

Fine-scale grassland assemblage analysis in Central Europe: ants tell another story than plants (Hymenoptera: Formicidae; Spermatophyta)

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Abstract

We address whether vascular plants can serve as a surrogate for ants in fine-scale assemblage studies by investigating assemblages of four plots of a dry steppe habitat in eastern Austria. We found that ants drew another picture than plants with respect to evenness, assemblage similarity, meta-similarity between single assemblage similarity matrices, and spatial species turnover. Ant data was more robust to data transformation than plant data. Differences between plant and ant assemblages levelled when data were reduced to presence-absence mode. We suspect that, in general, the correlation between plant and ant assemblages may be higher for coarse-scale studies involving pronounced ecological differences between habitats.

Key words: Community ecology, conservation biology, evenness, assemblage similarity, spatial species turnover, surrogacy, ants, vascular plants, temperate grassland, Central Europe

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Introduction

Conservation biologists are confronted with the difficult task of biodiversity monitoring – tracking changes in the biological integrity of ecosystems (ANDERSEN & al. 2004). This task actually encompasses very different things: from estimating global species numbers to assessing the impact of management practices on local communities. As conservation biology is a discipline with a deadline, researchers soon came to realise that they need to find biological indicators, i.e. representatives that allow retrieval of information on the whole. As no single taxon completely represents the whole, indicator taxa selection is crucial (LANDRES & al. 1988, HILTY & MERENLENDER 2000). Practical constraints (time, money, and availability of specialists) enforce the search for optimal trade-offs for combining indicator groups (e.g., HOWARD & al. 1998). Numerous studies have explored the adequacy of biodiversity surrogates, but the findings from different regions and among distinct taxa are inconsistent and controversial (e.g., NOSS 1990, PRENDERGAST & al. 1993, HOWARD & al. 1998, PANZER & SCHWARTZ 1998, PHARO & al. 1999, NEGI & GADGIL 2002, SAETERSDAL & al. 2003, WALDHARDT 2003, SAUBERER & al. 2004).

Plants have a long tradition as objects in community ecology, conservation biology and related fields (e.g., KERNER VON MARILAUN 1863, SCHROETER 1926, WHITTAKER 1956, BRAUN-BLANQUET 1961, BAKKER 1965, AUSTIN & HEYLIGERS 1989). This is due, among others, to the practicability of assessing sessile organisms, the importance of plants as primary producers and structural elements of habitats, and their well-studied information con-

tent on abiotic factors (e.g., ELLENBERG 1988). The occurrence and abundance of plant species enables ecologists to assess the prevailing environmental conditions (ENGLISCH & KARRER 2001). Thus vegetation data have become the prime source for habitat characterization (e.g., WHITTAKER 1973), in monitoring programmes (SPELLERBERG 1991), and for assessing global biodiversity hot-spots (e.g., MYERS & al. 2000).

Arthropods constitute the vast majority of global biodiversity. Among arthropods, ants are considered as ecologically dominant in most terrestrial environments. While ants have been increasingly appreciated as an indicator group in some regions (e.g., BESTELMEYER & WIENS 2001, ANDERSEN & al. 2004), their inclusion into conservation biology is still in its infancy in Central Europe (STEINER & SCHLICK-STEINER 2002). There are several parallels between plants and ants (ANDERSEN 1991, LÓPEZ & al. 1994), but the shared character most important for biological indication is their sessile life-style, which allows for a high exactness in topographical allocation of data (STEINER & SCHLICK-STEINER 2002).

There is an ongoing debate on whether plants can be surrogates for arthropods in biodiversity monitoring. Some argue that the distribution of arthropods is more finely patterned than that of plants (ANDERSEN & al. 2004, and references therein), others observed that conservation measures designed for plants are likewise beneficial for arthropods (e.g., PANZER & SCHWARTZ 1998). A series of biodiversity studies have compared plants with ants, but mostly with respect to species richness (e.g., NEGI & GADGIL

2002, DAUBER & al. 2003, SAUBERER & al. 2004). It is increasingly recognized that assemblage characteristics are preferable (SU & al. 2004), but only a few studies met this concern (GALLÉ 1980, GADAGKAR & al. 1993, DUELLI & OBRIST 1998, GALLÉ & al. 1998, OSBORN & al. 1999, BESTELMEYER & WIENS 2001, PFEIFFER & al. 2003). Their findings, however, were not unanimous: some found correlations between plants and ants across study sites, some did not.

Here, we address whether vascular plants can serve as a surrogate of ants in fine-scale assemblage studies in Central Europe. We compare vegetation (species assemblages with cover-abundance-data) and ant nest density data from different plots of a dry steppe habitat with respect to (a) species richness and evenness, (b) assemblage similarity, and (c) spatial species turnover.

