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Campylopus introflexus invasion in Icelandic high-temperature geothermal areas: widespread occurrence, weak geographic genetic structure, and lower native plant species richness.

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Abstract

The southern hemisphere moss *Campylopus introflexus* has spread widely across Europe, but only a little is known about its invasion in Icelandic geothermal habitats or its relationship with native vegetation. We surveyed the occurrence of *C. introflexus* in 16 high-temperature geothermal areas in Iceland, analysed its genetic variation using genotyping-by-sequencing, and studied plant communities in four geothermal areas. We detected the species in 12 of the 16 surveyed areas and at 1,241 of 2,896 survey points. Detection probability increased with soil temperature across the lower and middle part of the measured range, although the model was only moderately successful in predicting occurrence in areas excluded from model fitting. Genetic analyses showed no clear regional structure or isolation by distance, but strongly contrasting genotypes were found at two sites. Native plant richness was lower where *C. introflexus* was more frequent, after accounting for site and soil temperature. Richness was estimated to decrease by approximately 12% per 25 additional subquadrats occupied by *C. introflexus*. Evidence for this association was clearer for other bryophytes than for vascular plants, although their estimated responses were similar. Our results show that *C. introflexus* is widespread across the surveyed geothermal areas and is associated with lower native plant richness. Repeated surveys and genetic comparisons with populations outside Iceland are needed to better understand its spread and longer-term ecological effects.

Keywords

Campylopus introflexus; invasive alien bryophytes; geothermal habitats; genotyping-by-sequencing; plant invasion; species richness

Introduction

Invasive alien species are among the five major direct drivers of biodiversity loss worldwide (IPBES 2019, 2023), and therefore their establishment in habitats supporting distinctive communities and intraspecific genetic variation is a major conservation concern. Icelandic high-temperature geothermal areas form a scattered net of habitats characterised by steep local gradients in temperature, moisture, and soil chemistry. All geothermal habitat types recognised in Iceland's national habitat classification have been assessed as having high or very high conservation value (Ottósson et al. 2016) and previous research has identified distinct geothermal vegetation and plant species of conservation concern and has shown that species richness declines in the hottest and most acidic soils (Elmarsdóttir et al. 2003, 2015). Apart from being ecologically unique, on the community level these habitats also harbour unique genetic variation in some plant species: *Agrostis stolonifera* includes a lineage found only in geothermal areas, and *Cerastium fontanum* shows genetically based differences in flowering phenology along a soil temperature gradient (Nuppenau et al. 2023; Valdés et al. 2019). Thus, the establishment of a turf-forming non-native moss in these habitats raises questions about its impact on native vegetation.

Biological invasions involve several stages, including the arrival, establishment, and spread of species outside their native range (Richardson et al. 2000; Blackburn et al. 2011). Research carried out hitherto has shown that propagule supply has a direct effect on establishment opportunities, whereas local conditions and interactions with resident organisms determine which populations are able to persist and expand (Lockwood et al. 2005; Catford et al. 2009). Although most invasion research and conceptual frameworks have focused on vascular plants, it remains unclear how well these frameworks apply to bryophytes (Essl et al. 2014). Bryophytes differ considerably from vascular plants in their size, growth form, physiology, and ways of reproduction and dispersal. These differences may influence invasion processes, including the spatial scale at which invading species interact with resident vegetation. For example, in Dutch inland dunes, *C. introflexus* was more abundant than lichens at sites with higher atmospheric ammonia concentrations, and experimental growth increased with soil organic matter content (Sparrius and Kooijman 2011). It can be hypothesised that bryophyte invasions may not simply represent smaller-scale versions of vascular plant invasions, although the extent to which their underlying mechanisms differ remains poorly understood. Even for *C. introflexus*, one of the better-studied non-native mosses, quantitative studies of invasion impacts cover a limited range of habitats and regions (Essl et al. 2014). Investigating distribution patterns, population genetics, and vegetation data can help explain different parts of an invasion process, particularly where the invaded habitats are highly disjunct.

C. introflexus was first recorded outside its native range in Britain in 1941, and subsequently it has spread across much of Europe (Richards 1963; Hassel and Söderström 2005). The species has a wide ecological tolerance and occurs in both natural and human-transformed habitats, growing mostly in acidic substrates in dunes, heathlands, forests, dried-out peatlands, and even mine waste heaps (Hassel and Söderström 2005; Mikulášková et al.

2012a; Żarnowiec and Chmura 2019). Previous studies have also examined its habitat preferences and relationships with native vegetation, particularly in European dunes (e.g., Hasse 2007; Sparrius and Kooijman 2011). The species has been found on geothermal soils within its native (Given 1980; Convey and Lewis Smith 2006; Ochyra et al. 2008) and non-native ranges (Chiarucci et al. 2008; Llaneza García et al. 2016), but its invasion dynamics and impacts on native vegetation across these disjunct geothermal habitat systems have received little attention.

