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ORIGINAL PAPER

Mixed effects of the invasive moss *Campylopus introflexus* on spider and beetle communities in disturbed peatlands in southern Sweden

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Abstract Little is known about the effects of invasive bryophytes on native biodiversity. To date, the main documented effect is competition, mostly with other bryophytes. *Campylopus introflexus* is an invasive moss in Europe and North America that can form dense monocultural carpets that displace native vegetation and influence the composition of native arthropod communities. It was first recorded in Sweden in 1976, where it commonly invades disturbed peatlands and its invasion potential is currently assessed as 'severe'. Despite this long invasion history, little is understood about its local impacts, including on ground-dwelling arthropods. We analysed the effect of *C. introflexus* invasion on ground-dwelling beetle and spider communities at 14 sites in south-west Sweden. We collected arthropods along paired transects (50–200 m apart) in disturbed peatlands that were invaded or uninvaded by *C. introflexus*. Pitfall traps were emptied during the months of July, August, and September. We characterized the ground layer vegetation using quadrats (50 × 50 cm) centred over pitfall traps. We collected 2237 beetles belonging to 109 species from 18 families and 2139 spiders belonging to 85 species from 18 families. We found that *C. introflexus* invasion was associated with increased beetle abundance, richness, and diversity, but had no effect on spider abundance, richness, and diversity. We found no effect of *C. introflexus* invasion on beetle or spider community composition. Our results suggest that *C. introflexus* invasion into disturbed peatlands affects beetle communities, demonstrating that bryophyte invasions can have ecological consequences and highlighting the need for further research on this often overlooked group.

Keywords Invasive moss · Bryophyte · Peatlands · Disturbance · *Campylopus introflexus* · Arthropod communities

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Introduction

Biological invasions can threaten biodiversity directly through disease, predation and competition, and indirectly through trophic effects and by modifying ecosystem functioning (Mack et al 2000; Crooks 2002;

Katsanevakis et al 2014). Although the effects of invasive introduced vascular plants are well known (Pyšek et al. 2012; Kumar Rai and Singh 2020), there is limited evidence to date of the impacts of invasive bryophytes (mosses, hornworts and liverworts), despite their occurrence in terrestrial and freshwater ecosystems worldwide, from polar to tropical regions (Essl et al 2014). Bryophytes form a major component of plant biomass on Earth and play significant functional roles in ecosystem processes (Lindo and Gonzalez 2010; Turetsky et al 2012). We might therefore expect that bryophyte invasions could have negative effects on native vegetation and other species.

At least 139 bryophyte species have been introduced globally, of which seven have so far been documented to cause negative effects on biodiversity (Essl et al 2014). Quantitative studies are rare; the main documented impact from bryophyte invasions on native biodiversity occurs through competition, mostly with other bryophytes and lichens, resulting in altered species composition (Essl et al 2014). Disturbance can facilitate biological invasions, and most habitats invaded by bryophytes are previously modified environments such as roadsides and ruderal vegetation (Essl et al 2014; Orbán et al 2021). Records of bryophyte introductions per region have risen strongly in recent decades (Essl et al 2013), indicating that the impacts of bryophyte invasions may continue to increase, and more studies are needed to further understand the effects of bryophyte invasions on biodiversity.

Campylopus introflexus is a perennial, medium-sized moss forming carpets 0.5–10 cm high. Native to the southern hemisphere, it has become invasive in central and western Europe and western North America (Żarnowiec et al 2019) and is the only bryophyte among the 54 invasive plant species listed as "of greatest concern in Europe" (Nentwig et al 2018). In Europe, it occurs in coastal and inland acidic sand-dunes, drift sands, peatlands, *Sphagnum* bogs and heathland (Ketner-Oostra and Sýkora 2008; Klinck 2009; Richards and Smith 1975). It commonly invades disturbed habitats, such as peat extraction sites, ruderal vegetation and roadsides (Richards 1963; Richards and Smith 1975; Piessens et al 2008; Priede and Mežaka 2016). In sand-dunes, *C. introflexus* carpets were found to replace native bryophyte cover, alter soil pH, reduce feeding activity of soil-inhabiting organisms and alter communities of habitat-specialist arthropods (Hasse 2007; Isermann 2005; Pehle and Schirmel 2015; Vogels et al 2005; Schirmel et al 2011; Schirmel 2011; Schirmel and Buchholz 2013). In Sweden, *C. introflexus* was first discovered in the south-west in 1976 (Johansson 1977; Hallingbäck et al 1985), and it is now distributed from the southernmost tip of Sweden to north of Stockholm (Artportalen 2024). Despite this 45-year invasion history, its ecological impacts in Swedish habitats remain poorly understood. The national Swedish assessment of invasive species classifies the invasion potential of *C. introflexus* as 'severe', the highest of four risk classes (Strand et al 2018), yet quantitative data supporting this assessment are lacking. Initial surveys in south-west Sweden suggest the species commonly establishes along the edges of disturbed peatlands, forming bands a few metres wide (unpubl. data).

