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Phytosociology, ecology and aspects of fitness of *Pulsatilla pratensis* subsp. *nigricans* (Störck) Zämelis in the northern foothills of the Harz Mountains (Saxony-Anhalt, Germany)

Phytosoziologie, Ökologie und Aspekte der Fitness von *Pulsatilla pratensis* subsp. *nigricans* (Störck) Zämelis im Nordharzvorland (Sachsen-Anhalt, Deutschland)

Tim Meier[1 *], Norbert Rußwurm[2] & Uwe Wegener[3]

[1]Kröllwitzer Straße 20, 06120 Halle (Saale), Germany;
[2]Brinckmeierstraße 13, 06493 Ballenstedt, Germany;
[3]Meisenweg 27, 38820 Halberstadt, Germany
**Corresponding author, e-mail: tim.meier1@t-online.de*

Abstract

Over the last 25 years, central German dry grasslands have experienced a dramatic loss of species of typical, often threatened grassland specialists. Main drivers are global warming, atmospheric nitrogen deposition and changes in land use, all of which can contribute to reduced growth and fitness of such species, which in turn may lead to the extinction of their mostly small and isolated populations. Particularly, in the northern foothills of the Harz Mountains (Saxony-Anhalt, Germany), *Pulsatilla pratensis* subsp. *nigricans* appears to be increasingly threatened with extinction, as individuals have been counted in several populations for more than 40 years and dramatic declines in these populations have been documented since 2018. Therefore, we aimed to examine the occurrence of the species in various plant communities in the northern foothills of the Harz Mountains and to compare the growth and fitness of different populations. Additionally, management recommendations for conservation should be highlighted. We selected 11 populations in the northern foothills of the Harz Mountains and additionally one population in the Harz Plateau, determined their population size, conducted vegetation surveys and soil analyses and measured functional traits. We found that in 2023 most populations of *P. pratensis* subsp. *nigricans* were very small, occurring within the Harz region in different associations of the class *Festuco-Brometea*: *Festuco-Stipetum*, *Stipetum stenophyllae*, *Festuco-Brachypodietum*, *Adonido-Brachypodietum*, *Onobrychido-Brometum*, *Gentiano-Koelerietum*. An NMDS ordination revealed no preferences of *P. pratensis* subsp. *nigricans* for certain habitats, but population size decreased with increasing soil depth and increased with increasing soil carbon and soil nitrogen content. Vegetative and generative traits of *P. pratensis* subsp. *nigricans* differed significantly between the different sites to their varying ecological conditions. For example, higher values for plant height, leaf length, leaf area and seed mass were detected for the species mainly within the semi-dry grasslands. Population size as well as soil properties and mean indicator values had mostly significantly negative effects on the growth and fitness traits of this species, whereas soil depth and the mean indicator values for continentality, temperature, moisture and reaction had the greatest influence on the plant performance. Moreover, larger populations of *P. pratensis* tended to show lower values in their functional traits when soil depth is lower, water availability limited and soil dryness increases.

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Although most of these populations are remnant populations of *P. pratensis* subsp. *nigricans*, which are currently able to reproduce themselves, we found that these species had a relatively large environmental range. We assume that extreme prolonged periods of heat and drought will pose the main threat to the growth performance of *P. pratensis* subsp. *nigricans* in future. For the conservation of this species, we recommend optimal sheep grazing in a wide enclosure.

Keywords: climate warming, *Festuco-Brometea*, functional traits, nature conservation, *Pulsatilla pratensis* subsp. *nigricans*, soil factors, vegetation survey

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Dry and semi-dry grasslands are characterised by a high biodiversity of vascular plant species (Visconti et al. 2018) and contain a large proportion of rare and threatened species (Dengler et al. 2020). However, over the last 25 years, dry grasslands in Central Germany have experienced a dramatic loss of species of typical, often threatened and critically threatened grassland specialists (Meier et al. 2021, 2022). Processes of ongoing global change, such as climate warming and atmospheric nitrogen deposition, as well as changes in land use, such as the cessation of grazing and mowing, can be considered as the main drivers (Bobbink et al. 2010, Dupré et al. 2010, Hülber et al. 2017, Diekmann et al. 2019). Extreme weather conditions, such as heatwaves and drought events, have intensified in Central Germany in recent years (especially in 2018 and 2019) (Boergens et al. 2020), which probably favoured the loss of threatened species in these grasslands.

Habitat degradation and fragmentation often lead to isolated populations and thus to a declining population size (Young et al. 1996, González et al. 2020). This may in the longer term result in reduced genetic diversity and reduced fitness due to inbreeding depression (Oostermeijer 1996, Dannemann 2000, Packer et al. 2005, Leimu et al. 2006). The so-called "extinction vortex" describes the process whereby ecological, genetic and demographic forces interact synergistically and reinforce each other over time, which often leads to the extinction of small and isolated populations (Gilpin & Soulé 1986). Furthermore, functional traits such as plant height, SLA (specific leaf area), LDMC (leaf dry matter content) and seed mass are closely linked to resource acquisition and the competitiveness of plants and thus have an indirect effect on the growth and fitness of individuals in a population (Garnier et al. 2016). Functional traits can also provide an indication of the rarity and extinction of specialised species (Gabrielová et al. 2013).

Particularly in Central Germany, genetic studies, e.g. for the threatened species *Biscutella laevigata* subsp. *gracilis* (Rosche et al. 2022), *Dictamnus albus* (Hensen & Oberprieler 2005) and *Pulsatilla vulgaris* (Hensen et al. 2005), have shown that small populations in fragmented habitats exhibited low genetic diversity, which can lead to the local extinction of such populations. Another species that is potentially threatened by extinction in Central Germany is *Pulsatilla pratensis* subsp. *nigricans*, which occurs mainly in the Kyffhäuser (Thuringia) and Saale-Unstrut-Triasland as well as in the northern foothills of the Harz Mountains (Saxony-Anhalt) (Herdam 1995, Barthel & Pusch 1999). The latter region represents the main area of the species (NetPhyD & BfN 2013) that occurs here in various dry and semi-dry grassland communities.

Since 1982, detailed counting series of *P. pratensis* subsp. *nigricans* have been available for the Harslebener Berge (Wegener & Eberspach 1996, Wegener & Wolff 2007, Wegener & Rußwurm 2022). Wegener & Rußwurm (2022) presented an overview of the population dynamics of this species for this area and revealed the dramatic declines in the local populations after 2018, which forms the background for the present study. The aim of our investigation was to examine the occurrence of *P. pratensis* subsp. *nigricans* in different plant communities in the northern foothills of the Harz Mountains under changing environmental conditions and to compare the growth and fitness of several populations. Therefore, we addressed the following questions: (1) In which plant communities does *P. pratensis* subsp. *nigricans* occur in the northern foothills of the Harz Mountains? (2) Are there differences in the vegetative and generative traits of *P. pratensis* subsp. *nigricans* between the different populations? (3) Do habitat characteristics and population size have an influence on the growth and fitness of *P. pratensis* subsp. *nigricans*? Additionally, management recommendations for the future conservation of this species will be presented.

2. Material and methods

2.1 Study species

Pulsatilla pratensis subsp. *nigricans* (Störck) Zämelis (Abb. 1) belongs to the family *Ranunculaceae* and forms, next to *Pulsatilla pratensis* subsp. *pratensis* (L.) Mill. a subspecies of *Pulsatilla pratensis*. In general, *P. pratensis* is a perennial deciduous hemicryptophyte with a plant height of between 10 and 50 cm, with a purple or black-violet, always nodding flower and a deep root system (Müller et al. 2021). Flowering season is from the end of March to May, the flowers are pollinated by insects and the seeds are mainly dispersed anemochorously. *Pulsatilla pratensis* is widespread in the submeridional-temperate zone of Eurasia, occurring in continental sandy and siliceous dry and semi-dry grasslands and in dry pine and oak forests.

Fig. 1. *Pulsatilla pratensis* subsp. *nigricans* at peak flowering in April at the Weinberg near Börnecke (Photo: T. Meier, 07/04/2019).

Abb. 1. *Pulsatilla pratensis* subsp. *nigricans* in Vollblüte im April am Weinberg bei Börnecke (Foto: T. Meier, 07.04.2019).

The morphologically most distinctive characteristics of the subspecies *nigricans* compared to the subspecies *pratensis* are a perigone with short, non-shiny hairs, which is dark purple on the inside, and a perianth that is evenly divided into simple, narrow tips (Müller et al. 2021). The subspecies *nigricans* is classified as critically threatened (endangerment category 2) according to both the Red List of Germany (Metzing et al. 2018) and that of Saxony-Anhalt (Frank et al. 2020) and is strictly protected under the Federal Species Protection Ordinance. In our study areas, only the subspecies *nigricans* occurs, hereafter abbreviated as *P. pratensis*.

2.2 Study sites

A total of 11 populations of *P. pratensis* were studied in the northern foothills of the Harz Mountains and additionally one population near Elbingerode in the Harz Plateau (Table 1, Fig. 2). However, in the Harslebener Berge, these are more likely to be separate subpopulations of this species, relating directly to the 'observation sites' counted since 1982. In 2023, no individuals of *P. pratensis* could be detected at the two former sites HA4 and HA5 (cf. Wegener & Rußwurm 2022), so no investigations were conducted at these sites. Instead, an additional site in the Harslebener Berge, previously not included in the counts, was examined, which we here named HA9.

The region is characterised by a continental climate. The town Quedlinburg, about 3 to 6 km away from most of the studied sites, had an average annual temperature of 11.4 °C in 2022, a very high sunshine duration of 2146.9 h and an annual precipitation of only 321.6 mm, ranking it as the driest place in Germany for that year (Wetterkontor 2024). In 2022, the average spring temperature (March to May) was 9.5 °C and the average summer temperature (June to August) was 20.0 °C. Although the same average annual temperature of 11.4 °C was recorded for Quedlinburg in 2023, the annual precipitation was significantly higher at 749 mm and the average temperature during the study period in April and May was 10.6 °C (Wetterkontor 2024).

Table 1. Studied populations of *Pulsatilla pratensis* subsp. *nigricans* (see also Fig. 2) and their phyto-sociology as well as population size (flowering individuals) in 2023 (population size at Bollenkopf near Elbingerode was estimated). The plant communities were determined according to Schubert et al. (1995). Moreover, for each site the respective coordinates are given.

Tabelle 1. Untersuchte Populationen von *Pulsatilla pratensis* subsp. *nigricans* (siehe dazu auch Abb. 2) und deren Vergesellschaftung sowie Populationsgröße (blühende Individuen) im Jahr 2023 (Populationsgröße am Bollenkopf bei Elbingerode wurde geschätzt). Die Bestimmung der Pflanzengesellschaften erfolgte nach Schubert et al. (1995). Außerdem sind für jeden Standort die jeweiligen Koordinaten angegeben.