In Iceland, *C. introflexus* was first collected at a geothermal site near Mývatn in 1983 (Bergþór Jóhannsson 1991). Before the present surveys began in 2023, fewer than ten records of the species were available in the plant distribution database of the Natural Science Institute of Iceland. These records came from local botanical surveys, and the wider distribution of the species in Iceland remained very poorly known. The geographical separation of Icelandic geothermal areas, resulting in a network of highly disjunct "environmental islands", raises questions about whether invaded areas contain highly differentiated populations or whether their genetic variation is not highly structured. On the one hand, *C. introflexus* can spread over long distances through wind-dispersed spores, while deciduous shoot tips and turf fragments mainly contribute to local spread. On the other hand, geographic isolation may still limit dispersal between geothermal areas and allow populations to diverge. Hitherto, molecular studies have examined the relationship of *C. introflexus* with related species using nuclear and plastid sequences (Gama et al. 2017) and focused on genotyping methods like AFLP (Mikulášková et al. 2012a, b). However, compared with AFLP markers, genotyping-by-sequencing (GBS) can provide substantially more sequence-based SNP markers, allowing more detailed assessment of genetic structure.

The ecological significance of the formation of dense *C. introflexus* turfs in geothermal areas of Iceland is a separate question. Native plants may be less frequent where *C. introflexus* dominates, but this could reflect either suppression by the moss or differences in soil conditions that could favour *C. introflexus* over other species. Here, we combine point detections and apparent nondetections from high-temperature geothermal areas surveyed across Iceland, genotyping-by-sequencing, and vegetation surveys in four geothermal areas. We investigated (1) how widespread *C. introflexus* is across the geothermal areas in Iceland and how detection relates to soil temperature and substrate; (2) whether genetic variation is geographically structured; and (3) how native bryophyte and vascular-plant richness and composition vary with moss frequency after accounting for site and soil temperature, with pH examined where measurements are available.

Materials and methods

Study areas

During 2023–2024, we surveyed 16 of the 20 high-temperature geothermal areas in Iceland (Fig. 1, Table S1). The remaining four highland areas were not surveyed because of access and logistical constraints.

Occurrence surveys and environmental modelling

Where we found the species, we selected a measurement point at random within the occupied patch. In case of non-detection records, we selected a point at random within a visually inspected area where *C. introflexus* was apparently absent. Geographical coordinates of detection and non-detection points were recorded with a Garmin GPSMAP 67i in WGS 84 (EPSG:4326). The survey comprised 2,896 detection and non-detection points in total.

Soil temperature measured at 10 cm depth was used to characterise local geothermal intensity at each survey point. We distinguished three substrate classes based on field observations: (1) lava (comprising geothermally heated lava surfaces with little or no soil development), (2) hot soil (comprising geothermally heated mineral or organic soils), and (3) wetland (comprising water-saturated ground influenced by geothermal activity). Elevation was extracted from the ArcticDEM v3.0 digital elevation model (Porter et al. 2018), while distance to the nearest road was calculated using the IS 50V Transportation dataset. Elevation was included to account for broad environmental variation across surveyed areas. Distance to roads was included as a proxy for human disturbance and propagule pressure from human-related activities.

We analysed detection of *C. introflexus* at surveyed points using records with measured soil temperature. Nine wetland observations, all of which were nondetections, were excluded because their small number and lack of detections prevented reliable estimation of substrate effects. The final dataset comprised then of 1,590 observations from lava and hot-soil substrates across 16 geothermal areas. The response variable was the presence or apparent absence of *C. introflexus* at each sampling point, coded as a binary variable (1 = detected, 0 = not detected). We fitted binomial generalised additive models (GAMs) with a cubic regression spline for soil temperature at 10 cm depth (basis dimension k = 8), elevation per 100 m, log(1 + distance to the nearest road in km), substrate class, and a geothermal-area random intercept. Models were fitted by restricted maximum likelihood. We also fitted a model with a linear temperature term for comparison. Predictive performance in geothermal areas withheld from fitting was assessed by leave-one-area-out cross-validation using models without the area intercept, which cannot be estimated for a new area. We calculated the Brier score for every withheld area and the area under the receiver operating characteristic curve (AUC) for the 12 areas containing both detections and nondetections.

Genomic sampling and population genetic analyses

Candidate sampling locations were selected from georeferenced *C. introflexus* occurrence records. All records of the moss in Iceland were clustered using DBSCAN in QGIS 3.34.14, with a maximum inter-point distance of 100 m. We generally selected one location per cluster to reduce repeated sampling of neighbouring patches. In small or remote populations, additional samples were collected at shorter distances to maintain representation. In total, 96 georeferenced locations were sampled across Iceland. Collected moss shoots were air-dried before DNA extraction. The specimens used for genotyping were identified as *Campylopus introflexus* (Hedw.) Brid. by Mariusz Wierzgoń and Pawel Wasowicz. Voucher specimens

for all 96 samples collected for genotyping were deposited in the AMNH herbarium of the Natural Science Institute of Iceland in Akureyri (voucher numbers AMNH XXXX–XXXX) (final voucher numbers will be available upon acceptance).

Genotyping by sequencing was performed by LGC Genomics GmbH (project NGS4526) on 96 samples originally. Libraries were prepared using MslI and sequenced on an Illumina NovaSeq platform with 150-bp paired-end reads, generating approximately 144 million read pairs. Reads were demultiplexed with bcl2fastq v2.20, adapter-clipped, filtered for the restriction site and quality-trimmed. Reads containing ambiguous bases or shorter than 20 bp after trimming were discarded. Combined reads were clustered with CD-HIT-EST v4.6.1, allowing up to 5% sequence difference and retaining clusters supported by at least 20 reads. Quality-trimmed reads were aligned to this de novo reference using Bowtie2 v2.4.2, and variants were called with FreeBayes v1.2.0.

