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Carnivorous sundews (*Drosera rotundifolia*) are more carnivorous in high-light bog microhabitats that are not also nutrient-rich

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Abstract

1. Carnivorous plants adapt to variations in nutrient availability and shade by altering investment in carnivory in response to different environmental conditions. It is not clear, however, how carnivorous plants might alter investment in carnivory in relation to habitat heterogeneity at small scales. We hypothesised that the carnivorous plant *Drosera rotundifolia* would alter investment in carnivory and the amount of plant nitrogen (N) derived from prey in response to differences in shade and nutrients between hummock and hollow microforms on patterned peatlands.
2. We investigated *D. rotundifolia* growing on three peatlands in Northern Europe: Scotland, Sweden, and Finland where we expect microhabitat variability to differ between peatlands due to differences in the ratio of precipitation to evapotranspiration. We measured differences in the density of sticky leaf tentacles (investment in carnivory) and the proportion of plant N that was prey-derived (%N_{dfp}) for plants growing on hummocks and hollows at each peatland.
3. At the Finland site P:ET ratio was lowest (1.86), and root N availability was similar for hollows and hummocks. Here, tentacle density and %N_{dfp} were ~50% higher for plants on hollows than on the more shaded hummocks. At the Scotland site P:ET was highest (5.40), root N availability was lower for hummocks than for hollows, and hummocks were more shaded. Here, there was little difference in tentacle density and %N_{dfp} between plants growing on hummocks and hollows. The Sweden site was intermediate in terms of P:ET ratio (2.63), habitat heterogeneity, and carnivory.
4. Our results are consistent with the predictions of an evolutionary cost–benefit model for plant carnivory in which the marginal benefits of carnivory decrease with increasing root nutrient availability and decreasing light. This model predicted carnivorous plant phenotypic variability at small scales in response to different extents of habitat heterogeneity at our three study sites.

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5. Our study demonstrates the capacity for a carnivorous plant species to vary investment in carnivory, adjusting the proportion of prey-derived N, in response to small-scale habitat heterogeneity. We suggest that as well as an adaptation to low-nutrient conditions, carnivory may also provide a means for plants to adapt to and persist in heterogeneous habitats.

KEYWORDS

carnivorous plant, *Drosera rotundifolia*, hollow, hummock, microhabitat, peatland, phenotypic variation, sundew

1 | INTRODUCTION

At this present moment I care more about *Drosera*
than the origin of all the species in the world

—Charles Darwin, 1860, in a letter to Charles Lyell

Carnivorous plants supplement root nutrients by trapping and digesting animal prey usually via modified leaves (Adamec, 2013). Charles Darwin first demonstrated almost 150 years ago that carnivorous plants digest insect prey and assimilate their nutrients, postulating that carnivory was an adaptation to low-nutrient environments (Darwin, 1875). Theoretical advances such as the development of a cost–benefit model for the evolution of plant carnivory (Givnish, 2015; Givnish et al., 1984), and empirical evidence from observations and experiments demonstrate that carnivorous plants tend to be restricted to light, wet, low-nutrient environments (Ellison et al., 2003; Ellison & Gotelli, 2009; Forterre et al., 2005; Thorogood et al., 2017). Carnivorous plants also exhibit phenotypic variability in carnivorous traits in response to environmental variability (Abbott & Brewer, 2020; Brewer, 2003, 2019; Ellison & Gotelli, 2002; Holloway & Brewer, 2022; Pavlovič et al., 2010; Segala & Horner, 2023), and their reliance on prey nutrients can vary (Adamec & Pavlovič, 2018; Cook et al., 2018; Millett et al., 2015). However, our understanding of how these environment–trait interactions operate at small spatial scales remains limited.

Habitats vary at a range of temporal and spatial scales, to which plants must adapt (de Smedt et al., 2018; Molina-Montenegro et al., 2010). Flexibility in the traits associated with carnivory provides a mechanism for adapting to this variability (Adamec et al., 2021). Studies of variability in carnivorous plant traits have generally considered broad-scale continental differences among sites (Millett et al., 2015; Millett, Svensson, et al., 2012), are manipulative studies in situ and ex situ (e.g. Abbott & Brewer, 2020; Holloway & Brewer, 2022) or consider within-site temporal variation (Brewer, 1999). However, it has not been well demonstrated how these responses translate into patterns of carnivorous plant traits at small spatial scales. Spatial patterns of habitat variability tend to persist for long periods (e.g. bog hummocks can persist for hundreds of years, Barber, 1978; Conway, 1948; Tolonen, 1971), providing more time for phenotypic or genetic adaptation to environmental differences than short experimental studies. However, greater

gene-flow between closely situated populations might reduce the possibility of genetic adaptation compared with variation between sites. Additionally, the patterns of variation within a site will differ from those among sites as some environmental conditions will be more similar within a single site.

Carnivorous plant trait–environment relationships generally follow the predictions of the cost–benefit model for the evolution of carnivory (Givnish, 2015; Givnish et al., 1984, 2018). For example, in an ex situ experiment, the round-leaved sundew *Drosera rotundifolia* increased allocation to carnivory (increased leaf trap stickiness) in low-nutrient and high-light conditions (Thorén et al., 2003) and in situ plants had decreased prey nitrogen (N) uptake when growing on peatlands with increased atmospheric N deposition (and so root N availability; Millett et al., 2015; Millett, Svensson, et al., 2012). *Sarracenia purpurea* altered pitcher morphology in response to experimental N addition and among sites along an N deposition gradient (Ellison & Gotelli, 2002), and *Sarracenia alata* altered pitcher morphology in a manipulative in situ light experiment (Segala & Horner, 2023). *Pinguicula vallisneriifolia* and *P. moranensis* increased mucilage secretion (a sticky glue used to capture prey) and/or digestive gland density in response to increased light in situ (Alcalá & Domínguez, 2005; Zamora et al., 1998). These results underscore the importance of altering investment in carnivory as a mechanism for adaptation to variable habitat conditions. We predict that the same patterns will occur within sites in response to small-scale habitat variability.