Material and Methods

Sampling

The study site was a semi-natural dry grassland extensively grazed by sheep (phytocoenosis: *Ranunculo illyrici-Festucetum valesiacae*, ENGLISH & JAKUBOWSKY 2001) on Hundsheimer Berg (eastern Austria, 465 - 470 m a.s.l., 48° 07' N, 16° 56' E; Fig. 1). Four 20 × 20 m plots (1 - 4) were selected (Fig. 1). Plot selection aimed at minimum among-plots variation with respect to vegetation (based on data from ENGLISH & JAKUBOWSKY 2001), exposition (WSW), inclination (c. 2 %), distance to the nearest wood margin (c. 150 m) and grazing regime over the past 20 years (E. Zillner, pers. comm). Vegetation structure was relatively homogeneous within plots.

Vascular plants were assessed in 5 × 5 m quadrats located in the centre of each plot (Fig. 1). Plant species assemblage and vegetation cover was investigated in 2004 at different phenological states, from late spring to late summer. ADLER & al. (2004) was used as the standard reference for flowering plants and ferns. Quantitative plant cover estimates were obtained for each species applying the Londo's decimal scale (LONDO 1976) adjusted for low cover values. Mean percentage values of the respective cover classes were deployed for untransformed abundance values.

Ants were assessed inside two 5 × 5 m quadrats, adjoining but not overlapping plant quadrats, per plot in May 2004. We aimed at a complete search for ant nests in the quadrats by carefully cm-wise pushing apart of the vegetation using small rakes and by screening of the soil surface. Upon any signs of ant nests, such as nest entrances, little heaps of soil, disposal, dead ant workers or workers returning to the nest with food, the soil was opened and ant nests were sampled (cf. SEIFERT 1986). Ants were determined according to SEIFERT (1996) or – two samples of *Lasius* (*Chthonolasius*) – by B. Seifert. In addition to morphology-based determination, DNA sequences (1000 bp of the mitochondrial gene COI; methods in STEINER & al. 2005) of five samples of *Tetramorium* were compared with GenBank entries AY641728, AY641659 and AY641661 – species identification of some Central European *Tetramorium* species entirely based on morphology is less reliable than a combined approach using morphological and molecular methods (cf. STEINER & al. 2005). Reference specimens are kept in the collection of BCS & FMS. Nest densities (nests per m²) were calculated by pooling data from the two sub-plots.

Assemblage statistics

To characterise the plant and ant assemblages of the single plots, we calculated evenness *E* as the portion (%) of the Shannon diversity index *H'* (SHANNON & WEAVER 1949), based on *ln*, of the maximum value of *H'* for the observed number of species.

As a measure of assemblage similarity across plots, we computed Wishart's similarity ratio, a semi-metric measure suitable for R-mode analysis of ecological data matrices with various double-zero values (WESTHOFF & VANDER MAAREL 1978). Analyses were performed with untransformed data, with data after square root transformation and with data reduced to presence-absence mode. For visualisation we chose diagrams of hierarchical cluster analysis (average linkage between groups, LEGENDRE & LEGENDRE 1998) using SPSS 10.0.7 (SPSS INC. 1999).

Subsequently, we computed a meta-similarity between plant and ant assemblages. Similarity ratios of the single assemblages were compared by calculating a similarity value between all pairs of matrices, using Spearman rank-correlation by 2Stage analysis in PRIMER 5.2.9 (CLARKE & GORLEY 2001). Non-Metric Multi Dimensional Scaling (NMDS, KRUSKAL 1964) analysis was conducted from the resulting matrix of the 2Stage analysis (similarities converted to distances) in order to examine differences in compositional patterns of ant and plant assemblages. The placement of plots and number of axes in the NMDS ordination were calculated as the solution minimizing the final divergence between the dissimilarities in the original data matrix and the dissimilarities in the reduced ordination matrix. The distortion of the final model was measured by Kruskal's STRESS (Standardized Residual Sum of Squares), ranging from 0 to 1, with lower values indicating better reproduction of the original dissimilarities (see LEGENDRE & LEGENDRE 1998).

To assess spatial species turnover, we computed Jaccard's Index from presence-absence data of the plant and ant data matrix ($JI = a / (a + b + c)$), where *a* are species in common for two plots compared, *b* is the species loss, and *c* is the species gain in relation to the first plot (LEGENDRE & LEGENDRE 1998), and expressed it in terms of dissimilarity ($JD = 1 - JI$). *JD* varies from 0 (identical species composition) to 1 (no overlap of species across plots).

Results

In vascular plants, total species richness *S* was 74, for single plots it varied from 39 to 51. The percentage cover for single species ranged from 0.1 to 40, the sum of mean cover from 146 to 163 (Tab. 1). Ant sampling yielded a total of 160 nests of eight species. For single plots species richness varied from five to six, with a total of 33 to 50 nests per plot (Tab. 1). Values of evenness *E* ranged from 68.1 to 78.7 % for plants, and from 45.8 to 97.5 % for ants for every plot. The low values of plant evenness are due to the high abundance of the grass species *Festuca valesiaca* SCHLEICH. ex GAUDIN and *Koeleria macrantha* SCHULT., which form from 30 to 42 % of the total plant cover. The five most abundant species result in about 50 to 56 %, while the rarest 25 per plot sum up to a maximum of 20 % cover. The broad range over which evenness varies in ants is mainly due to very high abundance and percentage abundance values of *Lasius alienus* (FÖRSTER, 1850) in plot 1. While this ant has the highest percentage

