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Influence of *Sphagnum* harvesting on arthropod fauna and vegetation with a focus on beetles (Coleoptera) and ants (Hymenoptera: Formicidae)

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Abstract The harvesting of living peat moss (*Sphagnum* spec.) for various industrial applications has become increasingly prevalent. The harvesting process involves manual or mechanical extraction of *Sphagnum* fragments with minor to significant alterations of the habitats. This study investigates the impact of *Sphagnum* harvesting on arthropod fauna and vegetation structure at two donor sites with small-scale *Sphagnum* harvest in northwestern Germany. In the first year after the harvest, comparative surveys were carried out between harvested and unharvested reference areas. Arthropods living in and on the upper *Sphagnum* layer were studied by manually extracting quadrat samples. Vegetation surveys focused on the vascular plant composition and *Sphagnum* layer thickness as key habitat parameters. Results indicate no substantial effects on the total numbers for most arthropod orders. In contrast, the frequency of ant workers and the number of ant nests were considerably lower in harvested areas compared to reference areas. Vegetation analysis revealed that the shortening of the *Sphagnum* hummocks led to a homogenization of the vegetation structure and alterations in species composition in favor of moisture-loving species. Although no significant effects on total beetle populations were observed, the abundance of bog generalists and specialists was significantly reduced in harvest areas. Certain species displayed preferences for harvested or reference areas. Future harvesting practices should consider preserving vulnerable arthropod species and restricting harvesting to a small scale to mitigate adverse effects on bog ecosystems.

Keywords Invertebrates · Peat mosses · Vascular plants · Quadrat samples · Bogs · Peatlands

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Introduction

Harvesting living peat moss (*Sphagnum* spec.) fragments in raised bogs or at cultivation sites (*Sphagnum* farming) meets the increasing demand for this renewable raw material. Due to its ability to maintain moisture, inhibit the growth of bacteria and fungi, slow decomposition, and good aeration, *Sphagnum* biomass can be used as a high-quality constituent for growing media in horticulture and orchid industry as well as for diverse further applications like insulation and packaging material or pet terrariums (Domínguez 2014; Oberpaur et al. 2010; Whinam et al. 2003). Horticultural trials show it is an equivalent substitute for the mainly used horticultural slightly decomposed white peat (Jobin et al. 2014; Kumar 2017; Müller and Glatzel 2021). In some countries, such as Australia/Tasmania, New Zealand, and Chile, *Sphagnum* harvesting at semi-natural or natural stands is a major

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regional industry (Buxton et al. 1996; Díaz et al. 2012; Domínguez 2014; Whinam et al. 2003; Zegers et al. 2006). New approaches to growing *Sphagnum* moss at cultivation sites ('*Sphagnum* farming ') are being tested, for example, in Germany and Canada (Gaudig et al. 2018; Grobe et al. 2021; Pouliot et al. 2015). At cultivation sites, living fragments of *Sphagnum* mosses are spread on the bare peat surface, which may then form a closed *Sphagnum* carpet. *Sphagnum* biomass can be harvested every 3–5 years for further processing (Gaudig et al. 2014; Krebs et al. 2018).

Another reason for gathering or growing *Sphagnum* fragments, especially hummock-forming species, is to use them to accelerate the establishment of hummock-forming *Sphagnum* mosses during the restoration of degraded bogs (Caporn et al. 2017; Hölzel et al. 2023; Quinty and Rochefort 2003). *Sphagnum* mosses are particularly important, as they are keystone species for peat formation, maintaining a high water table, and decreasing pH levels (van Breemen 1995). The reintroduction of *Sphagnum* mosses can greatly accelerate the regeneration of characteristic *Sphagnum*-dominated bog vegetation, as shown, for example, in cutover bogs after peat extraction in Canada or the Baltic countries (González et al. 2014; Karofeld et al. 2016). For restoration purposes, *Sphagnum* fragments are harvested at natural donor sites and then transferred to the target sites. This is known as the "moss layer transfer technique" (Quinty and Rochefort 2003).

The implementation of *Sphagnum* harvesting ranges from minor interventions to comprehensive removal of the complete *Sphagnum* layer. In Germany, where 99% of peatlands are degraded (Joosten and Clarke 2002), harvesting of only small amounts is carried out for scientific or restoration purposes, sometimes harvesting 5–10 cm fragments of only half of the individual hummocks to limit the damage (Grobe 2023). In the Australasian and Chilean peatlands, *Sphagnum* harvesting is commonly implemented by hand but results in comprehensive removal of the top 25 cm up to the complete *Sphagnum* layer (Diaz and Silva 2012; Domínguez 2014; Whinam et al. 2003). For mechanical harvesting, excavators are used at forestry-drained peatlands in Finland and *Sphagnum* cultivation sites (Kumar 2017; Silvan et al. 2017). To obtain restoration material, *Sphagnum* biomass is also gathered mechanically with rotavators and bulldozers in areas intended for peat extraction in Canada (Quinty and Rochefort 2003).

