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ORIGINAL ARTICLE

Xerothermophilous species of rove beetles (Coleoptera: Staphylinidae) in dry-warm habitats prefer their wetter niches

ANDREAS KLEEBERG[1], **UDO STEINHÄUSER**[2] and **GUNNAR LISCHEID**[3,4]

[1] Zum Alten Windmühlenberg 26, D-12524 Berlin, Germany; e-mail: a.g.kleeberg@t-online.de

[2] Millionenweg 7, D-19395 Plau am See, Germany; e-mail: udosteinhaeuser@aol.com

[3] Leibniz Centre for Agricultural Landscape Research (ZALF), Eberswalder Straße 84, D-15374 Müncheberg, Germany; e-mail: lischeid@zalf.de

[4] University of Potsdam, Institute of Environmental Science and Geography, Karl-Liebknecht-Strasse 24–25, D-14476 Potsdam, Germany

Key words. Heathland, beetles, water loss, habitat preference, data logger, air temperature, humidity, Germany

Abstract. High temperatures that prevail at sun-exposed sites such as heaths, depressions, or on slopes, increase the risk of desiccation for rove beetles (Staphylinidae). Therefore, atmospheric and sub-atmospheric humidity determine the microclimates and thus habitat preference and activity of xerothermophilous species. In the nature reserve Marienfließ, a heathland in the south of Mecklenburg-Western Pomerania, Northeast German Lowlands, air temperature and humidity were recorded year-round along a transect at 10 sites, i.e. where the vegetation was more dense and more humid than where the vegetation was sparse and it was drier, using data loggers placed in the litter layer that recorded the conditions every 30 min in 2021. Monthly visits were made to determine the biomass of vegetation, soil and litter properties, edaphic rove beetle fauna and total abundance and and that of individual species at 1 m^2 sites. Statistical analysis of 365 diurnal cycles per site, with pronounced amplitude in air temperature and humidity, clearly delineated the cooler and more humid sites from warmer and drier ones. Between 10 and 22 of the 30 xerothermophilous species (73.3%), such as, e.g. *Quedius persimilis* Mulsant & Rey, 1876, *Xantholinus gallicus* Coiffait, 1956, *Cousya longitarsis* (Thomson, 1867) and *Euaesthetus superlatus* Peyerimhoff, 1937, were recorded only at the cooler and moist sites on the heath. Comparison of the abundances and distribution of species revealed that the xerothermophilous heath-dwelling and desiccation-prone species prefer rather constant environmental conditions, i.e. niches in cool and moist habitats on warm and dry heathland.

INTRODUCTION

Xerophily (ancient Greek: xerós – dry, arid, and philos – loving, friend) is characteristic of organisms preferring dry habitats. Organisms with these preferences are called xerophiles, and those that prefer dry warm habitats are called xerothermophiles (Schaefer, 2003). Among xerophilous animals, two types are distinguished according to the presence or absence of a transpiration guard (Müller, 1991). The grasshopper type has no mechanism to restrict loss of water by transpiration and compensates for this loss by ingesting water-containing food. The anobial type uses various adaptations (e.g., thick cuticle in insects) to reduce transpiration and survive drought over long periods of time. Rove beetles do not belong to either of these types and use other strategies to restrict water loss (Klimaszewski et al., 2018).

Of the 2111 species of rove beetles (Staphylinidae) listed in the Beetles of Central Europe (Koch, 1989), 1193 species (56.5%) are listed as hygrophilous, 97 species (4.6%) as xerophilous and 55 species (2.6%) as thermophilous, with the remaining species assigned to other categories. With their slender habitus, short elytra and freely movable abdomen (non-sclerotized ligaments), rove beetles are adapted to live in gaps in soil and (moist) litter (Schatz, 2004). As their body is covered by a thin layer of cuticular lipids (Eisenbeis & Wichard, 1999), they are very sensitive to desiccation (Henneberg, 2004; Klimaszewski et al., 2018). This is generally also true for their developmental stages, i.e. eggs (Lincoln, 1961), larvae and pupae (Bong et al., 2013, 2021). Furthermore, water loss of flying beetles is higher due to an increased transpiration rate, even if they have the protection of wax-coated integuments (Hoffmann, 1995) as is the case in some insects. In some species of the Paederinae, Euaesthetinae, Osoriinae and to some extent Steninae, the tergites, paratergites, and sternites are fused into rings around each segment, which probably reduces water loss (Frank & Thomas, 2016).

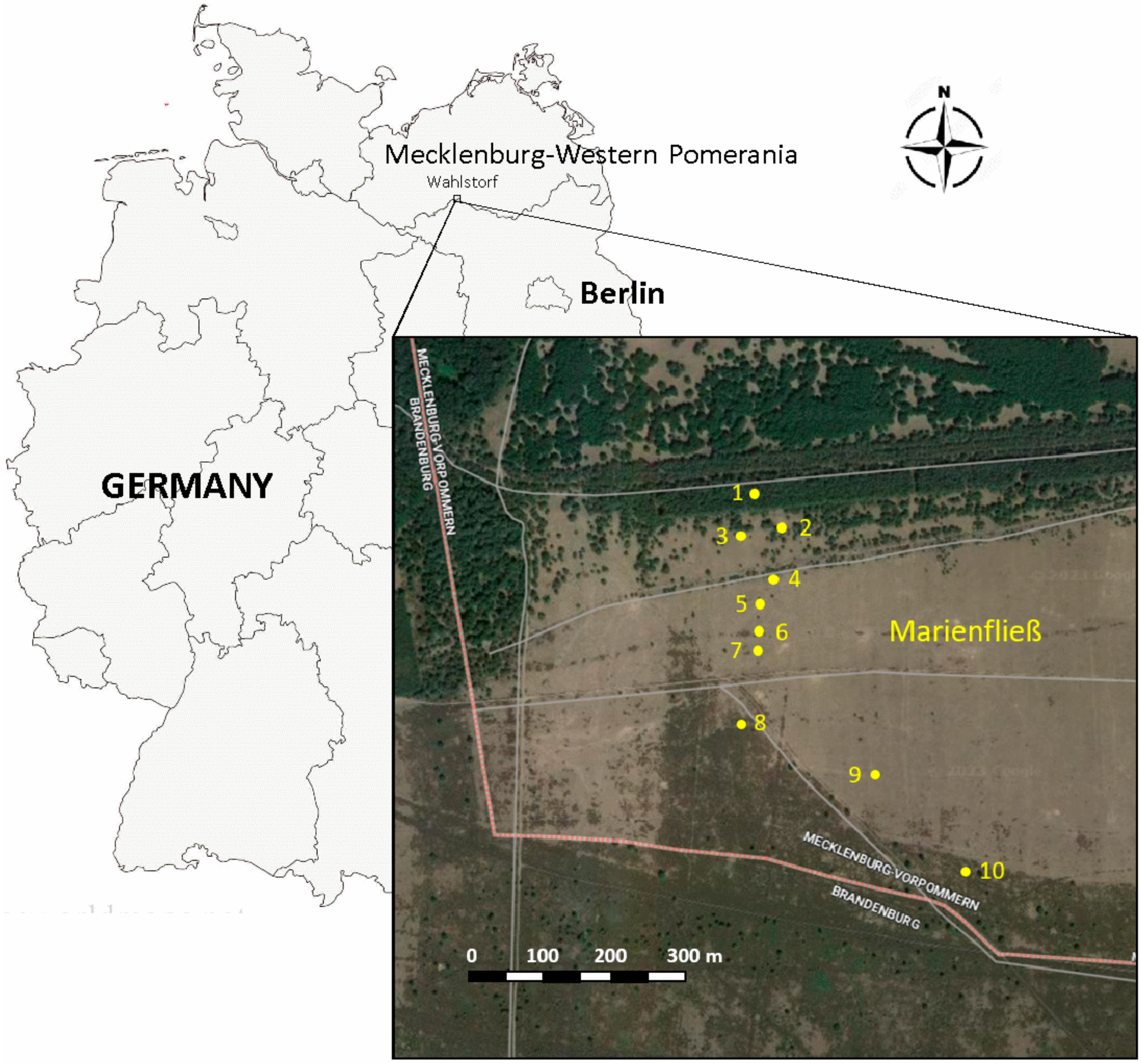

Fig. 1. Map of Germany showing the location of the area studied, the Marienfließ Nature Reserve, on the southern border of Mecklenburg-Western Pomerania. An insert on the map shows the location of the 10 sites studied along a transect from forest to open heath.