From the delivered VCF, we kept biallelic SNPs passing the site filter and accepted genotype calls with read depth ≥8. Because the sampled shoots are haploid gametophytes, the reference (0/0) and alternative (1/1) calls in the diploid-coded VCF were recoded as 0 and 1, respectively, and apparent heterozygous calls (0/1) were treated as missing. Five samples with a call rate <50% in an initial panel of SNPs were removed, leaving 91 samples to screen for candidate loci. Candidate loci had to have a call rate >=70%, a minor allele frequency >=0.05 and <=5% apparent heterozygous calls among these 91 samples.

We then excluded 21 samples having more than 5% apparent heterozygous calls as well as one sample that was an apparent repeat collection but with lower SNP call completeness. This exclusion left a final set of 69 samples. Minor allele frequencies were recalculated for these samples, and loci were required to have ≥90% genotype calls within each geographic region. One SNP per provisional de novo reference cluster was selected, prioritising call completeness. The principal panel contained 1,557 SNPs. For sensitivity analyses, we also assembled a 319-SNP panel requiring no apparent heterozygous calls among the intermediate set of 91 samples.

Plant community surveys and analyses

In summer 2024 we surveyed plant communities. Four areas (Bjarnaflag and Þeistareykir in northern Iceland and Grændalur and Hveradalur in southwestern Iceland) were surveyed at 1-7 selected sites per area, 12 sites in total, of which eight sites had been invaded by *C. introflexus*. Research was restricted to hot-soil habitats to reduce variation associated with differences in substrate, as geothermal lava habitats and hot soil support distinct plant communities and are therefore not directly comparable.

At invaded research sites, two perpendicular transects were placed to cross the widest part of the *C. introflexus* turf and extended approximately 2 m beyond its edges. A 50 × 50 cm plot was placed at the transect intersection and at 2 m intervals along each transect, including plots outside the turf. At uninvaded sites, we used the same design, but plots were placed across a local vegetation and temperature gradient. Each plot was divided into 100

subquadrats of 5 × 5 cm. For each vascular plant and bryophyte taxon, including *C. introflexus*, we recorded the number of subquadrats in which it occurred. Unidentified bryophyte taxa were retained as distinct, consistently coded morphotaxa. In total, we examined 113 50x50 cm plots across four areas. Soil temperature was measured at 10 cm depth at the intersection of the transects and at 1 m intervals towards plots beyond the turf. Soil for pH analysis was collected from the upper 3 cm at the same place. At uninvaded sites, temperature and soil samples were taken at plot centres. Soil samples were air-dried at room temperature for at least one week, sieved through a 2 mm mesh and ground with a mortar and pestle. Four grams of soil were mixed with 10 g of water, shaken, allowed to settle and measured for pH within 30 minutes.

Native taxon richness was the number of recorded taxa per plot, excluding *C. introflexus*. To compare plots within sites, richness models used 72 plots at eight sites containing both moss-present and moss-absent plots. We fitted quasi-Poisson models with the site as a fixed factor and soil temperature as a covariate. Moss frequency was entered either per 25 occupied subquadrats or as three descriptive groups: 0, 1–74 and 75–100. We also analysed other bryophytes and vascular plants separately and assessed sensitivity to available pH measurements and omission of individual sites.

For community composition, we used 60 plots at seven sites that contained at least one native taxon. We used Hellinger-transformed subquadrat frequencies and partial redundancy analysis to test the association with moss frequency while accounting for soil temperature and conditioning on site. Significance was assessed with 4,999 permutations restricted within sites. Analyses were conducted in R 4.4.2 using vegan 2.7-1 and permute 0.9-8.

Results

C. introflexus was detected in 12 of the 16 surveyed geothermal areas and at 1,241 of 2,896 surveyed points (Fig. 1, Table S1). Soil temperature was available for 1,599 points. Missing measurements were more frequent at detections (707/1,241; 57.0%) than at nondetection points (590/1,655; 35.6%). After excluding nine measured wetland points, the environmental analysis comprised 1,590 points on hot soil or lava.

