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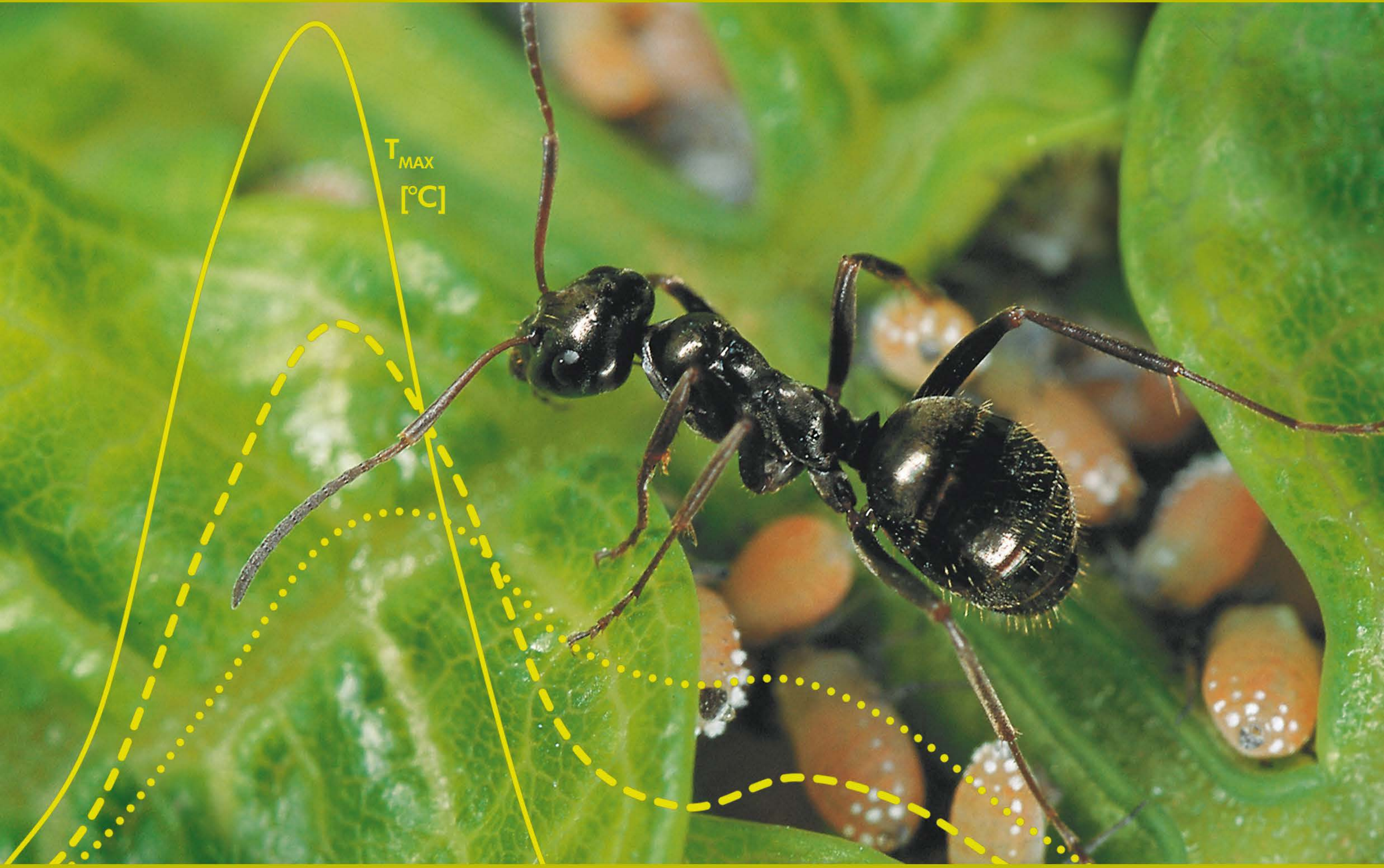

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The ecology of Central European non-arboreal ants – 37 years of a broad-spectrum analysis under permanent taxonomic control

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Abstract

– Methods: A broad spectrum analysis on ant ecology was carried out in Central Europe in 1979–2015, including 232 study plots from 5 to 2382 meters a.s.l. Basically each type of terrestrial, non-arboreal ant habitat was investigated. The full gradient for nearly each environmental variable was covered. The whole study was under permanent taxonomic control, assisted by holding a curated museum collection with updating of the data regarding newly discovered cryptic species. Ant biodiversity and abundance recording was based on direct localization of altogether 17,000 nest sites with nest density determination per unit area. Two new biomass and species richness calculation methods are introduced. Recorded niche dimensions included 6 physico-chemical, 7 structural and 4 species-defined factors. The paper represents the first ecological study with a thorough application of the soil temperature determination system *CalibSoil* which provides comparability of data on thermal behavior of hypo- and epigaean organisms within the context of global warming. It is shown that approximations of fundamental niche space and niche overlap are possible from field data based on 3 factors: (a) temporal disclosure of hidden fundamental niche space during dynamic processes, (b) mathematic decoupling of fundamental niche space from particular study plot situations by subdivision of niche dimensions into classes and (c) idealization of niche space by smoothing of frequency distributions for all niche variables. A method to estimate interspecific competitive exclusion based on a model that relates realized niche overlap to fundamental niche overlap is provided.

– Results: Thanks to the broad environmental gradients considered and the high number of data points, highly significant relations of species richness and biomass of ant assemblages to nearly each investigated environmental variable could be shown with curve characteristics mostly resembling skewed or unskewed optimum curves whereas quasi-linear relations were rare. The most important directly niche-segregating factors are soil moisture and maximum and mean soil temperature whereas herb-layer phytodensity, ranking at the penultimate place among the assessed environmental variables, is thought to have strong indirect effect by altering moisture and temperature conditions. The distribution of 86 ant species relative to environmental variables is shown. 27 habitat categories were compared for species richness and biomass. Xerothermous to mesoxerophytic grasslands on limestone showed the highest average species richness and biomass of open land habitats with 13.1 species / 100 m² and 8.8 g fresh weight / m². Xerothermous to tempered *Quercus* wood (12.5 species / 100 m², 5.5 g fresh weight / m²) and mature *Fagus* woods (0.35 species / 100 m², 0.07 g fresh weight / m²) showed the richest and poorest ant assemblages within woodland habitats. Convincing evidence was presented for E. Odum's theory that narrow niche spaces increase the number of species a habitat may hold. Species richness and evenness of ant assemblages showed a clearly positive correlation. Gause‘s Law is demonstrated to be valid on the biocenotic level: interspecific competitive displacement increases with growing relatedness – 20 pairs of sibling species had significantly lower coexistence values than 214 congeneric pairs of all other species from the genera to which the sibling species belonged (ANOVA $F_{1,232} = 9.98$, $p < 0.002$). It is shown that predictions of zoogeographic shifts due to global warming based on only meteorological simulations will remain inaccurate because 22–31% of variance of mean seasonal soil temperature T_{MEAN} was attributable to the habitat-specific factors stratification and density of phytolayers, orography (aspect) and properties of ground material.

Keywords ant biomass | ant species richness | realized and fundamental niche | sibling species | Gause's Law, calibrated soil temperature | global warming | range prediction | nature conservation

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1. Introduction

1.1 Aim of the study

In 1979, when this study was launched, ecological research in ants was not only impeded by taxonomic naivety (see section 1.2) but also by absence of concrete, objective data. The distribution of ant species over the habitats was described in that time by very rough subjective descriptions such as 'thermophilic, Mediterranean species nesting in dead wood of sun-exposed forest margins.' This situation has not improved substantially up to the present – those few pages with detailed numeric data on ecological preferences of Central European ants hidden in the book of Seifert (2007) largely escaped the attention of myrmecologists. Yet, a predictive ecology determining the position of an organism in a habitat needs concrete, testable and (in the ideal case) calibrated data on the distribution over a multitude of different niche dimensions. George Evelyn Hutchinson's conception of the ecological niche as a set of points in an abstract Cartesian space in which the coordinates are various environmental factors which influence the survival of the species (Hutchinson 1957) has paved the road towards a practical, predictive ecology. Following this basic model, the emphasis of later modifications was put on functionality, regarding the ecological niche as function of given environmental factors ('post authorized in the budget of nature') and the genetically determined potency of a species ('vocation'). Accordingly, Müller et al. (1977) defined the ecological niche to be formed by the fitting together (the congruence) of a n-dimensional valency volume of the habitat with the n-dimensional ecological potency volume of an organism. I follow this concept in this monograph and want to present concrete data on the relations of ant species to different environmental variables and to shed light on interspecific relations between ants. This, hopefully, will facilitate the understanding of the biology of Central European ants.

It is an inescapable fate of terrestrial ecologists that extremely large variance of data may occur for reasons that nobody understands in the first instance. A coefficient of variance of 50 % is a normal situation and 100 % are not rare. Two plots on the same limestone grassland, separated by some 50 meters and showing no apparent differences in structure and plant species composition, may show very different ant assemblages. It were such early findings that influenced the basic strategy of this study very soon. In order to work out fundamental distributional pictures with acceptable expense, I found it better to investigate a particular plot with comparably low effort and instead to increase the number of studied plots and to extend the spectrum of habitats to any conditions under which ants are able to reproduce.

Recent publications on community ecology of ants in Central Europe are not rare and a number of these are not suspected to suffer from wrong taxonomy (e.g. Dahms et al. 2005, 2007; Dauber & Wolters 2004, 2005; Rohe 2003; Wiezik et al. 2011, 2013). Yet, it is problematic and often impossible to derive reliable generalizations even from the cited studies because these considered only small segments within the fundamental niche space, operated with a much too small sample size and provided no comparability due to missing standardization in data recording. These disadvantages in combination with the high noise of ecological field data reduce the value of these studies considerably.

Apart from providing detailed information on ecological potencies and interspecific relations of ant species, the study also aims to give answers to more general questions of community ecology such as changes of species richness and biomass in dependency from diverse environmental variables, relations of species richness and niche width or the validity of the competitive exclusion principle. There is also hope that some of the methodological approaches introduced or re-described in this monography would find some followers within the next generation of ant ecologists.

This study extended over almost four decades but is, in the true sense of the word, no long-term study because a thorough re-investigation of same plots after a longer time interval was only rarely performed. Anyway, I consider the data of 232 study plots presented in the supplementary file as a unique and outstanding source of information on Central European ant communities and their habitats by the end of the 20th and beginning of 21st century. The precise determination of geographic position of the plots will allow future ecologists a direct re-investigation after 50 or 100 years and will provide a sound basis for an unprecedented monitoring of long-term changes. Follow-up investigations after a sufficiently long time could also provide answers to questions in the context of global warming: (a) did the ants change their thermal preferences by changing physiological parameters, (b) did the ants change to cooler habitats while maintaining their physiological parameters or (c) did they die out because no adaptation was possible?

I am willing to provide on request the complete digital data of all 232 study plots in order to allow other scientists to do their own, alternative analyses – perhaps advanced forms of multiple regressions or ordination approaches.

1.2 A good ecology is not possible without a sound taxonomic knowledge

There is a big difference between the identification of elements of biodiversity and those of technological diversity. Identification errors in the field of techno-diversity are automatically punished soon or later: building in a wrong switch element in an electronic instrument will lead to immediate malfunction or, to give another example, confusing an aluminum with a titanium screw in the wing of a jet plane may cause its crash. The result is immediately evident. Identification errors in biodiversity studies, in contrast, are not under this kind of automatic control – ecologists are basically free to publish swarms of wrong hypotheses with a low risk of punishment. This obscurity increases the importance of self-control and responsible behavior of scientists in this field of research.

Psycho-sociological reasons for violation of responsible behavior in biosciences have already been analyzed in the famous field study of Latour & Woolgar (1986). In the late 1970s, these authors observed the behavior of biologists in a laboratory of the renowned Salk Institute in a similar way as human ethologists would study an ethnic group in Japan or Africa. They came to the conclusion that the result of scientific activity was not objective and clean recognition but a scientific output distorted by self-justification, career goals, prejudice and fight for funding. I can witness by my own observations – as a directly involved, active participant of the academic business – that there is no change of the psycho-sociological background up to the year 2017.

Taxonomic expertise which is able to link species delimitation with Linnean nomenclature is vanishing at the beginning of the 21st century. Even well-funded research projects on ecology are run without experts who have sufficient taxonomical experience on the evertebrate groups they deal with to correctly identify these down to species level. Reasons for this development that started in the mid 1960s have been outlined, for instance, by Boero (2010) – research policy and structural chances in the institutions are a major theme here. With no taxonomic experts being available, scientists continue to launch ecological projects. Large parts of their research activity and thinking are concentrated on writing elaborate grant applications but the detailed scientific and logistic consequences of this proposal are of secondary importance in many research groups at this stage. If the application was successful, which appears often like winning in a lottery, the hasty search begins for somebody who could identify the species in this research project. A frequent decision is then: let us take some master student, ‘broadband’ entomologist or guest researcher to identify a certain group of arthropods.

The consequences for the value of the scientific publication finally released may be disastrous. If one finds in an ecological study on ants of the Harz Mountains performed by Srour et al. (2012) that 30% of the ‘identified’ species have never been observed before in that intensively studied geographical region or these kinds of habitats and if one looks at the impossible number of 41 species within as few as 971 trapped ants in these rather cool, low-diversity habitats, it is clear without direct examination of specimens that the ‘determinations’ were fully randomized and that all conclusions in that paper are completely invalid. For comparison: 38 ant species (number adjusted to the taxonomic concept of 2017) were identified among 15,000 pitfall-trapped and Berlese-extracted ant workers in an outstanding species richness hot spot, the Leutra Valley near Jena, some 110 km SW of the Harz Mountains (Seifert 1982). The case of Srour et al. (2012) is probably only the tip of the iceberg. I made a similar experience in a contact with a research project at another German university in which even ant subfamilies were confused. The problem named here for ants seems to be a general one for most groups of organisms as it was outlined by Bortolus (2008) who made an analysis of the taxonomic background of 80 selected papers in high-impact, peer-reviewed ecological journals. If ecologists take their job seriously they must be the first in the scientific community to raise their voice for strengthening education and funding of taxonomic research. Building skyscrapers in drift sand is no acceptable perspective for science.

The taxonomic problem became clear in my own scientific biography. I started ecological field research in 1979 and published the precursor of the present monograph seven years later (Seifert 1986). Following the species concepts of that time, 44% of the ant nests found in the study were considered by me of belonging to only six species: *Lasius alienus*, *Lasius niger*, *Myrmica sabuleti*, *Formica cunicularia*, *Temnothorax nylanderi* and *Tetramorium caespitum*. These determinations resulted in assuming six species with a broad ecological potency – e.g., ‘*Lasius niger*’ was believed to occur from the wettest parts of quaking bogs, over shaded forest and short-grassy park lawns to paved road sides in hot city centers. It was just in 1984 that I increasingly doubted the truth of these traditional species concepts (see also Seifert 2009) and decided to address the major part of my future research activity to ant taxonomy and evolution. In the following years, I could show that these six entities really consisted of 13 different species with a less broad ecological potency (Seifert 1991, 1992, 1995, 1997, 2000). In other words, 44% of the samples considered in Seifert (1986) were not correctly determined to species level, reducing the value of this paper to some methodological aspects and few general statements that were not seriously affected by wrong taxonomy.

Taxonomic errors in the monograph presented here were reduced to a minimum and there is much hope that the discovery of cryptic species in Central Europe approaches a saturation point. I personally performed species determination in most of the 17,000 ant nests found. Furthermore, I checked questionable determinations in direct contacts with Armin Lude, Sonja Weber, Thomas Nocke or Wolfgang Münch when their censuses, using similar ant recording methods, were incorporated in this paper. In fact, there seem to remain only few taxonomic problems within the 86 ant species found on the study plots. A very small error rate seems possible in the identification of the three species of the *Tetramorium caespitum* complex as this was frequently done by simple eye inspection based on expert experience instead of performing the safer, but very time-consuming, NUMOBAT procedures (e.g., Seifert et al. 2013).

The only problematic taxonomic borderline case within the 86 species found on the study plots is *Myrmica scabrinodis* in which East and West European populations show significant morphological differences. The mean error of four exploratory data analyses NC-Ward, NC-UPGMA, NC-K-Means and NC-NMDS-K-means (for methods see Seifert et al. 2013) was 3.8% in a meta-analysis of Palaearctic populations. This is above the 3% error threshold recommended by the Pragmatic Species Concept (Seifert 2014) or just below the 4% threshold later considered to be more adequate for cryptic species in ants (Seifert & Csösz 2015, Seifert 2016b, Seifert & Galkowski 2016). The decisive point against a subdivision in an eastern (*M. scabrinodis* Nylander) and western (*M. rugulosoides* Forel) species was in this case a significant morphological convergence in the broad sympatric zone ranging from 6°E to 17.5°E compared to the allopatric population east and west of this zone. This is a clear signal for frequent hybridization and introgression and I hypothesize the two populations as insufficiently separated.

2. Study area and study plots

The study was carried out in the years 1979 to 2015 and included 232 study plots in Central Europe within 46.5° N to 54.1° N, 9.3°E to 15.6°E and from 5 to 2382 m above sea level. Basically each type of terrestrial, non-arboreal habitat in which ants are able to reproduce was investigated. Within the system of study plots, maximum calibrated soil temperature of the summer season (see section 3.6.1) ranged from 7.4°C in a subalpine fir forest to 33.5°C in a plot on bare basalt rock whereas the seasonal mean of calibrated soil temperatures varied from 5.7°C in an alpine pasture to 18.4°C in a lowland sand dune with *Corynephorus*. As result of global warming, the mean air temperature [2 m] from 1 May to 31 August increased in the study area by 1.3°C during the period 1979 to 2015. The moisture gradient ranged from extremely dry in the top of a drift sand dune at the margin of a brown-coal strip mine to complete wetness in a quaking bog. The majority of study plots was investigated in only a single season. Expenditure of time for ant collecting and recording of habitat parameters ranged between 3 man-hours per plot in simply structured habitats with easily detectable nests (e.g. drift sand dunes with only *Formica cinerea*) but up to 32 man-hours per plot in habitats with a high structural diversity, hidden nest sites and high species richness. An approximate grouping of the 232 investigated plots into 27 habitat categories is given in Tab. 11 in section 4.3.

A more detailed characteristics of the 232 study plots is given in the supplementary information (www.senckenberg.de/soil-organisms/2017/study_plots_Seifert). Each characteristics presents data on geographic situation, plot size, date of investigation, investigator, orography, soil conditions, management and history of the habitat, structure in four phytostrata, plant species composition, soil temperature, moisture, nutrient figure, calcium figure, phytodensity in the herb layer, stone density, nest density of ant species and species richness.

3. Methods

3.1 Methods for search of ant nests

Recording of ant biodiversity and abundance was thoroughly based on direct localization of nest sites and determination of nest density per unit area. In contrast to more frequently used variants of trapping, baiting or sifting methods (reviewed in Agosti et al. 2000) which mainly record activity and behavior of foragers, localization of nest sites provides an approximation to the really existing ant population. Furthermore it gives insights into nest composition and biological properties of the ants themselves and allows, as a useful additional effect, collecting of clean nest populations of defined kinship needed for taxonomic or genetic investigations. Considering these advantages, it is surprising that Agosti et al. (2000) spared only one and a half pages for describing and commenting the method of nest density recording within a 280-pages book on standard methods for measuring and monitoring ant biodiversity.

The minimum condition for considering a finding on a certain spot as an ant nest was the association of workers with broods or of a queen with at least a single worker and some broods. This qualification was necessary to avoid two types of error leading to overestimation of nest densities. These are erroneous interpretations as nests in case of clusters of many workers at food sources (e.g., at subterranean aphid colonies) or of queens in founding chambers with broods. The latter finding does not necessarily indicate that a certain habitat will provide the conditions to establish a colony. Queens of some ant species do not seem to have a very selective habitat recognition system after nuptial flight and try to found also in places providing low chances for successful colony foundation. For example, founding queens of *Lasius platythorax* are frequently observed in open arable land (a habitat from which no established nests of this species are known so far) or founding queens of *Camponotus herculeanus* are abundant in tree stumps of large clear cuttings – a habitat where food sources are insufficient for this species. The definition of an ant nest given above does not distinguish between nests of monodomous and polydomous colonies. Aggression between closely neighboring nests was occasionally tested in the field for informal reasons but the results of these tests did not change the final quantitative assessment. The question in which way nest densities can be used for estimates of total ant biomass is considered in section 3.3.

Localization of nest sites in this research project focused on hypo- and epigaean strata. In shrub or woodland habitats, the study considered all ant nests below 2.0 meters height. Arboreal nest sites above this level were excluded from investigation except for very few plots inviting for easy and riskless tree climbing without equipment. A complete recording of hidden subterranean ant nests is in the majority of situations only possible when soil is dug thoroughly by closely-spaced cuts of spade and careful disintegration of the clods. This radical method of survey causes strong habitat destruction and was not acceptable for reasons of nature conservancy – the more as many plots were situated in protected areas. For reasons of comparability, this method was also not applied in the rather rare cases with no objections from the perspective of nature conservation or ground owners. However, nest densities recorded during this study with the moderately destructive methods explained below compare very well with data found by total digging (Galle 1972a, 1972b, 1978a, 1980; Nocke 1998). This positive impression refers to the majority of ant genera. Yet, the less radical method implies a significant underestimation of nest densities in small-sized subterranean ants with small nest populations and low above-ground foraging activity – namely *Ponera, Myrmecina* and *Stenamma.* In order to compensate for underestimation in these ants, the finding of already a single worker (or of several workers on the same spot) was considered as an indication for a nest nearby. This practice is justified under certain conditions also for epigaean species with very small foraging distances when these are present in low nest densities – e.g., the finding of a single *Temnothorax* or *Leptothorax* worker on a spot was considered as indication for a nest when no nest of this species was discovered within a radius of 1.5 meters (for foraging distances in these species see Fokuhl et al. 2012, Bengston & Dornhaus 2013, Seifert et al. 2013, Seifert et al. 2016).

In addition to nest samples, grab samples of foraging ant workers were taken from the plots. These data may provide information on possibly overlooked species or nests and may supplement quantitative assessment of nest density. If, for instance, five nests of *Leptothorax acervorum* and two nests of *L. muscorum* were found per unit area but the grab sample of all *Leptothorax* workers from the same area contained 15 % *L. gredleri*, one can assume that at least one *L. gredleri* nest was overlooked. Data of inferred nest presence were integrated in the final whole-community nest counts.

Localization of ant nests was performed as a sequence of three (sometimes four) different modes of recording: scrutiny search **(S-search)** is performed on a smaller-sized S-area, quick search (**Q-search**) was done on a larger-sized Q-area and spot inspection (**SI-search**) was carried out without reference to an area size (Fig. 1). In few cases a large-scale search (**L-search**) was applied. S-search, done on areas between 15 and 80 m², is a careful investigation of basically each square decimeter of soil and substrate surface. This includes the turning of any movable stone, ablation of bark pieces or loose-fitting stone plates on rock, opening of dead wood, of hollow acorns, nuts, old snail shells, galls or any other habitat structure potentially offering space for an ant nest. Suspicious soil spots were probed and opened a few centimeters deep with sharp steel instruments to provoke a response of ants. Grass and moss bults were ruptured and litter was carefully raked. Frequently mowed park lawns with completely smooth, homogenous surface, giving no indications to hidden ant nests, were aggressively scrubbed throughout their surface in order to provoke ants to appear on surface. Hidden ant nests of less populous ant species may be indicated by a few food remains or tiny material ejections or are located by observing the movements of workers returning with food. Expenditure of time for S-search varied. Habitats with complicated structure providing many microhabitats and high nest densities frequently required 30 minutes per m² for nest density recording alone. Complete disintegration of nests for taxonomic purposes could increase working time considerably. As the opposite extreme, open areas of fine sand with extremely sparse vegetation, where each nest entrance is easily visible, may require only 2 minutes search time per m². The applied recording method undoubtedly lead to a partial destruction of microhabitats but had no long-lasting effect at least on vascular plants which appeared unaffected during visits in the next season.

S-search aimed at realistic recording of nest densities of ants with hidden nests such as *Leptothorax*, *Temnothorax* or *Myrmecina* or with frequently hidden nests such as *Lasius* or *Myrmica*. The high expenditure of time reduced the size of S-areas to usually below 50 m² which was frequently not large enough to achieve a sufficient number of findings of larger species with lower nest densities, less hidden nests and larger territories. Recording realistic nest densities in these species groups – typically *Formica*, *Camponotus* and rarer *Lasius* species – was the main aim of Q-search during which microhabitats where no longer thoroughly investigated. Yet, data of the hidden species occasionally found during Q-search were integrated into the final whole-community nest density data as it is described below. The size of Q-areas is finally calculated by addition of the areas subject to S- and Q-search and ranged between 50 and 400 m².

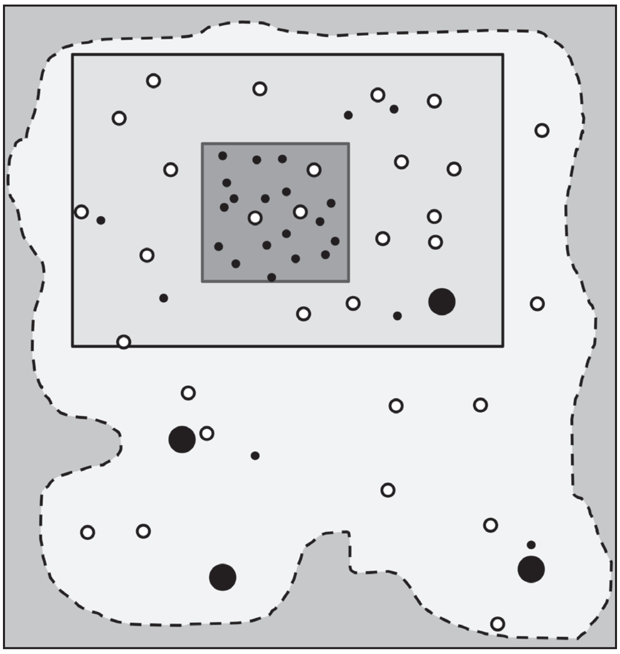


Figure 1. Three-level procedure for recording ant nest densities. The dashed line marks the border of a more or less homogenous habitat. Scrutiny search (S-search) for discovery of very hidden nests of usually smaller species (small black dots) is performed in the small inner square with high expenditure of time per unit square. Quick search (Q-search) for discovery of more easily detectable nest of larger species (white, medium-sized and big black dots) is done on the larger square with a lower expenditure of time per unit area. Spot inspection (SI-search) is done in the light grey zone without area-reference only on selected spots which appear most promising to find an ant nest – this increases the number of nest findings per unit time considerably. Data from S-, Q- and SI-search were finally collated to compute integrated nest densities.

The third search method, spot inspection without reference to an area size, named SI-search, was done in parts of the habitat immediately adjacent to S- and Q-areas and having the same habitat structure. SI-search selected spots most promising to find an ant nest – thus increasing the number of nest findings per unit time considerably. This allowed discovering nests of the rare species such as social parasites of the genus *Lasius* or *Formica.* These data were also integrated into the final whole-community density data by the procedures described below.

The fourth search method, large-scale search or L-search, was only exceptionally applied because of limitations in habitat area or time budget. L-search is a nest-density estimate for the easily visible nests of mound building wood ants performed by slowly walking over areas of one hectare or more.

3.2 The calculation of integrated nest density data, recording groups and pseudo-areas

The final abundance structure of the whole ant community is described by nest-density data which are integrated values when different search methods were combined. Integrated density values were always determined via allocating a species into a given recording group (RG). Recording groups describe the probability of finding an ant nest per unit investigation time. This probability is determined by position, type, size and density of the nests. Five recording groups are informally defined ranking from lowest to largest perceptibility.

RG *i*: Nests very difficult to find. Complete density recording is usually only possible by full-area digging and complete disintegration of soil clods. Subterranean, weakly populated nests in micro-spaces with workers exclusively foraging in soil or in litter (*Ponera*, *Hypoponera*).

RG *ii*: Nests difficult to find. Small-sized species with small nest populations living in frequently hidden micro-spaces located very near to substrate surface but with workers showing significant surface foraging (*Temnothorax, Leptothorax* and their social parasites, *Myrmecina*, *Stenamma*).

RG *iii*: Nests more easy to find. Medium-sized species with significant surface foraging and moderately populated nests of medium extension (subgenus *Lasius str., Myrmica*, *Tetramorium, Tapinoma*) or small- to medium-sized, completely subterranean species with large nest populations and more extended nest space (genera *Solenopsis*, *Tetramorium* and subgenera *Lasius str., Cautolasius*, *Chthonolasius*, *Austrolasius*).

RG *iv*: Nests with usually good perceptibility. Bigger species with intensive surface foraging and usually larger nest diameters and nest populations (subgenera *Serviformica, Raptiformica, Coptoformica, Dendrolasius*).

RG *v*: Nests immediately perceptible during walking over ground. Bigger species with intensive surface foraging and constructing big, strongly populated nest mounds – typically the mound building wood ants of the subgenus *Formica*.

This subdivision in five recording groups considers average relations over all habitats and is of informal value – i.e., it is a generalization on different perceptibility of nests depending on the ant group considered. In practice, an experienced myrmecologist should manage the issue with flexibility depending on the special situation in a particular habitat. To give an example, species of the subgenus *Serviformica* are normally placed in RG *iv* but an extremely dense *Formica* (*Serviformica*) *fusca* population along the margin of a xerothermous oak forest, for instance, is better downgraded to RG *iii*, sharing the grouping with *Lasius* or *Myrmica*.

Basically a myrmecologist has to ask two questions. The first question reads: The density of which species cannot be recorded realistically by the applied methods? These were in most of the study plots RG *i* species because of extremely hidden nests and RG *v* species because the investigated Q-area was too small and because a L-area was not investigated. The second question reads: The density of which recording groups is expected of having been determined realistically during S-search, Q-search or L-search (if the latter was done)?

Table 1 explains the calculation of integrated species-specific nest density values (ISSD) on the basis of a fictitious (but realistic) example of nest search in a xerothermous limestone grassland. Three single workers of *Ponera coarctata* (RG *i*) were found under three stones during S-search on 50 m² and considered to indicate three different nests. S-search furthermore resulted in the finding of 21 nests of RG *ii* (*Temnothorax* species), 38 nests of RG *iii* (*Lasius* and *Myrmica* species) and of 2 nests of RG *iv* (*Formica* species and *Polyergus rufescens*). This resulted in a total density of 6 nests/100 m² for RG *i*, 42 nests/100 m² for RG *ii*, 76 nests/100 m² for RG *iii*, 4 nests/100 m² for RG *iv* and 0 nests/100 m² for RG *v*. S-search was now considered to indicate a realistic overall density for RG *ii* and RG *iii* and these densities are now taken as fixed recording-group-specific total density (FRSD). The inevitably underestimated FRSD of RG *i* is also fixed at this stage but that of RG *iv* remains yet undetermined because the search area is too small. Subsequent Q-search on 100 m² area resulted finding 2 nests of RG *ii*, 16 nests of RG *iii* and 3 nests of RG *iv*. Because Q-search allowed a realistic density assessment of only RG *iv* and because S- and Q-areas sum up to 150 m², FRSD of RG *iv* is now fixed as 3.33 nests/100 m² – from 5 nests/150 m². SI-search, as the last recording method in this example, resulted in the finding of 1 nest of RG *ii*, 18 of RG *iii*, 8 of RG *iv* and 1 of RG *v*. Now the so called **pseudo-areas** come into play. Pseudo-areas are calculated for recording groups separately and provide a measure of the total intensity of investigation on a certain study plot. A pseudo-area may be understood as the area equivalent needed in a recording group to find the sum of nests recorded by S-, Q- and SI-search. The pseudo-area is the S+Q+SI search sum of nests divided by the FRSD value fixed for a recording group. Data of pseudo-areas are frequently useful for adjustment of species richness calculations when Q-areas are larger than 200 m² (see section 3.4).

The **integrated species-specific density** (ISSD) is finally calculated as the sum of nests found during S-, Q- and SI-search divided by the pseudo-area of the recording group to which a particular species belongs. Accordingly, the ISSD value of a rare species such as *Polyergus rufescens* is calculated in the given example as 1 nest/390.4 m² or 0.26 nests/100 m². This example shows the value of SI-search during which, with comparably low time requirement, the abundance of rare species can be estimated realistically. *Formica pratensis* remains in this example without density value because an L-search over an area of one ha was not performed – it is simply recorded here as present ('x').

3.3 The estimation of ant biomass

Nest density data can be used to estimate ant biomass if mean individual body mass and the mean number of individuals per nest population are known. I provide here a biomass estimation method which realistically describes a general distribution picture over all habitats in 232 study plots in relative terms. The main aim is here to correctly show the basic relationship of overall ant biomass to particular environmental factors or to habitat types. Note that no claim for precision of absolute values for particular study plots can be raised because of the large potential errors described in the next section.

3.3.1 Comment on error sources

The first problem is the absence of a linear relationship between recorded nest density and ant biomass because decreasing habitat quality does not only reduce nest density but also mean size of nest populations and mean worker body weight. This was a general impression during four decades of field work. To mention one obvious example, *Lasius platythorax* nests at the margin of a productive broad-leafed woodland are subjectively estimated to have approximately fivefold the average biomass compared to conspecific nests in the wet oligotrophic Sphagnetum of a quaking bog. The exact way to solve this problem would be direct evaluation of mean biomass per nest, species and habitat in the study plots by complete nest excavation and complete collecting of foragers. This approach was not possible due to limitations in working capacity and restrictions imposed by nature conservation laws. Yet, the error produced by a nonlinearity of nest density and biomass should not seriously distort the picture because the ranking of habitats is not affected.

The second problem is that nest density recording in this study also counted small initial nests (e.g., a founding queen with the first nanitic worker/s) whereas the many published censuses of size and composition of nest populations usually overlooked such nests or excluded them from evaluation. Accordingly, multiplying nest density data of this study with published data on mean nest populations will expectably result in an overestimation of biomass.

The third problem is that number and biomass of broods and freshly produced sexuals is much less well known than that of workers and more variable depending on time within the season, maturity of nests and environmental conditions (e.g. Buschinger & Heinze 2001, Nielsen 1978). The mean production of sexuals in *Lasius niger* or *Tetramorium caespitum*, for example, amounts 25 % and 33 % of the mean summer ant nest biomass respectively (Brian et al. 1967, Nielsen 1974a, Peakin 1972, Boomsma et al. 1982). In monogynous ant species tending for separation of queenless summer nests in order to maximize sexual production (e.g. Partridge et al. 1997), the conditions may become extreme: eggs, larvae and pupae amounted for 65 % of the total fresh weight of a queenless nest of *Temnothorax crassispinus* with 45 workers in early July before hatching of the alates. The calculation system presented here did not consider biomass of broods and sexual production. This results in an underestimation of mean annual biomass which compensates to some degree for the error mentioned in the previous section.

3.3.2 The biomass calculation system

After commenting on three major error sources, the biomass calculation system will be explained. The first factor to be determined was mean worker individual fresh weight. The more frequent use of dry weight in biomass investigations compared to fresh weight is usually explained by a better reproducibility. Yet, use of dry weight is problematic in its biological significance or comparability within groups of morphologically heterogeneous organisms. There are very strong differences between ants in thickness of cuticle. Dry weight in heavily armored ants such as *Myrmica* or *Tetramorium* is about 40 % of fresh weight whereas it may be as low as 25 % in the soft-bodied *Lasius flavus* (my own unpublished investigations). Considering these facts, I decided to use fresh weight for biomass calculations

Table 1. Fictitious example of a nest density recording combining the three search methods S search, Q search and SI search. RG = recording group, n = number of nests found, FRSD = fixed, recording-group specific total density [nests/100 m²] , ISSD = integrated species-specific density [nests/100 m²], n.d. = not determined.

	RG	n S-area 50 m²	FRSD after S	n Q-area 100 m²	FRSD after S+Q	n SI-search	n S+Q+SI search	Pseudo-area [m²]	ISSD
Ponera coarctata	*i*	3	6.0	0	6.0	0	3	50.0	6.0
Temnothorax albipennis	*ii*	13	42.0	1	42.0	0	14	57.14	24.5
Temnothorax tuberum	*ii*	8		0		1	9		15.8
Temnothorax interruptus	*ii*	0		1		0	1		1.8
Lasius alienus	*iii*	32	76.0	10	76.0	16	58	94.74	61.2
Lasius niger	*iii*	3		0		0	3		3.2
Lasius jensi	*iii*	0		1		0	1		1.1
Myrmica sabuleti	*iii*	3		2		1	6		6.3
Myrmica specioides	*iii*	0		3		0	3		3.2
Myrmica schencki	*iii*	0		0		1	1		1.1
Formica cunicularia	*iv*	2	n.d.	1	3.33	2	5	390.39	1.3
Formica rufibarbis	*iv*	0		2		5	7		1.8
Polyergus rufescens	*iv*	0		0		1	1		0.3
Formica pratensis	*v*	0	n.d.	0	n.d.	0	0	n.d.	x
sum		**64**		**21**		**28**	**113**		**127.6**

because weight in living condition tells us more about the metabolic status of an organism than dry weight (see also Dunger 1968 for soil organisms). I measured fresh weight of ants in the condition as they were present in the nest during the summer season because catching foragers alone would lead to a higher error. First of all there may be enormous variance in forager weight due to inflation of gaster by heavy crop fillings with liquid food. In the honey-dew feeder *Lasius fuliginosus* crop loads lead to an average weight increase by 55 % (F. Steiner pers. comm., supplemented by own data). On the other hand, foragers in many ant groups have reduced fat bodies and ovaries compared to young innendienst workers. This reduces mean forager weight compared to the total nest mean. The mean weight of *Formica polyctena* foragers, for instance, is only 72 % of that of workers from the nest core (Otto 1960).