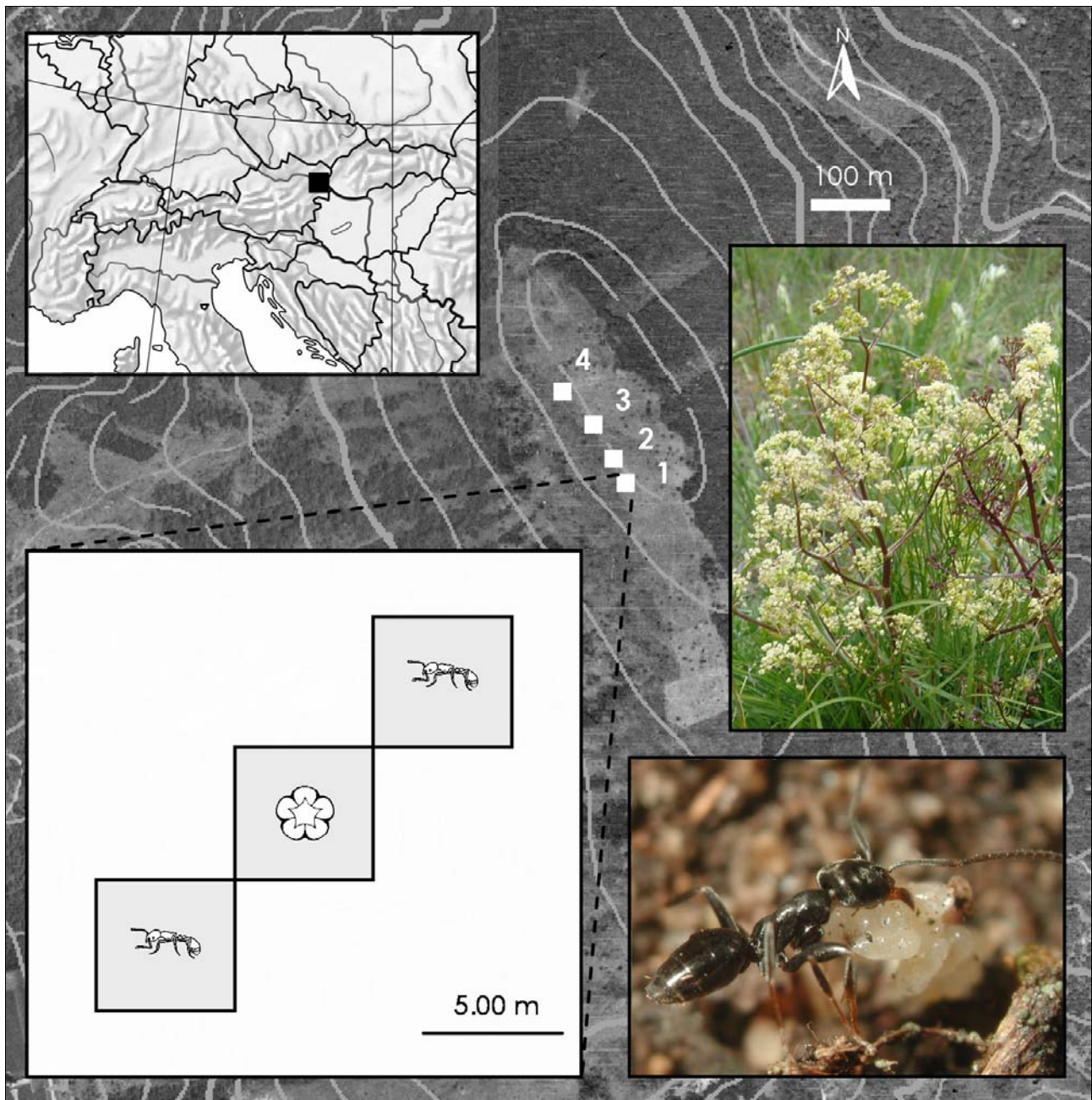


Fig. 1: Partial map of Central Europe with indication of study site (left upper corner), orthophoto of the study site showing plots 1 - 4; position of plant and ant subplots within plots, as indicated by symbols (left lower corner), and photographs of each a plant (*Trinia glauca* (L.) DUMORT., a dioecious Umbelliferae) and an ant (*Tapinoma erraticum* (LATREILLE, 1798)) typical for the study site.

abundance in every single plot, in plot 1 it reaches 80.0 %, compared to 30.3 - 35.3 % in the other plots.

Cluster diagrams of Wishart's similarity ratio values across plots (Fig. 2) illustrated differences between plants and ants. (a) Branching order was converse, irrespectively of data transformation: Plot 1 was least similar to all other plots in ants, but among the plots with highest similarity ratio values in plants. (b) The range over which similarities varied differed between plants and ants: Three of four ant assemblages clustered closer than any plant assemblages did, while one (plot 1) was more distant to the others than any plant assemblages were. (c) Plant and ant data

responded differently to transformation: Transformation caused a shift in branching order in plants, but branching order did not change with transformation in ants.