Study site/ Population	**Plant community**	**Population size [*n*]**	**Coordinates**
Harslebener Berge (HA)			
HA1	*Festuco-Brachypodietum*	38	51°49'54.00" N; 11°4'44.00" E
HA2	*Festuco-Stipetum*	3	51°49'53.32" N; 11°4'41.72" E
HA3	*Festuco-Stipetum*	3	51°49'54.06"N; 11°4'37.07"E
HA6	*Festuco-Stipetum*	3	51°50'5.15"N; 11°3'49.35"E
HA7	*Festuco-Brachypodietum*	16	51°50'10.30"N; 11°3'44.85"E
HA8	*Festuco-Brachypodietum*	15	51°50'13.78"N; 11°3'45.63"E
HA9	*Stipetum stenophyllae*	40	51°49'45.41"N; 11°4'30.46"E
Bollenkopf Elbingerode (ELB)	*Gentiano-Koelerietum*	~3000	51°46'32.81"N; 10°50'6.66"E
Arnstein (ARN)	*Festuco-Stipetum*	88	51°40'56.13"N; 11°25'1.90"E
Schalkenburg Quenstedt (SCH)	*Gentiano-Koelerietum*	26	51°41'21.10"N; 11°26'31.17"E
Weinberg Börnecke (BÖR)	*Adonido-Brachypodietum*	15	51°49'40.73"N; 11°2'49.80"E
Kleines Kamel Westerhausen (KAM)	*Onobrychido-Brometum*	47	51°48'0.19"N; 11°5'15.16"E

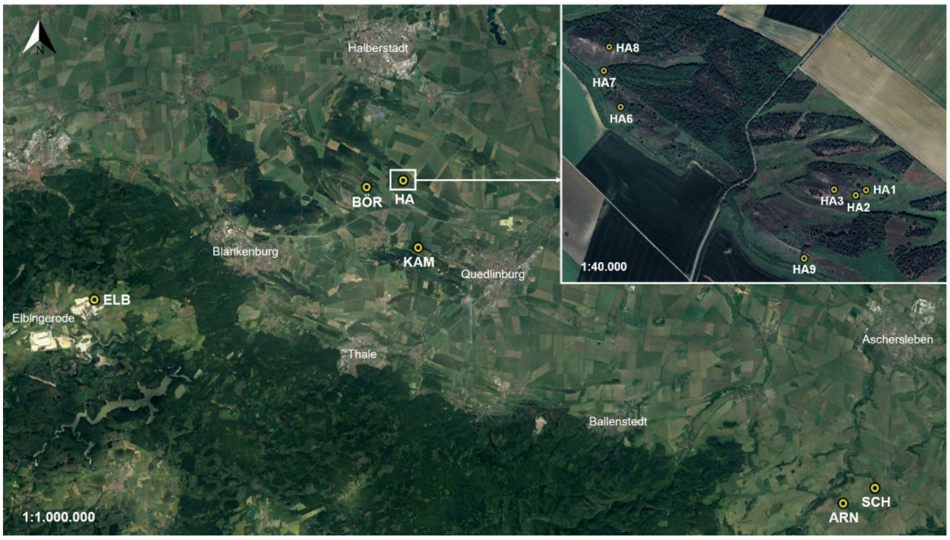

Fig. 2. Map of the studied *Pulsatilla pratensis* subsp. *nigricans* sites in the northern foothills of the Harz Mountains (HA, BÖR, KAM, ARN, SCH) and in the Harz Plateau (ELB). Detailed map of the sites in the Harslebener Berge top right (images from Google Earth, date: 06.04.2023). For abbreviations and coordinates, see Table 1.

Abb. 2. Karte zu den untersuchten Standorten von *Pulsatilla pratensis* subsp. *nigricans* im Nordharzvorland (HA, BÖR, KAM, ARN, SCH) und in der Harzhochfläche (ELB). Detaillierte Karte der Standorte in den Harslebener Bergen oben rechts (Luftbilder entstammen aus Google Earth, Aufnahmedatum: 06.04.2023). Abkürzungen und Koordinaten siehe Tabelle 1.

In the northern foothills of the Harz Mountains, the largest occurrences of *P. pratensis* are found on loess-covered sandy soils with low water storage capacity (Wegener & Eberspach 1996, Wegener & Wolff 2007, Wegener & Rußwurm 2022). All sites are heat-exposed, but the species apparently has a broader temperature amplitude, otherwise its occurrence in the Harz Plateau at approx. 470 m a.s.l. could not be explained.

The study sites contain a large number of threatened and rare species and are therefore subject to nature conservation management. More than half of the investigations took place in the nature conservation area “Harslebener Berge und Steinholz”, which is part of the Natura 2000 site “Harslebener Berge und Steinholz nordwestlich Quedlinburg” (EU FFH code: DE 4132-301, federal code: FFH0084, 261 ha) (Jentzsch & Reichhoff 2013). The Schalkenburg and Arnstein are part of the Natura 2000 site “Brummtal bei Quenstedt” (EU FFH code: DE 4334-303, federal code: FFH0189, 82 ha) and in the Harz Plateau the nature monument area “Bollenkopf und Schwefeltal” is part of the Natura 2000 site “Devonkalkgebiet bei Elbingerode und Rübeland” (EU FFH code: DE 4231-302, federal code: FFH0082, 424 ha) (Jentzsch & Reichhoff 2013). The Weinberg near Börnecke and Kleines Kamel near Westerhausen are protected as nature monument areas, but are not part of the surrounding Natura 2000 sites (Funkel et al. 2003).

Within the last 20 years, it was not possible to establish a grazing regime for *P. pratensis* in the northern foothills of the Harz Mountains based on scientific principles, especially in the Harslebener Berge. Since 2003, sheep grazing has been irregular, i.e. in some years grazing did not take place, while in other years overgrazing occurred, e.g. by placing the sheep in pens and keeping them on the same area at night, which did not benefit the nutrient-poor sites of *P. pratensis* (Wegener & Rußwurm 2022). The sites near Elbingerode were also not grazed for the last 20 years. However, to date, comprehensive shrub removal measures are carried out at least once or twice a year in the northern foothills of the Harz Mountains as part of work campaigns to eliminate emerging woody vegetation.

2.3 Vegetation surveys and soil analyses

Field work was conducted at the end of April 2023 during peak flowering of *P. pratensis*. Population size was determined exactly on the basis of all flowering individuals, as the counts were recorded using the same methodology since 1982 (cf. Wegener & Rußwurm 2022). However, there was an exception concerning the Bollenkopf near Elbingerode, where the population size could only be estimated due to the high number of individuals.

As many populations were very small, only one vegetation survey could be carried out for each site (Supplement S1). Plot size was 4 m^2 and geographical data, such as GPS coordinates (Tab. 1), were noted. The cover of the herb and cryptogam layer was estimated in %, but cryptogams were not identified on the species level, while cover of the vascular plant species was determined according to the 9-degree Braun-Blanquet scale (Reichelt & Wilmanns 1973). The identification of species was based on Müller et al. (2021), whose nomenclature was checked according to the floristic list for vascular plants of Germany (Hand et al. 2023), and the identification of plant communities was based on Schubert et al. (1995).

For each site, soil depth [cm] was measured using a metal rod with five different punctures. Moreover, a mixed sample of the mineral topsoil (A horizon) was taken from each site using a spade with up to five punctures and stored in plastic bags for transport. Soil samples were dried in the laboratory at air temperature and then the pH_{H2O} value (Microprocessor pH-Meter [pH537 WTW], Schütt Labortechnik GmbH), carbon content [%], nitrogen content [%] and carbon/nitrogen ratio (C/N analyser; vario EL cube, Elementar Analysensysteme GmbH) were measured.

2.4 Measurement of functional traits

Depending on the population, functional traits were measured on 15–20 flowering individuals of *P. pratensis*, which in some cases already covered the entire population size of some populations. At sites HA2, HA3 and HA6, only three flowering individuals could be investigated, respectively. As the species has a nodding flower, we specifically defined the plant height [cm] by measuring between the base of the plant and the highest point of the plant, which usually represented the bend of the shoot in the downward direction of the flower or the highest leaf tip of the bract. In addition, leaf length of the longest leaf [cm] and flower length [cm] were measured. One young, but preferably fully developed leaf per individual was harvested, these samples were kept moist with water in plastic bags and stored in the fridge for further analyses. Fortunately, there were still two vegetative individuals at site HA2 and sufficient vegetative individuals at site HA3, of which we sampled seventeen, so that at least the leaf traits at these sites could be recorded. All measurements and leaf sampling were carried out for each site at the same time as the vegetation survey and soil sampling, as the shoots of *P. pratensis* are erecting for fruit ripening.

Leaf trait analyses were conducted in the laboratory according to a standardised protocol (Perez-Harguindeguy et al. 2013). The leaves were scanned with a flatbed scanner (resolution: 300 dpi) and their leaf areas [cm^2] were analysed with the WinFOLIA Pro S software. Afterwards, leaves were separately freshly weighed, transferred to paper bags, dried in a drying cabinet at 60 °C for 72 h and then weighed again (leaf dry mass [mg]). SLA (specific leaf area; ratio between leaf area and leaf dry mass in mm^2/mg) and LDMC (leaf dry matter content; ratio between leaf dry mass and leaf fresh mass in mg/g) were calculated.

At the end of May 2023, all sites were revisited and as many seeds as possible were collected from fruiting individuals and stored in paper bags at room temperature. Here, no differentiation was made between separate individuals; instead a seed mixture per population was compiled, as the fruit set of the individuals was extremely poor. In the laboratory, 50 seeds per population were weighed separately to determine seed mass [mg], then scanned and measured with the WinSEEDLE software to obtain seed area [mm^2]. Due to the insufficient seed material, the initially planned studies on the germination rate were not possible.

2.5 Data analysis

For statistical analyses, the cover estimate value 2m was converted into the estimate value 1 and then Braun-Blanquet coverage values were transformed as follows: r = 0.1%, + = 0.5%, 1 = 2.5%, 2a = 10%, 2b = 20%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%. Moreover, unweighted mean Ellenberg indicator values for light, temperature, continentality, moisture, reaction and nutrients (Ellenberg et al. 2001), the proportions of functional species groups (annuals, graminoids, forbs), the proportions of main life forms (therophytes, chamaephytes, hemicryptophytes) and proportions of main strategy types (Grime 2001) (CS – competition-stress, CSR – competition-stress-ruderal, SR – stress-ruderal) per relevé were calculated and compared between the different study sites.

All statistical analyses were performed in R 3.6.0 (R Core Team 2019) and considered significant if $p < 0.05$. Floristic-ecological gradients in the vegetation between the different *P. pratensis* sites were examined applying non-metric multidimensional scaling (NMDS) (McCune & Grace 2002) with Bray-Curtis as distance metric. Therefore, all explanatory variables (total species number, cover of herb layer and cryptogams, soil properties, mean Ellenberg indicator values, functional groups, life forms, strategy types) were log-transformed and cover values were (x+1)-logarithmised to give less weighting to rarer species. With the function metaMDS, 100 iterations were calculated to determine the starting configuration, in which the lowest stress value for the two-dimensional NMDS solution was 16.54. The significance of the effects of all explanatory variables within the whole model was checked using the Monte-Carlo test (9999 permutations). Explanatory variables that significantly correlated ($p < 0.05$) with the axes of the ordination were post hoc fitted to the ordination diagram as vectors (function: envfit). NMDS was conducted using the packages vegan (Oksanen et al. 2020) and ggplot2 (Wickham et al. 2020).

Linear regressions were performed to identify significant relationships between population size (as logarithm) and soil properties. One-way analyses of variance (ANOVA) with subsequent Tukey's post-hoc tests using the multcomp package (Hothorn et al. 2008) were applied to reveal significant differences in the functional traits of *P. pratensis* between the different study sites. For functional trait analyses, the data from population HA2 was integrated into population HA3, as the sites were close to each other and the species composition was similar. Instead, population HA6 was removed from the functional analyses. Multiple linear regression models were used to investigate the effect of both soil properties and mean Ellenberg indicator values on the functional traits of *P. pratensis*. Here, soil properties and mean Ellenberg indicator values were the independent variables, while the growth and fitness traits, respectively, were the dependent variables. Additionally, population size was included as an independent variable in each model. All variables were log-transformed and the package corrplot (Wei & Simko 2021) was used to generate a correlation matrix of the pairwise correlations of all measured soil properties and mean Ellenberg indicator values to detect intercorrelated variables (Supplement E1). Before modeling, we removed the intercorrelated variables soil nitrogen content, soil carbon content and mean indicator value for light. Afterwards, we used Akaike Information Criterion (AIC) (Burnham & Anderson 2003) to find the linear models with the best fit, simplifying the regression models.

3. Results

3.1 Sociological and ecological affiliation

In 2023, the population sizes of *Pulsatilla pratensis* in the northern foothills of the Harz Mountains were very small, as many populations had fewer than 50 flowering individuals and some populations in the Harslebener Berge even consisted of only three flowering individuals (Tab. 1). The Harz Plateau on the Bollenkopf near Elbingerode had by far the largest population with ~3000 flowering individuals. Based on the vegetation surveys, it was found that *P. pratensis* in the northern foothills of the Harz Mountains occurred in different associations of the class *Festuco-Brometea* Br.-Bl. & Tx. ex Klika & Hadač 1944, i.e. the continental dry and semi-dry grasslands (Tab. 1), mainly on south-west to south-east exposed, slightly to moderately steep slopes (Supplement S1). Across all plots, the species achieved a mean cover of 15.26%. High cover values of *P. pratensis* were recorded at Bollenkopf near Elbingerode, near Arnstein, at Weinberg near Börnecke and at Kleines Kamel near Westerhausen (Supplement S1).