If the *Sphagnum* layer is completely removed for commercial harvest, only bare peat or dead moss layer remains at the natural or semi-natural donor sites, where *Sphagnum* regenerative capacity is low or non-existent, sometimes causing long-term damage to entire areas (Diaz and Silva 2012; Whinam et al. 2003; Zegers et al. 2006). But if at least 30% of actively growing plant parts of *Sphagnum* remain in the area, either due to small-scale harvest, low harvesting depth, or reseeding of fragments, and the hydrological conditions for moss growth are still optimal, they can regrow in three to 30 years (Benson et al. 2019; Buxton et al. 1996; Diaz and Silva 2012; Silvan et al. 2012; Whinam et al. 2003).

The effects of the *Sphagnum* harvest on the epigeic arthropod communities associated with the *Sphagnum* layer remain to be determined. So far there has been a small-scale study in New Zealand (Sanders and Winterbourn 1993), but further research is needed in other regions both at the quantitative level on faunal biomass and qualitatively at the species level. Epigeic arthropods, such as ants, beetles, and spiders, form the largest faunal biomass in *Sphagnum* habitats and include many highly specialized species (Rydin and Jeglum 2006; Spitzer and Danks 2006). These species have particularly close connections at the microhabitat level with the vegetation structure and especially with the *Sphagnum* layer (Hollmen et al. 2008; Muster et al. 2020; Powell et al. 2013; Sushko 2017; Tobisch et al. 2023; Zoch et al. 2024). These connections are partly direct when species feed on plant material (e.g., Byrrhidae) but can also be indirect since the vegetation influences the microclimatic conditions (Brigić et al. 2017; Ries et al. 2021; Spitzer et al. 1999). At the same time, there is an increasing decline in *Sphagnum* bogs and, thus, also in the distribution and relative abundance of specialized bog fauna species worldwide as a result of land-use changes for agricultural and forestry cultivation, drainage, nutrient inputs, and industrial peat extraction (Habel et al. 2019; Parish et al. 2008; Sperle and Bruelheide 2021; van Grunsven et al. 2020; Vries and Boer 1990).

It can be assumed that *Sphagnum* harvesting can weaken arthropod populations because of biomass removal, mechanical shredding, and changes in the habitat structure. Our study aimed to assess the effect of small-scale *Sphagnum* harvesting on epigeic arthropods at two near-natural donor sites in Germany. Therefore, we analyzed the influence of harvest on the following parameters:

- the total number of epigeic arthropod individuals in the top 5 cm of the *Sphagnum* layer,
- the number of different species of beetles and ants, as well as bog-typical and threatened species,
- the vegetation structure as an essential habitat characteristic.

Material and methods

Study sites

The surveys were conducted at two near-natural bogs ('Wildes Moor' 53° 02′ N, 7° 29′ E and 'Meerkolk' 52° 38′ N, 07° 08′ E) in northwestern Germany, near the Dutch-German border. The region was originally covered by extensive peatlands, which are now degraded mainly by agricultural use and peat extraction. The two bogs are called 'near-natural' because they have been affected by human activities such as intermittent drainage. Nevertheless, typical vegetation of ombrotrophic bogs with a high cover of hummock-forming *Sphagnum* mosses (mainly *S. papillosum, S. medium*) exists, which makes them suitable for *Sphagnum* harvest. In October 2015 (Wildes Moor) and in October 2016 (Meerkolk), *Sphagnum* fragments were harvested for the installation of two nearby experimental *Sphagnum* cultivation sites (Grobe et al. 2021; Zoch et al. 2024).

Sphagnum harvesting was conducted manually with hedge trimmers, cutting and raking aside the vascular plants, and then cutting and collecting the *Sphagnum* fragments. Harvesting was not carried out over the entire area but only in small sections of a few square meters to limit vegetation damage and promote regeneration. *Sphagnum* fragments were only harvested to a 5–10 cm depth. *Sphagnum* was cut from small patches, which covered an area of around 1 ha at Wildes Moor and 0.6 ha at Meerkolk. The study was conducted in these harvest areas (Fig. 1a; Table 1). The adjacent areas unaffected by harvesting had comparable vegetation and were included in the study as reference areas (Fig. 1b; Table 1).

Arthropods sampling, determination, and classification

The surveys were conducted from 2016 to 2017 in the first year after the harvest, respectively. Arthropods living in and on the upper *Sphagnum* layer were studied by manually extracting quadrat samples. Quadrat samples primarily capture species residing between the vegetation, while highly mobile species are only caught with single individuals (Coulson and Butterfield 1985; Zoch et al. 2024). It can, therefore, be assumed that the species caught are strongly linked to the location where they were found so that conclusions can be drawn about absolute densities of individuals and, thus, about the influence of harvesting (Andersen 1995; Coulson and Butterfield 1985).

