


Mapping an invasive bryophyte species using hyperspectral remote sensing data

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Abstract Reliable distribution maps are crucial for the management of invasive plant species. An alternative to traditional field surveys is the use of remote sensing data, which allows coverage of large areas. However, most remote sensing studies on invasive plant species focus on mapping large stands of easily detectable study species. In this study, we used hyperspectral remote sensing data in combination with field data to derive a distribution map of an invasive bryophyte species, *Campylopus introflexus*,

on the island of Sylt in Northern Germany. We collected plant cover data on 57 plots to calibrate the model and presence/absence data of *C. introflexus* on another 150 plots for independent validation. We simultaneously acquired airborne hyperspectral (APEX) images during summer 2014, providing 285 spectral bands. We used a Maxent modelling approach to map the distribution of *C. introflexus*. Although *C. introflexus* is a small and inconspicuous species, we were able to map its distribution with an overall

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accuracy of 75 %. Reducing the sampling effort from 57 to 7 plots, our models performed fairly well until sampling effort dropped below 12 plots. The model predicts that *C. introflexus* is present in about one quarter of the pixels in our study area. The highest percentage of *C. introflexus* is predicted in the dune grassland. Our findings suggest that hyperspectral remote sensing data have the potential to provide reliable information about the degree of bryophyte invasion, and thus provide an alternative to traditional field mapping approaches over large areas.

Keywords *Campylopus introflexus* · Dunes · Heathland · Imaging spectroscopy · Maxent · Moss

Introduction

Reliable distribution maps are crucial for the management of invasive plant species, but classical field surveys are not always efficient for large areas. In addition to being time-consuming and cost-intensive, especially for large and remote areas and repeated measurements, there is high observer-dependent variation (Fitzpatrick et al. 2009). In order to allow a cost-efficient eradication, invasive species must be detected as early as possible (Simberloff et al. 2013).

Advanced airborne remote sensing data can be a viable alternative to field surveys as they cover large areas and may enable the detection of species that are difficult to map in the field (Asner 2013). As the reflectance signal of plants is generally determined by their biochemical and biophysical characteristics (Asner 1997; Ollinger 2011), the invasive target species must have some unique biochemical, structural or related phenological characteristics in order to be detectable with remote sensing. To date, different types of remote sensing data have been used for the detection of invasive plants, depending on the characteristics of the study species and the project goals (see Huang and Asner 2009 for a review), from aerial photos to multi- and hyperspectral satellite, airborne or UAV data.

A very promising technique is to use hyperspectral remote sensing data. Characterized by a large number of spectral bands as compared to multispectral remote sensing data, hyperspectral data are regularly used in a wide range of fields such as geology, agriculture,

military surveillance and ecology. Hyperspectral imagery is also the type of data that is most commonly applied for invasive plant species (Bradley 2013), as the large number of spectral bands allows differentiation of even subtle differences in plant chemistry in order to detect the target species.

A number of studies using hyperspectral data for the detection of invasive plant species have relied on characteristic features of the target species, such as plant physiological traits, flower colours or phenology to differentiate them from the surrounding vegetation. For instance, Underwood et al. (2003) focused on spectral bands related to water absorption to detect the succulent species *Carpobrotus edulis* in coastal dune scrub and maritime chaparral. Andrew and Ustin (2008) were able to discriminate the weed *Lepidium latifolium* in Californian wetlands by means of its characteristic white flowers. Ishii and Washitani (2013) used spring images to detect the weed *Solidago altissima* in riparian wetlands before the seasonal development of the indigenous tall grass species. Only few studies so far have attempted to detect less conspicuous species, such as the thistle *Carduus nutans*, in a non-flowering state (Mirik et al. 2013). Likewise, only very few studies (e.g. Lass et al. 2005) have evaluated the potential of hyperspectral data for early detection, probably because later invasion stages where the invasive species are covering large areas are much easier to detect from remote sensing data.

Our objective was to assess the potential of hyperspectral remote sensing to detect the invasive bryophyte species, *Campylopus introflexus* (Hedw.) Brid, which was introduced less than 50 years ago to the coastal dunes of the island of Sylt in Northern Germany. More specifically, our goal was to develop an approach that is easy to replicate for other study areas and species, and to contribute to more efficient monitoring of invasive plant species, as well as to early detection. The invasive moss *C. introflexus* was selected as target species as it is especially difficult to map: it lacks conspicuous features such as colourful flowers, individual plants are small, and patches are often irregular and intermingled with other species.

This paper aims at answering the following questions: (1) How accurately can we detect an invasive moss species with hyperspectral data? (2) Can we detect early invasion stages as well? (3) Which vegetation types within the study site are most susceptible to invasion by *C. introflexus*?

Materials and methods

Study site

The island of Sylt extends about 30 km in north–south direction, but most parts of the island are only between 500 and 1500 m wide. Sylt is located in Northern Germany (Fig. 1) and has a temperate climate with medium temperatures of 1.7 °C in February and 17 °C in August. The annual mean temperature is 9 °C, and the annual precipitation is 717 mm with monthly values between 45 and 89 mm [weather station located in List, Northern Sylt, reference period 1981–2010 (DWD 2015)]. The soils in the dune areas on the west coast are mainly loose immature soils and podsolized regosols consisting of dune sand. Towards the centre, mainly on the east coast, the dominating soils are pseudogleys—brown earth and plaggen soils (BGR 2009). Formerly being part of the mainland, Sylt only took its current shape about 400 years ago. Today, large amounts of sand are artificially deposited on the west coast every year in order to counteract the natural erosion and prevent land loss.

The dune areas on the island formerly consisted mainly of shifting sand dunes without much vegetation cover, and grasses were first sown in the 16th century in order to fix the dunes. After 1790, grass planting with *Ammophila arenaria* became more common and frequent, but targeted mainly the central area around the islands main village. A fundamental change in dune management occurred when the Prussians took over the island in 1864. They introduced and financed a range of new efficient measures, among them the planting of tree species such as *Pinus nigra* and *Pinus montana* in the dune valleys. Those measures finally resulted in a fixation of most of the dune areas and prevented the evolution of new shifting dunes, only three of which have survived until today in the northern part of the island (Bartels 2013). The land use was also very important for the development of the dune areas: until about 1950, the heathlands were mostly grazed, and another common practice was to remove the topsoil together with the vegetation, then to put it in the stables or use it as fuel, along with any kind of emerging woody vegetation.