We measured, in situ, the response of a carnivorous plant species (*D. rotundifolia*) to naturally occurring microhabitat variation in shade and nutrient availability on patterned peatlands. We measured this response at sites across a wide geographic area, where we expected differences in precipitation and evapotranspiration to drive differences in patterns of microhabitat variation, providing a novel ‘natural experiment’ where different components of the microhabitat environment vary systematically and independently. *Drosera rotundifolia* has a circumboreal distribution, typically growing on patterned peatlands across the range of microforms. Patterned peatlands are characterised by the spatial organisation of microforms (also referred to as microhabitats or Scale Level 1 features—see Baird et al., 2013), most clearly defined by raised hummocks (also known as strings) and lower hollows (also known as flarks; with lawns often

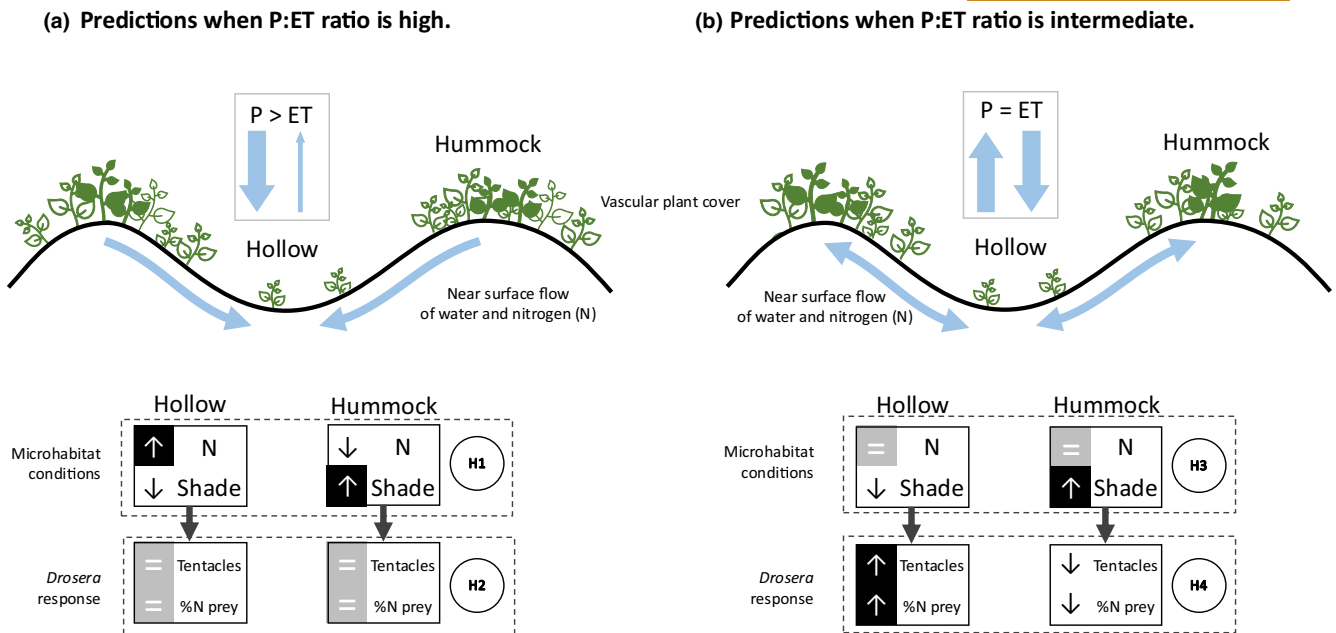


FIGURE 1 Top: Peatland processes predicted to impact P:ET-driven (precipitation: Evapotranspiration ratio) flow of water and nitrogen to hummocks and hollows. Bottom: Graphical hypotheses (H1–H4) showing predicted impacts of peatlands processes on microhabitat conditions and *Drosera rotundifolia* responses to those conditions. Presented are expected differences between hummocks and hollows for shade, nitrogen (N), tentacle density (investment in carnivory) and percentage of prey-derived N (%N prey) when P:ET is high (a) and intermediate (b).

grouped within hollows) across the surface of a peatland (Eppinga et al., 2010; Nungesser, 2003). The organisation of peatlands into these microform patterns means that these habitats are extremely variable at small scales.

Drosera rotundifolia can usually be found across a range of microhabitats, including hummocks and hollows (Baranyai & Joosten, 2016). Raised drier hummocks have relatively high vascular plant cover which impacts the sub-canopy light environment (Korrensalo et al., 2018), and lower wetter hollows and lawns are typified by non-vascular vegetation (Rietkerk et al., 2004; Rydin & Jeglum, 2006; van der Molen et al., 1994). Patterned peatlands typically receive most of their nitrogen from atmospheric deposition, which moves with water flow (Limpens et al., 2006; Lovett et al., 2009). Where flow is from hollows to hummocks (when precipitation < evapotranspiration), nitrogen accumulates in hummocks; where flow is from hummocks to hollows (when precipitation > evapotranspiration), nitrogen accumulates in hollows (Figure 1a, Eppinga et al., 2008). This results in large-scale variability in small-scale nitrogen distribution, impacting peatland formation in response to differences in climate (Eppinga et al., 2010). Thus, the extent of habitat microvariability that *D. rotundifolia* plants experience will vary for different patterned peatlands. This physical process provides the context in which we tested our hypotheses (Figure 1).

Our aim was to determine, for the first time, how P:ET-driven small-scale resource (light and nitrogen, N) variability impacts plant nutrition and variability in investment in carnivory, and how this trait variability changes with local climate. We predicted that even at small scales (i.e. within 1 m), light and N availability will alter *D.*

rotundifolia investment in prey capture: plants growing in higher light and lower N habitats will increase investment in prey capture and reliance on prey-derived N. We tested the hypotheses that (Figure 1):

1. For higher P:ET sites, nitrogen accumulates in hollows according to the directional flow of water, but hummocks are more shaded than hollows, and as a result;
2. Investment in prey capture, and prey N uptake by *D. rotundifolia* at these sites is the same for plants growing in hollows and hummocks due to the relatively greater benefit of carnivory in low root N microhabitats and the relatively elevated cost of carnivory in low-light microhabitats, that is, hummocks in higher P:ET sites, but
3. When P:ET decreases, the distribution of N changes, with N evenly distributed between hummocks and hollows or accumulating in hummocks, resulting in
4. Greater investment in prey capture and prey N uptake for *D. rotundifolia* in the lower N, less shaded hollows.

2 | MATERIALS AND METHODS

2.1 | Site information and plot selection

Fieldwork was conducted from July to August 2017. Measurements were made at three patterned ombrotrophic peatlands in Europe, across a longitudinal gradient, which differed in P:ET ratio (Figure 2, Table 1). Fieldwork permissions were obtained from the National Trust for Scotland (Scotland), the Swedish Integrated Monitoring



FIGURE 2 Left: Study site locations across Europe (southwest to northeast: Inverewe, Scotland; Hallebomossen, Sweden; Siikaneva, Finland). Indicative distribution of peatlands shown in green (taken from PEATMAP, Xu et al., 2018). Right: Indicative overview photo of each site.

