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Quantifying the recent expansion of native invasive rush species in a UK upland environment

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Abstract

Rushes, such as soft rush (*Juncus effusus* L.), hard rush (*Juncus inflexus* L.), and compact rush (*Juncus conglomeratus* L.) have become problem species within upland grasslands across the United Kingdom and the coastal grasslands of western Norway. Indeed, being largely unpalatable to livestock and having a vigorous reproductive ecology means that they can rapidly come to dominate swards. However, rush dominance results in a reduction in grassland biodiversity and farm productivity. Anecdotal evidence from the United Kingdom suggests that rush cover within marginal upland grasslands has increased considerably in recent decades. Yet, there is currently no published evidence to support this observation. Here, we use recent and historical Google Earth imagery to measure changes in rush frequency over a 13-year period within four survey years: 2005, 2009, 2015, and 2018. During each survey year, we quantified rush presence or absence using a series of quadrats located within 300 upland grassland plots in the West Pennine Moors, United Kingdom. Data were analysed in two stages, first, by calculating mean rush frequencies per sample year using all the available plot-year combinations (the full dataset), and second by examining differences in rush frequency using only the plots for which rush frequency data were available in every sample year (the continuous dataset). The full dataset indicated that rush frequency has increased by 82% between 2005 and 2018. Similarly, the continuous dataset suggested that rush frequency has increased by 174% over the same period, with the increases in frequency being statistically significant ($p < .05$) between 2005–2018 and 2009–2018. We discuss the potential drivers of rush expansion in the West Pennine Moors, the ecological and agronomic implications of grassland rush infestations, and priorities for future research.

KEYWORDS

Google imagery, habitat change, hill farming, *Juncus* spp., native invasive species, upland breeding birds, upland habitats, upland land management

1 | INTRODUCTION

Soft rush (*Juncus effusus* L.), hard rush (*Juncus inflexus* L.), and compact rush (*Juncus conglomeratus* L.) (henceforth known as "rushes" in this research paper) are native to the British Isles and occur throughout its many habitats (Preston, Pearman, & Dines, 2002). Rushes are generally tussock-forming, slowly spreading perennials that have a preference for wet, acidic, and nutrient-poor environments (Hill, Preston, & Roy, 2004; Richards & Clapham, 1941b, 1941c, 1941d). Nevertheless, they can establish and proliferate under a broad range of environmental conditions (Hill et al., 2004; Richards & Clapham, 1941b, 1941c, 1941d). However, the complete range of conditions under which rushes can survive (i.e., their fundamental niche) remains largely unknown (see, e.g., Hamilton, Ross, Silcock, & Steer, 2018).

In contrast, we do know about the reproductive ecology of rushes. For example, they can produce between 4,500 and 8,500 seeds per stem per year (Kaczmarek-Derda et al., 2014; McCarthy, 1971), which, on rush infested ground, equates to 4–6.7 million seeds per square metre per season (Ervin & Wetzel, 2001; Moore & Burr, 1948). To produce such large amounts of seed, a single rush plant only uses 0.27% of its annual net biomass production (Ervin & Wetzel, 2001). Depending on species, seeds ripen between July and September and are shed (mainly by the wind during dry conditions) up to the following spring (Richards & Clapham, 1941a, 1941b, 1941c). After shedding, seeds can remain dormant at the soil surface for up to 60 years (Moore & Burr, 1948), and, during this time, they may be dispersed by wind or surface run-off and/or germinate in areas disturbed by cultivation or livestock poaching (Agnew, 1961; Cairns, 2013; McCarthy, 1971). Once established, rushes persist for a long time and usually expand clonally via a shallow system of short rhizomes (Kaczmarek-Derda, Østrem, Myromslien, Brandsæter, & Netland, 2019), which ultimately leads to the formation of dense stands covering entire fields.

The vigorous reproductive ecology of rushes may be a contributing factor behind their recent invasion of upland grasslands across the United Kingdom and the coastal grasslands of western Norway (Cherrill, 1995; Østrem, Folkestad, Solhaug, & Brandsæter, 2018). Indeed, there is anecdotal evidence from farmers and ecologists in the United Kingdom of rush infestations within upland grasslands (Hamilton et al., 2018). Such infestations are problematic because they significantly reduce the agricultural and conservation value of the land (Cairns, 2013; Coyle, Whitehead, & Baines, 2018). However, while there have been several static assessments of grassland rush infestation in the United Kingdom (e.g., Cherrill, 1995; Hopkins, Matkin, Ellis, & Peel, 1985), there are currently no peer-reviewed studies that have attempted to measure changes in grassland rush expansion over time (but, e.g., within the grey literature, see: O'Reilly, 2011; Hamilton et al., 2018). The present study aims to address this research gap by providing a direct quantitative assessment of changes in grassland rush frequency between 2005 and 2018 within a large upland area: The West Pennine Moors Site of Special Scientific Interest (SSSI). In addition to presenting our results, we discuss the potential drivers of rush expansion in the West Pennine Moors (WPM), the agronomic and ecological implications of grassland rush infestations, and future research priorities.