Peatlands are wetlands where organic matter accumulates faster than it decomposes due to saturated, anaerobic soil, with high water tables, low pH and low nutrient concentrations. Mosses constitute a large portion of the boreal peatland biomass (Rydin et al 2013), providing habitat, food, and oviposition sites for ground-dwelling beetles and spiders, and host prey species such as nematodes, tardigrades, collembolans and chilopods (Glime 2017). Peatlands host many specialized arthropods, fungi and plants (Desrochers and Duinen 2006; Spitzer and Danks 2006; Kędzior et al 2022). Some specialist arthropods feed only on plants that are associated with peatlands, and peatland specialist spiders can serve as an indicator species for peatland condition (Neet 1996). Peat extraction sites, where *C. introflexus* is commonly recorded (Żarnowiec et al 2019; Priede and Mežaka 2016; Jukonienė et al. 2015), are peatlands from which peat was partially removed for commercial purposes. Peat extraction alters hydrology, substrate, and vegetation cover and composition, creating bare surfaces for colonization by invasive plants (Räsänen et al 2023), yet the impact of *C. introflexus* invasion on arthropod communities in disturbed peatlands remains unknown.

In this study we aimed to explore the effects of *C. introflexus* invasion on peatland arthropods. We tested whether variation in *C. introflexus* ground cover is related to arthropod abundance, diversity and richness, and whether invaded areas host a different community composition compared to uninvaded areas.

Because *C. introflexus* increases moss cover compared to the mostly bare surfaces left by peat extraction, we hypothesised that invaded sites will have: (1) higher beetle and spider species richness, diversity, and abundance, and (2) altered beetle and spider community composition relative to uninvaded sites.

Methods

Study area

We conducted this study in the provinces of Småland and Skåne in south-west Sweden in the hemiboreal vegetation zone (Fig. 1). The study area ranges from 80 to 150 m above sea level and consists of a mosaic of land-use types, including mixed coniferous–broadleaf forests used for timber production, agricultural cropland, peatlands (including those from which peat has been extracted), and urban areas. Mean annual temperature ranges from 6.5 to 7.5 °C, with a mean temperature during the study period (July to September) of 15.4 °C (Osby Weather Station [Fig. 1]; SMHI 2021a, 2021b). Mean annual precipitation ranges between 700–900 mm and a total of 204 mm rain fell during the study period (Osby Weather Station [Fig. 1]; SMHI 2021c, 2021d).

Sampling design

To assess the effects of *C. introflexus* invasion on arthropod communities, we collected pitfall trap samples from along transects in invaded and uninvaded areas of disturbed peatlands. After an initial survey of disturbed peatlands across south-west Sweden, we selected 14 sites that had high *C. introflexus* cover, but also areas that were free of invasion. The 14 sites were at least 1000 m apart from each other. In each site we placed two 3.8 m long transects, 50–200 m apart, such that one transect had average *C. introflexus* cover > 25% and one transect had no *C. introflexus* cover (0%) (Fig. 1). *Campylopus introflexus* commonly grows along the perimeter of peatlands; as a result, this was often where our transects were located (both invaded and uninvaded). Using a paired plot design allowed us to select transects that were similar in terms of soil type, tree cover, slope, aspect, and overall vascular plant species composition, but differed in whether they were invaded by *C. introflexus*. Transects with comparable bryophyte cover could not be selected, as uninvaded transects generally exhibited low cover. Whilst the distances between paired transects were insufficient to prevent arthropod dispersal between them, this design captured differences in arthropod activity (i.e. usage) of *C. introflexus* invaded and uninvaded transects.