The NMDS ordination based on the meta-similarity values (Fig. 3) gave a very good representation of the matrix (STRESS = 0.0). It visualized a higher impact of data transformation on plants (longer distances between data points in the plot) than on ants. Additionally, meta-similarity values of plants and ants were ordinated closest when based on presence-absence data.

Spatial species turnover (JD) ranged from 0.39 to 0.51 in plants and from 0.00 to 0.43 in ants for the adjacent

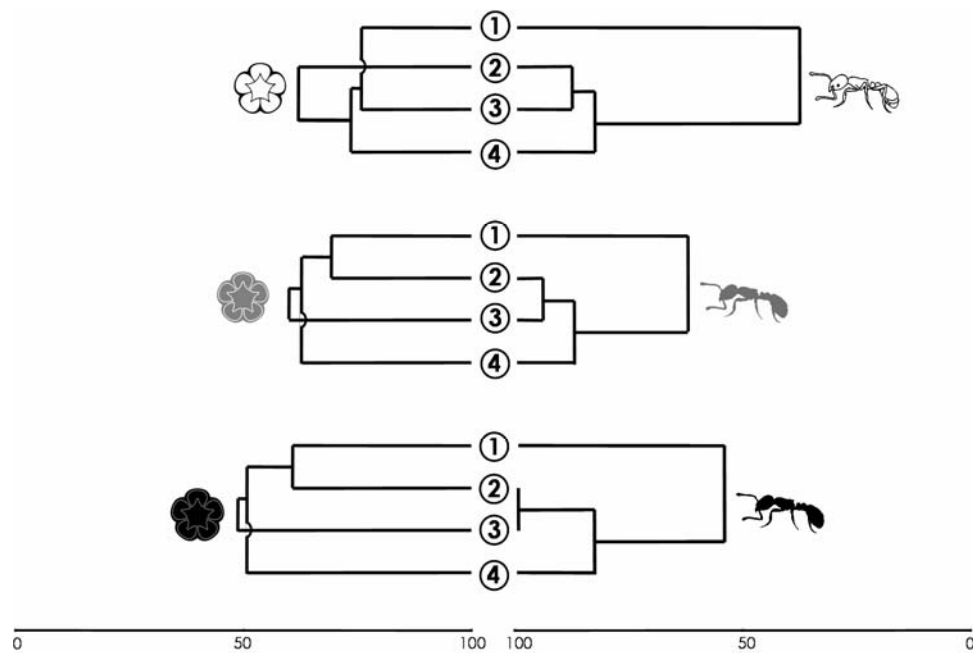


Fig. 2: Similarity between the plant and ant (indicated by symbols) assemblages of the four plots 1 - 4: cluster diagrams (average linkage between groups) of Wishart's similarity ratio values of untransformed data (white symbols), data after square root transformation (grey symbols) and data reduced to presence-absence mode (black symbols).

Tab. 1: Characteristics of plant and ant assemblages of the four plots (1 - 4) on Hundsheimer Berg: abundance (total sum of mean abundance / 25 m² in plants, nests / 50 m² in ants), species richness S, Shannon diversity index H', evenness E (%).

Plot	Group	Abundance	S	H'	E
1	plants	155	39	2.88	78.7
	ants	50	6	0.82	45.8
2	plants	150	43	2.76	73.4
	ants	34	5	1.42	88.2
3	plants	163	43	2.56	68.1
	ants	33	5	1.57	97.5
4	plants	146	51	2.87	73.0
	ants	43	6	1.56	87.2

plot comparisons (Tab. 2). The mean turnover was 0.48 for plants and 0.27 for ants. Despite generally lower values of spatial species turnover, higher variability among plots was indicated in ants.

Tab. 2: Spatial species turnover expressed as dissimilarity (JD) for the four-plot-sequence (1 / 2 / 3 / 4) and overall value (arithmetic mean) for plants and ants.

Plots	Geographic distance (m)	Plants (JD)	Ants (JD)
1 / 2	34	0.39	0.43
2 / 3	50	0.49	0.00
3 / 4	57	0.51	0.17
overall spatial species turnover		0.48	0.27

Discussion

In our study, plant species richness is in an order of magnitude characteristic for temperate grassland which is given as 30 to 60 species (ELLENBERG 1988, BARTHOLOTT & WINIGER 1998). Vegetation shows a high homogeneity across plots as reflected by abundance, species richness and evenness (Tab. 1), and similarity of assemblages (Fig. 2). The high values of spatial species turnover in plant assemblages (Tab. 2) are largely caused by infrequent ("satellite") species. Satellite species comprise species with broad