Another strategy to counteract desiccation or reduce water loss, used by desert and steppe dwellers, is to seek places in which to avoid exposure to solar radiation or reduce transpiration (Müller, 1991; Bong et al., 2021). Thus, humidity is crucial for the distribution of staphylinids (Ottesen, 1996; Holland et al., 2007; Irmler & Lipkow, 2018) and vegetation and ground litter are important factors determining their habitat preference and activity (Irmler, 2012; Irmler & Lipkow, 2018). Accordingly, it is hypothesized that xerothermophilous species of rove beetles in dry-warm habitats also (necessarily) have a preference for moist habitats and niches.

Thus, the present study aims to answer the following questions. What influence do the environmental factors, biomass of vegetation, temperature and especially humidity have on the occurrence and abundance of rove beetles? What is the habitat or niche preference of species classified as xerothermophilous in dry-warm heathlands? Can species communities be characterized or specific species be distinguished from each other in their requirements (preference, tolerance) based solely on humidity in the litter layer at the ground?

MATERIAL AND METHODS

Area studied

The nature reserve Marienfließ is located in the southwest of Mecklenburg-Western Pomerania, bordering Brandenburg (Fig. 1). It consists of a 610 ha of heathland, which was previously part of an airfield (since 1936) and military training area (since 1945) (Steinhäuser, 2013). This area is described in detail elsewhere (Martin, 2019; Deutschmann & Steinhäuser, 2020).

Weather data from Marnitz (DWD, 2022), a meteorological station 12 km away, reveal that Marienfließ has experienced changes in climate. The annual air temperature increased from 7.5 ± 0.6°C (1881–1890) to 9.8 ± 0.6°C (2012–2021) whereas the sum of annual precipitation did not change, with 608 ± 109 mm (1881–1890) and 625 ± 138 mm (2012–2021) (Fig. S1). Based

Table 1. Designation, location and brief characterization of the sites at which data loggers were installed (EL-USB2 and EL-USB2+*) for recording temperature and humidity (01/01/ to 12/31/2021) in the nature reserve Marienfließ (MF).

No. of site	GPS-coordinates	Site description
MF_1*	N 53° 21.004´ E 12° 05.233´	light pine forest, with 60- to 80-year-old trees, total reserve
MF_2	N 53° 20.985´ E 12° 05.266´	open pine stand at forest edge, moss under overhanging pine branches
MF_3	N 53° 20.981´ E 12° 05.217´	sloping wind-protected open space between single pine trees
MF_4	N 53° 20.954´ E 12° 05.250´	south of a path adjacent to a stand of *Calluna* and small pines
MF_5	N 53° 20.931´ E 12° 05.239´	incipient open space with stand of wiregrass and sheep´s fescue
MF_6	N 53° 20.913´ E 12° 05.237´	open area with sparse stand of *Calluna*
MF_7	N 53° 20.900´ E 12° 05.235´	open area in a shallow depression with little vegetation
MF_8	N 53° 20.847´ E 12° 05.223´	open area with closed stand of *Calluna* and a solitary pedunculate oak (*Quercus robur* L.)
MF_9	N 53° 20.813´ E 12° 05.375´	open area with low vegetation consisting of hawkweed and sheep’s fescue and a solitary hawthorn bush
MF_10*	N 53° 20.747´ E 12° 05.485´	open area in the middle of a closed stand of *Calluna* with two oak trees

on a first survey of rove beetles (Kleeberg, 2020), surveys were continued in 2021 in areas in Mecklenburg-Western Pomerania south of Wahlstorf (Fig. 1).

Sites sampled and weather data logging

After visual assessment, 10 sites that differed in vegetation-cover or plant biomass, which indicate a temperature or moisture gradient, were selected on 12/28/2020 (Table 1).

To record air temperature, humidity and dew point temperature continuously, an EasyLog data logger (EL-USB2 or EL-USB2+) was placed on the ground at each of the 10 sites on 12/28/2020 (Table 1). The 11-cm-long data loggers, powered by Li batteries (1/2AA size, 3.6 V), can store 16382 records for two parameters (temperature from –35 to 80 ± 0.2°C, humidity from 0 to 100 ± 2%). From these parameters, the dew point (in °C), the temperature at which water vapour begins to condense from the air, was automatically calculated. With the configuration and evaluation software EL-USB-WIN a recording frequency of 10 s to 12 h can be selected; 30 min (= 11 months data storage capacity or theoretical runtime) was set. The data loggers were deployed on 12/28/2020. Data were recorded throughout 2021. To achieve the minimum disturbance during the installation of the data loggers, a hole approximately 15 cm deep was drilled through the vegetation into the frozen ground, using a cordless electric drill and a cylindrical wire bird-feeder, made of wire mesh (height 22 cm, Ø 7 cm), was inserted to protect the data-logger (Fig. 2). The loggers were hung inside so that they measured within the litter layer at the ground surface. The data loggers were read for the first time on 04/22/2021 and batteries were changed; they were uninstalled on 01/06/2022. The 2021 data (air temperature, precipitation, relative humidity) from the Marnitz station (12 km air distance) were used as a reference (Fig. S1, DWD 2022).

Vegetation, soil and beetles

The transect (Fig. 1) was sampled monthly from March to November 2021 on nine dates in terms of vegetation, soil and rove beetles. The weather conditions are summarized in Table S1.

Along the transect, 10 circular areas exactly 1 m^2 were demarcated with a commercial plastic enclosure (3.55 m × 0.2 m). The biomass of vegetation, litter and top (1–2 cm) soil layer within the enclosure was completely removed and sieved through an 8 mm sieve (Fig. 2). The proportion > 8 mm was placed in~~to~~ 120 L plastic rubbish bags. The fresh weight (f.w.) was determined gravimetrically on site with a digital spring balance (PS 7600, up to 40 kg, Burg-Wächter, Germany), the accuracy of which over the range 960 g to 8,800 g was between 1.4% to 0.1%. Of the biomass 20.3–44.2% was taken to the laboratory for determination of the dry weight (d.w.). The entire portion < 8 mm was placed in cloth bags and also weighed on site. The entire contents of the bags were sieved through a kitchen sieve (2 mm) and the beetles removed. The d.w. of the three sieve fractions [BM – biomass > 8 mm, CS – coarse soil > 2 mm (litter), FS – fine soil < 2 mm (sand)] was determined by drying (40°C, 2 d). The organic content of the CS and FS was determined as loss on ignition (LOI, 550°C, 3 h). Mostly, the mean value (Mv) ± standard deviation (SD) was calculated.

