Analysis of the regional distribution of epigeic arthropods 1. Distribution models for ground beetles

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Synopsis

Distribution models for ground beetles

Distribution patterns of carabid beetles were investigated in a c. 4 km^2 area of continuous beechforests on limestone by pitfall sampling. GIS based habitat parameters were used to derive models predicting the quantitative distribution of single species in the study area. The extraction of factors that provide an optimum description of the data is detailed in the instance of *Pterostichus madidus*. A two-factor model is presented that predicts the distribution in three classes of activity density from a soil moisture classification and a specific north/south area differentiation. The model describes 61% of the catches correctly, and only 2% deviate extremely, i.e. by two density classes. An alternative model is presented that is based on a combination of moisture and relief classifications. This alternative model has a lower correspondence with the data (56% correct, 6% extreme deviations) but is not area-specific and can thus be transferred to other regions.

Carabidae, Pterostichus madidus, modelling, ecogeography

1 Introduction

The distribution patterns of species can be studied on a wide range of spatial scales from microhabitats to global range (WIENS 1989). We adressed the question of predictability of species' quantitative distribution on a meso-scale, i.e. in a c. 4 km^2 landscape section of continuous beechforests on limestone. While the range of habitats was limited by geology and vegetation type, there was a high degree of variability due to different ages of harvested forest stands and varied topography. The carabid fauna of the wider area has been reviewed by DORNIEDEN (1997).

This contribution describes the development of a factorial distribution model for *Pterostichus madidus* (FABRICIUS). The aim of the study is a predictive model based on habitat parameters available for the entire study area. The necessary handling of large spatial datasets was accomplished with a geographic information system (GIS). This technology is increasingly applied in ecogeographic studies at large scales (HAINES-YOUNG & al. 1993, MILLER 1994).

2 Material and methods

2.1 Study area

The study area of 3.8 km^2 is situated at the south-eastern edge of the extended limestone plateau »Göttinger Wald« which is largely covered by harvested beechforests. The topography is characterized by large plateau areas, while a number of valleys and the edge of the plateau form moderate to steep slopes. The altitude of the study area varies from 270 to 420 m a.s.l., yearly climatic means are 700 mm rainfall (DAMMANN 1969) and 7–8°C (HÖVERMANN 1957). Soils are a range of rendzinas and loess-derived brown soils (THÖLE & MEYER 1979), the vegetation is classified as Carici- and Melico-Fageta (BÖTTCHER & al. 1981, DIERSCHKE 1989).

2.2 Habitat parameters

A range of habitat parameters of different quality, measurement scale, and resolution were available from GIS databases (cf. DÖRING 1996): (i) high-resolution data on aspect, slope, and elevation from a digital elevation model based on a 25 m grid (»DGM5«), (ii) a soil moisture classification from a coarse-grained soil status mapping (»Standortkartierung«), and (iii) information on tree species composition, age, and density averaged for harvesting units of several hectares from a forestry inventory (»Forsteinrichtung«). ARC/INFO was used for handling and combining the different datasets.

The soil moisture classification was in some parts inaccurate, due to either digitizing errors or inconsistent applications of the classification scheme. Still it is in large parts adequate and it was used for modelling because it is the best available continuous representation of moisture conditions for the entire study area. Other abiotic parameters have been determined as point data around the traps (DORNIEDEN, unpubl. Diploma thesis, Göttingen 1996). These data are not considered in this study because they cannot be extrapolated to larger areas and thus cannot be used for continuous spatial modelling.

2.3 Sampling

Carabid beetles were sampled with 189 pitfall traps for 1 year from July 1994 through July 1995 (cf. DORNIEDEN & al. 1996). Sampling followed a factorial design with 4 habitat parameters predefining local habitats. Sampling sites were determined as combinations of these parameters each differentiated into 3 classes: aspect (north, south, other), slope (flat, medium, steep), canopy age (young, medium, old), and soil moisture (dry, medium, wet). Only areas of 50x50 m^2 minimum size and 25 m distance to interior and exterior borders were considered as potential sampling sites so as to minimize influences of adjacent areas and artefacts from GIS data layer intersection. Under these conditions, 69 different factor combinations were realized in the area. For most of these combinations 3 replicate sampling plots were determined. For some combinations it was only possible to delineate 1 or 2 replicate plots resulting in a total of 189. Traps were operated with ethylene glycole, exchanged biweekly, and closed in mid-winter.