2 | MATERIALS AND METHODS

2.1 | Site description and justification

The WPM Site of SSSI is situated in the North West of England (Figure 1). The site covers an area of 76 km^2 and an elevation range of 100–450 m. It was designated as a SSSI in 2016 because of its extensive mosaic of upland and upland-fringe habitats, which support significant populations of breeding birds, including waders such as curlew (*Numenius arquata* L.), snipe (*Gallinago gallinago* L.), and lapwing (*Vanellus vanellus* L.) (Natural England, 2016). The Centre for Ecology & Hydrology (CEH) Land Cover Map (LCM) data from 2015 (Rowland et al., 2017) indicates that the dominant upland habitats within the SSSI are blanket bog, acid grassland and heather moorland; however, there are also substantial areas of improved grassland and broadleaved woodland (Figure 1).

We chose to measure rush expansion within the WPM SSSI for two reasons. First, the SSSI contains large areas of marginal grassland, that is, semi-improved and enclosed permanent pasture at or below the moorland line (above this line the land is generally unimproved and unenclosed). These grasslands are vital to hill farmers because they tend to be the most productive areas of their farm (Mansfield, 2008; Nielsen & Søegaard, 2000). Also, by providing suitable nesting habitat, marginal grasslands can support large populations of wading bird species (Baines, 1988; Dallimer et al., 2010; Dallimer, Skinner, Davies, Armsworth, & Gaston, 2012). Crucially, the value of marginal grasslands to both farmers and birds decreases as rush cover increases: rushes are generally less palatable and digestible to livestock than other grassland species (Grant, Bolton, & Russel, 1984; Nielsen & Søegaard, 2000; Tweel & Bohlen, 2008), so increases in rush cover reduce grassland productivity and milk/meat production (Cairns, 2013); likewise, for wading birds, grasslands where rush cover exceeds 30% become suboptimal nesting habitat (RSPB, 2017). The second reason for choosing the WPM SSSI is that there are anecdotal reports from Natural England advisors and farmers of substantial increases in grassland rush cover over the past 20 years (K. Rogers, personal communication, April 15, 2019).

2.2 | Detecting rush (*Juncus* spp.) using Google Earth imagery

Rush tussocks are visible on colour aerial imagery, but only within habitats where the surrounding vegetation is much shorter and of a different colour or tone. The marginal grasslands within the WPM SSSI meet these criteria. For example, Figures 2 and 3 demonstrate that, compared to other upland habitats, there is a considerable height and colour differential between rush tussocks and the surrounding vegetation (mainly Poaceae spp.) within these grasslands, and these