To characterize the physical properties of CS and FS, the storage density (synonyms of dry bulk density, soil density), the porosity (synonyms of pore fraction, pore volume) and the water retention curve were determined (Durner & Iden, 2011). The storage density ρB (g cm^{-3}) is the quotient of the mass of solid components and the soil volume. The porosity ε (%) is given by $(1 - \rho B/\rho M) \times 100$. Since CS and FS are substrate mixtures with different organic contents, a mixing density ρM was calculated. The weighted arithmetic means takes into account the percentage of inorganic (100 – LOI, 2.65 g cm^{-3}) and organic components (LOI, 1.5 g cm^{-3}).

The water retention curve was determined by an evaporation experiment. For this purpose, dry, sieved material (CS, FS) collected on 05/16/2021 was placed in paper cups that were filled up to the top (volume 281 cm^3), with the area exposed to the atmosphere equal to 40.7 cm^2 and weighed (storage density). Each sample was moistened with 50 ml of cold tap water (12°C), which is equivalent to 12.3 mm of precipitation. The cups were then placed outdoors for 33 days (06/26–07/28/2021) on a lawn that was not shaded for most of the day. When it rained, the cups were placed under a roof. The paper cups with the slowly drying substrates were repeatedly weighed. At the same time, the air temperature was measured using a digital thermometer (TFA Dostmann) and the temperature of the surface of the substrate using an IR thermometer (Lasergrip 1080, Ektekcity).

To determine the habitat preference and abundances (ind. m^{-2}), which are rarely reported in the literature (Irmler & Lipkow,

Fig. 2. Photographs taken at the nature reserve Marienfließ (MF) in 2021. (a) Cordless electric drill with circular saw attachment, for drilling holes into the frozen ground into which cylindrical wire bird feeders were placed with the sensors of the data loggers suspended inside. (b) Data logger placed in an open area between solitary pine trees (MF_3). (c) Single standing pine with branches almost resting on the ground (MF_2). (d) Open area of heath with sparse stands of *Calluna*. The enclosed area is 1 m^2 and is the area from which all the vegetation was harvested (biomass). (e) Data logger in a stand of *Calluna*. (f) Over the course of the growing season the data logger was completely overgrown (MF_4). (g) Enclosed open area with *Deschampsia flexuosa* (L.) Trin. and *Festuca ovina* agg. L. prior to harvest of vegetation (MF_5). (h) Same site after vegetation is collected (biomass) and the litter including the epigeic rove beetles is sieved through a conventional 8 mm sieve.

2018), all staphylinids were counted and determined to species level. For the determination of beetle biomass, the body length and mass (Sartorius micro balance) of 10 individuals of each of the 11 species occurring in the area studied were determined using tin boats (4 × 4 × 11 mm).

The rove beetles were examined, and genitalia mostly dissected, using an Olympus SZX10 stereomicroscope at a magnification of 4.7–71.2×. The keys of Lohse (1964), Franz & Besuchet (1971), Besuchet (1974), Benick & Lohse (1974) and Assing & Schülke (2012) were used to identify the species of the Staphylinidae sensu latissimo (Grebennikov & Newton, 2009). For the naming, the nomenclatural and taxonomic changes in Assing & Schülke (2007) were considered. The species are arranged alphabetically following the Palaearctic Catalogue of Coleoptera (Schülke & Smetana, 2015) in subfamilies or within genera. Individuals of species that are faunistically remarkable or rare in Mecklenburg-Western Pomerania were retained in the private collection of the first author.

Data analysis

For each site, mean values of air temperature, humidity and dew point temperature were calculated for the year 2021. In addition, in order to account for temporal patterns varying between sites, the total set of 30 time series (10 sites × the three above features) was subjected to a principal component analysis (Jolliffe, 2002).

For the subsequent analysis, each site was characterized by six micro-meteorological variables (mean values of three features, and loadings on the first three principal components). To visualize the differences between the sites in this six-dimensional phase space Self-Organizing Maps, combined with Sammon Mapping (SOM-SM), were used (Kohonen, 2001; Lischeid, 2009). This approach aims to represent the sites by different symbols in a 2D plot in a way that the distances between the symbols are proportional to the differences between the sites in terms of the six variables. Thus, only distances between symbols can be interpreted and the axes do not contain any information.

These statistical analyses were done using R (R Core Team, 2022), version 4.1.3 (2022-03-10). In addition, the packages “som” (Yan, 2016) and MASS (Venables & Ripley, 2002) were used for the SOM-SM analysis.

The regression analyses were carried out using the data analysis ToolPak in Microsoft Excel 2016. Unless otherwise stated, the significance level α was set at 0.05 (5% or **) for all tests in the field study. The p-value corresponds to the test result, which indicates the probability of whether the observed difference is due to chance.

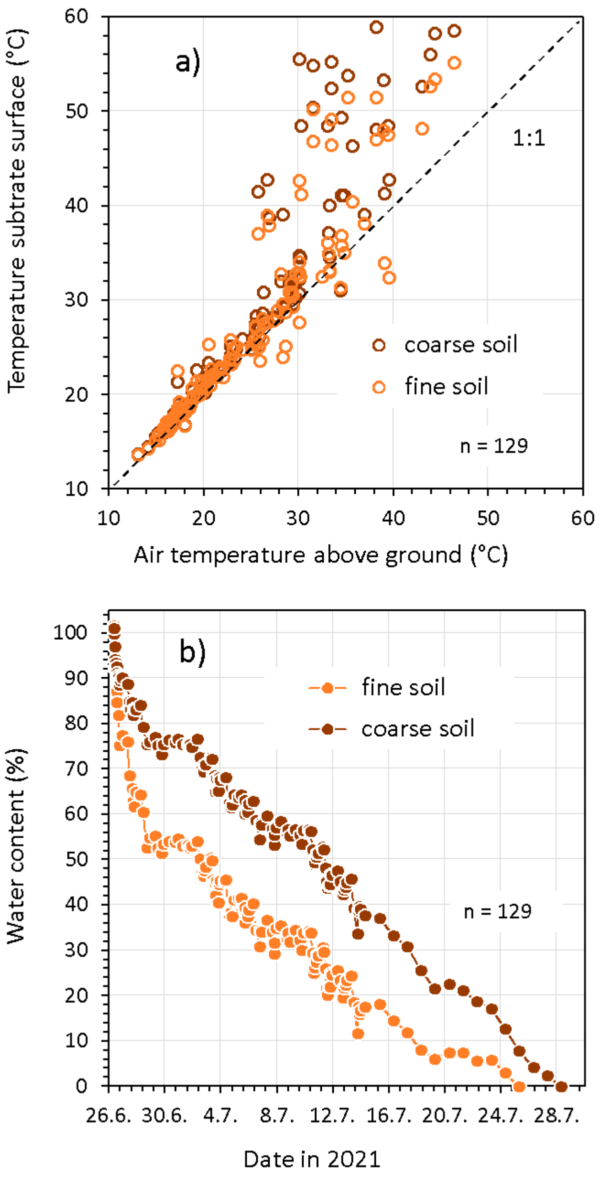

Fig. 3. (a) Air temperature 10 cm above ground vs. temperature on the substrate surface of the coarse soil (litter) and the fine soil (sand) of the 10 logger sites measured between 06/26 and 07/28/2021. (b) Course of water content of both substrates in the same period of time.

Table 2. Mean value ± standard deviation of water content (% fresh weight, f.w.) and content of organic matter in terms of loss of weight on ignition (% dry weight, d.w.) recorded for 10 sites in the nature reserve Marienfließ (MF) between 6 March and 10 November 2021, n = 9 sampling occasions. MF_1, the pine forest, is the reference. MF_2 to MF_10 are the sites with dense vegetation and MF_3 to MF_9 those with sparse vegetation (see Table 1).