Arthropod sampling was conducted on four to five dates each year from April to October. At the harvest and reference areas of Wildes Moor, five samples were taken on each date, for a total of 20 samples (Table 1). At Meerkolk, ten samples were taken on each date, and 50 samples were taken per treatment. The quadrat samples were randomly positioned, with samples placed only in hummocks of the target *Sphagnum* species *(S. papillosum, S. medium)* in the harvest and reference areas, while hollows were left out. In the sample frame (30 cm × 30 cm), the top layer of living *Sphagnum* (maximum 5 cm) and other vegetation or litter was cut off and examined by careful hand sorting. All arthropods were collected by hand from the material and taken for identification in the laboratory. Nymphs of Araneae in cocoons or on the backs of female adults were excluded.

The arthropods, including larvae, were identified at the order level according to Müller and Bährmann (2015). Ants and adult beetles were determined to species level according to Seifert (2007) and Lompe (2002). Critical beetle species were confirmed by various experts (see Acknowledgements). Fifteen beetles were determined only to genera (*Euaesthetus* and *Gabrius*) or subfamily (*Aleocharinae*). These individuals were indicated with spec. or agg. and the genera or subfamily count as one additional species in the total number of species.

For all determined species, a classification as "threatened" (categories 1, 2, 3, G on the German Red List, see Appendix for abbreviations), "near-threatened" (category V), or "not threatened" (category *) (Binot-Hafke et al. 2011; Gruttke et al. 2016;

Fig. 1 **a** Harvest and **b** reference area at Wildes Moor in May 2016 (7 months after the harvest)

Table 1 Harvest and reference areas of the study sites with area [ha], harvesting time, years of surveys, number of arthropod samples and vegetation plots

Study sites	Treatment	Area [ha]	Harvesting time	Year of surveys	No. of arthropod samples	No. of vegetation plots
Wildes Moor	Harvest	1.0	10/2015	2016	n = 20	n = 10
	Reference	0.4		2016	n = 20	n = 10
Meerkolk	Harvest	0.6	10/2016	2017	n = 50	n = 10
	Reference	0.6		2017	n = 50	n = 10

Ries et al. 2021) was made. The strength of their association with bogs in northwestern Germany was divided into three classes: tyrphobiont species were classified as “bog specialists”, tyrphophilous species or those with focal occurrence in raised bogs as “bog generalists”, and all other species with primary habitats outside bogs were labeled “bog tolerant” (Bräunicke and Trautner 2009; Koch 1989; Lompe 2002; Peus 1928; Seifert 2007; Sonnenburg 2009).

Vegetation surveys

Vascular plant species and *Sphagnum* spec. were examined at all sites in July of the first year after harvesting, as they form the essential habitat structures for the epigeic arthropod fauna (Table 1). For this purpose, ten representative plots (5 m × 5 m) were positioned at each treatment area in hummocks of the target *Sphagnum* species. Within the plots, the occurrence of all vascular plant species was recorded. As trees were not affected by the manual harvest, they were excluded. Cover of vascular plants and *Sphagnum* spec. was estimated according to a scale of Londo (1976). The mean values of the scale classes were used for analysis. Additionally, the thickness of the *Sphagnum* layer (the height of living mosses) was measured with a yardstick at five points (four corners and middle) in each plot, starting from the peat layer. For analysis, the mean value of the five points was used.

Data analysis

Statistical analysis was conducted using R software (R version 4.3.2, R Core Team 2023). To interpret and summarize major patterns of variation in vegetation structure between treatments, principal component analysis (PCA) was performed with the package ‘FactoMineR’ (Le et al. 2008). PCA biplot was produced using the packages ‘ggplot2’ and ‘factoextra’ (Kassambara and Mundt 2020; Wickham 2016). The variables included were the cover of individual vascular plant species that occurred in more than ten plots, the cover of *Sphagnum spec*., and the *Sphagnum* layer thickness.

Differences between the harvest and reference areas were tested using generalized linear mixed models (GLMM, with negative binomial error distribution) with the study site as a random effect in the model (significance level of $p < 0.05$). The number of arthropod individuals per sample at the order level, the number of different beetle species per sample for all species, bog generalists and specialists, near-threatened and threatened species, and the cover of plant species and *Sphagnum* layer thickness per plot were tested for differences. For arthropods, the analyses were only carried out for orders with more than 100 individuals in total, and ants were excluded as they live in nests. For the vascular plants, a selection was made based on their frequency in the plots. Only species that occurred in at least 10 of the 40 plots were analyzed. The package ‘glmmTMB’ (Brooks et al. 2017) was used to model the GLMMs. For graphical presentation, the R packages ‘ggplot2’ and ‘hrbrthemes’ were used (Rudis 2020; Wickham 2016).

As ants live in nests, individual numbers cannot be used to analyze this species group. For this reason, the frequency of ant species in the samples was compared. In addition, nest locations were derived from the number of individuals per sample (only workers). If there were more than ten workers of an ant species in a sample, a nest was assumed (directly in the sample or very close to it).

Results

Vegetation structure

The two dimensions of the PCA could explain 52.4% of the vegetation data (Fig. 2). Dimension 1 (horizontal axis) captured 29.1% of the variance, mainly showing the vegetation differences between the study sites’ reference areas. In dimension 1 was a gradient from a vegetation characterized by *Molinia caerulea, Erica tetralix,* and *Calluna vulgaris* in the reference areas of Wildes Moor to a vegetation formed by *Vaccinium oxycoccos, Andromeda polifolia, Sphagnum* spec. and *Eriophorum angustifolium* in the reference areas of Meerkolk.

