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Effects of landscape elements on the distribution of the rare bumblebee species *Bombus muscorum* in an agricultural landscape

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Abstract. The regional distribution pattern of *Bombus muscorum* was studied in an agricultural landscape of central Germany, one of two remaining areas with the occurrence of this nationally endangered species in the Land Hesse. To determine the landscape characteristics that facilitate the occurrence of *B. muscorum*, grid-based observation records were analysed in a GIS environment at a regional scale. A significantly negative effect of the number of trees on the occurrence of *B. muscorum* and a significantly positive one of the proportion of arable land, strongly support the species' preference for open landscapes. Yet, apart from open landscapes additional landscape features were shown to be important. A significantly positive effect of ditches in the final model revealed the importance of this landscape element for the occurrence of *B. muscorum*. This finding was additionally supported by recordings of nest-searching queens, nests, and flower visits along dithes. The positive effects of clover and fallow land indicate the species' need for suitable food resources throughout the season. Because *B. muscorum* exhibits small foraging ranges, it is essential that landscape elements that provide nesting sites, foraging habitats and undisturbed hibernation structures are next to each other. The low numbers of individuals of *B. muscorum* recorded indicate that the supply of these habitat elements may have reached a critical threshold in the study region.

Introduction

Since the intensification of agriculture during the 1950s the hitherto positive correlation between agricultural practices and species diversity became negative (Stoate et al. 2001). Declines in number of species in agricultural landscapes have been shown for plants and numerous animal groups (Sotherton and Self 1999). Pollinators, one of the most important functional groups in the landscape, are also negatively affected by modern agricultural techniques and the concurrent landscape changes (Williams 1989; Osborne and Corbet 1994; Buchmann and Nabhan 1996). In this regard, bumblebees are no exception; several species in Europe show diminishing ranges and declines in numbers (Williams 1986; Rasmont 1988; Williams et al. 1991).

The conversion from hay to silage production as well as the intensification of grassland management (Stoate 1996) has reduced suitable habitats for bumblebees. Furthermore, continuing enlargement of arable fields results in increasing fragmentation of remaining biotopes, such as hedgerows, field boundaries, ditches or path margins. The composition of the landscape is being severely altered (Meeus 1993), yet, the close proximity of certain habitats is often essential for the survival of species in a given landscape. Especially in the case of bumblebees, as central-place foragers, the spatial neighbourhood of nesting sites and foraging habitats, as well as the existence of undisturbed places for hibernation is essential (Svensson et al. 2000; Carvell 2002).

The maintenance of a diverse set of species within the taxon of bumblebees (*Bombus*) is of great value, not only from a conservational point of view, but also from an economical one. Besides many wild flowers, bumblebees pollinate numerous cultivated crops (Free 1993; O'Toole 1993; Watanabe 1994). Flowers with long corollas are especially dependent on the long-tongued species of bumblebees, such as *B. muscorum* (Rasmont et al. 1993). Whereas numerous studies have addressed foraging behaviour and distribution patterns of bumblebees at a small scale, such as within and between patches of flowers (Thomson 1996; Goverde et al. 2002), only recently has movement of bumblebees been studied at a landscape scale (Osborne et al. 1999; Walther-Hellwig and Frankl 2000; Bhattacharya et al. 2003; Kreyer et al. 2004). Analysing the effect of landscape structure on species richness and abundance of all species of bumblebees together, Steffan-Dewenter et al. (2002) did not find any significant result at neither spatial scale considered. However, it is highly probable that bumblebee species display species-specific activity ranges (Walther-Hellwig and Frankl 2000) and therefore react to the landscape structure at species-specific spatial scales.

B. muscorum, a species showing small activity ranges (Walther-Hellwig and Frankl 2000), occurs throughout Europe but disappeared from most of its range in the UK (Goulson 2003 and references therein) and is listed as endangered on the red list in Germany (Westrich et al. 1998).

The aim of the present study was to define the landscape characteristics that facilitate the occurrence of the critically endangered species *B. muscorum* in the 'Amöneburger Becken'. A geographic information system (GIS) was used to analyse this intensively used agricultural landscape, accommodating one of the remaining two verified populations of *B. muscorum* in the Land Hesse, Germany (Frommer 2001; Tischendorf 2001).