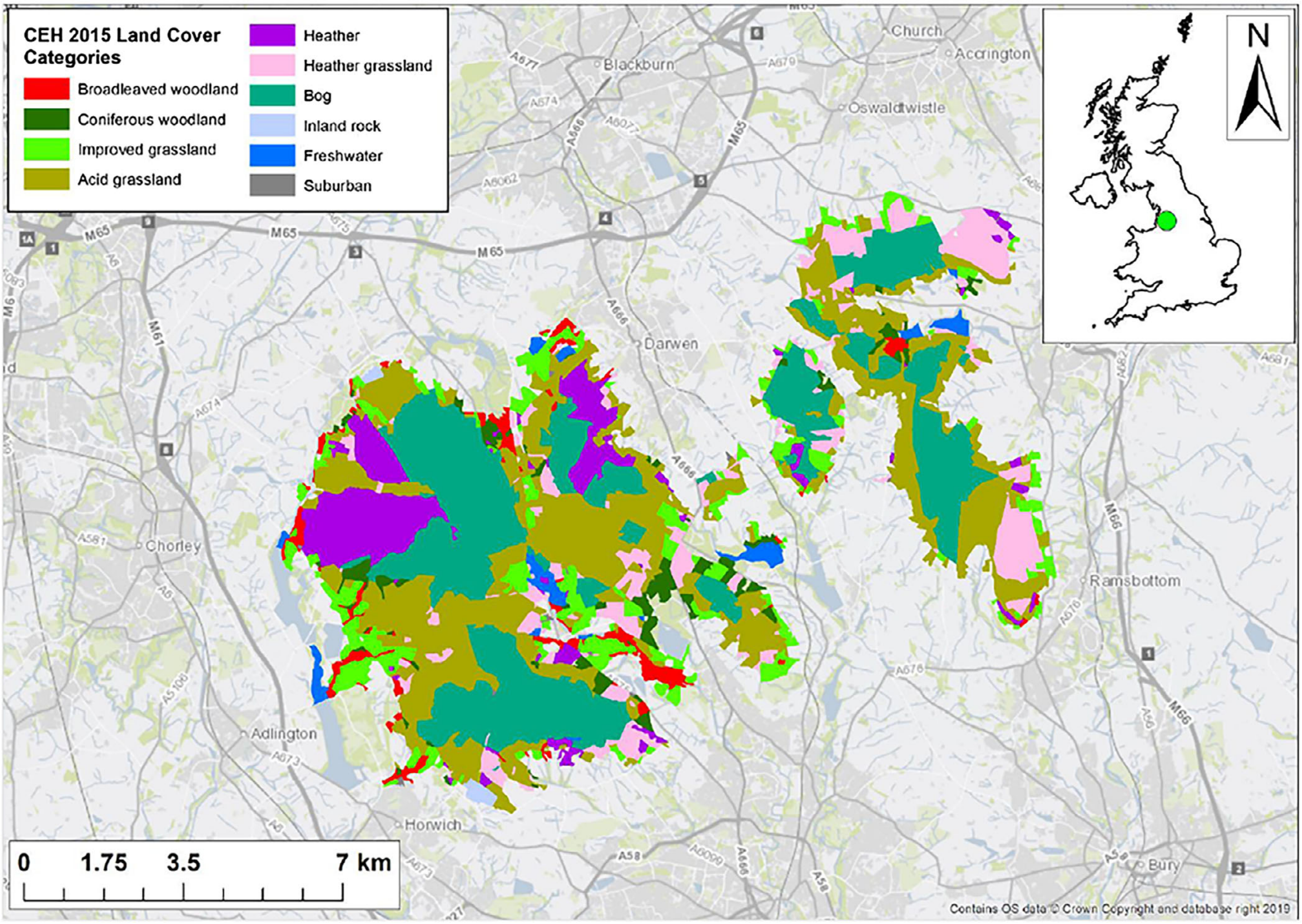

FIGURE 1 CEH land cover categories present within the West Pennine Moors SSSI (Rowland et al., 2017). Inset: Location of the West Pennine Moors SSSI (green circle) in the United Kingdom. The base map used is the Ordnance Survey Open Background map accessed through ArcGIS 10.4. CEH, Centre for Ecology & Hydrology

differences mean that rush tussocks are clearly visible on the corresponding aerial imagery. Thus, rush frequency within marginal grasslands can be quantified using aerial imagery and, if historical aerial imagery is available, one can measure changes in rush frequency over time. Google Earth (Google, Inc.) provides historical aerial imagery of the WPM SSSI for 2005, 2009, 2015, and 2018. However, images from 2009 and 2015 only provide partial coverage of the SSSI. Using the available Google Earth imagery data, we aimed to quantify changes in rush frequency within the marginal grasslands of the WPM SSSI during four time periods: 2005, 2009, 2015, and 2018.

We decided to use aerial imagery instead of field surveys because there is a lack of historical field data on rush expansion within the marginal grasslands of the WPM SSSI. Furthermore, while field surveys are likely to be more accurate, rush expansion can be measured more efficiently using aerial imagery, which means that larger areas of grassland can be surveyed. Furthermore, the use of aerial imagery is much more convenient for sampling more remote or inaccessible areas and you do not require prior permission from landowners.

2.3 | GIS selection of marginal grassland parcels

We used CEH LCM 2015 vector data (Rowland et al., 2017) to select marginal grassland parcels that lay within or intersected the WPM SSSI boundary. Because the CEH LCM 2015 does not have a "Marginal grassland" land cover category (Rowland et al., 2017) we adopted the "Improved grassland" land cover category as a surrogate because Google Earth aerial imagery revealed this to be the best proxy for marginal grassland within the WPM SSSI. According to the CEH LCM 2015, "Improved grassland" is "characterised by vegetation dominated by a few fast-growing grasses such as *Lolium* spp., and also white clover (*Trifolium repens*), on fertile, neutral soils. Improved Grasslands are typically either managed as pasture or mown regularly for silage production" (NERC, 2017).