Site code	Water content (% f.w.)			Loss on ignition (% d.w.)	
	Biomass	Litter	Fine soil	Litter	Fine soil
MF_1	44.6±20.3	38.4±18.2	31.3±14.9	73.6±16.5	63.7±14.0
MF_2	41.6±18.9	31.1±12.5	17.3±8.6	34.5±16.8	22.4±18.0
MF_4	39.0±8.3	19.9±8.9	10.0±4.4	23.9±15.0	12.6±9.5
MF_8	38.8±10.8	22.8±14.1	12.5±7.1	39.1±24.3	19.5±16.4
MF_10	35.2±11.2	24.6±11.1	14.2±5.8	42.1±22.3	20.1±13.4
MF_3	23.6±10.0	11.9±7.0	11.5±13.4	15.1±11.1	8.0±3.3
MF_5	22.2±9.2	10.7±5.1	7.9±4.0	12.7±6.0	8.7±2.0
MF_6	31.8±12.2	19.2±16.2	9.5±6.7	23.4±16.5	14.7±14.5
MF_7	20.3±6.8	10.3±5.1	5.8±3.6	13.2±9.8	7.5±3.6
MF_9	24.0±11.8	10.0±5.7	7.3±4.7	10.6±6.2	9.8±5.3

RESULTS

Site characterization (biomass, soil factors)

The transect included a sequence of areas of open pine forest to open heathland at different stages of succession (Fig. 2, Table 2).

The biomass (BM) of pine forest MF_1 (excluding the trunks of the pines) consisted mainly of an approximately 10 cm thick layer of recent and old needle litter. Water content of CS was on average 7.2 ± 4.3% higher than that of FS. Organic matter content (LOI) was on average 18.9 ± 11.4% higher than that of FS. There was a significant linear relationship between LOI and water content (Table 2) for both CS ($y = 0.448x + 6.028$; $n = 9$, $R^2 = 0.966$, $p = 0.602$) and

Table 3. Storage density and porosity of coarse soil (CS, litter, > 2 mm) and fine soil (FS, sand, < 2 mm) from sites with dense vegetation (MF_1 to MF_10) and open sparse vegetation (MF_3 to MF_9) based on the biomass recorded (> 8 mm, Table 2). Mv – mean value, SD – standard deviation.

Site	Storage density (g cm^{-3})		Porosity (% d.w.)	
	CS	FS	CS	FS
MF_1	0.2	0.6	86.5	70.1
MF_2	0.4	0.7	81.5	66.2
MF_4	0.6	1.1	74.5	54.5
MF_8	0.3	0.8	82.5	61.7
MF_10	0.4	0.9	78.5	61.8
Mv	0.4	0.8	80.7	62.9
SD	0.1	0.2	4.5	5.8
MF_3	0.9	1.1	63.6	53.8
MF_5	0.9	1.0	61.5	56.9
MF_6	0.3	0.9	80.0	62.3
MF_7	0.7	1.1	67.6	53.9
MF_9	0.7	1.0	69.1	56.1
Mv	0.7	1.0	68.4	56.6
SD	0.2	0.1	7.2	3.4

FS ($y = 0.426x + 4.77$; $n = 9$, $R^2 = 0.936$, $p = 0.602$) indicating the higher the percentage organic matter the higher the water binding capacity.

Retention curve for water, storage density and porosity

Depending on the quality and moisture of the substrate, the water content of CS (litter) ranges from 16.8% f.w. (MF_3) to 48.0% f.w. (MF_1), Mv ± SD 27.8 ± 10.3% f.w., and of FS (sand) from 13.9% f.w. (MF_4) to 24.0% f.w. (MF_1), Mv ± SD ($n = 10$) 16.5 ± 3.2% f.w. In order to compare the decrease in water content of the substrates over time, it was normalized to 100% (Fig. 3).

The temperature at the surface of the substrate was on average 3.8 ± 5.9 K (CS) and 2.3 ± 4.3 K (FS) higher than air temperature above the ground (Fig. 3a) in 96.1% (CS) and 86.0% (FS) of the 129 measurements. An initial high water loss from the surface of moist substrates in the first two days (CS: 0.14 L m^{-2} d^{-1}; FS: 0.25 L m^{-2} d^{-1}) was followed by lower rates (CS: 0.04 L m^{-2} d^{-1}; FS: 0.04 L m^{-2} d^{-1}) and a continuous evaporation of water (CS: 0.09 L m^{-2} d^{-1}; FS: 0.07 L m^{-2} d^{-1}) (Fig. 3b). Rainy days during the experiment, in combination with a slight cooling of the air, were accompanied by a slight uptake of water and a subsequent slow decrease in desiccation (plateaus). Under the given experimental conditions, especially when precipitation was excluded, it took 30 days for a 9 cm thick layer of litter and sand (Mv of all 2 × 10 substrates) to dry out completely (Fig. 3b). The organically richer CS (Table 2) dried out 3 days later than FS (Fig. 3b).

The storage density of the substrates at sites with dense vegetation (and higher organic matter, Table 2) was lower than that of the sites with sparser vegetation, and were more distinct for CS than for FS (Table 3). In contrast, the porosity of the substrates at sites with dense vegetation are higher than that of sites with sparse vegetation and were more distinct for CS than for FS (Table 3). There was a logarithmic significant relationship between LOI (Table 2)

Table 4. Abundance (mean Mv ± standard deviation SD, plus range) of rove beetles at Marienfließ (MF) compared to that recorded in the literature. Numbered notes indicate the source of data: [1]Assing (1993), [2]Assing (2009), [3]Irmler & Lipkow (2018). For a detailed description of the sites see Table 1.