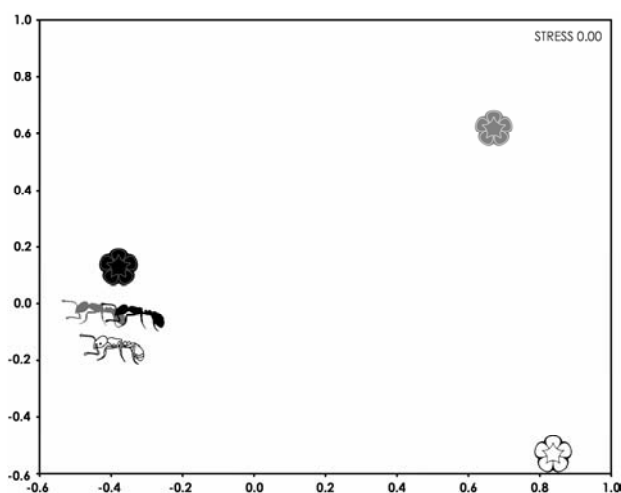


Fig. 3: Meta-similarity between plant and ant assemblages: Two-dimensional NMDS ordination of Wishart's similarity values between similarity ratio matrices of the single plant and ant assemblages (indicated by symbols; data points in centre of flower symbol and in centre of ant mesosoma), of untransformed data (white), data after square-root transformation (grey) and data reduced to presence-absence mode (black); Kruskal's STRESS value given.

ecological amplitude, species for which nutrient-poor habitats offer only suboptimal conditions (e.g., ruderals: *Plantago lanceolata*, *Stellaria media*), and species that substitute each other due to similar functional roles (e.g., short-lived annuals: *Erophila verna* (L.) CHEVALL., *Holosteum umbellatum* L.). On the other hand, the core set of plant species, forming the diagnostic species combination of the studied vegetation type, does not vary much across plots, which corresponds to other grassland studies (e.g., PÄRTEL & al. 2001).

Ant species richness values are rather low compared to other Central European grassland studies (SEIFERT 1986, SCHLICK-STEINER & al. 2003): this might be due to within-habitat homogeneity of vascular plants (KASPARI & al. 2000). Abundance and species richness are rather constant across plots, but a pronounced heterogeneity of ant assemblages is revealed by evenness, similarity of assemblages and spatial species turnover. A clumped distribution of *Lasius alienus* nests may be suspected, as was suggested by GALLÉ (1978) for "*Lasius alienus*" = *Lasius psammophilus* (SEIFERT, 1992) according to today's taxonomy (L. Gallé, pers. comm.).

Overall, from our study on species assemblages of a Central European dry grassland, ants drew another picture of their habitat than vascular plants. Our results agree with a number of studies which likewise revealed that variation of ant assemblages frequently does not correlate with that of vegetation (GALLÉ 1980, DUELLI & OBRIST 1998, GALLÉ & al. 1998, OSBORN & al. 1999, BESTELMEYER & WIENS 2001). In contrast, two other studies found a correlation between assemblage characteristics of plants and ants, namely in Indian forest habitats (GADAGKAR & al. 1993) and in Mongolian steppe and desert habitats (PFEIFFER & al. 2003). However, among-site variations of habitat quality were much more pronounced in those studies than in

the present case. We guess that plant and ant assemblages increasingly co-vary at larger geographic scale or with increasing habitat heterogeneity.

Ant data in our study turn out to be more robust with respect to data transformation than plant data, as illustrated by the constant branching order in the cluster diagrams of the similarity ratio values (Fig. 2) and by smaller differences of meta-similarity between ant assemblages after different data transformations (Fig. 3). OSBORN & al. (1999) also observed greater robustness of ant versus vegetation data for Venezuelan forests. Our study once again highlights the importance of quantitative data on plant and ant assemblages: Ecosystem function is not influenced solely by species richness, but species identity, abundance, and functional traits of species are moreover important for community structure, interactions, productivity and stability (HECTOR & al. 1999, LOREAU & al. 2001). The extant differences between plants and ants were less well highlighted when presence-absence data were used only (Fig. 3).

Plant species composition and quantitative cover differences essentially determine habitat structure, and are especially important for small and herbivorous species (BROWN & al. 1990, DENNIS 2003) exhibiting strong effects on insect species richness and abundances (e.g., HADDAD & al. 2001). The pattern exclusively detected based on the ant assemblage analysis is relevant for community ecology and conservation biology: On the one hand, ant assemblage characters constitute important habitat characters themselves (CRIST & WIENS 1996) because ants play important roles in their ecosystem with respect to biomass and energy turnover and are among the most important invertebrate predators and soil engineers (reviewed by STEINER & SCHLICK-STEINER 2002). On the other hand, ants were repeatedly found to serve as indicators of other habitat characters such as disturbance, successional change and rangeland condition (e.g., BURBIDGE & al. 1992, HOFFMANN 2000, SCHLICK-STEINER & al. in press).

In conclusion, plants are clearly no surrogate for ants in fine-scale community ecology studies and this may well apply to a range of other invertebrate groups as well (cf. ANDERSEN & al. 2004, DANGERFIELD & al. 2003). Nevertheless, for coarser studies of clearly differing habitats, ants may not yield that much additional information. In terms of applied conservation biology, our finding is a further argument in favour of selecting more than one taxon as a biodiversity indicator and of integrating ants into multi-taxa approaches to define conservation priorities and implement biodiversity monitoring programs (NOSS 1990, KOTZE & SAMWAYS 1999, BESTELMEYER & WIENS 2001).