Methods

Study area and sampling

The study was conducted in the 'Amöneburger Becken', a basin landscape near Marburg, Hesse (Germany). Bumblebees were surveyed in an area of 60 km^2

(Gauss-Krueger coordinates of the centre point: 3492000, 5627500), ranging from 200 to 305 m above sea level. Ditches and brooks drain this formerly wet basin landscape, allowing for intensive agriculture on the predominant loess soils in the area. Except for small villages often surrounded by orchards, the landscape is open showing only few vertical landscape elements (Figure 1).

To create distribution maps of *B. muscorum* Reinig, a 1 km^2 grid was projected on the study area. Quadrats to be investigated were chosen systematically. In total, 31 out of 60 quadrats were sampled (Figure 2). Each of the sample quadrats chosen was investigated on five dates.

On each observation date, 70 min were spent in a quadrat to search for *B. muscorum*: spots of aggregated food resources were investigated for 30 min altogether, preferably six different locations were sampled for 5 min each; the remaining 40 min were available for the location of aggregated food resources along linear landscape elements (e.g. road and field margins, hedges, ditches and forest edges). Species name, sex, caste, and visited food resource as well as the quadrant (0.5 km × 0.5 km) in which a bumblebee was encountered were recorded during stationary observations and transect walks. Abundances were noted during transect walks only, to avoid double counts. Walking distances during the search for food resources were kept to around 3 km per quadrat and investigation. Landscape elements checked for bumblebees differed in width but showed a total width of around 2 m most of the time. All accessible linear

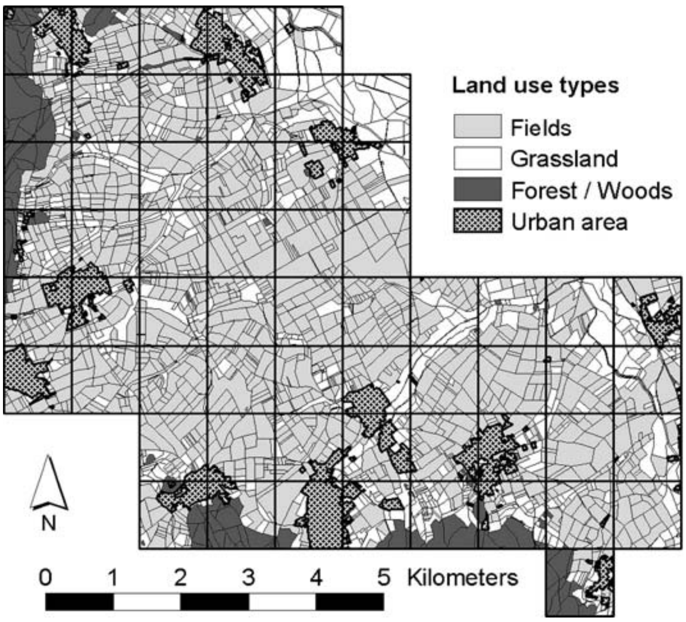

Figure 1. General map of the study area 'Amöneburger Becken' and distribution of main land use types.

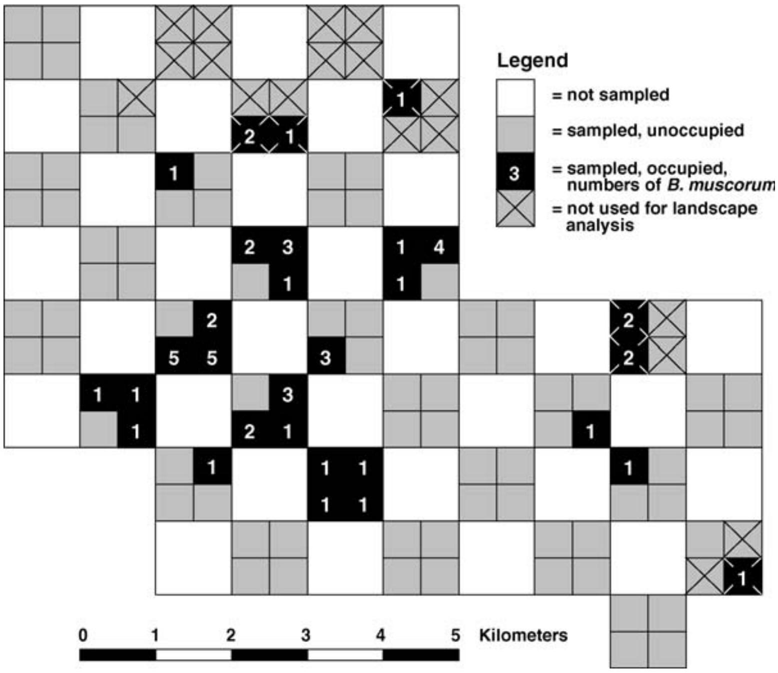

Figure 2. Distribution patterns of *Bombus muscorum* within the 'Amöneburger Becken'. Sampling units are underlayed in grey; presence of *Bombus muscorum* is indicated by black colour. Digits show abundances. Due to missing information for the landscape model, crossed sampling units were not used for spatial analyses.