Site or species name	Abundance (ind. m^{-2})	
	Mv ± SD	Range
Xantholinus gallicus Coiffait, 1956[1]	4.4±2.8	0–9
Othius subuliformis Stephens, 1833[1]	6.9±4.8	2–19
Ochthephilum fracticorne (Paykull, 1800)[2]	2.7±0.6	1.7–3.4
Agricultural areas[3]	29±11	
Dry pastures[3]	84±33	
Wet pastures[3]	169±28	
Alder (*Alnus*) forest[3]		350–470
MF_1 pine forest	3.3±6.0	0–153
Geostiba circellaris (Gravenhorst, 1806)	35.1±48.4	1–153
Othius subuliformis Stephens, 1833	14.0±10.1	4–29
Oxypoda annularis (Mannerheim, 1830)	8.8±11.0	1–28
Atheta amplicollis (Mulsant & Rey, 1873)	3.8±6.0	1–16
MF_2 moss under pine branches	2.9±2.6	1–38
Anthobium unicolor (Marsham, 1802)	10.8±10.7	3–29
Quedius persimilis Mulsant & Rey, 1876	10.5±14.7	1–38
Othius subuliformis Stephens, 1833	8.8±10.4	1–29
Oxypoda annularis (Mannerheim, 1830)	7.0±0.0	0–7
MF_3 open area among pines	1.9±1.5	0–6
Philonthus cognatus Stephens, 1832	6.0±0.0	0–6
Xantholinus longiventris Heer, 1839	5.0±0.0	0–5
Philonthus carbonarius (Gravenhorst, 1802)	3.0±0.0	0–3
Quedius persimilis Mulsant & Rey, 1876	2.3±1.3	1–4
MF_4 *Calluna* stand	2.1±2.5	1–30
Quedius persimilis Mulsant & Rey, 1876	13.3±13.1	2–29
Stenus impressus Germar, 1824	11.3±16.2	1–30
Oxypoda abdominalis (Mannerheim, 1830)	5.8±4.3	2–12
Aleochara bipustulata (Linnaeus, 1760)	4.0±0.0	0–4
MF_5 open area with wiregrass and sheep's fescue	1.1±0.3	0–2
Quedius levicollis (Brullé, 1832)	2.0±0.0	0–2
Amischa analis (Gravenhorst, 1802)	1.0±0.0	0–1
Atheta amplicollis (Mulsant & Rey., 1873)	1.0±0.0	0–1
Euaesthetus superlatus Peyerimhoff, 1937	1.0±0.0	0–1
MF_6 open area with sparse stand of *Calluna*	2.5±2.5	1–25
Atheta orbata (Erichson, 1837)	10.2±9.3	1–25
Oxypoda abdominalis (Mannerheim, 1830)	8.4±9.5	3–25
Mycetoporus baudueri Mulsant & Rey, 1875	6.5±7.8	1–12
Oxypoda brachyptera (Stephens, 1832)	5.0±0.0	0–5
MF_7 open area with sparse vegetation	1.3±0.5	0–3
Mycetoporus baudueri Mulsant & Rey, 1875	2.0±0.0	0–2
Oxypoda abdominalis (Mannerheim, 1830)	2.0±0.0	0–2
Xantholinus longiventris Heer, 1839	2.0±0.0	0–2
Quedius persimilis Mulsant & Rey, 1876	1.7±1.2	1–3
MF_8 closed stand of *Calluna*	2.0±1.5	0–20
Quedius persimilis Mulsant & Rey, 1876	6.1±6.6	1–20
Anthobium unicolor (Marsham, 1802)	5.0±0.0	0–5
Othius subuliformis Stephens, 1833	4.8±1.7	3–7
Stenus geniculatus Gravenhorst, 1806	4.0±0.0	0–4
MF_9 open area with sparse vegetation	1.7±0.9	0–4
Amischa analis (Gravenhorst, 1802)	3.0±0.0	0–3
Oxypoda soror Thomson, 1855	3.0±0.0	0–3
Atheta orbata (Erichson, 1837)	2.0±1.7	1–4
Liogluta alpestris (Heer, 1839)	1.5±0.7	1–2
MF_10 open area with stand of *Calluna*	2.0±1.4	1–10
Anthobium unicolor (Marsham, 1802)	6.0±2.8	4–8
Quedius persimilis Mulsant & Rey, 1876	5.1±3.4	1–10
Olophrum piceum (Gyllenhal, 1810)	4.0±0.0	0–4
Amischa nigrofusca (Stephens, 1832)	2.0±0.0	0–2

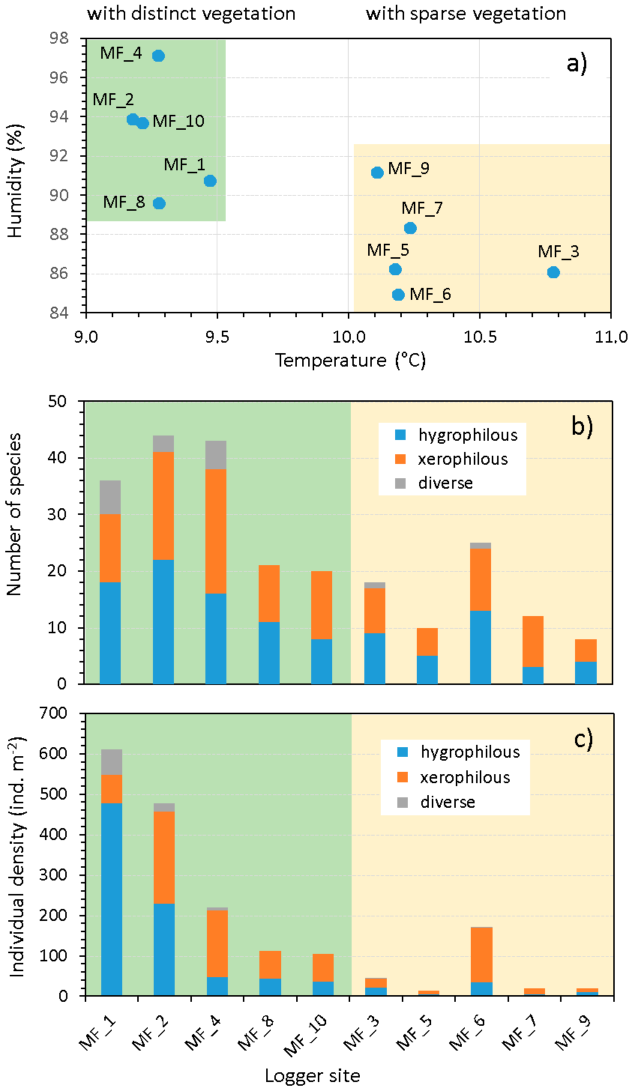

Fig. 4. (a) Mean annual air temperature vs. humidity of 10 plots in the heath Marienfließ in 2021. Distribution of species of rove beetles on the plots with distinct and low vegetation, specified according to their ecological humidity preference with (b) the number of species, and (c) the total individual abundance.

and porosity (Table 3) ($y = 11.716\ln(x) + 36.695$; n = 20, $R^2 = 0.84$, $\alpha = 0.01$, $p = 0.696$).

Species inventory of rove beetles

A total of 1789 rove beetles belonging to 72 species were collected on the nine occasions they were sampled at the 10 sites (Table S1). There was a significant nonlinear relationship between the number of individuals and the number of species collected at the 10 sites ($R^2 = 0.646$, $\alpha = 0.05$, $p = 0.587$). The relationship for MF_2 (moss below pine branches) was more distinct (n = 9, $R^2 = 0.933$, $\alpha = 0.001$, $p = 0.873$) than for the other sites.

About half of the species (44.4%) were hygrophilous (humicole) as were half of the individuals (50.8%). The other half consisted of xerophilous (humicole) or thermophilous species (41.7%), and species (13.9%), which are silvicolous or specialists with other preferences (Koch, 1989) (Table S3). Their abundances indicate the preference of certain species for site-specific temperature and moisture conditions (Table 4). Their abundances were comparable to those reported in other studies and sorted in descending order.

Body length varied between 1.5 mm (*Euaesthetus superlatus*) and 25.2 mm (*Ocypus olens*) (Table S2). The weighted arithmetic mean of all speciemens was 4.1 mm, which indicates the dominance of small species. The allometric relationship of the biomass of beetles was derived from the significant exponential relationship between the body length (mm) and weighted body weight (mg d.w.): biomass (mg) = $0.1884e^{0.2734 \text{body length}}$ (n = 11, $R^2 = 0.914$, $\alpha = 0.001$, $p = 0.873$). The biomass of the edaphic rove beetles at a site was calculated as a weighted mean by including the number of individuals. For example, the small *Geostiba circellaris* (2.6 mm) was abundant (350 ind. m^{-2}) and its biomass (134 mg m^{-2}) was almost as high (226 mg m^{-2}) as that of the biggest species *Ocypus olens* (25 mm), with only 2 ind. m^{-2} (Fig. S2).