TABLE 1 Environmental and geographic information for study sites. Predicted nutrient accumulation based on definitions of Eppinga et al. (2010).

Study site (site code)	Lat, long	Precipitation P (mm year ⁻¹) ^a	Evapo-transpiration ET (mm year ⁻¹) ^a	P:ET ratio	Climate classification ^b	N deposition (kg ha ⁻¹ year ⁻¹) ^c	Predicted nutrient accumulation
Inverewe, Scotland (Sc)	57.46, 5.33	1700	315	5.40	Cfb Temperate, oceanic	7.7	Hollows
Hallebomossen, Sweden (Sw)	59.73, 14.98	741	282	2.63	Dfb Continental, warm summer	4.5	Even distribution
Siikaneva, Finland (F)	61.84, 24.29	707	380	1.86	Dfc Continental, sub-arctic	7.4	Weakly hummock

^aClimate data derived from; Scotland: (Eppinga et al., 2010), Sweden: Kindla II weather monitoring site mean for 1996–2016, Finland: (Korhonen et al., 2013) and Siikaneva and Hyytiala weather monitoring stations 1986–2016.

^bClimate classifications follow Koppen–Geiger typology (Kottek et al., 2006).

^cAtmospheric N deposition is modelled total (reduced and oxidised, wet and dry) (APIS, 2016; Korhonen et al., 2013; SUAS, 2017; Weldon, 2022).

Programme (Sweden), and the Integrated Carbon Observation System team (Finland). All three sites had relatively low levels of atmospheric N deposition. Peatlands were characterised by hummock–hollow microtopography with regular variation in surface topography of approximately 0.5–1 m difference in height between hummocks and hollows. This is usual for such patterned peatlands (and hummocks may differ by only 0.05 m to an adjacent hollow microform; Baird et al., 2016), and creates clear small-scale patterns in plant communities, and variation in peatland processes such as hydrology (Eppinga et al., 2010).

Hollows were systematically (qualitatively) wetter than hummocks, as expected because they are closer to the water table. These hydrological differences drive variation in the plant communities found within the microforms. At all sites, vascular vegetation on hummocks was dominated by *Calluna vulgaris* (common heather), an ericaceous shrub that forms a dense canopy ~0.5 m above-ground. Vascular vegetation in hollows was predominantly low-growing *Carex* spp. (the sedges) present at low cover (~5% ground coverage)

in hollows so did not form a continuous canopy. *Drosera rotundifolia* were present across both microforms. *Drosera rotundifolia* are an obligate wetland species restricted to very wet areas of peatlands, therefore although hummocks are characterised by *Calluna vulgaris* (which can persist in dry substrates), hummocks within this study are permanently very wet.

Fifty 25 × 25-cm plots containing *D. rotundifolia* plants growing in *Sphagnum* spp. were selected using a stratified random design at each site. Two strata consisted of hummocks or hollows, and plots were distributed evenly among these (25 in hummocks and 25 in hollows), with a total of five hummocks and five hollows selected randomly per site (five plots per hummock or hollow).

2.2 | Measurements

The objective was to quantify differences between microforms in habitat characteristics and *D. rotundifolia* traits relating to prey

capture and nutrient acquisition. We focussed on two habitat characteristics: the light environment (as moderated by above-ground plant–plant interactions) and nitrogen availability. Though hydrological differences are present between hummocks and hollows, we assume the influence of these differences on the expression of carnivory is much smaller than the impact of shade and nutrient availability given the inherent carbon costs associated with carnivorous traits and the nutritional benefit gained from carnivory. We measured vascular plant cover and light interception as a measure of the impact of other co-occurring vascular plants on the light environment experienced by *D. rotundifolia*; we used N concentration in *Sphagnum* sp. as a bioindicator of differences in N availability which provides a baseline of nutrient availability in hummocks and hollows.

Sphagnum spp. intercept and accumulate in their tissues N from atmospheric deposition (Bragazza et al., 2005; Limpens et al., 2017). Where most of peatland N is received from atmospheric deposition, high tissue retention times make *Sphagnum* good indicators of nutrient availability in peatlands, particularly under low levels of atmospheric N deposition (Aldous, 2002; Williams et al., 1999). As such, *Sphagnum* tissue N concentrations are a sensitive indicator, up to a critical threshold, for 5–40 *Sphagnum* species (Zhou et al., 2021), with, for example, *Sphagnum fuscum* having a critical threshold of 14.8–15.7 kg ha⁻¹ year⁻¹ (Vitt et al., 2003), where uptake of nutrients is likely restricted to some extent by some other limiting factor (Bragazza et al., 2005). The field sites for this experiment have sufficiently low N deposition (Table 1) that we are confident that *Sphagnum* tissue nutrient concentrations indicate within-site variability in N availability (Zhou et al., 2021). Therefore, general patterns can be used to compare nutrient status of *D. rotundifolia* across sites in relation to nutrient availability within microforms.

Our focus was on two key plant traits: leaf tentacle density, and the proportion of plant N that is derived from prey. *Drosera rotundifolia* catches prey using leaves which have tentacles, on the end of which sticky mucilage is secreted to form a 'flypaper' trap. Previous in situ and ex situ studies have demonstrated differences in leaf-stickiness to quantify variation in investment in prey capture in response to differences in N availability (Cook et al., 2018; Thorén et al., 2003). Stickiness is, however, problematic for quantitative comparisons in practice because precipitation removes or dilutes trapped mucilage. Therefore, we used tentacle density as a more consistent measure of investment in prey capture given the short time available at each site for sampling, and the differences in sampling date and potentially weather at the three sites. Tentacle density has also been used previously as a measure of investment in prey capture (Crowley et al., 2013), and for other carnivorous species differences in leaf tentacle density have been linked to relative investment in prey capture (Alcalá & Domínguez, 2005; Cook et al., 2018; Jennings et al., 2016; Zamora et al., 1998). The proportion of N derived from prey demonstrates the nutritional impact of variation in investment in prey capture and root N availability. We measured the proportion of N derived from prey using stable isotopes to estimate the relative contribution of two N sources to a single pool (Schulze et al., 1991). Animals tend to have

a higher $\delta^{15}\text{N}$ compared with their local vegetation, that is, lower trophic levels (Boecklen et al., 2011), because ^{14}N tends to be excreted. It is therefore possible to determine the relative contribution of N that is root-derived or prey-derived by measuring $\delta^{15}\text{N}$ of the target plant and the two N sources.

