoparius* [L.] LINK) stands are important seminatural habitats in cultural landscapes of Germany. High structural diversity of broom stands is reflected by a high species diversity of the flora and fauna, giving them a high value for biodiversity conservation. The aim of this study was to assess the composition and structure of ant assemblages among successional stages of Scotch Broom stands, and compare these with assemblages in arable land and the climax forest habitat. We addressed, whether ant species richness in successional broom stands differ with respect to the dominant grass species, shrub cover and other structural variables describing vegetation. Furthermore, we studied whether ant species composition relates to plant species composition, and whether site productivity or structural vegetation properties are more important for ant species composition. We found that initial and climax stages of the succession constitute habitats which are very different from the "Scotch Broom stages" of succession. Ant species richness was not correlated to plant species richness but was best predicted by the two variables "moss cover" and "soil moisture". Path Analysis revealed that both site productivity and vegetation structure had an independent and significant effect on ant species composition. The estimate of the explanatory power of the "Productivity" path was twice the magnitude of "Structure". The successional dynamics within stands of Scotch Broom created complex habitat structures that provide diverse microhabitats for ants. The type of grassland vegetation was of little importance and therefore, schemes to maintain these old fields as ant habitats do not necessarily need to manage for a particular plant species composition but for dynamic and structurally rich sites. Due to site specific differences in soil attributes, legacy of former land use and Scotch Broom dynamics, single sites are of very individual character and harbour different ant assemblages. This causes high beta diversity and thus high ant species richness in Scotch Broom stands at the landscape scale. Therefore, conservation strategies for Scotch Broom stands should focus on maintaining a high number of sites widely dispersed within the landscape.

Key words: Succession, old field, *Cytisus scoparius*, conservation biology, assemblage similarity, site productivity, vegetation structure, temperate grasslands, Central Europe.

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Introduction

Scotch Broom (*Cytisus scoparius* [L.] LINK) stands are important seminatural habitats in cultural landscapes of Germany. Particularly in the agricultural regions of the Rhenish Uplands (Rheinisches Schiefergebirge), *C. scoparius* stands constitute a striking structural landscape element, covering extensive areas on unproductive sites, namely abandoned agricultural fields, clearings and open forests. The biology of Scotch Broom shows specific characteristics, which lend this plant and its stands a distinct status among Central European shrubs (reviewed in SIMMERING & al. 2001). The rapid growth and periodical diebacks owing to hard frosts lead to a considerable spatial variation of shrub cover in broom stands. Dense thickets are thus alternating with open areas featuring well developed, grass-dominated herb layers.

According to differences in origin and site productivity, the accompanying herb layer of Scotch Broom stands can be classified into three distinct plant communities (SIMMERING & al. 2000, 2001): (1) Very poor, acidic, and dry sites of clearings and abandoned pastures often carry a vegeta-

tion dominated by Wavy Hairgrass (*Avenella flexuosa* [L.] DREJER). This community may sometimes also be found on abandoned fields, but due to their slightly higher productivity, old fields usually carry a grassland type, (2) dominated by Red Fescue and Colonial Bentgrass (*Festuca rubra-Agrostis tenuis* community). This community is typical of poor, unimproved grasslands of the region (ELLENBERG & al. 1996), and has high proportions of low-nutrient indicators. In many stands, Scotch Broom is found within patches of a third grassland community, (3) dominated by the mesophytic Tall Oatgrass (*Arrhenatherum elatius* L.) and co-occurring nitrophytes. The leguminous Scotch Broom is potentially able to enrich sites with mineral nitrogen through symbiotic nitrogen-fixation. Therefore it has been argued that *A. elatius*-patches develop from broom stands of the *Festuca rubra-Agrostis tenuis* type, triggered by this nutrient enrichment. Broom thus acts as an "ecosystem engineer" through facilitative effects (SIMMERING & al. 2001). However, different optional and intermediate successional stages (mainly characterised by other shrubs) follow the

¹ This work is dedicated to the memory of Stefan Schödl.

establishment of dense broom thickets and lead finally to stages of young forest. In these young forest patches, broom still occurs but will eventually be shaded out.

The high structural diversity of broom stands is reflected by a high species diversity of the flora and fauna (KRÄMER & TOPP 1999, DAUBER & WOLTERS 2000a, KNECHT & al. 2000, MEMMOTT & al. 2000, PFAFF & WOLTERS 2000, SIMMERING & al. 2000, 2001, MEYER & al. 2004, PURTAUF & al. 2004, DAUBER & al. 2005, SIMMERING & al. 2006), giving Scotch Broom stands a high value for biodiversity conservation in agricultural landscapes.

Ants are an important component of the fauna of Scotch Broom stands. They might be important for the establishment and dispersal of Scotch Broom itself because the seeds of this shrub are partially ant dispersed (HEGI 1925). In general, ants are important predators in grasslands (KAJAK & al. 1972), and due to the high densities of ground nests in the old fields (DAUBER & WOLTERS 2000a) they can significantly affect soil properties and other soil organisms (PETAL 1980, DAUBER & WOLTERS 2000b). Furthermore, they increase small-scale patchiness and structural heterogeneity in the open areas of Scotch Broom stands (SIMMERING & al. 2003). The current abundance of Scotch Broom stands in the Rhenish Uplands is mainly owing to historic forms of land use, such as the agri-silvi-pastoral "Haubergswirtschaft" (FICKELER 1958) and other traditional coppice and farming systems. As these are no longer practised today, broom stands are historic relicts. The long-term conservation of these successional habitats can only be achieved by management. Ants, studied in combination with other focal taxa, might serve as biodescriptors for the development of sustainable management strategies (STEINER & SCHLICK-STEINER 2002).