Beetles in relation to site and microclimatic conditions

There was a significant exponential correlation between the biomass and abundance of rove beetles at the 10 sites, i.e. $y = 0.103e^{0.141x}$ ($R^2 = 0.895$, $\alpha = 0.01$, $p = 0.794$). In addition, the abundances of the beetles is associated with the proportion of organic matter (LOI), with the correlation for CS $y = 0.021x^{1.858}$ ($R^2 = 0.786$, $\alpha = 0.02$, $p = 0.745$) and for FS $y = 1.242x + 2.083$ ($R^2 = 0.648$, $\alpha = 0.05$, $p = 0.648$). This is also the case for the relationship between water content and beetle abundance for CS, with the regression $y = 0.0046x^{2.65}$ ($R^2 = 0.895$, $\alpha = 0.01$, $p = 0.794$) and a polynomic relationship for FS, with $y = -0.026x^2 + 3.75x - 22.34$ ($R^2 = 0.792$, $\alpha = 0.02$, $p = 0.745$). These relationships indicate that the abundance of staphylinids is linked to the biomass of vegetation, its organic matter content (water retention capacity, food source for prey animals) and water content of the substrates (CS, FS).

As shown for the temperature at the surface of the substrate (Fig. 3), the small rove beetles (Fig. S2) are sometimes exposed to high air temperatures. For example, the maximum range in temperatue in 2021 at sites MF_1, MF_2 (Fig. 2c) and MF_3 (Fig. 2b) was 1.5–27.5°C (26 K), 6.5–27°C (20.5 K) and –5–33°C (38 K) on different days, i.e. March 31, June 16 and April 27 (Fig. S3). These differences are remarkable, as the three sites are only 30 to 40 m apart (Fig. 1).

The sites with dense vegetation were cooler and more humid than the open sites with sparse vegetation (Fig. 4a). The highest number of individual beetles were recorded at the sites with dense vegetation, i.e. from the pine forest towards open sites (Fig. 4b).

Only the first three components of the principal component analysis were included in the subsequent analysis, which accounted for about 95.4% of the variance. The first component, the mean temporal behaviour, accounted for 76.8% of the variance and the second 15.9%. The latter firstly indicates positive deviations in air humidity in the first half of the year at some sites and higher dew point temperatures in two short periods in April and June 2021.

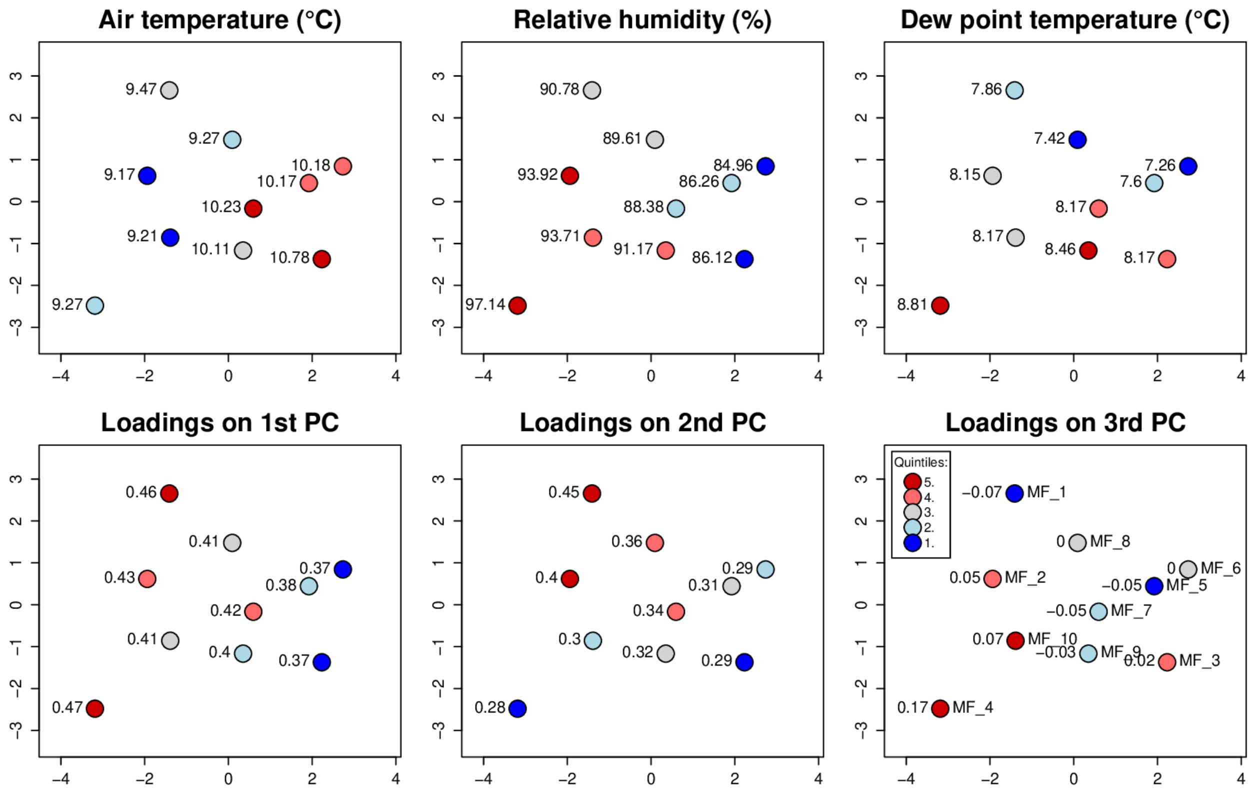

Fig. 5. Visualization of the data recorded at ten sites using SOM-SM (Self-Organizing Map, combined with Sammon Mapping). The location of symbols is identical in all panels. Site names are indicated in the lower right panel. Colours of the symbols indicate the quintiles of the respective features. Scores of mean values (upper row) and of mean loadings on respective principal components (lower row) are indicated to the left of the respective symbols.

The third principal component was primarily characterised by a clear difference in air humidity at site MF_4, a small stand of *Calluna*.

The SOM-SM of the sites measured accounted for 94% of the total variance in the 2d graph (Fig. 5). In each panel there are clear patterns. For example, the sites with the highest mean air temperature are close to the right margin of the graph and those with the lowest mean values to the left. The pattern for relative humidity is the opposite (Fig. 5).

As shown for representative species, hygrophilous and xerothermophilous species have a specific site preference (Fig. 6). For example, *Mycetoporus rufescens* and *Geostiba circellaris* clearly preferred sites with a low mean air temperature and high relative humidity. In contrast, the preference of *Xantholinus longiventris* was not clearly associated with any of the six variables depicted in Fig. 5.

DISCUSSION

Presence of small hygrophilous rove beetles in heathland is dependent on the existence of moist niches

Insects have a large surface area to volume ratio (e.g., O'Donnell, 2022). Because of their small size they can inhabit endogeic habitats. Thus, the dominance of rove beetles (Fig. S2) is associated with their body size as small species are the most abundant (Table S2). In addition, the fact that almost half of the species are hygrophilous (Table S3) indicates that there must be sufficient humid niches for them in the dry-warm Marienfließ heathland. Species that are considered to be xerothermophilic (Table S2) are most abundant in the cool and moist niches (Table 4). This is associated with the vegetation (canopy) cover, which modulates both litter input and evaporation, which favours the growth and reproduction of their prey (e.g., Trekels et al., 2017).