Mean worker fresh weight FW of nest population can be described within a group of related ants with similar body shape as a function of mean head size CS (the arithmetic mean of maximum measureable head length and width):

$$FW = SH * CS^3$$

where SH is a group-specific or species-specific shape factor. Large SH indicate a more thick-set or compact body shape. SH was determined in a small number of exemplary species of a species group with similar basic morphology. SH differed for instance between members of the subgenera *Serviformica* and *Formica*. Because population means of CS were available for any species of the study system thanks to the extensive NUMOBAT files of the author, fresh weight could be predicted for those (many) species where no samples of living ants were at hand (Tabs 2 and 3).

After having addressed mean worker fresh weight determination, we have to find reasonable estimates for the mean nest population of workers. The basic procedure was comparing published censuses, assessing the habitat quality attributable to these censuses and relating these to assumed average conditions over all habitat types. This included averaging of data of different authors but also a subjective adjustment of these data according to my individual experience in the field.

Good knowledge on size of nest population exists in small myrmicine ants such as *Leptothorax*, *Temnothorax*, *Myrmecina* or *Stenamma*. These ants have a smaller worker number, a low forager ratio and do frequently live in well-circumscribed nest spaces. Collecting of nearly complete nest populations is quite easy in these ant groups and there was a good supplementation of published censuses by my own data collected over three decades. Data on nest populations of *Leptothorax* species were given by Felke & Buschinger (1999), Heinze et al. (1992, 1995), Heinze & Lipski (1990), Heinze & Ortius (1991) and Lipski et al. (1992, 1994), of *Harpagoxenus* by Buschinger (1978), Buschinger et al. (1975), Bourke et al. (1988) and Winter & Buschinger (1986), of *Temnothorax* species by Foitzik et al. (1997, 2003), Martin et al. (1995), Mitrus (2013), Partridge et al. (1997), Seifert (2007) and Ticha (2002), of *Myrmecina* by Buschinger & Schreiber (2002), and of *Stenamma* by Lawitzky (1988), Buschinger & Heinze (2001) and Seifert (2007). Comparably good is also the knowledge in *Myrmica* species thanks to data published by Brian (1972), Petal (1972), Elmes (1973, 1975, 1987), Elmes & Abbot (1981), Elmes & Petal (1990), Elmes & Wardlaw (1981, 1982), Pech (2013), Pedersen & Boomsma (1999) and Seifert (2007).

More difficult is the situation in the genera *Tetramorium*, *Solenopsis*, *Lasius* or *Formica* because an exact census of the frequently large nest populations requires a complete (or at least sectorial) excavation of considerable mound and soil volumes. The problem is increased by high variance in nest population numbers caused by intraspecific social polymorphism (monogyny vs. polygyny), habitat quality and stage of succession. The census methods applied by different authors varied between direct excavation, mark-recapture estimates and determination of forager populations by traffic counts or exhaustive catches. The first step for assessment of mean nest populations in these genera was collating heterogeneous data of repeatedly studied focal species and determining from these data reasonable mean values. I took these means then as ‘calibration points’ for experience-based relational guesses of the situation in related species for which no or only anecdotal data were available. The focal species and the reference authors were: *Tetramorium caespitum* (Brian et al. 1967, Nielsen 1974a), *Lasius psammophilus* (Nielsen 1972, 1974a, 1975b, 1978), *Lasius niger* (Nielsen 1974a, Petal 1976, Boomsma et al. 1982, Holec & Frouz 2005), *Lasius flavus* (Nielsen et al. 1976, Nielsen 1977, Pontin 1978, Holec & Frouz 2005), *Formica cunicularia* (Holec & Frouz 2005), *Formica polyctena* (Horstmann 1982, Rosengreen & Sundström 1987, Sörensen & Schmidt 1987, Seifert 2016a), *Formica lugubris* (Breen 1979, Chen & Robinson 2013, Seifert 2016a) and *Formica sanguinea* (Marikovsky 1967, Kupyanskaya 1990, Holec & Frouz 2005).

3.4. The calculation of species richness

The species number S found in a certain habitat is a function of sampling effort E (‘Erfassungsintensität’

Table 2. Mean head size CS, shape factor SH, mean fresh weight and mean nest populations of worker ants for species of the subfamilies Ponerinae and Myrmicinae found in the study system. When two figures of CS and SH are given for a species, the first number refers to the minor caste and the second one to the majors. [1] mean of a nest population with 75 % minor workers and 25 % majors.

Species	CS [µm]	SH	fr. weight [mg]	mean nest population
Harpagoxenus sublaevis (Nylander 1849)	961	1.239	1.100	41 + 243 slaves
Leptothorax acervorum (Fabricius 1793)	816	1.480	0.804	180
Leptothorax gredleri Mayr 1855	709	1.480	0.527	33
Leptothorax muscorum (Nylander 1846)	647	1.480	0.401	47
Manica rubida (Latreille 1802)	1548	1.519	5.635	500
Myrmecina graminicola (Latreille 1802)	752	1.921	0.800	45
Myrmica constricta Karavajev 1934	966	1.419	1.309	875
Myrmica curvithorax Bondroit 1920	1098	1.419	1.922	382
Myrmica gallienii Bondroit 1920	1128	1.419	2.084	836
Myrmica lobicornis Nylander 1846	1062	1.419	1.739	280
Myrmica lobulicornis Nylander 1857	1073	1.419	1.794	600
Myrmica lonae Finzi 1926	1190	1.419	2.447	562
Myrmica rubra (Linnaeus 1758)	1138	1.419	2.140	1600
Myrmica ruginodis Nylander 1846	1209	1.419	2.566	800
Myrmica rugulosa Nylander 1849	983	1.419	1.379	1200
Myrmica sabuleti Meinert 1861	1158	1.419	2.255	650
Myrmica scabrinodis Nylander 1846	1081	1.419	1.834	600
Myrmica schencki Viereck 1903	1183	1.419	2.404	350
Myrmica specioides Bondroit 1918	1048	1.419	1.671	450
Myrmica sulcinodis Nylander 1846	1260	1.419	2.905	460
Myrmica vandeli Bondroit 1920	1137	1.419	2.086	850
Myrmoxenus ravouxi (André 1896)	623	1.733	0.419	33 + 140 slaves
Ponera coarctata (Latreille 1802)	639	1.564	0.408	50
Ponera testacea Emery 1895	586	1.564	0.315	50
Solenopsis fugax (Latreille 1798)	420/527	1.417/1.483	0.133[1]	50000
Stenamma debile (Förster 1850)	764	1.718	0.766	56
Strongylognathus testaceus (Schenck 1852)	670	1.240	0.373	600
Temnothorax affinis (Mayr 1855)	689	1.540	0.504	100
Temnothorax albipennis (Curtis 1854)	607	1.540	0.344	110
Temnothorax corticalis (Schenck 1852)	674	1.540	0.472	63
Temnothorax crassispinus (Karavajev 1926)	648	1.540	0.419	80
Temnothorax interruptus (Schenck 1852)	554	1.540	0.262	141
Temnothorax nigriceps (Mayr 1855)	629	1.540	0.383	126
Temnothorax nylanderi (Förster 1850)	652	1.540	0.427	85
Temnothorax parvulus (Schenck 1852)	575	1.540	0.293	61
Temnothorax saxonicus (Seifert 1995)	625	1.540	0.376	142
Temnothorax tuberum (Fabricius 1775)	624	1.540	0.374	150
Temnothorax unifasciatus (Latreille 1798)	642	1.540	0.407	134
Tetramorium alpestre Steiner et al. 2010	748	1.154	0.483	15000
Tetramorium caespitum (Linnaeus 1758)	774	1.268	0.588	15000
Tetramorium impurum (Förster 1850)	766	1.193	0.536	15000

Table 3. Mean head size CS, shape factor SH, mean fresh weight and mean nest populations of worker ants for species of the subfamilies Dolichoderinae and Formicinae found in the study system. When two figures of CS and SH are given for a species, the first number refers to the minor caste and the second one to the majors. [1] mean of a nest population with 75 % minor workers and 25 % majors.

Species	CS [µm]	SH	fr. weight [mg]	mean nest population
Camponotus fallax (Nylander 1856)	1508	1.954	6.7	300
Camponotus herculeanus (Linnaeus 1758)	2487	1.714	26.36	3000
Camponotus ligniperda (Latreille 1802)	2496	1.818	27.06	3000
Camponotus piceus (Leach 1825)	1045/1542	1.94/1.66	3.186[1]	400
Dolichoderus quadripunctatus (Linnaeus 1771)	841	1.77	1.052	300
Formica (Serviformica) cinerea Mayr 1853	1351	1.94	4.78	2000
Formica (Serviformica) clara Forel 1886	1475	1.94	6.23	2000
Formica (Serviformica) cunicularia Latreille 1798	1375	1.94	5.05	1400
Formica (Serviformica) fusca Linnaeus 1758	1304	1.94	4.30	1500
Formica (Serviformica) fuscocinerea Forel 1874	1307	1.94	4.33	2000
Formica (Serviformica) lemani Bondroit 1917	1268	1.94	3.96	1500
Formica (Serviformica) picea Nylander 1846	1211	1.94	3.44	650
Formica (Serviformica) rufibarbis Fabricius 1793	1439	1.94	5.78	2000
Formica (Serviformica) selysi Bondroit 1918	1354	1.94	4.82	2000
Formica (Formica) aquilonia Yarrow 1955	1504	2.561	8.71	150000
Formica (Formica) lugubris Zetterstedt 1838	1735	2.561	13.38	60000
Formica (Formica) paralugubris Seifert 1996	1603	2.561	10.55	150000
Formica (Formica) polyctena Förster 1850	1606	2.561	10.61	200000
Formica (Formica) pratensis Retzius 1783	1736	2.561	13.40	60000
Formica (Formica) rufa Linnaeus 1761	1812	2.561	15.24	60000
Formica (Formica) truncorum Fabricius 1804	1689	2.561	12.34	20000
Formica (Coptoformica) exsecta Nylander 1846	1391	2.561	6.89	25000
Formica (Raptiformica) sanguinea Latreille 1798	1823	2.561	15.26	5000 + 1000 slaves
Lasius (Lasius) alienus (Förster 1850)	823	1.656	0.923	5000
Lasius (Lasius) brunneus (Latreille 1798)	933	1.656	1.345	5000
Lasius (Lasius) emarginatus (Olivier 1792)	966	1.656	1.493	5000
Lasius (Lasius) niger (Linnaeus 1758)	977	1.656	1.544	5000
Lasius (Lasius) paralienus Seifert 1992	867	1.656	1.079	5000
Lasius (Lasius) platythorax Seifert 1991	970	1.656	1.511	5000
Lasius (Lasius) psammophilus Seifert 1992	841	1.656	0.985	5000
Lasius (Cautolasius) flavus (Fabricius 1782)	828	1.656	0.940	10000
Lasius (Cautolasius) myops Forel 1894	739	1.656	0.668	10000
Lasius (Chthonolasius) jensi Seifert 1982	977	1.656	1.544	10000
Lasius (Chthonolasius) meridionalis (Bondroit 1920)	996	1.656	1.636	10000
Lasius (Chthonolasius) mixtus (Nylander 1846)	1042	1.656	1.874	10000
Lasius (Chthonolasius) umbratus (Nylander 1846)	1096	1.656	2.180	10000
Lasius (Austrolasius) reginae Faber 1967	905	1.656	1.227	10000
Lasius (Dendrolasius) fuliginosus (Latreille 1798)	1403	1.590	4.39	30000
Polyergus rufescens Latreille 1798	1550	1.940	7.50	1500 + 15000 slaves
Plagiolepis vindobonensis Lomnicki 1925	479	1.656	0.182	15000
Tapinoma erraticum (Latreille 1798)	739	1.656	0.668	2000
Tapinoma subboreale Seifert 2011	683	1.656	0.528	1500

in Seifert 1986) which is quantified in this study by square meters of searched ground area. Assuming that the number of species a habitat can hold is finite, S follows a saturation curve. This relation was described by Kylin (1926) and Seifert (1986) by a function of the type $S = Q\ (1\text{-}e^{E})$ where Q is the maximal possible species number for a habitat that is limited by the overall species number existing in the corresponding geographic region and the ecological potency of particular species. However, a practical application of this function is problematic because Q remains nearly always unknown. Attempts to estimate Q for infinite E by a double-reciprocal plotting analogous to approaches in enzyme kinetics (Michaelis & Menten 1913) resulted in both credible as well as utterly impossible figures for the 232 study plots considered here (data not presented). A more reasonable estimate of Q within the investigation system applied here will probably require well-censused search areas of at least 1000 m² – a condition unrealizable in practice. As a consequence, I abandoned this form of describing species-accumulation curves and changed to functions based on natural logarithm (see below).

The first step in developing a method for calculation of species richness was calculating extrapolated species accumulation curves for each study plot under exclusion of data points resulting from SI- and L-search (section 3.1). The assumptions and algorithms were as follows. If n species were found on a Q-area, if i = 1 designates the most abundant and i = n the rarest species, and if D_1 is the sum of all nest densities d_i of n species

$$D_1 = \sum_{i=1}^{n} d_i \qquad [1],$$

the first species (i.e., the first nest finding) is expected statistically after having searched an area of $E_1 = 1/D_1$. Because the first finding will belong with the highest probability to the most abundant species with i = 1, the data of this species are removed from the data set and there remains a nest-density sum of

$$D_2 = \sum_{i=2}^{n} d_i \qquad [2].$$

The finding of the second abundant species is then predicted after having searched an area of $E_2 = 1/D_2$. The procedure is continued until the finding of the rarest species within the Q-area has been predicted. Fig. 2 shows the species accumulation curve of study plot SP 159 approximated in this way. This approach represents another variant of constructing so called Rarefaction Curves (Sanders 1968, Siegel 2006).

Within groups of species having comparable space utilization (e.g., within Collembola, within ants or within passerine birds), species accumulation curves show approximately equal stretching factors which are proportional to the minimal areal size. Recording 50 % of putatively present species requires a 10–20 fold larger area in ants compared to springtails (D. Russell pers. comm.). If the stretching factor can be considered as equal within a particular group of organisms, the slopes of species accumulation curves are proportional to species richness of a habitat. It was evident for ants that species accumulation curves of habitats differing in species richness did only exceptionally intersect for E > 15 m² – Figs 3–5 show the situation in three different types of habitats with only a few examples shown for each habitat. In other words, a study plot A showing a larger species number than a plot B after 20 m² of area have been searched is most likely to do so after a search over 100 or 200 m². This may be called the law of proportionality of species numbers.

A series of tests showed that empirical species accumulation curves of the data set of this study are best described by a logarithmus naturalis function of the type S = a Ln E + b. Exponential, power or polynomial functions showed a significantly worse fitting. This finding is confirmed for ants by Campbell et al. (2015) who found that species accumulation and extrapolation curves of data for ant assemblages in savannah, saltpan and desert sites were best fitted by logarithmic descriptions. A logarithmus naturalis fitting was also the best solution in oribatid mites recorded by pitfall trapping or soil cores (H.D. Engelmann pers. comm. 1985). In agreement with Stirling & Wilsey (2001), I consider the use of logarithmic functions as the best solution for describing species accumulation curves in general. In the ant data set of this study, the mean coefficient of correlation was 0.9835 for logarithmic fittings of extrapolated species accumulation curves for 192 study plots with at least three recorded species. The mean species accumulation curve derived from these data was

$$S_M = 1.6042\ \mathrm{Ln}\ E + 0.8476 \qquad [3].$$

The function $S_M = f(E)$ may be considered as description of the average behavior of ant assemblages within the study system. The absence of intersection points in species accumulation curves for E > 15 m² allows a calculation of a species number S_{100} referring to 100 m² of searched area. This can be done either by upward projection from study areas smaller or downward projection from areas larger than 100 m². The value S_{100} is used here as standard measure for species richness. It provides a direct, transparent information about an important ecological parameter without the need for interpretation as it is often required for the abstract figures of other diversity indices. The determination of S_{100} is done in two steps. At first, a

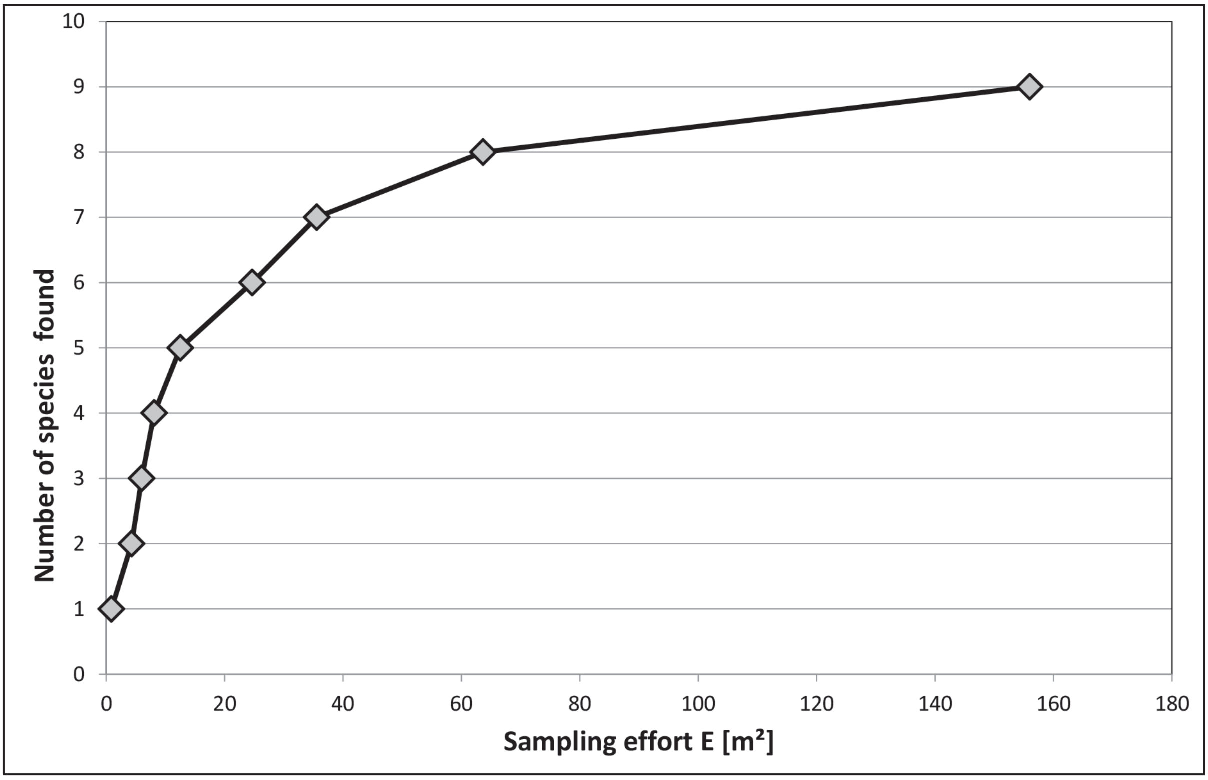


Figure 2. Extrapolated species-accumulation curve of study plot SP 159.

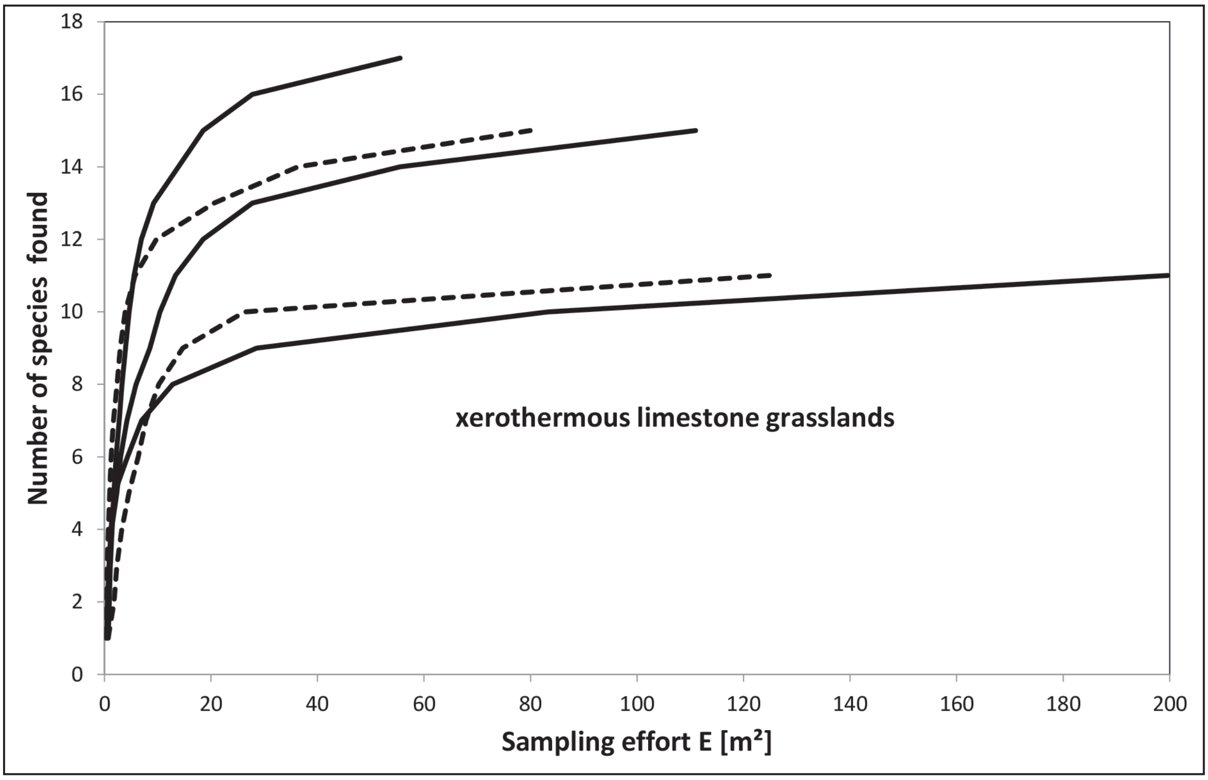


Figure 3. Extrapolated species accumulation curves for five study plots in xerothermous limestone grasslands.

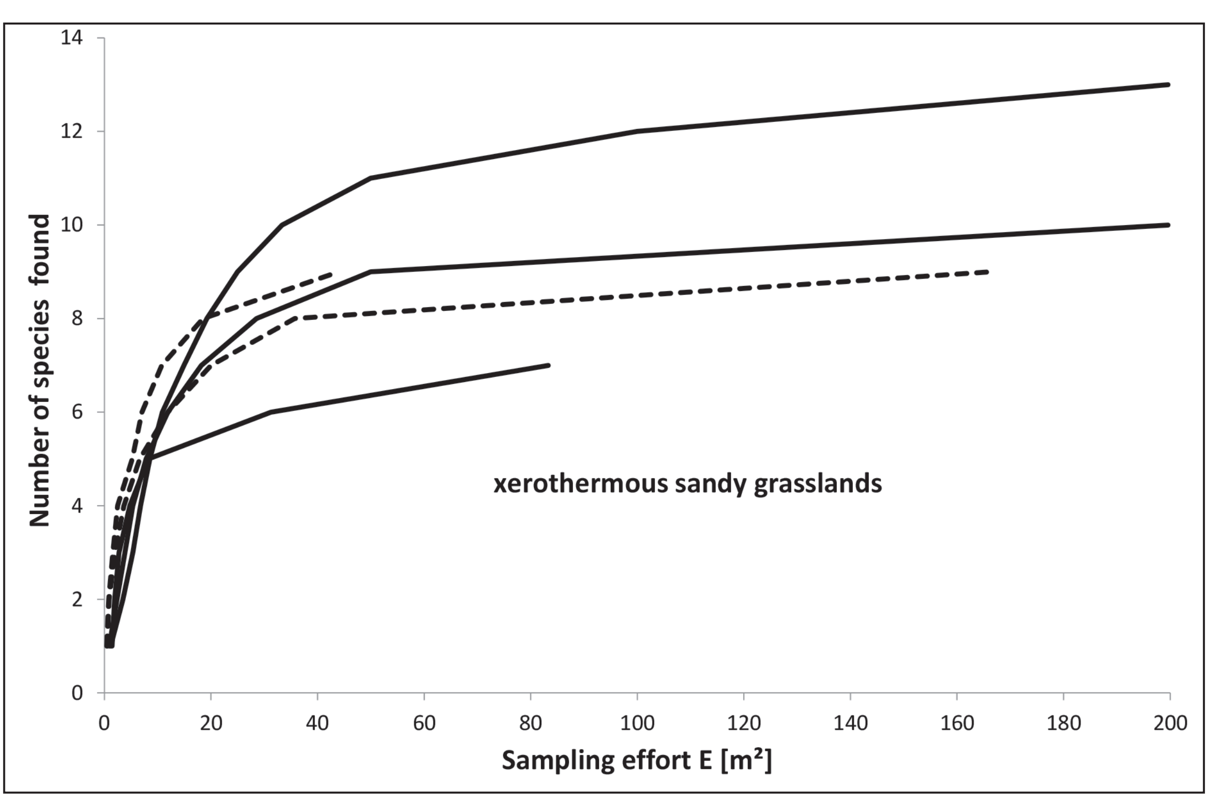


Figure 4. Extrapolated species accumulation curves for five study plots in xerothermous sandy grasslands.

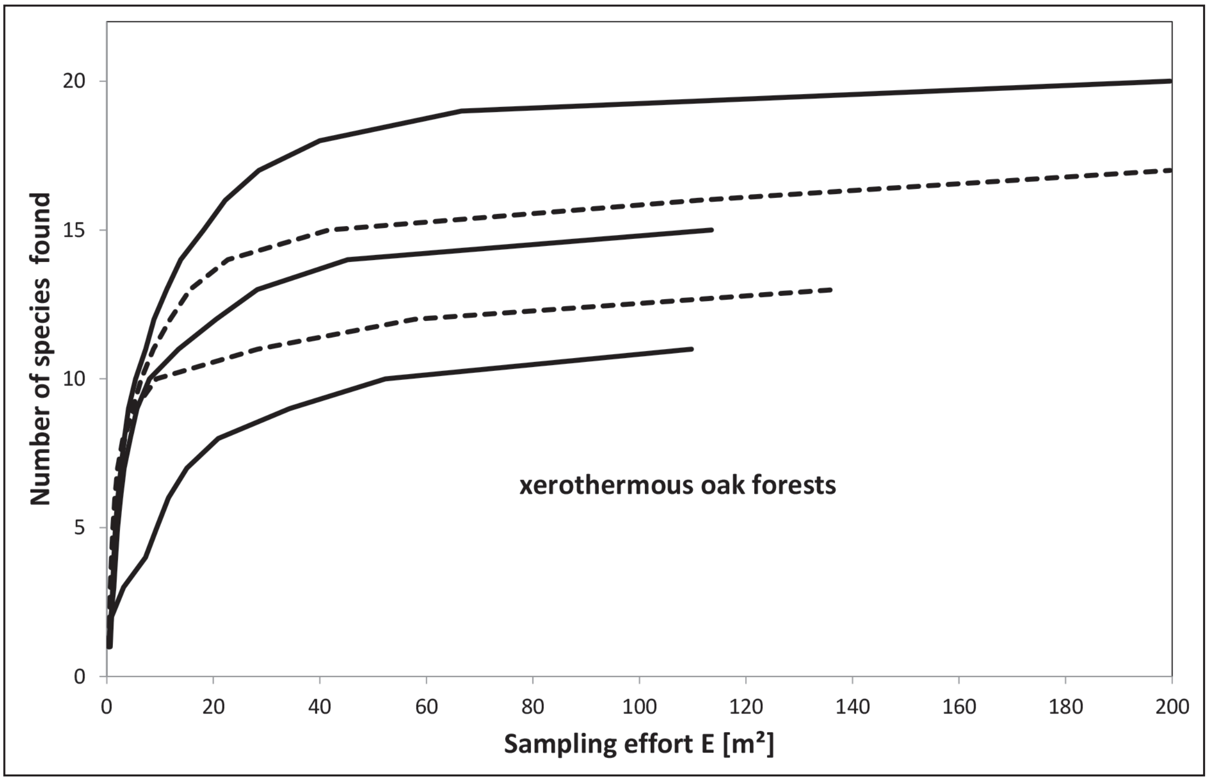


Figure 5. Extrapolated species accumulation curves for five study plots in xerothermous oak forests.

relative species richness index r of a study plot *i* with a given species number S_i and a given search area E_i is calculated by weighting against the standard function $S_M = f(E_i)$

$$r = S_i/S_M \qquad [4].$$

Accordingly, a habitat with r = 2 is calculated to have twice the species number of the ant system average predicted by the mean species accumulation curve. Because the latter function results in an absolute species number of 8.24 for a search area of 100 m² the predicted species number of S_{100} for this particular habitat is

$$S_{100} = 8.24\ r \qquad [5].$$

If S-areas and Q-areas are distinguished, species richness S_{100} is calculated from the arithmetic mean of the r values of both areas. To give an example, the species accumulation curve of study plot UF 159 (Fig. 2) predicts the finding of the penultimate (8th) species within the S-area after 66.7 m² and that of the last (9th) species within the Q-area after 156.0 m². The ant system average $S_M$for these areas is 7.59 and 8.95 respectively resulting in r values of 8/7.59 = 1.054 and 9/8.94 = 1.006. With a mean value of r = 1.02, S_{100} is calculated here as 1.02*8.24 = 8.40. A problem occurs with species numbers of Q-areas larger than 200 m² which are most likely under-recordings – at least in certain habitat types. Data from such study plots should have affected the confidence of the standard species accumulation curve for E > 200 m². It is advised in such cases to use the pseudo-area that is closest to 100 m² instead of referring to the Q-area.

The method described above is a two-step procedure taking a detour over an interim value representing a calibration against the system average S_M. It might be asked in this context if the calculation of S_{100} should not better be done by direct use of the individual logarithmic descriptions valid for each study plot. This can be rejected clearly. First of all, direct calculation is problematic or even mathematically impossible for those 17 % of study plots were between 0 and 2 species have been found. Furthermore, many search areas were clearly smaller than 100 m² and determination of S_{100} has to be done by a risky upward projection. Direct upward projections calculated for such areas resulted in impossibly large species numbers for a big fraction of study plots – though less frequent than in double-reciprocal plotting analogous to Michaelis & Menten (1913). The failure of both methods is largely explained by the frequently strong slopes of species accumulation curves for small E and weak support by too few data point in species-poor habitats.

3.5 The calculation of evenness

Several authors have recommended a separate calculation of the two main parameters of community ecology, species richness and evenness, to provide a meaningful insight into community function (Whittaker 1965; Tramer 1969; Hurlbert 1971; Mc Naughton 1977, Seifert 1986, Magurran 1988; Legendre & Legendre 1998; Weiher & Keddy 1999). Biodiversity indices which are influenced by both parameters in an unpredictable way are of little, if any, use. Highly questionable, for instance, is the heuristic value of the original Shannon-Wiener formula

$$H' = -\sum_{i=1}^{n} p_i * \mathrm{Log}_2\, p_i \qquad [6]$$

when it is used as a biodiversity index. One of the arguments against the application of this formula is that habitats of most different community structure may come out with the same value of H. This may apply when a habitat A shows a high species number but extremely low evenness and a habitat B low species number but high evenness (Seifert 1986).

According to these considerations, a separate calculation of species richness and evenness requires that the mathematics of evenness determination must be independent from species richness. This condition is given in the evenness index V of Hurlbert (1971) with

$$V = (H' - H_{MIN})/(H_{MAX} - H_{MIN}) \qquad [7]$$

where H' is the given Shannon entropy and H_{MAX} and H_{MIN} are the maximum and minimum Shannon entropy theoretically possible for the given species number S, given species-specific nest density d_i, and total nest density D. Thereby H' is calculated as

$$H' = \left| \sum_{i=1}^{S} (d_i/D * \mathrm{Ln}\,(d_i/D)) \right| \qquad [8].$$

The theoretical maximum H_{MAX} that is given when all species are found in equal nest densities is calculated as

$$H_{MAX} = \mathrm{Ln}\ S \qquad [9].$$

The theoretical minimum H_{MIN} is given when all but one dominant species are represented by the minimum possible nest density d_{MIN} (i.e., only a single nest found in each species) whereas the dominant species is represented by the maximum possible nest density $d_{MAX} = D - d_{MIN}\,(S-1)$. H_{MIN} is then calculated as

$$H_{MIN} = \left| (d_{MIN}/D * \mathrm{Ln}\,(d_{MIN}/D)*(S\text{-}1) \right| + \left| d_{MAX}/D * \mathrm{Ln}\,(d_{MAX}/D \right| \qquad [10].$$

3.6 The recording of niche dimensions

A total of 17 niche dimensions were recorded: 6 physico-chemical factors, 7 structural factors and 4 species-defined factors. The physico-chemical factors were maximum calibrated soil temperature $\mathbf{T_{MAX}}$, mean calibrated soil temperature $\mathbf{T_{MEAN}}$, soil humidity **F**, soil calcium **R**, nutrient supply **N** and mechanical stress on top soil **M**. The structural characters were phytodensity **PD**, cumulative cover of shrubs and trees **ShTrC**, cover of herb layer **HeC**, cover of moss layer **MoC**, cover of litter layer **LiC**, cover of dead wood **DWC** and cover of stones **StC.** Species-defined factors were strata of foraging **SF**, nest microhabitat **NM**, fields of nutrition **FN** and body size **BS.**

The physico-chemical factors F, R and N were determined by the indicator plant system of Ellenberg et al. (2001), updated by data given in Jäger & Werner (2005) and supplemented for the southern Alps by the system of Landolt et al. (2010). The indication in this study was largely based on vascular plants and to a lower degree on mosses and lichens. Plot-specific mean indicator values were computed only by presence – i.e., without weighting by cover percentage. There is no evidence over all studies that this weighting yielded higher correlations with measured data of soil parameters than the simple qualitative approach. Instead, there are several studies in which weighting by cover percentage affected the results – this disturbance is explained by the individual growth strategy of particular plant species having a high indicative power but growing only as single, highly dispersed individuals (Ellenberg et al. 2001, Käfer & Witte 2004). The Ellenberg indicator values, which are basically ordinal variables, are treated here as interval-scaled data which is unlikely to result in wrong indications.

Computation of probabilities for niche overlap and niche width calculations required defining classes for each factor. No transformation of raw data was done in the factors T_{MAX}, T_{MEAN}, F, N, R, PD, HeC, ShTrC, MoC and LiC before assigning these data to classes. However, coverage data of stones StC and dead wood DWC were square-root transformed. This was indicated by the following arguments. Stones and dead wood found on soil surface play an outstanding role as nest habitat for ants and nest density is a saturation function of available nest microhabitats with an upper value of nest density limited by the minimum possible distance between nests. The maximum density of ant nests observed from any habitat in the system of 232 study plots was below 6 nests per/m². Accordingly, a supply of suitable nest items much above this density should not have an influence on overall ant density – e.g., an increase of stone density from 15 to 50 per m² should be meaningless for ants from the perspective of housing space. On the other hand, an increase from 1 to 4 stones per m² at the lower end of the density scale is likely to have a big effect on the ants. Accordingly, a square-root transformation of microhabitat density data appeared as best solution providing a finer assessment for smaller and broader one for big microhabitat density. Tabs 4 and 5 show the subdivision of classes for the physico-chemical and structural niche variables. The subdivision of classes in the categorial niche variables M, SF , NM and FN is given farther below.

3.6.1 Maximum, mean and basal calibrated soil temperature T_{MAX}, T_{MEAN} and T_{BAS}

Temperature of top soil was measured in a depth of 35 mm. Calibrated maximum, mean and basal soil temperatures T_{MAX}, T_{MEAN} and T_{BAS} were calculated as basically described by Seifert & Pannier (2007). Deviating from these authors, who calibrated against a fixed 30-year period 1977–2006, calibration was done here against a dynamic 10-years standard that considers local climate changes due to global warming. Calculation of T_{MAX}, T_{MEAN} and T_{BAS} was done with the software package *CalibSoil* freely downloadable under http://www.senckenberg.de/files/content/forschung/abteilung/zoologie/pterygota/calibsoil.zip.

The *CalibSoil* software package contains a text file ‘CalibSoil-Derivation-of-Method.pdf’ in which the derivation and aim of the method is thoroughly explained. As the system is very complex, I give here only a short information. *CalibSoil* is a calculation system enabling direct comparisons of single-day allochronic and allotopic soil temperature measurements in natural ecosystems by calibration against astronomical and meteorological standard conditions. *CalibSoil* answers the question which temperatures are expected for a spot if a particular measurement had been taken within a climatic context matching the average situation from May to August of the previous 10 years. *CalibSoil* makes a single-day soil temperature measurement in a lowland spruce forest of Poland during the cold summer of 1987 directly comparable with a single-day measurement taken in a high-mountain spruce forest of Switzerland in the extremely hot and dry summer of 2015. Within the algorithms of *CalibSoil*, the average climatic situation is determined by the data of the next meteorological station(s): the mean air temperature TAS and mean sunshine duration from 1 May to 31 August over the 10 years prior to the actual year of measurement. This adaptive, or shifting, 10-year standard is short enough to visualize global climatic developments yet long enough to give a reliable indication of the medium-term temperature history of a site.