The aim of this study was to assess the composition and structure of ant assemblages among successional stages of Scotch Broom stands, and compare these with assemblages in arable land and the climax forest habitat. Specifically, we addressed the following questions:

(I) How does ant species composition and richness in broom stands differ from those of arable land and forest, the initial and climax stages of succession?

(II) Does ant species richness differ between successional broom stands that vary with respect to grassland community, shrub cover and other structural variables describing vegetation? Is there a relation between ant and plant species richness?

Vegetation of broom stands reflects underlying differences in site productivity, which is expressed by the three different grassland communities. However, the high spatial and temporal dynamics in broom cover and other related structural vegetation properties, such as cover of mosses, herb layer etc. lead to fundamentally contrasting living conditions for ants. Hence, we amended our analysis by focussing on the composition of ant assemblages:

(III) How does ant species composition relate to plant species composition? Which underlying gradients in the vegetation of broom stands – site productivity or structural properties – are more important for ant species composition?

Material and methods

Study region and study sites: The study sites were located in the Lahn-Dill-Bergland, a region covering about

900 km² at the eastern ridge of the Rhenish Uplands (Central Hesse, Germany; 200 - 600 m a.s.l.; mean annual temperature: 6 - 8 °C; average annual precipitation: 650 - 1100 mm; soil: small scale patterns of acidic shallow regosols to cambisols over Devonian clay slates and greywackes on upper to mid-slopes, and planosols to gleysols on lower slopes). Due to the unfavourable abiotic conditions, traditional heritage customs creating small field sizes (around 0.4 ha), and predominance of part-time farming, the region is marginal in terms of agricultural production (FREDE & BACH 1999). In the middle of the 20th century a high percentage of agricultural fields were abandoned ("Sozialbrache"; NOWAK 1988). These old fields are currently managed as grassland (WALDHARDT & OTTE 2003) or are covered with extensive Scotch Broom stands.

We selected a total of 30 study sites within the study region. Arable land represents the starting point of secondary succession. Thus we sampled six arable fields, three of them cultivated with wheat (ALc1 - ALc3) and three in the state of a one-year fallow (ALf1 - ALf3) sown with White Clover. All arable sites were lacking Scotch Broom. Traps on site ALc2 were destroyed by field management and were hence lost for the analyses. Six forest sites marked the climax stages of the succession, with three young forest sites in a transitional state from broom stand to forest (Fy1 - Fy3), and three old forest stands (Fo1 - Fo3) without Scotch Broom. The character of the three old forest stands was stamped by silvicultural management over the last decades or even centuries and it was not possible to decide whether they once originated from spontaneous succession. Dominant tree species were Beech (*Fagus sylvatica* L.) and Oak (*Quercus robur* L. & *Q. petraea* [MATT] LIEBL.).

Eighteen sites were successional Scotch Broom stands. Based on a preceding phytosociological study (see SIMMERING & al. 2001 for details), sites were classified according to the dominant grass species and the estimated density of the *C. scoparius* cover, leading to six distinct categories: (I) acidic and nutrient poor sites dominated by *Avenella flexuosa* in the herb layer with open (< 30 %, Afo1 - Afo3) and dense (> 60 %) *C. scoparius* cover (Afd1 - Afd3); (II) *Festuca rubra*-*Agrostis tenuis* community with open (Fro1 - Fro3) and dense *C. scoparius* cover (Frd1 - Frd3); (III) more productive sites dominated by *Arrhenatherum elatius* with open (Aeo1 - Aeo3) and dense *C. scoparius* cover (Aed1 - Aed3). All study sites had dry to mesic soils, and were either situated on planar surfaces or on moderate slopes with southern aspect.

Sampling: Ants were sampled with pitfall traps (ø: 2 cm; killing and preserving agent: ethanol : glycerine [2 : 1] solution) within a 64 m² plot at each study site. Nine traps were placed on each site in an 8 × 8 m square located at the interior crossing points of a 2 × 2 m grid. The square was situated with a distance of 2 m to the border of the study area. Ants were collected during a one-week period in late June in 1999. All individuals were determined to species level according to SEIFERT (1996). Specimens are kept in the private collection of Jens Dauber. Only worker ants were considered in statistical analyses.

Vegetation of the 18 Scotch Broom stands and the three young forest sites was sampled between late June and early July of the same year. Percentage cover values for all cryptogams and vascular plant species within the 64 m²-

plots were visually estimated applying the Braun-Blanquet cover classes (KENT & COKER 1992, WILMANN 1998). Estimates of vegetation structure included the total percentage cover of mosses, herb, shrub and tree strata, as well as their minimum and maximum heights. Additionally, we recorded the percentages of open soil, (grass-) mat cover and (leaf) litter. Plant nomenclature follows ELLENBERG & al. (1992).

Data analysis: Judging from our experience with the ant fauna of broom sites (DAUBER & WOLTERS 2000a, 2004), we assumed that sampling was equally efficient at all sites. Instead of applying richness estimators, we therefore simply used the cumulative number of ant species found in the nine traps as response variable, i.e., species richness per site (S). Considering the small number of traps, and given the problems occurring with the application of species richness estimators (cf. KING & PORTER 2005), we viewed this measure as the most appropriate.