Measurements were made on five 25-cm² plots on each of five hummocks and five hollows at each site. Within each plot, five *D. rotundifolia* plants were identified and photographed for tentacle density analysis. These same plants were then harvested, removing all above-ground, plus living below-ground tissues for tissue analysis. Plants were pooled per plot. To provide endpoints for estimating the proportion of *D. rotundifolia* N from prey, and to quantify relative plant N availability between microforms, one 5 × 5 × 2-cm (width, length, depth) sample of *Sphagnum* spp. capitula was collected from each plot. Potential prey was sampled by placing a 10 × 5-cm sheet of yellow flypaper at each plot; captured insects were collected daily for 4 days. Insects likely to be too large to be captured by *D. rotundifolia* (i.e. >10-mm length) were not included in this sample.

We used photographs of each plant rosette to calculate the tentacle number and lamina area. Each plant was photographed from directly above the plant using a narrow depth of field ($F=2.4$), with a ruler for scale. This was done at least twice per plant and the clearest photograph was used for measurement, ensuring the scale and the entire plant were in focus. Photographs were taken using a Sony SLR SLT- α 37 fitted with a SAL-100M28 Sony 100 mm F/2.8 macro lens and saved in RAW format. Photographs of plants were completed within 5 days per site to capture microform contrast rather than temporal change.

To provide quantification of the light environment at each plot, photosynthetically active radiation (PAR=400–700 nm wavelengths) was measured directly above the shrub canopy height, and at ground level using a quantum sensor (SKP 200 PAR Quantum Sensor, Skye Instruments Ltd., Wales UK). These measurements were made at five locations for each plot between 10:00 and 14:00. The light environment will change through the year, but because the objective of this study was to compare microforms within each location, these data provide a robust comparison. It is likely that the relative differences between microforms will be relatively constant throughout the year because they are dominated by persistent evergreen shrubs. Vascular vegetation cover was estimated by eye and vegetation height was measured at three points per plot using a tape measure.

All tissue samples were stored with desiccant before being oven-dried. As soon as possible and within 48 h, plant and insect samples were dried to a stable mass in a forced-air oven at 70°C for 72 h. Plant samples were ground to a fine homogenised powder using a ball mill, insects were ground using a pestle and mortar, to ensure sample homogeneity.

2.3 | Nitrogen isotope and tissue nutrient concentration

Drosera rotundifolia, *Sphagnum* spp., and prey samples (one sample of each per plot, 150 plots in total) were analysed for $\delta^{15}\text{N}$ and N

concentration at the NERC Life Science Mass Spectrometry Facility, UK. Nitrogen isotope ratios were analysed using a Thermo Scientific DELTA V Plus isotope ratio mass spectrometer (Thermo Scientific Germany) interfaced with a Costech ECS 4010 elemental analyser (Costech Instruments, Italy). Three in-house standards (alanine, gelatine, and glycine) were run every 10 samples for quality assurance. All data were reported with respect to the international standard of atmospheric N_2 (AIR) for $\delta^{15}N$. Results were reported in the δ notation as the deviation from standards in parts per mille (‰) where (Equation 1):

$$\delta^{15}N = \left[\frac{\frac{^{15}N}{^{14}N} \text{ sample}}{\frac{^{15}N}{^{14}N} \text{ reference}} - 1 \right] \times 1000 \quad (1)$$

The proportion of prey-derived N and corresponding root-derived N of *D. rotundifolia* was calculated by using the $\delta^{15}N$ of *D. rotundifolia*, $\delta^{15}N$ of *Sphagnum*, and $\delta^{15}N$ of prey into a single isotope ratio, two end-point linear mixing model (Equation 2) (Shearer & Kohl, 1989). The assumption of the model is that non-carnivorous plants can be used as a proxy for $\delta^{15}N$ of carnivorous plants that have obtained none of their N from prey and prey $\delta^{15}N$ can be used as a proxy for carnivorous plants that rely on prey for all their N.

$$\% N_{\text{derived from prey}} = \frac{\delta^{15}N_{\text{Drosera rotundifolia}} - \delta^{15}N_{\text{Sphagnum}}}{\delta^{15}N_{\text{Prey}} - \delta^{15}N_{\text{Sphagnum}}} \quad (2)$$

This model takes advantage of the inherent difference in $\delta^{15}N$ between trophic levels to discern the proportional contributions of two isotope ratio sources (prey or root-derived) into a single sink (*D. rotundifolia* $\delta^{15}N$). This has been widely used to estimate differences in the amount of N in carnivorous plants that are derived from prey (Butler & Ellison, 2007; Friday & Quarmby, 1994; Givnish & Shiba, 2022; Lin et al., 2021; Millett, Svensson, et al., 2012; Schulze et al., 1991).

Sphagnum spp. are a good indicator of N availability and $\delta^{15}N$ signature because they are sensitive to within-site variation in availability and $\delta^{15}N$ signature (Bragazza et al., 2005). Nitrogen availability in the surveyed sites is almost exclusively rain-fed or atmospherically deposited. The $\delta^{15}N$ signature of the sites varies, likely due to differences in deposition levels and the ratio of reduced vs. oxidised N in deposition. Additionally, hummock and hollow signatures within sites may also vary. *Sphagnum* $\delta^{15}N$ data were therefore collected for each plot. This enables comparison of the contrast between microforms within and among sites. *Drosera rotundifolia* has a similar rooting depth to and is rooted within the *Sphagnum*. *Sphagnum* therefore serves as a baseline for the $\delta^{15}N$ signature for non-carnivorous species and for *D. rotundifolia* that attain all their nutrients via roots. Other potential end points, for example, other non-carnivorous vascular plants are not adequately present in hummocks and hollows and contain more woody tissues with higher C:N ratios which may affect their $\delta^{15}N$ signature (Givnish & Shiba, 2022). For all plants, all above- and below-ground plant tissues were removed (Millett et al., 2003). Atmospheric N fixation can be an N-source for *Sphagnum* on ombrotrophic bogs, in addition to precipitation, which will alter $\delta^{15}N$. We consider this to be an additional reason

for using *Sphagnum* spp. rather than other plants. This is because this end point is analogous to a carnivorous plant that has obtained all its nitrogen through root uptake, and we would expect that any N from atmospheric fixation would also be available for root uptake by *Drosera rotundifolia*. Transfer of N from atmospheric fixation to non-N fixing plants has been demonstrated in other systems (Millett, Godbold, et al., 2012), and we expect that is also likely in the present system. Given that all the *D. rotundifolia* in this study were rooted within the *Sphagnum* and are known to interact with them in terms of N uptake (Svensson, 1995), we think it is, therefore, reasonable to assume that the $\delta^{15}N$ of N taken up by *D. rotundifolia* roots is very close to that of the *Sphagnum* they are growing in, but likely consists of N from precipitation plus N fixation. We do recognise, however, that this is an assumption and one which remains untested, but N fixation by *Sphagnum* on ombrotrophic bogs in Europe is likely quite low (Van Den Elzen et al., 2020), so any error will be small.