Along each transect, we placed four 50 × 50 cm quadrats alternatively 50 cm either side of the transect and spaced 1.6 m apart (Fig. 1). Pitfall traps were placed in the centre of each of the four quadrats along a transect (Fig. 1) to sample beetle and spider assemblages. Pitfall traps capture arthropods by intercepting individuals moving across the ground surface. This method somewhat limits our assessment to the effect of *C. introflexus* on ground-dwelling and active arthropods, while less mobile taxa such as web-building spiders may be under-sampled. Along each transect, we placed four pitfall traps, one in the centre of each quadrat (Fig. 1). Each pitfall trap was 6 cm in diameter, 9 cm deep and filled with a 50:50 water to monopropylene glycol solution and a few drops of detergent. To protect from rain and reduce evaporation, we covered each pitfall trap with a square piece of grey foam (approx. 7 × 7 cm), elevated 10 cm above the trap on wooden stakes.

Data collection

Between the 3rd of August and 7th of September 2021, we recorded the vascular plant, bryophyte, and lichen species in each quadrat. We also estimated the percent area covered to the nearest 5% in each quadrat for leaf litter, bare ground, rocks, *C. introflexus*, all bryophytes and lichens jointly (including *C. introflexus*), and all vascular plants combined (Table 1). Some plant and lichen species were identified in the laboratory using standard identification literature.

We set up pitfall traps between the 12th and 15th of July, and emptied them on three occasions, resulting in three sampling periods: 3–6 August (20–26 sampling days), 2–7 September (28–36 sampling days) and 14–17 September (8–16 sampling days). Traps were drained of liquid and emptied into labelled tubes filled with 70% ethanol. In the laboratory, we sorted and identified beetles and spiders to the genus level. Species level identification was conducted by specialists; however, some taxa could only be identified to the genus level. For ease of terminology, we hereafter