The mean indicator value for nutrients ranged from 2.22 to 3.22, indicating that all sites were comparatively nitrogen-poor (Tab. 2). The low mean indicator values for moisture and consistently high mean indicator values for reaction also pointed to dry and slightly alkaline soils.

Table 2. Comparison of *Pulsatilla pratensis* subsp. *nigricans* sites regarding their vegetation plot properties, soil properties, mean Ellenberg indicator values, proportions of functional species groups, proportions of main life forms and proportions of main strategy types (CS – competition-stress, CSR – competition-stress-ruderal, SR – stress-ruderal).

Tabelle 2. Vergleich der Standorte von *Pulsatilla pratensis* subsp. *nigricans* hinsichtlich ihrer Gesamt-Vegetationseigenschaften der Aufnahmefläche, Bodeneigenschaften, mittleren Ellenberg-Zeigerwerte, Anteile der funktionellen Artengruppen, Anteile der wichtigsten Lebensformen und Anteile der wichtigsten Strategietypen (CS – Konkurrenz-Stress-Strategie, CSR – Konkurrenz-Stress-Ruderal-Strategie, SR – Stress-Ruderal-Strategie).

Parameter	HA1	HA2	HA3	HA6	HA7	HA8	HA9	ELB	ARN	SCH	BÖR	KAM
Vegetation plot properties												
Cover herb layer [%]	99	85	70	80	70	98	85	60	80	50	95	95
Cover cryptogams [%]	1	10	20	5	20	2	10	10	15	10	5	3
Species number [n]	32	26	31	23	26	34	31	18	27	24	29	20
Soil properties												
Soil depth [cm]	25.6	27.1	16.8	21.5	24.9	25.1	24.1	6.1	9.6	10.4	20.1	22.5
pH value	7.0	6.1	8.0	7.9	6.8	7.4	5.9	7.5	5.1	4.8	6.7	7.3
Nitrogen content [%]	0.21	0.11	0.21	0.24	0.24	0.17	0.32	1.33	0.46	0.42	0.21	0.42
Carbon content [%]	2.81	1.44	4.02	3.49	3.20	2.34	4.15	24.72	6.06	5.11	2.62	6.29
C/N ratio	13.08	13.06	19.09	14.34	13.49	13.96	13.11	18.64	13.15	12.09	12.39	14.84
Mean indicator values												
Light (mL)	7.09	7.48	7.57	7.35	7.58	7.24	7.57	7.67	7.50	7.35	7.28	7.25
Temperature (mT)	5.76	6.14	6.04	6.20	5.87	5.87	6.15	5.67	5.92	5.95	5.68	6.19
Continentality (mK)	4.71	4.88	5.04	5.19	4.58	4.66	4.86	4.29	4.32	4.41	4.56	4.41
Moisture (mF)	3.45	3.08	3.00	3.04	3.20	3.47	3.00	3.00	3.25	3.35	3.36	3.22
Reaction (mR)	7.31	6.91	7.25	7.19	6.52	6.83	6.52	6.60	6.57	6.44	7.22	6.82
Nutrients (mN)	2.68	2.61	2.36	2.55	2.23	3.20	2.22	2.24	2.41	3.22	2.70	3.00
Functional groups												
Annuals [%]	6.25	15.38	12.90	17.39	30.77	29.41	16.13	22.22	22.22	37.50	6.90	10.00
Graminoids [%]	21.88	26.92	29.03	21.74	15.38	17.65	29.03	33.33	11.11	8.33	31.03	30.00
Forbs [%]	71.88	57.69	58.06	60.87	53.85	44.12	54.84	44.44	66.67	62.50	62.07	60.00
Life forms												
Therophytes [%]	6.25	15.38	12.90	17.39	30.77	29.41	16.13	22.22	22.22	37.50	6.90	10.00
Chamaephytes [%]	9.38	15.38	9.68	17.39	7.69	0.00	12.90	16.67	7.41	16.67	6.90	15.00
Hemicryptophytes [%]	84.38	73.08	83.87	69.57	65.38	70.59	77.42	66.67	70.37	45.83	86.21	70.00
Strategy types												
CS [%]	25.00	19.23	29.03	30.43	26.92	17.65	22.58	22.22	22.22	8.33	27.59	20.00
CSR [%]	56.25	57.69	61.29	47.83	38.46	38.24	58.06	55.56	37.04	37.50	48.28	60.00
SR [%]	6.25	11.54	9.68	13.04	26.92	11.76	16.13	22.22	18.52	20.83	6.90	5.00

In the Harslebener Berge (HA), *P. pratensis* occurred both in the steppe grasslands of the *Festuco valesiacae-Stipetum capillatae* (Libbert 1931) Mahn 1959 and *Stipetum stenophyllae* (Podp. 1930) Meusel 1938 as well as in the *Festuco rupicolae-Brachypodietum pinnati* Mahn 1959 (Tab. 1). In the steppe grasslands, this species was associated with at least one dominant species of *Stipa*: *S. capillata* (HA2, HA3), *S. pennata* (HA6), *S. tirsa* (HA9). The nitrogen-poorer sites HA2 and HA3 (Tab. 2) were characterised by a medium cover of *Anthericum liliago* and *Salvia pratensis* and additionally at site HA3 by a medium cover of *Galatella linosyris*. The *Festuco-Brachypodietum* at site HA1 was characterised by a high cover of *Brachypodium pinnatum*, but a low cover of *Festuca rupicola*, while fringe species (e.g. *Agrimonia eupatoria*, *Astragalus glycyphyllos*, *Fragaria viridis*) occurred with medium cover. A moderate cover of *F. rupicola* and, surprisingly, a relatively high proportion of annual species (e.g. *Draba verna*, *Myosotis stricta*) were found at sites HA7 and HA8 (Supplement S1, Tab. 2). Interestingly, *Carex supina* also occurred with low to medium cover at the almost flat sites HA6, HA7 and HA8.

At Arnstein, *P. pratensis* occurred in a *Festuco valesiacae-Stipetum capillatae* (Libbert 1931) Mahn 1959 and at Schalkenburg near Quenstedt in a *Gentiano-Koelerietum pyramiddatae* Knapp 1942 ex Bornk. 1960 (Tab. 1) on a shallow, nitrogen-rich and acidic substrate (Tab. 2). Here, the lowest proportions of graminoids per plot were found of all investigated sites (Tab. 2). Only *Festuca valesiaca* was one of the few graminoids with a high cover at Arnstein (Supplement S1), while the proportion of annuals was highest at Schalkenburg compared to all other sites (Tab. 2).

Pulsatilla pratensis was found at Weinberg near Börnecke in an *Adonido-Brachypodietum pinnati* (Libb. 1933) Krausch 1961 together with the named character species *Adonis vernalis* and *Brachypodium pinnatum* (Tab. 1, Supplement S1). Instead, the species occurred at Kleines Kamel near Westerhausen in an *Onobrychido-Brometum erecti* Th. Müll. 1968, which was characterised by a high dominance of *Bromus erectus*. These two sites had the highest proportion of graminoids of all sites (Tab. 2). At Weinberg, besides *B. pinnatum*, also *B. erectus*, *Festuca rupicola* and *Helictochloa pratensis* were present with low to medium cover, while at Kleines Kamel, *B. erectus* and *Poa angustifolia* were found with medium cover (Supplement S1). Moreover, both sites were comparatively nitrogen-rich and generally had a high cover of the herb layer, but a low proportion of annuals (Tab. 2).

On the other hand, *P. pratensis* occurred in the Harz Plateau at Bollenkopf near Elbingerode in a sparse and species-poor *Gentiano-Koelerietum pyramidatae* Knapp 1942 ex Bornk. 1960 on Devonian limestone (Tab. 1 and 2). This site was very shallow and characterised by a very relatively high soil nitrogen and carbon content compared to all other sites in the northern foothills of the Harz Mountains (Tab. 2). Here, the character species *Koeleria pyramidata* appeared, typical grassland specialists such as *Allium oleraceum*, *Helianthemum nummularium* and *Sanguisorba minor* showed a medium cover and many annuals (e.g. *Arenaria serpyllifolia*, *Draba verna*, *Holosteum umbellatum*) were recorded (Supplement S1).

NMDS revealed no preferences of *P. pratensis* for certain habitats, but soil depth and soil nitrogen content, the mean indicator value for continentality and the proportion of therophytes, competition-stress-ruderalists and stress-ruderalists were significantly correlated with both axes (Fig. 3).

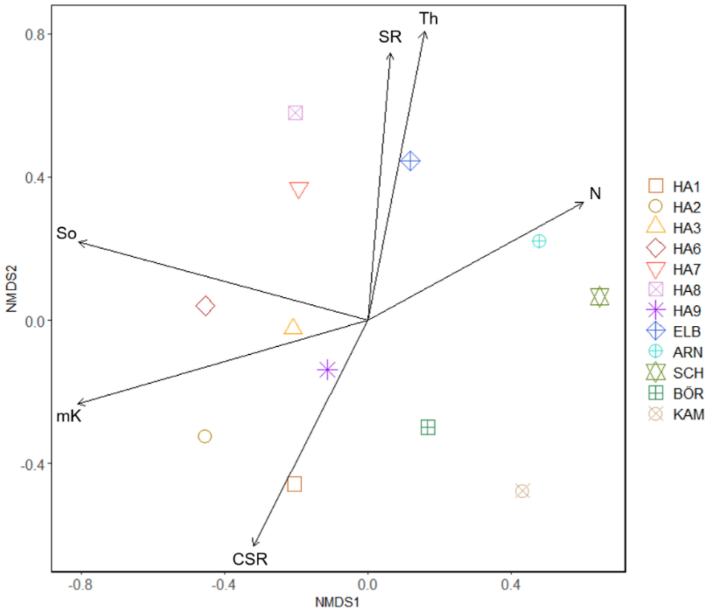

Fig. 3. Non-metric multidimensional scaling (NMDS) of the vegetation relevés for the different *Pulsatilla pratensis* subsp. *nigricans* sites (see legend on the right; abbreviations as in Tab. 1). Minimal stress of axis 2 is 16.54. Ecological parameters, which are significantly correlated ($p < 0.05$) with the axes of the ordination, are shown as vector arrows (So – soil depth, N – soil nitrogen content, mK – mean indicator value for continentality, Th – proportion of therophytes, CSR – proportion of competition-stress-ruderalists, SR – proportion of stress-ruderalists).

Abb. 3. Nichtmetrische multidimensionale Skalierung (NMDS) der Vegetationsaufnahmen für die verschiedenen Standorte (siehe Legende rechts; Abkürzungen siehe Tabelle 1) von *Pulsatilla pratensis* subsp. *nigricans*. Der minimale Stresswert von Achse 2 beträgt 16,54. Ökologische Parameter, die signifikant mit den Achsen der Ordination korreliert sind, sind als Vektorpfeile dargestellt (So – Gründigkeit, N – Bodenstickstoffgehalt, mK – mittlerer Zeigerwert für Kontinentalität, Th – Anteil an Therophyten, CSR – Anteil an Konkurrenz-Stress-Ruderal-Strategen, SR – Anteil an Stress-Ruderal-Strategen).