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Zusammenfassung

Liefern Gefäßpflanzen in kleinräumigen Gemeinschaftsstudien ausreichend Information, um die Untersuchung von Ameisengesellschaften zu ersetzen? Auf vier Flächen eines Trockenrasenlebensraums in Ostösterreich ergaben Ameisen ein anderes Bild als Pflanzen, hinsichtlich Evenness, Gemeinschaftsähnlichkeit, Meta-Ähnlichkeit zwischen Ähnlichkeitsmatrizen und räumlichem Wechsel des Artenbestandes ("Artenaustausch"). Ameisendaten waren robuster gegenüber Transformationen als Pflanzendaten. Unterschiede zwischen Pflanzen- und Ameisengemeinschaften zeigten sich weniger deutlich, wenn ausschließlich qualitative Daten herangezogen wurden. Wir vermuten, dass die Korrelation zwischen den zöologischen Kennwerten von Pflanzen- und Ameisengemeinschaften in großräumigeren Untersuchungen und bei stärkeren ökologischen Unterschieden zwischen den Lebensräumen zunimmt.

References

- ADLER, W., OSWALD, K. & FISCHER, R. 1994: Exkursionsflora von Österreich. – Ulmer, Stuttgart, 1180 pp.
- ANDERSEN, A.N. 1991: Parallels between ants and plants: implications for community ecology. In: HUXLEY, C.R. & CUTLER, D.F. (Eds.): Ant-plant interactions. – University Press, Oxford, pp. 539-553.
- ANDERSEN, A.N., FISHER, A., HOFFMANN, B.D., READ, J.L. & RICHARDS, R. 2004: Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. – *Austral Ecology* 29: 87-92.
- AUSTIN, M.P. & HEYLIGERS, P.C. 1989: Vegetation survey design for conservation: Gradsect sampling of forests in North-Eastern New South Wales. – *Biological Conservation* 50: 13-32.
- BAKKER, A. 1965: Botanical grassland research and nature conservation. – *Netherlands Journal of Agricultural Science* 13: 190-200.
- BARTHOLOTT, W. & WINIGER, M. 1998: Biodiversity. A challenge for development research and policy. – Springer, Berlin Heidelberg New York Tokyo, 448 pp.
- BESTELMEYER, B.T. & WIENS, J.A. 2001: Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. – *Ecological Applications* 11: 1123-1140.
- BRAUN-BLANQUET, J. 1961: Die inneralpine Trockenvegetation von der Provence bis zur Steiermark. – *Geobotanica Selecta* 1: 1-273.
- BROWN, V.K., GIBSON, C.W.D. & STERLING, P.H. 1990: The mechanisms controlling insect diversity in calcareous grasslands. In: HILLIER, S.H., WALTON, D.W.H. & WELLS, D.A. (Eds.): Calcareous grasslands - ecology and management. – Bluntisham Books, Bluntisham UK, pp. 79-87.
- BURBIDGE, A.H., LEICESTER, K., MCDAVITT, S. & MAJER, J.D. 1992: Ants as indicators of disturbance at Yanchep National Park, Western Australia. – *Journal of the Royal Society of Western Australia* 75: 89-95.
- CLARKE, K.R. & GORLEY, R.N. 2001: PRIMER v5: User Manual/Tutorial. – PRIMER-E, Plymouth, 91 pp.
- CRIST, T.O. & WIENS, J.A. 1996: The distribution of ant colonies in a semiarid landscape: implications for community and ecosystem processes. – *Oikos* 76: 301-311.
- DANGERFIELD, J.M., PIK, A.J., BRITTON, D., HOLMES, A., GILLINGS, M., OLIVER, I., BRISCOE, D. & BEATTIE, A.J. 2003: Patterns of invertebrate biodiversity across a natural edge. – *Austral Ecology* 28: 227-236.
- DAUBER, J., HIRSCH, M., SIMMERING, D., WALDHARDT, R., OTTE, A. & WOLTERS, V. 2003: Landscape structure as an indicator of biodiversity: matrix effects on species richness. – *Agriculture, Ecosystems and Environment* 98: 321-329.