landscape elements were covered over the whole sampling period. All individuals assigned to the species *B. muscorum* were caught with an insect net and checked for the absence of black hairs on the thorax to prevent mistake with *B. humilis*.

The order of quadrats to be investigated was changed randomly. Sampling took place from the beginning of June to the end of August 2001, between 0800 and 2000 h at temperatures above 12 °C on days without rain and stormy wind.

Landscape-models and analysis

Intensive mapping of land use and landscape elements within the study area during the years 1999 and 2000 (Walther-Hellwig 2001), as well as aerial photographs from 1999, provided the landscape information used in the present vector based GIS-landscape-models. The vertical structure, the potential supply of pollen and nectar and the suitability for nesting and hibernation of landscape elements guided the model-building. Models encompassed field crops with a detailed mapping of potential food resources including orchards, semi-natural landscape elements, single trees as well as woodlands and urban structures (Table 1). The topology of woodlands and urban areas as well as of semi-natural landscape elements, such as hedgerows, banks, ditches etc. showed only marginal changes over the mapping period. Superabundant food resources such as rape, clover, beans etc. were updated by additional mapping during fieldwork.

All spatial analyses were performed in ArcView 3.2 (ESRI Geoinformatik, Hannover, Germany) enhanced by several scripts and extensions, using the 0.5 km × 0.5 km grid. Due to missing landscape information on the margins of the study area, only a subset of 100 sampling units (Figure 2) could be considered while analysing the occurrence of *B. muscorum* in relation to landscape

Table 1. Landscape elements mapped as polygons, lines or points.

	LE	V
Polygon-Layer	[%]	
Camelina sativa (L.) Crantz	<0.1	1
Helianthus annuus L.	<0.1	1
Phacelia tanacetifolia Bentham	<0.1	1
Sinapis arvensis L.	0.1	1
Solanum tuberosum L.	0.4	1
Legumes	0.1	1
Pisum sativum ssp. L.	1.0	
Vicia faba L.	1.0	
Brassica napus L.	6.0	
Trifolium pratense L.	0.9	2
Trifolium repens L.	0.2	2
Fallow land	1.1	
Arable land	51.7	
Grassland	22.3	
Hedgerows and groves	0.5	3
Woodland	6.6	3
Orchards	0.5	4
Rural settlements	8.0	4
Line-Layer	[km]	
Brooks	47.9	
Ditches	18.3	
Flower-rich banks	14.8	5
Flower-rich structures	3.1	5
Grassland elements	6.8	
Flower-rich hedgerows	1.5	6
Hedgerows	10.3	6
Rows of trees	4.4	6
Field paths	355.9	
Streets	82.2	
Point-Layer	[*n*]	
Trees	2416	

LE = quantities of mapped landscape elements in the Amöneburger Becken; V: '#' variables assigned to new groups.

structure. The reduced area comprised only 24 of the 30 sampling units found to be occupied by *B. muscorum*. A multiple logistic regression was performed on the occurrence of *B. muscorum* in quadrants (0.5 km × 0.5 km) against the numbers of bumblebees encountered besides *B. muscorum* and the landscape variables mapped. Several landscape variables were combined in ecologically meaningful groups prior to analysis to prevent problems in convergence. The following groups were established: flower resources of rare crops (1), clover (2), woody structures (3), adjacent vertical structures (4), linear flower resources (5), and linear vertical structures (6) (Table 1). The new variable (3) was log-transformed to prevent the Hauck–Donner effect (Hauck and Donner 1977). Stepwise backward selection using the stepAIC procedure was applied for model reduction. All statistical analyses were performed using the statistical software R, version 1.7.1. (The Free Software Foundation Inc., Boston, USA).