3.2 Growth and fitness

Population size decreased significantly with increasing soil depth (Fig. 4a), but increased significantly with increasing soil carbon and soil nitrogen content (Fig. 4b, c). In contrast, soil C/N ratio and pH value had no significant influence on the population size (Fig. 4d, e).
There were significant differences in the vegetative traits of *P. pratensis* between the different sites (Fig. 5). The highest plant height was found at Kleines Kamel and the lowest at site HA7 of the Harslebener Berge, although high values for plant height were also verified at Weinberg near Börnecke (Fig. 5a). Leaf lengths were highest at Weinberg near Börnecke and Kleines Kamel and differed significantly from those in the Harslebener Berge (Fig. 5b). Leaf dry mass was significantly higher at sites ARN, SCH, BÖR and KAM than at all other sites (Fig. 5c). A similar pattern was revealed for leaf area, with the exception of site HA8, where individuals at Weinberg near Börnecke had the highest leaf area (Fig. 5d). SLA was significantly higher at sites HA3, HA7 and KAM than at sites ELB, ARN and SCH (Fig. 5e). But LDMC of individuals at Bollenkopf near Elbingerode was significantly higher than at site HA7 (Fig. 5f).

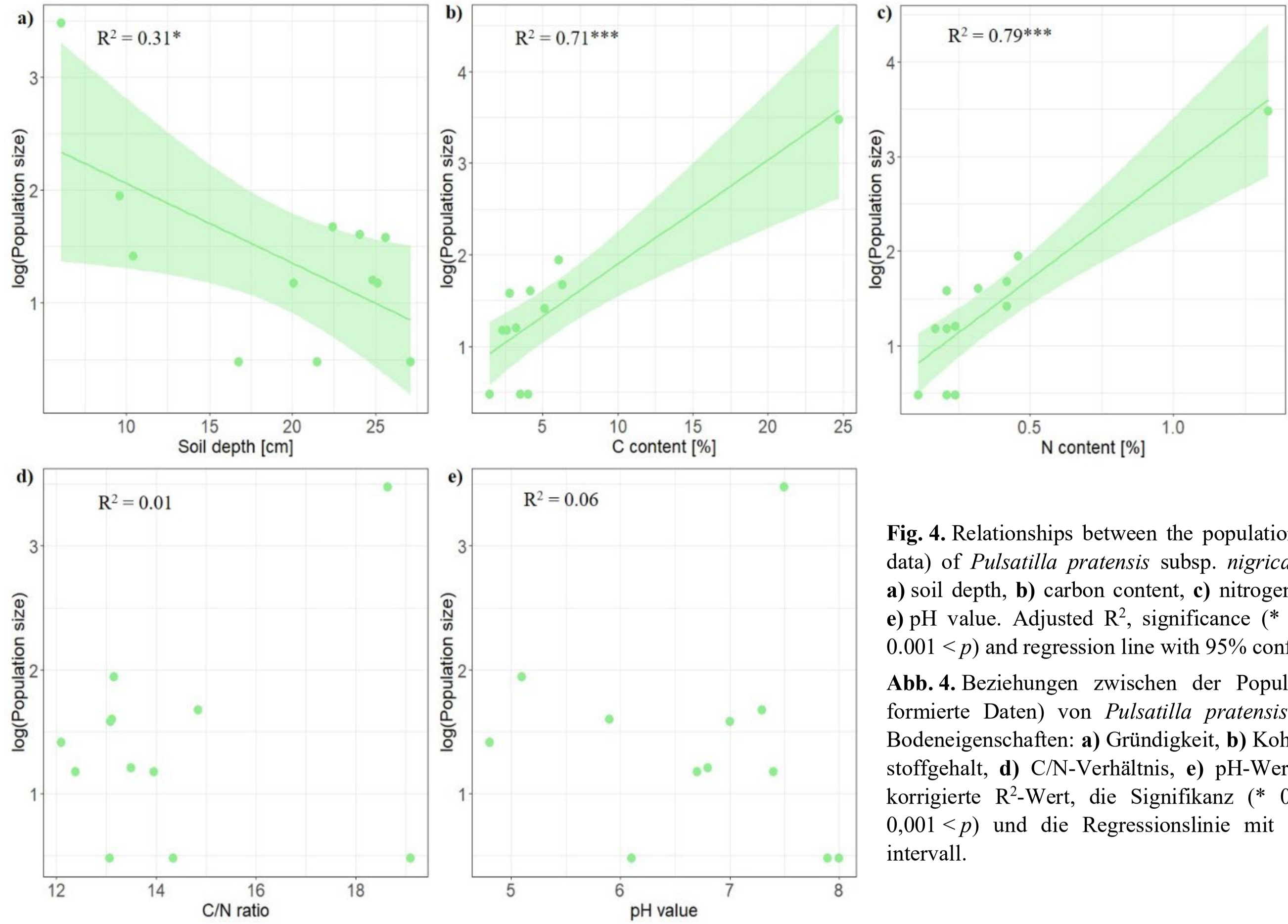

Fig. 4. Relationships between the population size (log-transformed data) of *Pulsatilla pratensis* subsp. *nigricans* and soil properties: **a)** soil depth, **b)** carbon content, **c)** nitrogen content, **d)** C/N ratio, **e)** pH value. Adjusted R^2, significance (* $0.01 \leq p < 0.05$, *** $0.001 < p$) and regression line with 95% confidence level are given.

Abb. 4. Beziehungen zwischen der Populationsgröße (log-transformierte Daten) von *Pulsatilla pratensis* subsp. *nigricans* und Bodeneigenschaften: **a)** Gründigkeit, **b)** Kohlenstoffgehalt, **c)** Stickstoffgehalt, **d)** C/N-Verhältnis, **e)** pH-Wert. Angegeben sind der korrigierte R^2-Wert, die Signifikanz (* $0{,}01 \leq p < 0{,}05$, *** $0{,}001 < p$) und die Regressionslinie mit dem 95 % Konfidenzintervall.

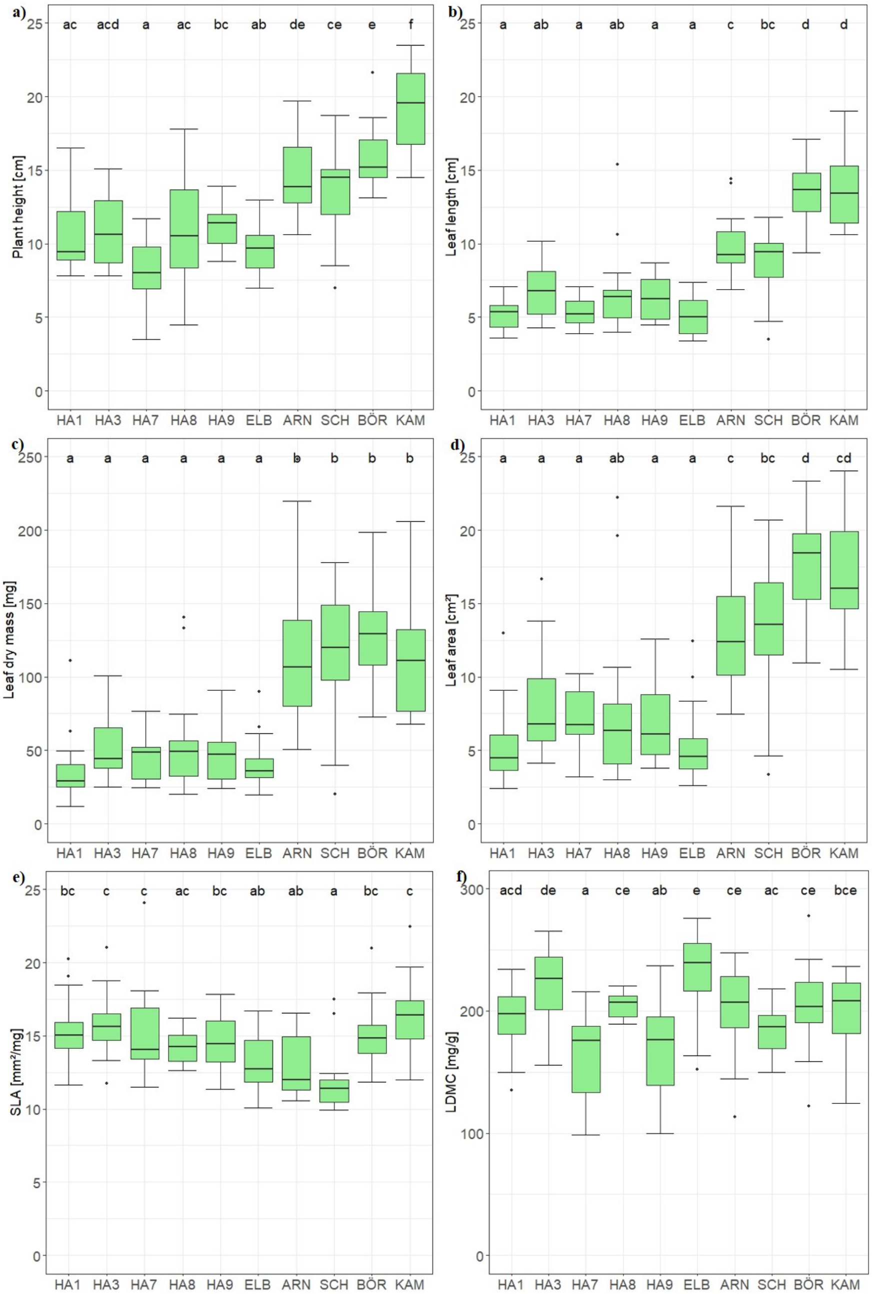

Fig. 5. Vegetative traits of *Pulsatilla pratensis* subsp. *nigricans* compared between the different sites (abbreviations as in Tab. 1): **a)** plant height, **b)** leaf length, **c)** leaf dry mass, **d)** leaf area, **e)** SLA, **f)** LDMC. Different letters indicate significant differences at $p < 0.05$.

Abb. 5. Vegetative Merkmale von *Pulsatilla pratensis* subsp. *nigricans* im Vergleich der verschiedenen Standorte (Abkürzungen siehe Tabelle 1): **a)** Wuchshöhe, **b)** Blattlänge, **c)** Blatttrockenmasse, **d)** Blattfläche, **e)** SLA, **f)** LDMC. Unterschiedliche Buchstaben bedeuten signifikante Unterschiede bei $p < 0{,}05$.

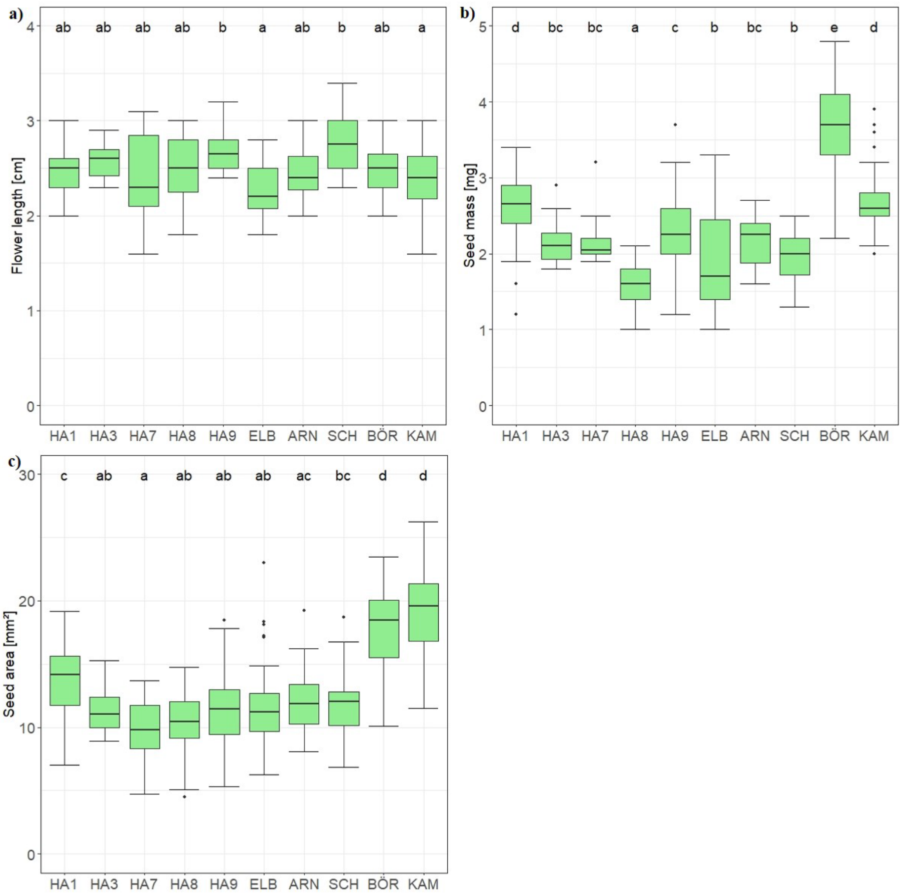

Fig. 6. Generative traits of *Pulsatilla pratensis* subsp. *nigricans* compared between the different sites (abbreviations as in Tab. 1): **a)** flower length, **b)** seed mass, **c)** seed area. Different letters indicate significant differences at $p < 0.05$.