The main target value **T_{MAX}** is calibrated for the condition of a ‘Standard Radiation Day’. The Standard Radiation Day is defined by a sunshine duration equal to 80% of astronomically possible sunshine duration and an air temperature equal to the mean recorded between 1 May and 31 August of the 10 years before the year of investigation. T_{MAX} is the most important thermal parameter for soil organisms during the main growth season because it is not only a good indicator of heat stress but is largely responsible also for differences of mean between-habitat temperatures if the study plots are embedded within the same climatic context. On the other hand, overall growth rates, ontogenetic development or mean metabolism should more strongly depend on mean soil temperatures during the whole season. These mean temperatures **T_{MEAN}**, a value integrated over all weather situations during the season, can be estimated when the local or regional sunshine duration is taken into consideration.

The number of required temperature measuring points per habitat depends on its structure. In very homogenous habitats, only three thermometers, positioned some two meters from each other, may be sufficient. In heterogeneous habitats, all microhabitats (surface components) of differing heating properties must be measured simultaneously. The overall-habitat temperature is then calculated from the data of the different microhabitats weighted by their percentage of surface cover. A total of 12 or more measuring points, with two or three points per microhabitat, may be necessary in such cases. Fig. 6 shows the situation in a xerothermous habitat with extremely different microhabitat temperatures. All niche space, richness or biomass calculations in this study constantly refer to overall-habitat temperatures as weighted average of microhabitat temperatures in 35 mm depth.

The mean error of a single-day determination of T_{MAX} from the seasonal mean was 1.97°C in 54 full-insolation habitats (i.e., fully sun-exposed bare soil) and 0.73°C for 103 measurements in a zero-insolation habitat (i.e., a forest with full canopy closure situated at a steep northern

Table 4. Class definitions in the physico-chemical niche variables the meaning of which is explained in sections 3.6.1 to 3.6.4.

Class	T_{MAX} [°C]	T_{MEAN} [°C]	F	N	R
1	(6,8]	(5,6]	≤3.01	≤2.09	≤2.03
2	(8,10]	(6,7]	(3.01,3.79]	(2.09,2.87]	(2.03,2.82]
3	(10,12]	(7,8]	(3.79,4.58]	(2.87,3.65]	(2.82,3.62]
4	(12,14]	(8,9]	(4.58,5.36]	(3.65,4.43]	(3.62,4.42]
5	(14,16]	(9,10]	(5.36,6.14]	(4.43,5.21]	(4.42,5.21]
6	(16,18]	(10,11]	(6.14,6.92]	(5.21,5.99]	(5.21,6.01]
7	(18,20]	(11,12]	(6.92,7,71]	(5.99,6.77]	(6.01,6.80]
8	(20,22]	(12,13]	(7.71,8.49]	(6.77,7.55]	(6.80,7.60]
9	(22,24]	(13,14]	(8.49,9.27]	> 7.55	> 7.60
10	(24,26]	(14,15]	> 9.27		
11	(26,28]	(15,16]			
12	(28,30]	(16,17]			
13	(30,32]	(17,18]			
14	(32,34]	(18,19]			
15	(34,36]	(19, 20]			

Table 5. Class definitions in the structural niche variables the meaning of which is explained in sections 3.6.6 to 3.6.12. Square-root transformed data are used in StC and DWC.

Class	PD	LiC, MoCHeC, ShTrC	$StC^{0.5}$	$DWC^{0.5}$
1	(0,200]	≤0.11	(0,0.6]	(0,0.08]
2	(200,406]	(0.11,0.22]	(0.6,1.2]	(0.08,0.16]
3	(406,683]	(0.22,0.33]	(1.2,1.8]	(0.16,0.24]
4	(683,1033]	(0.33,0.44]	(1.8,2.4]	(0.24,0.32]
5	(1033,1455]	(0.44,0.55]	(2.4,3.0]	(0.32,0.40]
6	(1250,1948]	(0.55,0.66]	(3.0,3.6]	(0.40,0.48]
7	(1764,2514]	(0.66,0.77]	> 3.6	(0.48,0.56]
8	(2401,3152]	(0.77,0.88]		(0.56,0.64]
9	(3136,3861]	> 0.88		> 0.64
10	(3969,4643]			
11	(4900,5497]			
12	(5497,6422]			

slope). Averaging three single-day measurements spaced over the season reduces the mean error close to 1°C and 0.5°C respectively (Seifert & Pannier 2007). In study plots where a direct measurement of T_{MAX} failed due to absence of sufficient solar radiation during the investigation time, a prediction of T_{MAX} was necessary. This was possible using a catalogue of guiding values of microhabitat and habitat temperatures standardized for 51°N, 11°E, 300 m a.s.l. and zero inclination of ground (Seifert & Pannier 2007). These guiding values were then adopted to a particular situation by correcting for deviations in geographical and orographic parameters and plant coverage. These predictions, which are basically interpolations between known comparable situations, proved to be more exact than a direct single-day measurement (Seifert & Pannier 2007).

Data of the basal calibrated soil temperature $\mathbf{T_{BAS}}$ are required for calculation of T_{MEAN} and for estimating the partial contributions of macroclimate and habitat factors on the temperatures finally achieved in a soil (section 4.6). T_{BAS} represents a prediction of the mean calibrated soil temperature achieved in a study plot if solar radiation would be completely shielded all over the season. T_{BAS} is a hypothetic value for an open habitat but becomes a real figure in woodland habitats situated at steep northern slopes (e.g. in study plots SP 50 or SP 98). Seifert & Pannier (2007) have called such conditions a zero-insolation soil (ZIS) as opposed to a full-insolation soil (FIS) such as, for example, an open sand dune. Neglecting the very rare cases of strong geothermal heat emission, a temperature increase above T_{BAS} is almost always of solar origin and determined by habitat structure and orography. In ZIS habitats, T_{BAS} is strongly correlated with the standard air temperature TAS provided by meteorological stations but it is in absolute value significantly lower because of heat loss by soil evaporation and the rather slow heat absorption in spring and summer. This retarded temperature dynamics is explained by the fact that heat flow goes from a moderately warmer air body to a solid substrate and by the fact that soils of ZIS habitats are usually covered by an isolating litter layer. The significant reduction of T_{BAS} in ZIS habitats, its quantification and relation to minimum soil temperature T_{MIN} in FIS habitats is explained in the text file 'CalibSoil-Derivation-of-Method.pdf' of the internet source cited above. According to this source there is the empiric relation

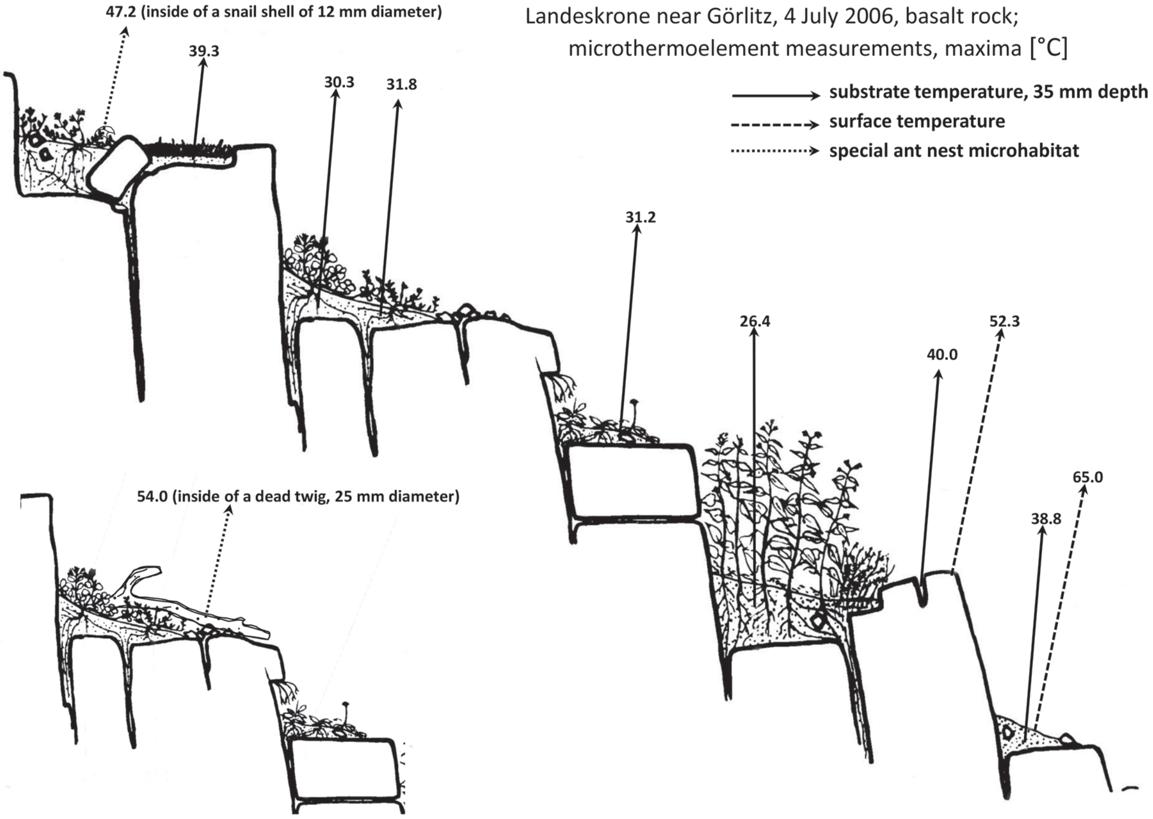


Figure 6. Measurement of spot temperatures in a xerothermous habitat on basalt rock. Arrows in solid lines point to temperatures taken 35 mm below soil/rock surface – from left to right these are: below moss crust, below *Sedum telephium* pad, below *Thymus* pad, below *Hieracium pilosella* plants, in *Cynanchum vincetoxicum* stand, in cleft of basalt rock, in bare soil over basalt rock. Arrows in dashed lines point to surface temperatures and those in dotted lines to nest sites of *Temnothorax* ants on soil surface.

$$T_{MIN} \text{ of FIS habitats} \approx T_{MEAN} \text{ of ZIS habitats} \approx T_{BAS} \approx TAS - 3.3°C \quad [11]$$

which allows to use T_{BAS} as standard value for calculation of calibrated mean soil temperature T_{MEAN} for any habitat irrespective of its position within the FIS-ZIS gradient. For further details of calculation see functions [31] to [35] in the text file 'CalibSoil-Derivation-of-Method.pdf' of the internet source cited above.

3.6.2 Soil moisture figure F

The soil moisture figure F (from German 'Feuchte') belongs to the more reliable (and useful) variables within the indicator plant system founded by Ellenberg in 1950. The high performance of F for fine differentiation of moisture on a local scale is well established (examples in Ellenberg et al. 2001, Oddershede et al. 2015). F shows a high correlation with direct long-term measurements of average lowest moisture contents in summer and the annual average ground water level. Furthermore, the ranking of F data calculated in this study was in no case in severe conflict with my own subjective expectations derived from the orography observed in the field. Yet, the moisture indication (as it is with other Ellenberg indicator values) becomes less accurate when remote parts of Central Europe are compared without regional calibration.

3.6.3 Nutrient figure N

Ellenberg originally proposed his figure N to indicate mineral nitrogen content in the soil but recent surveys suggest that it better describes the nutrient supply in a broader sense – mineral and organic nitrogen but also phosphorus. Accordingly, the value of N should better be named the productivity figure of a soil (Schaffers & Sykora 2000, Wagner et al. 2007). However, maintaining Ellenberg's letter N, I propose to name it herewith 'nutrient figure'.

3.6.4 Calcium figure R

The figure R was proposed by Ellenberg to indicate the soil reaction. Yet, there is a better correlation of this figure with the total amount of calcium (exchangeable Ca^{2+} plus Ca from carbonates) than with soil pH (Schaffers & Sykora 2000, see also Szymura et al. 2014). This can be explained at least in part by a much stronger short-term variability of pH compared to calcium (Degorski 1982). Accordingly, R should better be named 'calcium figure'.

3.6.5 Mechanical stress M

This figure intends to estimate the degree of mechanical stress or pressure on soil surface exerted by animals, humans or machines. Data on this physical niche variable are not based on measurements but were determined by subjective estimation according to inspection of the surface structures and knowledge about mechanical stress factors usual for that type of habitat or explicitly known for a study plot. Including intermediate situations, seven classes were distinguished:

1 = no stress or pressure.
Examples: *Sphagnum* associations in quaking bogs, steep scarps
3 = weak stress or pressure.
Examples: mowing with light machines once or twice a year; sheep pasturing for one day in intervals of 2–4 weeks; occasional visits by humans or big mammals
5 = mean stress or pressure
Examples: intensive grazing by big mammals for a maximum of three weeks per year; permanent sheep pasturing in lower density (< 10 animals per ha); park or garden lawns visited by humans during weekends and cut in weakly or in two-weeks intervals by very light machines; agriculturally used cut meadows mowed twice a year by heavy machines.
7 = strong stress or pressure
Examples: permanent grazing by cattle throughout the season; regularly used football places, picnic areas or core zones of populated beaches; unpaved driveways or sidewalks; main activity spots of military training areas with heavy equipment.

3.6.6 Cover of stones StC

Stones and the hypolithic space have an extraordinary importance as nest microhabitats for ants in open, sun-exposed habitats because of providing favorable thermic conditions for brood development (Seifert 1986). Large stones may also reduce predation by woodpeckers. The value StC aims to determine the number of stones potentially providing a hypolithic nest habitat for ants. The recording considered only stones at soil surface, having at least their upper surface freely exposed (i.e., not covered by soil material or organic litter) and having a minimum diameter of 4 cm. Square-root transformation of raw data (given in stones/m²) was performed for the reasons explained under 3.6. There is some weakness in the recording schedule because the investigation protocol developed in the year 1979 (and maintained until about 2000) did not include estimates of total surface coverage by stones and also not numeric data on their spacing. Five stones with an average diameter of 5 cm were considered in that time to have the same meaning for ants as five stones of 10 cm diameter which is not realistic – e.g., from the perspective of nesting space needed by different ant genera. There was also some bias of the investigator, with all other habitat parameters being equal, to select an area showing a distribution and number of stones that facilitated nest discovery. StC was estimated by averaging 5–10 subjective estimates in homogenously spaced patches of one m². Because of the inconsistent mode of recording over the 37-years investigation period, I decided not to include StC into the calculation of niche space but the data are given for informal reasons in the characteristics of study plots

3.6.7 Cover of litter layer LiC

Decaying litter is an important habitat for prey organisms of some ant groups – in the studied system typically for members of genera such as *Ponera*, *Stenamma*, *Myrmecina*, *Leptothorax* or *Temnothorax*. On the other hand, a thick layer of dry and loose litter is a strong thermal insulator and hampers heat absorption of soil. This may represent a problem for ants needing higher temperatures for brood development. The investigation protocol required recording the cover percentage and mean thickness of the litter layer including its early decomposition stages but excluding mull or raw humus. Any kind of organic litter is considered regardless if originating from broad-leafed or coniferous trees, shrubs, dwarf-shrubs or grasses. LiC was estimated by averaging 5–10 subjective estimates in homogenously spaced patches of one m².

3.6.8 Cover of dead wood DWC

Dead wood is a favored nest habitat for many ants. This refers to dead wood remaining in situ as well as to material fallen to ground. The value of DWC considers only the cover percentage of fallen dead wood estimated by vertical projection plus the basal area of tree stumps or standing dead trees. This refers to any kind of material from thick tree stems down to twigs of 1 cm diameter. Square-root transformation of raw data (given in % of cover) was performed for the reasons explained under 3.6. DWC was estimated by averaging 5–10 subjective estimates in homogenously spaced patches of one m².

3.6.9 Cover of the moss layer MoC

The investigation protocol required recording of the cover percentage and mean height of mosses including lichens. MoC was estimated by averaging 5–10 subjective estimates in homogenously spaced patches of one m².

3.6.10 Cover of the herb layer HeC

The cover percentage of the herb (field) layer may be an important structural niche variable for large, fast-moving ants with wide foraging distances through its effect on spatial resistance. HeC was estimated by averaging 5–10 subjective estimates in homogenously spaced 1-m² patches.

3.6.11 Plant density PD

The plant density value PD considers all plant species typically forming the moss and herb layer but includes all specimens of shrub and tree species if their height does not exceed 80 cm – i.e., saplings and young plants of an oak, for instance, were included. PD is calculated as the product of cover percentage and mean height of these vegetation elements. A xerothermous grassland with a mean vegetation height of 15 cm and a cover of 90%, for example, has a plant density figure of 15*90 = 1350. Mean height measurement was done by horizontal projection and averaging over all plant elements present – e.g., a moist meadow with the tips of *Alopecurus pratensis* florescences reaching up to 110 cm may be estimated to have a mean height of only about 50 cm because of being composed of lower and taller grasses and other herb species. Furthermore, recording aimed to estimate a seasonal average of plant height. An unmown tall herb community with *Filipendula ulmaria* and *Cirsium oleraceum*, for instance, achieving its maximum mean height of 80 cm by mid July is estimated to have a seasonal average of 60 cm or, to give another example, a periodic sheep pasture with a mean plant height fluctuating in 3-week intervals between 3 and 15 cm is assessed to have a seasonal average of 9 cm. Dry weight of the considered plant elements can be described as a linear function of PD but the correlation is rather weak due to big differences in mean water content between different phytoassociations – errors may reach 50 % of the true value (Seifert 1986). As a consequence, attempts to directly estimate epigaean phytomass by PD data were given up. Class intervals were subdivided according to a square-root rule because a change of PD from 200 to 1200 has a much bigger effect on ants than a change from 4500 to 5500 considering temperature, moisture and feeding conditions.

3.6.12 Cumulative cover of the shrub and tree layer ShTrC

The investigation protocol included recording cover percentage and mean height of shrubs taller than 80 cm and cover percentage, mean height and mean diameter at breast height of trees. As tree-dwelling ants are not the focal group of this study, the shrub and tree layers were evaluated preferentially for its effects on ants with epigaean or subterranean nest sites. These are, apart from providing arboreal foraging space and food resources, mainly the effect of shading, increased air humidity and litter production. As these factors are cumulative effects of both shrub and tree layer which are hardly separable in a reasonable way, I decided to sum up the data of both strata in a single value. The consequence is that ShTrC may achieve values > 100 % in forests with high crown density of trees and a well developed understory of smaller trees and shrubs.

3.6.13 Nest microhabitat NM – extended species-level data

Selection of nest microhabitats is an important niche variable in ants. NM data are based on my records in field books entered during this ecological study but to a larger part entered during collecting for other (mainly taxonomic) purposes. The data finally used were no simple addition of data but were modified in each species by subjective intervention that attempted to consider if local peculiarities might have distorted the data. Data of other collectors deposited in the files of SMN Görlitz were not used because there is a strong danger for wrong indication due to a personal sampling bias. If, for instance, a leading myrmecologist was specialized on *Temnothorax* or *Leptothorax* ants he will have made the experience that the biggest sampling success occurred through disintegrating dead wood, splitting off stone plates or bark pieces, turning small stones or cracking special microspaces such as snail shells or acorns. Following this experience he will have overlooked, for instance that a substantial part of *Temnothorax interruptus* nests, in contrast to its congeners, are located in solid moss pads. Another, very active, collector in Germany was biased to discover nests of larger ant species such as *Myrmica*, *Lasius*, *Formica* and his picture of microhabitat selection of the comparably few *Temnothorax* nests which he found will have underestimated nests in microspaces.

I resigned to make a distinction between nests under stones and soil nests without stone covering. This may appear surprising if one considers the significant microclimatic differences often observed between such nest spots. The resignation is explained (a) by errors through a collecting bias (i.e., turning of relatively more stones than probing soil spots), (b) by frequent cases where a distinction between under-stone and soil-only nests was virtually impossible due to big lateral extensions of the nests away from the stone and (c) by the argument that under-stone nests are basically excavated in soil. Finally, seven microhabitat qualities were distinguished. The estimates consider to which percentage different strata contribute to the true nest space. In a big nest of *Formica*, for example, which is roughly classified as a soil nest, some 10 % of the true nest space may be excavated in the root felt of grasses. A small *Temnothorax* nest, in contrast, will usually occupy only a single microhabitat stratum or quality. Acronyms and definitions of the seven microhabitat qualities were as follows:

SOILSTO	- in soil and/or under stones
MOSS	- in moss layer
LITTER	- in litter
TURF	- in upper root felt and lowest epigaean parts of grasses
WOOD	- in wood and bark, without distinction if belonging to standing or fallen trees or if in situ or representing detached parts.
ROCK	- in rock crevices and between loose-fitting stone plates
MICRO	- in special microspaces: nuts, acorns, galls, snail shells

3.6.14 Strata of foraging SF – extended species-level data

The strata of foraging SF describe the probability of an ant worker to forage in several vertical strata from deep soil up to tree canopies. SF data are a subjective synthesis of (a) my personal experience gathered in the field during digging for ants nests, (b) my personal observation of forager movements in the field and (c) published or otherwise communicated knowledge of other researchers on ant biology. Calibration of assessments by numeric data was a rare exception. For example, a correction of the assessment for foraging in the herb layer was performed by relating sweep net catches to pitfall catches using data provided by University of Jena in 1986. Foraging includes predation, picking up solid items or imbibing liquid food sources such as honey dew, nectar or plant sap. Six strata of foraging were distinguished with the acronyms meaning

DeepSoil	- foraging in deeper soil at depths of at least 10 cm

TopSoil - foraging in top soil including the root layer of herbs in depths < 10 cm
MossLitter - foraging in the moss and litter layer
FreeSurf - foraging on free, above-ground surfaces except of those on herbs, shrubs and trees
Herb - foraging in the herb layer
ShrubTree - foraging on shrubs and trees, ascending 2 meters at least

The assumption that surface or herb foraging was probably underestimated because there was no direct observation of nocturnal activity is unlikely because the evaluation of some 100 000 pitfall-trapped ants in many research projects outside this study would have shown undetected movements. Anyway, SF was excluded from calculation of niche spaces because the data are strongly deficient for many species and the reader is advised to consider the SF data given in the results section as personal opinion of an expert.

3.6.15 Fields of nutrition FN – extended species-level data

The fields of nutrition FN describe the probability to use four major food categories based on a subjective synthesis of my personal experience and published food analyses of other authors. Four categories are distinguished

Zoopha - zoophagous (predatory or scavenging)
Nectar - feeding on nectar and other plant saps
Tropho - trophobiosis with Aphidina, Coccidoidea, Lycaenidae, Heteroptera and Symphyta or, if not trophobiotic, licking up honey dew from surfaces.
PlantPart - feeding on seeds, elaiosomes, pollen and other parts of plants

FN was excluded from calculation of niche spaces because the data are strongly deficient for many species and the reader is advised to consider the NU data given in the results section as personal opinion of an expert.

3.6.16 Body size BS – supplementary species-level data

After having described where foraging occurs (SF) and which food qualities are taken up (NU), another important variable describing the food niche of ant species has to be added: worker body size BS. Body size has a significant influence on the size of food items retrieved and the size of prey organisms that can be overwhelmed – even if cooperative transport and killing, highly effective weapons and disintegration of large food items at the site of discovery of a booty can compensate for disadvantages of small body size. Body size is also most important for the fine differentiation of the fields of foraging. It determines which cleft spaces can be penetrated by an ant worker without spending extra energy.

Body size will be used here as one niche dimension for calculating the overlap of the fundamental niche space (see section 3.7.3) and I will explain in the following how a simplified estimate of this parameter was derived. The first consideration refers to head size of an ant and the penetration of cleft spaces. Assume for a habitat with a multitude of homogenously distributed cleft widths, that the smallest cleft can be penetrated by the smallest ant species A in the system with a head size CS_A and that the largest cleft can be penetrated by all ant species of any size. From this it follows that the smallest species A has the maximum possible niche width for the ability of cleft invasion and that niche width decreases with growing head size. The niche width *w* of a species I with a head size CS_I is then proportional to CS_A/CS_I and the niche overlap OV_{IJ} between two species J and K (with J representing the larger-headed species) proportional to CS_K/CS_J.

Muscular strength is also a function of body size estimated here by CS. While CS as a one-dimensional body measure is proportional to ability of cleft space penetration, the square of CS is proportional to the weight of food items that can be transported because muscular strength is a function of the cross-sectional area of a muscle. Taking both things together, I propose as an adequate estimate of body-size related niche overlap O_{size}

$$O_{size} = [CS_{min} / CS_{max} + (CS_{min} / CS_{max})^2] / 2 \qquad [12]$$

where CS_{min} and CS_{max} is the head size of the smaller and larger species respectively.

3.7 The calculation of niche space

As mentioned in the introduction, I follow here a conception of the ecological niche as a set of points in an abstract Cartesian hyperspace space in which the coordinates are various environmental factors which influence the survival of the species (Hutchinson 1957). Considering the ecological niche as function of given environmental factors and the genetically determined potency of a species, Müller et al. (1977) defined the ecological niche to be formed by the fitting together (the congruence) of a n-dimensional valency volume of the habitat with the n-dimensional ecological potency volume of an organism. The niche space calculations presented here have two main aims. The first is estimating interspecific spatial displacement as function of genetic relatedness by describing the realized niche overlap as a function of fundamental niche overlap. This approach wants to give evidence if Gause's Law of competitive exclusion – shown to be valid for Protozoa under simplified laboratory conditions (Gause 1932, Violle et al. 2011) – is valid for ants also under conditions of natural ecosystems. The second aim is estimating to which degree an environmental factor determines the spatial segregation of ants using factor-specific data of mean niche width and mean overlap of fundamental niche spaces.

3.7.1 Preparation of frequency distributions of niche dimensions – weighted and unweighted approaches

The ecological potency or position of an organism is most clearly shown if different qualities and quantities of environmental factors or resources are provided with equal probability. Yet, it is nearly impossible to match this condition in field studies of complex ecosystems distributed over most different landscapes. Over all 232 study plots there was, for instance, a bias to investigate xerothermous habitats – the median of moisture figure F was 4.53 within a total range running from 2.25 to 9.75 and the median of mean soil temperature T_{MEAN} was 14.6° within a total range between 5.7 and 18.4°C. This over-representation of warm habitats could possibly cause some increase in the resulting mean value of T_{MEAN} above the values expected when the 'supply' over all temperature classes was equal. In order to correct for such distortions, Seifert (1987) proposed a weighting of niche dimensions inversely proportional to the number of study plots falling into a certain class. If $p_{A,k}$ is the unweighted probability of a species A to fall into a class *k*, if n_k is the absolute number of study plots falling into class k and if L is the total number of classes, the weighted probability $p_{A,k}$' is then

$$p_{A,k}' = p_{A,k} / (n_k * \sum_{k=1}^{L} p_{A,k} / n_k) \qquad [13]$$

It will be shown in the results section if such a weighting may finally provide an advantage if all pros and cons are considered. In species with lower frequencies, say those being present on only 3–8 % of study plots (quite many species!), these corrective calculations are likely to produce much accidental variation and are suspected to generate more damage than improvement of the picture.

The weighted and unweighted frequency distributions describing the behavior of a species against certain factor were smoothed according to the ascending interpolation algorithm $(p_{i-1} + 2\ p_i + p_{i+1})/4$. However, if the upper and lower extreme classes (marginal classes – e.g., classes 1 and 15 in T_{MAX}), were occupied by a species, they were treated in a different way because this algorithm is not applicable there. In this cases the value of the marginal class was fixed at 75 % of the primary value. This fixation, furthermore, had the positive effect that extremely eccentric frequency distributions – e.g. of very xerothermous species – could not be manipulated in a misleading way. The data resulting from this smoothing procedure were finally adjusted to probability values summing up to 100 %.

3.7.2 Fundamental and realized niche – basic considerations

The concepts of fundamental and realized niche introduced by Pianka (1976) are of central importance for the understanding of the mathematical model presented here. The fundamental niche is considered as that space of the n-dimensional hypervolume occupied by a species if competitors are absent whereas the realized niche is the smaller part of this hypervolume really occupied under natural (coenotic) conditions with diverse interspecific effects. In other words, the fundamental niche is an expression of the maximum possible potency volume. For example, there is a wide 'fundamental' potency of *Rattus norvegicus* for running, climbing and diving but it cannot successfully compete with a squirrel in a woodland in harvesting hazel nuts or with an otter in a pond in catching fishes. The usual presence of competitors in natural ecosystems, in combination with the fact that even such a broad field study as presented here will not cover the whole fundamental niche space for each dimension and species, raises the question if it is possible to calculate fundamental niche spaces from field data. The answer is that field data cannot describe the fundamental niche space in its total extension but there is a good chance that approximations of fundamental niche spaces are possible without experimental settings in laboratories. This position was already expressed by Seifert (1987). There are three factors allowing approximations of fundamental niche space and of overlap of fundamental niche spaces by field data:

(a) temporal disclosure of hidden fundamental niche space during dynamic processes,

(b) mathematic decoupling of fundamental niche space from particular test plot situations by subdivision of niche dimensions into classes and
(c) idealization of niche space by smoothing of frequency distributions for all factors.

The first phenomenon is temporal disclosure of hidden fundamental niche space during dynamic processes. This refers to a situation where main competitors may be absent from a site for reasons independent from competition or independent from their normal behavior regarding particular environmental factors. This may be explained by example of a single species pair: There is a general observation all over Central Europe that *Lasius psammophilus* replaces (competes out) *Lasius niger* in permanent xerothermous grasslands on sand. Imagine now a region not providing this kind of habitat for geological reasons in which *L. niger* is abundant whereas *L. psammophilus* is extremely rare or absent. This is given, for example, in the loamy hill country of W Sachsen. In the 1960s, open sandy heath areas were generated in this region near the town of Zwickau by strip mining of deeper deposits of late Eocenic sand and gravel and this was followed by a massive colonization of these sites by *L. niger* before any of the better adapted *L. psammophilus* could move in from other regions. A similar situation was found in post-mining successions on sandy xerothermous ground in the huge brown-coal strip mining areas of the Lausitz were no *L. psammophilus* but many *L. niger* survived the devastating impact on a whole landscape. To stay with this species pair and going now to sandy areas in the lowlands of N Sachsen where both species are abundant and closely neighboring for probably 600 years, we find *L. niger* to strongly dominate over *L. psammophilus* in just those sandy xerothermous grasslandpatches in military training areas subject to strong mechanical stress on topsoil caused by movements of heavy vehicles. In other words, new man-made habitats provided the condition for *L. niger* to display its fundamental potency of getting along with very high soil temperatures and very low moisture. Clear cuttings inside of large forests areas, to give another example, may show hidden potencies of typical forest species. Thanks to the fact that it is always a multiplication of several factors that decides who wins the competition game, parts of a fundamental niche dimension which are usually hidden may become exposed under certain conditions. Similar effects, of course, may be produced by natural processes during successions after strong river floods, rock falls, woodland fires or in ecotones.

In the same sense as field data will underestimate the absolute size of the fundamental niche this logically applies to fundamental niche overlap. Yet, this underestimation will apply to all species in the system and it is sufficient to work with relative values and approximations for the purposes of this monograph: estimation of interspecific displacement, ranking of the niche-segregating effect of a factor, and comparative estimation of the ecological potency. The subdivision of each environmental factor in classes in order to generate frequency distributions based on probability of occurrence causes the next approximation of fundamental niche space. This generates a mathematic decoupling of fundamental niche space from particular study plot situations – explicitly, the high number of 232 study plots compared to the number of occupied classes (the maximum was 15 classes in soil temperature), implies the theoretical extreme that two species may have identical frequency distributions for a given niche dimension even if not coexisting on a single study plot. In fact, such situations were frequently approached in pairs of closely related species (see results). In other words, a high overlap in a fundamental niche dimension (and of the whole fundamental niche space) may be calculated even if the realized niche overlap is close to zero due to competitive exclusion. In this sense, subdivision into classes provides a relative independence of our calculation system from competition.

The third factor approximating data of fundamental niche space overlap to theoretical expectations is the mathematical smoothing of frequency distributions. Smoothing is demanded by theory as fundamental niche spaces should have some regular, predictable shape and smoothing should contribute to independence of extrapolated fundamental niche spaces from competition. Why? There may be, for instance, a reduced probability in a certain class of the primary (unsmoothed) frequency distribution of a niche dimension in a species A while a species B shows in exactly that class an increased probability and just this disparity may be an expression of interspecific displacement or competitive exclusion. This phenomenon is less likely in unsmoothed data sets when each of the compared species is present on more than 15 study plots but it may become significant for the quite many species with frequencies lower than 15.

3.7.3 The calculation of niche overlap and niche width

The formula for calculation of niche overlap O used here is mathematically equivalent to formulae of Renkonen (1938) and Schoener (1974). It is basically a percent overlap of frequency distributions and in contrast to other niche overlap formulae most easy to interpret:

$$O = 1 - 0.5 \sum_{i=1}^{n} |p_{i,A} - p_{i,B}| \qquad [14a]$$

or more simple

$$O = \sum_{i=1}^{n} \min(p_{i,A}, p_{i,B}) \quad [14b].$$

This is the basic formula where $p_{i,A}$ and $p_{i,B}$ are the probabilities of a species A and B to occur in a certain study plot *i* (when realized niche overlap O_R is calculated by formula 15) or the probabilities to occur in a certain class *i* of an environmental factor (when fundamental niche overlap O_F is calculated, see formula 18).

The calculation of **realized niche overlap** included three steps. Following the basic formula [14b], a primary value of the realized niche overlap O_P was calculated as

$$O_P = \sum_{i=1}^{n} \min(p_{i,A}, p_{i,B}) \quad [15]$$

where $p_{i,a}$ is the quotient of the nest density of species A on study plot *i* divided by the sum of nest densities of species A over all n = 232 study plots ($p_{i,B}$ is calculated accordingly). O_P is strongly influenced by the number (frequency) of study plots occupied by the species A and B. If the frequencies of the considered species differ strongly, the value of O_P will be lower which leads to distortions in the calculation of interspecific displacement. This suggests the need for a calibration of O_P against a maximum possible value O_{MAX} under the condition that the absolute frequencies of the species in the system are maintained. O_{MAX} is achieved if each species is present on all plots it occupies with equal abundance and if there is a maximum possible syntopic occurrence of both species. With n_{MIN} representing the number of plots occupied by the rarer and n_{MAX} representing the number of plots occupied by the more abundant species the maximum is then

$$O_{MAX} = 0.5 + n_{MIN} / (2 * n_{MAX}) \quad [16].$$

O_{MAX} is 1.0 if both species have equal frequencies but, for example, only 0.60 if the more abundant species is five times more frequent than the rarer one. The corrected, finally used value of realized niche overlap O_R is then

$$O_R = O_P / O_{MAX.} \quad [17]$$

The **overlap of the fundamental n-dimensional niche space** O_F is calculated here as the simple geometric mean of the overlap data of n factors

$$O_F = (O_1 * O_2 ... * O_n)^{1/n} \quad [18].$$

For reasons of inadequate recording or danger of subjective assessment bias (see section 3.6) , the factors StC, FS and FN were excluded from calculation of fundamental niche spaces which were finally recorded along only 14 niche axes. When calculated overlap data were < 0.001 for a certain factor, these data were substituted by the value of 0.001 in order to avoid fundamental niche overlap values of zero.

In contrast to calculations within the context of factorial and niche overlap, arithmetic mean and tolerance for a particular factor were calculated from the primary, unsmoothed and unweighted frequency distributions. Factorial width *w* (synonymous with tolerance), as one dimension of overall niche width, was calculated as the square root of summed squared deviations from the mean – this is basically a standard deviation. The sum *S* of squared distances from the arithmetic mean m_A of a species A is for a number of L classes in a factor

$$S = \sum_{k=1}^{L} p_{A,k} * (m_A - k)^2 \quad [19]$$

with $p_{A,k}$ being the probability to fall in class k. Factorial width *w* as the square root of *S* should be calibrated in a way allowing an easier interpretation and comparison between the data of different factors. This adjustment determines a value of 1 for a maximum factorial width – i.e., for a homogenous (rectangular) distribution over all classes. For the condition of a rectangular distribution and the factors considered here, the square root of *S* is a function of the number of classes L as

$$\text{sqrt } S = 0.2900 \text{ L} - 0.0286 \quad [20].$$

This empirically determined function had a linear correlation coefficient of 1.000 for L ranging from 4 to 15 as given for the factors used in the niche model. Accordingly, the calibration of factorial niche width component *w* to maximum values of 1 can be done as follows

$$w = \text{sqrt } S / (0.2900 \text{ L} - 0.0286) \quad [21].$$

It should be noted, that factorial niche width *w* may achieve values larger than 1 in exceptional cases of a very eccentric bimodality of frequency distributions.

The overall niche width *W* for n considered factors is then calculated as the geometric mean

$$W = (w_1 * w_2 ... * w_n)^{1/n} \quad [22].$$

3.7.4 The model to estimate interspecific competitive exclusion

The fundamentals of this approach have been outlined by Seifert (1987) and I present here a modified argumentation. As pointed out above, the fundamental niche spaces and the overlap of these spaces describe a theoretical situation in the absence of favorable or suppressing interspecific effects. The realized niche space, in contrast, is formed when these interspecific effects are working and is always smaller than the fundamental niche space that describes the full range of the ecological potency of a species. Accordingly, a realized niche cannot be formed outside the frame defined by the fundamental niche and it is a reasonable expectation that realized and fundamental niches show a significant correlation when all species pairs over the whole investigation system are considered. The same will apply to the overlap of niche spaces. If the average behavior of the system is described by a function $O_R = f(O_F)$, positive deviations of O_R from the function value should indicate a tendency for coexistence or facilitation but negative ones a tendency for interspecific displacement or competitive exclusion. A visualization of this idea is provided by Fig. 7.