Results

Presence, absence, abundance and food resources

During the present study 7 queens, 44 workers and 2 males of *B. muscorum* were recorded, representing 1.7% of the total number of bumblebees observed. *B. muscorum* was present in 30 of 124 quadrants (0.5 km × 0.5 km) (Figure 2). Individuals of *B. muscorum* were found visiting 13 different plant species; eight individuals were observed in flight. *Trifolium pratense* was most frequently used. Four out of 21 flower visits to *T. pratense* were recorded on agricultural cultivations (Table 2).

Table 2. Plant species utilized by *Bombus muscorum* and number of individuals observed on each plant species.

Species	Number of observed individuals of *Bombus muscorum*
Trifolium pratense L.	21
Trifolium repens L.	8
Vicia cracca L.	3
Lotus corniculatus L.	2
Lotus pedunculatus Cav.	2
Phacelia tanacetifolia Benth.	2
Stachys palustris L.	1
Centaurea jacea L.	1
Vicia sepium L.	1
Cirsium vulgare (Savi) Ten.	1
Lythrum salicaria L.	1
Galeopsis pubescens Bess.	1
Lathyrus pratensis L.	1

Table 3. Results of the multiple logistic regression (based on the presence of *Bombus muscorum*, numbers of individuals of other bumblebee species, and landscape composition).

Variable	Estimate	SE	*z*-value	*p*
Intercept	−4.194e + 00	1.480e + 00	−2.834	0.005
Clover (2)[a]	8.674e−05	5.813e−05	1.492	0.136
Arable land	1.727e−05	6.857e−06	2.519	0.012
Fallow land	9.305e−05	5.800e−05	1.604	0.109
Trees	−1.002e−01	4.326e−02	−2.318	0.020
Ditches	3.381e−03	1.589e−03	2.128	0.033

Originally, all 20 variables were fitted; the model was reduced using a stepwise backward selection with the AIC as criterion to omit terms.
[a]Clover is a combined variable, see Table 1.

Landscape analysis and evaluation of landscape elements

The predominant landuse in the 'Amöneburger Becken' is arable agriculture including several crops (60.7% of study area). Furthermore, intensively used meadows can be found on 22.3% of the area, in large parts along the river Ohm. Rural settlement structures make up an area percentage of 8%. Villages are often surrounded by orchards (0.5%). Forests, mainly found at the southern and western margins of the basin cover 6.6% of the study area. Table 1 contains area percentages (plane), lengths (linear) and numbers (punctual) of all landscape elements investigated.

The stepwise backward selection for the logistic regression retained five of 20 variables that were included in the original model (Table 3). The final model contained the variables arable land and ditches that showed significantly positive effects on the occurrence of *B. muscorum*. Also the presence of clover and fallow land contributed to the occurrence of the species in a positive way. In contrast, the number of trees showed a significantly negative effect on the presence of *B. muscorum* (Table 3).

Discussion

Most *B. muscorum* were found in the central parts of the study area, matching exactly those areas most intensively used for agricultural purposes. However, this surprising observation mirrors the distinctive habitat requirements of *B. muscorum*.

The significantly negative effect of the number of trees on the occurrence of *B. muscorum* reflects the species' preference for open landscapes (Dylewska 1957; Reinig 1970). This is supported by the observation that out of 24 analysed sampling units occupied by *B. muscorum* two only included rural settlements and none woodland. Accordingly we assume that the significantly positive effect of the landscape variable arable land on the occurrence of *B. muscorum* is not caused by the type of crop cultivated, but the absence of vertical landscape elements on the area under crop within the inner part of the study area.

The avoidance of vertical landscape structures at a regional scale mirrors the species' main distribution along coastal areas at the biogeographical scale (Reinig 1970; Wagner 1971; Peters 1972; Westrich 1990; Pekkarinen and Teras 1993; Plowright et al. 1997). Under natural conditions, *B. muscorum* probably mainly occurs in the open landscapes of coastal areas. It seems that the increase of open landscapes in the interior, due to human activities, caused an expansion of the distribution ranges of *B. muscorum*. Accordingly, *B. muscorum* has been recorded in open regions of the interior by several authors (Dylewska 1957; Reinig 1970; Westrich 1990).

However, despite the omnipresence of open landscapes, such as intensively used agricultural landscapes (Statistisches Bundesamt 2002), *B. muscorum* is regarded as an endangered species in Germany (Jedicke 1997; Westrich et al. 1998) and appears to be very rare in the interior (Wolf 1985; Hagen 1994).