Abb. 6. Generative Merkmale von *Pulsatilla pratensis* subsp. *nigricans* im Vergleich der verschiedenen Standorte (Abkürzungen siehe Tabelle 1): **a)** Blütenlänge, **b)** Samenmasse, **c)** Samenfläche. Unterschiedliche Buchstaben bedeuten signifikante Unterschiede bei $p < 0{,}05$.

Furthermore, significant differences in the generative traits of *P. pratensis* were detected between the different sites (Fig. 6). The flowers at site HA9 in the Harslebener Berge and at Schalkenburg were significantly longer than at sites ELB and KAM (Fig. 6a). The highest seed mass was recorded at site BÖR and the lowest seed mass at site HA8, although high values for this parameter were also determined for sites HA1 and KAM (Fig. 6b). The highest seed area was evident at Weinberg near Börnecke and Kleines Kamel and differed significantly from all other sites (Fig. 6c).

Soil properties and mean Ellenberg indicator values had significant effects on the growth and fitness traits of *P. pratensis* (Supplement S2). Population size had a significantly negative influence on leaf length, leaf dry mass, leaf area and seed mass, while the other traits were unaffected by population size. Soil depth, the mean indicator value for temperature and that for continentality, moisture and reaction showed the strongest relationships with the growth and fitness of *P. pratensis* populations. Particularly, leaf length, leaf dry mass, leaf area and seed mass were significantly negatively affected by soil depth and soil C/N ratio. The pH value had a negative effect on plant height and flower length, whereas it showed a positive influence on LDMC, seed mass and seed area. The mean indicator values for continentality and moisture were negatively related to leaf dry mass, leaf area and LDMC. The mean indicator values for temperature and reaction were positively related to, e.g., plant height, leaf length, leaf area, SLA and seed mass. Among all traits, seed mass was most strongly affected by the soil factors and mean indicator values.

4. Discussion

In the northern foothills of the Harz Mountains, i) *Pulsatilla pratensis* occurred in one dry grassland community (*Festuco-Stipetum*) and in five semi-dry grassland communities (*Stipetum stenophyllae*, *Festuco-Brachypodietum*, *Adonido-Brachypodietum*, *Onobrychido-Brometum*, *Gentiano-Koelerietum*). ii) There were significant differences in the vegetative and generative traits of *P. pratensis* between the different populations. The growth performance was partly higher in semi-dry grasslands than in dry grasslands. iii) Habitat characteristics and population size had mostly significantly negative effects on the growth and fitness of *P. pratensis*. Larger populations of *P. pratensis* (e.g. Elbingerode) tended to show lower values in their growth and fitness traits.

The effects of the sharp decline in *P. pratensis* populations after severe drought events in 2018 and 2019 were clearly noticeable (e.g. population size in 2015 for site HA1 in total 137 individuals and for site HA3 in total 3214 individuals (cf. Wegener & Rußwurm 2022); population size in 2023 for site HA1 in total 38 individuals and for site HA3 in total 3 individuals), but Wegener & Rußwurm (2022) reported that considerable fluctuations in population size from year to year seem to be common at the edges of the species' range. In 2023, many sites had only a small population size and the fruit set of the individuals was relatively low. One exception, however, was the population at Bollenkopf near Elbingerode, where the very high population size has remained relatively constant over decades (Wegener verbal information). In this area, on average 200 mm more precipitation than in the northern foothills of the Harz Mountains is recorded (Groß et al. 1982), which could have positively affected the stability of the local *P. pratensis* population.

Indeed, the smallest population sizes were documented in the *Festuco-Stipetum* at Harslebener Berge. Such a dry grassland community often occurs on extreme sites with steeper slopes and less vegetation cover, and is subject to higher solar radiation and drought (Schubert et al. 2001), which is particularly true for site HA3 (steep south-facing slope) in the Harslebener Berge. Extreme heat and severe drought events during the summer months cause soils to heat up and dry out more quickly, leading to an increase of short-lived annuals but lethal effects on perennial plants (Fischer et al. 2020), which may have been the case for *P. pratensis* despite its deep root system. Contrary, Harzé et al. (2016) showed that dry grassland species on shallow sites with high solar radiation can better tolerate higher environmental stress by selectively adapting their functional traits. Although we could confirm this adaptation of the traits of *P. pratensis* in the *Festuco-Stipetum*, we assume exactly the opposite trend, that this species 'suffers' from increasing environmental stress.

Most of these investigated populations are remnant populations of *P. pratensis* that are able to reproduce. Small populations can be quite stable, which is the case for the Red List species *Aster alpinus* (Meier 2023), *Iris aphylla* (Meier 2022) and *Scorzonera purpurea*

(Meier 2021) in the Harz region, as their isolated occurrences have been confirmed even after decades. But it should be considered that only flowering individuals of *P. pratensis* were recorded since the beginning of the count series and demographic studies have not yet been studied. Such investigations have already been conducted for *P. patens* both in the NSG “Garchinger Heide” north of Munich and in the Natura 2000 site “Grasslands in the Military Training Grounds in Orzysz” in the Masurian Lake District in Poland, whereby juvenile, vegetative and flowering individuals were divided (Röder & Kiehl 2006, Juśkiewicz-Swaczyna 2010). Both studies showed that the proportion of non-flowering individuals was always higher than that of flowering individuals. In future, it would be advisable to realise demographic studies on *P. pratensis* in the northern foothills of the Harz Mountains, as the “actual” population size, including non-flowering individuals, may differ significantly from those documented in our study, especially as vegetative individuals were also spotted at many sites. Interestingly, single individuals of *P. pratensis* can reach an age of over 40 years, enabling them to survive on suboptimal sites (i.e. with high dominance of graminoids) (Wegener & Rußwurm 2022). Overaged populations of this species are unable to reproduce, which was already shown in small populations in Brandenburg (Fischer et al. 1982).

Based on soil properties, we detected that *P. pratensis* had a relatively large environmental range, as it colonised deep to shallow, alkaline to slightly acidic and nitrogen-rich to nitrogen-poor sites. This is emphasised by the fact that *P. pratensis* occurred in one dry grassland community and five semi-dry grassland communities in our study region. Similar findings were also confirmed for this species in the Žumberak Mountains of north-western Croatia, where it grows on two soil types: rendzina on dolomite and calcomelanosol on limestone (Vbrek 2001).

In semi-dry grassland communities (*Adonido-Brachypodietum* and *Onobrychido-Brometum*), *P. pratensis* tended to exhibit higher vegetative and generative trait values. This result can be compared to the study by Hensen et al. (2005), who demonstrated for *P. vulgaris* in Central Germany that a high population size led to increased seed production and seed mass, resulting in a positive effect on their fitness. Such fitness traits are highly dependent on population size, genetic diversity and habitat characteristics (González et al. 2020), which underlines our result that seed mass of *P. pratensis* was most influenced by the measured environmental variables.

Soil depth and the mean indicator value for continentality were significantly related to community composition (NMDS) and, together with the mean indicator value for reaction, had the greatest influence on the growth and fitness of the *P. pratensis* populations. However, population size decreased with increasing soil depth, suggesting that, on deeper soils, competition from other, presumably suboceanic and more nutrient-demanding species may be higher. Nevertheless, population size and, for example, soil depth and the mean indicator value for moisture had mostly negative effects on specific vegetative and generative traits of *P. pratensis*. Some evidence indicates that *P. pratensis* exhibits higher intraspecific competition at larger population sizes when soil depth is lower, water availability limited and soil dryness increases, leading to a decrease in certain trait values, such as leaf dry mass, leaf area and seed mass.

Furthermore, in the *Adonido-Brachypodietum* and *Onobrychido-Brometum*, not only a high cover of *P. pratensis*, but also of e.g. *Bromus erectus* was detected. During the last two decades, in particular *B. erectus* has become increasingly dominant in dry and semi-dry grasslands of Central Germany, which has led to a decline in species richness in these plant communities due to its increased competitive ability (Meier et al. 2021, 2022). This stress-tolerant grass accumulates higher layers of litter and can significantly reduce the growth of neighbouring species due to lower light availability on the ground (Ridding et al. 2020), which has already been confirmed for *P. vulgaris* (Walker & Pinches 2011). In the Czech Republic, declining population trends of *P. grandis* were verified from 2005 to 2023, mainly as a result of the accumulation of layers of litter (Tichý et al. 2025). However, we assume that extreme prolonged periods of heat and drought will pose the main threat to the growth performance of *P. pratensis* in future, presumably due to higher competition from neighbouring species as a result of limited resource acquisition.

Besides extreme weather events, herbivory also seemed to be an increasingly serious problem for *P. pratensis*. We suggest that adult individuals of oil beetles (*Meloe proscarabaeus*) had considerably eaten the flowering shoots of *P. pratensis*, resulting in no development of a fruit set. Comparable findings were also reported in Saxony (Zöphel & Pfeiffer 2020), but further studies would be useful to investigate this issue.

5. Recommendations for nature conservation

Populations of *Pulsatilla pratensis* often colonise different vegetation types (i.e. dry and semi-dry grasslands) in our study region. Therefore, we recommend sheep grazing in a wide enclosure as the best option for the future conservation of *P. pratensis* in the northern foothills of the Harz Mountains. Paddock grazing during the day on the sites and at night outside the protected areas is generally possible, but not an optimal solution because a relatively large amount of faeces is deposited by sheep in a small area and trampling damage can arise. Moreover, the shepherd should pass across the sites with the stock of sheep at least twice a year to remove standing biomass from grasses. If sheep grazing is not possible, the sites should be mowed to prevent the *P. pratensis* stands from overgrowing with grass species, while mechanical cutting is also useful to prevent shrub encroachment. Burning would generally be a suitable measure for creating open soil patches by removing litter, but this is difficult to organize for the *P. pratensis* sites and requires public statement. With increasing dry periods in spring and summer, promoting the remaining populations of *P. pratensis* on the southern slopes is obviously no longer optimal, but rather that of the populations on the western and eastern slopes. However, the suitability of semi-shaded sites for future conservation is currently being investigated in comparative studies of two sites in Brandenburg (unpublished data). The creation of appropriate restoration sites is also helpful, as the direct sowing of seeds from local *P. pratensis* populations in previously damaged areas by removing topsoil requires further investigation, but has already been realised with positive results for *P. patens* in the NSG “Garchinger Heide” (Röder & Kiehl 2008). In contrast to *Jurinea cyanoides* (Tischew & Kommraus 2009) and *Scorzonera purpurea* (Kienberg et al. 2013), transplanting *P. pratensis* individuals cultivated in a greenhouse into the field without sufficient aftercare failed (personal investigations, unpublished data). But positive results were reported in the natural monument “Zechstein” in Saxony by transplanting pre-grown *P. pratensis* individuals into the field (Zöphel & Pfeiffer 2020). Finally, only such aforementioned management practices can help to prevent a local extinction of *P. pratensis* in the Harz region under future changing weather conditions.