2.4 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Microform (hummock or hollow)	Pooled plots	15, 15
Site	Site	3

2.5 | Data analysis

2.5.1 | Trait measurement using Adobe Photoshop

Plant measurements were taken through pixel counts converted to metrics in Adobe Photoshop CC v2015.1 (2015) and saved to a CSV file.

For each plant, we measured the leaf lamina area and number of tentacles. Tentacle counts were completed on a sub-sample of the area of each lamina, for efficiency. The sub-sample was tentacles terminating within the border of the circumference of the lamina. Measurements of plants within a plot were averaged. All data analyses were conducted using R within Rstudio v 2022.02.3+492 (R Core Team, 2022; RStudio Team, 2022). Tentacle density was calculated using Equation 3. Phytovolume was calculated using Equation 4.

$$\text{Tentacle density} = \frac{\text{Number of tentacles terminating within area of leaf lamina}}{\text{Lamina area (mm}^2\text{)}} \quad (3)$$

$$\text{Phytovolume (m}^3\text{ m}^{-2}\text{)} = \text{Mean vegetation height of plot (m)} \times \text{mean vegetation coverage of plot (m}^2\text{ m}^{-2}\text{)} \quad (4)$$

For measures of *D. rotundifolia* traits and habitat characteristics, we analysed differences between microforms using nested

ANOVA, with peatland microform nested within peatland. A priori contrasts (planned comparisons) were used to determine pairwise comparisons of differences in these measurements between microforms within each site. Assumptions of normality and homoscedasticity were tested using Q–Q plots and Shapiro–Wilk tests. Tentacle density was log-transformed for analysis because this reduced skewness in the original data and tentacle density followed a log-normal distribution.

To test for differences in how the hummock–hollow trait contrast varied between the three peatlands we followed the method of Eppinga et al. (2010). We calculated for each site an index of ‘trait contrast’ which provides a relative measure of the hummock–hollow difference in the trait value and compared this index between sites. We did this for two reasons: (1) to achieve this comparison with linear modelling would require paired plots, and this was not the design we adopted, (2) our trait ratio evaluates relative differences, removing absolute differences between sites. The trait contrast for a trait X within a site was calculated using Equation 5 where TC_X is a dimensionless unit for the contrast in trait X in a site, and overbars indicate averages (mean).

$$TC_X = \frac{\overline{X_{\text{hummock}}} - \overline{X_{\text{hollow}}}}{\overline{X_{\text{hummock}}} + \overline{X_{\text{hollow}}}} \quad (5)$$

The value of TC_X can range between -1 (which means a value of zero in the hummocks) and 1 (which means a value of zero in the hollows); a value of zero indicates that the trait was the same in hummocks and hollows at that site. To calculate, TC_X requires pairwise coupling of hummocks and hollows. As we did not pair plots in this way, we used a resampling approach to construct bootstrap replicate hummock–hollow pairs from the original data, with replacement. In R within Rstudio v 2022.02.3+492 (R Core Team, 2022; RStudio Team, 2022), we generated 1000 bootstrap replicates of the trait measurement in one randomly selected hummock and hollow. For each replicate, we calculated TC and used the mean and standard deviation of these TC measurements to test for differences between sites using a t -test for two populations. We used a Bonferroni adjustment to p -values to account for the elevated probability of Type 1 errors consequential of multiple pairwise comparisons (between three sites). Data are openly available via Loughborough University Research Repository (Hatcher & Millett, 2024).

3 | RESULTS

Microhabitat conditions varied between hummocks and hollows for all sites (Figure 3A–H). Hummocks were more shaded than hollows: vascular vegetation cover, phytovolume, and light interception were consistently higher on hummocks than on hollows for all sites. These differences were statistically significant (Figure 3B,D,F, Table S1). Nitrogen availability (indicated by *Sphagnum* sp. tissue N concentrations) was greater in hollows than hummocks, but this difference

decreased along the P:ET gradient, being greatest in the Scotland site (P:ET = 5.40) and negligible in the Finland site (P:ET 1.86; Figure 3H, Table S1).

Drosera rotundifolia traits varied between hummocks and hollows, but these differences varied among peatlands (Figure 4A–F). In the Finland and Sweden peatlands, *D. rotundifolia* growing on hummocks had lower leaf tentacle density and lower proportion of N derived from prey than those growing in hollows, these differences were statistically significant; in the Scottish peatland leaf tentacle density and proportion of N derived from prey did not differ between hummocks and hollows (Figure 4B,D respectively, Table S2). *Drosera rotundifolia* tissue %N was greater in hollows than hummocks in the Scotland site, lower in hollows than hummocks in the Sweden site (these differences were statistically significant, Table S2), and did not differ in the Finland site (Figure 4F).

Trait contrasts for measures of habitat heterogeneity were consistently strongly positive for vegetation cover and phytovolume, reflecting more vascular plant cover on hummocks than hollows (Figure 3A,C, Table S3). The strength of this difference was slightly lower for the Swedish peatland vegetation cover than for the other two sites and slightly greater for Scotland phytovolume compared with the other two sites. Trait contrasts for canopy light transmission were strongly negative, reflecting greater transmission of incident light for hollows than hummocks (Figure 3E, Table S3). Canopy light transmission was slightly more evenly distributed between hummocks and hollows in the Finnish peatland. These patterns indicate that P:ET ratio had little influence on between-microform variation in the light environment at the peatland surface. The contrast in *Sphagnum* sp. N concentrations, which we are using as a bioindicator of N availability, changed from negative to neutral as P:ET ratio decreased (Figure 3G, Table S3). This indicates that N accumulated in hollows at the site with higher P:ET ratio (Scotland), and this accumulation decreased with no difference between hummocks and hollows in the site with lowest P:ET ratio (Finland).

The contrast between carnivorous plants growing on hummocks and hollows for traits relating to an investment in prey capture and prey N uptake also varied along the gradient of P:ET ratio. For plants growing in the high P:ET ratio site (Scotland), investment in prey capture (tentacle density) and the proportion of plant N derived from prey capture was the same on hummocks and hollows (Figure 4A,C, Table S4). For the lower P:ET ratio sites, the trait contrast for investment in prey capture and the proportion of N derived from prey, was strongly negative. This indicates higher investment in prey capture for plants growing in hollows. There was a clear trend of increasingly more negative trait contrast for the proportion of prey-derived N as P:ET ratio increased. *Drosera rotundifolia* tissue N concentrations followed the opposite pattern (Figure 4E, Table S4): the negative contrast became less negative as P:ET ratio increased. That is, higher *D. rotundifolia* N content in hollows at high P:ET ratio (Scotland), but no difference between microforms, or higher N content on hummocks at lower P:ET ratios.