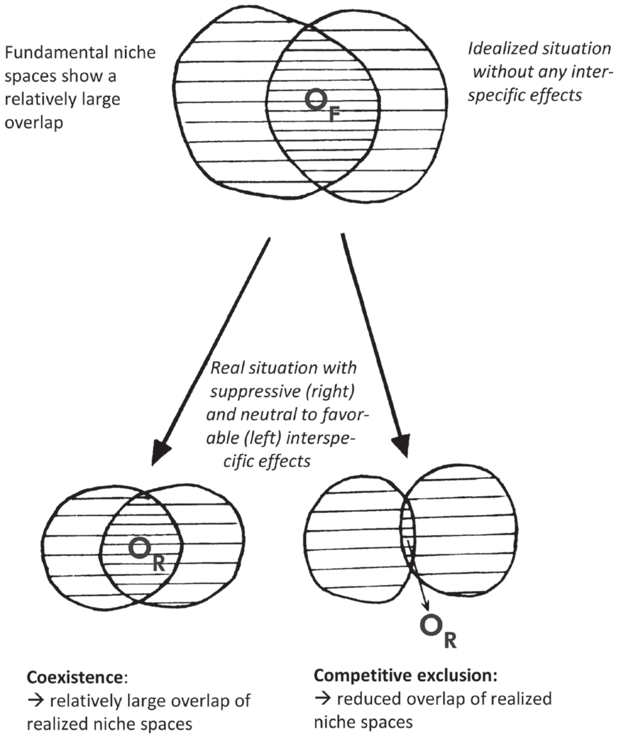


Figure 7. The model to estimate interspecific competitive exclusion (modified from Seifert 1987).

4. Results and discussion

4.1 The ant species found, their abundance and behavior regarding selected niche dimensions

This section provides an overview about the 86 ant species found in this ecological study. Tabs 6–7 show the overall sum of nest density, the presence, the mean values and factorial niche width (tolerance) for eight selected environmental factors and the overall niche width as geometric calculation from only these eight factors. Tables 8–9 show the strata of foraging (SF), the fields of nutrition (FN) and the composition of nest microhabitats (NM). As stated in the methods section, the reader should be aware that many statements regarding the factors SF and FN have to be understood as a subjective expert opinion due to the most fragmentary data basis available here. Discussing the particular behavior of 86 species in respect to 36 parameters would go beyond the scope of this monography. Examples of few selected species are discussed in the sections 4.2.1 to 4.2.11 which consider the influence of twelve environmental factors on species richness and ant biomass.

4.2 The influence of environmental factors on richness and biomass of ant assemblages

This section considers the influence of the 12 environmental factors T_{MAX}, T_{MEAN}, F, N, PD, StC, R, M, MoC, LiC, ShrTrC and DWC on species richness and ant biomass on the community level and discusses the reaction of particular, selected species. The first general finding on the community level is that linear or quasi-linear relations between environmental factors and species richness or biomass are rare. The highest correlations and most reasonable descriptions of the real relations are usually achieved by polynomial functions (Figs 8–18). These show in 80 % of the cases that the optima of richness and biomass are not at the upper or lower end of an environmental gradient which makes simple linear descriptions inappropriate. The second general finding is that richness and biomass behave in a similar way regarding the same environmental factor – the optima of biomass are often found at very similar positions along an environmental gradient. The main reason for this congruence is the rare association of species-poor or even monospecific ant assemblages with a high overall ant biomass. The third general result is that 88 % of the descriptions are significant for $p < 0.001$ thanks to the large sample size of 232 plots and the very

Table 6. Unweighted data of niche dimensions (see sections 3.7.1 to 3.7.3) in ant species belonging to the subfamilies Formicinae and Dolichoderinae. Acronyms: sum – sum of nest densities, n – number of occupied study plots, W_8 – niche width considering the eight environmental factors given in the table, m – arithmetic mean, *w* – factorial width (a value of 1.0 corresponds to a rectangular distribution over the whole measured range, see section 3.7.3). For proper explanations of T_{MAX}, T_{MEAN} (maximum and mean soil temperature), F (soil moisture), N (soil nutrients), R (soil calcium), ShrTrC (additive cover of shrubs and trees), LiC (litter cover) and PD (plant density in the moss and herb layer) see section 3.6. All data refer to classes and were calculated from class probabilities but the mean temperature data were secondarily transformed into °C.

	sum	n	W_8	T_{MAX}		T_{MEAN}		F		N		R		ShrTrC		LiC		PD	
				m	*w*	m	*w*	m	*w*	m	*w*	m	*w*	m	*w*	m	*w*	m	*w*
Camponotus fallax	10.16	4	0.30	20.6	0.21	15.7	0.16	2.66	0.22	4.32	0.76	4.52	0.38	7.08	0.37	2.50	0.19	4.72	0.42
Camponotus herculeanus	12.90	10	0.36	20.0	0.25	12.4	0.17	4.44	0.31	4.69	0.45	2.95	0.26	1.16	0.38	4.61	0.70	2.24	0.66
Camponotus ligniperda	73.30	21	0.39	25.6	0.46	15.5	0.22	2.23	0.22	2.52	0.30	6.18	0.82	2.92	0.75	1.58	0.32	3.78	0.42
Camponotus piceus	2.10	1	0.09	31.0	0.07	16.6	0.07	1.00	0.10	2.00	0.11	9.00	0.11	1.00	0.11	1.00	0.11	2.00	0.09
Dolichod. quadripunctatus	31.08	8	0.33	20.4	0.22	15.3	0.28	2.92	0.19	4.76	0.63	4.69	0.43	7.21	0.35	2.83	0.30	4.63	0.45
Formica aquilonia	0.12	1	0.09	15.0	0.07	7.6	0.07	4.00	0.10	2.00	0.11	3.00	0.11	6.00	0.11	4.00	0.11	2.00	0.09
Formica cinerea	161.10	21	0.31	30.3	0.32	16.5	0.19	2.14	0.33	2.98	0.55	6.01	0.72	1.40	0.30	1.02	0.08	2.40	0.44
Formica clara	22.26	16	0.24	29.7	0.16	17.3	0.25	1.93	0.20	2.62	0.23	4.57	1.03	1.00	0.11	1.06	0.16	2.64	0.33
Formica cunicularia	136.53	50	0.36	25.3	0.54	15.4	0.32	2.26	0.30	3.13	0.50	7.41	0.72	1.30	0.42	1.03	0.08	4.30	0.49
Formica exsecta	0.14	1	0.09	23.0	0.07	7.6	0.07	4.00	0.10	2.00	0.11	3.00	0.11	1.00	0.11	1.00	0.11	3.00	0.09
Formica fuscocinerea	33.68	5	0.23	26.3	0.24	16.8	0.13	4.00	0.48	3.03	0.54	8.01	0.04	3.04	0.55	1.69	0.20	4.67	0.25
Formica fusca	297.55	58	0.57	22.1	0.59	14.8	0.31	2.93	0.52	3.22	0.54	4.98	0.82	4.20	0.96	1.82	0.58	3.73	0.50
Formica lemani	262.98	21	0.42	19.4	0.41	8.4	0.42	4.17	0.44	2.59	0.40	4.74	0.95	1.26	0.21	1.19	0.28	3.36	0.58
Formica lugubris	0.12	2	0.18	16.4	0.37	7.6	0.07	3.83	0.13	2.83	0.14	6.33	0.58	1.83	0.14	1.00	0.11	2.67	0.24
Formica paralugubris	0.02	1	0.09	7.0	0.07	6.6	0.07	4.00	0.10	3.00	0.11	3.00	0.11	8.00	0.11	9.00	0.11	1.00	0.09
Formica picea	63.40	7	0.22	22.2	0.27	14.9	0.15	8.46	0.22	1.29	0.22	1.54	0.38	1.43	0.26	1.00	0.11	5.68	0.29
Formica polyctena	0.39	3	0.28	18.7	0.10	14.3	0.22	3.18	0.13	4.62	0.36	6.38	0.36	7.67	0.30	2.69	0.85	5.85	0.35
Formica pratensis	1.09	5	0.23	25.8	0.30	15.7	0.13	1.88	0.11	2.85	0.20	6.11	1.20	1.00	0.11	1.37	0.19	4.08	0.37
Formica rufa	0.87	3	0.35	24.0	0.62	16.0	0.21	2.51	0.29	2.74	0.17	3.23	0.16	6.25	1.15	6.92	1.35	2.80	0.15
Formica rufibarbis	89.21	38	0.33	27.2	0.46	15.6	0.23	1.92	0.24	2.81	0.52	7.56	0.69	1.30	0.36	1.00	0.11	3.46	0.41
Formica sanguinea	50.64	39	0.66	24.3	0.69	15.1	0.61	2.98	0.55	3.13	0.52	3.86	0.97	2.08	0.75	2.14	0.62	3.55	0.64
Formica selysi	17.70	6	0.13	25.7	0.14	13.9	0.13	3.31	0.16	2.06	0.13	8.97	0.06	1.74	0.19	1.00	0.11	2.62	0.18
Formica truncorum	0.27	2	0.22	18.6	0.33	14.3	0.33	3.26	0.15	3.26	0.17	8.00	0.11	2.04	0.68	1.52	0.34	7.00	0.09
Lasius alienus	1774.02	48	0.35	26.5	0.50	15.3	0.26	1.91	0.18	2.48	0.34	7.57	0.69	1.66	0.59	1.13	0.14	3.69	0.45
Lasius brunneus	133.33	22	0.51	17.7	0.51	13.8	0.32	3.75	0.38	5.34	0.56	5.42	0.49	7.26	0.62	3.48	0.72	3.22	0.63
Lasius emarginatus	131.17	18	0.37	25.3	0.49	15.4	0.25	1.88	0.18	2.29	0.27	4.56	0.52	3.58	0.83	1.70	0.31	2.77	0.41
Lasius flavus	2092.84	73	0.41	23.8	0.51	14.8	0.27	2.66	0.41	3.42	0.70	7.07	0.71	1.44	0.48	1.08	0.13	4.31	0.44
Lasius fuliginosus	6.90	10	0.40	15.8	0.28	13.2	0.18	3.65	0.17	5.91	0.70	6.24	0.67	7.53	0.56	3.97	0.63	4.67	0.46
Lasius jensi	28.30	12	0.21	25.8	0.33	15.0	0.18	1.97	0.14	2.53	0.38	8.76	0.27	1.00	0.11	1.00	0.11	3.92	0.35
Lasius meridionalis	2.27	1	0.09	29.0	0.07	16.6	0.07	1.00	0.10	2.00	0.11	9.00	0.11	1.00	0.11	1.00	0.11	3.00	0.09
Lasius mixtus	8.80	1	0.09	19.0	0.07	13.6	0.07	3.00	0.10	4.00	0.11	5.00	0.11	1.00	0.11	1.00	0.11	5.00	0.09
Lasius myops	103.20	10	0.22	29.4	0.19	16.4	0.16	1.58	0.17	2.52	0.37	8.10	0.56	1.00	0.11	1.00	0.11	2.88	0.37
Lasius niger	1271.50	75	0.45	24.5	0.60	15.5	0.40	3.14	0.33	4.74	0.62	5.86	0.67	1.54	0.55	1.06	0.16	3.92	0.54
Lasius paralienus	133.20	6	0.31	26.3	0.30	15.2	0.21	2.22	0.22	2.22	0.24	7.83	0.67	1.68	0.52	1.22	0.24	5.02	0.32
Lasius platythorax	482.35	49	0.70	19.5	0.45	14.1	0.39	5.11	0.91	3.15	0.70	3.26	0.76	4.37	1.05	2.49	0.81	4.80	0.77
Lasius psammophilus	183.91	20	0.31	29.0	0.41	16.7	0.26	1.59	0.22	2.23	0.32	2.86	0.64	1.25	0.25	1.17	0.20	2.10	0.37
Lasius reginae	25.20	6	0.18	28.6	0.29	16.3	0.24	1.85	0.13	2.00	0.15	8.60	0.19	1.00	0.11	1.00	0.11	2.92	0.34
Lasius umbratus	7.68	9	0.55	22.7	0.75	14.7	0.33	2.62	0.32	3.95	0.67	6.94	0.73	3.28	1.04	2.13	0.67	4.47	0.32
Plagiolepis vindobonensis	20.50	3	0.14	28.3	0.12	16.2	0.12	1.37	0.17	1.85	0.14	8.63	0.19	1.00	0.11	1.00	0.11	3.34	0.23
Polyergus rufescens	1.50	2	0.12	27.0	0.07	15.6	0.07	2.00	0.10	2.53	0.19	8.53	0.19	1.00	0.11	1.00	0.11	3.53	0.16
Tapinoma erraticum	334.42	15	0.19	26.6	0.34	15.2	0.21	1.64	0.17	2.35	0.23	8.81	0.16	1.11	0.20	1.00	0.04	3.76	0.42
Tapinoma subboreale	191.25	17	0.21	27.2	0.31	15.7	0.19	1.81	0.20	2.02	0.23	8.25	0.35	1.05	0.09	1.00	0.11	3.31	0.36

Table 7. Unweighted data of niche dimensions in ant species belonging to the subfamilies Ponerinae and Myrmicinae. Acronyms: sum – sum of nest densities, n – number of occupied study plots, W_8 – niche width considering the eight environmental factors given in the table, m – arithmetic mean, *w* – factorial width (a value of 1.0 corresponds to a rectangular distribution over the whole measured range, see section 3.7.3). For proper explanations of T_{MAX}, T_{MEAN} (maximum and mean soil temperature), F (soil moisture), N (soil nutrients) , R (soil calcium) , ShrTrC (additive cover of shrubs and trees) , LiC (litter cover) and PD (plant density in the moss and herb layer) see section 3.6. All data refer to classes and were calculated from class probabilities but the mean temperature data were secondarily transformed into °C.

	sum	n	W_8	T_{MAX}		T_{MEAN}		F		N		R		ShrTrC		LiC		PD	
				m	*w*	m	*w*	m	*w*	m	*w*	m	*w*	m	*w*	m	*w*	m	*w*
Anergates atratulus	2.10	1	0.09	29.0	0.07	15.6	0.07	1.00	0.10	1.00	0.11	8.00	0.11	1.00	0.11	1.00	0.11	2.00	0.09
Harpagoxenus sublaevis	9.89	5	0.33	16.8	0.13	13.6	0.21	4.31	0.34	3.14	0.43	1.81	0.15	5.39	0.81	1.86	0.60	3.72	0.46
Leptothorax acervorum	322.75	33	0.63	18.8	0.37	13.0	0.62	4.47	0.64	3.15	0.63	2.80	0.72	4.05	0.89	2.14	0.82	4.18	0.48
Leptothorax gredleri	155.59	7	0.35	18.3	0.25	14.4	0.22	3.61	0.17	4.77	0.36	4.42	0.65	6.29	0.48	2.67	0.87	3.61	0.24
Leptothorax muscorum	191.47	13	0.47	18.8	0.43	14.1	0.21	3.30	0.36	3.13	0.55	3.25	0.94	4.85	0.40	2.27	0.94	3.85	0.36
Manica rubida	123.31	16	0.52	26.4	0.40	16.6	0.47	3.51	0.47	3.17	0.48	6.57	0.86	2.76	0.67	1.84	0.36	4.28	0.60
Myrmecina graminicola	144.54	27	0.37	26.0	0.41	15.2	0.28	2.00	0.20	2.40	0.26	8.04	0.60	2.10	0.64	1.25	0.35	4.08	0.43
Myrmica constricta	51.29	9	0.42	27.5	0.49	16.8	0.17	2.58	0.42	2.44	0.33	6.45	0.82	2.90	0.64	1.74	0.28	4.11	0.60
Myrmica curvithorax	56.71	5	0.22	23.8	0.34	15.3	0.16	6.60	0.34	6.19	0.29	7.28	0.37	1.00	0.11	1.01	0.05	2.83	0.55
Myrmica gallienii	215.50	12	0.30	18.9	0.33	14.2	0.29	6.99	0.57	5.75	0.61	7.29	0.26	1.00	0.11	1.00	0.11	6.80	0.70
Myrmica hirsuta	42.00	3	0.13	22.8	0.16	14.5	0.08	2.09	0.10	3.09	0.11	7.93	0.12	2.44	0.56	1.00	0.11	4.09	0.09
Myrmica lobicornis	51.89	15	0.51	20.7	0.43	10.6	0.89	3.13	0.24	2.33	0.32	4.48	0.78	2.27	0.73	1.37	0.44	2.25	0.14
Myrmica lobulicornis	85.15	6	0.17	18.0	0.27	7.5	0.05	4.00	0.10	3.49	0.46	6.03	0.48	1.25	0.17	1.00	0.11	2.25	0.14
Myrmica lonae	84.00	9	0.51	20.6	0.35	14.3	0.23	3.46	0.70	2.43	0.41	4.36	1.01	4.43	0.85	1.77	0.45	3.74	0.49
Myrmica myrmicoxena	1.79	1	0.09	15.0	0.07	7.6	0.07	4.00	0.10	3.00	0.11	7.00	0.11	2.00	0.11	1.00	0.11	3.00	0.09
Myrmica rubra	736.93	71	0.63	18.2	0.43	14.2	0.24	5.64	0.72	4.85	0.85	5.85	0.88	3.59	1.24	1.44	0.49	5.90	0.76
Myrmica ruginodis	513.22	76	0.68	17.3	0.32	13.2	0.48	4.57	0.59	4.05	0.75	4.29	0.93	5.34	1.14	2.76	0.83	5.11	0.75
Myrmica rugulosa	219.02	20	0.41	24.3	0.50	15.6	0.30	3.42	0.37	5.19	0.63	5.98	0.57	2.83	0.93	1.21	0.16	3.02	0.27
Myrmica sabuleti	743.94	65	0.40	24.4	0.46	15.1	0.29	2.16	0.23	2.71	0.40	6.94	0.81	2.23	0.77	1.21	0.21	3.85	0.43
Myrmica scabrinodis	864.92	51	0.47	21.7	0.47	13.6	0.59	6.60	0.84	2.57	0.52	3.97	0.90	1.12	0.30	1.03	0.14	4.96	0.50
Myrmica schencki	152.11	46	0.33	27.0	0.56	15.9	0.25	2.08	0.26	2.50	0.37	6.68	0.71	1.39	0.44	1.04	0.07	3.45	0.45
Myrmica specioides	411.28	38	0.28	27.8	0.39	15.6	0.25	1.81	0.26	2.46	0.35	8.17	0.67	1.16	0.21	1.01	0.08	2.95	0.36
Myrmica sulcinodis	56.89	8	0.36	19.4	0.30	11.5	0.49	4.10	0.16	4.57	0.38	3.37	0.35	1.16	0.14	3.20	0.65	2.93	0.89
Myrmica vandeli	11.00	2	0.19	18.0	0.21	12.6	0.07	8.00	0.10	3.51	0.33	5.77	0.83	1.00	0.11	1.00	0.11	7.26	0.41
Myrmoxenus ravouxi	10.50	2	0.11	30.4	0.12	16.6	0.07	1.00	0.10	1.66	0.18	9.00	0.11	1.00	0.11	1.00	0.11	1.00	0.09
Ponera coarctata	186.57	20	0.37	25.3	0.36	15.6	0.24	2.41	0.30	2.76	0.33	7.73	0.46	2.90	0.58	1.56	0.30	4.40	0.55
Ponera testacea	13.40	5	0.22	29.4	0.26	16.0	0.20	1.58	0.17	2.32	0.28	6.69	0.79	1.00	0.11	1.00	0.11	2.88	0.25
Solenopsis fugax	731.60	35	0.25	28.2	0.30	15.8	0.20	1.74	0.16	2.13	0.30	7.64	0.69	1.11	0.21	1.03	0.10	3.09	0.38
Stenamma debile	155.91	18	0.54	18.1	0.47	13.4	0.24	3.55	0.37	4.77	0.86	5.55	0.87	6.97	0.74	4.07	0.74	2.92	0.44
Strongylognathus testaceus	9.65	5	0.20	30.0	0.28	18.0	0.24	2.69	0.16	4.19	0.50	3.64	0.23	1.00	0.11	1.08	0.11	3.06	0.20
Temnothorax affinis	73.42	7	0.30	21.5	0.25	15.2	0.27	2.18	0.15	2.69	0.55	4.60	0.49	6.18	0.46	2.16	0.17	3.90	0.31
Temnothorax albipennis	100.50	13	0.23	27.7	0.38	15.8	0.23	1.53	0.17	2.28	0.25	8.57	0.19	1.40	0.25	1.00	0.11	2.63	0.36
Temnothorax corticalis	10.46	3	0.23	20.8	0.15	15.7	0.09	3.48	0.25	5.45	0.53	5.35	0.40	7.11	0.24	2.24	0.17	4.35	0.31
Temnothorax crassispinus	1693.54	26	0.46	19.4	0.31	14.9	0.20	3.09	0.25	3.89	0.72	4.26	0.78	6.70	0.52	3.97	0.85	3.82	0.49
Temnothorax interruptus	336.60	23	0.26	28.7	0.31	15.8	0.19	1.45	0.20	1.76	0.30	7.84	0.60	1.12	0.21	1.03	0.09	2.57	0.50
Temnothorax nigriceps	275.20	11	0.41	28.3	0.45	15.9	0.17	2.10	0.34	2.34	0.30	6.01	0.79	2.15	0.65	1.50	0.30	3.21	0.64
Temnothorax nylanderi	1033.71	10	0.43	17.9	0.45	13.7	0.20	3.38	0.27	4.28	0.36	4.84	0.49	7.48	0.71	4.97	0.91	2.00	0.43
Temnothorax parvulus	404.72	6	0.31	22.1	0.28	14.6	0.12	2.50	0.17	3.03	0.52	4.13	0.40	5.96	0.58	2.40	0.26	3.23	0.48
Temnothorax saxonicus	37.91	5	0.29	22.4	0.18	15.2	0.21	2.15	0.13	2.57	0.55	5.10	0.47	5.16	0.57	2.13	0.14	2.34	0.56
Temnothorax tuberum	216.20	11	0.32	25.3	0.39	14.0	0.79	2.03	0.31	2.29	0.23	7.87	0.68	1.35	0.23	1.00	0.11	3.18	0.32
Temnothorax unifasciatus	858.78	31	0.40	25.5	0.51	15.0	0.24	2.00	0.19	2.23	0.28	5.81	0.86	3.20	0.77	1.50	0.29	3.36	0.49
Tetramorium alpestre	41.81	3	0.15	22.8	0.07	7.6	0.07	3.37	0.17	2.00	0.11	3.57	0.68	1.00	0.11	1.00	0.11	2.03	0.36
Tetramorium caespitum	983.95	49	0.34	28.2	0.32	16.3	0.30	2.01	0.31	2.69	0.41	6.85	0.88	1.21	0.23	1.14	0.21	3.03	0.33
Tetramorium impurum	743.17	44	0.41	28.0	0.51	15.6	0.24	1.86	0.25	2.25	0.34	6.41	0.80	2.09	0.69	1.30	0.30	2.98	0.47

Table 8. Strata of foraging, main fields of nutrition and nest microhabitats of species belonging to the subfamilies Formicinae and Dolichoderinae. For more detailed explanations see sections 3.6.13 to 3.6.15. Cells marked with ‘n.f.’ belong to permanent social parasites which do not forage.

	Strata of foraging SF						Fields of nutrition FN				Nest microhabitat NM						
	Deep Soil	Top Soil	Moss Litter	Free Surf	Herb	Shrub Tree	Zoopha	Nectar	Tropho	Plant Part	Soil Stone	Rock	Moss	Turf	Litter	Wood	Micro
Camponotus fallax	0.00	0.00	0.00	0.06	0.02	0.92	0.58	0.13	0.21	0.08	0.00	0.02	0.00	0.00	0.00	0.98	0.00
Camponotus herculeanus	0.02	0.04	0.01	0.13	0.04	0.76	0.23	0.05	0.67	0.05	0.09	0.01	0.00	0.00	0.00	0.90	0.00
Camponotus ligniperda	0.03	0.06	0.01	0.21	0.07	0.62	0.27	0.05	0.63	0.05	0.31	0.09	0.00	0.00	0.00	0.60	0.00
Camponotus piceus	0.00	0.10	0.05	0.30	0.40	0.15	0.45	0.20	0.20	0.15	0.80	0.11	0.02	0.03	0.03	0.01	0.00
Dolichod. quadripunctatus	0.00	0.00	0.01	0.07	0.07	0.85	0.61	0.13	0.13	0.13	0.00	0.01	0.00	0.00	0.00	0.98	0.02
Formica aquilonia	0.00	0.07	0.03	0.30	0.10	0.50	0.30	0.03	0.65	0.02	0.77	0.02	0.00	0.01	0.00	0.20	0.00
Formica cinerea	0.01	0.07	0.01	0.58	0.15	0.18	0.50	0.05	0.40	0.05	0.92	0.03	0.00	0.04	0.00	0.01	0.00
Formica clara	0.01	0.09	0.03	0.60	0.24	0.03	0.60	0.05	0.29	0.06	0.92	0.03	0.00	0.05	0.00	0.00	0.00
Formica cunicularia	0.01	0.11	0.02	0.45	0.36	0.05	0.58	0.05	0.32	0.05	0.87	0.02	0.00	0.10	0.00	0.01	0.00
Formica exsecta	0.01	0.20	0.03	0.43	0.18	0.15	0.40	0.02	0.56	0.02	0.95	0.00	0.00	0.05	0.00	0.00	0.00
Formica fuscocinerea	0.01	0.07	0.01	0.58	0.15	0.18	0.50	0.05	0.40	0.05	0.92	0.03	0.00	0.04	0.00	0.01	0.00
Formica fusca	0.01	0.14	0.05	0.33	0.30	0.17	0.50	0.10	0.35	0.05	0.59	0.07	0.01	0.07	0.02	0.24	0.00
Formica lemani	0.01	0.15	0.05	0.40	0.30	0.09	0.56	0.11	0.27	0.06	0.74	0.05	0.01	0.12	0.00	0.08	0.00
Formica lugubris	0.00	0.05	0.05	0.30	0.10	0.50	0.30	0.03	0.65	0.02	0.77	0.02	0.00	0.01	0.00	0.20	0.00
Formica paralugubris	0.00	0.05	0.05	0.30	0.10	0.50	0.30	0.03	0.65	0.02	0.77	0.02	0.00	0.01	0.00	0.20	0.00
Formica picea	0.01	0.21	0.48	0.15	0.10	0.05	0.23	0.09	0.63	0.05	0.20	0.00	0.59	0.20	0.00	0.01	0.00
Formica polyctena	0.00	0.07	0.03	0.30	0.10	0.50	0.30	0.03	0.65	0.02	0.77	0.02	0.00	0.01	0.00	0.20	0.00
Formica pratensis	0.01	0.15	0.03	0.45	0.20	0.16	0.41	0.02	0.55	0.02	0.88	0.01	0.00	0.04	0.00	0.08	0.00
Formica rufa	0.00	0.07	0.03	0.30	0.10	0.50	0.30	0.03	0.65	0.02	0.77	0.02	0.00	0.01	0.00	0.20	0.00
Formica rufibarbis	0.01	0.10	0.02	0.50	0.32	0.05	0.59	0.05	0.31	0.05	0.87	0.03	0.01	0.09	0.00	0.01	0.00
Formica sanguinea	0.01	0.10	0.02	0.53	0.09	0.26	0.48	0.02	0.48	0.02	0.80	0.05	0.00	0.05	0.00	0.10	0.00
Formica selysi	0.01	0.07	0.01	0.70	0.10	0.11	0.66	0.02	0.30	0.02	0.94	0.04	0.00	0.01	0.00	0.01	0.00
Formica truncorum	0.00	0.05	0.05	0.30	0.10	0.50	0.30	0.03	0.65	0.02	0.62	0.10	0.00	0.03	0.00	0.25	0.00
Lasius alienus	0.03	0.22	0.04	0.31	0.18	0.22	0.39	0.18	0.37	0.06	0.82	0.03	0.00	0.09	0.01	0.05	0.00
Lasius brunneus	0.00	0.09	0.10	0.25	0.05	0.51	0.30	0.05	0.60	0.05	0.06	0.00	0.00	0.00	0.04	0.90	0.00
Lasius emarginatus	0.01	0.07	0.03	0.40	0.18	0.31	0.45	0.05	0.44	0.06	0.31	0.51	0.00	0.00	0.02	0.16	0.00
Lasius flavus	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.85	0.02	0.02	0.10	0.00	0.01	0.00
Lasius fuliginosus	0.00	0.17	0.03	0.30	0.03	0.47	0.25	0.07	0.64	0.04	0.30	0.00	0.00	0.00	0.00	0.70	0.00
Lasius jensi	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.90	0.00	0.00	0.10	0.00	0.00	0.00
Lasius meridionalis	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.90	0.00	0.00	0.10	0.00	0.00	0.00
Lasius mixtus	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.85	0.00	0.00	0.10	0.02	0.03	0.00
Lasius myops	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.92	0.03	0.00	0.05	0.00	0.00	0.00
Lasius niger	0.02	0.16	0.04	0.34	0.19	0.25	0.34	0.05	0.56	0.05	0.83	0.06	0.00	0.04	0.00	0.07	0.00
Lasius paralienus	0.03	0.22	0.04	0.31	0.18	0.22	0.39	0.19	0.36	0.06	0.85	0.01	0.00	0.13	0.00	0.01	0.00
Lasius platythorax	0.02	0.10	0.08	0.31	0.17	0.32	0.34	0.05	0.56	0.05	0.16	0.01	0.12	0.05	0.01	0.65	0.00
Lasius psammophilus	0.04	0.29	0.04	0.21	0.20	0.22	0.35	0.14	0.50	0.01	0.92	0.02	0.00	0.05	0.01	0.00	0.00
Lasius reginae	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.92	0.03	0.00	0.05	0.00	0.00	0.00
Lasius umbratus	0.16	0.78	0.05	0.01	0.00	0.00	0.20	0.00	0.80	0.00	0.84	0.02	0.00	0.05	0.02	0.07	0.00
Plagiolepis vindobonensis	0.01	0.12	0.12	0.35	0.35	0.05	0.33	0.32	0.33	0.02	0.81	0.10	0.01	0.03	0.01	0.03	0.01
Polyergus rufescens	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.81	0.04	0.01	0.08	0.00	0.07	0.00
Tapinoma erraticum	0.00	0.09	0.10	0.40	0.40	0.01	0.60	0.13	0.20	0.07	0.75	0.01	0.07	0.14	0.03	0.00	0.00
Tapinoma subboreale	0.00	0.09	0.10	0.40	0.40	0.01	0.60	0.13	0.20	0.07	0.75	0.01	0.07	0.14	0.03	0.00	0.00

Table 9. Strata of foraging, main fields of nutrition and nest microhabitats of species belonging to the subfamilies Myrmicinae and Ponerinae. For more detailed explanations see sections 3.6.13 to 3.6.15. Cells marked with 'n.f.' belong to permanent social parasites which do not forage.

	Strata of foraging SF						Fields of nutrition FN				Nest microhabitat NM						
	Deep Soil	Top Soil	Moss Litter	Free Surf	Herb	Shrub Tree	Zoopha	Nectar	Tropho	Plant Part	Soil Stone	Rock	Moss	Turf	Litter	Wood	Micro
Anergates atratulus	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.85	0.03	0.02	0.10	0.00	0.00	0.00
Harpagoxenus sublaevis	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.87	0.06	0.02	0.05	0.00	0.00	0.00
Leptothorax acervorum	0.00	0.21	0.41	0.36	0.01	0.01	0.87	0.02	0.07	0.04	0.03	0.04	0.04	0.00	0.00	0.88	0.01
Leptothorax gredleri	0.00	0.21	0.41	0.33	0.01	0.04	0.87	0.02	0.07	0.04	0.00	0.01	0.01	0.00	0.00	0.82	0.06
Leptothorax muscorum	0.00	0.22	0.43	0.34	0.01	0.00	0.87	0.02	0.07	0.04	0.03	0.02	0.02	0.00	0.00	0.92	0.01
Manica rubida	0.00	0.00	0.05	0.70	0.10	0.15	0.84	0.03	0.11	0.02	0.93	0.02	0.00	0.05	0.00	0.00	0.00
Myrmecina graminicola	0.05	0.36	0.54	0.05	0.00	0.00	0.99	0.00	0.00	0.01	0.88	0.03	0.00	0.03	0.06	0.00	0.00
Myrmica constricta	0.02	0.18	0.18	0.45	0.17	0.00	0.68	0.04	0.25	0.03	0.83	0.00	0.02	0.15	0.00	0.00	0.00
Myrmica curvithorax	0.02	0.25	0.10	0.48	0.15	0.00	0.56	0.04	0.35	0.05	0.83	0.00	0.02	0.15	0.00	0.00	0.00
Myrmica gallienii	0.01	0.18	0.23	0.32	0.21	0.05	0.60	0.06	0.32	0.02	0.84	0.00	0.07	0.09	0.00	0.00	0.00
Myrmica hirsuta	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.73	0.03	0.07	0.13	0.01	0.03	0.00
Myrmica lobicornis	0.02	0.15	0.39	0.39	0.05	0.00	0.72	0.04	0.20	0.04	0.75	0.00	0.03	0.10	0.08	0.04	0.00
Myrmica lobulicornis	0.02	0.15	0.35	0.38	0.10	0.00	0.72	0.04	0.20	0.04	0.50	0.10	0.05	0.30	0.00	0.05	0.00
Myrmica lonae	0.02	0.10	0.26	0.37	0.18	0.07	0.54	0.04	0.35	0.07	0.72	0.01	0.10	0.10	0.01	0.06	0.00
Myrmica myrmicoxena	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.50	0.10	0.05	0.30	0.00	0.05	0.00
Myrmica rubra	0.02	0.15	0.19	0.26	0.19	0.19	0.48	0.05	0.37	0.10	0.62	0.00	0.08	0.12	0.00	0.18	0.00
Myrmica ruginodis	0.01	0.15	0.18	0.26	0.18	0.22	0.53	0.02	0.30	0.15	0.48	0.00	0.07	0.10	0.07	0.28	0.00
Myrmica rugulosa	0.02	0.17	0.19	0.52	0.10	0.00	0.64	0.08	0.25	0.03	0.48	0.20	0.08	0.24	0.00	0.00	0.00
Myrmica sabuleti	0.02	0.10	0.21	0.40	0.20	0.07	0.51	0.07	0.37	0.05	0.74	0.05	0.05	0.15	0.00	0.01	0.00
Myrmica scabrinodis	0.02	0.18	0.15	0.42	0.20	0.03	0.51	0.06	0.40	0.03	0.59	0.01	0.20	0.20	0.00	0.00	0.00
Myrmica schencki	0.02	0.15	0.20	0.41	0.22	0.00	0.58	0.10	0.27	0.05	0.75	0.05	0.05	0.15	0.00	0.00	0.00
Myrmica specioides	0.02	0.18	0.18	0.42	0.20	0.00	0.51	0.05	0.41	0.03	0.82	0.01	0.01	0.15	0.01	0.00	0.00
Myrmica sulcinodis	0.02	0.20	0.20	0.45	0.13	0.00	0.55	0.08	0.30	0.07	0.71	0.03	0.05	0.20	0.01	0.01	0.00
Myrmica vandeli	0.02	0.17	0.21	0.40	0.20	0.00	0.59	0.07	0.30	0.04	0.59	0.01	0.20	0.20	0.00	0.00	0.00
Myrmoxenus ravouxi	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.08	0.40	0.07	0.01	0.01	0.23	0.20
Ponera coarctata	0.27	0.43	0.26	0.04	0.00	0.00	1.00	0.00	0.00	0.00	0.80	0.05	0.00	0.10	0.05	0.00	0.00
Ponera testacea	0.27	0.43	0.26	0.04	0.00	0.00	1.00	0.00	0.00	0.00	0.80	0.05	0.00	0.10	0.05	0.00	0.00
Solenopsis fugax	0.29	0.58	0.10	0.03	0.00	0.00	0.50	0.00	0.50	0.00	0.81	0.03	0.01	0.15	0.00	0.00	0.00
Stenamma debile	0.08	0.35	0.49	0.08	0.00	0.00	0.95	0.00	0.02	0.03	0.89	0.01	0.03	0.00	0.05	0.02	0.00
Strongylognathus testaceus	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	n.f.	0.87	0.06	0.02	0.05	0.00	0.00	0.00
Temnothorax affinis	0.00	0.00	0.00	0.01	0.01	0.98	0.88	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.01
Temnothorax albipennis	0.00	0.08	0.21	0.28	0.41	0.02	0.80	0.15	0.05	0.00	0.16	0.25	0.09	0.09	0.01	0.16	0.24
Temnothorax corticalis	0.00	0.00	0.00	0.01	0.01	0.98	0.88	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.01
Temnothorax crassispinus	0.00	0.08	0.36	0.29	0.22	0.05	0.95	0.02	0.03	0.00	0.04	0.02	0.01	0.02	0.08	0.35	0.48
Temnothorax interruptus	0.00	0.07	0.31	0.31	0.31	0.00	0.80	0.15	0.05	0.00	0.31	0.12	0.33	0.18	0.00	0.01	0.05
Temnothorax nigriceps	0.00	0.14	0.21	0.32	0.33	0.00	0.80	0.15	0.05	0.00	0.00	0.96	0.02	0.00	0.00	0.01	0.01
Temnothorax nylanderi	0.00	0.08	0.37	0.30	0.23	0.02	0.95	0.02	0.03	0.00	0.04	0.02	0.01	0.02	0.04	0.24	0.63
Temnothorax parvulus	0.00	0.08	0.38	0.31	0.23	0.00	0.95	0.02	0.03	0.00	0.13	0.01	0.01	0.00	0.13	0.24	0.48
Temnothorax saxonicus	0.00	0.06	0.27	0.34	0.16	0.17	0.95	0.02	0.03	0.00	0.03	0.80	0.03	0.00	0.00	0.06	0.09
Temnothorax tuberum	0.00	0.07	0.13	0.27	0.53	0.00	0.80	0.15	0.05	0.00	0.25	0.42	0.15	0.06	0.01	0.02	0.09
Temnothorax unifasciatus	0.00	0.06	0.24	0.24	0.46	0.00	0.80	0.15	0.05	0.00	0.07	0.39	0.10	0.02	0.02	0.16	0.24
Tetramorium alpestre	0.17	0.34	0.03	0.43	0.03	0.00	0.34	0.05	0.36	0.25	0.85	0.05	0.00	0.10	0.00	0.00	0.00
Tetramorium caespitum	0.17	0.34	0.03	0.43	0.03	0.00	0.26	0.04	0.35	0.35	0.85	0.03	0.02	0.10	0.00	0.00	0.00
Tetramorium impurum	0.17	0.34	0.03	0.43	0.03	0.00	0.26	0.04	0.35	0.35	0.83	0.08	0.02	0.07	0.00	0.00	0.00

broad environmental gradient studied. The goodness of the polynomial descriptions was estimated by the critical values of Pearson's correlation coefficient. These are in a two-tailed test for 232 study plots with 230 degrees of freedom 0.1287 ($p < 0.05$), 0.1687 ($p < 0.01$) and 0.2147 ($p < 0.001$). The parameters of the polynomial functions written in the diagrams (Figs 8–18) are strongly rounded which may result in big disagreements to the true values depicted by the curve progressions in the figures.