Erweiterte deutsche Zusammenfassung

Einleitung – Innerhalb der letzten 25 Jahre zeigte sich für die mitteldeutschen Trockenrasen ein dramatischer Artenverlust von gefährdeten und stark gefährdeten Graslandspezialisten (Meier et al. 2021, 2022). Haupttreiber sind die Prozesse des fortwährenden „Globalen Wandels", wie z. B. Klimaerwärmung und atmosphärische Stickstoffdeposition, sowie rückläufige Landnutzungspraktiken (Bobbink et al. 2010, Dupré et al. 2010, Diekmann et al. 2019). Außerdem haben in den Jahren 2018 und 2019 extreme Witterungsbedingungen, wie Hitzewellen und Dürren, in Mitteldeutschland verstärkt zugenommen (Boergens et al. 2020), was wahrscheinlich den Verlust von gefährdeten Arten begünstigt hat. Schlechte Lebensraumbedingungen führen oftmals zu räumlich isolierten Populationen und somit zu einer abnehmenden Populationsgröße (González et al. 2020). Pflanzliche funktionelle Merkmale wirken indirekt auf das Wachstum und die Fitness von Individuen einer Population (Garnier et al. 2016), können jedoch auch einen Hinweis auf die Seltenheit und das Aussterben von spezialisierten Arten liefern (Gabrielová et al. 2013). Eine in Mitteldeutschland vorkommende stark gefährdete Art ist *Pulsatilla pratensis* subsp. *nigricans*, deren Hauptvorkommen auf das Nordharzvorland beschränkt ist (NetPhyD & BfN 2013). Wegener & Rußwurm (2022) stellten für das Gebiet der Harslebener Berge einen Überblick über die Populationsdynamik dieser Art dar und konnten dabei die dramatischen Einbrüche der dortigen Populationen nach 2018 aufzeigen. Ziel unserer Studie war es im Hinblick auf die sich verändernden Umweltbedingungen, sowohl die Einnischung von *P. pratensis* subsp. *nigricans* in die verschiedenen Pflanzengesellschaften im Nordharzvorland zu untersuchen als auch das Wachstum und die Fitness einzelner Populationen zu vergleichen. Zusätzlich sollen Managementempfehlungen für den zukünftigen Erhalt dieser Art aufgezeigt werden.

Material & Methoden – Insgesamt wurden 11 Populationen von *Pulsatilla pratensis* im Nordharzvorland und zusätzlich eine Population in der Harzhochfläche untersucht (Tab. 1, Abb. 2). Die Populationsgröße wurde anhand der blühenden Individuen ermittelt (cf. Wegener & Rußwurm 2022). Ende April 2023 wurde pro Standort eine Vegetationsaufnahme an Stellen mit hohen Deckungswerten von *P. pratensis* durchgeführt (Beilage S1) und anhand dieser die jeweilige Pflanzengesellschaft bestimmt (Tab. 1). Für jeden Standort wurde die Gründigkeit des Bodens gemessen und eine Bodenprobe zur Analyse des pH_{H2O}-Wertes, Kohlenstoffgehaltes, Stickstoffgehaltes und Kohlenstoff/Stickstoff-Verhältnisses entnommen. Je nach Population wurden möglichst an 15–20 blühenden Individuen von *P. pratensis* folgende funktionelle Merkmale erhoben: Wuchshöhe, Blattlänge, Blütenlänge, Blattfläche, Blatttrockenmasse, SLA (spezifische Blattfläche), LDMC (Blatttrockenmasseanteil). Ende Mai 2023 wurden alle Standorte erneut aufgesucht und von fruchtenden Individuen Samen geerntet. Es wurde jedoch pro Population nur eine Samenmischung erstellt, wobei von jeweils 50 Samen pro Population die Samenmasse und Samenfläche einzeln ermittelt wurde. Anhand der Vegetationsdaten wurden die Standorte von *P. pratensis* u. a. hinsichtlich ihrer mittleren Zeigerwerte nach Ellenberg, Anteile funktioneller Artengruppen, Lebensformen und Strategietypen gegenübergestellt. Die Bodeneigenschaften wurden ebenfalls miteinander verglichen. Floristisch-ökologische Gradienten in der Vegetation zwischen den Standorten wurden mittels einer nicht-metrischen multidimensionalen Skalierung (NMDS) aufgedeckt. Lineare Regressionen dienten zur Ermittlung von signifikanten Beziehungen zwischen der Populationsgröße und den Bodeneigenschaften. Einfaktorielle Varianzanalysen (ANOVA) mit anschließenden Tukey-post-hoc-Tests wurden durchgeführt, um signifikante Unterschiede in den funktionellen Merkmalen von *P. pratensis* zwischen den verschiedenen Standorten nachzuweisen. Multiple lineare Regressionsmodelle wurden verwendet, um den Effekt sowohl der Bodeneigenschaften als auch der mittleren Zeigerwerte und zusätzlich der Populationsgröße auf die funktionellen Merkmale von *P. pratensis* zu untersuchen.

Ergebnisse – Im Jahr 2023 waren die Populationsgrößen von *Pulsatilla pratensis* bis auf eine Ausnahme sehr klein gewesen (Tab 1). Anhand der Vegetationsaufnahmen zeigte sich, dass im Nordharzvorland *P. pratensis* in einer Trockenrasengesellschaft (*Festuco-Stipetum*) und in fünf Halbtrockenrasengesellschaften (*Stipetum stenophyllae*, *Festuco-Brachypodietum*, *Adonido-Brachypodietum*, *Gentiano-Koelerietum*, *Onobrychido-Brometum*) vorkam (Tab. 1) und eine durchschnittliche Deckung über alle Aufnahmen hinweg von ca. 15,26 % hatte. Die mittleren Nährstoff-, Feuchtigkeits- und Reaktionszeigerwerte deuteten darauf hin, dass es sich um vergleichsweise stickstoffarme, trockene und schwach basische Standorte handelte (Tab. 2). In den Steppenrasen war *P. pratensis* mit mindestens einer dominierenden *Stipa*-Art vergesellschaftet, während in den anderen Pflanzengesellschaften andere Graminoide (z. B. *Brachypodium pinnatum*, *Bromus erectus*) z. T. eine mittlere Deckung aufwiesen (Tab. 2). Ebenfalls konnten erkennbare Unterschiede in den Bodeneigenschaften, wie Gründigkeit und Stickstoffgehalt, zwischen den Standorten erfasst werden (Tab. 2). Die NMDS ergab keine Präferenzen von *P. pratensis* für bestimmte Habitate, aber die Gründigkeit und der Stickstoffgehalt des Bodens, der mittlere Zeigerwert für Kontinentalität sowie der Anteil der Therophyten und der der Konkurrenz-Stress-Ruderal-Strategen und Stress-Ruderal-Strategen waren mit beiden Achsen signifikant korreliert (Abb. 3). Die Populationsgröße nahm mit zunehmender Gründigkeit signifikant ab und mit zunehmendem Kohlenstoff- und Stickstoffgehalt des Bodens signifikant zu (Abb. 4). Es zeigten sich signifikante Unterschiede in den vegetativen und generativen Merkmalen von *P. pratensis* zwischen den unterschiedlichen Standorten (Abb. 5, 6), was generell auf deren ökologischen Bedingungen zurückzuführen ist. So wurden für *P. pratensis* z. B. höhere Werte bei der Wuchshöhe, Blattlänge, Blattfläche und Samenmasse hauptsächlich innerhalb der Halbtrockenrasen erfasst. Nicht nur die Populationsgröße, sondern auch die Bodeneigenschaften und mittleren Zeigerwerte hatten einen signifikanten, z. T. negativen, Effekt auf die vegetativen und generativen Merkmale von *P. pratensis*, wobei die Gründigkeit des Bodens sowie die mittleren Zeigerwerte für Temperatur, Kontinentalität, Feuchtigkeit und Reaktion den größten Einfluss ausübten (Beilage S2). Die Samenmasse wurde am meisten von der Populationsgröße und den Habitateigenschaften beeinflusst.

Discussion – Die Auswirkungen des Einbruches der Populationen von *Pulsatilla pratensis* im Nordharzvorland nach den schweren Dürreereignissen der Jahre 2018 und 2019 waren eindeutig spürbar. Viele Standorte wiesen nur noch eine kleine Populationsgröße auf und der Fruchtansatz der Individuen war verhältnismäßig gering, vor allem im *Festuco-Stipetum*, der einer stärkeren Sonneneinstrahlung und Trockenheit ausgesetzt ist (Schubert et al. 2001). Extreme Trockenheit und schwere Dürreereignisse während der Sommermonate führen dazu, dass sich die Böden schneller aufheizen und austrocknen und es somit zu lethalen Effekten ausdauernder Pflanzen kommen kann (Fischer et al. 2020), was vermutlich der Fall bei *P. pratensis* gewesen sein könnte. Die meisten dieser untersuchten Populationen sind Restpopulationen von *P. pratensis*, die sich aktuell noch selbstständig reproduzieren können. Jedoch sind kleine Populationen durchaus stabil, was für die Rote Liste-Arten *Aster alpinus*, *Iris aphylla* und *Scorzonera purpurea* im Harzgebiet zutrifft, da deren isolierte Vorkommen auch noch nach Jahrzehnten wiederbestätigt werden konnten (Meier 2021, 2022, 2023). Dabei sollte berücksichtigt werden, dass seit Beginn der Zählreihen nur blühende Individuen von *P. pratensis* erfasst wurden (cf. Wegener & Rußwurm 2022) und Untersuchungen zur Demographie bisher nicht erfolgten. Anhand der Bodeneigenschaften konnten wir feststellen, dass *P. pratensis* eine größere ökologische Valenz aufweist, da sie auf tief- bis flachgründigen, alkalischen bis leicht sauren und stickstoffreichen bis -armen Standorten siedelte. Tendenziell wies *P. pratensis* in den Halbtrockenrasen (insbesondere im *Adonido-Brachypodietum* und *Onobrychido-Brometum*) höhere Wachstums- und Fitnesswerte auf, was in Beziehung zur Studie von Hensen et al. (2005) gesetzt werden kann, die für *P. vulgaris* in Mitteldeutschland nachweisen konnten, dass eine große Populationsgröße zu einer erhöhten Samenproduktion und Samenmasse und somit zu einem positiven Effekt auf deren Fitness führte. Solche Fitnessmerkmale sind stark von der Populationsgröße, der genetischen Vielfalt und den Habitateigenschaften abhängig (González et al. 2020), was unser Ergebnis unterstreicht, dass die Samenmasse von *P. pratensis* am stärksten von den gemessenen Umweltvariablen beeinflusst wurde. Dennoch übten sowohl die Populationsgröße als auch u. a. die Gründigkeit des Bodens und der mittlere Zeigerwert für Feuchtigkeit negative Effekte auf einzelne vegetative und generative Merkmale von *P. pratensis* aus. Die Art scheint eine höhere intraspezifische Konkurrenz bei höherer Populationsgröße aufzuweisen, wenn bei einer geringeren Gründigkeit die Wasserverfügbarkeit gehemmt ist, die Bodentrockenheit zunimmt und dies zu einer Abnahme einzelner Merkmalswerte, wie Blatttrockenmasse, Blattfläche und Samenmasse führt. In den beiden Halbtrockenrasengesellschaften *Adonido-Brachypodietum* und *Onobrychido-Brometum* konnte nicht nur eine hohe Deckung von *P. pratensis*, sondern auch von

Bromus erectus erfasst werden. Diese stresstolerante Grasart hat in Mitteldeutschland zunehmend an Dominanz erlangt (Meier et al. 2021, 2022), akkumuliert höhere Streuschichten und kann somit das Wachstum von benachbarten Arten erheblich beeinträchtigen (Ridding et al. 2020), was bereits für *P. vulgaris* bestätigt wurde (Walker & Pinches 2011), wir jedoch davon ausgehen, dass extrem langanhaltende Hitze- und Dürrephasen die Hauptgefahren auf die Wachstumsleistung von *P. pratensis* in Zukunft darstellen.