Dimension 2 (vertical axis), describing a supplemental 23.3% variance, reveals vegetation differences between the treatments. The species that made the greatest contribution to dimension 2 were *Rhynchospora alba*, *Drosera intermedia*, and *D. rotundifolia.* In addition, dimension 2 was mainly influenced by the thickness of the *Sphagnum* layer. The data of

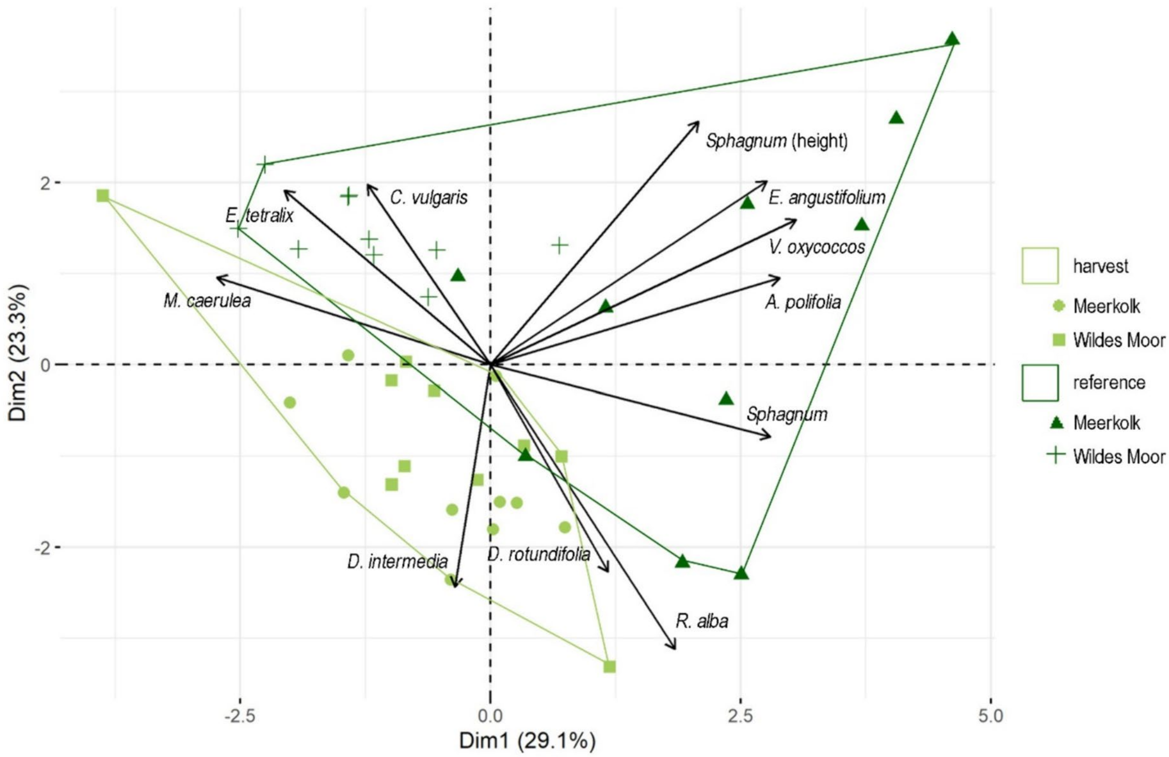

Fig. 2 Principal Component Analysis (PCA) Biplot of the vegetation in n = 20 plots per treatment. Each dot represents one plot of Meerkolk and Wildes Moor study sites at which the vegetation was assessed. Convex hulls are drawn for the harvest and reference areas. Black vectors represent the cover of different vascular plant species and *Sphagnum* spec. and *Sphagnum* layer thickness (height). Only species that occurred in more than ten plots are shown. See Table 2 for abbreviations of plant species

the two treatments showed only a small overlap and revealed a greater homogeneity of vegetation in the harvest areas (smaller convex hull) of both study sites. In contrast, the vegetation of the reference areas showed more variation as the vegetation of the study sites differed. The slight angles of the vectors reveal a close correlation between the cover of some plant species, for example *Drosera rotundifolia* and *Rhynchospora alba*.

The vegetation of all areas was characterized by a high *Sphagnum* cover (Table 2). While there were no differences in *Sphagnum* cover between the harvest and reference areas, there was a significantly lower *Sphagnum* layer thickness in the harvest areas, with a mean height of 8.7 cm in the harvest and 20.0 cm in the reference areas. The dominant vascular plant species were *Erica tetralix, Molinia caerulea*, and *Rhynchospora* alba, with a mean cover of around 13 to 29%. Differences were found between the vegetation of the harvest and reference areas, with a significantly lower cover of *Andromeda polifolia*, *Erica tetralix* (nearly significant with p = 0.06), *Eriophorum angustifolium,* and *Vaccinium oxycoccos,* and a significantly higher cover of *Drosera intermedia* at the harvest areas (Table 2). Non-significant differences, but still visible tendencies, were observed for *Drosera rotundifolia* and *Rhynchospora alba,* with a higher cover in the harvest areas.