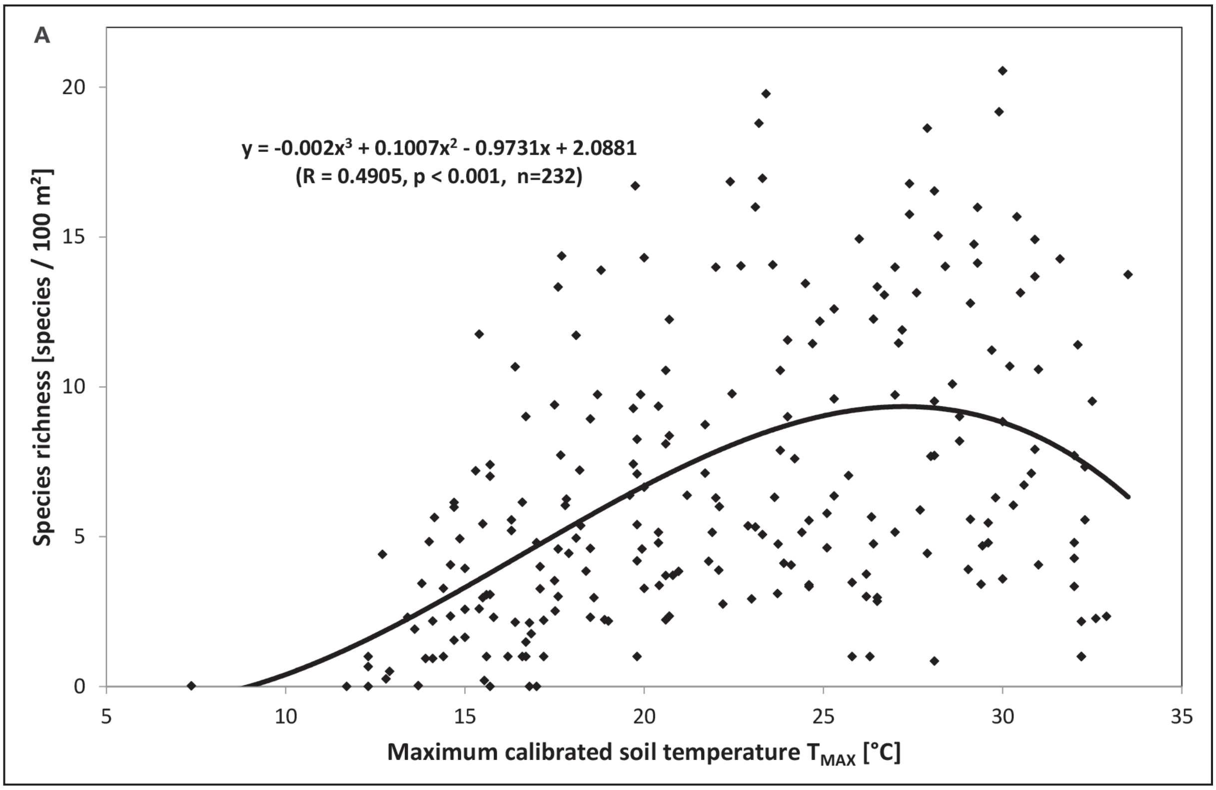
4.2.1 The influence of maximum and mean soil temperatures

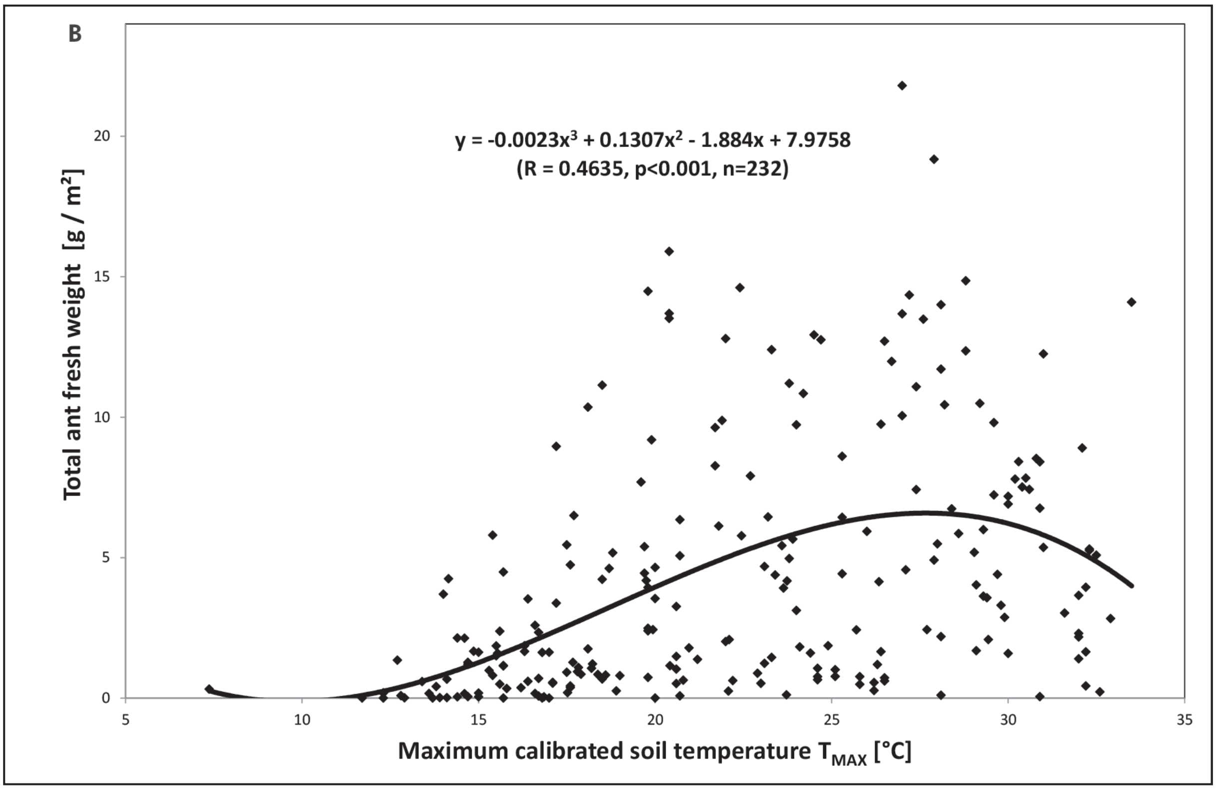
The reaction of ants regarding soil temperature are very clear and Pearson's correlation coefficient is > 0.3926 ($p << 0.001$) in any of the four polynomial descriptions (Figs 8A–9B). For maximum calibrated soil temperature T_{MAX}, ranging in the study plots from 7.4°C to 33.5°C, the maximum species richness of 9.9 species/100 m² and the maximum biomass of 7.2 g/ m² is achieved at 27.5°C (Figs 8A, B). In mean calibrated soil temperature T_{MEAN}, ranging from 5.7°C to 18.4°C, the maximum species richness of 9.7 species/100 m² and the maximum biomass of 6.2 g/m² are achieved at 16.5°C (Figs 9A, B). These data confirm the view that ants are a very thermophilic insect group. The drop of richness and biomass in extremely hot habitats is probably an effect of too high temperatures for many species but also of increasing scarcity of food resources.

It has to be kept in mind that the habitat temperatures in Tabs 6–7 always refer to a standardized measuring depth of 35 mm below soil or substrate surface. It is reasonable to assume that these data give us a good indication of the within-genus ranking of species in thermal behavior. Yet, comparative laboratory investigations to check these field data are nearly lacking. Elmes & Wardlaw (1983) investigated the temperature dependency of developmental time of the last larval stage until pupation in *Myrmica ruginodis*, *M. rubra*, *M. scabrinodis* and *M. sabuleti* (all four species were correctly determined). There was a full rank correlation of the integrated developmental temperatures of Elmes & Wardlaw with both the T_{MAX} and T_{MEAN} data in Tab. 7.

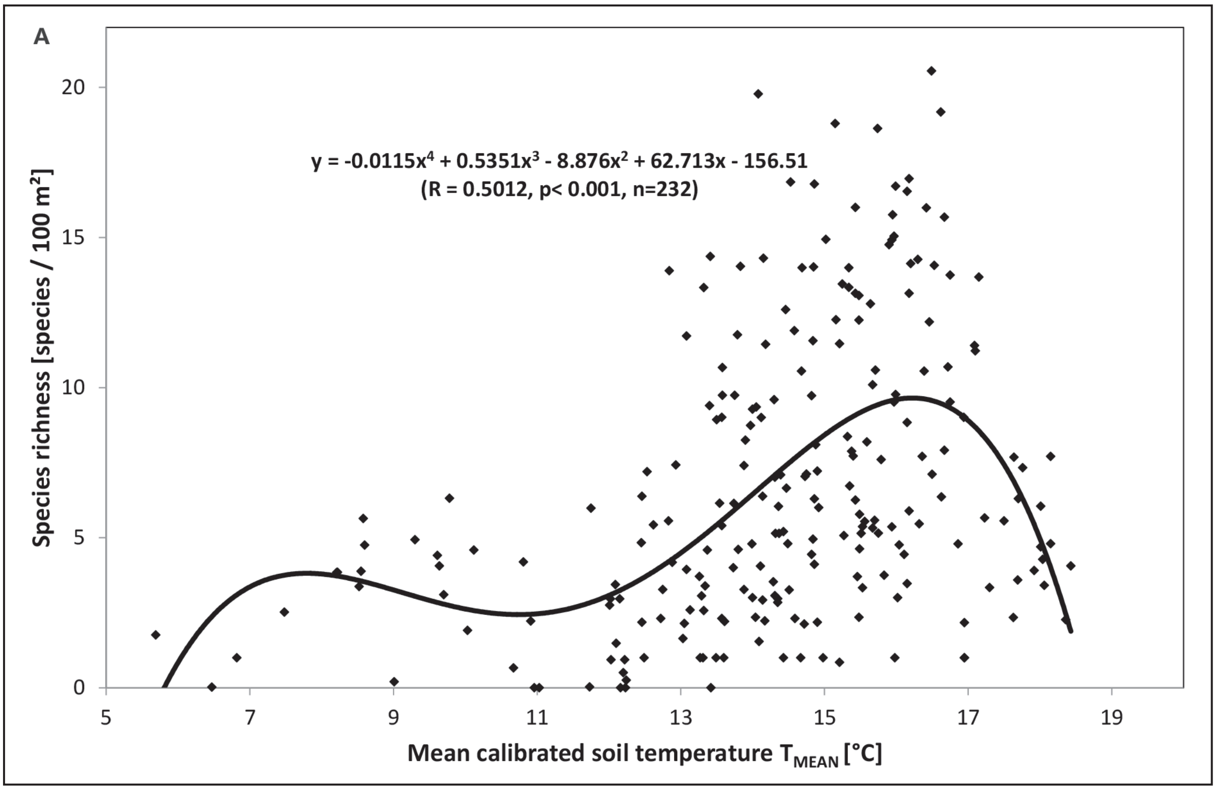
Conclusions on physiological adaptations of species are possible also from field data if T_{MAX} and T_{MEAN} data are considered against the position of the nest centers with the broods relative to surface and if there is knowledge on the temperature behavior of different soil strata in open and woodland habitats (Seifert & Pannier 2007). This shall be explained in four examples. *Temnothorax* and *Leptothorax* species prefer nest sites in 1–3 cm³ large microspaces placed few millimeters above or below the soil surface and there is no option to avoid extreme temperatures by vertical movements within the nest throughout the year. The other ant genera in the study construct much deeper, vertically structured nests allowing a flexible up and down movement to levels with more favorable temperature and moisture conditions. The example of two most different ant species frequently sharing the same macrohabitats shows these between-genus differences: The overall means of T_{MAX} and T_{MEAN} of 28.7 and 15.8°**C** in *Temnothorax interruptus* and of 29.0 and 16.7°C in *Lasius psammophilus* are nearly equal but the thermophysiological behavior differs strikingly. During a standard radiation day in a sandy xerothermous grassland with $T_{MAX} = 29.0$°C , broods of *L. psammophilus* will be concentrated in nest chambers in deeper soil layers where temperatures achieve a maximum of 27°C whereas broods and adults in a *T. interruptus* nest in the moss crust 10 mm below surface will experience a maximum temperature of 41°C – a temperature *L. psammophilus* larvae would not survive three hours. To give a further example, maximum calibrated soil temperatures in 35 mm depth were 30.9°C in study plot SP 122 – a former limestone quarry almost without vegetation and no humus horizon. Broods and adults of *Temnothorax nigriceps* nested here 12 mm below surface between loose-fitting limestone plates. According to micro-thermoelement measurements of 17 July 2006, they survive noon temperatures of at least 50.4°C without any mortality and temperature is expected to drop in this nest spot to 9°C during the coldest days of the summer season. The adaptation of *Temnothorax* and other small ants of the tribe *Formicoxenini* to more or less strong circadian temperature amplitudes evolved in a way that these changes are virtually required for brood development (Buschinger 1973).

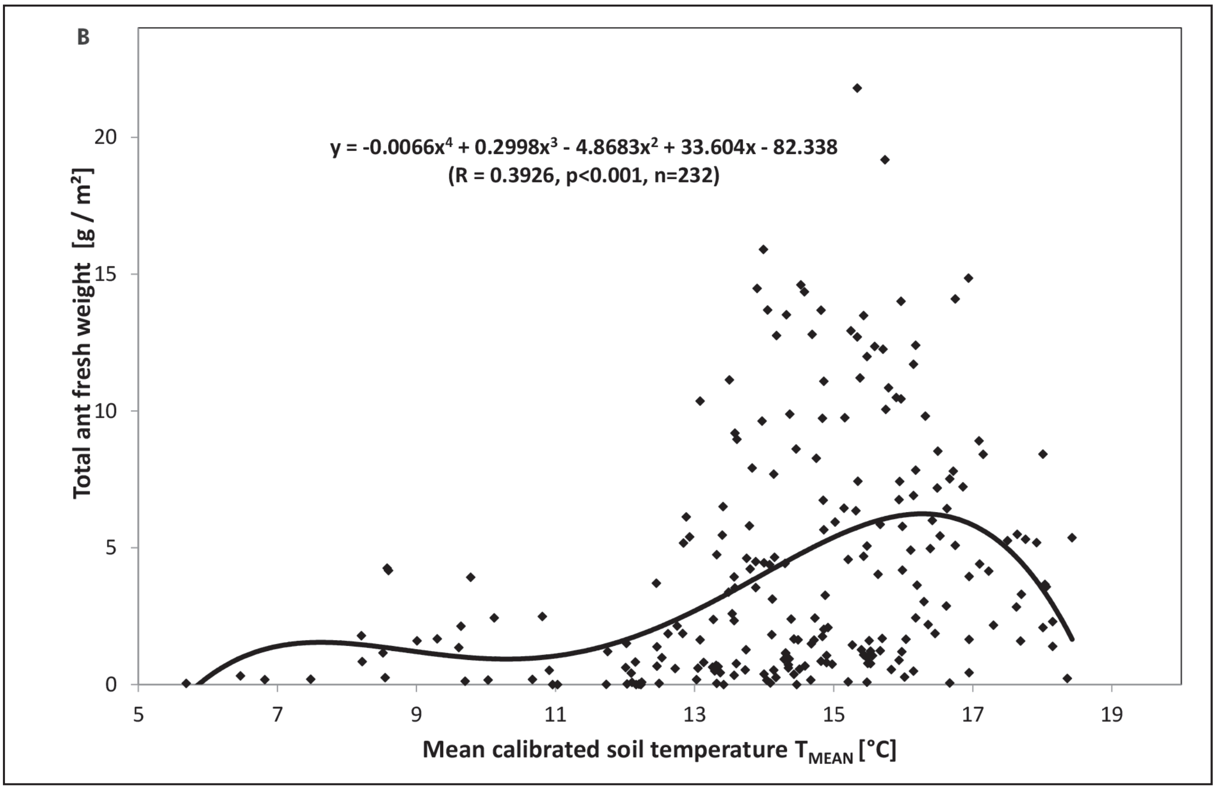
This situation is contrasted by the oligostenothermous species *Stenamma debile* which typically nests in topsoil of shady forests with well developed litter layer. The daily temperature in a typical nest site of this species under a basalt stone in study plot SP 164 varied from only 14.6 to 15.4° (0.8 K) while air temperature outside the forest varied from 18.0 to 36.5°C (18.5 K) as measured 30 May 2003. T_{MAX} and T_{MEAN} are a good indication for the true temperature conditions in *Stenamma debile* nests as their depth usually corresponds to the measuring depth for calibrated temperatures. *S. debile* populations were found within and outside this study in habitats with T_{MEAN} ranging between 12.5 and 17.0°C. Considering that these data are calibrated seasonal means and that mean soil temperatures increase by about 8°C from May to August in such woodland habitats (Seifert & Pannier 2007), one may expect an upper limit of soil temperature of about 21°C in years with normal macroclimatic conditions.





Figures 8. (**A**) Relation of maximum calibrated soil temperature and species richness of ant assemblages. (**B**) Relation of maximum calibrated soil temperature and biomass of ant assemblages





Figures 9. (**A**) Relation of mean calibrated soil temperature and species richness of ant assemblages. (**B**) Relation of mean calibrated soil temperature and biomass of ant assemblages.

Above-average nest temperatures during a critical phase of larval development may cause all diploid larvae to develop into workers and, accordingly, to a complete failure of gyne production – this was observed in the warm season of 1997 in most regions of South Germany (Buschinger 1999). Laboratory investigations (Lawitzky 1988) confirm the oligostenothermy of *S. debile*: The optimum for brood development was 20.5°C at 95% relative air humidity and a temperature increase above 26°C at 95% as well as lowering of air humidity below 80% at 20.5°C caused a rapid emigration to other brood chambers.

A completely different example is *Temnothorax tuberum*. This ant occurs in the geographic area considered here in open, usually stony, xerothermous grasslands from the planar up to the subalpine zone (2300 m, here only nesting below heat-collecting stones at southern slopes). According to my own unpublished taxonomic investigations, the planar and subalpine populations in the reference area (but not outside!) are conspecific and we have to accept a very wide altitudinal range in a single species. Remarkably, there is a rather low niche width in maximum calibrated soil temperatures ($w = 0.39$) but a big one in mean calibrated soil temperatures ($w = 0.79$) over the eleven study plots where *T. tuberum* was found (Tab. 7). These data show that maximum temperatures are probably more important for niche formation in this species than mean temperatures which vary strongly due to the wide altitudinal range.

Increased niche width data found in the present regional study do also correlate with large-scale geographic distributions. *Formica sanguinea* is found in Europe from Sicily to North Cape in warm to very hot, more or less sun-exposed habitats and it shows a very wide factorial niche width for both T_{MAX} ($w = 0.69$) and T_{MEAN} ($w = 0.61$). There is also no morphological indication that this euryoecious species could be split into different species even over the whole range east to Mongolia and Tibet.

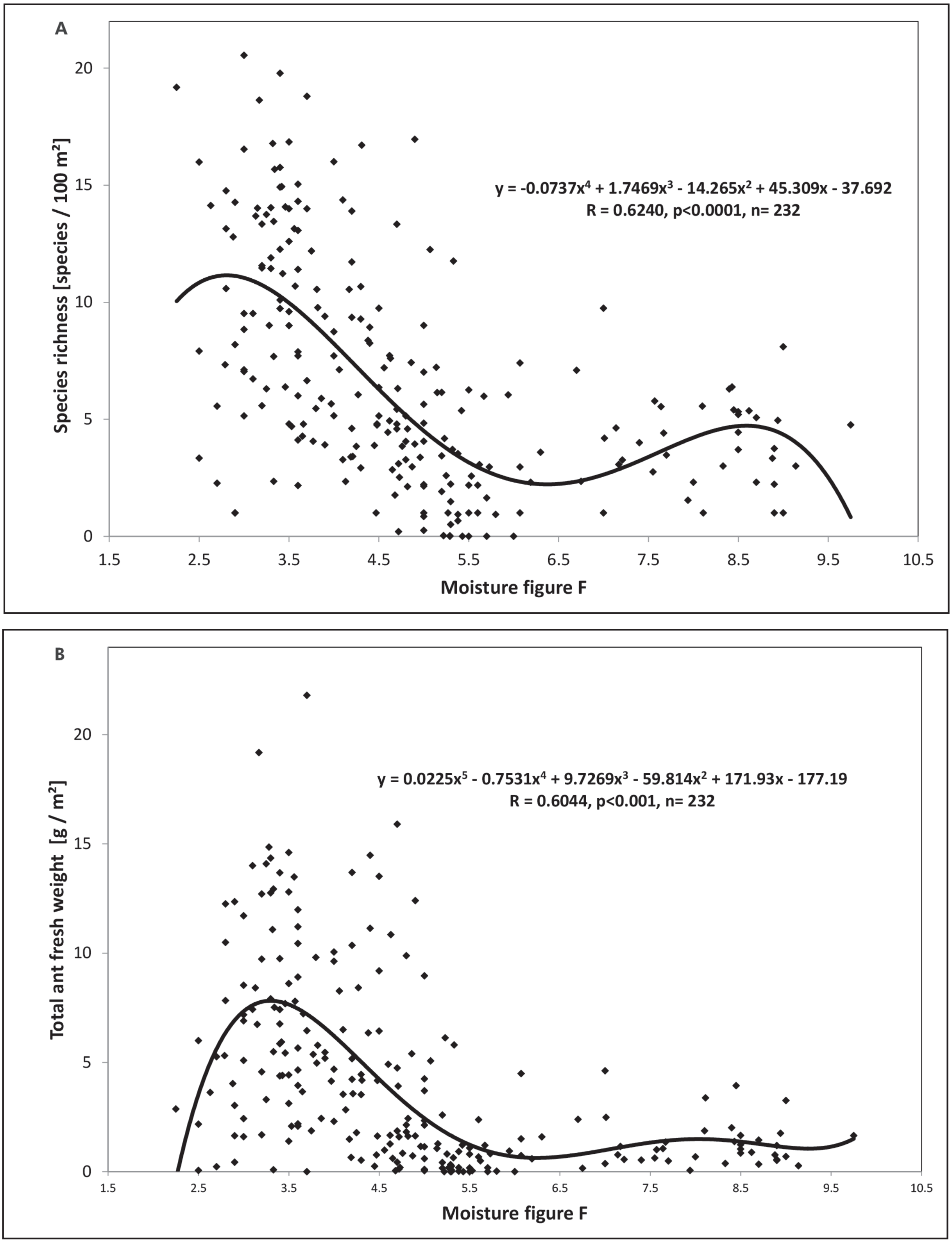
4.2.2 The influence of soil moisture F

The reaction of ants regarding moisture appears to be even stronger than on temperature and it seems to be the most significant among all environmental variables considered in this study (see also section 4.2.12). The data clearly confirm that highest ant species richness and biomass is found in the temperate zone of Europe at dry to very dry soil conditions. The Pearson correlation coefficients for the polynomial descriptions are 0.624 in species richness and 0.604 in ant biomass ($p << 0.001$, Figs 10A, B). The optimum of species richness with $S_{100} = 11.4$ is achieved at a moisture figure of 2.8 corresponding to very dry conditions and the maximum of ant biomass with 7.8 g/m² at a moisture figure of 3.3 corresponding to dry conditions. Above these optima follows a constant decline of both richness and biomass to only 2.3 species/100 m² and 0.6 g/m² achieved at a moisture figure of 6.0. The curves continue with a strong increase of richness to 4.7 species/100 m² achieved at a moisture figure of 8.6 and an insignificant increase of ant biomass to 1.5 g/m² achieved at a moisture figure of 8.1. The increase of richness from mean to very wet moisture conditions is explained by the association of high wetness with high temperatures in the open *Sphagnum*-dominated peat bog habitats where the basically adverse influence of wetness is compensated by optimum thermic conditions provided by the moss pads having T_{MAX} ranging between 24 and 29°C.

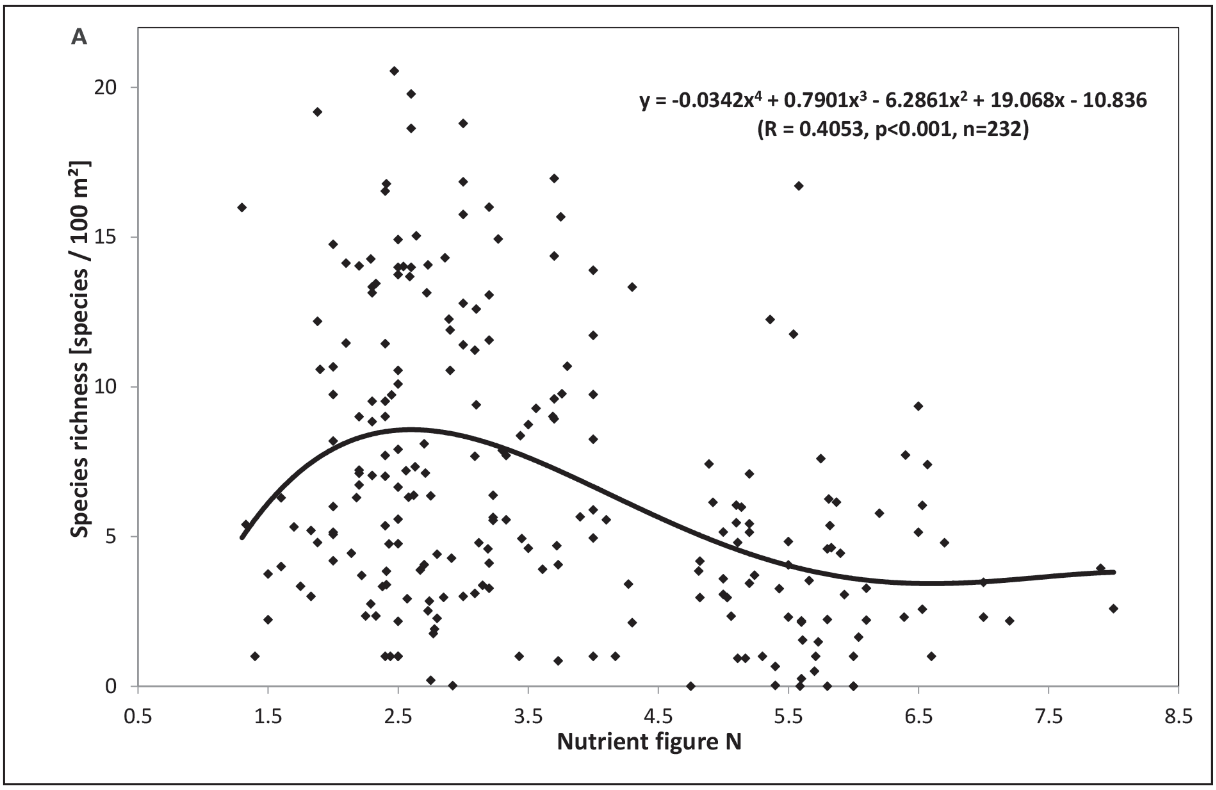
The preferences of individual ant species (Tabs 6 and 7) begin with a mean moisture figure of 1.45 in *Temnothorax interruptus* or of 1.58 in *Lasius myops* and *Ponera testacea,* which are indicator species of extremely dry habitats, and end with a value of 8.47 in *Formica picea* which is characteristic for the wettest parts of peat bogs. Niche width for moisture is generally small over all ant species in the study but there are few exceptions. One of these is *Myrmica scabrinodis* ($w = 0.84$) that may develop extremely dense populations both in the *Sphagnum* pads of quaking bogs and in fresh-dry grassland (compare, for instance, study plots SP 85 and SP 220). The frequency distribution of moisture preference in this species is bimodal but intensive taxonomic studies did not give even a suggestion that *M. scabrinodis* has to be split in two species with most different habitat selection. If evidence for a splitting into two species *M. scabrinodis* Nylander and *M. rugulosoides* Forel could be given some day, both cryptic species will show the same eccentric bimodality (my own unpublished investigations). *Myrmica lonae* represents a similar, but less extreme, case of bimodal habitat selection from dry grassland to boggy habitats with $w = 0.70$ (see also Seifert 2000).

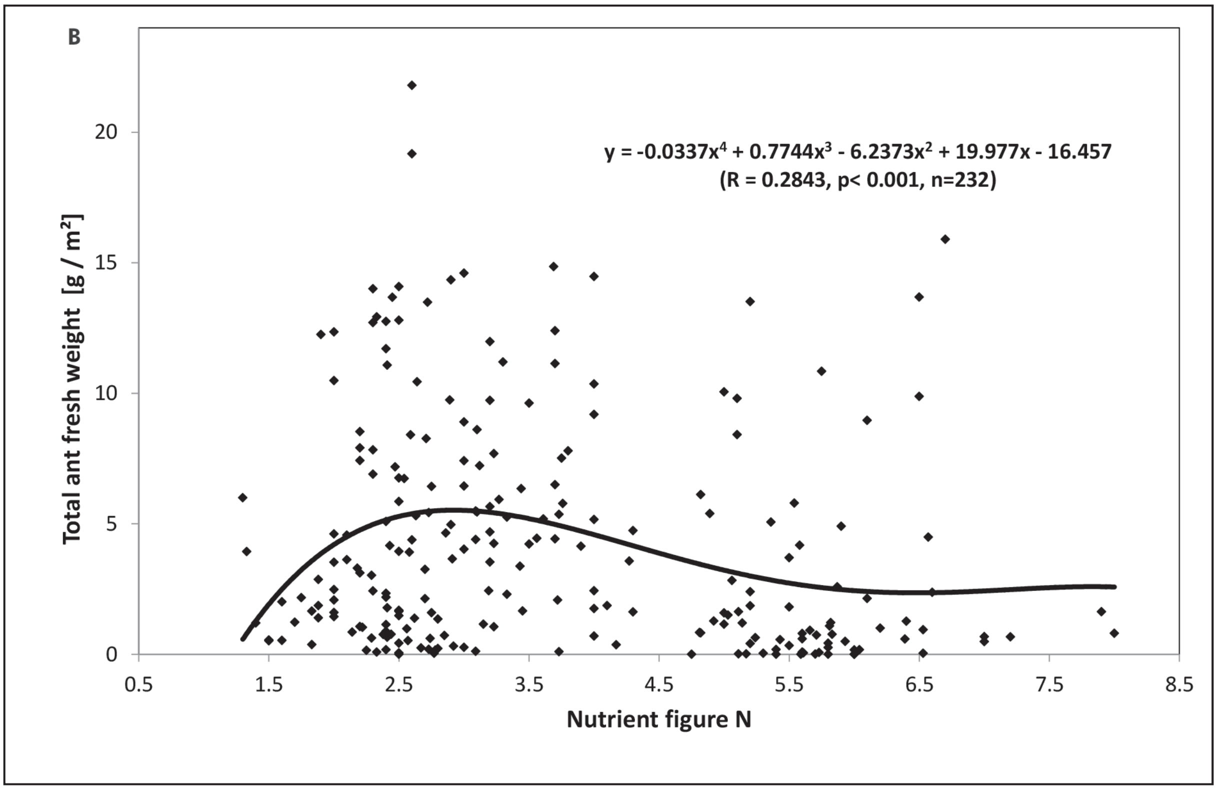
4.2.3 The influence of nutrient figure N

The distribution of ants relative to nutrient figures shows a highly significant picture. The Pearson correlation coefficients for the polynomial descriptions are 0.405 in species richness and 0.284 in ant biomass ($p << 0.001$, Figs 11A, B). Maximum species richness with $S_{100} = 8.5$ is achieved at a nutrient figure of 2.6 and the maximum of ant biomass with 5.5 g/ m² at a nutrient figure of 2.8. Above these optima follows a constant decline of both richness and biomass to 3.5 species/100 m² and 2.5 g/m²



Figures 10. (**A**) Relation of soil moisture F and species richness of ant assemblages. (B) Relation of soil moisture F and biomass of ant assemblages.





Figures 11. (**A**) Relation of nutrient figure N and species richness of ant assemblages. (B) Relation of nutrient figure N and biomass of ant assemblages.

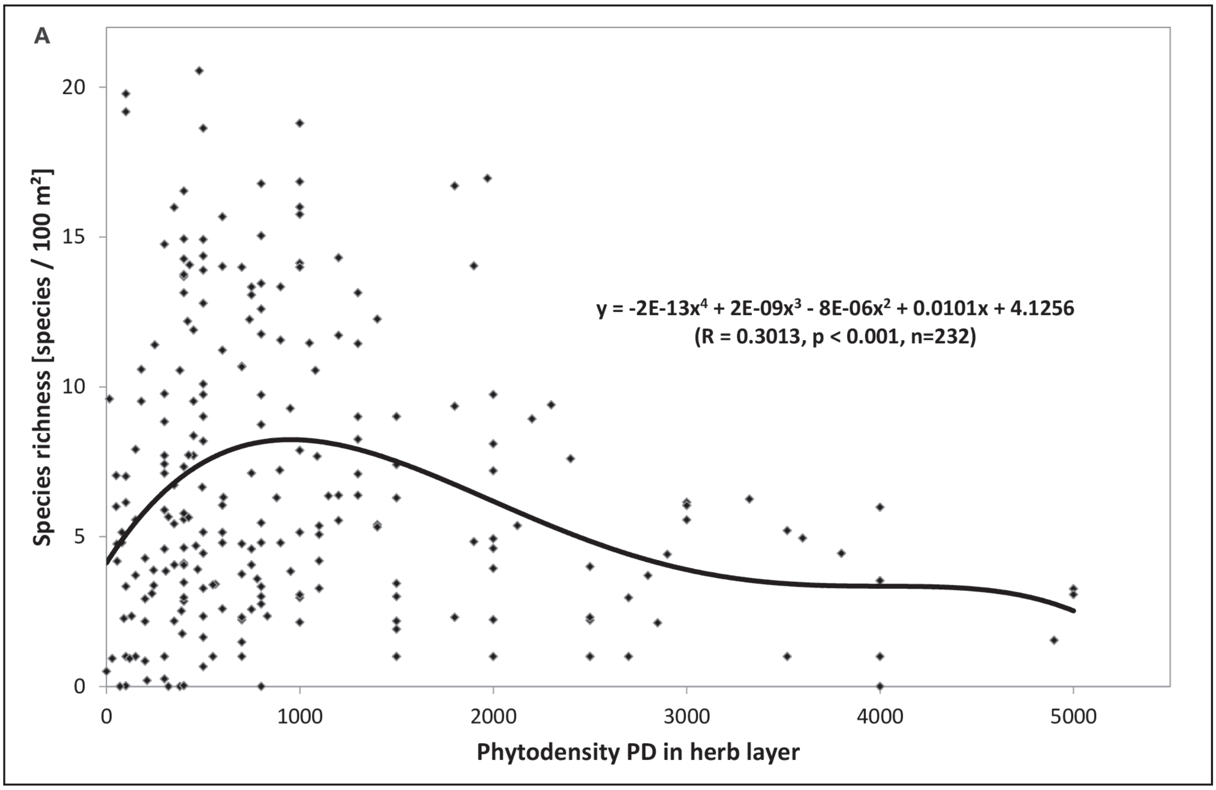
achieved at a nutrient figure of 6.5. These values remain constant up to the maximum nutrient figure of 8.0. There is expectably no direct reaction of ants to plant nutrients such as organic and mineral nitrogen or phosphorus but the ants react to complex habitat factors correlated with nutrient figures. The most important of these factors is increased density and height of herb layer plants caused by eutrophication leading to unfavorable changes in soil temperatures and moisture which decreases ant species richness and biomass. The drop of richness and biomass in extremely nutrient-poor habitats is largely a consequence of the weaker food supply in marginal habitats such as peat bogs or humus-deficient raw soils. Because there are no suggestions of a direct influence of plant nutrients on ants, the relations of particular ant species to this factor are not discussed.