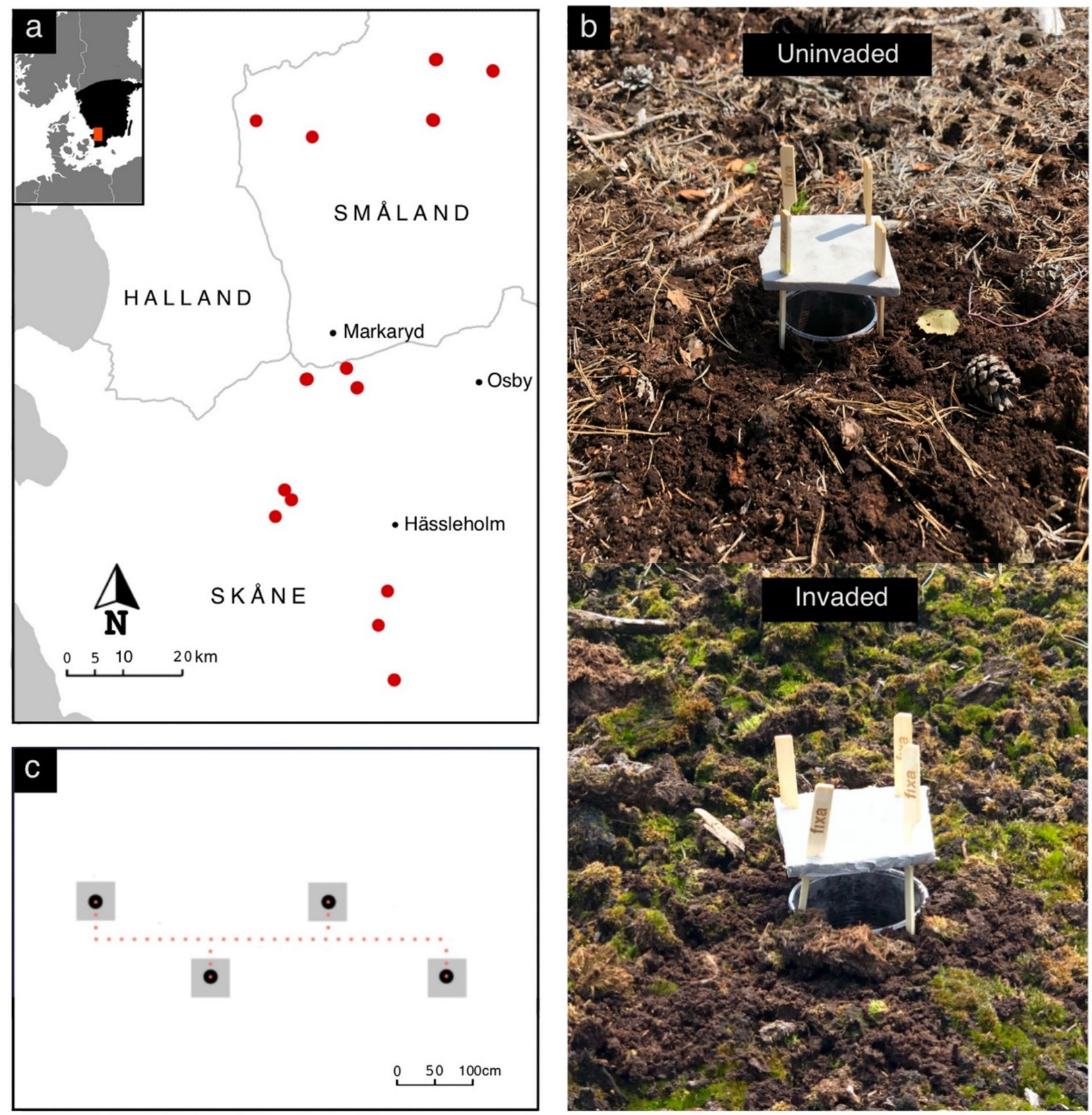


Fig. 1 Study overview: **a** The 14 study sites of disturbed peatlands in two provinces in south-west Sweden (red circles) (see Supplementary Material, Table S1) and the distribution of *Campylopus introflexus* in Sweden at the time of the study (shown in black in insert panel). **b** Pitfall traps installed in typical examples of disturbed peatland that were (top) uninvaded and (bottom) invaded with *C. introflexus*. **c** Overview of the transect survey design (length was 3.8 m). Grey squares represent the quadrats (50×50 cm) from which covariate data were surveyed, and black circles represent the location of the four pitfall traps

refer to all identified taxa as "species" throughout the text. Spiders were recorded as either adults, juveniles or spiderlings, and adults were further identified as male or female when possible. Spiderlings were excluded from the abundance assessments and subsequent analyses. Spider taxonomy followed the World Spider Catalog (World Spider Catalog 2023). The carrion-feeding beetle families Leiodidae and

Table 1 Range, mean, standard deviation (SD) and 95% confidence interval (CI) of the covariates recorded from paired transects invaded or uninvaded by *Campylopus introflexus* ($n = 14$ each). For each transect, the mean value for each covariate was calculated as the mean from four quadrats

Covariates	Invaded				Uninvaded			
	Range	Mean	SD	CI	Range	Mean	SD	CI
C. introflexus cover (%)	26–92	45	17.2	39–51	0–0	0.0	0.0	0–0
Bryophyte and lichen cover (%)	31–93	48.3	16.8	43–54	0–25	5.5	7.4	2–8
Vascular plant cover (%)	0–60	19.2	16.2	13–25	2–52	26.2	15.2	18–31
Leaf litter cover (%)	5–60	19.6	14.2	16–29	4–46	19.1	13.1	15–24
Bare soil cover (%)	3–44	15.8	11.3	12–20	12–82	47.6	24.6	38–57
Rock cover (%)	0	0	0	0	0–65	1.6	8.8	0–4