Nowadays, wet lowlands seem to be the only remaining habitat in the interior suitable for *B. muscorum* (Westrich 1990; Treiber 1998). The significantly positive effect of ditches on the occurrence of *B. muscorum*, together with the frequently observed nest-searching behaviour of queens and the two findings of nest along brooks and ditches, leads us to the assumption that these landscape elements are essential to meet the habitat requirements of this bumblebee species (see also Reinig 1970). Comparably high shares of brooks and ditches occur within the central part of the formerly wet floodplain 'Amöneburger Becken' (Rittweger 1997), and are therefore regarded to be the main reason for this landscape harbouring one of the two remaining populations of *B. muscorum* in the Land Hesse (Frommer 2001; Tischendorf 2001).

In addition to their location on the north-facing slope of a small brook the observed nests of *B. muscorum* were close to fields of *T. pratense*. With regard to this observation, the positive effects of clover and fallow land, and the recordings of flower visits, an additional requirement essential for the presence of *B. muscorum* became apparent – the provision of suitable food resources in spatial proximity to nesting-sites. Long-tongued bumblebee species, such as *B. muscorum*, show comparably low competition abilities on super-abundant flower resources like rape (Heinrich 1974; Ranta and Vepsalainen 1981; Plowright et al. 1997). Furthermore, in most years there is only a small overlap of this particular resource with the seasonal occurrence of *B. muscorum*, as this species is emerging relatively late. In accordance, recorded flower visits showed that agricultural cultivations of plants with long corollas such as *T. pratense* and *T. repens* are frequently utilized by this bee. *T. pratense* is grown extensively throughout the 'Amöneburger Becken' and is harvested on demand during a great part of the growing season. Contrary to modern silage production, this technique results in a higher percentage and a greater continuity of flowering plants. However, the periodicity of agricultural resources makes alternative foraging habitats, such as fallow land, essential (Backman and Tiainen 2002; Croxton et al. 2002).

Flower visits to the important forage species *T. pratense* and *T. repens* were also frequently recorded on plants growing on taluses, path- and field-margins. *Vicia cracca*, *V. sepium* and *Lotus corniculatus* occur in these linear grassland elements, too. Furthermore, *B. muscorum* was recorded on *L. pedunculatus*, *Lythrum salicaria*, *Galeopsis pubescens* and *Stachys palustris* all growing along brooks and ditches. This shows that besides the required nesting-sites brooks and ditches also supply valuable food resources. With the exception of *Phacelia tanacetifolia*, all floral resources visited by this bumblebee species underline the importance of non-cultivated flower-rich elements (Kells and Goulson 2003) or semi-natural grasslands (Söderström et al. 2001) within the open landscape.

Continuous enlargement of agricultural fields and the disappearance of extensively used grasslands or non-crop features such as field margins and ditches (Stoate et al. 2001) result in an impoverished landscape not only in terms of nectar and pollen resources but also in terms of suitable sites for nesting and hibernation (Riemann 1987; Jennersten et al. 1993). Increasing levels of competition for the remaining resources between different species of bumblebees or within the guild of pollinators might be a consequence. This seems not yet to be the case in the study area as the present analysis did not reveal any effect of numbers of individuals of other bumblebee species recorded in the area on the occurrence of *B. muscorum*.

Actual sizes of agricultural fields below the regional average (Hessisches Statistisches Landesamt 1999) might indicate a higher proportion of edge structures within the 'Amöneburger Becken' compared to other intensively used agricultural areas in the Land Hesse. This circumstance, besides the numerous brooks and ditches draining this basin landscape, seems to be another landscape characteristic that allows *B. muscorum*, a species supposed to have comparatively small foraging ranges (Walther-Hellwig and Frankl 2000) and presumably low competitive abilities on mass-flowering crops, to still exist in this area.

Although Williams (1986, 1989) argues that the patterns of abundance of bumble species in the UK are best explained by their climatic optima and declining populations as observed in *B. muscorum* might also be affected by climatic shifts (cf. Thomas et al. 2004), we regard the continuing impoverishment of the landscape in terms of semi-natural landscape elements as one of the main factors that negatively affects population sizes and distributions ranges of *B. muscorum*. The survival of *B. muscorum* within the 'Amöneburger Becken' will be crucially dependent on the establishment and the spatial connectivity of landscape elements providing habitats for nesting, foraging and hibernating such as ditches and flower-rich fields, margins or banks.

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