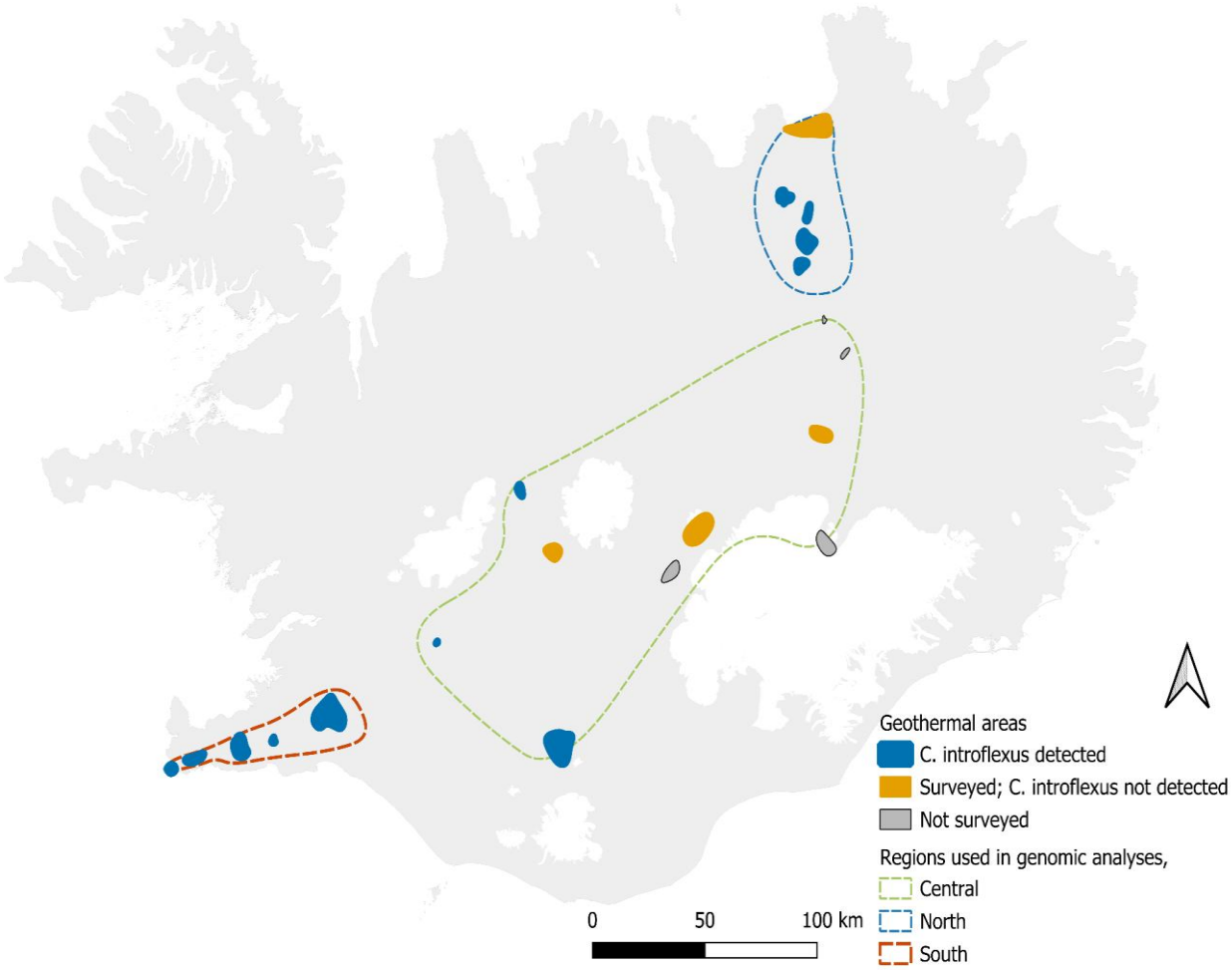


Fig. 1 Occurrence of *C. introflexus* in Icelandic high-temperature geothermal areas surveyed in 2023–2024. Blue indicates detection, orange indicates surveyed areas without a detection, and grey indicates areas not surveyed. Dashed lines indicate the boundaries between the North, Central and South regions used in genetic analyses.

Detection of *C. introflexus* increased with soil temperature across the lower and middle part of the measured range after accounting for elevation, road distance, substrate and differences among geothermal areas (Fig. 2). For a hot-soil point at median elevation and road distance, with the area effect set to zero, the fitted detection probability was 0.012 at 10 °C and 0.293 at 70 °C. The curve levelled off at higher temperatures, but uncertainty does not support identifying a distinct thermal optimum. Increasing the basis dimension of the temperature smooth from five to eight had little effect on the curve or predictive performance. Coefficients from the linear-temperature model and the missing-temperature sensitivity analysis are presented in Table S2. When entire geothermal areas were withheld, the k = 8 model had a mean area AUC of 0.671 across the 12 evaluable areas and a pooled Brier score of 0.209 across all 16 areas (Table S3). The corresponding values for the linear-temperature model were 0.668 and 0.209, indicating little predictive advantage from the nonlinear term.