Effect of *Sphagnum* harvesting on arthropod fauna

In total, we collected 2,197 arthropod individuals belonging to twelve orders (without ants). Of these, 1175 individuals were present in the reference areas, more than in the harvest areas (1022). The dominant orders were Araneae, Hemiptera, and Coleoptera, with about 170 to 470 individuals per treatment and a relative abundance of 20–40% of all individuals.

Table 2 Summary table with mean values and ± standard deviation for the cover of vascular plants and *Sphagnum* spec. as well as *Sphagnum* layer thickness (height) in n = 20 plots per treatment (harvest and reference)

		Harvest	Reference	Estimate	Standard error	p
Cover [%]	*Andromeda polifolia*	0.3 ± 0.7	4.3 ± 6.5	− 2.573	0.760	***
	Calluna vulgaris	1.5 ± 2.3	1.5 ± 1.6	0.0165	0.635	ns
	Erica tetralix	16.8 ± 11.4	28.8 ± 17.8	− 0.428	0.229	ns
	Eriophorum angustifolium	3.2 ± 2.0	9.7 ± 15.0	− 0.987	0.356	**
	Drosera intermedia	1.2 ± 1.4	0.3 ± 0.6	2.200	0.868	*
	Drosera rotundifolia	3.2 ± 2.6	2.3 ± 2.2	0.312	0.259	ns
	Molinia caerulea	16.2 ± 9.9	16.4 ± 11.1	0.012	0.202	ns
	Rhynchospora alba	18.8 ± 11.9	12.7 ± 13.4	0.700	0.395	ns
	Sphagnum spec	84.3 ± 13.3	86.4 ± 9.8	− 0.025	0.046	ns
	Vaccinium oxycoccos	2.0 ± 2.3	8.2 ± 9.5	− 1.368	0.426	**
Height [cm]	*Sphagnum spec*	8.7 ± 2.4	20.0 ± 4.7	− 0.832	0.091	***

Only species that occurred in more than ten plots are shown

The influence of *Sphagnum* harvest was tested using GLM with negative binomial error distribution

Level of significance ($p \leq 0.05$): ns (not significant, $p > 0.05$), *($p < 0.05$), **($p < 0.01$), ***($p < 0.001$)

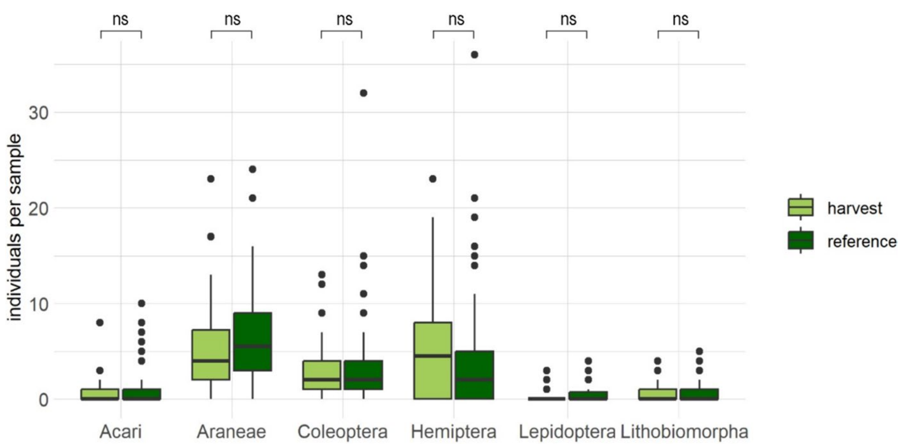

Fig. 3 Number of individuals per sample for different arthropod orders in harvest and reference areas in n = 70 samples per treatment. Only orders with more than 100 individuals in total are shown. Differences between the sites tested using GLMM with negative binomial error distribution and study site as a random effect. Level of significance ($p \leq 0.05$), ns (not significant, $p > 0.05$)

The orders Lithobiomorpha, Acari, and Lepidoptera made up 2–5% of all individuals, with 30 to 70 individuals per treatment, whereby only caterpillars and no adults of Lepidoptera were found. Six orders (Diptera, Geophilomorpha, Hymenoptera (without ants), Pseudoscorpiones, Orthoptera, Opiliones) were not included in the further analyses because they were found with only less than five individuals overall.

There were no significant differences in the number of arthropod individuals per sample between the reference areas, with an average of 16.8 ± 13.0 individuals per sample compared to an average of 15.0 ± 8.8 individuals in the harvest areas. The same applies to the different orders with no significant differences in individual numbers per sample between the treatments (Fig. 3). On average, the number of individuals was higher on the reference sites, except for the Hemiptera, for which it was higher in the harvest areas.