Differences in S between arable land (n = 5), Scotch Broom stands (n = 18), and forest (n = 6) were tested by unbalanced analysis of variance (ANOVA). To find the best model explaining S in the 21 successional stands (18 broom stands and three young forests), we applied General Regression Model with forward selection procedure (GRM) as implemented in Statistica 6.0 software package (STATSOFT INC. 2001). Categorical predictors used for GRM were plant community (Af, Fr, Ae, Fy) and density of broom (o = open / d = dense). Continuous predictor variables were the estimates of vegetation structure listed above. Further, we calculated mean Ellenberg Indicator values for moisture (M), soil reaction (R) and nutrient status (N) from the species list of each site (ELLENBERG & al. 1992), as well as plant species richness and Evenness of the herb layer (MAGURRAN 2004).

All variables representing proportion data were arcsin-squareroot transformed (SOKAL & ROHLF 1995). Prior to analyses we checked for homogeneity of variances (Levene's Test) and for normality of data. GRM was calculated with standardised data to receive a zero-intercept in the model. Percentages of variation explained (% EV) in the GRM were calculated from the ratios of the sums of squares of a significant predictor variable to total sum of squares.

Multivariate analysis of ant species composition was restricted to the 18 Scotch Broom stands and the three young forests. In order to assess and illustrate multivariate relations between vegetation properties and ant assemblages, we applied (Bray-Curtis) Polar Ordination (PO) on ant species employing the PC-Ord-Package (MCCUNE & MEFFORD 1999, MCCUNE & GRACE 2002). A species-by-site matrix of arcsin-squareroot transformed frequencies of the eight ant species, which were occurring in at least three sites, was constructed and submitted to ordination. In Polar Ordination, samples are arranged between endpoints of a distance matrix. As it is the most straightforward measure of community structure in species-poor communities and performs well for small data sets (fig. 6.6 in MCCUNE & MEFFORD 1999), we chose Euclidian distance as distance measure.

According to our hypothesis regarding the dependence of ant species composition on site productivity and vegetation structure, we restricted the PO to two axes. The maximum-range method (Bray-Curtis original) was applied for

endpoint selection of both axes. Plot scores were calculated by weighted averaging. Passive correlations between ordination axes and vegetation properties were shown as vector overlays in the ordination diagram for illustrative purposes (Fig. 1).

To quantify the relative impact of site productivity vs. vegetation structure as explanatory variables of ant assemblages, we carried out a Path Analysis based upon distance matrices and Mantel matrix correlations (cf. LEDUC 1992, LEGENDRE & LEGENDRE 1998). A path model was constructed for the relations between site productivity, vegetation structure and ant assemblages (Fig. 2). For each of these variables, a matrix of the Euclidian distance between sites was calculated.

The response distance matrix, "Ants", was calculated from the species-by-site matrix also used in PO. The matrix for vegetation structure ("Structure") was derived from a set of seven arcsin-squareroot transformed variables that showed the highest correlations with PO axes, and thus ant community structure. The distance matrix for site productivity ("Productivity") was calculated from the Ellenberg Indicator-values M (moisture value), R (reaction value) and N (nutrient value) as correlates of overall productivity (ELLENBERG & al. 1992). The underlying assumption was that in the relatively poor broom sites higher values of these three fundamental site conditions indicate overall higher soil productivity.

A fourth matrix, "Plants", was calculated from the Euclidian distances between vegetation relevés (containing all 45 species occurring in more than two sites). We tested the relation between the plant composition matrix and the other matrices with simple Mantel tests. However, the plant composition matrix was not independent of the indicator value matrix and we hence did not include it into the Path Model.

Pearson correlation coefficients from simple Mantel Tests (Mantel r) were used to calculate path coefficients, which are standardised regression coefficients (SOKAL & ROHLF 1995). Pearson correlation coefficients as well as Path Analysis both assume linearity. As the gradients studied were rather short (dry to mesic, open to dense, poor to moderate nutrient), and Pearson correlation is also known to be robust, we consider it justified to expect a quasi-linear response of ant species with transformed data.

Partial Mantel Tests served to assess the significance of path coefficients (cf. LEDUC & al. 1992, LEGENDRE & LEGENDRE 1998, DE BLOIS & al. 2001). Significance of simple and partial Mantel coefficients was tested by 9999 Monte Carlo permutations using the XLSTAT 2006 Excel-Add-In (ADDINSOFT 2006).

Results

A total of 3999 ants belonging to 19 species of 7 genera were sampled at the 29 study sites (Tab. 1). The species covered a wide spectrum of habitat preferences, ranging from disturbance tolerant, open habitat species (e.g., *Lasius niger* (LINNAEUS, 1758), *Myrmica rubra* (LINNAEUS, 1758)), via species typical for dry and warm open grasslands (e.g., *Myrmica schencki* VIERECK, 1903, *Myrmica sabuleti* MEINERT, 1861) and species preferring cooler and moister semi-open habitats (e.g., *Myrmica ruginodis* NYLANDER, 1846), to typical wood-living ants (e.g., *Lasius platythorax* SEIFERT, 1991, *Temnothorax nylander* (FÖRSTER,

Tab. 1: Frequencies [%] of ant species in the 29 study sites. Number of species per site is shown on the bottom of the table. Aeo = *Arrhenatherum elatius* dominated sites with open (< 30 %) *C. scoparius* cover; Aed = *Arrhenatherum elatius* dominated sites with dense (> 60 %) *C. scoparius* cover; Afo = *Avenella flexuosa* dominated sites with open *C. scoparius* cover; Afd = *Avenella flexuosa* dominated sites with dense *C. scoparius* cover; ALc = arable field cultivated with wheat; ALf = one-year fallow sown with White Clover; Fo = old forest stands; Fro = *Festuca rubra*-*Agrostis tenuis* community with open *C. scoparius* cover; Frd = *Festuca rubra*-*Agrostis tenuis* community with dense *C. scoparius* cover; Fy = young forest sites in a transitional state from broom stand to forest.