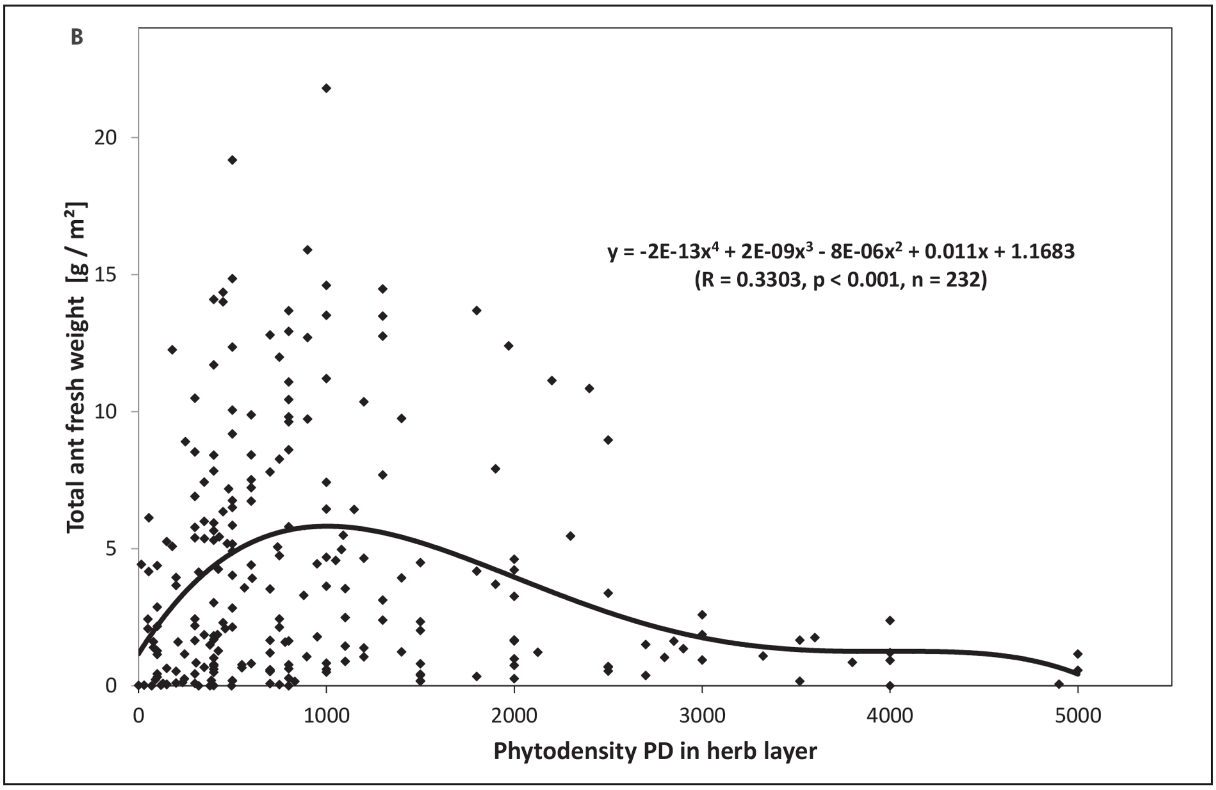
4.2.4 The influence of phytodensity PD

The polynomes describing ant distribution relative to phytodensity PD are very similar in shape to the picture seen in nutrient figure N and highly significant. The Pearson correlation coefficients are 0.301 in species richness and 0.330 in ant biomass ($p << 0.001$, Figs 12A, B). Maximum species richness with $S_{100} = 8.0$ is achieved at a PD value of 950 and the maximum of ant biomass with 5.8 g/ m² at a value of 1000. Above these maxima follows a constant decline of both richness and biomass to 3.3 species/100 m² and 1.4 g/ m² achieved at a PD value of 3500. These values remain constant up to the maximum PD value of 5000. A direct, positive influence of phytodensity on ant species richness and biomass is certainly given for PD values < 900. In this lower range, an increase of phytodensity results in an improvement of food supply for ants while the moisture and temperature conditions remain favorable for most ant species. Yet, when PD grows above the value of 1200, deterioration of the conditions for brood development increasingly outbalances the productivity advantage, causing a decrease of species richness and biomass. Up to a phytodensity of 3500, typically corresponding to a mean height of herb layer of 35 cm and 100 % cover percentage, some species of *Lasius*, *Myrmica* and *Serviformica* can save favorable breeding conditions by increasing the height of their mineral mounds. In the extreme, these mounds may have a height of twice the basal diameter but continuing this constructive measure when the height of the herb layer grows further is beyond the capacity of these ants. The consequences of mean plant height on soil temperatures have been described by Fig. 6 in Seifert & Pannier (2007): In a grassland of 100 % cover, situated at 51°N, 11°E and 300 m altitude, T_{MAX} falls from 23.5°C at a mean height of 5 cm to 16.5°C at 35 cm and to 14.4°C at 50 cm. There are very few ant species which can tolerate phytodensities above 3100 (above PD class 8) – the biggest tolerance is found in *Myrmica rubra*, *M. ruginodis* and *Lasius platythorax*. The unweighted probabilities (see section 3.7.1) of these ants to occur at PD > 3100 and the niche width for factor PD are 15.7 % and 0.76 in *M. rubra*, 10.3 % and 0.75 in *M. ruginodis* and 12.0 % and 0.77 in *L. platythorax* respectively. For comparison: the average of these data in the remaining 83 species within the study system is 0.46 % and 0.38. Apart from these clear influences in particular cases, phytodensity PD seems to have a remarkably weak effect on niche segregation of ants – it occupies the penultimate rank among twelve environmental variables assessed (see section 4.2.12, Tab. 10). This ranking probably indicates that the direct effect of height and density of herb layer plants on ants is moderate – plant structure as such, in its material properties, is not of very high importance for ants. Contrastingly, however, as it is more deeply discussed in section 4.7, PD causes very strong indirect effects by altering epigaean and subterranean temperature and moisture conditions.

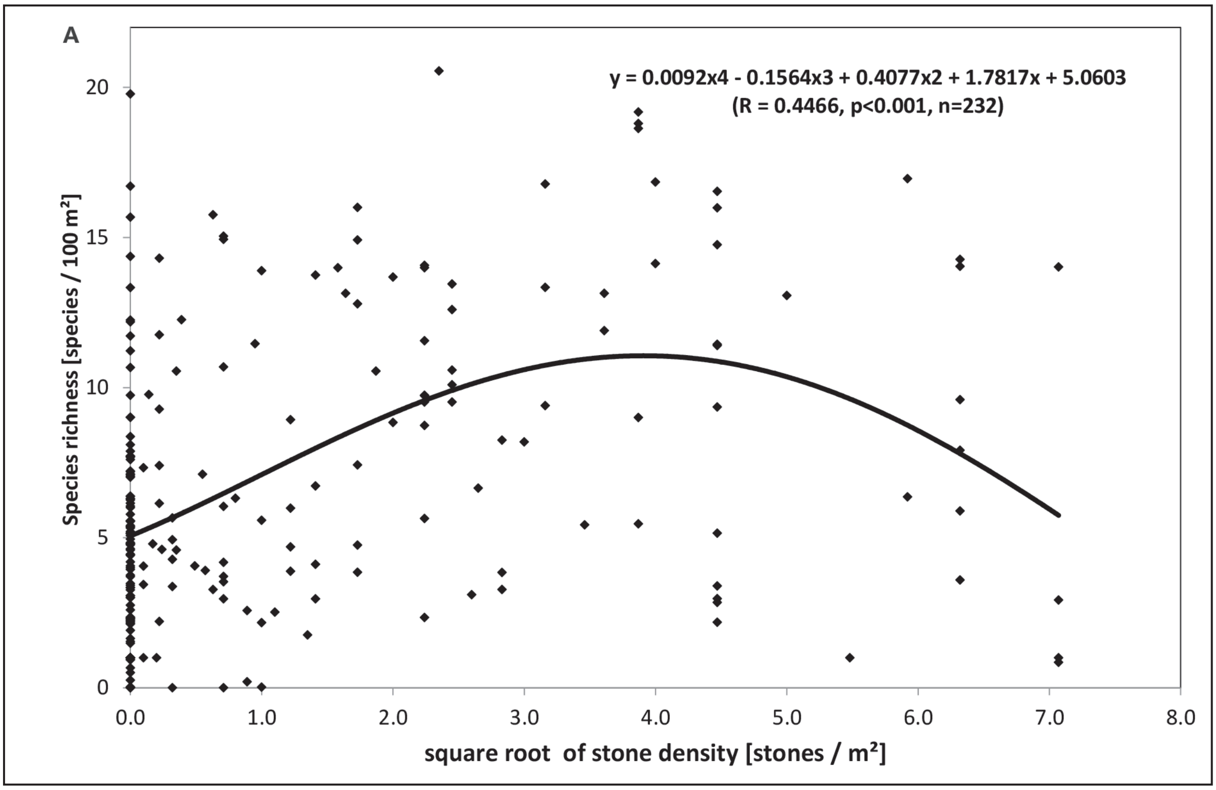
4.2.5 The influence of surface stone density StC

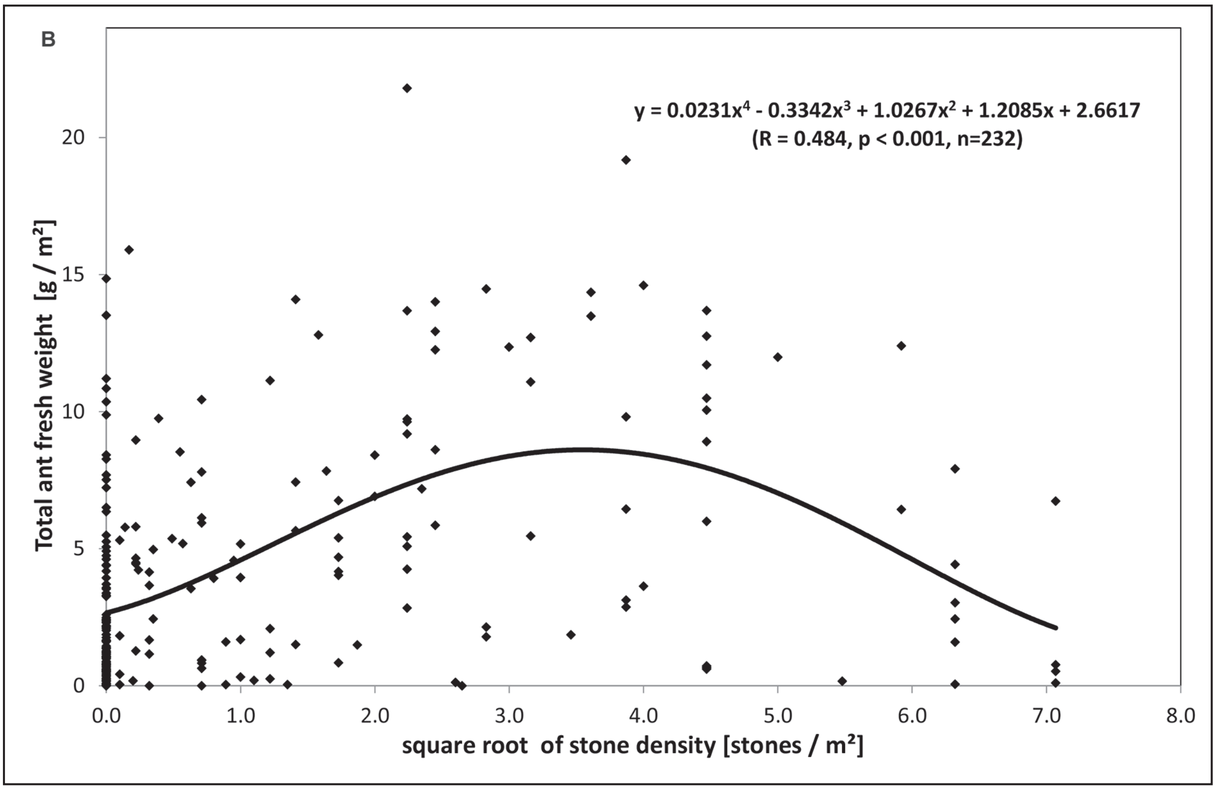
Stones and the hypolithic space have an extraordinary importance as nest microhabitats for ants in open, sun-exposed habitats because of providing favorable thermic conditions for brood development (Seifert 1986). Large stones may also reduce predation by woodpeckers. The polynomes describing ant distribution relative to stone density StC are highly significant – the Pearson correlation coefficients are 0.447 in species richness ($p << 0.001$) and 0.234 in ant biomass ($p < 0.001$, Figs 13A, B). There is a constant increase of species richness and biomass from zero stones to optimum values of species richness of 11.0 species/100 m² at a StC value of 3.9 and of ant biomass with 8.6 g/m² at a StC value of 3.6. These optima translate into a mean distance between stones of 28 and 26 cm and can be explained as the best compromise between supply of nest sites and supply of food sources by primary and secondary producers. When stone density increases above the optima, both species richness and biomass drop to 5.8 species/100 m² and 2.1 g/m² achieved at a StC value of 7.0. This depletion of ant assemblages is explained by a strong reduction of food sources due to poor plant growth in the herb layer – StC values of 7 basically indicate rubble fields with extremely low primary production.



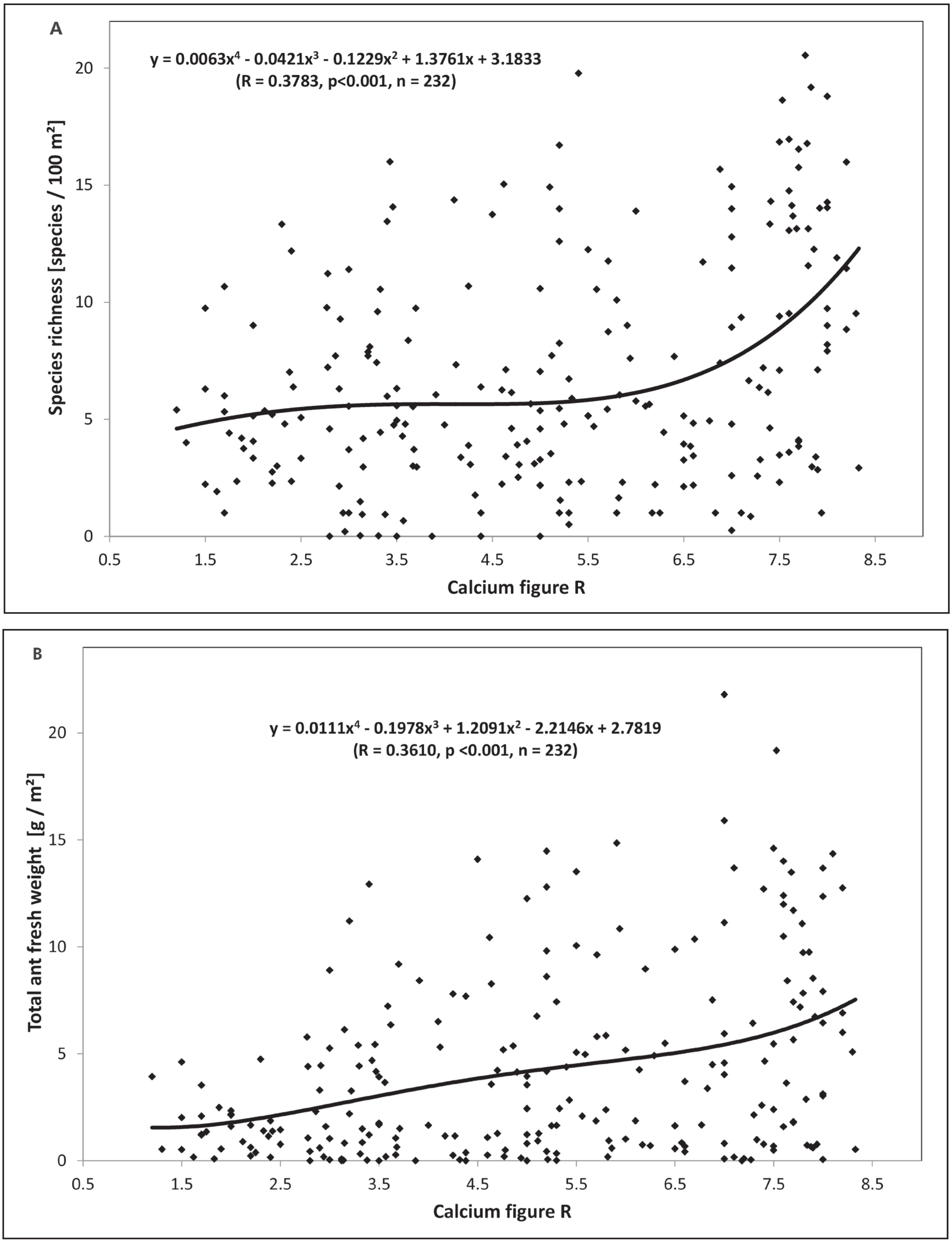


Figures 12. (**A**) Relation of phytodensity in the herb layer and species richness of ant assemblages. (B) Relation of phytodensity in the herb layer and biomass of ant assemblages.





Figures 13. (**A**) Relation of stone density on soil surface and species richness of ant assemblages. (B) Relation of stone density on soil surface and biomass of ant assemblages.



Figures 14. (**A**) Relation of calcium figure R and species richness of ant assemblages. (B) Relation of calcium figure R and biomass of ant assemblages.

4.2.6 The influence of calcium figure R

It was stated in the methods section that Ellenberg's figure R is a better correlated with total soil calcium than with pH values. Yet, both parameters should be discussed here because metabolism and productivity of many soil organisms and plants strongly depend on pH. Ants are expected to be comparably insensitive to increasing soil acidity. Firstly, species with sufficiently large nest populations and long-term stable nest positions accumulate exchangeable cations at the nest spot (e.g. Jacubczyk et al. 1972, Dean & Yeaton 1993) which increases the buffer capacity of brood chambers – a general trend seems to be that intranidal pH is increased in acidic soils and decreased in basic soils (Dlussky 1967, Frouz et al. 2003, Frouz & Jilkova 2008). Secondly, the broods of weakly populous ants nesting in closed microspaces such as acorns, nuts or snail shells – typically *Temnothorax* species – should be well protected from adverse soil chemistry. Thirdly, and perhaps representing the most important factor, permanent brood care with licking and cleaning of eggs and larvae will certainly improve brood survival under conditions of chemical stress.

The data of the study show that species richness remains at a constantly low level of about 5 species/100 m² at calcium figures between 1.2 and 6.5 but then increases strongly to 12.2 species/100 m² achieved at a calcium figure of 8.3 (Fig. 14A). The polynomial description of this relation is highly significant ($r = 0.378$, $p \ll 0.001$) and the strongly increased richness data for calcium figures above 6.5 compared to those at lower figures is confirmed by an ANOVA ($F_{1,230} = 423.7$, $p \ll 0.001$). Ant biomass shows a constant, quasi-linear relation against the calcium figure: it grows from 1.5 g/m² at a calcium figure of 1.2 to 7.6 g/m² at a calcium figure of 8.3 (Fig. 14B). The polynomial description is highly significant ($r = 0.361$, $p \ll 0.001$).

Giving a reasonable explanation for these two clear relations is difficult. A strong direct effect of pH and/or soil calcium on physiology of ant broods seems rather unlikely for the reasons mentioned above. Looking at the data, it becomes clear that the many study plots with very rich ant assemblages on raw or protorendzina soils on limestone ground in Thüringen and Sachsen-Anhalt are responsible for the strong increase of species richness for calcium figures > 6.5. I suppose indirect, correlated effects of temperature and moisture connected with xerothermous limestone soils as most likely explanation for the apparently clear relation of richness and biomass to calcium figures. The high correlation of calcium figure with maximum soil temperature ($r = 0.217$, $p < 0.001$) and soil moisture ($r = 0.375$, $p \ll 0.001$) found over all 232 study plots supports this idea.

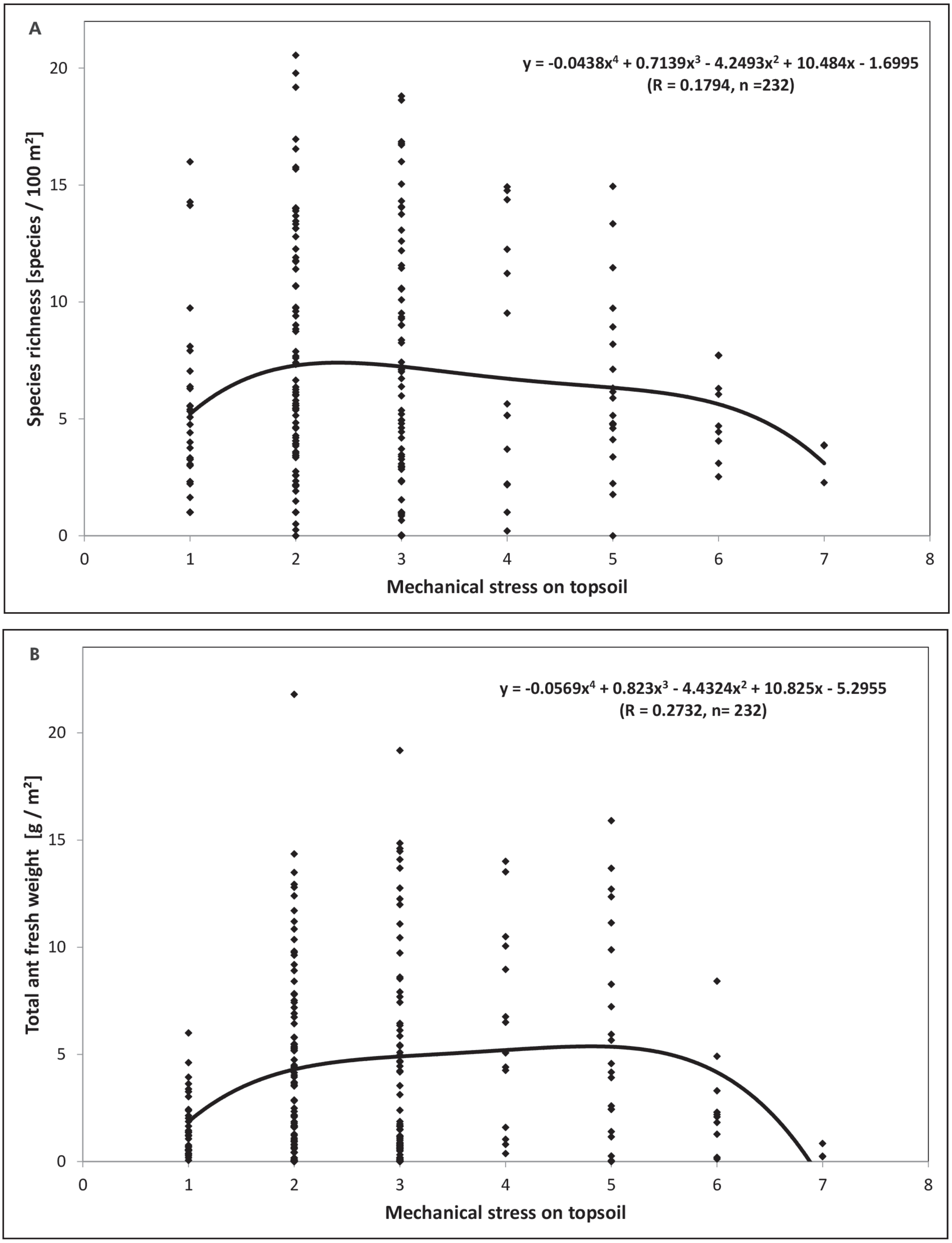
4.2.7 The influence of mechanical stress M

The assessment of the influence of this factor on ant assemblages suffers from the low number of study plots in the upper two stress classes 6 and 7. The polynomial description of the relation between species richness and mechanical stress on topsoil shows a weak correlation ($R = 0.1794$) and significance calculations appear problematic because the distinction of only seven different M values caused a strong reduction of degrees of freedom (Fig. 15A). Richness remains rather constant for M classes 2–5 but there is a decrease in class 1 and probably the upper two classes. The behavior of biomass relative to mechanical stress is similar and somewhat clearer ($R = 0.2732$) but we have the same problem with degrees of freedom.

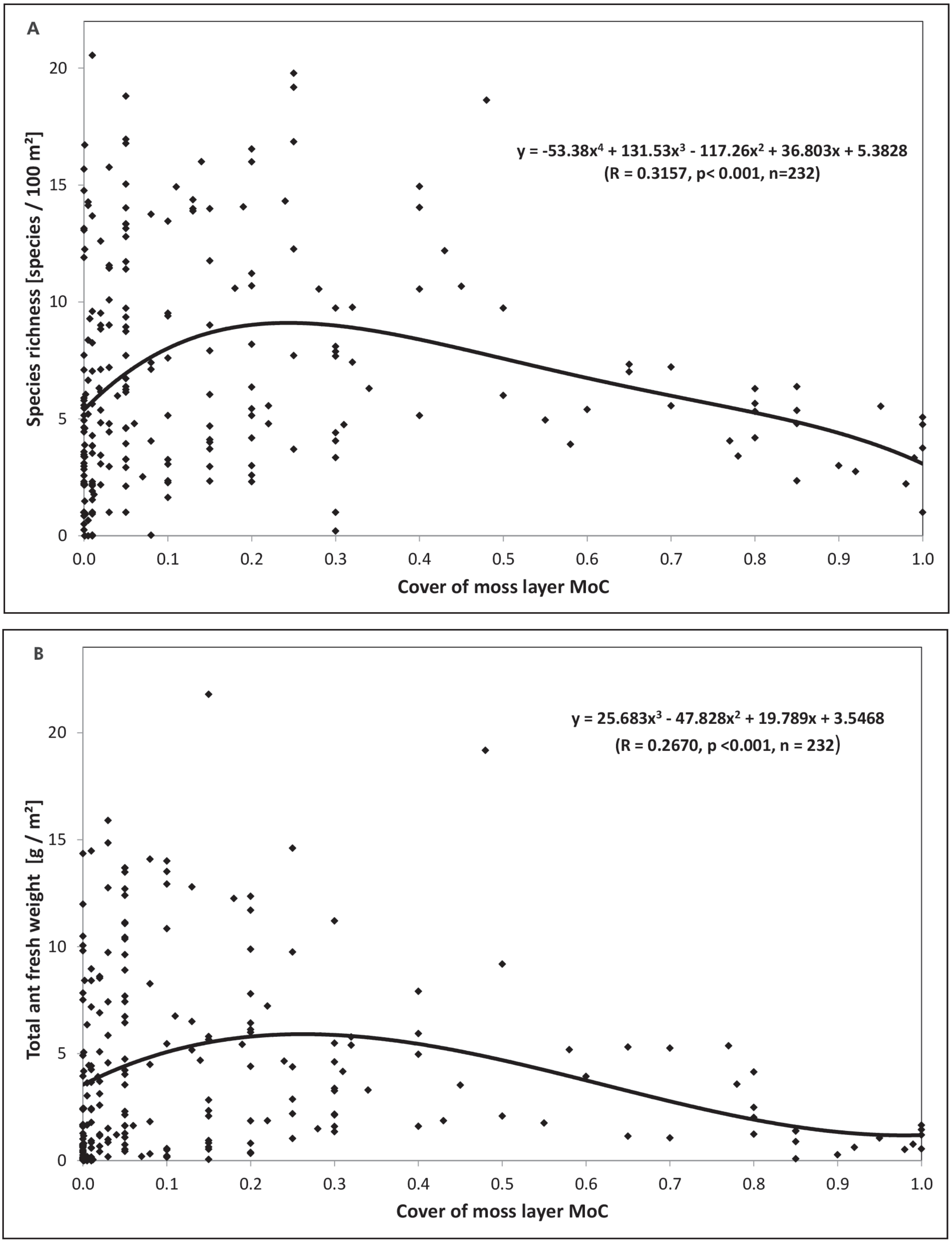
The drop of richness and biomass in M class 1 (meaning zero stress) is no effect of mechanical stress but an expression of the low productivity or food supply in habitats falling into this class. These habitats are quaking bogs or steep rocky scarps with zero human management or movement and no motivation or possibility for larger mammals to walk or feed there. On the other hand, the decline of biomass in the upper two stress classes 6 and 7 compared to classes 2–5 is certainly a direct influence of this factor if we look at the following data. The mean temperature (T_{MAX}), moisture (F) and phytodensity (PD) figures of the study plots in stress classes 6–7 are 25.7°C, 4.16 and 406 and those of stress classes 2–5 are 22.2°C, 4.51 and 977. Multiplying the influence of these three most influential factors on biomass (Figs 8B, 9B, 12B), study plots in stress classes 6–7 are predicted to have a higher biomass than those in classes 2–5. Mechanical stress at the upper end of the scale, accordingly, should directly cause a depression of biomass development.

Some outstanding aspects of behavior of species or genera regarding mechanical stress shall be considered here. First of all, the high tolerance of *Myrmica* species regarding this factor is remarkable. Considering only species present on more than five study plots and using unweighted data, niche width for factor M is 0.600 ± 0.185 for 13 *Myrmica* species and 0.438 ± 0.172 for 46 species of other genera (ANOVA, $F_{1,57} = 8.70$, $p < 0.005$). Furthermore the mean values of M are significantly higher in *Myrmica* with 3.12 ± 1.09 compared to the other species with 2.65 ± 0.49 (ANOVA, $F_{1,57} = 5.09$, $p < 0.028$). A typical example is *Myrmica rugulosa* that reproduces in habitats such as walkways, picnic places, strongly trampled grassland on beaches or clip lawns.

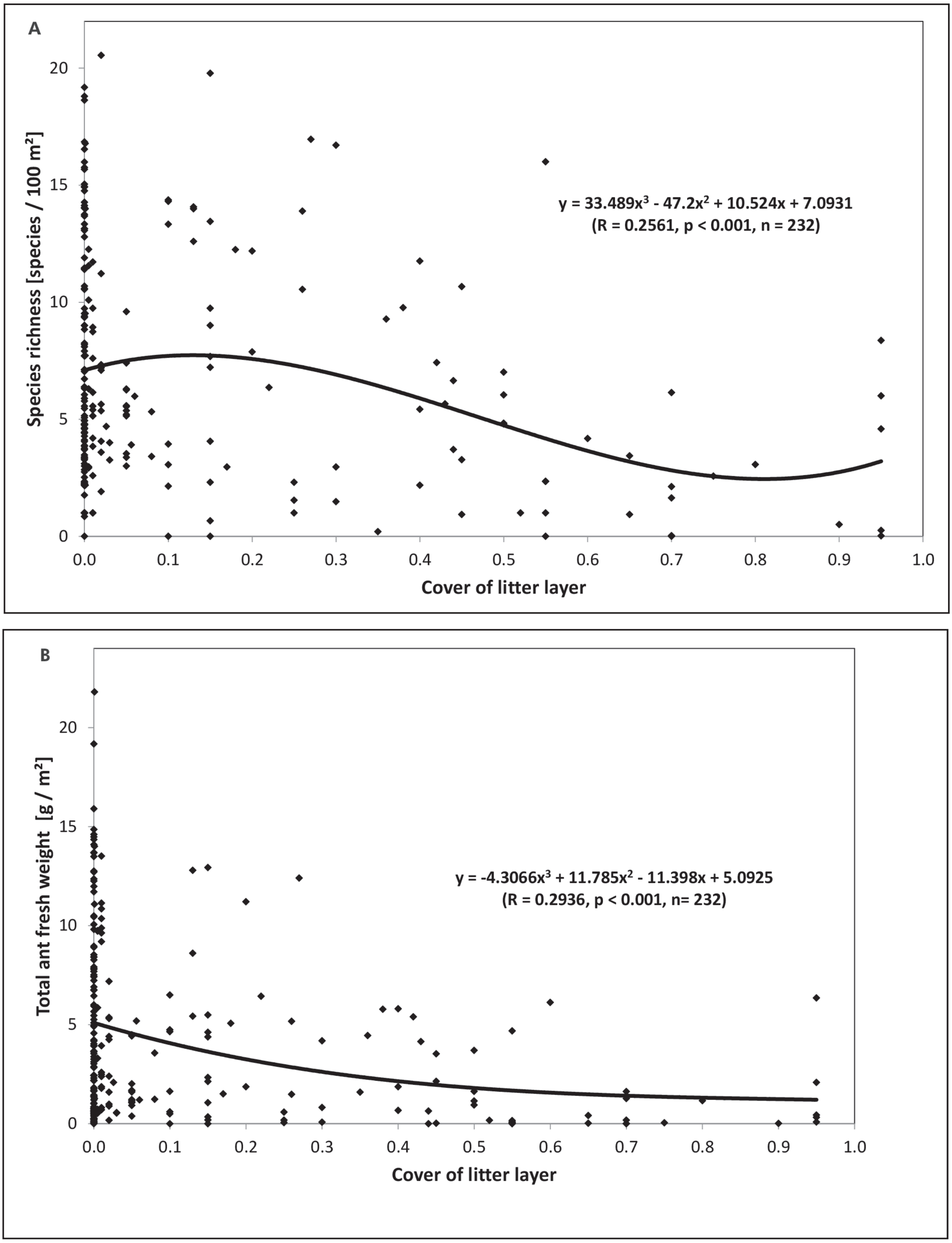
Different tolerance against mechanical stress may also cause an intrageneric niche segregation. It is a general picture all over Central Europe (and within this study) that *Lasius psammophilus* replaces (competes out) *Lasius*



Figures 15. (**A**) Relation of mechanical stress on topsoil and species richness of ant assemblages. Significance level p was not calculated here due to problems caused by reduction of degrees of freedom. (**B**): Relation of mechanical stress on topsoil and biomass of ant assemblages. Significance level p was not calculated here due to problems caused by reduction of degrees of freedom.



Figures 16. (**A**) Relation of moss cover and species richness of ant assemblages. (**B**): Relation of moss cover and biomass of ant assemblages.



Figures 17. (**A**) Relation of litter cover and species richness of ant assemblages. (**B**) Relation of litter cover and biomass of ant assemblages.

niger in permanent xerothermous grasslands on sandy ground. Yet, in sandy xerothermous grasslands in military training areas, *L. niger* dominates over *L. psammophilus* in just those patches subject to strong mechanical stress on topsoil caused by movements of heavy vehicles or infantry (see study plots 125, 131, 157, 158, 163). The main reason for this suppression of *L. psammophilus* in a basically adequate habitat are deleterious soil compaction effects on its major food source – root-sucking aphids which are usually concentrated in the upper 15 cm of soil. The larger flexibility in food selection and relative independence from subterranean trophobionts allows *L. niger* to become dominant here. The different tolerance of mechanical stress in *L. psammophilus* and *L. niger* finds its expression in mean M values of 2.81 in the former and 3.56 in the latter.

4.2.8 The influence of moss cover MoC

The polynomial descriptions of the relation of moss and lichen cover to species richness ($R = 0.316$, $p < 0.001$, Fig. 16A) and biomass ($R = 0.267$, $p < 0.001$, Fig. 16B) are highly significant but an explanation appears difficult as a direct influence of MoC on ants is difficult to separate from correlated effects of other factors. Moss as such has little meaning for ants from a nutritional point of view. The material properties of moss, considering all pros and cons, do also not favor it as a means for nest construction. The significant portion of cut-off moss particles often seen in *Formica* mounds in peat bogs is largely explained by the easy availability and lack of other materials. However, living moss in particular is important through its thermic effects on nest climate in sun-exposed habitats. This becomes most obvious in *Sphagnum* stands in open quaking bogs. Moss is always an excellent absorber of solar energy and the high moisture content within the moss pad and the high water table generate a big thermal capacity of the upper 15 cm of this particular habitat. Sun-exposed quaking bogs behave like a dark water body with fixed strata – i.e., without heat exchange by convection currents. This results in higher average temperatures and a slower temperature drop compared to open and dry sun-exposed soils of mineral material when clouds screen the sun. *Sphagnum* pads in open peat bogs have a guiding value T_{MAX} of 25.5°C for a latitude of 51°N, a longitude of 11°E and an elevation of 300 m when calibrated against the average climatic background of the years 1977–2006 (Seifert & Pannier 2007) – this is near to the thermal optimum for ants (see section 4.2.1).