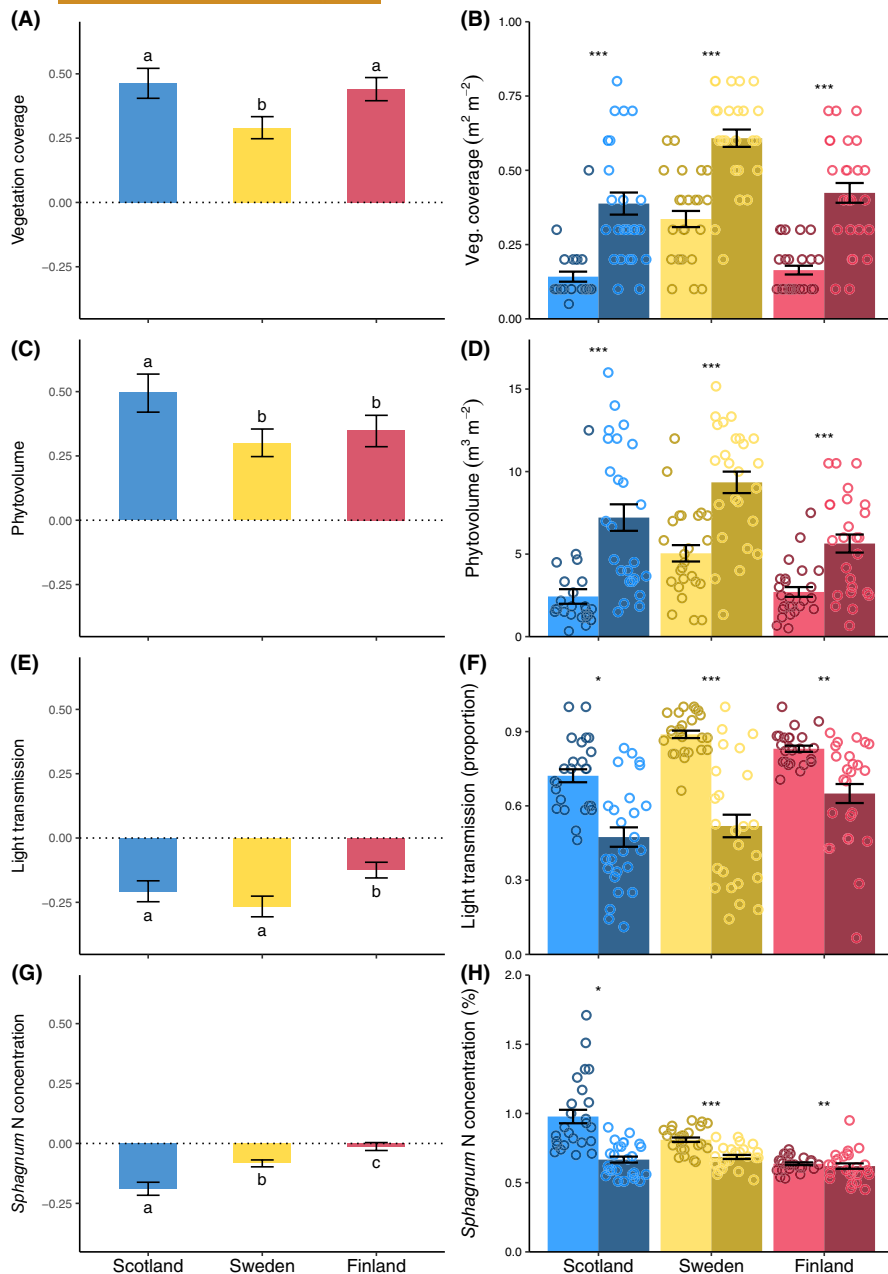


FIGURE 3 Hummock-hollow resource contrasts (dimensionless, A, C, E, G) and raw hummock and hollow values (B, D, F, H) for vegetation cover (A, B), phytovolume (C, D), light transmission (E, F), root N availability as a function of *Sphagnum* tissue N % (G, H). In all panels P:ET ratio decreases from left (Scotland) to right (Finland). Differing letters among bars indicate significant differences ($p_{adj} < 0.05$), asterisks among bars indicate significant differences between hummock and hollow (* $\equiv p < 0.05$, ** $\equiv p < 0.005$, *** $\equiv p < 0.001$, (* $\equiv p < 0.1$, ns \equiv not significant), error bars are 95% confidence intervals.