Species	ALc		ALf			Afo			Afd			Fro			Frd			Aeo			Aed			Fy			Fo				
	1	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3		
<i>Lasius niger</i> (LINNAEUS, 1758)		11	67	89	22																										
<i>Myrmica rugulosa</i> NYLANDER, 1849		11																													
<i>Myrmica rubra</i> (LINNAEUS, 1758)	100	22										11			78	100	56			29	22										
<i>Myrmica scabrinodis</i> NYLANDER, 1846		11				22	63	67	44	50	89	67	100		100	100	22	78	89	57	22									11	
<i>Myrmica sabuleti</i> MEINERT, 1861						88	67	25		13	22		11			11		11	22	43		33								11	
<i>Lasius flavus</i> (FABRICIUS, 1782)						25	33	50		11	22									22	29										
<i>Myrmica lobicornis</i> NYLANDER, 1846						44	63	50	33	63	22	44		11			33	33		29	11	33									
<i>Tapinoma erraticum</i> (LATREILLE, 1798)						56	38		22													11									
<i>Myrmica schencki</i> VIERECK, 1903							25	17		38	78									11	14										
<i>Formica fusca</i> LINNAEUS, 1758									50						11							33									
<i>Myrmica ruginodis</i> NYLANDER, 1846						11		33	67	25	56	78		89	11		78	33	44	56	43	100	67	86	100	100	100				
<i>Temnothorax nylanderi</i> (FÖRSTER, 1850)																											11	33	78		
<i>Lasius platythorax</i> SEIFERT, 1991																											11		22		
<i>Leptothorax acervorum</i> (FABRICIUS, 1793)													11	11																	
<i>Formica rufibarbis</i> FABRICIUS, 1793																	11														
<i>Myrmica lonae</i> FINZI, 1926											13																				
<i>Lasius alienus</i> (FÖRSTER, 1850)											13																				
<i>Tetramorium</i> cf. <i>caespitium</i> (LINNAEUS, 1758)										25																					
<i>Lasius fuliginosus</i> (LATREILLE, 1798)																											43				
Number of species (S)	1	4	1	1	1	2	6	6	5	5	8	4	6	2	3	2	3	2	3	5	2	5	7	5	4	2	3	2	5		

1850)). Two species, *L. niger* and *Myrmica rugulosa* NYLANDER, 1849, were exclusively found in arable land, whereas two other species, *L. platythorax* and *T. nylanderi*, were exclusively found in forest sites (Tab. 1). Of the nine more frequent species, which occurred in most of the Scotch Broom stands and in the forest, only *M. rubra* and *M. scabrinodis* NYLANDER, 1846 were also found within the arable land sites. Seven species, none of which can be considered rare in general, were found at one or two study sites only.

Ant species richness of study sites ranged from one to four species in arable land, and from two to five species in forest. Variability of ant species richness was highest in the Scotch Broom stands, ranging from two to eight (Tab. 1). Mean species richness was significantly lower in ar-

able land (1.6 ± 0.8 SD) than in Scotch Broom stands (4.2 ± 0.4 SD) and forest (3.5 ± 0.7 SD) (ANOVA: $df = 2$, $F = 4.4$, $P < 0.05$).

However, taking only the successional stages of Scotch Broom stands and young forests into account, GRM revealed that neither grassland type (i.e., Af, Fr, Ae, Fy) nor broom cover (open vs. dense) had any significant effect on ant species richness (Tab. 2). In contrast, the best model predicting ant species richness, accounting for 56.3 % of total variation, contained the two variables "moss cover" and "Ellenberg M-value". Both variables had negative parameter estimates, indicating that highest ant species richness is found in dry sites without a prominent moss layer. Moss cover in our data is mainly determined by the abundance of the common moss species *Rhytidiadelphus*