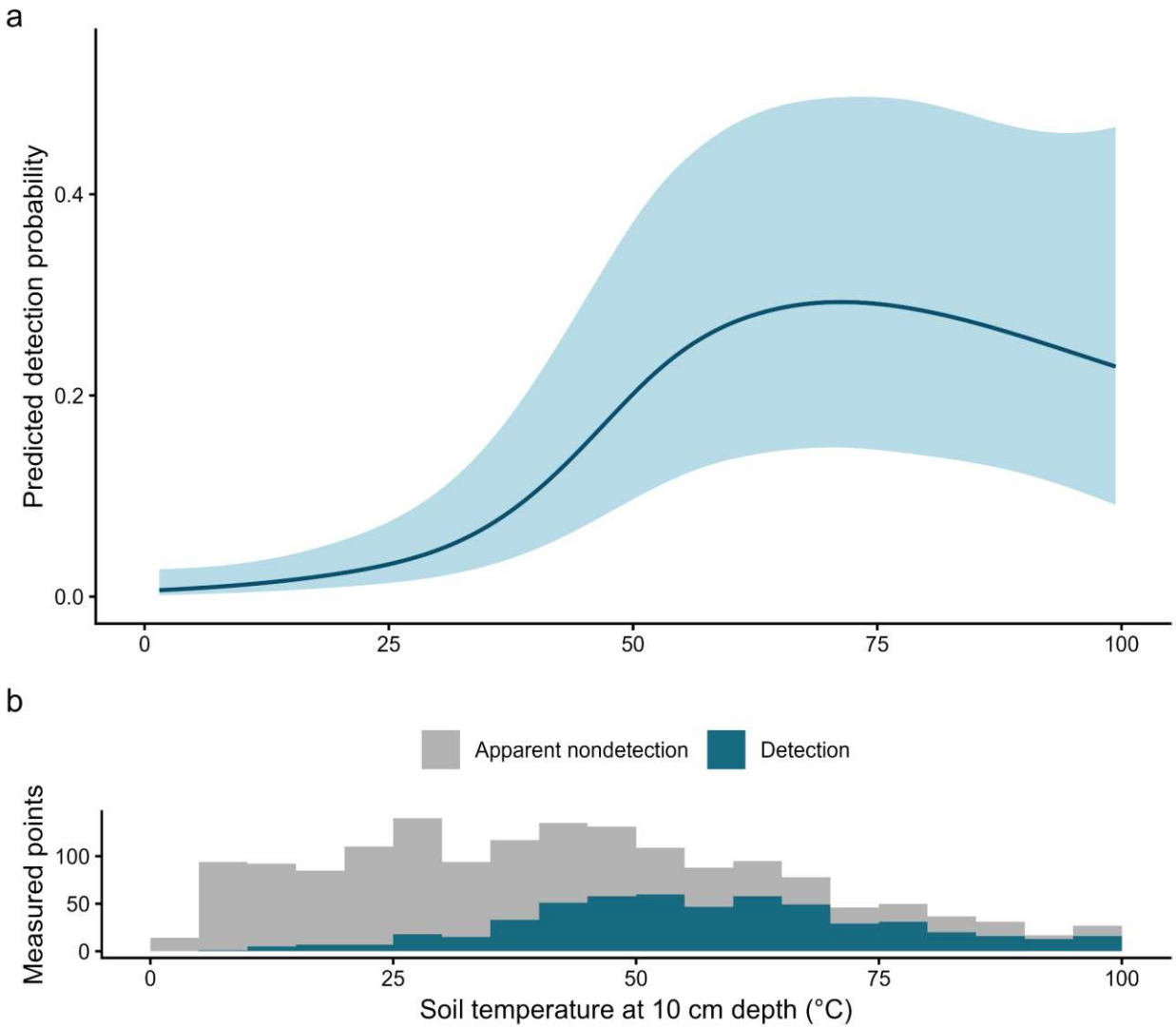


Fig. 2 Detection of *C. introflexus* in relation to soil temperature at 10 cm depth. (a) GAM predictions for hot soil at median elevation and road distance, with the geothermal-area effect set to zero; shading shows pointwise 95% confidence intervals. (b) Unadjusted counts of detections and apparent nondetections in 5 °C bins.

Population genetic structure

Quality filtering retained 69 of 96 sequenced samples from 21 sampling sites (Table S4). In a PCA based on 1,557 SNPs, samples from northern, central and southern Iceland broadly overlapped. PC1 and PC2 explained 5.2% and 4.5% of the variation, respectively (Fig. 3). Site-level genetic distances showed no detectable regional separation (mean difference between and within regions = 0.0004; permutation $P = 0.917$) or isolation by distance (Spearman's $\rho = -0.071$; permutation $P = 0.506$). Both tests used 4,999 permutations. Results were also nonsignificant with a stricter 319-SNP panel ($P = 0.398$ and 0.493, respectively; Table S5).

Despite the limited genetic structure overall, some sites contained contrasting genotypes, and we found them in two small populations: at Leirhnjúkur in northern Iceland (LEL) and

Stórihver in the central highlands (STO). In the primary 1,557-SNP panel, LEL02 and LEL03 differed at only 1 of 1,535 jointly called SNPs (0.07%), whereas each differed from LEL01 at 312 shared SNPs (20.90–21.12%). Similarly, STO03 and STO04 differed at 4 of 1,554 jointly called SNPs (0.26%), whereas comparisons between STO03 or STO04 and STO01 or STO02 differed at 23.18–24.85% of shared SNPs. The same pattern was retained in the stricter 319-SNP sensitivity panel (Table S6). These percentages, however, refer to selected polymorphic GBS markers, not genome-wide sequence divergence.