Pitfall traps give useful results only for adult carabids' population parameters (LÖVEI & SUNDERLAND 1996), and for the study area no information is available on true population densities, reproduction or larval survival. Pitfall catches are the population parameter that is measured, modelled and predicted in this study.

2.4 Statistical analysis

The evaluation of factors to be included in distribution models was by means of analysis of variance (ANOVA) of the original catch data, the evaluation of factorial distribution models was by means of contingency table analysis of original and model-predicted data after a transformation to 3 abundance-classes. SAS/STAT 6.11 procedures were used for computations. General Linear Models (GLM) were applied for the analysis of variance, data were log-transformed, and factor sum of squares (SS) were computed with a type III error assumption. Contingencies are described by the γ-coefficient for ordinal data and tested by χ^2.

3 Results

3.1 Original 4-factor model

The sampling design gives rise to an analysis of variance based on the original 4-factor classification. The results are presented for all 6 species of *Pterostichus* recorded (Table 1). This genus illustrates the array of distribution patterns from the dominant *P. burmeisteri* which was caught nearly everywhere and on the average in high numbers, to species caught in ±low numbers in ±large parts of the area *(P. madidus, P. melanarius, P. oblongopunctatus)*, to species caught only incidentally *(P. niger, P. strenuus)*. All Pterostichus species with notable frequencies were affected by at least one of the original habitat factors, and each factor had a significant influence on the distribution of at least two *Pterostichus* species (Table 1). But the overall explanation of the observed variance in numbers by this 4-factor model is very low, at most 25% in the case of *Pterostichus melanarius*. The analytic steps to derive better distribution models are subsequently described for *Pterostichus madidus*. This species was sampled in intermediate numbers and frequency and occurred mostly in the southern part of the study area (Fig. 1).

Table 1
Population parameters and primary distribution models for *Pterostichus* species.

Pterostichus spp.	Σ N	freq. (%)	med. (N>0)	GLM model R^2	GLM model P	model factors (P): aspect	slope	moist.	age
burmeisteri	5380	95	26	0.22	0.0001	0.055	**<0.001**	0.240	**<0.001**
madidus	1347	62	6	0.19	0.0001	**0.005**	**0.003**	**0.014**	0.614
melanarius	283	39	2	0.25	0.0001	**0.005**	**0.001**	**0.016**	**<0.001**
oblongopunct.	194	42	2	0.15	0.0003	0.418	**<0.001**	0.535	0.822
niger	25	6	1.5	0.08	0.0693	0.222	0.290	0.794	0.026
strenuus	1			0.04	0.5872				

Population parameters are the number of specimens sampled in 1 yr, the frequency in all 189 traps, and the median abundance in those traps where the respective species was caught. A General Linear Model without interaction is computed for ln(N+1) with aspect, slope, moisture, and age in 3 classes each. Significant (P < 0.05) factor-P's are in bold for overall significant models.