Edaphic rove beetles actively search for moist niches

The edaphic rove beetles recorded (Table S1) belong to the following three groups defined by Irmler & Lipkow (2018): (i) species that forage at random on the surface of the soil and litter (e.g., *Ocypus olens*, *Philonthus carbonarius*), (ii) species that orient visually while walking slowly on the surface of litter or on bare soil (e.g., *Stenus impressus*, *Quedius nigriceps*), and (iii) litter-dwelling species (e.g., *Othius subuliformis, Xantholinus linearis*) and hemiedaphic species (e.g., *Drusilla canaliculata*, *Geostiba circellaris*). All these species can move between nearby areas with vegetation and open areas (Figs 1–2), or actively seek moist niches (Figs 4–6). In addition to the diurnal movements of beetles, seasonal changes in location are also reported (Assing, 1993). Moreover, certain developmental stages are found only in very specific types of biotopes (Kratochwil & Schwabe, 1984).

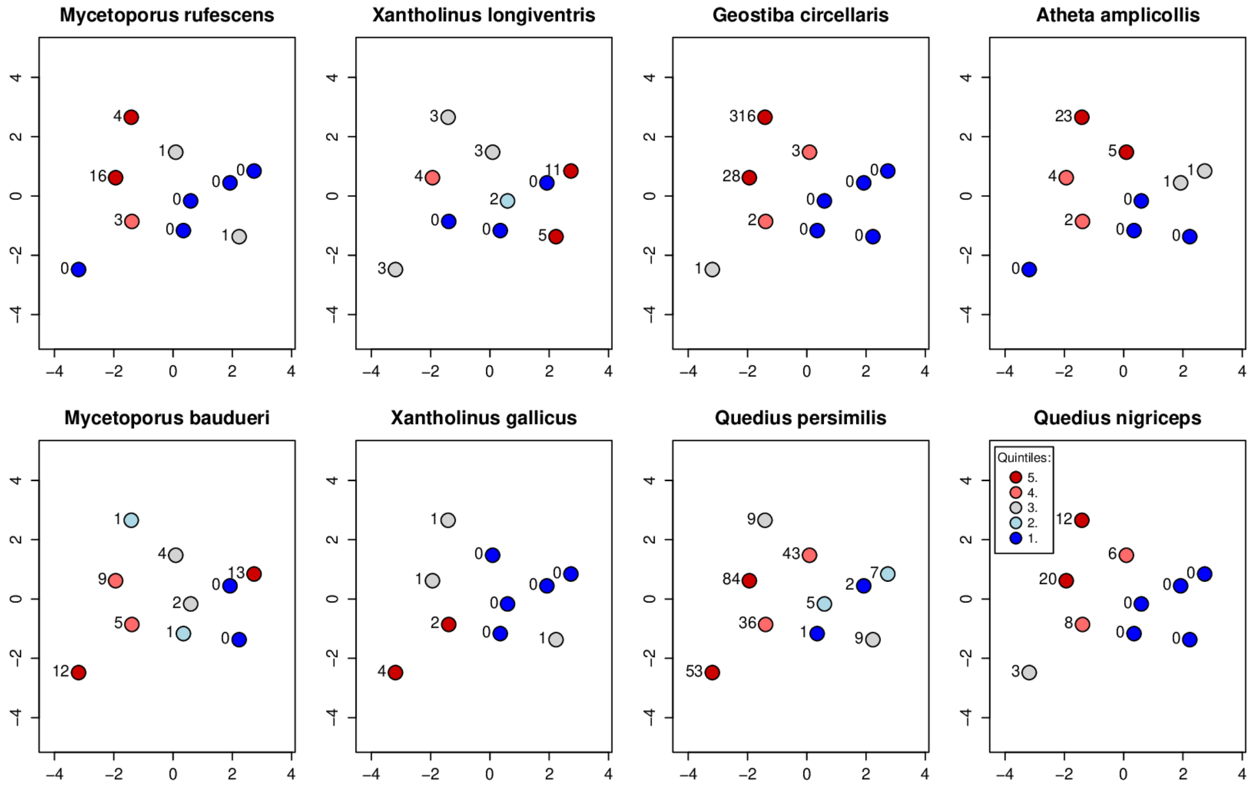

Fig. 6. Total number of speciemens of hygrophilous (upper row) and xerothermophilous (lower row) species collected at the ten sites in 2021 (numbers are close to the symbols). Symbol colouring indicates the quintiles of numbers of specimens. Arrangement of symbols for the 10 sites is identical to that in Fig. 5.

Vegetation and the quality of its litter is important in enabling rove beetles to avoid desiccation

As expected, hygrophilous species were most abundant in pine forest (MF_1) (Fig. 4), which is therefore a reference habitat for these species (Table S1). The high levels of shade and litter there may also account for the highest densities recorded in this habitat. The thickness of the litter layer in the open sites (MF_5 to MF_9) is less than in MF_1, as in the former more of the mineral soil is exposed and as a consequence they tend to be drier (Table 2, Fig. 3) and a less favourable habitat for rove beetles.

Because of its mean organic matter and higher water content (Table 2), especially in spring (March to May), the litter in the moss-covered site (MF_2, Fig. 2c), is a very favourable habitat for small hygrophilous species (Table 2, Fig. 4) (Table S2, Fig. S2), which in dry habitats quickly dessicate.

The high temperatures at the surface of substrates that are exposed to sunlight result in rapid but varying rates of drying (Fig. 3). The coarse and darker litter (CS) has a higher organic content than sandy soil (FS, Table 2), and a higher water binding capacity and a lower potential for desiccation (Fig. 3b). The development of moisture-retaining substrates (moss, needles, leaves) depends on the vegetation (Fig. 2). In adition, the minimum water content of CS and FS over the course of the year (June, August; not shown) indicates the importance of summer precipitation. Mean precipitation (nearby meteorological station Marnitz) over the last 10 years (2011–2020) was 644 mm. Thus 2021 was a 'normal' year, with 676 mm.

Due to a very high reflectivity (albedo) of sand (almost 40% of the total radiation) and low absorption the air layers near the ground it can become hot, which determines the microclimate. This is especially true for more wind-protected areas (MF_3) with sparse vegetation, where there can be very little air movement. The reflection of visible light is one third higher from dry than wet sand and UV reflection about twice as high (Kratochwil & Schwabe, 1984).

The sieved substrates (CS, FS) had a lower storage density (Table 3) than the para-brown earth (luvisol), prevailing in the young moraine landscapes in the NE of Germany, with 1.16–1.70 g cm^{-3} (Amelung et al., 2018). Consequently, the porosity (Table 3) is higher than that of the young morainic soils, with 36–56%. The larger pore volume provides a suitable habitat for the majority of small rove beetles (Table S2) and it is also important for thermal conductivity. The lower the storage density or larger the pore volume, the lower the thermal conductivity, which helps them survive the often high temperature gradients that develop during the course of a day (Fig. S3), with sometimes extremely high temperatures on the surface of the substrate (Fig. 3). As measured in the desiccation experiment, the maximum as well as minimum values of the soil temperature in the uppermost 5–7 cm of plant-free soil are almost always 7–10°C higher than the maximum or minimum values of the air temperature recorded at meteorological stations, 2 m above ground (Amelung et al., 2018).

Species-specific rove beetle abundances indicate their habitat preference

The abundances recorded at Marienfließ indicate the habitat preference of the different species of rove beetle (Tables 4 and S3). There are very few reports of the abundance of rove beetles (Irmler & Lipkow, 2018) in the literature (for the temperate zone), both total and for individual species. Note that the individual abundances determined here are for the edaphic fauna of a 1 m^2 plot. Nevertheless, e.g. those for *Othius subuliformis* (Table 4) are in the same range as those collected using pitfall traps (Assing, 1993). Based on the features of the sites (Tables 1 and 2) and the highest abundances of the different species in the different microhabitats their preferences become clear (Tables 4 and S3).