4 | DISCUSSION

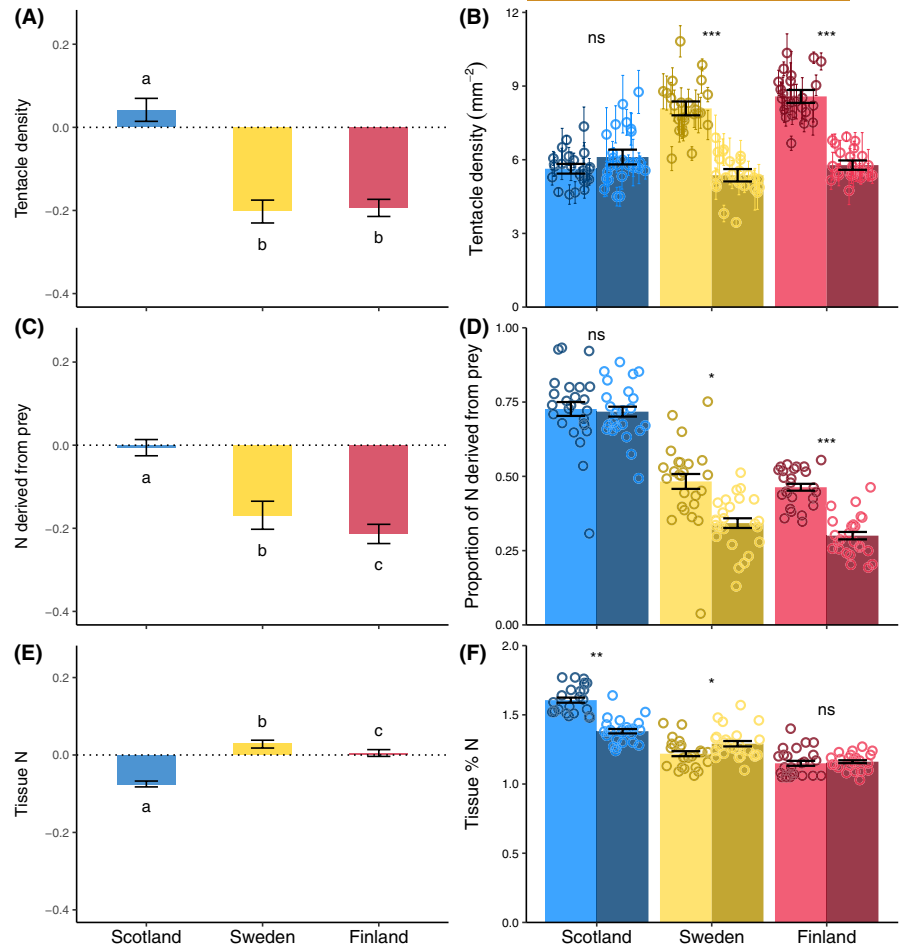
We found evidence that *D. rotundifolia* adapts to microhabitat variability between hummocks and hollows by altering investment in carnivory by changing the density of leaf tentacles and by altering prey N uptake. The clear patterns in these traits over very small scales (<1 m) suggest that plant carnivory provides a mechanism of adaptation to small spatial scale habitat heterogeneity. Our results demonstrate that P:ET ratio creates among-site differences in small-scale patterns of N availability (supporting hypotheses 1 and 3), while wetter hollows are consistently less shaded. This habitat heterogeneity drives patterns of *D. rotundifolia* carnivorous traits and nutrition (supporting hypotheses 2 and 4) and is consistent with the predictions of the cost-benefit model for plant carnivory (Givnish et al., 1984, 2018). *Drosera rotundifolia* plants are more carnivorous

(higher tentacle density and greater N from prey) in unshaded, low-nutrient microhabitats.

The cost-benefit model predicts that N derived from carnivory is more valuable when N is more limited, which is the case at microsites which are sunnier and have lower levels of root N availability, and that carnivorous plants will invest more resources in prey capture in these situations. Previous studies have demonstrated carnivorous plant adaptation that follows these predictions (Brewer, 2019; Bruzese et al., 2010; Millett et al., 2015; Segala & Horner, 2023). Our results extend this understanding of the adaptive function of plant carnivory to much smaller spatial scales than previously considered and demonstrate the ecological impact of climate-driven variation in within-habitat heterogeneity.

Eppinga et al. (2010) showed that P:ET ratio controls nutrient distribution in patterned peatlands. When P:ET ratio is lower, N

FIGURE 4 Hummock–hollow resource contrasts (dimensionless, A, C, E) and raw hummock and hollow values (B, D, F, where hummocks are the left lighter shade bar within sites and hollows are the right darker shade bar within sites, points are the mean plot value) of *Drosera rotundifolia* for tentacle density (A, B), N derived from prey (C, D), tissue % N (E, F). In all panels P:ET ratio decreases from left (Scotland) to right (Finland). Letters among bars indicate significant differences ($p_{adj} < 0.05$), asterisks among bars indicate significant differences between hummock and hollow ($* \equiv p < 0.05$, $** \equiv p < 0.005$, $*** \equiv p < 0.001$, ns not significant), error bars are 95% confidence intervals for microform bars (and standard error for plot points in A). Note that tentacle density (B) was log-transformed prior to analysis but raw data are presented.



accumulates in hummocks; when P:ET ratio is higher, N accumulates in hollows. We predicted that the pattern of shading would be consistent, so the distribution and presence of different microhabitats (defined by N and shade) would be dependent on P:ET ratio (Figure 1). We expected the impacts of microhabitat changes on investment in prey capture and prey N uptake for *D. rotundifolia* to follow the predictions of a cost–benefit model for plant carnivory (Givnish et al., 1984): that investment in prey capture (and so prey nutrient uptake) will be greatest in unshaded, nutrient poor habitats, where the marginal benefit of carnivory is predicted to be greatest. Thus, we expected more investment in prey capture and prey N uptake in the low-N, high-light hollows compared with high-N, low-light hummocks.

Our results confirm these predictions. At the site where P:ET ratio was highest (Scotland), *Sphagnum* N content and light reaching the peatland surface were higher in hollows than hummocks, which is consistent with nutrient accumulation in hollows (Eppinga et al., 2010). At this site, investment in prey capture (tentacle density) and the proportion of N derived from prey did not differ between hummocks and hollows. At the site with lowest P:ET ratio (Finland), *Sphagnum* N content was evenly distributed between hummocks and hollows, consistent with equal nutrient accumulation between microforms (as predicted by Eppinga et al., 2010). At this site, allocation to carnivory and N from prey varied between microforms, being higher in hollows than hummocks. We interpret this as being due to the impact of differences

in shading between hummocks and hollows at this site. The Sweden site was intermediate in P:ET ratio and phenotypic variability. These results demonstrate that the impacts of climate variability on nutrient distribution in patterned peatlands (Eppinga et al., 2010) alter the phenotypic expression of *D. rotundifolia* in addition to within-site variability in the distribution of vascular vegetation and subsequent shade. The changes in within-habitat investment in carnivory and N acquired from prey are, therefore, likely a result of the counteracting impacts of different resource limitations—increased light increasing the marginal gain from allocation to carnivory through tentacle production, and increased root N availability reducing the marginal gain from additional investment in carnivory.

Local climate regimes (P:ET contrast), nutrient flows, and vegetation coverage are predicted to be consistent on patterned peatlands across their range (Eppinga et al., 2008; Korrensalo et al., 2018; Pastor et al., 2002; Rydin & Jeglum, 2015), so it is likely that the impacts of these controls on within-site phenotypic variability in *D. rotundifolia* can be similarly generalised. In this study, we demonstrate that the influence of nutrient accumulation patterns within peatlands on phenotypic variability in plants is driven by the local climate regime. This is the first such demonstration that the P:ET-driven mechanism of nutrient accumulation in patterned peatlands impacts the biota. Thus, we demonstrate the potential for climate variability to indirectly impact phenotypic variability, which may

have implications for understanding plant and community responses to climate change.