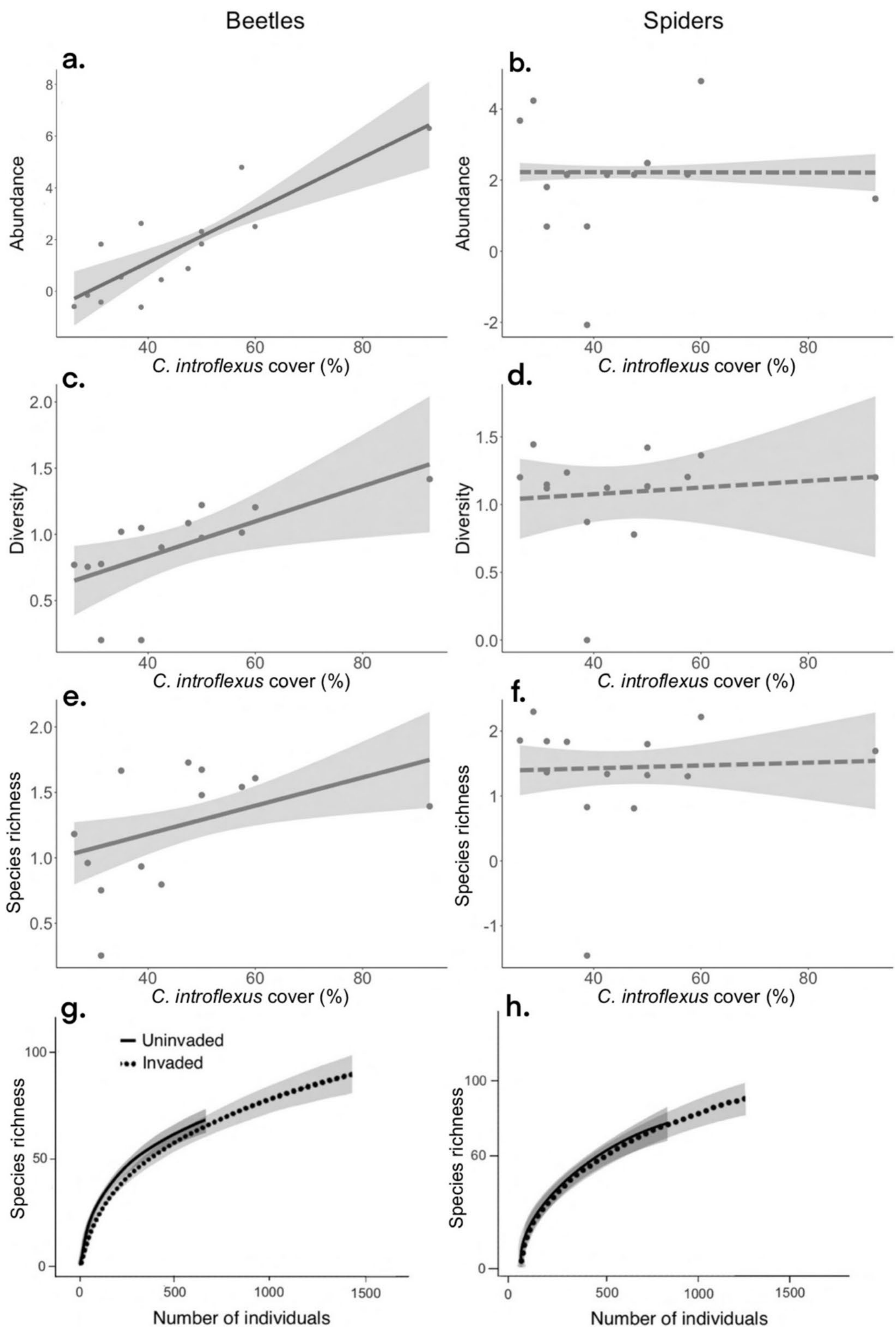
Silphidae were excluded from any analysis because they did not randomly fall in traps but were instead attracted to traps that contained decaying vertebrates (e.g. shrews, frogs and lizards). Selected arthropod and plant voucher specimens were deposited at the Swedish Museum of Natural History. Beetle and spider records have been entered into ArtPortalen, the Swedish website for species occurrence records (www.artportalen.se).

Data analyses

To test whether *C. introflexus* invasion was related to the abundance, species richness, and diversity (Shannon diversity index; Shannon 1948) of beetles and spiders, we fitted linear models (LMs) and generalized linear models (GLMs) using the mean percent cover of *C. introflexus* per transect as a continuous predictor. We ran the models with the invaded transects only, and beetles and spiders were analysed separately. For abundance, richness and diversity, we calculated mean values of the four pitfall traps per transect for each sampling period, and then the means across all three sampling periods. We calculated mean values to overcome uneven samples between invaded and uninvaded transects, as some pitfall traps were destroyed by wild animals, and these samples were excluded from the mean. We modelled abundance and richness using a Poisson distribution and rounded mean abundance and richness values to meet the assumptions of Poisson modelling. Diversity was modelled using a Gaussian distribution. We checked for overdispersion and used a quasi-Poisson distribution in the case of overdispersion. We calculated mean values across the four quadrats per transect of the covariates used in the models (leaf litter cover, bare soil cover, vascular plant cover and rock cover; Table 1). To avoid collinearity, we assessed correlations between the covariates (Supplementary Material, Table S4). Combined bryophyte and lichen cover was excluded from the models as it was highly correlated with *Campylopus introflexu*s cover (Supplementary Material, Table S4). None of the remaining covariates used in the models were highly correlated ($r > 0.7$) (Supplementary Material, Table S4). We used stepwise removal of non-significant covariates ($p > 0.1$) to simplify models and avoid overfitting, while retaining those with potential ecological relevance despite not reaching the conventional significance threshold of 0.05. Model assumptions were checked using residual plots and tests for overdispersion. To obtain *p*-values we used the Anova function with Type II sum of squares from the "car" R package (Fox and Weisberg 2019). All statistical analyses were done with R (R version 4.5.1).