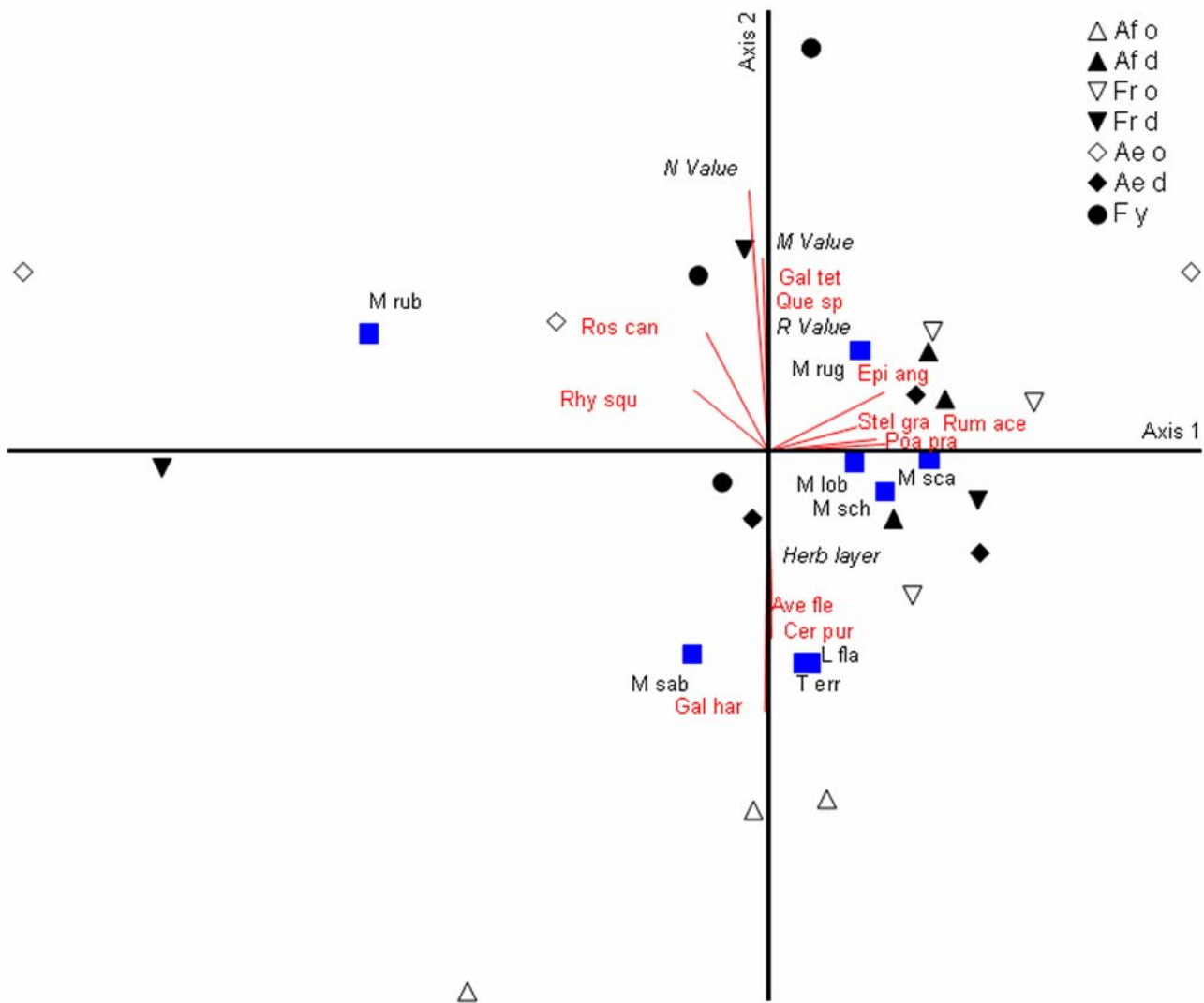


Fig. 1: (Bray-Curtis) Polar Ordination (PO; Euclidian distance; restricted to two axes) based on species-by-site matrix of arcsin-squareroot transformed frequencies of eight ant species, which were occurring in at least three sites. Passive correlations between ordination axes and vegetation properties are shown as vector overlays. M, R, N Value = Ellenberg M (moisture), R (soil reaction), and N (nutrients) Indicator-values. Vascular plants: Ave flex = *Avenella flexuosa*; Epi ang = *Epilobium angustifolium*; Gal tet = *Galeopsis tetrahit*; Gal har = *Galium harynicum*, Poa pra = *Poa pratensis*; Que sp. = *Quercus* sp.; Ros can = *Rosa canina*; Rum ace = *Rumex acetosa*; Stel gram = *Stellaria graminea*; Mosses: Cer pur = *Ceratodon purpureus*; *Rhytidiadelphus squarrosus*. Ants: L fla = *Lasius flavus*; M lob = *Myrmica lobicornis*; M rub = *Myrmica rubra*; M rug = *Myrmica ruginodis*; M sab = *Myrmica sabuleti*; M sca = *Myrmica scabrinodis*; M sch = *Myrmica schencki*; T err = *Tapinoma erraticum*. Sites: Afo / Afd = acidic and nutrient poor sites dominated by *Avenella flexuosa* in the herb layer with open (< 30 %) and dense (> 60 %) *C. scoparius* cover; Fro / Frd = *Festuca rubra*-*Agrostis tenuis* community with open and dense *C. scoparius* cover; Aeo / Aed = more productive sites dominated by *Arrhenatherum elatius* with open and dense *C. scoparius* cover; Fy = young forest sites in a transitional state from broom stand to forest.

squarrosus (HEDW.) WARNST., which occurred with highest abundance in shaded areas of broom stands. Plant species richness was not significantly correlated with ant species richness and was also excluded from the GRM model.

The cumulative variance of ant species composition explained by Polar Ordination was 49 %. Axis 1 accounted for 31.6 % of the original distance matrix and was correlated with three variables accounting for vegetation structure: The proportion of open soil ($r = 0.24$), moss cover ($r = -0.32$), and maximum height of the herb layer ($r = -0.20$). Vector overlays of single plant species along this axis indicated the co-occurrence of species often found in mesic

grassland communities, such as *Rumex acetosa* L., *Poa pratensis* L. and *Stellaria graminea* L., but also of species more typical of scrubs (*Epilobium angustifolium* L.). Positively correlated with this axis were the ant communities of the more mesic broom stands (Fr and Ae) with open and dense broom cover. Axis 2 accounted for 18.4 % of the original distance. It was positively related to all three Ellenberg Indicator-values (M: $r = 0.58$; R: $r = 0.42$; N: $r = 0.67$), but correlated also with four structural variables: Tree cover ($r = 0.36$) and litter cover ($r = 0.45$) were positively correlated, while the cover of herb layer ($r = -0.44$) and mat cover ($r = -0.21$) showed the opposite relation. According-