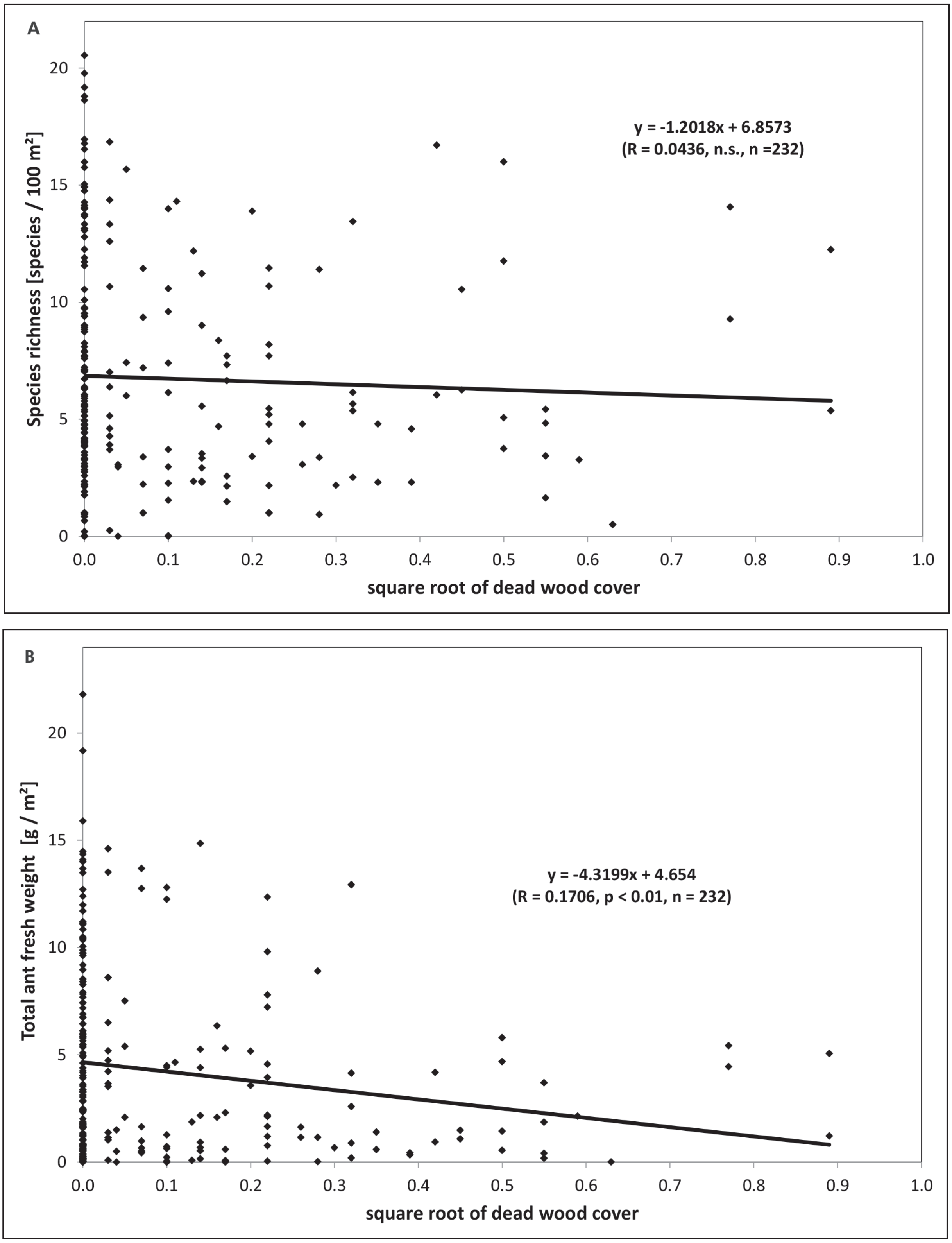
Coming back to the data suggested by Figs 16A and 16B, a flat optimum for both species richness and biomass appears to be at MoC values of about 0.25 and the pessimum occurs at MoC values > 0.7. The latter data always refer to weakly productive and comparably species-poor *Sphagnum* stands in peat bogs. Regarding species richness, the thermal advantage provided by *Sphagnum* mosses in peat bogs can compensate to a certain degree for disadvantages caused by low habitat productivity and low structural diversity – richness drops here for MoC 0.9 to about 48 % of the maximum value achieved at a MoC value of 0.25. This thermal advantage has no effect on biomass that decreases at MoC values of 0.9 to 20 % of the maximum because very low habitat productivity is here the limiting factor.

4.2.9 The influence of litter layer LiC

Despite significant development of litter in some open habitats such as *Calluna*, *Vaccinium*, *Erica* or *Calamagrostis* stands, the cover of litter layer is very strongly and linearly correlated with the cumulative cover of the shrub and tree layer ($r = 0.725$, $p \ll 0.001$, $n = 232$). The consequence is that the synergistic action of two factors – (a) shading by shrubs and trees and (b) the thermal insolation of soil by a litter layer – prevents the warming of top soil by solar radiation. The strong decrease of soil temperatures in test plots with much litter is indicated by a very close correlation of LiC and T_{MAX} ($R = 0.549$, $p \ll 0.001$). In other words, the significant decrease of both species richness ($R = 0.256$, $p < 0.001$) and biomass ($R = 0.294$, $p < 0.001$) with growing litter cover shown by the polynomial functions (Figs 17A, B) is largely due to thermal effects. Positive counter-effects of litter development by providing accessory food sources for ants with high foraging activity in this stratum cannot compensate significantly because such ant species are not abundant in Central Europe (Tabs 8 and 9) and have a comparably low biomass (*Myrmecina*, *Leptothorax*, *Temnothorax*, *Myrmica*). It should be mentioned in this context that supercolonies of mound building wood ants of the *Formica rufa* group may develop a very high biomass in forest habitats with strong litter cover. Yet, the investigation schedule of this study with S-areas < 100 m² and Q-areas usually < 250 m² did not allow a reasonable recording of these ants – even more, sampling in the territory of *Formica rufa* group supercolonies was clearly avoided because there was suppression of other ant species.

4.2.10 The influence of dead wood cover DWC

The complete failure to demonstrate any relation of dead wood cover on ant species richness or biomass (Figs 18A, B) appears surprising in the first instance since



Figures 18. (**A**) Relation of dead wood cover and species richness of ant assemblages. (**B**) Relation of dead wood cover and biomass of ant assemblages.

dead wood is crucially important as nest habitat at least for canopy ants (Seifert 2008). The negative result for epigaean ants does also not change if extreme habitats with dead or heavily smoke-damaged spruce forest with masses of dead wood on ground (SP 168–170, SP 172–174, SP 176, SP 177) are excluded from analysis or if open and woodland habitats are considered separately. The main reason for this unexpected result is apparently that only 10% of the ant species in the system show a clear preference for wood as nesting substrate (Tabs 8 and 9) and that only 4% of epigaean ants do really need dead wood. Other ground species with rather frequent nesting in dead wood can use other microhabitats without suffering a disadvantage. There is probably also a problem with the simple investigation method: the protocol required recording of the total cover percentage of dead wood only but not observing number, dispersion and mean size of the items. Many rather small pieces of dead wood, well dispersed over the ground and summing up to 1% of cover may increase species richness (and perhaps also biomass) much more than few large items summing up to 3%. Furthermore, there was a poor differentiation within just the lowest DWC range where some effects on ants are likely to occur.

4.2.11 Comparing niche dimensions of closely related species

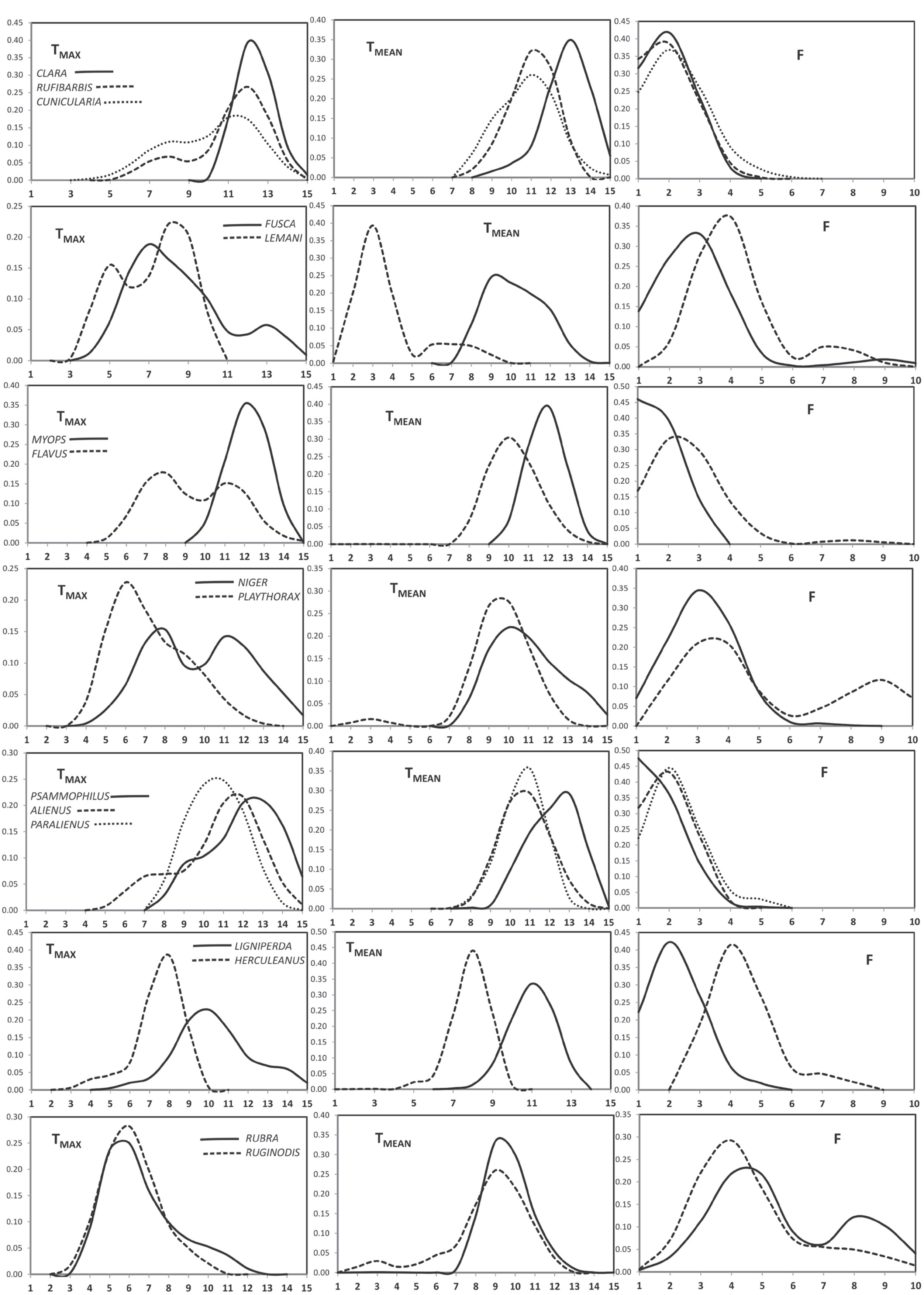
The niche hypothesis followed here implies the extreme that two species may form almost equal fundamental niche spaces in a sympatric area but simultaneously show a close-to-zero overlap of their realized niche spaces. This mutual spatial exclusion may be generated along the axes of environmental factors recorded in this study – then slightly different adaptations, for example to temperature or moisture, may explain the segregation of realized niche spaces. Yet, the true vectors for this exclusion remain often unclear and are frequently found in ethological aspects – interspecific behavior in particular (Seifert 1987). Clarity is provided here only by intimate knowledge of the specific biology and much direct observation in the field. Anyway, it seems interesting to see if relations to particular environmental axes may offer partial explanations for niche segregation in closely related ants.

A contrast between highly similar fundamental niche spaces and low spatial coexistence becomes more probable the closer related the species are (see section 4.5). Figs 19 and 20 show the smoothed frequency distributions of pairs or triples of 16 closely related species over the six niche dimensions T_{MAX}, T_{MEAN}, F, N, M and LiC. There are very weak differences of fundamental niche spaces in the triple *Formica clara*, *F. rufibarbis* and *F. cunicularia*. *F. clara* is exposed as the most xerothermophilous species (Fig. 19, 1st row) which is in agreement with the large-scale geographic distribution pattern: it clearly dominates over the other two species in the southern zone of continental steppes from Europe to Siberia (Seifert 1997, Seifert & Schultz 2009). A better adaptation of *Formica clara* to hot conditions is obvious (see also Tab. 6). On the other hand it appears doubtful if the higher probability of *F. clara* to occur on plots with stronger mechanical stress on topsoil M (Fig. 20, 1st row) is really a consequence of a better adaptation to this factor and not caused by other, correlated factors. The smaller peak at large figures of M is explained by a very strong dominance of *F. clara* on military training areas in the former East Germany.

An interesting disparity between maximum calibrated soil temperatures T_{MAX} and the calibrated seasonal mean T_{MEAN} is observed in the closely related species *Formica fusca* and *F. lemani*: mean soil temperatures differ strikingly with 14.8°C in *fusca* and 8.4°C in *lemani* but the maxima during standard radiation days are more comparable with 22.1°C in *fusca* and 19.4°C in *lemani* (Tab. 6; Fig. 19, 2nd row). It is predictable that laboratory experiments will show a much faster larval development at low temperatures in *F. lemani* but only weak interspecific differences in the upper ranges of foraging temperatures. It appears doubtful also in this species pair if there is a different adaptation to mechanical stress as Fig. 20 suggests – a big fraction of *F. lemani* was found in strongly grazed alpine cattle pastures but preferentially in areas where the nests were protected against trampling damage by sufficiently large cover stones.

Obvious differences are visible in the sibling species *Lasius myops* and *L. flavus* with the former being the much more xerothermophilic species (Tab. 6; Fig. 19, 3rd row). These data clearly indicate different species-specific adaptations to physical factors. The different ecological adaptations of both species have been thoroughly discussed by Seifert (1983) who quoted that soil moisture was probably the most segregating factor. The lower M values in *L. myops* are explained by the simple fact that xerothermous habitats with sparse herb layer were pastures for only sheep and goats but in no case for the much more heavy cattle. The situation in the study plot system provides no test for resistance of *L. myops* against mechanical stress. The high probability

► **Figure 19**. Relations of 16 closely related ant species to the niche axes T_{MAX}, T_{MEAN} and F. Only species names in capital letters are given. The full names are *Formica CLARA*, *Formica RUFIBARBIS*, *Formica CUNICULARIA, Formica FUSCA*, *Formica LEMANI*, *Lasius MYOPS*, *Lasius FLAVUS, Lasius NIGER*, *Lasius PLATYTHORAX*, *Lasius PSAMMOPHILUS*, *Lasius ALIENUS*, *Lasius PARALIENUS*, *Camponotus HERCULEANUS*, *Camponotus LIGNIPERDA*, *Myrmica RUBRA* and *Myrmica RUGINODIS.*


T_{MAX}
CLARA
RUFIBARBIS
CUNICULARIA
T_{MEAN}
F
T_{MAX}
FUSCA
LEMANI
T_{MEAN}
F
T_{MAX}
MYOPS
FLAVUS
T_{MEAN}
F
T_{MAX}
NIGER
PLAYTHORAX
T_{MEAN}
F
T_{MAX}
PSAMMOPHILUS
ALIENUS
PARALIENUS
T_{MEAN}
F
T_{MAX}
LIGNIPERDA
HERCULEANUS
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RUGINODIS
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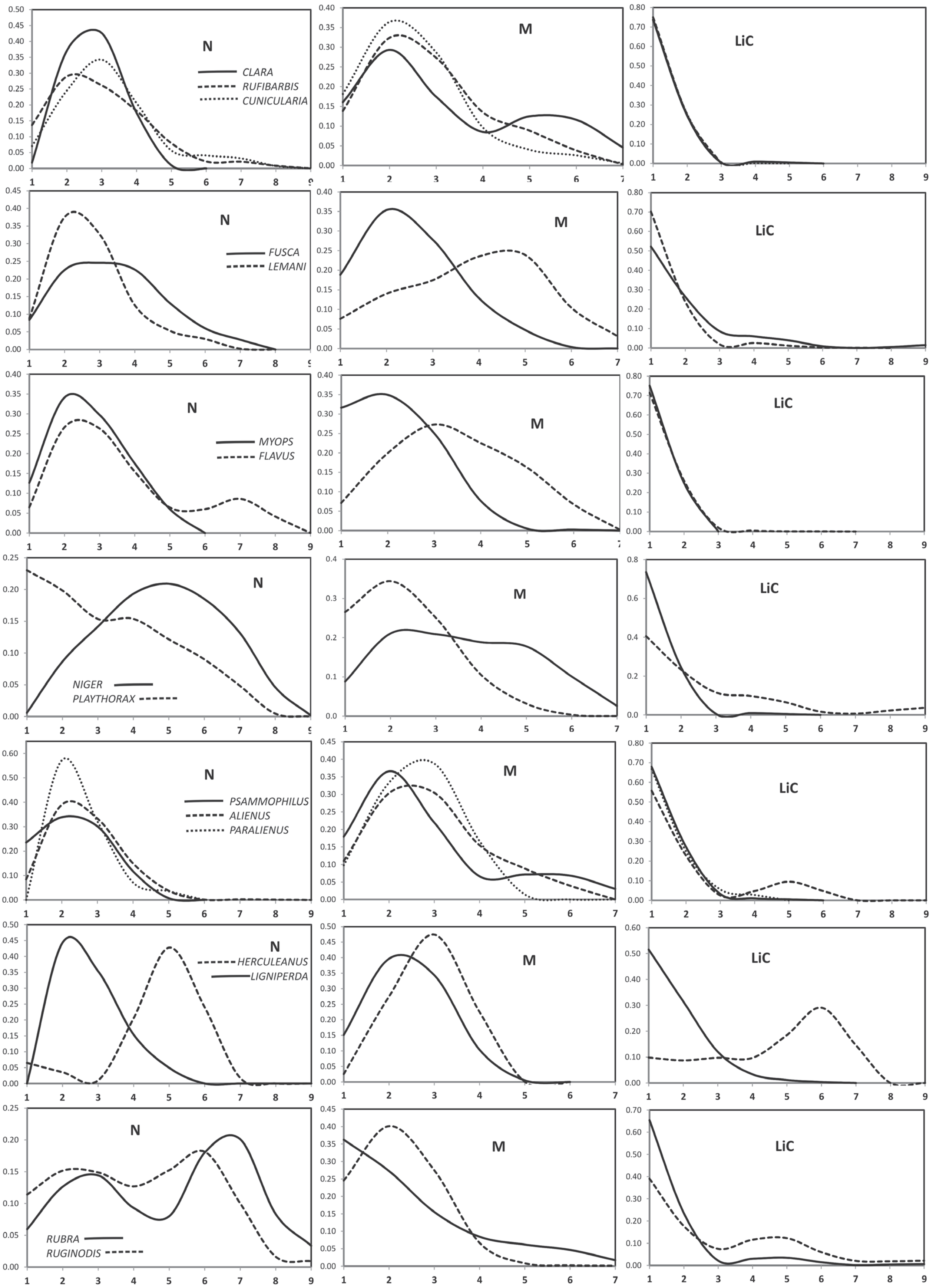
N
CLARA
RUFIBARBIS
CUNICULARIA
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LiC
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FUSCA
LEMANI
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LiC
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MYOPS
FLAVUS
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LiC
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NIGER
PLAYTHORAX
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ALIENUS
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of *L. flavus* to occur in medium-scale M classes signals at least some direct adaptation to this factor (Fig. 20, 3rd row. The mounds of these ants on cattle pastures show, in strong contrast to those of *L. niger*, a remarkably stable surface due to a very solid, compacted layer of root turf built up by the plants growing on mound surface. This undoubtedly reduces brood and adult mortality by cattle trampling.

The different ecological adaptations in *Lasius niger* and *L. platythorax* were already reported and discussed by Seifert (1991). The significant differences between both sibling species shown in Figs 19 and 20 are a reflection of the very different selection of main habitats: this is woodland and bogs in *L. platythorax* and rural and urban open habitats in *L. niger*. The deciding species-specific adaptation leading to this habitat segregation is most probably the higher tolerance of low temperatures and of high moisture in *L. platythorax* whereas the differences in the factors N, M, LiC should largely represent correlations to main habitat types rather than indicating specific adaptations to these factors.

Within the triple of the closely related species *Lasius psammophilus*, *L. alienus* and *L. paralienus*, the first shows the highest and the last the lowest xerothermy but the differences over all factors are very weak. The small peak of *L. alienus* (Fig. 20, 5th row in LiC) is a reflection of occurrence at sunny margins of broad-leafed woodland.

Camponotus herculeanus differs from its sister species *C. ligniperda* by its clearly lower xerothermy (Fig. 19, 6th row) leading to a strong segregation of main habitats which is montane to subalpine spruce forest in the former and sunny ecotones between broad-leafed woodland and xerothermous grassland in the latter. The clear differences in the factors N and LiC are consequence of this habitat selection and certainly no reflection of a special adaptation to these factors.

High similarity in their relations to nearly any factor is observed in the sister species *Myrmica rubra* and *M. ruginodis* (Figs 19 and 20). The general observation that *M. ruginodis* is much less frequent than *M. rubra* in cultivated land cannot be explained by the factors recorded in this study – differing species-specific physiological, morphological or nest-construction adaptations are unlikely to be responsible for the spatial segregation. One rather probable explanation is provided by colony demography: it seem reasonable that the more developed polygyny and polydomy in *M. rubra* makes it less sensitive to mechanic impacts by human management because the high productivity of the surviving, intact colony fragments can easily compensate the losses in destroyed parts of the colony.

4.2.12 Which environmental factors are most important for niche segregation of ants?

I made an attempt to assess the influence of particular environmental factors on niche segregation of ants based on data of those 59 species present on more than five study plots. The relations of ant species to a certain factor are in the majority of cases non-linear – symmetric or skewed optimum curves are typical (Figs 19 and 20) and non-linearity is also dominant in the behavior of whole ant assemblages when richness and biomass data are plotted (Figs 8–18). This may constitute a severe problem when linear ordination methods are used for estimating the contribution of a certain environmental factor on niche segregation. I tested here two alternative indicators: (a) factorial niche overlap *O* which considers the shape of frequency distributions on the species level and (b) the goodness of fitting of polynomial descriptions of species richness and biomass on the society level. Factorial niche overlap *O* was calculated in 1711 species pairs formed by 59 species present on more than five study plots. The final mean of factorial niche overlap was calculated as the arithmetic mean of data from the weighted and unweighted approach. A strong effect of a factor on segregation of niche spaces should be given when the mean factorial niche overlap is low. The alternative indicator, the goodness of polynomial descriptions of species richness and biomass on 232 study plots, is represented by Pearson's correlation coefficient R. A factor should have a strong effect on the distribution of ants when the correlation is large but R will be affected by different recording accuracies of the environmental factors.

Table 10 shows an attempt to rank the effect of environmental factors on distribution of ants in the studied Central European ecosystems. It should be kept in mind that the data represent the system's average and that certain factors which appear unimportant from a more general perspective may have strong effects in particular species (see the discussions under 4.2.1–4.2.10). According to the total evidence from both indicator systems indicated by the position value P, soil moisture F and maximum calibrated soil temperature T_{MAX} are the most important environmental variables followed by mean calibrated soil temperature T_{MEAN}, reaction (calcium) figure R and cumulative cover of shrubs and trees ShTrC. It is remarkable that moisture is in a leading position despite a less accurate, plant-indication-based recording compared to the more precise temperature data which are based on direct calibrated measurements or cross-referenced guiding values. The fourth rank of calcium figure R

◄ **Figure. 20**. Relations of 16 closely related ant species to the niche axes N, M and LiC.

should largely be a correlated effect of temperature and moisture conditions found in xerothermous limestone grasslands instead of representing a direct effect of chemicals (see also discussion in section 4.2.6). The position of ShTrC is partially explained by the effects of canopies on soil moisture and temperature but it should also reflect a segregation into guilds of woodland and open-land species.

It is in some way astonishing that plant density PD occupies the penultimate position within the twelve environmental variables ranked here. It is undisputed that excessive development of herb layer in open land habitats due to abandonment of extensive grassland management and hypertrophication by nitrogen immission is a major threat to biodiversity of thermophilous subterranean and epigaean arthropods (and other organisms). However, the data of this study support the idea that structural and nutritional effects of plant density are less important for ants of the temperate zone than its effect on soil temperature and moisture when the whole environmental gradient is considered. This does not exclude that plant density may be a deciding factor at the lower end of the gradient (see section 4.2.4).

4.3 Between-habitat comparison of ant species richness and biomass

Table 11 compares 27 habitat types in their mean ant nest density, species richness and biomass for both open and woodland habitats. The first general conclusion from the data is that average species richness and biomass is lower in woodland habitats than in open land. Averaging the data of 156 study plots in open habitats and the 76 study plots in woodland habitats, mean ant species richness in woodland is 86% and biomass only 52% of the mean in open habitats. These data are certainly typical for the temperate zone and differ strongly from the situation known from the tropics. Adding canopy ants to the whole calculation, species richness of temperate woodland will increase to about 90–95% of the open land figure but the biomass disadvantage remains because true canopy nesting ants amount for only 3–6% of total ant biomass in temperate forests (Seifert 2008).

The highest biomass and by far the highest species richness for any open land habitat is found in xerothermous to mesoxerophytic grasslands on limestone or chalk. This over-all-habitats maximum (OAHM) of 13.1 species/100 m² and 8.82 g fresh weight/m² is used as reference point for the comparisons in the sections below. In xerothermous to mesoxerophytic grassland on natural neutral to acid soils, there is a significant drop in species richness to 60% and in biomass to 67% of the OAHM. While moisture and temperature conditions in both habitat types are equally favorable, the advantage of habitats on limestone is explained by a higher number and diversity of nest microhabitats such as stones, limestone plates or snail shells. The larger plant diversity on calcareous soils (Dengler 2004) should also favor richer ant assemblages because it is likely to result in a wider spectrum of trophobionts and of primary and secondary consumers used by the ants as prey.

Neutral to acid xerothermous grassland habitats on heaped soil in the first 15 years of post-mining successions have physical and structural conditions similar to such habitats on natural ground but they have a clearly lower species richness achieving only 35% of the OAHM. This is caused by the following factors: (a) The early occupation of space and competition by the rapidly colonizing pioneer species *Lasius niger* and *Formica cinerea* hampers the immigration of congeneric species despite their basically good adaptation to such conditions. (b) The source populations of the latter species have rapidly declined due to loss of semi-natural xerothermous grassland by the changed human land use. (c) The build-up of a rich root aphid fauna needs a longer time – species of the subgenera *Cautolasius* and *Chthonolasius* depend on this food source. (d) These post-mining habitats develop usually in a free succession (i.e., not grazed or otherwise managed) and will rapidly transform to woodland before the missing species typical for xerothermous grassland can build up significant populations.

Despite a clear reduction of species richness to 58% of the OAHM value in fresh-dry, meagre grassland, biomass remains here very large with 98% of the OAHM value. Most of the study plots belonging to this habitat category were managed as extensive sheep pasture until about 1992 which offered best conditions for biomass development. Exemplary in this context is study plot SP 198 with a biomass of > 16 g/m² alone for *Lasius flavus* which was estimated by direct measuring of nest size in 437 mounds. The uncorrelated behavior of richness and biomass in fresh-dry, meagre grassland is explained by big densities of the high-biomass nests of *Lasius flavus, L. alienus* and *L. niger* species while species richness in genera with low mean nest biomass such as *Temnothorax* decreased considerably compared to limestone/chalk habitats.

Comparing fresh meadows and pastures in the planar to submontane zone with fresh montane to alpine pastures, we observe a similar species richness for both altitudinal zones (3.76 vs. 3.98 species/100 m²) but a strong decrease of ant biomass (5.36 vs. 1.74 g/m²) at higher altitudes. This is largely explained by the decreasing density of high-biomass *Lasius* nests and a bigger share of low-biomass *Myrmica* nests due

Table 10. Mean factorial niche overlap of the unweighted (O_U) and the weighted (O_W) approach derived from 1711 species pairs formed by 59 species. R_R and R_B are Pearson's correlation coefficients of polynomial descriptions of species richness and biomass respectively of ant assemblages on 232 study plots. O_M is the arithmetic mean of O_U and O_W. R_M is the arithmetic mean of R_R and R_B. Data are ordered according to a position value P which is the geometric mean of O_M and 1-R_M. The influence of a factor on distribution of ants is supposed to be the larger the smaller the value of P is.

factor	P	O_U	O_W	R_R	R_B	O_M	R_M	1- R_M
F	0.4617	0.5884	0.5165	0.6240	0.6044	0.5525	0.6142	0.3858
T_{MAX}	0.5038	0.4879	0.4827	0.4905	0.4635	0.4853	0.4770	0.523
T_{MEAN}	0.5394	0.5629	0.4890	0.5012	0.3926	0.5260	0.4469	0.5531
R	0.5568	0.4966	0.4871	0.3783	0.3610	0.4919	0.3697	0.6303
ShTrC	0.6088	0.5457	0.4556	0.2394	0.2800	0.5007	0.2597	0.7403
HeC	0.6125	0.5768	0.6074	0.4261	0.3066	0.5921	0.3664	0.6336
N	0.6227	0.6228	0.5609	0.4053	0.2843	0.5919	0.3448	0.6552
LiC	0.6737	0.7098	0.5420	0.2561	0.2936	0.6259	0.2749	0.7251
MoC	0.6742	0.7512	0.5315	0.3157	0.2670	0.6414	0.2914	0.7086
M	0.7216	0.7270	0.6192	0.1794	0.2732	0.6731	0.2263	0.7737
PD	0.7374	0.8178	0.7717	0.3013	0.3303	0.7948	0.3158	0.6842
DWC	0.7557	0.7042	0.5750	0.0436	0.1706	0.6396	0.1071	0.8929

Table 11. Comparison of 27 habitat categories in mean total nest density D [nests/100 m²], species richness S_{100} [species/100 m²] and biomass [fresh weight in g/m²]. The term 'grassland' means shrub- and treeless habitats with a small to large percentage of surface covered by grasses. Woodland or shrub habitats are shaded in grey. The sum of the number of study plots N is 238 (instead of 232) because few plots of intermediate classification were allocated to two categories.

Habitat	N	D	S_{100}	Biomass
xerothermous grassland on sand dunes	7	24.3	3.55	1.82
xerothermous to mesoxerophytic grassland on limestone/chalk	36	169.6	13.1	8.82
xerothermous to mesoxerophytic grassland on basalt	10	119.5	8.46	6.44
xerothermous to mesoxerophytic grassland on neutral to acid soils	17	96.0	7.83	5.94
neutral to acid xerothermous grassland in a post-mining succession	7	56.8	4.62	5.28
fresh-dry, meagre grassland	10	127.5	7.56	8.62
fresh meadows and pastures in the planar to submontane zone	5	66.7	3.76	5.36
fresh pastures in the montane to alpine zone	10	58.5	3.98	1.74
moist to wet meadows and sedge fens	6	39.9	2.79	1.00
dry to moist heath	4	37.7	5.95	4.41
peat bogs and fens	23	46.6	4.22	1.43
open saline habitats	5	46.9	4.66	1.07
open habitats on limestone gravel banks of rivers	8	24.0	2.99	1.42
tall herb communities	1	74.1	1.00	2.38
fallows of arable land	2	36.3	4.14	4.34
road margins	3	94.0	5.16	5.80
clip lawns	3	118.7	6.0	8.22
xerothermous to tempered *Quercus* woods	15	219.4	12.5	5.49
dry *Pinus* woods	7	96.4	8.52	2.97
mixed broad-leafed woods	11	127.9	4.74	1.70
alder carrs (*Alnus* fenwoods)	5	32.6	3.33	1.32
Fagus woods	4	0.32	0.35	0.07
fresh to moist *Pinus* woods	8	67.9	5.81	1.27
living, *Picea-abies*-dominated conifer forest	8	0.79	0.63	0.27
dead, *Picea-abies*-dominated conifer forest	8	0.62	0.49	0.02
clear-cuttings in former *Picea-abies*-dominated conifer forest	6	16.1	4.54	2.61
dense shrub stripes in open land	3	86.8	6.08	4.26
intermediate stages of succession from open land to woodland	6	123.3	7.70	4.77

to decreasing T_{MEAN} (13.9°C vs. 8.5°C) and increasing mechanical stress by more intensive cattle grazing (M 4.20 vs. 5.50) in the high-altitude grasslands.

In habitats where one or several environmental factors are at the pessimum, such as moist to wet meadows, sedge fens, salines and peat bogs, mean biomass is only 11–16% of the OAHM value while the reduction of species richness to 21–36% of the OAHM is less strong due to the presence of some specialized species.

Two open habitats subject to strong anthropogenous pressure, road side margins and clip lawns, both show above-average biomass data. The rather high rank of road margins is explained by an ecotone effect which is a small-scale association of favorable xerothermous conditions near to the pavement with sufficient plant productivity towards the roadside ditch. There is furthermore a splendid food supply for zoophagous ants due to the accumulation of dead or disabled insects skidded to the road margin after collision with vehicles. The high ant biomass in clip lawns of parks and settlement gardens is probably explained by the combination of (a) warm topsoil, (b) complete cover of grasses with strongly developed root layer as habitat for subterranean aphids, (c) artificial irrigation in case of extreme drought and (d) long-term habitat stability.

Within the woodland habitats, the highest species richness (95% of the OAHM value) and highest biomass (62% of the OAHM values) is achieved in xerothermous to tempered *Quercus* wood (Tab. 11). This is explained by weak to moderate soil moisture, rather warm topsoil and rich supply of microhabitats for nesting.

Rank two in species richness is occupied by dry *Pinus* forests showing 65% of the OAHM value. A good supply with nest microhabitats both by dead wood and pine bark, in situ or on ground, and favorable soil temperature and moisture conditions are responsible for a rather high species richness. Yet, because the special supply with nest microhabitats in pine forests favors in particular the low-biomass species of the genera *Temno-* and *Leptothorax*, there is a significant drop of biomass to 34% of the OAHM value.

Ecotone habitats such as shrub stripes in open land or habitats in transition from open land to forest show a rather big biomass with 48% to 54% of OAHM.

By far the poorest ant assemblages are found in *Fagus* or *Picea-abies*-dominated forests with a mean relative species richness of only 2.7% and 4.8% respectively and a biomass of 0.8% and 3.1% of the OAHM values respectively. Many pessimal factors are combined in these forests: very low soil temperatures, poor food availability due to sparse or missing development of herb layer and unfavorable properties of dead and decaying wood to serve as nest habitat for ants. The last place of pure *Fagus sylvatica* stands does also apply for those ants which were no focal group of this study: mound-building wood ants of the *Formica rufa* group do not inhabit pure beech woods if alternatives are available (Eichhorn 1963, Wellenstein 1967, my own experience). This appears surprising to some extent since at least the populous, polydomous colony types of these ants with their big actively thermo-regulated nests can easily get along with a cool habitat climate. Furthermore, the poor food supply on forest floor should not matter so much because food sources in the canopy are well within the foraging range of these ants. The build-up of significant *F. rufa* group populations in these forests is probably hampered by the synergetic action of four unfavorable factors. These are (1) unsuitability of the leaf litter for mound-building purposes, (2) the higher expense of energy and time during ground foraging over the heavily structured, uneven litter surface, (3) unmanageability of the thick litter layer by the ants preventing the construction of smooth, efficient trunk roads. Furthermore *Fagus* forests have (4) lower temperatures and (5) a poorer food supply compared to *Quercus* forests where, in addition, the negative effect of litter is less dramatic. The contrastingly high abundance of *F. rufa* group ants in planar and colline *Picea-abies*-dominated forests, which are comparable to *Fagus* forests in microclimate and food supply, is explained by the ideal properties of needle litter for mound construction.

4.4 The relation of evenness, fundamental niche width and species richness

The uncoupling or independent calculation of evenness and richness (see section 3.5) allows to investigate if both basic parameters of ecosystems stand in any relation. Excluding species-poor study plots with less than 6 ant species/100 m², a highly significant positive correlation between species richness S_{100} and Hurlbert's evenness index V can be shown (Fig. 21, $R = 0.401$, $n = 106$, $p << 0.001$). In other words, the higher the number of ant species in a habitat is the more even is the distribution of their nest densities. The biological or ecological meaning behind this relation is not really clear. One possible interpretation of these data is that eudominance of a single or very few euryoecious ant species becomes less probable when a multitude of environmental valencies is provided allowing the coexistence of many, on average more specialized species. This effect could be one explanation for the observation that invasion of introduced ant species into species-rich natural or semi-natural habitats often proceeds more slowly than in sites with strong anthropogenous disturbance or pressure (Walsh et al. 2004, Wittmann 2014, Zettler et al. 2004).

The idea that the carrying capacity of a habitat for species is increased when the species present are more specialized can be checked if species richness is described as a function of fundamental niche width. According to a hypothesis of Odum (Odum 1971, 1983), development of narrow niche spaces may be considered as a form of specialization. This specialization causes a higher efficiency in the utilization of resources and increases the diversity of a community but is paid with a lower adaptability. Overall fundamental niche width *W* of all species was calculated including all physico-chemical and structural niche dimensions described in section 3.6.1 to 3.6.12. This considered a total of 13 niche dimensions because T_{MAX} and T_{MEAN} were considered with good reasons as different niche variables. Excluding study plots with less than 2 species/100 m², ant species richness S_{100} showed a clearly negative correlation to mean width of the fundamental niche *W* of all ant species present on a plot (Fig. 22, R = 0.4766, n = 200, $p << 0.001$). Species richness was 11.7 species/100 m² for *W* = 0.30 and it decreases to 2.6 species for *W* = 0.67. This is convincing evidence for the theory of Odum: narrow niche spaces increase the number of species a habitat may hold. As it is difficult in coevolving systems to distinguish cause and effect, we may also reverse the argumentation: if an habitat offers a multitude of resources, specialized species with narrow niches may establish and reduce the chances for euryoecious species to become dominant. Thus we arrive at the same conclusion as we got it above from the richness-evenness relation.