We also compared beetle and spider abundance, richness, and diversity between invaded and uninvaded transects by using separate models with *C. introflexus* presence (present or absent) as a categorical predictor. Beetles and spiders were modelled separately, with site included as a random effect in linear mixed models (LMMs) and generalized linear mixed models (GLMMs), to account for non-independence of paired transects within the same site. We included the covariates as described above, with stepwise removal, keeping only explanatory variables with *p*-values lower than 0.1.

We assessed the effect of *C. introflexus* invasion on the community composition of beetles and spiders using a permutational multivariate analysis of



Beetles
Spiders
a.
b.
c.
d.
e.
f.
g.
h.
Abundance
Diversity
Species richness
C. introflexus cover (%)
Number of individuals
Uninvaded
Invaded

◂**Fig. 2** Regression plots showing the relationship between *Campylopus introflexus* (% cover) and beetle abundance (**a**), diversity (**c**) and richness (**e**) and spider abundance (**b**), diversity (**d**) and richness (**f**) in invaded transects at 14 sites in south-west Sweden. Lines represent fitted values from generalized linear models and shaded areas show the 95% confidence intervals. Solid lines denote statistically significant models, whereas dashed lines denote non-significant models. The y-axis shows the mean value of a pitfall trap taken as the average from four pitfall traps per transect and then averaged across three sampling periods. The species accumulation curves show the 95% confidence intervals of estimated beetle (**g**) and spider (**h**) richness sampled along transects invaded or uninvaded by *C. introflexus*

variance (PERMANOVA; using the 'adonis' function in the "vegan" package and including site as a random factor via the function 'strata'). We used Bray–Curtis distances on separate species-by-site matrices for beetles and spiders, respectively. Each cell value was the mean abundance for a given species, calculated as the mean per transect from the four pitfall traps and then averaged across the three sampling periods. We also ran the analysis after removing species with low abundances (mean abundance <0.1), to minimise the noise from rare taxa that can inflate dissimilarity measures. We performed non-metric multidimensional scaling (NMDS) to visually display the spatial ordination of beetle and spider communities sampled from invaded and uninvaded transects. To ensure that our results reflected the effects of *C. introflexus* cover, rather than of other species associated with invaded sites, we tested whether vascular plant composition differed between invaded and uninvaded sites. This was done using a PERMANOVA, NMDS, and indicator species analysis implemented in the 'indicspecies' R package (De Cáceres and Legendre 2009). Indicator species analysis identifies plant species that are significantly associated with either invaded or uninvaded sites, helping to determine whether particular species co-occur with *C. introflexus* and could influence arthropod communities.

Finally, to test the effect of *C. introflexus* invasion on total gamma diversity, we compared the beetle and spider species accumulation curves over pooled individual abundance across all transects and sites between invaded and uninvaded transects. We visually checked the 95% confidence intervals for any overlap as a test for significant differences in the accumulation curves.

Results

From 106 traps at 14 sites and three sampling periods, we collected and identified a total of 2237 individual beetles, belonging to 109 species from 18 families (excluding the carrion feeding beetle families Leiodidae and Silphidae). An additional 27 taxa could only be identified to the genus level. We collected a total of 2139 individual spiders (excluding spiderlings) and identified 85 species from 18 different families (Supplementary Material, Tables S5, S6). A total of 77% of the spiders belonged to the wolf spider family (Lycosidae). Finally, 28 taxa could only be identified to the genus level. Unidentified species within the same genus were grouped and treated as a single species (e.g., *Zelotes* sp.).

We found that beetle abundance, richness and diversity all increased in transects with higher *C. introflexus* cover (Fig. 2a, c, e, abundance: $p=0.001$, richness: $p=0.027$, diversity: $p=0.012$, Supplementary Material, Table S2), whereas *C. introflexus* cover was unrelated to spider abundance, richness and diversity (Fig. 2b, d, f, abundance: $p=0.968$, richness: $p=0.776$, diversity: $p=0.692$). Beetle abundance was also positively related to leaf litter cover, bare soil cover, and vascular plant cover (leaf litter cover: $p<0.001$, bare soil cover: $p<0.001$, vascular plant cover: $p<0.001$, Supplementary Material, Table S2). Beetle richness and diversity were positively correlated with leaf litter cover (richness: $p=0.003$, diversity: $p=0.001$, Supplementary Material, Table S2). No covariates were retained in the spider models (Fig. 2a–f, Supplementary Material, Table S2). We found no difference in mean abundance, species richness, and diversity of beetles and spiders between uninvaded transects and those invaded by *C. introflexus* (presence-absence analysis; Supplementary Material, Table S3, Fig. S2). No covariates were retained after stepwise removal of non significant variables ($p<0.1$) in both the beetle and spider models.