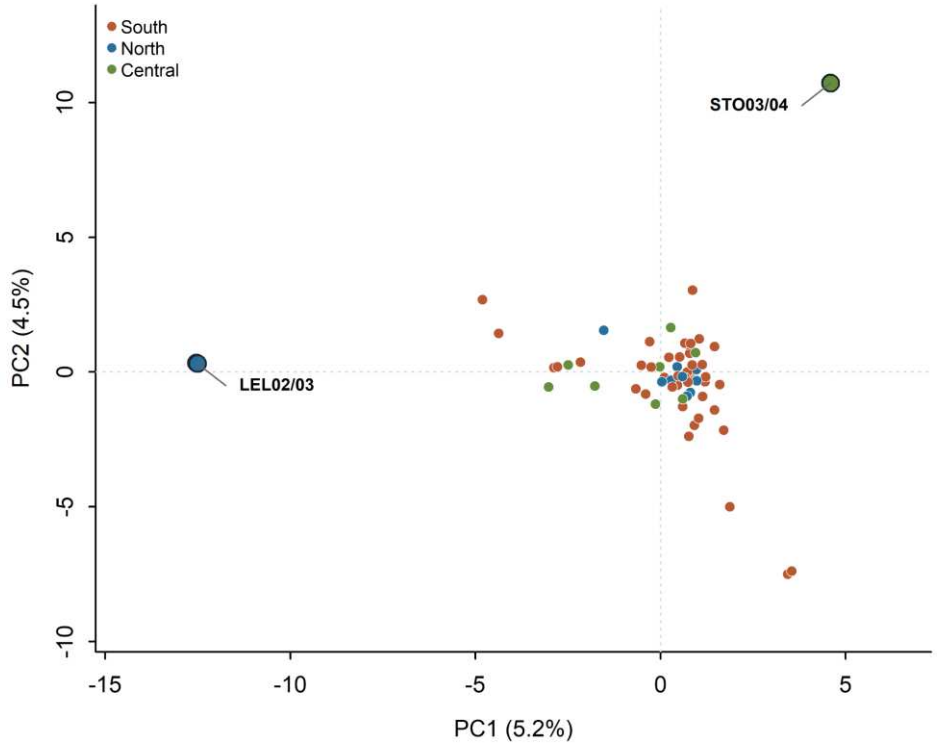


Fig. 3 Genetic variation in Icelandic *C. introflexus*. Principal component analysis of 1,557 SNPs from 69 samples; colours indicate geographic region. PC1 and PC2 explain 5.2% and 4.5% of the variation, respectively. Labels identify the distinctive samples LEL02, LEL03, STO03 and STO04

Native species richness

Within the geothermal areas included in the species richness assessment that had been invaded by *C. introflexus* (Bjarnaflag, Grændalur, Hveradalur), eight sites had both plots with and without *C. introflexus*, or 72 plots out of the total number of 113 plots surveyed, and could therefore be included in the species richness analysis. The frequency of *C. introflexus* in the 100 subquadrats was zero in 22 plots, 1–74 in 16 plots (median three) and 75-100 in 34 plots (Fig. 4a). Mean native taxon richness was 4.59, 5.75 and 2.71 in these groups, respectively. Dense turfs of *C. introflexus*, with patches of other vegetation remaining within the invaded ground, are illustrated in Fig. 5.

After adjusting for site and soil temperature, native taxon richness decreased with increasing *C. introflexus* frequency, with an estimated reduction of 12% per 25 additional occupied subquadrats (richness ratio = 0.880, 95% CI 0.814–0.951; P = 0.0016). When analysed separately, other bryophytes showed a similar negative association (richness ratio = 0.875, 95% CI 0.794–0.966), corresponding to a 12.5% reduction in richness per 25 additional occupied subquadrats. The estimated association was also negative for vascular plants (richness ratio = 0.903, 95% CI 0.782–1.042), although the confidence interval included no change (Table S7).

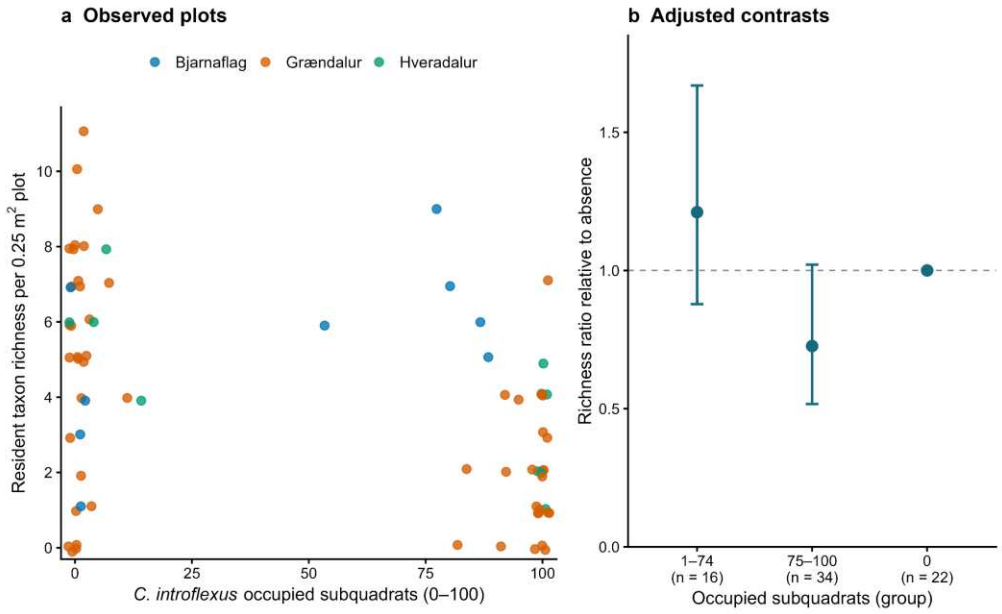


Fig. 4 Native plant richness and *C. introflexus* frequency in geothermal plots. (a) Richness of taxa other than *C. introflexus* in 72 plots from eight sites in three geothermal areas; points are jittered for visibility. *C. introflexus* frequency is the number of occupied subquadrats, not per cent cover. (b) Quasi-Poisson model ratios relative to plots without *C. introflexus*, adjusted for sampling site and soil temperature. Bars indicate 95% confidence intervals; the reference group has no interval. The 1–74 group contained predominantly low frequencies.

The negative association between *C. introflexus* frequency and native plant richness remained after accounting for soil pH. In the subset of 61 plots with pH measurements, the estimated richness ratio for plots with high moss frequency (75–100 occupied subquadrats) compared with plots without the moss was 0.615 without pH and 0.604 after including pH (Table S7).

Community composition was analysed in 60 plots from seven sites that contained at least one native plant taxon. After accounting for site and soil temperature, *C. introflexus* frequency explained 5.0% of the remaining variation in native plant community composition, but the association was not statistically significant (partial RDA, pseudo-F = 1.35, P = 0.114; Table S8).