A characteristic species of the heath, which occurred at six of the 10 sites and were the most abundant (Table 4), is the xerophilous and humicole *Quedius persimilis* (Koch, 1989). It was more abundant at sites with dense vegetation (5.1–13.3 ind. m^{-2}) than those with sparse vegetation (1.7–2.3 ind. m^{-2}). The former are the cooler and wetter habitats (Fig. 4), with an annual mean of humidity of 88.4–98.0%. In comparison, the hygrophilous rove beetle *Philonthus quisquiliarius* (Gyll.) was reared by García et al. (2012) in 3 L boxes, which were watered weekly with 200 ml of water, being equivalent to precipitation of 0.5 mm d^{-1}, and a humidity of 80 ± 5% at a temperature of 20 ± 0.3°C. At Marienfließ, *Quedius persimilis* experienced an average annual precipitation of 1.8–1.9 mm d^{-1} and sometimes extremely high temperatures for short periods (Fig. S3).

Examples of the preference of xerothermophilic species for cool and humid habitats

Between 10 and 22 of the 30 xerothermophilous species (73.3%, Table S3) were recorded in the cooler and moister sites on the heath (Fig. 4). *Xantholinus gallicus* occurred in the vegetated moist plots MF_2, MF_4 and MF_10 (Table 1). It is a Central European species, i.e. bioindicator of dry and/or warm slopes. It is common on all *Calluna* heaths in north-western Germany and their associated biotopes (sandy grasslands, pine forests, *Erica* heath) (Assing, 1993). This author reports the preference of *X. gallicus* for relatively stable biotopes on sandy-acid soils, but no clear relationship with specific moisture or temperature conditions. However, the logger measurements indicate that habitat preferences can be defined in terms of a high spatial and temporal resolution in terms of temperature and humidity (Fig. 6).

Xantholinus linearis was recorded only in vegetated plots MF_2 and MF_4 (Table S3). According to Assing (1993) it is a Euro-Mediterranean eurytopic species that prefers open terrain, especially in sandy grasslands. Remarkably, the two closely related *X. gallicus* and *X. linearis* co-occur in most *Calluna* heaths, rough grasslands and pine forests. Based on their very similar phenology, body size and food (non-specific carnivorous), they are likely to compete for resources (Assing, 1993).

Euaesthaetus superlatus differs from its Central European congeners in inhabiting open, semi-dry or dry warm habitats (Jałoszyński et al., 2018). It was only collected in a small stand of *Calluna* (MF_4, Fig. 2f). In Poland, it occurs in open habitats: regenerating heather that was burnt two years previously, and in a plot dominated by the purple moor-grass *Molinia caerulea* (L.) Moench (Jałoszyński et al., 2018).

Oxypoda brachyptera, epigaeically active from spring to late autumn, was collected at a vegetated (*Calluna*) site (MF_4) and open sites (MF_6, MF_7, Fig. 2g), which is in accordance with the finding that this species usually occurs in non-forest biotopes (Assing, 2012).

Cousya longitarsis is a very rare and local species. Assing (2018) states this species occurs mainly in more or less dry, unforested habitats with scattered vegetation (heathland, grassland) on sandy, calcareous and gravel soils. Remarkably, on the Marienfließ heath, this species has so far only been collected in cool and wet places, i.e. MF_2 (Fig. 2c) in May 2020 (Kleeberg, 2020) and MF_4 (Fig. 2f, Table S2).

The greater the structural diversity of a habitat (Table 1, Fig. 2), the more numerous the opportunities for individual species to take refuge there. Especially favourable are marginal areas (ecotones), e.g. shaded shrub and forest edges (Fig. 1, MF_2, MF_4) in direct contact with dry sites free of woody plants and overgrown only with low vegetation.

Communities consisting of both hygrophilous and xerothermophilous species

Although habitat preferences were recorded for all the species occurring at Marienfließ (Figs 4, 5) and of selected hygrophilous and xerothermophilous species (Fig. 6), the presence of species (Tables 4 and S3) is only slightly dependent on humidity. The separation of hygrophilous and xerothermophilous species was not always possible. For example, common and eurytopic species, such as *Anthobium unicolor* and *Olophrum fuscum* (Table S2) occur in dry and wet habitats (Assing & Schülke, 2012). This may be because the dependence of individual species of rove beetles on the environment is low, which makes a clear differentiation difficult. This is also confirmed by studies on the relationship of rove beetles to the degree of vegetation-cover, pH and organic content of the soil (Irmler & Gürlich, 2007). In addition, the classification into hygrophilous or xerothermophilous (Koch, 1989) is probably not specific enough for all species. Finally, rove beetles, in particular, are mobile enough to react quickly to short-term changes in air temperature and humidity (O'Donnell, 2022). Thus, longer and higher temporal resolution of beetles and autecological studies on individual species (Bong et al., 2013) are needed in order to highlight the differences more clearly.

Rove beetles as bioindicators of dry-warm *Calluna* heathlands

In the German lowlands, heathland is located in nature reserves and even then, only in small areas. Their existence is therefore highly endangered. There is no need for an assessment of the remnants that still exist today as every area of heathland is in need of protection (e.g., Kratochwil & Schwabe, 1984; Steinhäuser, 2013). Various ecological studies describe rove beetles as highly specialized and stenotopic, and bioindicators of changes in the environment (e.g., Boháč, 1990; Stasiov et al., 2021). Present results on their habitat preference in terms of substrate quality, water retention capacity, temperature and humidity (Tables 4 and S3, Figs 4–6) can be used to define the requirements of xerothermophilic species. Examples are *Cousya longitarsis* (Kleeberg, 2020), *Oxypoda vicina*, *Stenus geniculatus*, *Euaesthetus superlatus*, *Quedius nigriceps*, *Ocypus picipennis picipennis* and *Xantholinus gallicus* (Tables 4 and S2). It is reasonable to assume, that the disappearance of these stenotopic species indicates a change in the species spectrum towards eurytopic species and thus the eutrophication of an area.

CONCLUSIONS

In its current form, the Marienfließ nature reserve is a warm and dry site (under climatic stress, Fig. S1), whose biotic communities are dependent on human activity that has resulted in irreplaceable habitats for rare species of rove beetles. Understanding species-specific habitat requirements is important for their survival. The present study indicates the extent to which their diversity and habitat preferences are driven by local microclimatic conditions within heathland. Vegetation, and related temperature, humidity (dew point) and soil moisture (CS > FS, Table 2) were the most important factors determining the number and abundance of rove beetles with particular preferences. The species of rove beetles known to be xerothermophilous also prefer wetter niches (Table 3, Figs 4 and 6). Particularly valuable ecotones for species-rich staphylinid occurrences are the pine-covered marginal areas of the heath (MF_2, MF_4, Fig. 1). The open pine stands, especially the individual trees with their branches almost resting on the ground (MF_2, Fig. 2c), ensure a mosaic of moderate temperatures and humid habitats for xerothermophilous species. This implies, that the lowland heath Marienfließ requires management, which is dependent on a precise knowledge of how the habitat, niche structure and substrate properties will be affected by climate change (Fig. S1). As recently stated, comparable studies on insects will be important in predicting the effect of climate change on insect numbers and biodiversity (O'Donnell, 2022).

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Fig. S1. Weather data for 1881–2021 recorded at the nearby meteorological station at Marnitz.

Fig. S2. Relationship between body length and abundance of the rove beetles.

Fig. S3. Range in the maximum air temperature recorded at the 10 sites.

Table S1. Meteorological conditions recorded at the sites during sampling.

Table S2. Abundances of 72 species of rove beetles

Table S3. Number and abundance of species of rove beetles