The dunes located on the sea side (west coast) are mostly natural aeolian atlantic dunes, while the east coast was originally made up of pleistocene sands deposited during the ice age. The dominant vegetation

is *Empetrum nigrum* heathland (Hieracio-Empetretum, Calluno-Ulicetea), covering about two thirds of the study area, followed by grey dunes vegetation (Koelerio-Corynepherea), making up about 13 % of the total cover. Heathlands with high cover percentages of *Erica tetralix* sometimes in association with *Narthecium ossifragum* (Ericetum tetralicis, Oxy-cocco-Sphagnetea) and areas dominated by *A. arenaria* (Elymo-Ammophiletum, Ammophiletea) each cover about 4 %. About 3 % consist of shifting dunes and another 3 % are dominated by *Rosa rugosa*, another invasive species (Leguan 2012).

Study species

The heath star moss, *C. introflexus*, is the only bryophyte listed among the 100 worst invasive species for Europe (Essl and Lambdon 2009). Native to the southern hemisphere, the species was first observed in Europe in 1941 in Sussex, UK (Richards 1963), possibly introduced through its use as packaging material for the import of goods. From England, *C. introflexus* has spread over large areas in Europe, by long distance dispersal of spores transported by wind and dispersal of vegetative fragments through animals, vehicles and other pathways.

Invading coastal and inland dunes, it leads to a reduction of herbaceous plants in *Corynephorus canescens*-dominated communities, such as *Aira praecox*, *Jasione montana* and *Viola canina*, as well as a decrease in the diversity of mosses such as *Dicranum scoparium*, *Hypnum cupressiforme* and *Polytrichum piliferum* and lichens such as *Cladonia portentosa*, *C. strepsilis*, *C. uncialis* and *Stereocaulon condensatum* (Rabitsch et al. 2016). Moreover, it may change succession rates (Biermann and Daniels 1997; Ketner-Oostra and Sýkora 2004). Other studies, particularly on alkaline soils, found that the effect on lichens and other plant species might be only temporary (Hasse 2007; Klinck 2009; Sparrius and Kooijman 2012). However, the dense mats of *C. introflexus* induce changes in soil formation, water balance, and vegetation structure (Rabitsch et al. 2016) with negative consequences for other dune species such as carabid beetles and spiders (Vogels et al. 2005; Schirmel et al. 2011). By reducing arthropod abundance and diversity, it also contributed to a case of local extinction of the insectivorous bird *Anthus campestris* in the Netherlands (van Turnhout 2005).

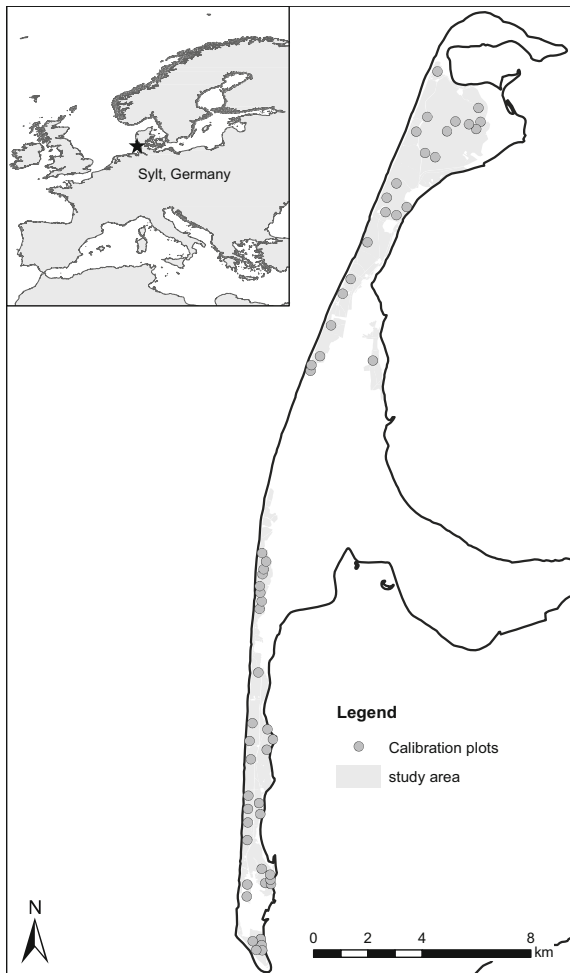


Fig. 1 Location of the North Frisian island Sylt (Germany) and the 57 plots used to calibrate prediction models for the invasive bryophyte *C. introflexus* based on hyperspectral remote sensing data

While Hahn (2006) concluded that a regeneration of the affected sandy xeric grasslands is rather improbable, other studies claimed that the effect is rather local and only temporary, particularly on less acidic sands with higher lime content. However, the long-term effect on succession in dune ecosystems is not yet clear (Hasse 2007). Possibly there will be a cyclic succession with native bryophytes and lichens. A succession to *Calluna vulgaris* heathland is likely in the long term, particularly under future climate warming. Equally unclear are the possible management options for heavily invaded areas. One option that has shown positive results is the deposition of sand. Boxel et al. (1997) found that *C. introflexus*

disappeared when more than a few millimetres of sand accumulated each year from blowouts. Research from Ketner-Oostra and Sýkora (2000) showed that reactivating blowouts and maintaining sandflow from foredunes is a useful management option, and that the addition of sand with neutral to subneutral pH, some lime and relatively high base content also had a positive effect on lichen richness. Furthermore, the restoration of dynamic dunes with blowing sand is known to support the native biodiversity in dunes (Geelen et al. 2015).

In Germany, *C. introflexus* was first detected in 1967 in several locations (Neu 1968; Benkert 1971; Düll and Meinunger 1989) and probably reached the island of Sylt some years later. On the island of Römö (Denmark), which is located North of Sylt, and is connected to Sylt by car ferry, it was first found in 1970 (Frahm 1971). Although most of the dune areas on the island of Sylt have been given the status of nature protection areas between 1972 and 1980, and access to those areas is largely prohibited today, the high number of tourists visiting the island each year and other human activities probably has had an impact on the species' spread in the past. The island of Sylt is connected to the mainland by a train, which is also transporting cars, and a ferry from Denmark, thus the establishment and spread of *C. introflexus* was probably supported by those connections. So far, no map of the species' distribution or analysis of its impacts on the island of Sylt exists.