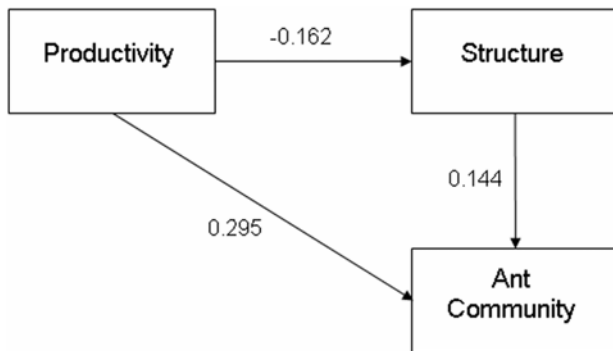


Fig. 2: Path Diagram showing the direct effects of abiotic site conditions (Ellenberg Indicator-values; Productivity) and vegetation structure (Structure) on ant species composition in successional broom stands and young forests ($n = 21$). All path coefficients are significant at the $P < 0.05$ level.

Tab. 2: GRM results (forward selection) on the effects of vegetation structure (field estimates) and site productivity measures (Ellenberg Indicator-values) on ant species richness.

	df	MS	F	p	% EV
Vegetation Structure					
Grassland type	0				
Dense / open broom cover	0				
Herb layer %	0				
Moss cover %	1	7.2	15.1	0.001	36.7 %
Open Soil %	0				
Mat Cover %	0				
Litter Cover %	0				
Evenness Herb layer	0				
Plant species richness	0				
Ellenberg Indicator-Values (Productivity)					
Moisture Value (M)	1	3.9	8.1	0.01	19.7 %
Soil Reaction Value (R)	0				
Nutrient Value (N)	0				
Error	18	0.5			43.7 %

ly, plant species overlays on Axis 2 clarify this mixed gradient from the open, dry sites of the *Avenella*-community with *Avenella flexuosa*, *Galium harcynicum* WEIGEL and *Ceratodon purpureus* (HEDW.) BRID. to young forest stands with *Quercus* trees and accompanying nitrophytes (*Galeopsis tetrahit* L.) and shrubs (*Rosa canina* L.). The cover of broom did not correlate with either one of the axes. In total, the descriptive ordination of ant species composition did not reveal a distinct pattern that may be clearly related to either site productivity or vegetation structure (Fig. 1). To separate effects of vegetation structure and productivity, we took into account the seven structural variables (listed above) correlating with both PO Axes for the calculation of a "Structure" distance matrix. The resulting matrix was submitted to Mantel Tests (Tab. 3) and Path Analysis (Fig. 2).

Tab. 3: Mantel coefficients ($P < 0.05$) of Matrix correlations on Euclidian distances of ant species (8 species) and plant species composition (45 species), site productivity (M, R, N Ellenberg Indicator-values), and vegetation structure (7 variables, see text).

	Ants	Plants	Structure
Plants	0.18	-	
Structure	n.s	0.14	-
Productivity	0.27	0.49	-0.16

Mantel test results indicated a significant correlation of plant composition ("Plant") and Ellenberg Indicator-value matrix ("Productivity"). Both matrices were also positively correlated with "Ants", while "Structure" was correlated with "Plants" but not significantly related to "Ants". The negative correlation (and path coefficient) between "Structure" and "Productivity" points to the fact that sites with a similar vegetation structure, e.g., Afo and Aeo, may differ strongly in Ellenberg values, i.e., overall site productivity. Other sites, in contrast, have comparable site conditions, but differ strongly in vegetation structure (e.g., Af vs. Fy). However, Path Analysis revealed that both gradients in our data sets have an independent and significant effect on ant species composition (Fig. 2). Although "Structure" was not significantly correlated with "Ants" in simple Mantel Tests (Tab. 3), the direct effect became apparent when accounting for differences in site productivity in Path Analysis. The estimate of the "Productivity" path was, however, twice the magnitude of "Structure". This result is in remarkable contrast to our analysis of ant species richness, where structural variables (moss layer) explained a much larger proportion of variation than site conditions (moisture).

Discussion

The present study on species richness and composition of ant assemblages in Scotch Broom stands affirmed the importance of this seminatural habitat in harbouring a species-rich ant fauna. The diversity of the ecological traits and niche preferences of the ant species found in the Scotch Broom stands underline the strong ecotonal character of these old fields which form a transition from open grasslands to forests. Both initial and climax stages of the succession constitute habitats which are very different from the "Scotch Broom stages" of succession. Arable fields have a strongly depleted ant community due to the adverse management practises (DAUBER & WOLTERS 2005), and older forest stands – depending on the forest type - might harbour equally species-rich, but very differently composed ant communities (EICHHORN 1971, DOROW 2001).

The number and composition of ant species found in the Scotch Broom stands is largely in accord with previous studies that have been carried out in the same region (DAUBER & WOLTERS 2000a, 2004). This result confirms that the sampling method (i.e., pitfall traps) used in the present study was adequate to address questions on ant species richness and composition within the focal habitat, because both observed species number and composition were comparable to the data sampled by combined census methods of nest counting and pitfall trapping used in the previous

studies. Such accordance between census techniques is not always given because sampling efficiency of the single methods depends to a great extent on the habitat characteristics and the foraging strategies of the ant species living in these habitats (SCHLICK-STEINER & al. 2006). Given the method applied in our study, the ant census is of course not complete and some species with hypogaean activity and small colonies might have been overlooked.