4.5 Interspecific competitive exclusion is increased with growing relatedness – Gause's law can be shown outside laboratory settings

A search in the Web of Science for the strings 'competitive' AND 'exclusion' OR 'Gause' in the title category conducted on 27 October 2016 resulted in 459 publications for the period since 1980. As much as 80% of these papers constituted in mathematic modelling of fictive data sets and empiric research in Procaryota, Protozoa, unicellular algae and even biomolecules. The remaining 20% referred to studies on Eumetazoa and vascular plants based on field studies with only 4% of these dealing with insects. The overall impression from these papers is that interspecific competitive exclusion is considered as an important variable for the shaping of biocenoses but its effects are discussed in a very different way depending on the context and the perspective or idiosyncrasy of the investigators. A challenging opinion such as of Walter (1988) that interspecific competition is usually too weak and intermittent a force to achieve

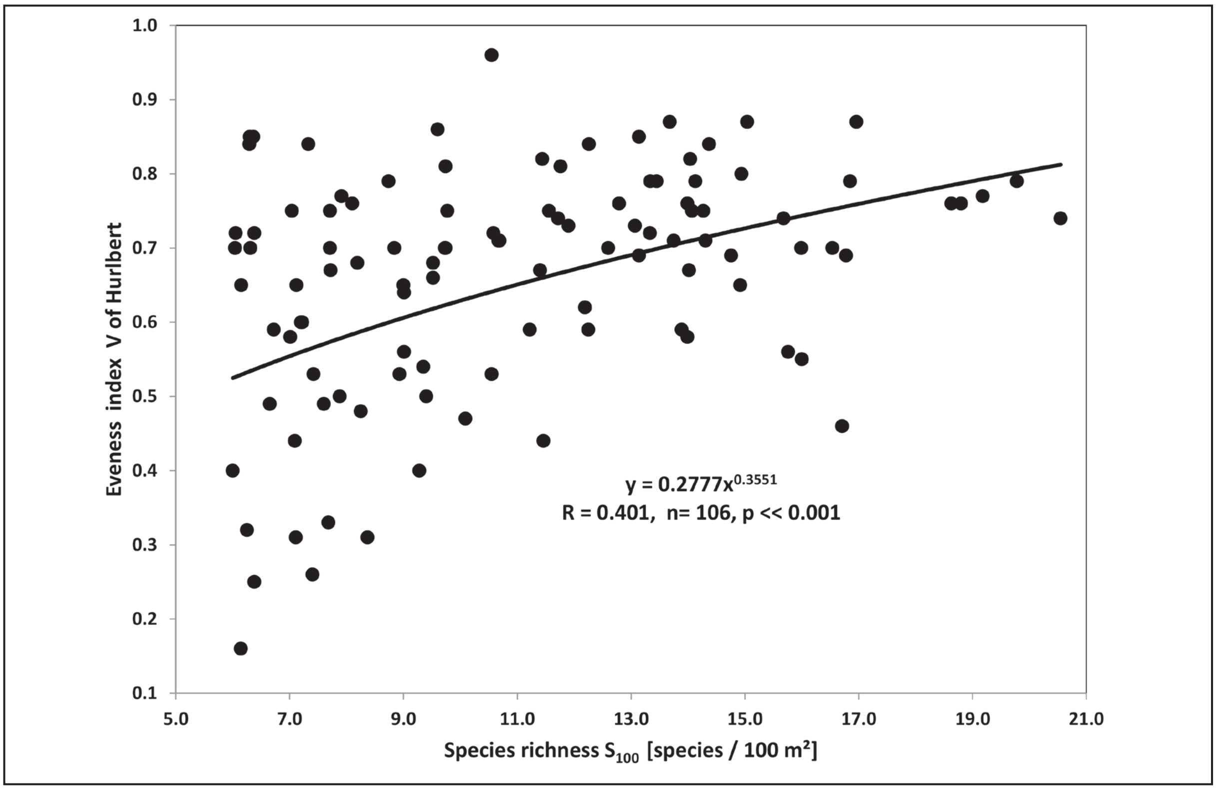

Figure 21. Relation of ant species richness and evenness in 106 study plots with more than five species per 100 m².

ecologically-significant results stands alone within the mainstream of ecological hypotheses which are represented, for example, by Finke & Snyder (2008) or Levine & Hille Ris Lambers (2009). Anyway, there is certainly a good portion of truth in the position of Walter – one of my main arguments in the methods section of this paper is in agreement with this: the temporal exposure of hidden fundamental niche space during dynamic processes (see section 3.7) is based on the fact that competitive exclusion does not play a significant role in particular (if not many) situations. Most of these 459 papers indicated by the search machine referred to competition between two or very few species whereas empirical studies on the community level were exceptional. This study seems to have a unique selling point by its approach to infer on species-specific situations from broad-scale whole-community data of multiple niche dimensions.

The analysis of interspecific competitive exclusion conducted here used the 14 niche variables T_{MAX}, T_{MEAN}, F, N, R, PD, M, HeC, ShTrC, MoC, LiC, DWC, NM and BS to calculate the overlap of fundamental niche space O_F. All calculations considered only those 59 species present on more than five study plots and not being true canopy dwellers. This gave a total of 1711 species pairs for calculation of fundamental niche overlap O_R and O_F. Plotting O_R against O_F (Fig. 23) resulted in a standard function $O_C = f(O_F)$ that describes the average behavior within the study system. This function is for the unweighted approach

$$O_C = f(O_F) = 1.6702\ O_F^3 - 1.4317\ O_F^2 + 0.4313\ O_F - 0.0419 \quad (R = 0.729,\ p<0.001) \qquad [23]$$

and very similar in the weighted approach:

$$O_C = f(O_F) = 1.5315\ O_F^3 - 0.8232\ O_F^2 + 0.1338\ O_F - 0.0049 \quad (R = 0.778,\ p<0.001) \qquad [24].$$

Interspecific competitive displacement is indicated when the coexistence value COEX

$$COEX = O_R - O_C \qquad [25]$$

is negative and coexistence when it is positive. The main hypothesis to be tested here is if interspecific competitive displacement grows with increasing relatedness. Closely related or cryptic species are expected to show a high overlap of their fundamental niche spaces and a contrastingly small overlap of their realized niche spaces. This should be indicated by low COEX values.

Three collectives of species pairs were selected and compared to test this hypothesis. The collective SIBLIN contained 20 pairs of closely related species – for simplicity of wording loosely called here „sibling species“ (but see the restricted meaning of the term in Seifert 2009). The collective CONSIB contained 214 congeneric pairs of all other species from only the genera to which the sibling species belonged and NONSIB all 1691 pairs formed by non-sibling species of any genus. The 20 species pairs in SIBLIN were

Camponotus herculeanus / *C. ligniperda*, *Formica clara* / *F. cunicularia*, *F. clara* / *F. rufibarbis*, *F. cunicularia* / *F. rufibarbis*, *F. fusca* / *F. lemani*, *Lasius flavus* / *L. myops*, *L. platythorax* / *L. niger*, *L. alienus* / *L. paralienus*, *L. alienus* / *L. psammophilus*, *L. paralienus* / *L. psammophilus*, *Leptothorax gredleri* / *L. muscorum*, *Myrmica constricta* / *M. rugulosa*, *M. constricta* / *M. specioides*, *M. lonae* / *M. sabuleti*, *M. rubra* / *M. ruginodis*, *M. lobicornis* / *M. lobulicornis*, *Tapinoma erraticum* / *T. subboreale*, *Temnothorax crassispinus* / *T. nylanderi*, *T. nigriceps* / *T. tuberum*, *Tetramorium caespitum* / *T. impurum*.

Most of these species pairs are so similar in morphology that they are likely to be confused by untrained investigators.

Tab. 12 shows the coexistence values COEX calculated from both unweighted and weighted data sets which provide very similar indications. Despite producing accessory random variance in species with lower frequency, the weighted approach seems to have a slightly better overall performance indicated by the better fitting in function [24] and stronger differentiation of COEX data. Using the arithmetic mean of the COEX data of the weighted and unweighted approach, the group SIBLIN shows significantly lower coexistence values than the

Table 12. Coexistence values COEX for pairs of closely related species (SIBLIN), for congeneric pairs of all other species from only the genera to which the sibling species belonged (CONSIB) and for all pairs formed by non-sibling species of any genus (NONSIB). COEX is given in units of 10^{-4} and in heavy type in the sequence arithmetic mean ± standard deviation [lower extreme, upper extreme] and n is the number of pairs in each collective. Results of a one-way ANOVA are placed in the line separating the compared data sets.

Collective	n	COEX, unweighted	COEX, weighted
CONSIB	214	**–151 ± 852 [-2754,+3787]**	**–70 ± 808 [-1887,+4028]**
	ANOVA	F=8.29, p< 0.004, df1=1, df2=232	F=11.13, p< 0.001, df1=1, df2=232
SIBLIN	20	**–739 ± 1078 [-3074,+1908]**	**–715 ± 1010 [-2989,+1858]**
	ANOVA	F=18.07, p< 0.000, df1=1, df2=1709	F=20.08, p<0.000, df1=1, df2=1709
NONSIB	1691	**+9 ± 778 [-2754,+4109]**	**+8 ± 713 [-2799,+4444]**

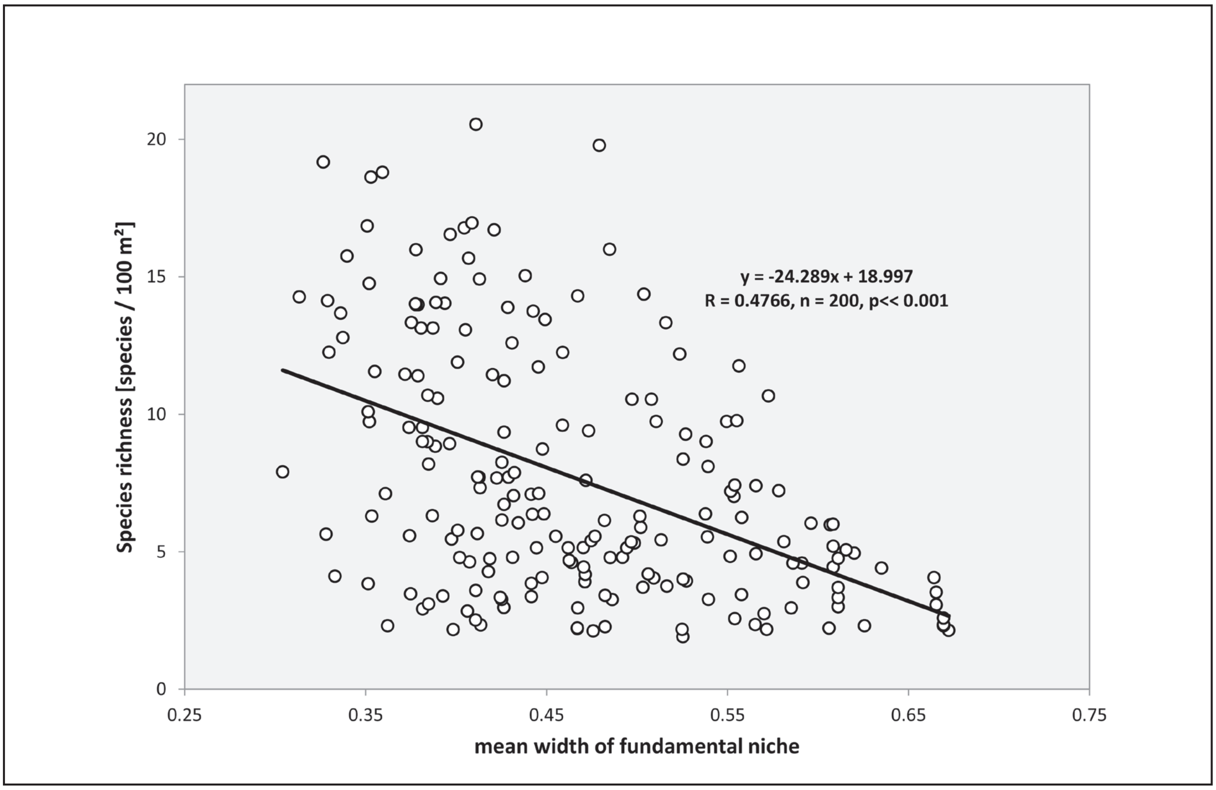

Figure 22: Relation between species richness an mean fundamental niche width within ant assemblages.

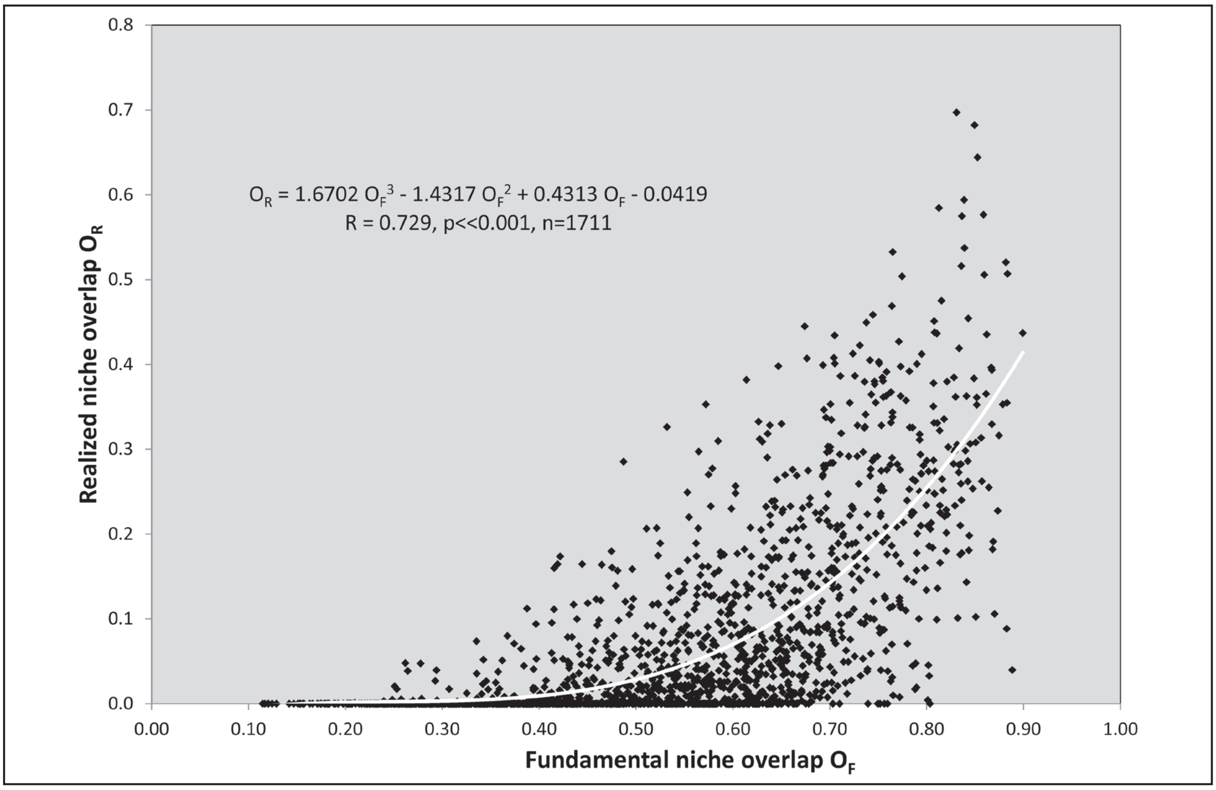

Figure 23: Plotting of realized niche overlap against fundamental niche overlap in 1711 species pairs.

group CONSIB and thus a clear trend for competitive exclusion (ANOVA $F_{1,232} = 9.98$, $p < 0.002$). This is a convincing indication that Gause's law is operating also in natural, multi-species communities with many resources and not only in simplified laboratory settings with only two species and a single food source.

The strong statistical evidence on the community level was allowed by a sufficiently large sample size but is it possible to derive conclusions also for particular species pairs? The answer is that a clear inference is not possible in many cases because the noise of data is too large and because the truth of an indication can only be assessed if the interspecific behavior of the confronted species is known. I discuss in the following only few, rather exposed examples based on data of the arithmetic mean between the weighted an unweighted approach.

The strongest negative coexistence value in the whole system of COEX = –3032 is calculated for the closely related dolichoderine species *Tapinoma erraticum* and *T. subboreale*. These were present on 15 and 17 study plots respectively but showed a realized niche overlap of 4.0 % only whereas the fundamental niche overlap was as large as 82.8 %. This situation is remarkable as the two species are sympatric in 85 % of the study area and are also found on closely neighboring plots. This competitive exclusion finds its expression also in a clear zonation in very large and coherent xerothermous grasslands such as in the Leutra Valley near Jena with *T. erraticum* occupying the Teucrio-Seslerietum and upper Festuco-Brometum and *T. subboreale* found in the lower Festuco-Brometum and upper Dauco-Arrhenatheretum phytoassociations (Seifert 1982). It remains to be studied by which form of interaction – scrambling competition, aggressive interference competition or a synergy of both – this spatial segregation is generated.

The strongly negative coexistence value of COEX = –1775 in the pair *Tetramorium caespitum* / *T. impurum* is most probably explained by a competition for exactly the same food resources (mainly seeds and subterranean trophobionts) in combination with a very high interspecific aggression leading to true wars of extermination (Seifert 2007). Remarkable is also the strong spatial exclusion of *Formica clara* and *F. rufibarbis* with COEX = –1754, O_R = 4.0 % and O_F = 74.1 %. There are no observations of interspecific behavior in these species but, concluded from the situation in non-supercolonial species of the subgenus *Serviformica*, fightings with masses of ants engaged are unlikely to occur. Spatial exclusion should be generated here largely by scrambling competition and aggressive interaction between single individuals during foraging – defense of territories is unknown in these ants but they tend to develop a homogenous spacing of nest sites (Gallé 1980). Unknown is also the interspecific behavior of the sibling species *Lasius alienus* and *L. paralienus* which show COEX = –2454, O_R = 10.2 % and O_F = 83.1 %. It seems likely that spatial exclusion in this species pair is caused by differences in humidity and temperature tolerance which, however, were not clearly exposed within the study plot system (Fig. 19). Yet, these differences in xerothermy are strongly suggested by altitudinal distribution within the German states Rheinland-Pfalz and Baden-Württemberg where *Lasius alienus* is more frequent in warm vine growing areas whereas *L. paralienus* dominates on the submontane to montane pastures of the Eifel and Schwäbische Alb.

At the other end of the scale we find species pairs with strongly positive coexistence values. A well-studied example is the pair *Lasius niger* and *Myrmica rugulosa* showing the data COEX = +2243, O_R = 53.7 % and O_F = 81.0 %. A remarkable behavioral mechanism observed by several investigators in exactly the same way (Czechowsky 1979, De Vroey 1978, Seifert 2007) ensures here that the frequent encounters of both species at food sources do not result in any injury or mortality and enables, in combination with the different foraging strategies, an extreme degree of coexistence. A high degree of coexistence is also indicated in *Temnothorax nigriceps* and *T. unifasciatus* with COEX = +3231, O_R = 58.4 % and O_F = 77.6 %. This coexistence is allowed by a very low interspecific aggression between foragers and a differing selection of nest microhabitats which are rock crevices in 96 % of the *T. nigriceps* nests whereas 61 % of the *T. unifasciatus* nests are found in other microhabitats. A similar avoidance of competition for nest sites is observed in *Temnothorax albipennis* and *T. tuberum* for which the data are COEX = +2284, O_R = 57.6 % and O_F = 83.1 %. In continental habitats with lying and standing dead wood and when the competing ground-nesting *T. tuberum* (or *T. unifasciatus*) are present, *T. albipennis* typically evades to dead wood 2–50 cm above ground. In the absence of competitors it is much more frequently nesting in microspaces on ground surface. No signs of aggression or displacement are also observed during the frequent encounters of foragers *Manica rubida* and *Myrmica constricta* and fightings enforced by the experimenter through artificial mixing of nest populations ended in a quick separation of the conflict parties without having generated mortality. The extreme data in this species pair of COEX = +4277, O_R = 69.7 % and O_F = 78.1 % confirm these observations and indicate a particular case of a peaceful coexistence.

4.6 Prediction of future zoogeographic shifts due to global warming will remain inaccurate when the habitat-dependent temperature component is not considered

The temperature to which a terrestrial organism is exposed is undoubtedly strongly influenced by macroclimate but it is known for a long time that these temperatures are also strongly determined by habitat factors or the biological microenvironment (e.g., Geiger 1927, Lützke 1958, Geiger 1961, Lache 1976, Seifert 1986, Stoutjesdijk & Barkman 1992, Kennedy 1997). Avoidance of extreme computing effort and lack of knowledge about the influence of special habitat parameters may explain that published predictions of future distributional ranges of species are based so far on simulations of meteorological data only but do not consider the thermal effects of habitat structure, orography or geological material. To give an example, it is expectable that really observed upper latitudinal extremes can go much beyond those predicted using meteorological simulations alone if there are special temperature-increasing orographic or edaphic conditions in a northern region. The northernmost populations of *Leptothorax acervorum* pass the Arctic tree line by 150 km (Francoeur 1983) and the Ust-Lenski Nature Reserve in the Lena delta at 73°N represents the most northern ant population of the world (Heinze & Hölldobler 1994). The range expansion into these permafrost areas is properly explained by orography and the particular soil conditions of the nest sites. Berman et al. (2010) intensively studied the habitat and microhabitat selection of *L. acervorum* in these regions and found nest densities fully comparable to those in Central Europe. According to these authors, *L. acervorum* nests are preferential built here on sufficiently drained, but not extremely dry, southern slopes of terraces and they emphasized the importance of both macro- and micro-relief and of material properties. A paradox cooling effect of habitat structures is discussed by Wallisdevries & Van Swaay (2006): strong early spring growth of herblayer plants caused by global warming and by excess nitrogen disturbed the ontogenesis of thermophilous egg- or larvae-hibernating butterflies whereas adult- or pupae-hibernators were not affected.

The determination of calibrated soil temperatures by *CalibSoil* allows to estimate the partial contributions of meteorological and habitat-specific factors on soil temperatures.

The key variables in this calculation are the calibrated basal soil temperature T_{BAS} and the calibrated mean soil temperature T_{MEAN}. It follows from section 3.6.1 and the internet source named there that T_{MEAN} is equal to T_{BAS} when habitat temperature is exclusively determined by the meteorological factors valid for certain geographical spot and that any increase of T_{MEAN} above T_{BAS} indicates the influence of habitat-specific factors. The latter include stratification and density of phytolayers, orography (aspect) and properties of ground material.

Fig. 24 shows a plot of T_{MEAN} against T_{BAS} with the dotted line indicating equality of T_{MEAN} and T_{BAS}. A big positive deviation from this line indicates a strong effect of habitat- dependent factors which may increase the mean seasonal soil temperatures strongly above the basal soil temperature – e.g., by 5.0°C in SP 119 (a xerothermous habitat on bare basalt rock) or by 5.1°C in SP 143 (a coastal sand dune). All data points very close to the dotted line, unexceptionally belonging to very shady forests, indicate a zero influence of direct solar heating. The average increase of mean soil temperatures by habitat-specific factors over all 232 study plots was 2.29 ± 1.31 °C. This figure alone illustrates the important influence of habitat-specific factors. The regression function of T_{MEAN} against T_{BAS}, indicated by the solid line in Fig. 24, is nearly parallel to the dotted line, suggesting that the solar heating up of alpine, subalpine and highly montane habitats (those with $T_{BAS} < 10°C$) is comparable to those of lower altitudinal levels. A regression coefficient of $R^2 = 0.69$ indicates that 69 % of the variance of T_{MEAN} may be explained by T_{BAS}. In other words, 31 % of variance within the present system of study plots is not explained by meteorological factors and is largely due to habitat factors. A related approach of estimating the contribution of habitat-specific factors is considering T_{BAS} as a partial quantity of T_{MEAN} and calculating the difference of the sums of deviation squares. The sum of deviation squares was 1270.1 in T_{MEAN} and 988.7 in T_{BAS}. The difference of 281.4 would indicate that 22.2 % of the total variance is not caused by meteorological factors. It is clear that the contribution of habitat-specific factors will grow with decreasing altitudinal and latitudinal variance in the system considered. Reducing the system to 178 study plots in the region of Thüringen, Sachsen-Anhalt and Sachsen, where altitude varied by 900 meters only and latitude by 1.8 degrees only, as much as 69.8 % of the variance is explained by non-meteorological factors according to the regression approach and 60.1 % according to the partial quantity approach.

4.7 Biodiversity conservation issues

A comprehensive consideration of the climatic, cultural, socio-economic and political factors shaping the species composition in the Central European cultural landscape from the Neolithic up to the present was given by Poschlod (2015). Accordingly, this section cannot provide anything what is essentially new but it may sharpen the view on the situation in ants.

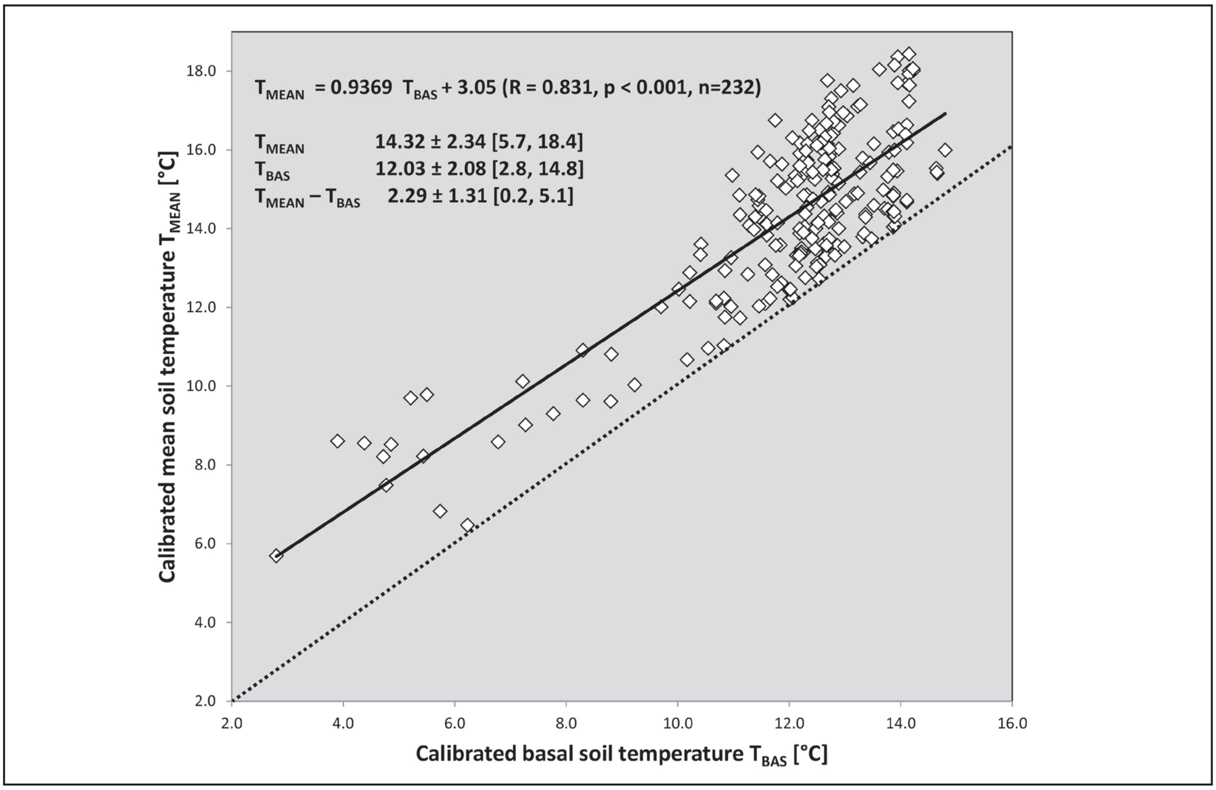

Figure 24. Plotting of calibrated mean soil temperature T_{MEAN} against calibrated basal soil temperature T_{BAS}. The deviation of T_{MEAN} from the dotted line quantifies the influence of habitat-specific factors.

Describing the general situation within the studied territory of Central Europe, ant species living in open landscape in particular have suffered a severe decline in population number and biodiversity due the socioeconomic and political changes of the last four decades. Most important is hypertrophication and excessive growth of herbs and scrub encroachment in oligotrophic open habitats or at margin lines between open land an forest. This was caused by excessive immission of atmospheric nitrogen and by agriculture in the form of mineral fertilizers or liquid manure, by a massive decline of shepherding, by natural woodland succession in former military training areas, afforestation of grassland on unproductive soils, by metastatic extension of settlement and business areas or by a loss of extensive forms of management due to the exodus of the young from traditional farms.

What was the overall situation within the system of 232 study plots considered here? Eight study plots or 3.4% of the total became basically uninhabitable for ants due to massive change of human use such as flooding, transformation into mining areas or yearly ploughing. In 65 study plots belonging to diverse types of open land habitats, the change of habitat structure was observed after a mean interval of 21 years (the mean year of thorough ant investigation was 1984 and the mean year of habitat re-assessment without a thorough ant recording was 2005). 44.6% of these plots showed weak or no changes in habitat structure. 33.8% were significantly changed due to moderately strong changes in management (e.g., transition from a pasture into a cut meadow) or due to some alteration of ground water level. Yet, 21.5% were extremely transformed – mainly by massive growth of herb layer plants, scrub encroachment, succession to woodland and in one case each by extreme cattle density and afforestation (Tab. 13). It is the latter degree of extreme habitat transformation, affecting 22% of all plots within some 20 years, that is responsible for in my opinion the most dynamic degradation of open-land ant biodiversity we have experienced in the region since the year 1800. The big losses in mesic and wet grasslands or bogs experienced in the same time, affecting other groups of organisms dramatically, did not have comparable effects on biodiversity of ants because these have only few species specialized for such types of habitats.

The data on the influence of certain environmental factors provided in section 4.2 and 4.3 have indicative value for assessment of nature conservation issues and present, for the first time in ants, a reliable indication how different environmental variables act on ant biodiversity in general and on particular species. This does not apply to ants only. Some of the described variables determine also the long-term survival of many other subterranean or epigaean organisms – at least of those open-land species requiring sufficient temperatures, moderate humidity and oligotrophic habitats with moderate herb layer development. The fates of indicator species such as Blue Grass (*Sesleria*), Weather Clock (*Carlina*), *Ophrys* orchids, *Bembix* wasps, *Oedipoda* grasshoppers, *Coronella* snakes, *Lacerta* lizards, of Wheatear (*Oenanthe*), Tawny Pipit (*Anthus*) or Grey Partridge (*Perdix*) – to name only a few – are closely associated with that of ants. This illustrates that optimum species conservation in the cultural landscape of Central Europe can only be intelligent, compromising habitat management.

I restrict here the considerations to five environmental variables of outstanding influence which does not say that other factors are meaningless. The deciding point is that most ant species preferring open land habitats need sufficiently high temperatures and a well-drained nest microhabitat for completing brood development. This is documented by the clear relation of ant distribution to soil moisture F (Fig. 10), maximum calibrated soil temperature T_{MAX} (Fig. 8) and mean calibrated soil temperature T_{MEAN} (Fig. 9). Maximum values of species richness and biomass occur in dry habitats (F = 2.7–3.6) with high maximum and mean soil temperatures (T_{MAX} 25–30°C, T_{MEAN} 16–17°C). These three factors are the most influential variables directing the distribution of ants as shown by the ranking attempt in section 4.2.12 that used data of niche segregation and correlations with polynomial functions (Tab. 10). Surprisingly, in the same ranking attempt, phytodensity in the herb layer PD seemed to have no strong direct influence of on ant distribution (Tab. 10) except for the lowest range of the gradient (see section 4.2.4). However, by strongly modifying soil temperature and moisture, phytodensity has an enormous indirect influence on ant distribution in open habitats. The thermal effect of PD in 162 open-habitat study plots becomes most obvious if the meteorological component of soil temperature is removed by subtracting the value of calibrated basal soil temperature T_{BAS} from T_{MAX} and T_{MEAN}. The difference $D_{MAX} = T_{MAX} - T_{BAS}$ follows a highly significant negative exponential function with

$$D_{MAX} = 17.958\ e^{-0.0005\ PD}\ (r = 0.842,\ n = 162,\ p << 0.001) \quad [26]$$

and the difference $D_{MEAN} = T_{MEAN} - T_{BAS}$ follows a basically similar relation with

$$D_{MEAN} = 4.034\ e^{-0.0005\ PD}\ (r = 0.840,\ n = 162,\ p << 0.001) \quad [27].$$

Furthermore, soil moisture F correlates with PD following a highly significant polynomial function with

$$F = 1*10^{-11} *PD^3 - 3*10^{-7}*PD^2 + 0.002*PD + 3.32$$
$$(r = 0.524,\ n = 162,\ p << 0.001) \quad [28].$$

Diagrams of the dependency of ant species richness and biomass on phytodensity PD in the 162 open-land study plots are not shown here because these are very similar in both curvature and correlation to the relations valid for all 232 plots (Fig. 12). Functions [26] – [28] and Fig. 12 provide overwhelming evidence that massive increases of phytodensity and scrub encroachment in open habitats, mainly caused by decline of grassland management, and of sheep grazing in particular, by excessive nitrogen immissions and by shutdown of military training areas are the most important threats to ant biodiversity in open habitats of the research area. There are few local studies which support these impacts also for regions outside the study area. Wiezik et al. (2013) showed that shrub encroachment altered the composition and diversity of ant communities in abandoned grasslands of the western Carpathians, and nitrogen immissions by intensive agriculture has been made responsible for a strong decrease of habitat quality for ants on forest borders adjoining farmland in Belgium and the Netherlands (Dekoninck et al. 2010, Mabelis & Korczyńska 2016).

Table 13. Code numbers of study plots listed up according to different degrees of habitat change. The three columns at left refer to 65 study plots in open habitats revisited after 21 years (mean year of thorough ant investigation 1984, mean year of habitat re-assessment 2005) which remained basically inhabitable for ants. The fourth column lists up the study plots, in this case both open and woodland habitats, that became fully uninhabitable by ants due to flooding, transformation into mining areas or yearly ploughing.

habitats remaining basically inhabitable for ants			
weak or no habitat change	**significant habitat change**	**extreme habitat change**	**habitats that became uninhabitable for ants**
SP 1, SP 2, SP 4, SP 7, SP 9, SP 10, SP 15, SP 17, SP 18, SP 19, SP 27, SP 39, SP 40, SP 50, SP 73, SP 78, SP 83, SP 94, SP 95, SP 101,SP 113, SP 117, SP 119, SP 155, SP 157, SP 158, SP 181, SP 196, SP 201	SP 8, SP 14, SP 23, SP 24, SP 25, SP 28, SP 29, SP 34, SP 35, SP 37, SP 43, SP 54, SP 64, SP 65, SP 72,SP 88, SP 96, SP 114, SP 122, SP 132, SP 163, SP 182	SP 3, SP 21, SP 22, SP 25, SP 30, SP 31, SP 33, SP 36, SP 77, SP 107, SP 121, SP 131, SP 142, SP 147	SP 48, SP 85, SP 86, SP 90, SP 91, SP 92, SP 93, SP 108 = 3.4% of 232 study plots
29 = 44.6%	**22 = 33.8%**	**14 = 21.5%**	

An important management issue is sheep pasturing and the way it is performed. Before the year 1990, sheep pasturing was a significant factor shaping the habitat structure in 32 study plots. 84 % of these were situated in the German federal states Thüringen and Sachsen-Anhalt and the southern Alps and mainly on shallow soils over limestone not adequate for any use other than pasturing or alpine skiing. In 27 study plots the development of management after the year 1990 was known. Sheep pasturing was given up after 1990 in 59 % of these plots and maintained in only 41 %.

I want to illustrate here, also as a story of personal observation beginning with the year 1966, the change in sheep farming in the territory of the former East Germany – now forming the federal states Thüringen, Sachsen-Anhalt, Sachsen, Brandenburg and Mecklenburg-Vorpommern. Sheep density per unit area was here in 1989 five times higher than in West Germany and of significant economic importance (Bundesministerium für Ernährung, Landwirtschaft und Forsten 1999). After this, there was not only a decline in absolute numbers of sheep in East Germany but also a profound change in the way of management: there was a profound shift from traditional shepherding to sheep paddocking. A traditional shepherd, today a profession at the brink of extinction, was responsible in the 1980s for different subareas within a total territory of perhaps 10–30 km² depending on landscape structure. He drove, typically assisted by two well-trained shepherd dogs, a herd of some 500 sheep over pastures but also over margin stripes of arable land or along rural lanes (and in autumn and winter additionally over sowings of clover or lucerne in stubble fields). The sheep moved by slow speed over the ground, cutting vegetation in a moderate way and compacting the soil rather weakly, thus allowing herb layer plants to flower and fruit within the interval to the next grazing. This also produced small-scaled mosaic patterns – small patches with ripping out of vegetation, approaching raw soil conditions, alternate with larger moderately affected areas. Additionally, the feces of sheep, being well distributed over the ground, provided food and microhabitats for coprophages or fungi – the former being important as food organisms for many predators and the latter being important, to give an example, for germination of some orchids or gentians (Hempel 2008). Furthermore, transport of seeds attached to the fur of wandering sheep facilitated genetic exchange between isolated populations of plants. This mode of management was ideal for maintaining a high grassland biodiversity. The currently applied paddocking, in contrast, often results in the stay of high sheep densities in a certain area over more than a week – sometimes even perverted by the provision of supplementary food. This management may leave a trampled ground with only few millimeters of brown above-ground vegetation remaining.

Transforming pastures into cut meadows, as observed in SP 34, SP 114, SP 115, causes a horizontal homogenization of habitat structure as well as mechanical and thermal stress to ant nests. The T_{MAX} of a horizontal cut meadow situated at 51°N, 11°E and 300 m a.s.l. is 15.5°C when grasses have grown up to a mean height of 40 cm (Seifert & Pannier 2007). Some ant species can compensate for this thermal deficiency by constructing high mounds of soil or plant particles to collect as much as possible solar radiation. Cutting then the meadow down to a height of some 8 cm causes a sudden dramatic impact on the ant mounds which are not only decapitated with the broods scattered over the ground but there is also an increase of T_{MAX} to 22°C and a rapid decline of epigaean humidity. There are no direct studies of the consequences for ant populations of transforming dry to fresh pastures into cut meadows and the data of this monograph with only few cut meadows investigated can also not answer this question. However, concluded from my subjective impression in the field gathered during random collection throughout three decades, I expect a significant reduction in species richness and an increase of stress-resistant euryoecious species. Accordingly, nature conservation management should try to maintain as much as possible extensive pasturing in order to maintain highest biodiversity levels.

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