Field data

For calibrating our distribution models, we surveyed a total of 57 plots each covering 3 m × 3 m where *C. introflexus* was present in June 2014. The cover of all occurring plant species including bryophytes was recorded. For lichens, the total cover was estimated. The plots were chosen using a stratified sampling design taking into account all relevant vegetation types as well as different stages of *C. introflexus* invasion.

For validating our models, 150 additional randomly located 3 m × 3 m plots were recorded in October and November 2014. For those plots, the percentage cover of *C. introflexus* and of all species with more than five percent of cover was determined. This dataset contains both presence and absence plots of the target species. For all plots, the GPS position was

taken in the plot centre using a Trimble GeoExplorer 6000. The position average was integrated over at least 100 measurements.

Remote sensing data

The airborne hyperspectral data for Sylt were acquired in a flight campaign on July 16th 2014, with a flight height of 2270 m, between 12:21 and 13:13 local time. The dataset was recorded in four flight lines covering the northern and two flight lines covering the southern part of the island, resulting in a total of 32 partly overlapping images. Each image consists of 285 spectral bands recorded with an APEX (Airborne Prism EXperiment) sensor covering a spectral range between 412 and 2432 nm. Each individual pixel of the image has the size of 1.8 m × 1.8 m on the ground. The Flemish Institute for Technological Research (VITO) pre-processed the hyperspectral data and included radiometric and geometric calibration, correction of spectral smile effects as well as geometric and atmospheric correction (VITO 2014).

Once pre-processed, the 32 separate hyperspectral images were combined in one mosaic. For the overlapping areas of the separate images, the mean value was calculated. For two images containing clouds or cloud shadows, the cloud-free image was chosen. A total of 146 bands that remained after the elimination of the bands disturbed by water vapour signal were included into further analysis. All pre-processing steps were performed in the R statistical environment (R Core Team 2015) using the packages “rgdal” (Bivand et al. 2015) and “raster” (Hijmans 2015).

Data analysis

The data analysis follows the work flow shown in Fig. 2. To define our study area, we used a biotope map (Leguan 2012) to exclude all urban structures, agricultural areas, roads, and areas with biotope types unsuitable for our target species, such as salt marshes (see Fig. 1). We also excluded the still sheep-grazed areas at the northern tip of Sylt (Ellenbogen) from our analysis, because of its rather different land use history and resulting vegetation composition.

As a classification algorithm for mapping the current distribution of *C. introflexus* across Sylt, we

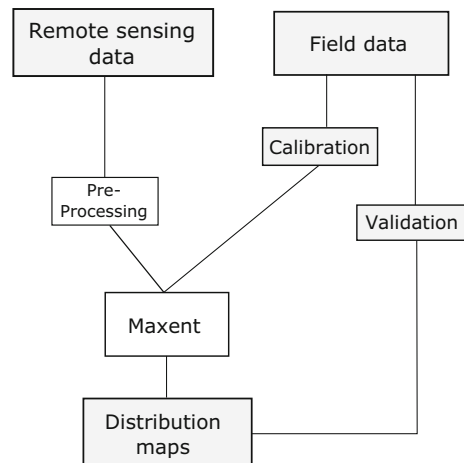


Fig. 2 Work flow of the analyses for calibrating and validating a Maxent model to map an invasive species using a combination of field and remote sensing data

used Maxent (Phillips et al. 2004). Maxent is a one-class-classifier that separates the target species from the background by using a maximum entropy approach. We chose Maxent because it is a widely used and state-of-the-art modelling tool in ecology (Merow et al. 2013; Elith et al. 2011). In order to model the species distribution, the approach requires independent predictor or explanatory variables. These variables are usually abiotic factors such as climate, topography, light or soil conditions that are relevant for plant physiology. In our model, we used the 146 spectral bands from our hyperspectral remote sensing dataset as predictors. Maxent basically compares probability densities. We know the conditional density of the predictors at the presence sites, as well as the unconditional density of the predictors across the study area, but not the prevalence. Maxent makes an estimate of the ratio between the two densities where the distance between the density at the presence sites and the density across the study area is minimized. The model can then be transformed from an exponential to a logistic model, providing us with the logistic output, which is an estimate of the probability that the species is present in a certain location. For detailed information on the model functioning see Phillips et al. (2006) and Elith et al. (2011).

As samples, we used the presence points of our calibration dataset, containing 57 observed presences, for which we extracted the spectra from the hyperspectral data. Additionally we extracted the spectra for 10,000 background samples that were randomly

Table 1 Schematic confusion matrix

		Map prediction	
		<i>Campylopus</i> present (1)	<i>Campylopus</i> absent (0)
Field observation	<i>Campylopus</i> present (1)	True positive (TP): correctly predicted presences	False negative (FN): mispredicted absences
	<i>Campylopus</i> absent (0)	False positive (FP): mispredicted presences	True negative (TN): correctly predicted absences

drawn from the biotope types where *C. introflexus* occurs or may potentially occur.

To assess the model performance we used the area under the curve (AUC) statistic. AUC evaluates to which degree the given distribution performs better than a random distribution. It ranges from 0 (wrong prediction) to 1 (perfect match), with 0.5 indicating the model performance for a random distribution of presences.

To transform occurrence probabilities into presence-absence data, a threshold was defined, and the final presence-absence map was created. The probability threshold can be selected manually for Maxent (Phillips et al. 2006). We chose to work with a medium high threshold, the '10 percentile training presence' threshold, which selects the value as threshold above which 90 % of the training samples are correctly classified. The threshold was chosen subjectively.

As external validation, we used the independent dataset containing the 150 presence and absence plots, and calculated the confusion matrix. From the confusion matrix (Table 1), we calculated the OAC (overall accuracy), MCC (Matthews's correlation coefficient), McNemar test as well as the user's and producer's accuracy.

The overall accuracy (OAC) is the proportion of true predictions among the sum of all values on the confusion matrix (Eq. 1):

$$OAC = \frac{(TN + TP)}{(TN + FN + FP + TP)} \quad (1)$$

where *TN* = true negatives, correctly predicted absences; *TP* = true positives, correctly predicted presences; *FN* = false negatives, mispredicted absences; *FP* = false positives, mispredicted presences.