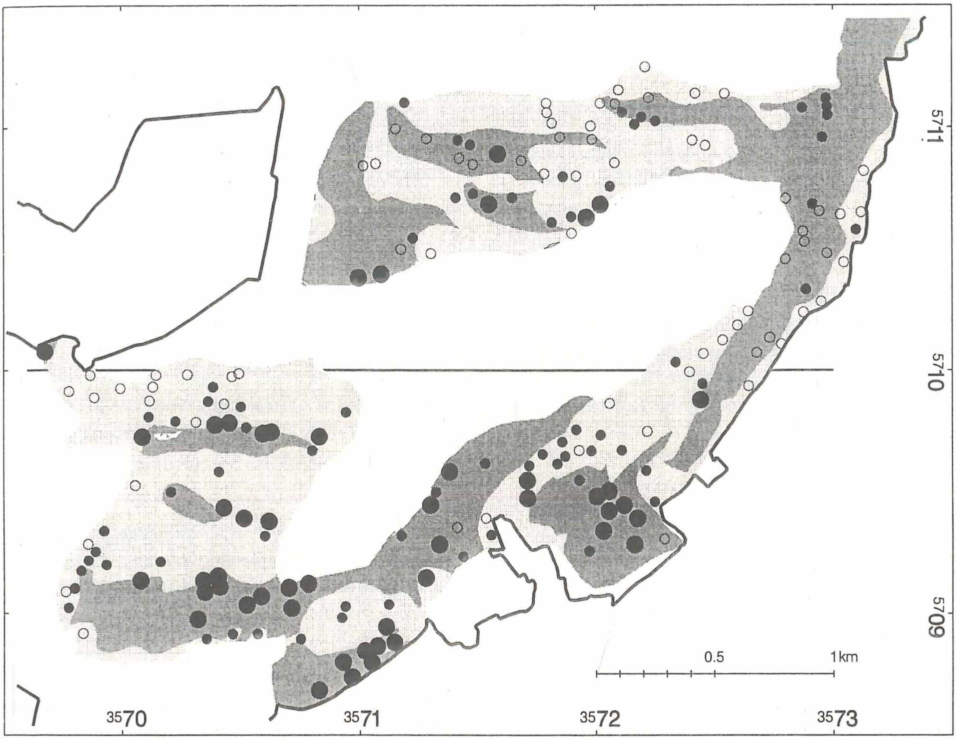

Fig. 1

Predicted abundance classes and sampling results for *Pterostichus madidus*. The study area is shaded in gray. The area is part of the forestry district Reinhausen-Wittmarshof. It is situated at the SE edge of the forested limestone plateau »Göttinger Wald«, the irregular lines delimit the exterior forest edge, NE of the study area a large open area is enclosed by the forest. At the margin coordinates of the Gauß-Krüger system are marked. The distribution model's area differentiation into a northern and a southern part is indicated by the horizontal line. Areas of relatively low and high predicted abundances in the respective part are shaded in light and dark gray, respectively. Actual pitfall catches in 1994/95 are given in 3 activity abundance classes: 0 specimens (open circles), 1–9 specimens (small dots), ≥10 specimens (large dots).

3.2 Optimized 2-factor model

The available habitat parameters (cf. 2.2) were tested in varying combinations to develop a modified ANOVA model. This iterative procedure cannot be regarded as a valid test of the resulting model but rather represents a heuristic tool to identify parameters of potential explanatory value. For the available dataset the best descriptive model consists of the soil moisture classification modified by an area differentiation. This differentiation was accomplished by simply deviding the area into north and south based on the centre of the N-S extension (cf. Fig. 1). The resulting ANOVA model (Table 2) identifies effects both of moisture classes and of N/S-location on the abundance of *P. madidus*, and there is also a significant interaction, i.e. the abundance at certain moisture class sites is modified by the location of these sites in the northern or southern area.

Abundances were classified as no occurrence, low and high densities, and factor class combinations were attributed to one of these classes following the actual average catch results. In the northern area, no occurrence is predicted except for low abundances in dry parts. In the southern area, low densities are predicted except for dry parts where high abundances are expected. A comparison of actual relative catch results with those predicted by the model reveals 61% correct descriptions (Table 3, cf. Fig. 1). There are only 3 traps (2%) with a deviation of the model prediction from the actual results by more than one density-class.

3.3 Model modification and operationalization

The revised model (3.2) represents an optimal model for the study area in terms of combining a minimum

Table 2

ANOVA of an optimized two-factor distribution model for *Pterostichus madidus*.

source	df	SS	MS	F	P
model	15	132.2	8.82	9.08	0.0001
error	173	168.0	0.97		
moisture	7	45.3	6.46	6.66	0.0001
area	1	45.5	45.47	46.84	0.0001
moist. x area	7	17.5	2.50	2.57	0.0151

A General Linear Model of ln(N+1) is computed with 8 moisture classes and 2 area classes with interaction, n=189, model R^2=0.44, factor SS's are type III. SS: sum of squares, MS: mean square, df: degrees of freedom.