Species composition of beetles and spiders did not differ between invaded and uninvaded transects (Beetles: PERMANOVA, $R^2=0.02$, $p=0.9$; Spiders: PERMANOVA, $R^2=0.03$, $p=0.34$) (Fig. 3), nor did it differ after removing low-abundance species (Supplementary Material, Table S2). Plant community composition differed between invaded and uninvaded transects (PERMANOVA, $R^2=0.06$, $p=0.003$).

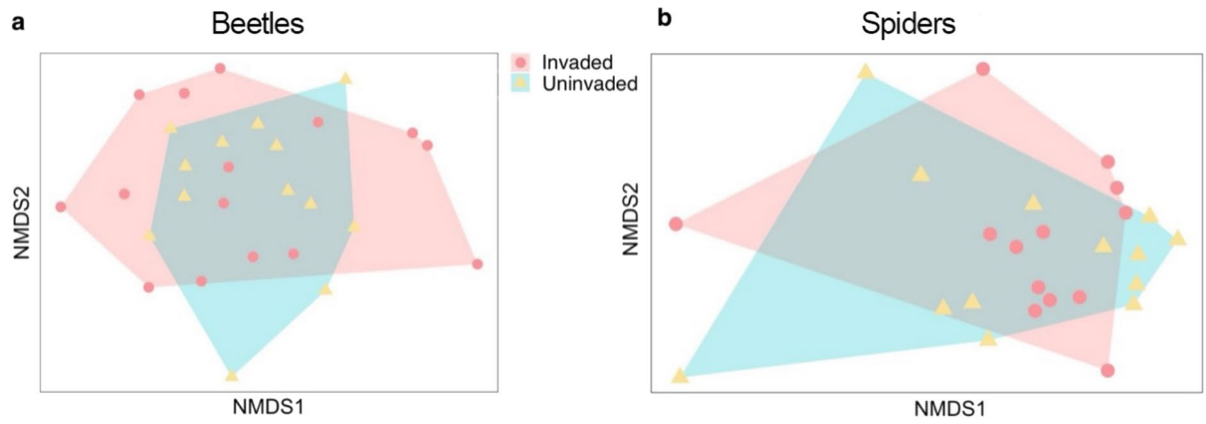


Fig. 3 Beetle (**a**) and spider (**b**) species composition sampled along transects invaded or uninvaded by *Campylopus introflexus* at 14 sites in south-west Sweden, using 2-dimensional NMDS ordination of occurrences to visualize results. Stress: beetles = 0.235, spiders = 0.132. Circles represent invaded transects and triangles represent uninvaded transects

Indicator species analysis identified a single sedge species, *Eriophorum vaginatum*, as being significantly more abundant and frequent along uninvaded transects (IndVal = 0.7, $p = 0.035$; Supplementary Material, Fig. S1).

Finally, there was consistent overlap in the 95% confidence intervals for species richness accumulation curves of both beetles and spiders along invaded and uninvaded transects. This suggests similar levels of gamma diversity across all pooled individuals regardless of invasion by *C. introflexus* (Fig. 2g, h).

Discussion

Our results suggest that *C. introflexus* invasion is positively associated with beetle abundance, diversity, and richness in disturbed peatlands in south-west Sweden. In contrast, spider abundance, diversity, and richness, as well as the overall community composition of both beetles and spiders, were not significantly affected by *C. introflexus* invasion. Based on these findings, *C. introflexus* invasion is unlikely to pose a significant threat to the ground-dwelling beetle and spider fauna in these habitats.

In line with our first hypothesis, beetle species richness, diversity and abundance were affected by *C. introflexus* invasion in these disturbed habitats. Beyond the sedge *Eriophorum vaginatum* being strongly associated with sites invaded by *C. introflexus*, the main difference between the transects was the total cover of bryophytes and lichens; 48% along invaded transects compared to 5% along uninvaded transects. Because most of this cover consisted of *C. introflexus*, the significant effects observed in beetle richness can likely be attributed to *C. introflexus* invasion. The higher beetle abundance, richness and diversity, especially at early stages of peatland succession, may be explained by the availability of moss habitat, which provides food for the bryophagous (moss-feeding) beetles, oviposition sites, and abundant prey species for predatory beetles, such as nematodes, tardigrades, springtails, collembolans and chilopods (Glime 2017). Through invasion of disturbed peatlands, *C. introflexus* appears to create moss habitat for beetles where little would otherwise be available.