The user's accuracy is the proportion of correctly predicted absences among the total number of predicted absences ($TN/(TN + FN)$) or correctly predicted presences among the total number of predicted presences ($TP/(TP + FP)$).

The producer's accuracy is the proportion of correctly predicted absences among the total number of observed absences ($TN/(TN + FP)$) or correctly predicted presences among the total number of observed presences ($TP/(TP + FN)$).

While the statistics above focus on the correctly classified values (TP and TN), Mathew's correlation coefficient (MCC) also considers the misclassified values (FP and FN) (Eq. 2):

$$MCC = \frac{TP * TN - FP * FN}{\sqrt{(TP + FP) * (TP + FN) * (TN + FP) * (TN + FN)}} \quad (2)$$

The McNemar test focuses even more on the misclassified values (*FP* and *FN*), and tests whether their values are imbalanced. This balance is quantified as the *Chi* value. If *p* is significant it means there is a significant difference.

As we suppose that we model both actual distribution and potential habitats due to the spectral similarity of the co-occurring vegetation, we additionally used a two-step modelling approach, which worked as follows: First, the model was run as described above. Next, a new set of 10,000 background points was selected from the area containing all presences resulting from the first modelling. Then, the model was run again.

Furthermore, we investigated on how the results depended on the number of calibration plots in order to assess how much field work is actually necessary and if our approach is also applicable to species with a more limited distribution, for example for species that just started invading the area. We therefore compared the outputs and performances of our Maxent runs while reducing the number of observed presences successively by five plots per run. In each step, we randomly removed presences, each belonging to one out of five different cover classes. For evaluation, we

Table 2 Accuracy assessment of the distribution map of *Campylopus introflexus* within the coastal dunes on the North Frisian island Sylt based on hyperspectral remote sensing and Maxent modelling

		Map prediction			Producer's accuracy (%)
		<i>Campylopus</i> present	<i>Campylopus</i> absent	Total	
Field observation	<i>Campylopus</i> present	27	21	48	56.3
	<i>Campylopus</i> absent	16	86	102	84.3
	Total	43	107	150	
User's accuracy (%)		62.8	80.4		
Overall accuracy (%)		75.3			
Matthew's correlation coefficient		41.8			
McNemar χ^2		0.40	<i>p</i>	0.51	

To generate the binary map, the '10 percentile training presence' threshold of 0.307 was applied. For the McNemar test a $p > 0.05$ indicates no significant difference between the proportions of FNs and FPs

used the different accuracy measures explained above (AUC, OAC, users and producers accuracies, MCC and McNemar test).

In order to investigate the susceptibility of different types of coastal vegetation to invasion, we differentiated the vegetation types according to the TMAP-code (Trilateral Monitoring and Assessment Programme, Petersen et al. 2014), a vegetation type classification which aims to harmonize vegetation mapping across the Wadden Sea area across the Netherlands, Germany and Denmark. We then calculated the amount of pixels predicted to contain *C. introflexus* in each vegetation type. For areas where more than one TMAP-code was assigned within the biotope mapping of the island in 2012, we assigned 60 % of the area to the primary and 40 % to the secondary TMAP type.

Results

Maxent modelling

The overall accuracy of the Maxent model was approximately 75 %, while Matthews's correlation coefficient was approximately 0.42 (see Table 2). The FNs and FPs in the confusion matrix were relatively balanced, according to the McNemar test. The AUC value was about 0.872. The amount of correctly classified presences (TPs) increases for high cover percentages of *C. introflexus* (Fig. 3).

As a result of the basic Maxent modelling, we derived a probability map and a presence–absence map for *C. introflexus*, (Fig. 4), using all available 57

presence points, and the '10 percentile training presence' threshold. The probability map shows five classes, three below and two above the threshold of 0.307, while the presence–absence map only shows all areas above the threshold. The visual inspection of the modelling results did not show any pattern or break-line in between the different flight lines. The misclassified validation plots were evenly distributed across the island.

All bands considered important in the model were located in the short wave infrared region (SWIR; Fig. 5). The three most important ones were located at 1736, 1988 and 1996 nm, all relatively close to the water absorption bands, making up about 40 % of the permutation importance, which is a measure of the final contribution of the different bands to the model. Only a few bands were located in the near infrared (NIR).

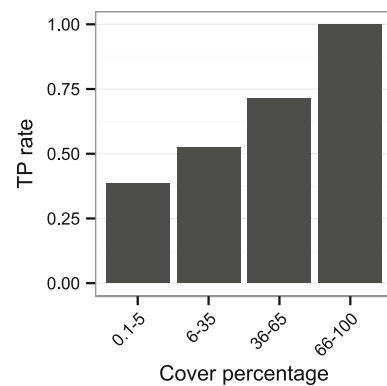


Fig. 3 Rate of correctly predicted presences of the validation dataset related to the cover percentage of the invasive bryophyte *C. introflexus* observed in the field