Combining the species records of the present and of our previous studies, a sum of 24 species is occurring in the Scotch Broom stands. This total number of ant species is considerably higher than the species richness recorded in managed grasslands (DAHMS & al. 2005, DAUBER & WOLTERS 2005), and arable fields (DAUBER & WOLTERS 2000a), while, in contrast, the average ant species richness of Scotch Broom stands is quite similar to that of managed grasslands (DAUBER & WOLTERS 2004, DAHMS & al. 2005). This indicates a higher beta-diversity (i.e., between-community diversity) of ant communities among Scotch Broom stands in comparison to managed grasslands, resulting in higher total species richness at the landscape scale (cf. LOREAU 2000).

Many studies suggest that species richness of ants is positively associated with habitat complexity and micro-structure diversity (ANDERSEN 1986, SEIFERT 1986, WEBER 2003, ARMBRECHT & al. 2004, but see LASSAU & HOCHULI 2004). Indeed, habitat complexity of Scotch Broom stands is high as a result of the particular dynamics of succession and patchy and sporadic anthropogenic disturbances (SIMMERING & al. 2001). In contrast, succession in constantly managed grasslands is leading to more homogeneous patterns of both vegetation (WALDHARDT & OTTE 2003) and ant communities (DAUBER & WOLTERS 2005). This comparison corroborates the findings that successional stages with a high level of structural vegetation diversity maintain high insect species richness (SOUTHWOOD & al. 1979), whereas anthropogenic disturbances affecting succession and reducing vegetation structure lead to lower diversity (BESTELMEYER & WIENS 1996).

In our study, ant species richness and composition varied considerably between the Scotch Broom stands, indicating a rather individual character of the single sites. Accordingly, the variation in ant species richness could not be attributed to the three categories of grassland vegetation types. Plant species richness was likewise no predictor of ant species richness. This confirms the results of studies conducted in managed grasslands, which showed that plant species richness is less important than, e.g., soil attributes in explaining variation in ant species richness (BOULTON & al. 2005, DAHMS & al. 2005). In contrast, SAUBERER & al. (2004), searching for correlations between species richness of plants and ants across different habitat types, found a positive correlation between ant and plant species richness. However, it was not determined whether the correlation was driven by habitat differences that affected plants and ants alike or was due to true synergistic relationships. Just as reported by the study of DAHMS & al. (2005) on ants in managed grasslands, ant species richness in the Scotch Broom stands was negatively affected by soil moisture. Furthermore, moss cover, indicating shading, had also a negative effect on ant species richness. Since ants in general are a thermophilic taxon (SEIFERT 1996, ANDERSEN 1997), increased soil moisture, often going along with

higher nitrogen content and denser vegetation structure as well as shading, tend to decrease ant species richness in temperate ecosystems (PETAL 1976, SCHLICK-STEINER & STEINER 2002; but see BAUSCHMANN 2000).

It is an open question, whether vegetation can be used as a surrogate for biodiversity with respect to conservation management and monitoring (e.g., SAUBERER & al. 2004, PANZER & SCHWARTZ 1998). The results of the studies conducted on this topic are quite contradictory, and do not raise much hope because it has been repeatedly shown, that vegetation is poorly correlated to invertebrate biodiversity patterns (e.g., CRISP & al. 1998, JONSSON & JONSELL 1999, VESSBY & al. 2002, ENGLISCH & al. 2005, but see DUELLI & OBRIST 1998). Results on the response of ant communities to vegetation developments in successional habitats are also contradictory. Most likely, they depend on the biogeographical region and the habitat type under investigation (compare, e.g., GALLÉ 1991, PUNTILLA & al. 1994, MAJER & NICHOLS 1998, ANDERSEN & al. 2006). In contrast to the grassland assemblage analysis done by ENGLISCH & al. (2005) in steppe habitats, ant assemblages found in our study did not draw a completely different picture of their habitat than plants. We found a positive correlation between similarities of ant species composition and plant species composition (Tab. 3). However, we rather expected vegetation structure and site productivity, both being closely correlated to plant community composition, to be the real causes of variation in ant species composition (KASPARI & al. 2000, LASSAU & HOCHULI 2004). Indeed, the Path Analysis revealed a clear significant relationship between site productivity and ant assemblages. Also, vegetation structure had a significant effect on ant assemblages, which was independent from site productivity but of lesser importance. The conclusion that vegetation structure might be less important than soil attributes in explaining variation in ant assemblages are corroborated by the studies of LOBRY DE BRUYN (1993), BOULTON & al. (2005), and DAHMS & al. (2005). Alternatively, the differences in ant assemblages between the open *Avenella*-community and the other Scotch Broom stands (Fig. 1) might be a legacy of the different pathways of the evolution of these habitats, with *Avenella*-communities partly originating from abandoned pastures and the other stands mostly from abandoned crop fields (cf. SIMMERING & al. 2001).