Including soil pH in the community-composition analysis did not change the overall result. In the subset of 52 plots with pH measurements, neither *C. introflexus* frequency (P = 0.451) nor pH (P = 0.095) showed a statistically significant association with native plant community composition (Table S8).



Fig. 5 Dense mats of *C. introflexus* in an Icelandic geothermal area at Grænadalur (S Iceland). The dark moss carpet represents extensive *C. introflexus* cover, while the lighter green patch (arrow) indicates native vegetation within the invaded site.

Discussion

C. introflexus was detected in 12 of 16 surveyed high-temperature geothermal areas, around four decades after its first record in Iceland. This shows an extensive establishment across a highly disjunct habitat system. In invasion frameworks, occurrence in separated areas reflects efficient dispersal, successful arrival, and establishment, but a present-day distribution alone does not reveal when each area was colonised (Blackburn et al. 2011). It is important to realise that the first collection need not coincide with the original introduction and that we do

not have access to historical data on *C. introflexus* distribution. Thus we can conclude that the invasion is already widespread, but the rate of expansion cannot be calculated from these data. Studies from Britain, the Czech Republic and Poland have documented fast spread of *C. introflexus* in Europe, providing useful comparisons with Iceland (Hassel and Söderström 2005; Mikulášková et al. 2012a; Żarnowiec and Chmura 2019).

In Iceland, detection of *C. introflexus* was associated with warmer soil across the lower and middle part of the measured temperature range. This agrees with a study of Californian geothermal bryophytes in which *C. introflexus* was associated with warmer microsites (Llaneza García et al. 2016), and it is consistent with local environmental conditions influencing establishment, as proposed by general invasion theory (Catford et al. 2009). However, we failed to establish a thermal optimum with the fitted relationship, and its performance in predicting detections in withheld geothermal areas was moderate. It can be hypothesised that successful establishment of bryophytes depends not only on propagule arrival but also on conditions allowing or facilitating germination and development in early stages. Environmental conditions such as moisture and other substrate properties could be particularly important here (Wiklund and Rydin 2004). Thus, the association between *C. introflexus* detection and soil temperature may partly reflect conditions affecting establishment, although our data do not allow us to identify the developmental stages involved. It is important to realise that substrate temperature measured at 10 cm depth is also a proxy for local geothermal influence, not the exact temperature where moss shoots live. Additionally, moisture, substrate chemistry and propagule pressure may contribute to the unexplained variation. As we did not measure propagule supply, we cannot distinguish limited arrival from failure to establish at otherwise suitable points.

The higher rate of missing temperature measurements at detection points (57.0%) compared to nondetections (35.6%) was due to a combination of physical, logistical, and protocol factors. First, *C. introflexus* often grew on hard lava crusts or very thin soils over lava, making it physically impossible to push the temperature probe 10 cm deep. Second, in some geothermal areas, measurements could not be taken safely because of extremely hot ground and the associated risk of burns. Third, inside large or highly clustered moss populations, temperature readings were taken representatively for the whole patch to avoid redundant measurements. Finally, because recording soil temperature requires the probe to stabilise at each point, temperature readings were occasionally skipped to maximise our geographical mapping footprint within limited field windows. Since we retained a very large sample of 1,590 fully measured points across all 16 areas, we would argue that the statistical power of our generalised additive models (GAMs) remained sufficient.

Within the Blackburn et al. (2011) framework, interpreting a species' present-day distribution requires disentangling the signal of active regional spread from historical arrival events. Most retained genomic samples in our study showed remarkably weak geographic separation across Iceland, with northern, central, and southern populations broadly overlapping in genetic space. This high degree of genetic homogeneity might be compatible with the spread stage of a not very diverse pool of genotypes expanding rapidly across a highly disjunct

geothermal network. Long-distance dispersal is common among bryophytes, but successful establishment does depend on local environmental conditions (Barbé et al. 2016). Such a dispersal pattern could contribute to the weak geographic genetic structure observed among Icelandic populations of *C. introflexus*, while differences in local conditions may influence where the species becomes established. Bryophyte spores and vegetative propagules can differ in their dispersal and establishment ability, and it seems that larger vegetative propagules often establish more efficiently under suitable conditions (Löbel and Rydin 2010). Both reproductive pathways could therefore contribute to the spread of *C. introflexus* across Icelandic geothermal areas, although their relative importance remains unknown and cannot be disentangled by the present study. During fieldwork, we noticed that sheep frequently used patches of geothermally heated soil as resting places and may therefore contribute to the local dispersal of *C. introflexus* by transporting its propagules. However, the importance of this dispersal pathway has not been investigated directly.

The lack of spatial genetic structure cannot be used to rule out the possibility of repeated introductions, particularly if introduced plants originated from genetically similar source populations. However, we found that Icelandic populations are not always genetically uniform, and in two cases we showed the presence of more genetically distinct genotypes within the same geothermal area. Quantitatively, these differences are similar to those found between populations in Iceland. Therefore, we cannot conclude that these genotypes represent separate evolutionary lineages or resulted from different introductions. Because populations outside Iceland were not included in our genetic analyses, the number and sources of introductions remain unknown.