Beetles

In total, we collected 376 adult individuals of 46 beetle species belonging to ten families (Appendix). Thirty-five species were found in each of the two treatments (Table 3). Of all species, 13 can be categorized as bog generalists and four as specialists. Seven species are considered threatened in Germany,

Table 3 Summary table with the species and individual numbers of adult beetles, and the mean number ± Standard deviation per sample for the harvest and reference areas, subdivided into all species, bog generalists (BG) or specialists (BS), and near-threatened (NT) or threatened (T) species

		Harvest		Reference		Estimate	Standard Error	p
		Total	Mean no. per plot	Total	Mean no. per plot			
No. of species	All	35	1.5 ± 1.4	35	1.7 ± 1.6	− 0.105	0.154	ns
	BG/BS	14	0.6 ± 0.8	15	0.8 ± 1.0	− 0.340	0.218	ns
	NT/T	10	0.5 ± 0.6	9	0.5 ± 0.6	− 0.031	0.248	ns
No. of individuals	All	153	2.2 ± 2.5	223	3.2 ± 4.7	− 0.342	0.200	ns
	BG/BS	53	0.8 ± 1.2	122	1.7 ± 4.0	− 0.813	0.283	**
	NT/T	43	0.6 ± 1.0	59	0.8 ± 1.4	− 0.316	0.280	ns

The influence of *Sphagnum* harvest was tested using GLMM with negative binomial error distribution and study site as a random effect;

*($p < 0.05$), **($p < 0.01$), ***($p < 0.001$), ns (not significant, $p > 0.05$)

and three species are near-threatened, although all of these species are bog generalists or specialists. With 223 individuals, there tended to be more individuals in the reference areas than in the harvest areas, with 153 individuals. Nevertheless, the number of species and individuals per sample showed no significant differences between the treatments except for bog species (Table 3). There were significantly more individuals of bog generalists and specialists in the reference areas than in the harvest areas.

There were primarily regional differences between the two study sites for the individual numbers of different species (Appendix). Some species also showed minor differences between the two treatments. The bog specialist *Philonthus nigrita* and the bog generalists *Pterostichus diligens, Cyphon hilaris,* and *C. variabilis* occur at both study sites but with higher individual numbers and frequencies or exclusive occurrence in the reference areas (Appendix, Table 4).

In contrast, the bog tolerant *Chaetarthria seminulum* and *Helophorus flavipes* were found only or with considerably higher individual numbers in the harvest areas (Appendix).

Ants

For ants, six species were found (Table 5) with 1279 individuals. *Formica picea* is the only bog specialist, while all other species are bog generalists. In addition, *Formica picea* is a threatened species, and *Myrmica scabrinodis* a near-threatened one. The most frequent species were *Lasius platythorax* and *Myrmica scabrinodis*, with a higher frequency in the reference areas (Table 5). For both species considerably more nests were found in the reference areas. The other species were found in less than five samples each, with *Formica picea, Myrmica rubra,* and *M. ruginodis* only found with a few workers in the reference areas and *Leptothorax acervorum* with one nest in a harvest area.

Discussion

Effects of *Sphagnum* harvesting

The study found different effects of *Sphagnum* harvesting on the arthropod fauna and the vegetation after 1 year. There were no significant effects on the individual numbers of arthropods at the order level. This may be related to the fact that the harvest areas were very small and surrounded by unharvested areas, so the arthropods could recolonize within the study period. Nevertheless, in the case of ants, the frequency of workers and the number of nests were considerably lower in the harvest areas. This is related to the destruction of nests in the *Sphagnum* harvesting process. Ants specializing in bogs build their nests in the *Sphagnum* carpet, with high nest densities of up to 100 nests per 100 m^2 in open *Sphagnum* areas (Seifert 2007). Even though the number of nests in the harvest areas was clearly reduced, some were still found here. Because ants do not reproduce in winter

Table 4 Pooled numbers of individuals and frequency (number of samples in which the species was detected) for bog specialists (BS) and bog generalists (BG) of beetles in n = 70 samples per treatment

		Peatland association	Harvest		Reference	
			Sum	Frequency	Sum	Frequency
Carabidae	*Acupalpus dubius*	BG	5	4	6	5
	Bradycellus ruficollis	BG	1	1	1	1
	Pterostichus diligens	BG			7	4
Chrysomelidae	*Altica ericeti*	BG	3	3	1	1
	Plateumaris discolor	BG	1	1	4	3
Dytiscidae	*Hydroporus obscurus*	BG	2	2	2	2
	Hydroporus scalesianus	BS	13	4	15	6
	Hydroporus tristis	BG	1	1	4	2
	Rhantus suturellus	BG	1	1		
Hydrophilidae	*Enochrus affinis*	BG			1	1
Noteridae	*Noterus crassicornis*	BG	1	1		
Scirtidae	*Cyphon hilaris*	BG	8	8	24	11
	Cyphon variabilis	BG	5	5	40	9
Staphylinidae	*Acylophorus wagenschieberi*	BS	6	6	3	2
	Lathrobium rufipenne	BS	3	2	3	2
	Olophrum piceum	BG			1	1
	Philonthus nigrita	BS	3	3	10	9