Table 3

Contingency table analysis of a distribution model for *Pterostichus madidus* predicting abundance classes from soil moisture classes and a north/south area differentiation.

predicted catch-classes	actual catch-classes 0	1	2	no. of traps (model classes)
0	36	10	2	48
1	34	52	19	105
2	1	7	28	36
no. of traps (actual classes)	71	69	49	189

The 3 classes of actual and predicted catches are defined as 0, 1–9, and ≥10. χ^2 test: P=0.001, γ=0.81.

of factors/classes and a maximum of correct description of the data. A shortcoming of this model is its restriction to the original area because of the specific area differentiation which cannot be easily transferred to other areas (cf. STROTHMANN & al. 1998). This limitation may be solved either by replacing the »area« factor by area-independent parameters, or by selecting a different factor combination, i.e. by replacing the optimized model by an alternative model. The possibly reduced goodness of fit would be balanced by an operationalization of the distribution model allowing a transfer to other areas.

For the present dataset it was possible to develop an alternative 2-factor model by combining the original soil moisture classification with a topographic relief analysis (R. SCHULZ, pers. comm.). No occurrence of *Pterostichus madidus* is predicted for moist areas in valleys or on north-facing slopes, a high abundance is predicted for dry areas on south-facing slopes. The correspondence of model predictions with the actual catches (γ=0.60, Table 4) is less than that for the above model (γ=0.81, Table 3), yet it is statistically significant and the amount of correct descriptions is similar (56% compared to 61%). Extreme mismatches are increased to 11 traps (6%) of which the 5 traps with no specimens expected and the highest class recorded require further exploration of possible causes, while the other 6 traps may be regarded as casual or unexplicable artefacts of reduced trap efficiency.

Table 4

Contingency table analysis of a distribution model for *Pterostichus madidus* predicting abundance classes from soil moisture classes and a topographic classification.

predicted catch-classes	actual catch-classes 0	1	2	no. of traps (model classes)
0	34	19	5	58
1	31	43	15	89
2	6	7	29	42
no. of traps (actual classes)	71	69	49	189

The 3 classes of actual and predicted catches are defined as 0, 1–9, and ≥10. χ^2 test: P=0.001, γ=0.60.

4 Discussion

The habitat parameters used in the above distribution models are not optimal in an ecological sense, if proximate factors governing certain species' distribution patterns are well-known at all (cf. THIELE 1977). Still they are useful in the present context because they are on the one hand the best data that are available for the entire study area, and on the other hand they are at least correlated with local micro- or meso-climate. Erratic effects are to be expected from many sources, like data resolution, sampling method, mobility of carabids, trap-point microhabitat peculiarities, or from spatio-temporal population dynamics. If the stochastic nature of the true underlying distribution pattern in the area is considered, the correspondence between the data and the above deterministic factorial models has to be regarded as a good fit. A number of mismatches appear to be explicable by neighbourhood effects of trap locations (cf. Fig. 1), but this aspect has not been elaborated so far.

It is possible to construct different alternative models, and autocorrelations may obscur causal relations (cf. ROTHLÄNDER & al. 1998). To decide about the adequacy of a model, statistical parameters like contingency coefficients can be used, or parameter effects may be judged by their ecological sense.

These aspects have to be considered in a first step of evaluating competing models, but the crucial step is an independent test of the predictions. Therefore, the above optimized but area-specific model (3.2) was tested and could be confirmed through sampling at new trap sites in the study area (STROTHMANN & al. 1998). If an area-independent model is needed, it is necessary to derive a model with parameters that are available in other target areas. A transferable model is presented above (3.3), and sampling in other beechforests on limestone will have to decide upon its adequacy.

Future refinements of distribution models will have to incorporate possible effects of microhabitat conditions, spatial autocorrelation or neighbourhood diffusion. Also, potential interspecific effects have been neglected in the analyses presented in this study.

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