The simultaneous influence of site productivity and vegetation structure was nicely depicted by the ordination of the ant species along the second axis of the Polar Ordination (PO). The lower part of Axis 2 represented a sequence from unproductive, open *Avenella*-communities to *Festuca*- and *Arrhenatherum*-communities, which was correlated to increasing soil moisture and nitrogen indicator-values (Fig. 1). This sequence was reflected in the decrease of the frequencies of *M. sabuleti*, *L. flavus* (FABRICIUS, 1782), and *T. erraticum* (LATREILLE, 1798), and an increase of the other *Myrmica* species. The sequence of sites along this second axis was further prolonged by a transition from Scotch Broom stands to young forest stands, which in turn was correlated to vegetation structure (i.e., tree and litter cover in particular). This structural gradient is followed by an increase in the frequency of *M. ruginodis*. The ordination of the ants along this sequence was largely in accordance with the known niche differentiations of the species (SEIFERT 1986, 1996, ELMES & al. 1998). However, the not-

able differences in vegetation structure among the open areas and dense thickets of the Scotch Broom stands, with the exception of open *Avenella*-communities, did not lead to a distinct pattern in ant composition. Only *M. rubra* was clearly separated from the other *Myrmica* species (Fig. 1), which was due to its high frequency in one of the *Arrhenatherum* dominated stands and to a correlation of its occurrence to an increase in moss cover. Within the Scotch Broom stands, the trend of a high species turnover from thermophilic open landscape species to woodland species was not as pronounced as reported from other habitats facing an increase of shrub cover (BAUSCHMANN 2000, WEBER 2003). This might be explained by the small-scale heterogeneity of the stands with warmer patches of short to medium vegetation and cooler patches of taller vegetation in close vicinity (SIMMERING & al. 2001), allowing the co-occurrence of ant species of different habitat preferences (e.g., *M. ruginodis* vs. *M. schencki*). Therefore, coarse vegetation or soil pattern describing the habitat at the site scale (in our case 64 m²) might not be sufficient in habitats of small scaled complexity to explain the occurrence of ants because their distribution depends on microhabitat availability and follows a higher spatial resolution (PIK & al. 2002).

To conclude, our study of ant assemblages in Scotch Broom stands has confirmed the important function of this seminatural habitat for biodiversity conservation in agricultural landscapes. The successional dynamics within stands of Scotch Broom create complex habitat structures that provide diverse microhabitats for ants. The type of grassland vegetation is of little importance and therefore schemes to maintain these old fields as ant habitats do not necessarily need to manage for a particular plant species composition but for dynamic and structurally rich sites. Due to site specific differences in soil attributes, legacy of former land use and Scotch Broom dynamics, the single sites are of very individual character and harbour different ant assemblages. This causes a high ant species richness in Scotch Broom stands at the landscape scale. Therefore, conservation strategies for Scotch Broom stands should focus on maintaining a high number of sites widely dispersed within the landscape, i.e., maximising the dissimilarity between Scotch Broom stands and promoting the large scale contribution of beta-diversity to regional species richness (cf. GABRIEL & al. 2006). Even small remnants of seminatural grasslands can harbour species rich ant assemblages (DAUBER & al. 2006), and therefore small and isolated stands of Scotch Broom should also be in the focus of conservation strategies for this historical landscape element.

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Zusammenfassung

Besenginster-Bestände (*Cytisus scoparius* [L.] LINK) stellen bedeutende seminaturliche Lebensräume in Deutschen Kulturlandschaften dar. Die Bestände sind durch eine hohe strukturelle Diversität charakterisiert, was wiederum einen

hohen Artenreichtum der assoziierten Flora und Fauna bedingt. Daher sind diese "Ginsterbrachen" von hohem Naturschutzwert. Ziel dieser Studie war es, Ameisengemeinschaften in verschiedenen Sukzessionsstadien von Besenginsterbeständen zu erfassen und diese mit Ameisengemeinschaften in Äckern und Wäldern der Region zu vergleichen. Die Äcker stellen hierbei den Ausgangspunkt und die Wälder den Endpunkt der Sukzession dar. Innerhalb der Besenginster-Bestände wurde untersucht, welchen Einfluss die in den Beständen etablierte Grünlandvegetation, die Verbuschung und andere Vegetationsstrukturen auf den Ameisenartenreichtum haben. Zudem wurde untersucht, welchen Einfluss Pflanzenartenkomposition, Standortproduktivität und strukturelle Parameter der Vegetation auf die Zusammensetzung der Ameisengemeinschaften haben. Sowohl die Initial- als auch die Klimaxstadien der Sukzession unterschieden sich deutlich von den Zwischenstadien, den Besenginster-Beständen. Der Artenreichtum der Ameisen zeigte keine Korrelation mit dem Artenreichtum der Pflanzen. Die besten Erklärungsvariablen für die Ameisenartenzahl waren die Deckung der Mooschicht und die Ellenberg-Feuchtezahl. Eine Pfad-Analyse zeigte signifikante und voneinander unabhängige Effekte der Standortproduktivität und der Vegetationsstruktur auf die Zusammensetzung der Ameisengemeinschaften, wobei die Standortproduktivität einen um das Doppelte höheren Einfluss aufwies. Die Sukzessionsdynamik in den Besenginster-Beständen erzeugt komplexe Habitatstrukturen, welche eine Vielzahl an Mikrohabitats für Ameisen bereitstellen. Die Ausprägung der Grünlandvegetation war nur von geringer Bedeutung und daher ist es im Rahmen eines Managements der Ginsterbestände zur Erhaltung einer diversen Ameisenfauna nicht notwendig, eine spezifische Pflanzengemeinschaft anzustreben. Allerdings sind die einzelnen Bestände, bedingt durch standortsspezifische Unterschiede, unterschiedliche Ausgangshabitate und die Sukzessionsdynamik sehr verschieden voneinander, so dass sie auch sehr unterschiedliche Ameisengemeinschaften beherbergen. Dies wiederum führt zu einem hohen Artenreichtum auf der Landschaftsebene. Daher sollten Naturschutzstrategien zum Erhalt der Ginsterbrachen bestrebt sein, eine große Anzahl an weit in der Landschaft verbreiteten Flächen zu schützen und zu fördern.

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