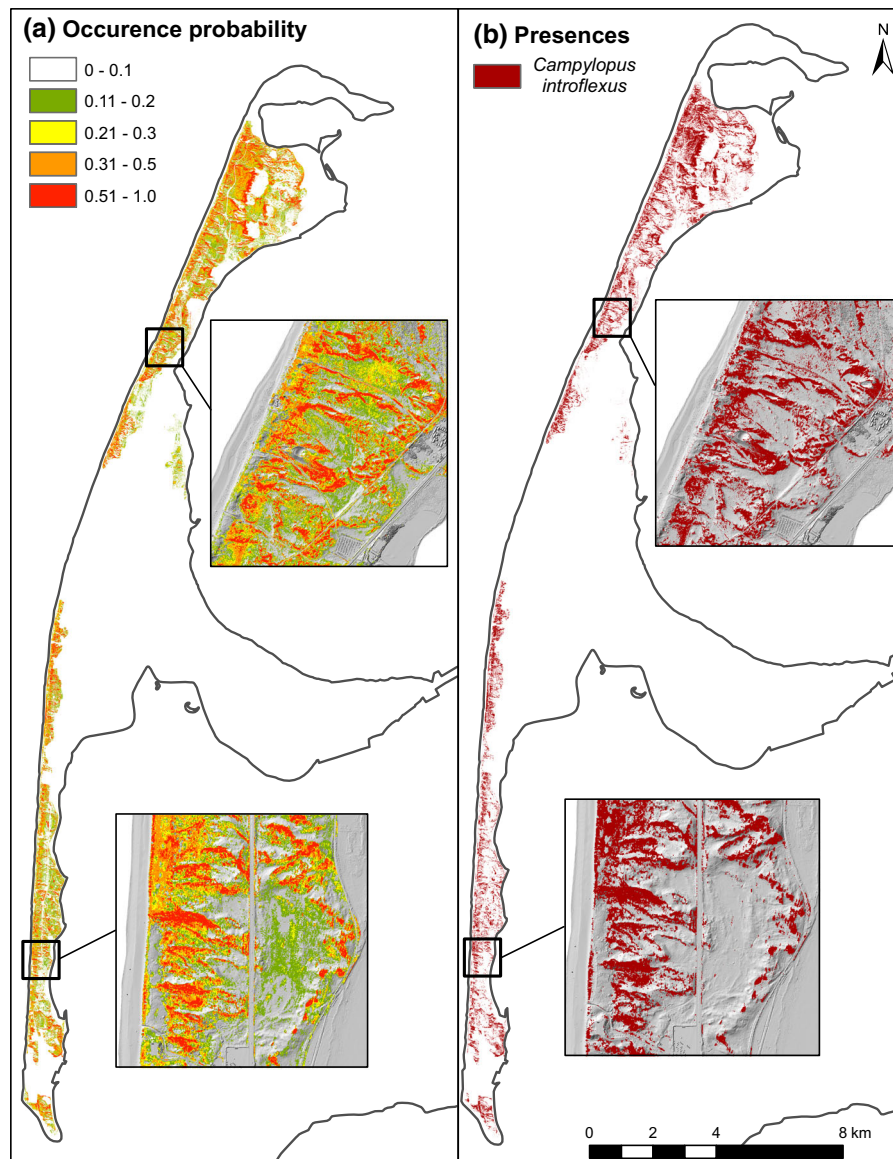


Fig. 4 **a** Probability map based on hyperspectral remote sensing and Maxent modelling and **b** model-based presence–absence map for the invasive bryophyte *C. introflexus* in the dune vegetation on the North Frisian island Sylt (Germany). The

presence–absence map is derived from the probability map by applying a probability threshold of 0.307. The background in the detailed maps is a LiDAR-derived relief hillshade

Two-step modelling

In the second run of the twostep modelling (re-analysis based on a reduced background set) a threshold of 0.371 (‘10 percentile training presence’) was applied. It produced an AUC value of 0.758 and the resulting overall accuracy did not change compared to the one step approach. Mathew’s

correlation coefficient slightly decreased to 0.38. This resulted in 95 out of 102 correctly classified absences, but only 18 out of 48 correctly classified presences, and while a smaller number of field absences were wrongly predicted, about 30 field presences out of 48 were not detected by the model (see Table 3). The McNemar test confirmed that this prediction was very unbalanced.

Fig. 5 Permutation importance of spectral bands used by Maxent modelling of the invasive bryophyte *C. introflexus* on the island of Sylt (Germany)

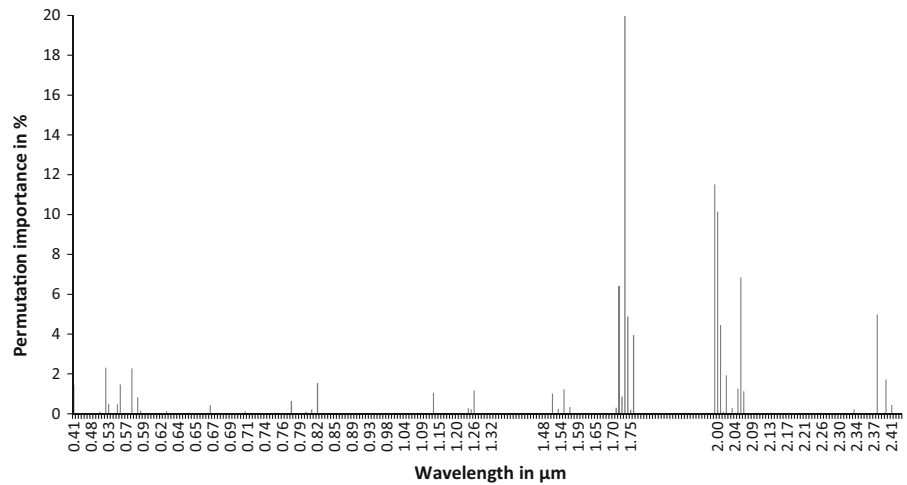


Table 3 Accuracy assessment of the distribution map of *Campylopus introflexus* within the coastal dunes on the North Frisian island Sylt based on hyperspectral remote sensing and a two-step Maxent modelling approach

		Map prediction			Producer's accuracy (%)
		<i>Campylopus</i> present	<i>Campylopus</i> absent	Total	
Field observation	<i>Campylopus</i> present	18	30	48	37.5
	<i>Campylopus</i> absent	7	95	102	
	Total	25	125	150	93.1
User's accuracy (%)		72.0	76.0		
Overall accuracy (%)		75.3			
Matthew's correlation coefficient		0.38			
McNemar χ^2		13.1	<i>p</i>	0.0003	

To generate the binary map, a '10 percentile training presence' threshold of 0.371 was applied. For McNemar test, a $p < 0.05$ indicates a significant difference between the proportions of FNs and fFPs

Percentage of *Campylopus introflexus* in different biotope types

The model predicted that *C. introflexus* is present in about 27 % of the pixels within our study area, which corresponds to a total area of 6.5 km². According to our model predictions, the North of the island seems slightly more invaded (31 %) than the South (26 %) and the centre (22 %).

Our model predicted that *C. introflexus* occurs in 52 % of the dune grassland pixels (TMAP-Code X.5), in 29 % of the dune slack heath pixels (H.3), in 25 % of the dune heath pixels (X.6), and in 16 % of the yellow dune pixels (X.4), see Fig. 6.