Many studies have shown that vascular plant invasions can reduce arthropod richness and abundance (Litt et al. 2014; Spafford et al. 2013) and declines in native plant diversity (Hejda et al. 2009; Vilà et al. 2011). Such reductions in native plant diversity may, in turn, limit food resources for herbivorous arthropods, particularly for species unable to utilize the invader as a food source (Strong et al. 1984). However, invasions can also have positive effects on certain arthropod groups. For example, detritivores often benefit from plant invasions, potentially due to increased productivity, greater litter input, and more favourable microclimatic conditions (Siemann et al. 2006; Bartomeus et al. 2008; Longcore 2003; Litt et al. 2014). By increasing ground cover, *C. introflexus* may similarly enhance the local availability of food for herbivorous beetles, at least for species capable of feeding directly on the moss. In our transects, however, *C. introlexus* cover was not positively correlated with increased leaf litter (Supplementary Material, Table S4). Dense moss cover may help buffer extreme surface temperatures, which in peatlands can fluctuate by up to 30 °C in a single day (Gerson 1969), providing thermal refuge for beetles. Furthermore, *C. introflexus* often naturally breaks into smaller, overturned patches, creating a structurally complex surface that may offer shelter from predators or habitat for prey. Despite these potential mechanisms, our second hypothesis was not supported: beetle community composition was unaffected by *C. introflexus* invasion. This suggested that it is not just a subset of beetle species active in *C. introflexus* mats, but rather the entire community.

Campylopus introflexus invasion did not affect spider species richness, diversity, abundance, or community composition, thereby rejecting our first and second hypotheses. Previous studies in sand-dune habitats detected effects on arthropods only where moss cover exceeded 80% (Vogels et al. 2005; Schirmel et al. 2011), substantially higher than the mean cover of 45% recorded in our invaded sites, which may explain the absence of comparable effects. Because pitfall traps are biased toward more active species (Lövei and Sunderland 1996; Lang 2000), our results primarily reflect responses of active taxa and may not adequately capture those of more sedentary species, such as web-building and ambush spiders. Future studies should therefore assess how these groups respond to *C. introflexus* invasion.

Spiders are primarily specialist predators of insects and other small arthropods, and plant invasions can alter prey availability, with cascading effects on spider communities (Gratton and Denno 2005; Litt et al. 2014). Although beetle abundance was higher in *C. introflexus*-invaded transects, an important prey source for spiders, this did not translate into a corresponding increase in spider abundance. Any increase in abundance associated with invaded sites may have been countered by reduced capture rates, as species likely moved more slowly through the dense moss cushions of *C. introflexus*-invaded transects compared to the smoother bare ground of uninvaded transects.

Conclusion

Campylopus introflexus is an early colonizer of disturbed peatlands (Jukonienė et al 2015, Priede and Mežaka 2016), and can increase bryophyte ground cover, an important habitat for arthropods (Glime 2017). In our study, spider communities were unaffected by invasion, whereas beetles showed higher abundance, richness and diversity in invaded transects. *Campylopus introflexus* does not appear to threaten peatland vegetation, nor vegetation recovery in peatlands and typically declines as systems regenerate (Priede and Mežaka 2016). Likewise, rewetting reduces *C. introflexus* cover, and has been associated with recovery of invertebrate communities in boreal and restored peatlands (Noreika et al., 2015; Watts and Mason 2015; Watts et al. 2008; Samson et al. 2024).

Overall, *C. introflexus* invasion in disturbed peatlands in south-west Sweden appears to pose little risk to ground-dwelling beetle and spider assemblages. However, impacts on less well-sampled taxa remain uncertain, including web-building and ambush spiders, moss-dwelling microfauna (e.g. nematodes, tardigrades, springtails, collembolans and chilopods), and species potentially affected by moss encroachment in other systems, such as digger wasps in sand-dune habitats. Further work should therefore extend to sandy substrates and coastal heathlands, which are considered especially vulnerable to plant invasions (SLU Artdatabanken 2025).

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Author contributions Conceptualization: I.B., K.H., and J.W.; Formal Analysis: J.W., K.H., and I.B.; Funding acquisition: K.H., and I.B.; Supervision: I.B., and K.H.; Writing—original draft: J.W.; Writing—review and editing: I.B., and K.H.

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Data availability All data is available as supplementary material.

Declarations

Conflict of interest The authors have no relevant financial or non-financial competing interests to disclose.

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