Naturschutzempfehlungen – Für den zukünftigen Erhalt von *Pulsatilla pratensis* im Nordharzvorland empfehlen wir optimaler Weise eine Schafbeweidung im weiten Gehüt. Die Koppelhaltung tagsüber auf den Flächen und nachts außerhalb der Schutzgebiete ist generell möglich, stellt aber keine optimale Lösung dar, weil relativ viel Kot der Schafe auf kleiner Fläche abgesetzt wird und Trittschäden entstehen können. Weiterhin ist es erforderlich, dass der Schäfer mindestens zweimal im Jahr mit der Schafherde über die Flächen gehen sollte, um möglichst viel Biomasse der Gräser zu entnehmen. Bei zunehmenden Trockenperioden im Frühling und Sommer ist es offensichtlich nicht mehr optimal, die Restbestände von *P. pratensis* an den Südhängen, sondern stärker die Vorkommen an den West- und Osthängen zu fördern. Hilfreich ist auch die Schaffung geeigneter Renaturierungsflächen, denn eine Direkteinsaat von Samen in vorgeschädigte Flächen mittels Oberbodenabtrag bedarf zwar einer weiteren Untersuchung, konnte jedoch bereits für *P. patens* mit positiver Bilanz realisiert werden (Röder & Kiehl 2008). Eine Nachpflanzung von im Gewächshaus angezogenen Individuen von *P. pratensis* ohne ausreichende Nachbetreuung hat sich bisher nicht bewährt.

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Author contributions

All authors participated in field work. TM developed the design for this study, conducted vegetation surveys, measured the plants and took leaf samples. NR counted the flowering individuals, UW took soil samples and both collected mature seeds. TM performed laboratory analyses, carried out statistical analyses and wrote substantially the manuscript. NR and UW supported the writing of the manuscript.

ORCID iDs

Tim Meier https://orcid.org/0000-0002-2718-540X

Supplements

Supplement S1. Vegetation relevés of investigated *Pulsatilla pratensis* subsp. *nigricans* sites in the Harz region.

Beilage S1. Vegetationsaufnahmen der untersuchten Standorte von *Pulsatilla pratensis* subsp. *nigricans* in der Harzregion.

Supplement S2. Multiple linear regressions after model simplification to test the influence of a) soil properties and b) mean Ellenberg indicator values (independent variables) on the respective growth and fitness traits (dependent variables) of *Pulsatilla pratensis* subsp. *nigricans*.

Beilage S2. Multiple lineare Regressionen nach Modellvereinfachung zur Überprüfung des Einflusses von a) gemessenen Bodenfaktoren und b) mittleren Ellenberg-Zeigerwerten (unabhängige Variablen) auf die jeweiligen Wachstums- und Fitnessmerkmale (abhängige Variablen) von *Pulsatilla pratensis* subsp. *nigricans*.

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Correlation matrix of pairwise correlations of all a) measured soil properties and b) mean Ellenberg indicator values (abbreviations as in Tab. 1).

Anhang E1. Korrelationsmatrix der paarweisen Korrelationen aller a) Bodeneigenschaften und b) mittleren Ellenberg-Zeigerwerte (Abkürzungen siehe Tabelle 1).

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Supplement S1. Vegetation relevés of investigated *Pulsatilla pratensis* subsp. *nigricans* sites in the Harz region. The cover values of the species were estimated using the 9-degree Braun-Blanquet scale (Reichelt & Wilmanns 1973). The plant communities were determined according to Schubert et al. (1995) and are listed in Tab. 1. The coordinates for each relevé are also in Tab. 1. Study sites: HA – Harslebener Berge, ELB – Bollenkopf Elbingerode, ARN – Arnstein, SCH – Schalkenburg Quenstedt, BÖR – Weinberg Börnecke, KAM – Kleines Kamel Westerhausen.

Beilage S1. Vegetationsaufnahmen der untersuchten Standorte von *Pulsatilla pratensis* subsp. *nigricans* in der Harzregion. Die Deckungsgrade der Arten wurden nach der 9-teiligen Braun-Blanquet-Skala (Reichelt & Wilmanns 1973) geschätzt. Die Pflanzengesellschaften wurden nach Schubert et al. (1995) bestimmt und sind in Tabelle 1 aufgeführt. Die Koordinaten für jede Aufnahme sind ebenfalls in Tabelle 1 zu finden. Untersuchungsgebiete: HA – Harslebener Berge, ELB – Bollenkopf Elbingerode, ARN – Arnstein, SCH – Schalkenburg Quenstedt, BÖR – Weinberg Börnecke, KAM – Kleines Kamel Westerhausen.

Study site	HA1	HA2	HA3	HA6	HA7	HA8	HA9	ELB	ARN	SCH	BÖR	KAM
Date	20.04.23	20.04.23	20.04.23	20.04.23	20.04.23	20.04.23	20.04.23	23.04.23	26.04.23	26.04.23	23.04.23	23.04.23
Exposition	E	SSE	SSE	SW	SSW	SSW	SW	SSE	S	SW	SW	SW
Inclination [°]	10	20	30	2	2	2	10	30	15	50	20	10
Altitude [m.a.s.l.]	153	148	158	178	166	197	172	469	216	204	198	187
Cover herb layer [%]	99	85	70	80	70	98	85	60	80	50	95	95
Cover cryptogams [%]	1	10	20	5	20	2	10	10	15	10	5	3
Species number [n]	32	26	31	23	26	34	31	18	27	24	29	20
Festucion valesiacae												
Festuca valesiaca	.	1	1	.	.	.	2m	1	4	2m	.	2m
Carex supina	.	.	.	2a	3	2m	.	.	.	.	.	2m
Stipa capillata	.	2b	3	.	.	.	.	.	.	.	.	.
Cirsio-Brachypodion												
Astragalus danicus	.	+	+	.	r	1	.	.	.	.	.	.
Scabiosa ochroleuca	+	1	+	.	.	.	1	.	r	.	.	.
Stipa tirsa	r	.	.	1	.	.	3	.	.	.	.	.
Adonis vernalis	.	.	.	.	.	.	.	.	.	.	2m	.
Festucetalia valesiacae												
Stipa pennata	.	.	1	3	.	.	+	.	.	.	.	.
Silene otites	.	.	.	.	.	.	r	.	.	r	.	.
Xerobromion erecti												
Helianthemum nummularium	+	.	2m	2a	r	.	.	2b	.	.	.	.
Mesobromion erecti												
Cirsium acaule	1	.	.	.	.	.	.	.	.	.	.	.
Medicago lupulina	r	.	.	.	.	.	.	.	.	.	.	.
Koelerio-Phleion phleoidis												
Koeleria macrantha	1	2a	1	1	2a	2m	1	.	2m	.	+	.
Brometalia erecti												
Dianthus carthusianorum	.	r	.	r	.	.	2m	.	1	+	r	r
Helictochloa pratense	+	.	r	.	.	+	2m	.	.	.	+	.
Bromus erectus	.	.	.	.	.	.	.	r	.	.	3	4
Koeleria pyramidata	.	.	.	.	.	.	.	2a	.	.	.	.
Carex caryophyllea	.	.	.	.	.	.	.	1	.	.	.	.
Arabis hirsuta	.	.	.	.	.	.	+	.	.	.	.	.
Festuco-Brometea												
Pulsatilla pratensis	2b	r	2m	+	1	2m	1	3	3	1	3	3
Potentilla neumanniana	.	+	1	1	+	2m	2a	1	2b	1	1	r
Euphorbia cyparissias	+	+	1	+	.	+	1	2m	.	2a	1	.
Galium verum	+	.	2m	2m	+	1	.	.	1	2m	2m	2b
Brachypodium pinnatum	4	2m	+	r	.	+	2m	.	.	.	2a	.
Festuca rupicola	1	.	1	.	2a	3	.	2b	+	.	1	.
Filipendula vulgaris	2a	2a	2m	2b	2m	1	2a	.	.	.	.	.
Carex humilis	1	2b	1	.	.	.	2m	.	.	.	2m	.
Eryngium campestre	.	.	2m	.	1	.	+	.	2b	.	+	.
Salvia pratensis	1	3	3	+	.	.	.	.	.	.	.	+
Sanguisorba minor	+	.	1	+	.	.	.	2b	+	.	.	.
Veronica spicata	2m	2a	.	2m	.	.	2b	.	.	.	.	2a
Asperula cynanchica	.	.	.	1	.	.	.	.	.	r	r	.
Galatella linosyris	.	.	2b	.	.	.	.	.	.	.	r	.
Allium oleraceum	.	.	.	.	.	.	.	2a	.	.	.	r
Trifolium montanum	.	.	.	.	.	+	.	.	+	.	.	.
Poa angustifolia	.	.	.	.	.	.	.	.	.	.	.	2b
Phleum phleoides	.	.	.	.	.	.	.	.	.	.	1	.
Senecio viscosus	.	.	.	.	.	1	.	.	.	.	.	.
Thymus praecox	.	.	.	.	.	.	.	.	.	+	.	.
Nardo-Callunetea												
Luzula campestris	1	1	.	.	.	.	+	.	.	.	2m	+
Sedo-Scleranthetea												
Achillea pannonica	+	+	.	1	+	1	1	.	+	.	+	1
Draba verna	r	2m	+	2m	+	+	+	2a	.	+	.	.
Arenaria serpyllifolia	+	1	1	3	2a	.	2m	2b	.	.	+	.
Myosotis stricta	.	.	.	+	+	+	+	.	2m	1	+	.
Cerastium semidecandrum	.	1	+	.	2b	.	2m	.	2a	.	.	.
Taraxacum sect. *Erythrosperma*	.	.	r	.	2b	1	+	2a	.	.	.	.
Holosteum umbellatum	.	.	.	.	2m	.	.	2m	+	2a	.	.
Artemisia campestris	.	1	.	.	.	.	.	.	1	2m	.	.
Trifolium arvense	.	.	.	.	1	.	.	+	2m	.	.	.
Veronica verna	.	.	.	.	.	+	.	.	2m	2a	.	.
Vicia hirsuta	.	.	.	.	.	+	.	.	1	.	r	.
Acinos arvensis	.	.	r	.	.	.	.	+	.	.	.	.
Arabidopsis thaliana	.	.	.	.	+	1	.	.	.	.	.	.
Erodium cicutarium	.	.	.	.	+	r	.	.	.	.	.	.
Veronica arvensis	.	.	.	.	.	+	.	.	2m	.	.	.
Valerianella locusta	.	.	.	.	.	.	.	.	r	r	.	.
Cerastium arvense	.	.	.	.	.	2b	.	.	.	.	.	.
Trifolium campestre	.	.	.	.	.	2a	.	.	.	.	.	.
Alyssum montanum	.	.	.	.	.	.	1	.	.	.	.	.
Spergula morisonii	.	.	.	.	+	.	.	.	.	.	.	.
Scleranthus annuus	.	.	.	.	.	.	.	.	.	+	.	.
Lamium amplexicaule	.	.	.	.	.	.	.	.	.	r	.	.
Molinio-Arrhenatheretea												
Plantago lanceolata	.	.	.	.	.	2m	.	.	1	.	r	.
Saxifraga granulata	.	.	.	.	.	.	.	.	2m	+	.	.
Prunella vulgaris	2a	.	.	.	.	.	.	.	.	.	.	.
widespread grassland species												
Pilosella officinarum	+	+	.	.	r	.	+	.	+	2m	+	1
Anthoxanthum odoratum	.	2b	+	.	.	.	2m	.	.	.	.	.
Agrostis capillaris	.	.	.	.	+	.	.	1	.	.	.	+
Plantago media	1	.	r	.	.	.	.	.	.	.	.	.
Rumex acetosella	.	.	.	.	+	.	r	.	.	.	.	.
Gagea pratensis	.	.	.	.	.	1	.	.	.	.	.	.
Lotus corniculatus	.	.	r	.	.	.	.	.	.	.	.	.
Vicia angustifolia	.	.	.	.	.	.	.	.	+	.	.	.
herbaceous fringe species												
Fragaria viridis	2b	.	+	.	2m	r	.	.	.	.	2a	.
Scabiosa canescens	1	.	2m	+	.	.	.	.	.	.	.	+
Agrimonia eupatoria	2a	r	.	.	.	.	.	.	.	.	r	.
Anthericum liliago	.	2b	3	.	.	.	+	.	.	.	.	.
Hypericum perforatum	.	.	.	.	.	.	+	.	.	.	+	.
Trifolium alpestre	.	.	.	.	.	+	2m	.	.	.	.	.
Viola hirta	+	.	.	.	.	.	.	.	.	.	r	.
Astragalus glycyphyllos	2a	.	.	.	.	.	.	.	.	.	.	.
other species												
Senecio vernalis	.	r	.	r	.	.	.	.	.	+	.	1
Viola arvensis	.	.	.	.	.	r	.	.	1	r	.	.
Bromus sterilis	.	.	.	.	.	r	.	.	.	2m	.	.
Carduus nutans	.	.	.	.	.	2a	.	.	.	.	.	.
Lactuca serriola	.	.	.	.	.	2m	.	.	.	.	.	.
Myosotis arvensis	.	.	.	.	.	2m	.	.	.	.	.	.
Veronica hederifolia	.	.	.	.	.	.	.	.	.	1	.	.
Echium vulgare	.	.	.	.	.	.	.	.	+	.	.	.
Falcaria vulgaris	.	.	.	.	+	.	.	.	.	.	.	.
Taraxacum sect. *Ruderalia*	+	.	.	.	.	.	.	.	.	.	.	.
Capsella bursa-pastoris	.	.	.	.	.	.	.	.	.	.	.	r
Dactylis glomerata	.	.	.	.	.	.	.	.	.	.	r	.
Moehringia trinervia	.	.	.	.	.	r	.	.	.	.	.	.
woody species												
Crataegus monogyna juv.	+	r	.	.	.	.	.	.	.	r	.	.
Ligustrum vulgare juv.	.	.	.	.	.	.	.	.	.	.	r	2m
Rosa rubiginosa juv.	.	.	.	1	.	.	.	.	.	.	.	+
Carpinus betulus juv.	r	.	.	.	.	.	.	.	.	.	.	.