Reduced number of calibration plots

The reduction of the number of calibration plots from 57 to about 17 plots did not necessarily lead to a decrease in prediction accuracy (see Fig. 7). However, McNemar test showed that model results were highly unbalanced when only 7 and 12 calibration plots were used. The model using 27 calibration plots also shows a highly imbalanced confusion matrix according to the McNemar test, but this was probably due to the relatively low value of the threshold for this model. A visual comparison of the resulting maps revealed that the general distribution pattern of *C. introflexus* does not change much for all of the models with 12–57

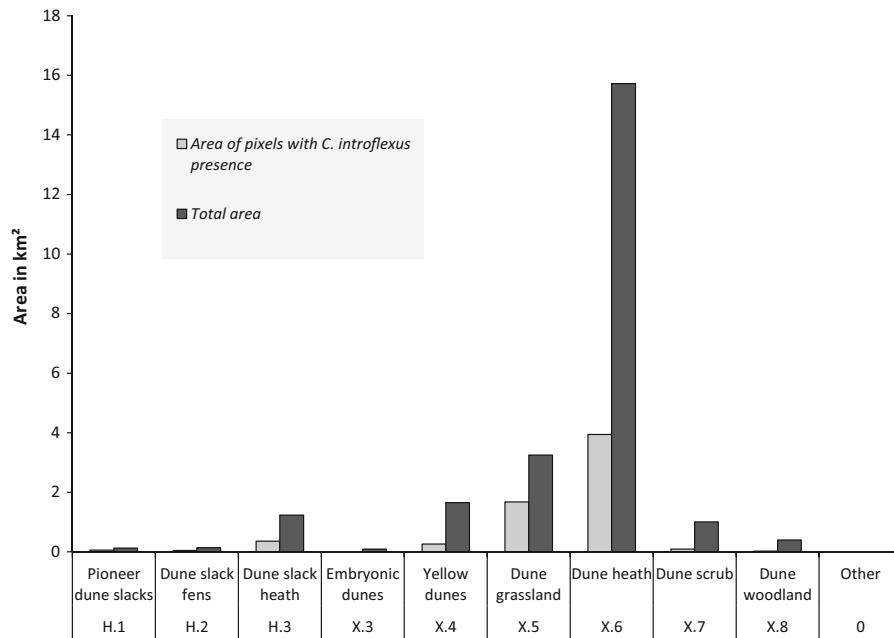


Fig. 6 Predicted percentage of pixels invaded by the invasive bryophyte *C. introflexus* for all TMAP vegetation types that cover a total area of at least 3 ha on the North Frisian island Sylt (Germany)

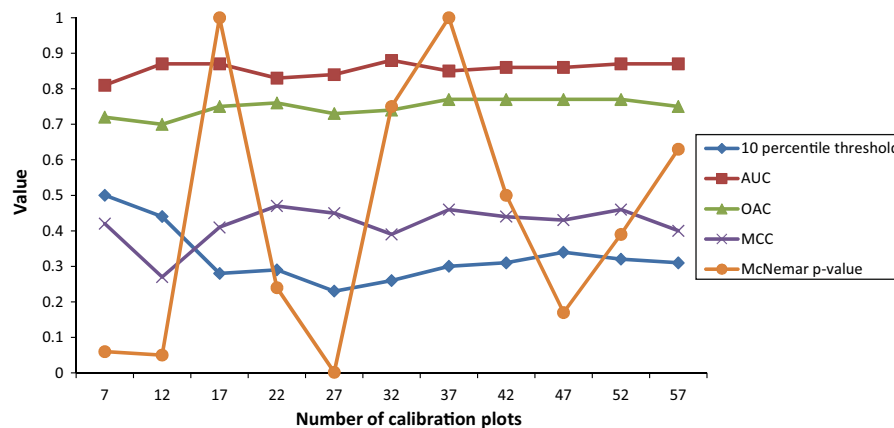


Fig. 7 Threshold value, area under the curve (AUC), overall accuracy (OAC), Matthews correlation coefficient (MCC) and p value of the McNemar test for different numbers of calibration plots ranging from 7 to 57 plots

calibration plots. Only the model with seven calibration plots showed a very different pattern in the prediction.

Discussion

How well can we map *Campylopus introflexus*?

The results of our modelling approach based on hyperspectral images show that it is possible to map

occurrences of *C. introflexus* in the dune areas of the island of Sylt with an overall accuracy of 75 %. This value is not extremely high compared to other studies using remote sensing to map invasive plant species, e.g. 93 % overall accuracy for *Solanum mauritianum* (Atkinson et al. 2014), 79 % and 91 % for *C. nutans* in preflowering and peak flowering state, respectively (Mirik et al. 2013), or 84.4 % for *S. altissima* (Ishii and Washitani 2013). However, taking into account the size and the inconspicuousness of the study species,

which mostly does not even covers a whole 1.8 m x 1.8 m pixel, and appears in very different forms and variable patch sizes, sometimes in very small quantities below the heathland shrubs, our results are considered sufficiently accurate.

The evaluation of the model with the independent validation dataset showed that most of the false negatives (*FNs*) are plots with less than 5 % cover of *C. introflexus* (nine plots out of 21). This means that the model is not able to detect very low cover fractions, which is not surprising as in those low cover plots *C. introflexus* usually appears below or between other species such as *E. nigrum* or *C. vulgaris*, and may thus not significantly contribute to the overall reflectance signal of the plot. Another four misclassified plots have higher cover, but are located less than one pixel away from predicted presences. This misclassification could be related to spatial inaccuracies in field and remote sensing data. This only leaves eight plots with medium to high cover of *C. introflexus*, which are mainly plots with a relatively high amount of *E. nigrum* and/or *C. vulgaris*, where *C. introflexus* occurs in between and below the other species. Therefore, the weighted mean of the reflection signal of the plot is probably dominated by the shrub signal.

This means that in practice, if using the maps for further analysis or for management, only eight plots with a significant cover of the target species would be overlooked. As the suggested management approach for *C. introflexus* (see introduction and last section of the discussion) does not necessarily require to precisely locate every single small occurrence, we judge that our resulting error to be within an acceptable range.

For the false positives (*FPs*), about four out of 16 plots have medium to high bare soil cover (white sand) similar to many invaded sites, which could be the reason for confusion. Another four plots are dominated by *A. arenaria*, here the contribution of the white sand to the overall reflection signal could also be responsible for the overprediction. Yet another four plots have heterogeneous vegetation cover. Here the misprediction could be due to confusion with lichens or bryophytes spectrally similar to *C. introflexus*. The remaining four plots are mainly dominated by *E. nigrum*, but do not have a high cover of bryophytes or lichens. Here the most probable explanation is a position uncertainty in combination with one of the explanations above, as the high number of true

negatives (*TN*) proves that model mostly succeeds in correctly classifying *E. nigrum* dominated areas without *C. introflexus* as such.