- DENNIS, P. 2003: Sensitivity of upland arthropod diversity to livestock grazing, vegetation structure and landform. – *Food Agriculture & Environment* 1: 301-307.
- DUELLI, P. & OBRIST, M.K. 1998: In search of the best correlates for local organismal biodiversity in cultivated areas. – *Biodiversity and Conservation* 7: 297-309.
- ELLENBERG, H. 1988: Vegetation ecology of Central Europe. – University Press, Cambridge, MA, 989 pp.
- ENGLISCH, T. & KARRER, G. 2001: Zeigerwertsysteme in der Vegetationsanalyse – Anwendbarkeit, Nutzen und Probleme in Österreich. – *Berichte der Reinhold-Tüxen Gesellschaft* 13: 83-102.
- ENGLISCH, T. & JAKUBOWSKY, G. 2001: Standortökologie, Chorologie und Diversität pannonischer Trockenrasen im NSG "Hundsheimer Berg - Braunsberg" (Hainburger Berge, Niederösterreich). – *Berichte der Reinhold-Tüxen-Gesellschaft* 13: 235-240.
- GADAGKAR, R., NAIR, P., CHANDRASHEKARA, K. & BHAT, D.M. 1993: Ant species richness and diversity in some selected localities in Western Ghats, India. – *Hexapoda* 5: 79-94.
- GALLÉ, L. 1978: Dispersion of the nests of an ant species (Hymenoptera: Formicidae). – *Acta Biologica Szeged* 24: 105-109.
- GALLÉ, L. 1980: Dispersion of high density ant populations in sandy soil grassland ecosystems. – *Acta Biologica Szeged* 26: 129-135.
- GALLÉ, L., KÖRMÖCZI, L. & KERÉKES, J. 1998: Structure of ant assemblages in a Middle-European successional sand-dune area. – *Tiscia* 31: 19-28.
- HADDAD, N.M., TILMAN, D., HAARSTAD, J., RITCHIE, M. & KNOPS, J.M.H. 2001: Contrasting effects of plant richness and composition on insect communities: A field experiment. – *The American Naturalist* 158: 17-35.
- HECTOR, A., SCHMID, B., BEIERKUHNLEIN, C., CALDEIRA, M.C., DIEMER, M., DIMITRAKOPOULOS, P.G., FINN, J., FREITAS, H., GILLER, P.S., GOOD, J., HARRIS, R., HÖGBERG, P., HUSS-DANELL, K., JOSHI, J., JUMPPONEN, A., KÖRNER, C., LEADLEY, P.W., LOREAU, M., MINNS, A., MULDER, C.P.H., O'DONOVAN, G., OTWAY, S.J., PEREIRA, J.S., PRINZ, A., READ, D.J., SCHERER-LORENZEN, M., SCHULZE, E.-D., SIAMANTZIOURAS, A.-S. D., SPEHN, E.M., TERRY, A.C., TROUMBIS, A.Y., WOODWARD, F.I., YACHI, S. & LAWTON, J.H. 1999: Plant diversity and productivity experiments in European grasslands. – *Science* 286: 1123-1127.
- HILTY, J. & MERENLENDER, A. 2000: Faunal indicator taxa selection for monitoring ecosystem health. – *Biological Conservation* 92: 185-197.
- HOFFMANN, B.D. 2000: Changes in ant species composition and community organisation along grazing gradients in semi-arid rangelands of the Northern Territory. – *Rangeland Journal* 22: 171-189.
- HOWARD, P.C., VISKANIC, P., DAVENPORT, T.R.B., KIGENYI, F.W., BALTZER, M., DICKINSON, C.J., LWANGA, J.S., MATTHEWS, R.A. & BALMFORD, A. 1998: Complementarity and the use of indicator groups for reserve selection in Uganda. – *Nature* 394: 472-475.
- KASPARI, M., O'DONNELL, S. & KERCHER, J.R. 2000: Energy, density, and constraints to species richness: Ant assemblages along a productivity gradient. – *The American Naturalist* 155: 280-293.
- KERNER VON MARILAUN, A. 1863: Das Pflanzenleben der Donauländer. – Universitätsverlag Wagner, Innsbruck, 238 pp.