We noticed that native taxon richness declined with increasing frequency of *C. introflexus* in plots compared within sites after adjustment for soil temperature. The estimated richness ratio was 0.88 per 25 additional subquadrats occupied by *C. introflexus*. Evidence of a negative association was clearer for other bryophytes than for vascular plants. Studies of vascular-plant invasions show that invader dominance can be important for community responses, although the response depends on the invader and resident community (Hejda et al. 2009). Earlier work on *C. introflexus* also suggests that outcomes may vary among habitats. In Dutch drift sands, conditions favouring moss dominance raised concern for lichen-rich vegetation (Sparrius and Kooijman 2011). In a five-year dune study, however, lichens recolonised moss-dominated plots, and *C. introflexus* had no major effect on the overall vegetation succession trajectory (Hasse 2007).

Our richness results suggest that the relationship between the non-native *C. introflexus* and native geothermal vegetation may follow a non-linear threshold-like pattern rather than a continuous linear decline. While native taxon richness remained stable when the *C. introflexus* abundance was low, a reduction was observed when the invading moss species achieved dominance in the subquadrats. This pattern agrees with broader invasion frameworks, showing that it is dominance, rather than the simple presence of an invading species, that is often the primary driver of community change (Hejda et al. 2009). It has been noticed that dense bryophyte turfs can act as physical filters at the soil surface, potentially

altering microsite conditions or limiting spore and seedling establishment (Sparrius and Kooijman 2011). However, such effects are not necessarily specific to *C. introflexus*, as native turf-forming bryophytes may also provide similar physical barriers. Due to the observational nature and localised scale of this study, we cannot definitively prove a direct competitive displacement. Our results, however, do suggest that potential negative impacts in these disjunct thermal systems may be connected to dense carpet formation rather than to early stages of invasion.

The richness result should also be considered together with the community-composition analysis, which gave less conclusive results. The latter analysis included only plots with at least one native plant taxon, because community composition cannot be compared in plots where no native plants were recorded. This is an important limitation, as plots containing only *C. introflexus* were excluded, meaning that the analysis could not account for the complete absence of native plants in these plots. The strongly uneven distribution of *C. introflexus* frequency, with most plots having either little or no moss or very high frequencies, further complicates the interpretation of these results. Our analysis found no clear relationship between *C. introflexus* frequency and native plant community composition after accounting for site and soil temperature. However, this does not mean that *C. introflexus* has no effect on native vegetation. Although we accounted for site and soil temperature, the negative relationship between *C. introflexus* frequency and native plant richness does not demonstrate that the moss caused a decline in richness. Other environmental factors that were not measured, as well as differences in patch history, may also have influenced the observed pattern. No lichens were found in the surveyed plots, so we could not assess their response to *C. introflexus.*

The frequency of *C. introflexus* was strongly uneven across plots. Most plots had little or no *C. introflexus* or had the moss species in at least 75 of 100 subquadrats, with only one falling between 25 and 74. This observation shows a clear spatial contrast between sparse, diffused occurrences and turf formation, but not the time needed to form a turf. In order to establish whether moss density increases rapidly and whether changes in native richness follow the same temporal pattern, repeated observations of changes along turf edges would be needed.

Our findings also have implications for the conservation of natural geothermal habitats in Iceland, which are classified as having high or very high conservation value (Ottósson et al. 2016). Having this in mind, the widespread colonisation of these habitats by *C. introflexus* is by itself of concern, especially where the species forms extensive dense mats. Such dominance by a non-native moss alters the structure, appearance, and most probably functioning of these geothermal ecosystems and at least reduces the space available for native species. Association between dense *C. introflexus* turfs and lower native plant richness established in this study adds to this concern. Regular monitoring of invaded sites, especially the expansion of dense mats and changes in native vegetation, would help determine the long-term consequences of this invasion.

The main contribution of this study is that it combines information on the distribution of *C. introflexus*, its genetic variation, and its relationship with local vegetation in Icelandic

geothermal areas. Earlier studies of invasive bryophytes have covered relatively few habitats (Essl et al. 2014), while research on *C. introflexus* has mostly focused on particular habitats or individual aspects of its invasion. Our findings show that the species is widespread in Icelandic geothermal areas and that its frequency is associated with lower native plant richness. We need studies using, for example, permanent plots, repeated distribution surveys, and genetic comparisons with populations outside Iceland, which would help us understand how these patterns change over time.

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Supplementary information

Online Resource 1. Supplementary Tables S1–S8 containing occurrence summaries, environmental model results, cross-validation, genomic filtering and genetic structure, pairwise genotype comparisons, and native vegetation analyses for *Campylopus introflexus* in Icelandic geothermal areas.

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Statements and Declarations

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Competing Interests

The authors declare no competing interests.

Author Contributions

PW conceived and coordinated the study, contributed to fieldwork, analysed the occurrence and genomic data, and led the writing of the manuscript. RS contributed to study design, fieldwork, vegetation data collection and preparation of the vegetation dataset. OKV contributed to study design, fieldwork, vegetation sampling and interpretation of the ecological analyses. MW contributed to bryophyte identification, interpretation of the results and manuscript development. ISJ contributed to study design, interpretation of the ecological results and manuscript development. All authors reviewed and approved the final manuscript.

Data Availability

The supplementary tables are provided as Online Resource 1. The occurrence and vegetation datasets, processed genomic data and analysis scripts will be deposited in a public repository upon acceptance of the manuscript. Raw GBS sequencing reads will be deposited in the European Nucleotide Archive (ENA) upon acceptance. Repository links and accession numbers will be provided in the final version of the manuscript.

Supplementary Files

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- ESM1.xlsx