Threatened and near-threatened species are underlined

Table 5 Frequency (number of samples in which workers were detected) and number of nests (samples with more than 10 workers) for all ant species in n = 70 samples per treatment

	Peatland association	Harvest		Reference	
		frequency workers	No. of nests (> 10 workers)	Frequency workers	No. of nests (> 10 workers)
Formica picea	BS			4	
Lasius platythorax	BG	15	3	19	8
Leptothorax acervorum	BG	1	1		
Myrmica rubra	BG			3	
Myrmica ruginodis	BG			1	
Myrmica scabrinodis	BG	33	2	45	15

The peatland association differs between bog specialists (BS) and bog generalists (BG). Threatened and near-threatened species are underlined

(Seifert 2007), one can expect that ants did not reproduce after the *Sphagnum* harvesting. Nests found in the next year in the harvest areas are most likely nests that were there before the harvesting, which were probably damaged but not wholly destroyed. The question is whether they can cope with the changed conditions after the harvest. The *Sphagnum* layer thickness of hummocks has been reduced significantly by the harvest, so the *Sphagnum* capitula and the surface of hummocks have been lowered towards the water table, even if the hummock-forming *Sphagnum* species are still alive and can likely regenerate. Moisture-loving plant species such as *Rhynchospora alba* and *Drosera intermedia* indicate that harvest areas have become wetter (Müller et al. 2021), even if the overall hydrology of the sites has not been changed. Moisture is a critical factor influencing the occurrence of arthropods in peatland areas (Hoffmann et al. 2016; Maes et al. 2019). The bog generalists *Myrmica scabrinodis, Lasius platythorax,* and *Leptothorax acervorum*, which were found with nests, can build their nests in very wet *Sphagnum lawns,* but are nevertheless dependent on the top part of the *Sphagnum* remaining dry for breeding development (Maes et al. 2003; Seifert 2007). *Formica picea, Myrmica rubra,* and *M. ruginodis* were found only with a few foraging workers, which does not allow any conclusions to be drawn about nest sites because they overcome long distances (Klarica and Glaser 2015). Nevertheless, it is known that the tyrphobiont *Formica picea* prefers to build its nests in dry hummocks with *Polytrichum spec*., *Ericaceae* and graminoids (Seifert 2007; Sonnenburg 2009). This study shows that these structures have been reduced by the harvest, which is why *Formica picea* is likely to be affected by *Sphagnum* harvesting. Due to the alterations of the harvest areas, they are probably unsuitable as nest sites for this ant species until the *Sphagnum* hummocks have reached a critical height again.

For beetles, no effects of the harvest on the total number of individuals and species were found, and most species show no differences in occurrence between harvest and reference areas. Nevertheless, it was revealed that some species react differently to the harvest. The aquatic hydrophilid species *Chaetarthria seminulum* and *Helophorus flavipes* have increased their presence in the harvest areas, possibly preferring the lower and, thus, wetter *Sphagnum* lawns, as the adults are detritivores, feeding on organic material in the water or near to it (Lompe 2002). In contrast, the abundance of bog generalists and specialists was significantly reduced, and single species like *Pterostichus diligens* could be found with lower individual numbers in the harvest areas. Zoch et al. (2024) and Muster et al. (2020) also show that a high *Sphagnum* layer thickness is a vital habitat structure and decisive for the occurrence of arthropods specialized in bogs, which may lose hiding and reproduction structures when the *Sphagnum* layer is reduced. Further effects on individual species could not be proven but can be surmised from the changes in the vegetation. Some beetles directly depend on specific plant species and vegetation structures (Brigić et al. 2017; Spitzer et al. 1999; Sushko 2017). Heather species such as *Andromeda polifolia* and *Erica tetralix* have declined in their cover in the harvest areas. This might impact dependent species, such as *Altica ericeti*, which lives on plants of the genus *Erica* (Rheinheimer and Hassler 2018). This leaf beetle species is threatened with extinction in Germany (Ries et al. 2021), and until the time of the study, it was not even known that it occurred in the state of Lower Saxony (Schacht and Mertens 2022). This shows that the arthropod fauna is often insufficiently studied (Kato et al. 2009) and should be assessed before any interventions.

Another effect that *Sphagnum* harvesting might have on all epigeic arthropods is the removal of individuals with the *Sphagnum* material from the area (Sanders and Winterbourn 1993). Derived from the individual numbers per sample in the reference areas (including ants), one could approximate that *Sphagnum* harvesting removed around 30 arthropod individuals per 1 m^2 and 550 individuals per 1 m^3 of mosses together with the upper *Sphagnum* layer at a cutting depth of 5 cm (this corresponds to the sample depth). It can be assumed that some of the arthropods removed will be transferred to the target areas and accelerate the colonization of typical bog species (Watts et al. 2008).