- KOTZE, D.J. & SAMWAYS, M.J. 1999: Support for the multi-taxa approach in biodiversity assessment, as shown by epigaeic invertebrates in an Afrotropical forest archipelago. – *Journal of Insect Conservation* 3: 125-143.
- KRUSKAL, J.B. 1964: Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. – *Psychometrika* 29: 1-27.
- LANDRES, P.B., VERNER, J. & THOMAS, J.W. 1988: Ecological uses of vertebrate indicator species: a critique. – *Conservation Biology* 2: 316-328.
- LEGENDRE, L. & LEGENDRE, P. 1998: Numerical ecology. Second edition. – *Developments in Environmental Modelling* 20. Amsterdam, Elsevier Scientific Publishing, 870 pp.
- LONDO, G. 1976: The decimal scale for relevés of permanent quadrats. – *Vegetatio* 33: 61-64.
- LÓPEZ, F., SERRANO, J.M. & ACOSTA, F.J. 1994: Parallels between the foraging strategies of ants and plants. – *Trends in Ecology and Evolution* 9: 150-153.
- LOREAU, M., NAEEM, S., INCHAUSTI, P., BENGTSSON, J., GRIME, J.P., HECTOR, A., HOOPER, D. U., HUSTON, M.A., RAFAELLI, D., SCHMID, B., TILMAN, D., & WARDLE, D.A. 2001: Biodiversity and ecosystem functioning: Current knowledge and future challenges. – *Science* 295: 804-808.
- MYERS, N., MITTERMEIER, R.A., MITTERMEIER, C.G., DA FONSECA, G.A.B. & KENT, J. 2000: Biodiversity hotspots for conservation priorities. – *Nature* 403: 853-858.
- NEGI, H.R. & GADGIL, M. 2002: Cross-taxon surrogacy of biodiversity in the Indian Garhwal Himalaya. – *Biological Conservation* 105: 143-155.
- NOSS, R.F. 1990: Indicators for monitoring biodiversity: a hierarchical approach. – *Conservation Biology* 4: 355-364.
- OSBORN, F., GOITIA, W., CABRERA, M. & JAFFÉ, K. 1999: Ants, plants and butterflies as diversity indicators: comparisons between strata at six forest sites in Venezuela. – *Studies on Neotropical Fauna and Environment* 34: 59-64.
- PANZER, R. & SCHWARTZ, M.W. 1998: Effectiveness of a vegetation-based approach to insect conservation. – *Conservation Biology* 12: 693-702.
- PÄRTEL, M., MOORA, M. & ZOBEL, M. 2001: Variation in species richness within and between calcareous (alvar) grassland stands: the role of core and satellite species. – *Plant Ecology* 157: 203-211.
- PFEIFFER, M., CHIMEDREGZEN, L. & ULYKPAN, K. 2003: Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. – *Journal of Biogeography* 30: 1921-1935.
- PHARO, E.J., BEATTIE, A.J. & BINNS, D. 1999: Vascular plant diversity as a surrogate for bryophyte and lichen diversity. – *Conservation Biology* 13: 2822-2892.
- PRENDERGAST, J.R., QUINN, R.M., LAWTON, J.H., EVERSAM, B.C. & GIBBONS, D.W. 1993: Rare species, the coincidence of diversity hotspots and conservation strategies. – *Nature* 365: 335-337.
- SAETERSDAL, M., GJERDEA, I., BLOM, H.H., IHLEN, P.G., MYRSETH, E.W., POMMERESCH, SKARTVEITB, R.J., SOLHØYB, T. & AAS, O. 2003: Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. – *Biological Conservation* 115: 21-31.
- SAUBERER, N., ZULKA, K.P., ABENSPERG-TRAUN, M., BERG, H.-M., BIERINGER, G., MILASOWSKY, N., MOSER, D., PLUTZAR, C., POLLHEIMER, M., STORCH, C., TRÖSTL, R., ZECHMEISTER, H. & GRABHERR, G. 2004: Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. – *Biological Conservation* 117: 181-190.
- SCHLICK-STEINER, B.C., STEINER, F.M. & MODER, K. 2003: Ant nests in linear habitats: A new technique for estimating the density of sedentary organisms. Simulation and case study. – *Sociobiology* 42: 163-174.
- SCHLICK-STEINER, B.C., STEINER, F.M. & STEINER, H.M. in press: Effect of extensification of coppice management on Central European ant assemblages (Hymenoptera: Formicidae). – *Entomologia Generalis*.
- SCHROETER, C. 1926: Das Pflanzenleben der Alpen. – Albert Rautenstein, Zürich, 1288 pp.
- SEIFERT, B. 1986: Vergleichende Untersuchungen zur Habitatwahl von Ameisen (Hymenoptera: Formicidae) im mittleren und südlichen Teil der DDR. – *Abhandlungen und Berichte des Naturkundemuseums Görlitz* 59: 1-124.
- SEIFERT, B. 1996: Ameisen: beobachten, bestimmen. – Naturbuch Verlag, Augsburg, 352 pp.
- SHANNON, C. & WEAVER, W. 1949: The mathematical theory of communication. – Urbana, University of Illinois Press, 117 pp.
- SPELLERBERG, I.F. 1991: Monitoring Ecological Change. – University Press, Cambridge, MA, 334 pp.
- SPSS INC. 1999: SPSS for Windows. Release 10.0.7, Standard Version. – SPSS Inc., Chicago, Illinois.
- STEINER, F.M. & SCHLICK-STEINER, B.C. 2002: Einsatz von Ameisen in der naturschutzfachlichen Praxis. Begründungen ihrer vielfältigen Eignung im Vergleich zu anderen Tiergruppen. – *Naturschutz und Landschaftsplanung* 34: 5-13.
- STEINER, F.M., SCHLICK-STEINER, B.C., SANETRA, M., LJUBOMIROV, T., ANTONOVA, V., CHRISTIAN, E. & STAUFFER, C. 2005: Towards DNA-aided biogeography: an example from *Tetramorium* ants (Hymenoptera, Formicidae). – *Annales Zoologici Fennici* 42: 23-35.
- SU, J.C., DEBINSKI, D.M., JAKUBAUSKAS, M.E. & KINDSCHER, K. 2004: Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. – *Conservation Biology* 18: 167-173.
- WALDHARDT, R. 2003: Biodiversity and landscape – summary, conclusions and perspectives. – *Agriculture, Ecosystems & Environment* 98: 305-309.
- WESTHOFF, V. & VAN DER MAAREL, E. 1978: The Braun-Blanquet approach. In: WHITTAKER, R.H. (Ed.): Classification of plant communities. – W. Junk, The Hague, pp. 287-399.
- WHITTAKER, R.H. 1956: Vegetation of the Great Smoky Mountains. – *Ecological Monographs* 26: 1-80.
- WHITTAKER, R.H. (Ed.) 1973: Ordination and classification of communities. – *Handbook of Vegetation Science* 5: 1-737.