The true positives (*TPs*) are plots with mostly medium to high *C. introflexus* cover fractions of between 5 and 100 %. As Fig. 3 shows, the model accurately detects almost all high cover plots, but makes more mistakes with decreasing cover percentages of *C. introflexus*. So even if we are potentially missing or overestimating some of the low cover plots, the map still gives us a very good idea of the overall distribution of *C. introflexus* on the island, which was completely unknown before.

We therefore conclude that the map we produced from remote sensing is a good alternative to a traditional field mapping approach for *C. introflexus*. One main reason is the difficulty to detect and accurately estimate this species in the field: small occurrences of the moss cannot be detected from a long distance. Even standing directly on a plot, an observer has to search carefully before all smaller occurrences are detected or its presence can be safely excluded. Another major obstacle to mapping *C. introflexus* on Sylt from field observations is due to the large size of the area. However, a major drawback to the wide use of hyperspectral remote sensing data is the high costs associated with flight campaigns (He et al. 2011).

What are we actually modelling?

The general assumption behind our modelling approach is that we can map the actual distribution after applying a threshold to the occurrence probability map. However, the model is trained with mixed stands of the target species and co-occurring vegetation that result in a mixed spectral signal. It is thus possible that we model not only the actual distribution, but also, partly, potential habitats. Due to a similar co-occurring vegetation, potential uninvaded habitats might have a reflectance signal that is very similar, especially to the plots with low *C. introflexus* cover. In order to verify to which extent our modelling results are correct and represent real presences, we validated against an independent dataset.

We tested a two-step modelling approach in order to differentiate between actual distribution and potential habitats, which are presumably both included in the basic modelling approach. Here the presumption is

that by running the model again on a background that is restricted to the results of the basic modelling, we can separate potential habitats from actual distribution, modelling only the latter. As the results show, the modelled presences are much more restrictive than the presences predicted by the basic modelling, and thus probably underestimate the real presences of *C. introflexus*.

A reason could be that the model is searching for reflectances similar to the ones in the calibration dataset. However, the model does not know how exactly the spectral signal of *C. introflexus* looks like, and will thus only model any reflectances similar to the mixed pixels containing a certain amount of *C. introflexus*. As shown in the analysis of the misclassified validation plots of the Maxent modelling, those include a variety of different types of plots, and we cannot say if they are classified incorrectly because of similar reflectances of potential habitats or because of similar reflectance signals of the co-occurring species. This could be especially true for plots with high covers of lichens and some mosses similar to *C. introflexus* in terms of structure, biomass etc. Presumably, the two-step modelling further narrows the similarity criteria, which is further restricting the presences, not necessarily to true presences but to similar reflectance of all sorts. We conclude that the two-step modelling did not provide a further improvement of the prediction in the case of our study species.

Another answer to the question of what we are actually modelling can be found in the band regions of the hyperspectral remote sensing data: which are the most important single bands and band regions indicating *C. introflexus* presences? The large majority is located in the short wave infrared (between 1300 and 2500 nm). This region is dominated by strong water absorptions, which not only affects certain bands, but has a carry-over effect on the region between the main absorption bands (Kumar et al. 2002). Plots dominated by *C. introflexus* have higher reflectances, indicating a lower water content of the plants. Furthermore, this spectral region is characterized by absorptions of biochemical compounds such as lignin, cellulose, starch, proteins and nitrogen, but the absorption of those molecules are rather low, and they are usually masked by water absorption in the case of fresh leaves (Kumar et al. 2002). Thus, our model may not only detect occurrences of *C. introflexus* but it may also detect other areas that have low water content, thus

possibly overestimating the total area invaded by *C. introflexus* on the island of Sylt. For example plots where *C. introflexus* is not present but with high covers of similar mosses, lichens, certain small grasses or a high bare soil cover could be misclassified for that reason.

The fact that our model relies on different areas of the spectrum, mainly on bands in the short wave infrared, also underlines the benefits of using data with a high spectral resolution for the analysis and suggests that the detection using remote sensing data with a lower spectral resolution might not be as successful. While associated with high costs, hyperspectral data also offers significant advantages for detecting invasive plant species due to the use of a wider range of the spectrum (see He et al. 2011). However, future research is needed to test whether the species might also be detectable using data with a lower spectral resolution, which is available for larger areas at lower costs.

Can we use this approach for early detection?

In order to answer the question whether our approach can support an early detection of invasive plant species, we will discuss the effects of thresholding, the reduction of the number of calibration plots and our model performance for low cover plots.

The selection of the threshold for a given model significantly influences the resulting binary presence–absence map. While some authors recommend to avoid setting thresholds whenever possible (Merow et al. 2013), it is necessary to use a threshold value in order to derive binary predictions from probabilities of presence, for example for management purposes or, in our case, to quantify the amount of *C. introflexus* in different biotope types. In our case the ‘10 percentile training presence’ showed good performances for different accuracy measures. However, it might be useful to vary the threshold depending on the purpose of the map. For a conservative estimate of the species’ overall presence in the area, a higher threshold might be useful, whereas a lower threshold could be employed if a land manager wants to identify all possibly invaded areas within an early detection and management framework. Another option would be to use the probability map, considering the classes above the threshold as areas where the species most probably occurs and the first class below the threshold as areas

that should additionally be searched if the goal is to find all occurrences.

Another question is whether our approach shows good results when having a limited number of calibration plots available, which would be the case for a species that recently invaded the area. As shown in Fig. 7, the model produces good results with a small number of calibration plots. The evaluation using different accuracy measures showed that 17 calibration plots are enough to produce a reliable model. The visual inspection of the projected map indicated that even with 12 calibration plots, our modelling approach can generate patterns similar to the ones with a much larger number of calibration plots. The small number of presences needed are in accordance with findings from (Baldeck and Asner 2014), who concluded that for differentiating savannah tree species, about 19 crowns were sufficient for calibrating the model. However, in those ecosystems, the crowns usually cover at least several pixels, while in our dune ecosystem, *C. introflexus* is usually mixed with many with other species. They concluded that the data-accuracy-relationship depends on the species and their spectral separability and expect the basic structure of the relationship to be similar for most datasets.