Supplement S2. Multiple linear regressions after model simplification to test the influence of a) soil properties and b) mean Ellenberg indicator values (independent variables) on the respective growth and fitness traits (dependent variables) of *Pulsatilla pratensis* subsp. *nigricans.* Population size is also included as an independent variable in each model. Adjusted R^2 and error probability p_{tot} (bold: $p \leq 0.05$) of the respective whole models are indicated. *b* – unstandardised coefficients, *SE* – standard error of the unstandardised coefficient, *ß* – standardised coefficients, *t* – *t*-value, *p* – significance of the independent variables.

Beilage S2. Multiple lineare Regressionen nach Modellvereinfachung zur Überprüfung des Einflusses von a) gemessenen Bodenfaktoren und b) mittleren Ellenberg-Zeigerwerten (unabhängige Variablen) auf die jeweiligen Wachstums- und Fitnessmerkmale (abhängige Variablen) von *Pulsatilla pratensis* subsp. *nigricans.* Die Populationsgröße wird zusätzlich als unabhängige Variable in jedes Modell miteinbezogen. Korrigierte R^2-Werte und Irrtumswahrscheinlichkeit p_{tot} (Fettdruck: $p \leq 0{,}05$) der jeweiligen Gesamtmodelle sind angegeben. *b* – unstandardisierte Koeffizienten, *SE* – Standardfehler des unstandardisierten Koeffizienten, *ß* – standardisierte Koeffizienten, *t* – *t*-Wert, *p* – Signifikanz der unabhängigen Variablen.

Source of variation	*b*	*SE*	*ß*	*t*	*p*	R^2	p_{tot}
1a) Influence of soil properties on plant height							
Intercept	1.381	0.139		9.953	**< 0.001**	0.019	0.079
Population size	-0.007	0.016	-0.037	-0.455	0.650		
pH value	-0.368	0.171	-0.168	-2.153	**0.033**		
2a) Influence of soil properties on leaf length							
Intercept	2.182	0.315		6.936	**< 0.001**	0.085	**< 0.001**
Population size	-0.056	0.023	-2.357	-2.443	**0.015**		
Soil depth	-0.213	0.091	-2.394	-2.343	**0.020**		
C/N ratio	-0.834	0.213	-2.966	-3.916	**< 0.001**		
3a) Influence of soil properties on leaf dry mass							
Intercept	5.050	0.445		11.351	**< 0.001**	0.215	**< 0.001**
Population size	-0.126	0.033	-3.873	-3.873	**< 0.001**		
Soil depth	-0.707	0.129	-5.501	-5.501	**< 0.001**		
C/N ratio	-1.910	0.301	-6.345	-6.345	**< 0.001**		
4a) Influence of soil properties on leaf area							
Intercept	3.596	0.448		8.033	**< 0.001**	0.160	**< 0.001**
Population size	-0.119	0.033	-0.335	-3.623	**< 0.001**		
Soil depth	-0.503	0.129	-0.381	-3.891	**< 0.001**		
C/N ratio	-1.608	0.303	-0.385	-5.306	**< 0.001**		
5a) Influence of soil properties on SLA							
Intercept	0.546	0.116		4.703	**< 0.001**	0.219	**< 0.001**
Population size	0.007	0.008	0.077	0.868	0.386		
Soil depth	0.204	0.034	0.573	6.073	**< 0.001**		
C/N ratio	0.303	0.079	0.269	3.849	**< 0.001**		
6a) Influence of soil properties on LDMC							
Intercept	2.213	0.084		26.394	**< 0.001**	0.137	**< 0.001**
Population size	-0.013	0.011	-0.119	-1.256	0.211		
Soil depth	-0.175	0.041	-0.418	-4.288	**< 0.001**		
pH value	0.381	0.091	0.295	4.205	**< 0.001**		
7a) Influence of soil properties on flower length							
Intercept	0.563	0.061		9.240	**< 0.001**	0.104	**< 0.001**
Population size	0.000	0.012	0.006	0.041	0.968		
Soil depth	0.063	0.039	0.213	1.602	0.111		
pH value	-0.307	0.084	-0.337	-3.672	**< 0.001**		
8a) Influence of soil properties on seed mass							
Intercept	1.258	0.178		7.076	**< 0.001**	0.130	**< 0.001**
Population size	-0.027	0.011	-0.162	-2.492	**0.013**		
Soil depth	-0.173	0.063	-0.279	-2.726	**0.007**		
pH value	1.050	0.196	0.548	5.365	**< 0.001**		
C/N ratio	-1.317	0.203	-0.697	-6.490	**< 0.001**		
9a) Influence of soil properties on seed area							
Intercept	1.751	0.201		8.706	**< 0.001**	0.053	**< 0.001**
Population size	-0.004	0.012	-0.023	-0.345	0.730		
Soil depth	-0.160	0.072	-0.238	-2.229	**0.026**		
pH value	0.965	0.221	0.465	4.359	**< 0.001**		
C/N ratio	-1.083	0.230	-0.528	-4.720	**< 0.001**		

Source of variation	*b*	*SE*	*ß*	*t*	*p*	R^2	p_{tot}
1b) Influence of mean indicator values on plant height							
Intercept	-3.914	0.971		-4.030	**< 0.001**	0.420	**< 0.001**
Population size	-0.025	0.017	-0.129	-1.442	0.151		
Temperature	6.840	0.852	0.611	8.031	**< 0.001**		
Continentality	-5.383	0.595	-0.836	-9.044	**< 0.001**		
Reaction	3.961	0.593	0.537	6.683	**< 0.001**		
2b) Influence of mean indicator values on leaf length							
Intercept	0.580	1.369		0.425	0.672	0.504	**< 0.001**
Population size	-0.166	0.025	-0.697	-6.718	**< 0.001**		
Temperature	5.278	1.029	3.761	5.130	**< 0.001**		
Continentality	-10.136	0.839	-1.256	-12.088	**< 0.001**		
Moisture	-1.616	0.610	-2.032	-2.647	0.088		
Reaction	4.803	0.682	5.188	7.041	**< 0.001**		
3b) Influence of mean indicator values on leaf dry mass							
Intercept	8.922	2.215		4.029	**< 0.001**	0.441	**< 0.001**
Population size	-0.316	0.040	-0.868	-7.878	**< 0.001**		
Temperature	2.861	1.668	0.134	1.715	0.088		
Continentality	-14.998	1.360	-1.217	-11.030	**< 0.001**		
Moisture	-3.024	0.990	-0.249	-3.056	**0.003**		
Reaction	3.125	1.106	0.221	2.826	**0.005**		
4b) Influence of mean indicator values on leaf area							
Intercept	6.299	2.086		3.020	**0.003**	0.476	**< 0.001**
Population size	-0.321	0.038	-0.906	-8.500	**< 0.001**		
Temperature	4.068	1.571	0.195	2.589	**0.010**		
Continentality	-15.154	1.281	-1.264	-11.834	**< 0.001**		
Moisture	-3.210	0.932	0.272	-3.445	**< 0.001**		
Reaction	4.388	1.042	0.319	4.212	**< 0.001**		
5b) Influence of mean indicator values on SLA							
Intercept	-0.832	0.567		-1.466	0.144	0.127	**< 0.001**
Population size	-0.003	0.009	-0.029	-0.306	0.760		
Temperature	1.317	0.480	0.235	2.743	**0.007**		
Reaction	1.239	0.325	0.335	3.816	**< 0.001**		
Nutrients	-0.139	0.091	-0.107	-1.527	0.128		
6b) Influence of mean indicator values on LDMC							
Intercept	3.451	0.937		3.684	**< 0.001**	0.168	**< 0.001**
Population size	0.004	0.015	0.033	0.248	0.804		
Temperature	-1.386	0.751	-0.210	-1.846	0.067		
Continentality	-1.052	0.529	-0.277	-1.991	**0.048**		
Moisture	-2.034	0.516	-0.544	-3.942	**< 0.001**		
Reaction	1.676	0.431	0.385	3.888	**< 0.001**		
Nutrients	0.565	0.186	0.370	3.046	**0.003**		
7b) Influence of mean indicator values on flower length							
Intercept	0.285	0.322		0.884	0.378	0.075	**0.003**
Population size	-0.001	0.011	-0.031	-0.031	0.975		
Continentality	0.939	0.401	2.340	2.340	**0.021**		
Moisture	0.603	0.324	1.859	1.859	0.065		
Reaction	-0.986	0.340	-2.896	-2.896	**0.004**		
8b) Influence of mean indicator values on seed mass							
Intercept	-2.688	0.774		-3.474	**< 0.001**	0.297	**< 0.001**
Population size	-0.060	0.013	-0.358	-4.789	**< 0.001**		
Temperature	3.195	0.648	0.324	4.932	**< 0.001**		
Continentality	-4.422	0.473	-0.733	-9.340	**< 0.001**		
Moisture	1.132	0.455	0.214	2.489	**0.013**		
Reaction	4.174	0.342	0.669	12.211	**< 0.001**		
Nutrients	-1.111	0.161	-0.544	-6.886	**< 0.001**		
9b) Influence of mean indicator values on seed area							
Intercept	-3.915	0.552		-7.086	**< 0.001**	0.350	**< 0.001**
Population size	-0.001	0.010	-0.007	-0.131	0.896		
Temperature	4.951	0.506	0.462	9.788	**< 0.001**		
Continentality	-4.348	0.369	-0.664	-11.783	**< 0.001**		
Reaction	4.881	0.337	0.721	14.470	**< 0.001**		

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Supplement E1. Correlation matrix of pairwise correlations of all a) measured soil properties and b) mean Ellenberg indicator values (abbreviations as in Tab. 1). Correlation coefficients (ranging from -1 to 1) and significance values (* 0.01 ≤ p < 0.05, ** 0.001 ≤ p < 0.1, *** p < 0.001) are given. Colours are used to visualise a positive (blue colours) or negative (red colours) correlation, and the size of the squares indicate the strength of the correlation.

Anhang E1. Korrelationsmatrix der paarweisen Korrelationen aller a) Bodeneigenschaften und b) mittleren Ellenberg-Zeigerwerte (Abkürzungen siehe Tabelle 1). Korrelationskoeffizienten (im Bereich von -1 bis 1) und Signifikanz-Werte (* 0,01 ≤ p < 0,05; ** 0,001 ≤ p < 0,1; *** p < 0,001) sind angegeben. Die Farben dienen zur Visualisierung einer positiven (blaue Farben) oder negativen (rote Farben) Korrelation, und die Größe der Quadrate gibt die Stärke der Korrelation an.