Conclusions

Sphagnum harvest mainly affects epigeic arthropod species building nests, like ants and species specializing in dry hummocks. In contrast, species that can cope with very wet *Sphagnum* are less likely to be affected or may even benefit from slightly wetter conditions caused by the reduced height of the *Sphagnum* layer. In addition, the shortening and leveling of *Sphagnum* hummocks led to a homogenization of the vegetation of both study sites, and the composition of vascular plant species was altered, at least temporarily. Murray et al. (2017) and Guêné-Nanchen et al. (2019) have also found alterations in plant composition due to *Sphagnum* harvesting with preferential plant species of wet microhabitats benefiting from wetter donor areas. In our study, the top parts of hummock-forming *Sphagnum* species were only cut off in small sections of a few square meters so that the mosses could regenerate rapidly, and it can be assumed that the arthropod fauna was not permanently damaged in its populations. This is consistent with Sanders and Winterbourn (1993), who found short-term effects of *Sphagnum* harvesting on the mean density and taxonomic richness (family level) of invertebrates in the *Sphagnum* layer, but little effect in the medium to long term. If equal patches of the donor site are left untreated, the invertebrate fauna can survive undamaged and recolonize the harvest areas. This approach will probably also encourage *Sphagnum* regrowth (Krebs et al. 2016; Whinam and Buxton 1997; Zegers et al. 2006). More negative effects can be expected from large-scale harvesting and removing the entire *Sphagnum* layer and, thus, the whole arthropod fauna, only re-spreading some of the material to stimulate regrowth (Buxton et al. 1996; Domínguez 2014). It is known that creating bare peat areas can negatively affect the occurrence and abundance of bog species (Zoch et al. 2024). *Sphagnum* harvesting should, therefore, only be done in patches or strips.

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Author contributions L.Z. and M.R. Reich created the study conception and design. Material preparation, data collection and analysis were performed by L.Z. The first draft of the manuscript was written by L.Z., and M.R. commented on previous versions of the manuscript. Both authors read and approved the final manuscript.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Appendix

See Table 6.

Table 6 Pooled numbers of individuals per treatment and study site (Meerk. = Meerkolk, Wild. = Wildes Moor) of all recorded beetle species with the indication of bog association (BS = bog specialists; BG = bog generalists; BT = bog tolerant) and the Red List Category in Germany according to Gruttke et al. (2016) and Ries et al. (2021) (1 = Threatened with Extinction; 2 = Highly Threatened; 3 = Threatened; G = Threat of Unknown Extent; V = Near Threatened; * = Not Threatened)

		Red List	Bog asso-coation	Harvest		Reference	
				Meerk	Wild	Meerk	Wild
Carabidae	*Acupalpus dubius*	V	BG		5		6
	Bradycellus ruficollis	3	BG		1		1
	Pterostichus diligens	*	BG			6	1
	Pterostichus vernalis	*	BT			1	
Chrysomelidae	*Altica ericeti*	1	BG		3		1
	Cryptocephalus ocellatus	*	BT		1		
	Plateumaris discolor	2	BG	1		4	
Curculionidae	*Micrelus ericae*	*	BT		1		
	Betulapion simile	*	BT	1			
Dytiscidae	*Hydroporus obscurus*	V	BG	1	1	2	
	Hydroporus scalesianus	2	BS	13		15	
	Hydroporus tristis	*	BG	1		4	
	Rhantus suturellus	V	BG	1			
Hydrophilidae	*Cercyon pygmaeus*	*	BT	1			
	Chaetarthria seminulum	*	BT	20	10	3	
	Coelostoma orbiculare	*	BT	1		4	
	Enochrus affinis	*	BG			1	
	Helophorus flavipes	*	BT	1	2		
Latridiidae	*Corticarina similata*	*	BT			1	
Noteridae	*Noterus crassicornis*	*	BG	1			
Pselaphidae	*Pselaphus heisei*	*	BT	1			
Scirtidae	*Cyphon hilaris*	G	BG	7	1	22	2
	Cyphon padi	*	BT	1		5	
	Cyphon variabilis	*	BG	5		40	
Staphylinidae	*Acylophorus wagenschieberi*	2	BS	6		3	
	Aleocharinae agg.					1	2
	Drusilla canaliculata	*	BT	5		5	
	Erichsonius cinerascens	*	BT	2	1		1
	Euaesthetus spec.			4		2	
	Gabrius spec.			1		1	
	Lathrobium rufipenne	G	BS	3		3	
	Myllaena intermedia	*	BT	27	1	48	1
	Myllaena minuta	*	BT	4			
	Ochthephilum fracticorne	*	BT	1	4	4	7
	Olophrum piceum	*	BG				1
	Philonthus carbonarius	*	BT	4		8	
	Philonthus cognatus	*	BT	2		1	
	Philonthus nigrita	*	BS	3		6	4
	Philonthus varians agg.		BT			1	
	Scopaeus laevigatus	*	BT	1			
	Stenus providus		BT				1
	Tachyporus chrysomelinus	*	BT			1	
	Tachyporus hypnorum	*	BT			1	
	Tetartopeus terminatus	*	BT	2		1	
	Xantholinus longiventris	*	BT			1	

Table 6 (continued)

	Red List	Bog asso-coation	Harvest		Reference	
			Meerk	Wild	Meerk	Wild
Xantholinus gallicus	*	BT	1			

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