This suggests that this approach can significantly reduce the field work effort, at least for the calibration plots, and that we can also use this approach for species that are not (yet) very widespread. For validation, however, we found that a larger dataset would allow more detailed conclusions on the model performance. The main challenge is to collect a balanced dataset: from our dataset of 150 random plots, only about one third were presence points. Depending on the size of the area and the previous knowledge of the target species, such data (presence for calibration, presence and absence for validation) can be collected within one to 4 weeks by one person, as our experience from this and other field campaigns has proven.

As discussed before, the model performance decreases for low cover plots (see Fig. 3). This means that we do have to deal with a certain amount of poor prediction accuracy for low cover plots. However, we can say that our approach gives good results even with reduced number of calibration plots; and setting a lower threshold, we have a good chance of also detecting recently invaded areas with low cover values, which can then be verified during field visits.

Overall, this approach could greatly reduce the overall searching effort for large areas.

How widespread is *Campylopus introflexus* in the different biotope types and what does that mean for the dune ecosystem?

We found that on the island of Sylt, *C. introflexus* is much more widespread than we anticipated. According to our model, it is present in about one quarter of the pixels in our study area. Even in the case that our model overestimates the distribution of *C. introflexus*, we still found a high level of invasion of this species on the island (cf. empirical data from the validation plots: 48 occurrences out of randomly located 150 plots). While the species spread was studied extensively on the East Frisian Islands (see Hahn 2006), no in-depth studies on the occurrence of *C. introflexus* on the island of Sylt have been carried out up to date.

The general underestimation of bryophyte invasion was also reported in recent studies that have evaluated the impact and the future spread of invasive bryophytes and estimated them to be much more widespread than currently known: Mateo et al. (2014) modelled the potential range of *C. introflexus* and two other invasive bryophytes in the Northern hemisphere and found that it is considerably larger than the realized range, encompassing large portions of central and eastern Europe, North America and eastern Asia. Essl et al. (2014) stated that bryophytes are a largely understudied group of invasives and found that the impact of invasive bryophytes will most likely increase in the future.

Our analysis of the different TMAP dune types showed that for the most abundant TMAP type, the dune heath, about one quarter of the pixels is predicted to be invaded by *C. introflexus*, while for the second most abundant TMAP-type, the dune grassland, about half of the area is predicted to be invaded pixels. *C. introflexus* usually invades sunny sites with low pH-values that have gaps in the vegetation cover (Frahm 1972) and benefits from nitrogen deposition and carbon-rich soils (Sparrius and Kooijman 2011). It expands rapidly in suitable areas. In coastal areas, it often becomes dominant in bryophyte- and lichen rich sandy xeric grasslands (grey dunes), but also establishes in the dune heath in gaps in the vegetation cover (Starfinger et al. 2003). In Denmark, Klinck (2009) examined about 5000 plots in dune areas and found

that *C. introflexus* was present in 15 % of the grey dunes, and 12 % of the dune heath. Our model is generally in accordance with those findings, as it predicts the highest values for dune grasslands (50 % of the pixels invaded), and lower values in the dry dune heath (25 % of the pixels invaded), but predicts higher total degrees of invasion in these habitat types than were found before. However, those percentages should be interpreted with caution, as they are potentially subject to misdetection. For the other TMAP-types present on the island, the model also predicts the invasion by *C. introflexus*, but due to the limitations mentioned before and the fact that most of the plots used to calibrate the model are located within the two most abundant biotope types, the dune grassland and the dune heath, the predictions for the other TMAP-types should be considered with caution. Regarding the question of transferability of our results to other study areas we therefore propose the following: it should be possible to apply the same model to study areas with similar biotope types, but probably would not work with a system where the characteristics of the surrounding vegetation substantially differ; future research is needed to prove those suggestions.

Given that up to one quarter of the pixels (about 6 km²) of our study area are probably invaded, we argue that *C. introflexus* will change the dune ecosystem and will likely negatively affect the dune habitat. We suggest that on the island of Sylt, the development of *C. introflexus* should be monitored closely in the future by establishing permanent plots. Moreover, the burial of *C. introflexus* with sand through the reactivation of dunes should be considered as a management option, as it is currently the most promising method to reduce the presence of *C. introflexus* without adversely affecting the surrounding vegetation (Boxel et al. 1997; Ketner-Oostra and Sýkora 2000). When the covered by sand, lichens and other pioneer species can establish upon the moss carpets and act as secondary pioneers (Ketner-Oostra and Sýkora 2004). It should further be determined which other factors (e.g. disturbances due to rabbit activity, lowering of the ground water table particularly in dune slacks) are actually driving the spread of *C. introflexus* on the island of Sylt and whether any action can be taken to limit this spread.

We presume that because of the small size and inconspicuous character of this species, and the fact that bryophytes are often not included in vegetation

surveys such as the recent biotope mapping from 2012 (Leguan 2012), its presence has gone mostly unnoticed in the recent years on the island of Sylt, and that on other dune areas, its presence might currently also be underestimated. We therefore recommend that the moss should be regularly included in large scale vegetation surveys such as the biotope mapping, and to constitute a separate TMAP-type and if available use hyperspectral remote sensing data in dune areas when it is known or suspected to be present. While small occurrences are difficult to map in the field, the larger mats are easy to recognize even from a distance without being a moss expert. As the species may cause severe impacts on the dune ecosystem, its spread should not go unnoticed.

Conclusion

Our study has demonstrated that hyperspectral remote sensing data can be used successfully to project the presence of an invasive moss species. Even with a certain degree of uncertainty, the projection is useful to understand the general distribution of the invasion over a large area. As invasive bryophytes are a largely understudied group of species, remote sensing provides a viable alternative to traditional field mapping for producing insights at larger scales, and to predict their presence in open areas such as dune ecosystems. Even though the acquisition of airborne hyperspectral data is very cost-intensive, it provides information and insights impossible to gather with traditional methods. While this study provides a baseline of the invasion impact and explores the feasibility of the approach, more research is needed in order to fully understand the impact of *C. introflexus* on the different biotopes on the island of Sylt as well as to explore the feasibility of possible management options.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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