Much of our current understanding of carnivorous plant nutrition depends on experimental prey addition or exclusion (Abbott & Brewer, 2020; Farnsworth & Ellison, 2007; Holloway & Brewer, 2022). These studies demonstrate for example that additional prey is less valuable when carnivorous plants are growing in more nutrient-replete substrates (Ellison & Gotelli, 2001). However, there is a clear need to determine how carnivorous plant nutrition varies under environmental variability, specifically under natural prey capture conditions. This is because prey availability can vary within and between sites, and also because adding or excluding prey will necessarily result in unrealistic prey capture rates. The approaches for doing so are difficult, requiring either surveys of prey capture (e.g. Cresswell, 1991; Zamora, 1995), or the use of stable isotope approaches (e.g. Ellison & Gotelli, 2001; Givnish & Shiba, 2022; Schulze et al., 1991), and very occasionally both (e.g. Cook et al., 2018). Our study demonstrates that the conclusions drawn from manipulative studies do tend to hold under real-world prey capture conditions. For example, the Scotland site (high P:ET) has a much higher proportion of prey-derived N in tissue compared with the other sites. Though not measured directly in this study, the frequency of midges, a major component of *D. rotundifolia* diet (Cook et al., 2018), was extremely high (pers. obs) at the Scotland site compared with the other three sites. Prey availability may therefore explain why the Scotland site had higher *D. rotundifolia* prey-derived N, and overall tissue %N than the other two sites (Figure 4D).

Comparisons between the three sites in terms of P:ET-driven microform patterns within each site remain valid despite potential differences in prey abundance, and the potential for between-site differences is the reason we used resource contrasts as Eppinga et al. (2010) also did, in addition to absolute values for our comparisons. Prey abundance has no impact on the nutrient accumulation mechanisms and therefore N accumulation was still present within this site. High prey abundance in the Scotland site may, however, explain why tentacle density was lower here than in the Finland and Sweden sites at the site level as carnivory can be invested to a lesser extent while still having a high probability of prey capture. Measuring the abundance and quality of potential prey would be beneficial for understanding the impact of habitat heterogeneity on carnivorous plants. For example, does prey availability also vary systematically at these small scales? Additional studies in situ exploring this dynamic would be of value for understanding the influence of prey availability and capture on plant trait expression under real-world ecological scenarios (Farnsworth & Ellison, 2007).

We used tentacle density as an indicator of investment in carnivory. This is because the tentacles carry the sticky mucilage which is used to capture prey. Though tentacle density and mucilage are identified as carnivorous traits, the specific contribution of these traits to overall prey capture and nutrient uptake has not been well quantified (Alcalá & Domínguez, 2005; Cook et al., 2018; Jennings et al., 2016; Zamora et al., 1998). It is reasonable to expect that more tentacles will result in more mucilage and so a greater prey

capture potential and tentacle density has been used as a proxy in other *Drosera* species for investment in carnivory in response to competition for prey (Crowley et al., 2013; Jennings et al., 2016). Tentacle density was not our only measure of carnivory, we also used N from prey, but this measure supports our results in ways that fit with our assumptions regarding tentacle density.

We did not quantify the influence of differences in hydrological status between microforms. Hummocks are drier than hollows, and this drives patterns of plant distribution. *Drosera rotundifolia* grows across wetter and drier microforms, but we cannot discount the possibility that differences in hydrological status may also influence investment in carnivory. If they do, the cost-benefit model for carnivory (Givnish et al., 1984, 2018) predicts that investment in carnivory would be greater in wetter habitats because of reduced allocation to roots (Brewer et al., 2011). Our data do support this, but we cannot disentangle variation in light from that in hydrology. Hummocks are shaded and drier, hollows are open and wetter. Separating these two factors in a correlative study like ours is not possible, and experimental approaches would be needed. Nonetheless, our study reflects the variability that *D. rotundifolia* experiences in real life, and so is a good test of the small-scale environmental controls over carnivory.

In conclusion, our results show clear and systematic phenotypic variability in carnivorous plant investment in carnivory and nutrition at small (<1 m) scales. These patterns follow those of key peatland processes, which create hummock-hollow topography, and which alter hydrology and nutrient flows within patterned peatlands. Precipitation: evapotranspiration ratio has been shown previously to impact nutrient distribution within peatlands, but we demonstrate for the first time that these changes will also likely impact plant intraspecific trait variation. *Drosera rotundifolia* is an iconic peatland species and is sensitive to environmental variability due to its narrow habitat affinity. We demonstrate that this sensitivity is realised clearly even within sites, extending previous understanding of how carnivorous plants vary among sites (Bruzzese et al., 2010; Cook et al., 2018; Zamora et al., 1998). The ability to adapt nutrient uptake mechanisms seems likely to contribute to *D. rotundifolia* persistence and may potentially be important for resilience to environmental change. This species might be a particularly useful model for understanding phenotypic adaptation with respect to nutrient uptake pathways, because of the relative ease of differentiating between root versus carnivorous nutrient uptake. Future work might concentrate on understanding the limits of this phenotypic variability, the extent of this effect in the lower P:ET peatlands, impacts on other carnivorous and non-carnivorous species, and the contribution of plastic vs. genetic mechanisms to this trait variability.

AUTHOR CONTRIBUTIONS

Christopher R. Hatcher and Jonathan Millett agree to be accountable for the aspects of the work that we conducted. Christopher R. Hatcher and Jonathan Millett conceived the ideas and designed the methodology. Christopher R. Hatcher collected the data. Christopher

R. Hatcher and Jonathan Millett analysed the data and Christopher R. Hatcher led the writing of the manuscript. Christopher R. Hatcher and Jonathan Millett contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Loughborough University Research Repository: <https://doi.org/10.17028/rd.lboro.21717983> (Hatcher & Millett, 2024).

STATEMENT ON INCLUSION

Our study involved fieldwork in three countries across Europe. We engaged with, and recognise the assistance of, academics and stakeholders in the completion of this research (see acknowledgements). The local engagement for this research was not sufficient for authorship but the nature and scope of the work carried out sits within the research priorities of those involved and have an agreement in place to present our findings upon publication. Had this project not been a substantial part of CH's PhD, engagement in data collection, analysis, or write-up would have involved these persons more and they would have been invited to be part of publication. For further work or future projects, we will strive to do better in providing opportunities for local collaborators to be authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary for hierarchical ANOVA analysis of environmental variables in hummocks and hollows across three sites (Sw = Sweden, F = Finland, Sc = Scotland).

Table S2. Summary for hierarchical ANOVA analysis of *Drosera rotundifolia* morphological measurements and nutrient status in hummocks and hollows across three sites (Sw = Sweden, F = Finland, Sc = Inverewe, Scotland).

Table S3. Hummock-hollow resource contrasts (dimensionless).

Table S4. Hummock-hollow trait contrasts (dimensionless).

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