In total, 340 improved grassland parcels lay within or intersected the WPM SSSI boundary. However, 40 grassland parcels were excluded from our survey because Google Earth imagery revealed that non-grassland habitats constituted ≥25% of their extent. We used the remaining 300 grassland parcels as discrete sampling units in which we measured temporal changes in rush frequency (see Supporting

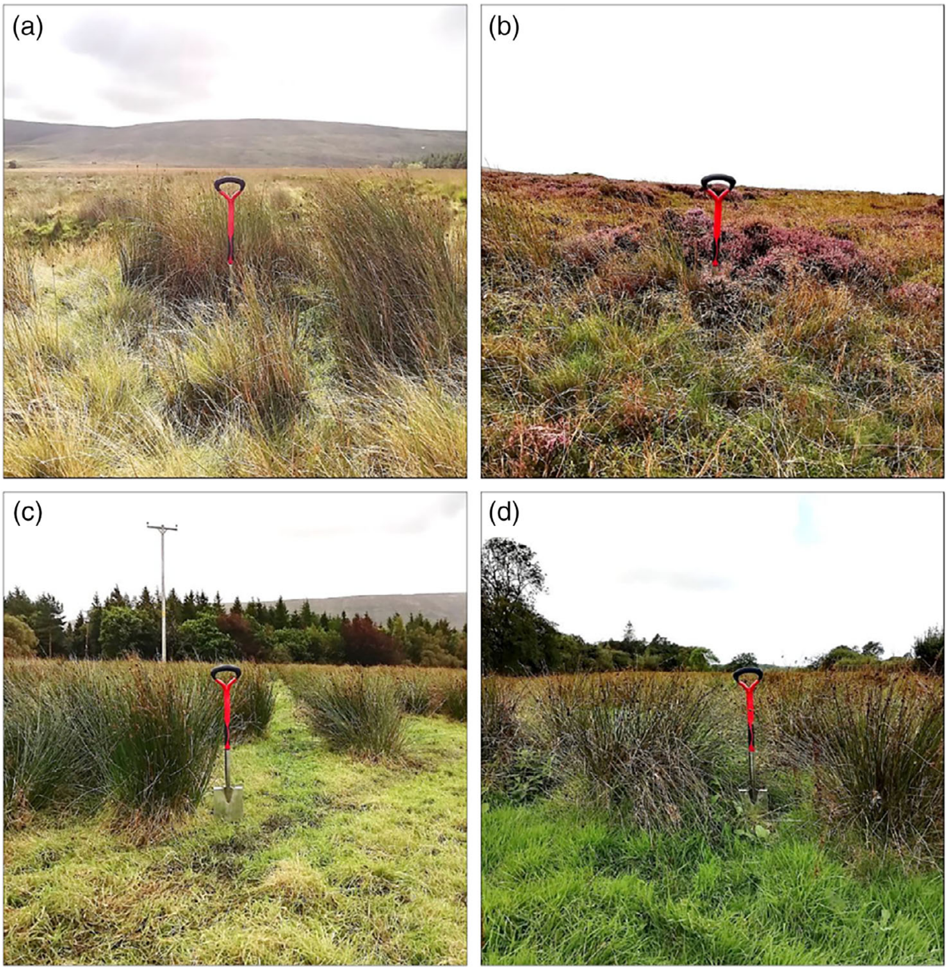

FIGURE 2 The upper photos show the homogeneous height and colour contrast found between rushes and the surrounding vegetation within (a) Acid Grassland and (b) Heather Moorland. The lower photos show the heterogeneous height and colour contrast found between rushes and the surrounding vegetation within the Marginal Grasslands (c and d). The large height and colour contrast between rushes and the surrounding vegetation within Marginal Grassland parcels mean that it is clearly visible on Google Earth imagery (see Figure 3). The spade pictured is 1 m tall. All photos were taken on the September 11, 2019

Information File 1). These parcels varied in size from 0.5 to 18.8 ha (mean parcel area of 2.8 ± 0.1 ha) and occurred at elevations ranging from 140 to 341 m (mean parcel elevation of 253.5 ± 2.4 m).

2.4 | Retrieval and processing of Google Earth imagery

We downloaded Google Earth images from 2005, 2009, 2015, and 2018 that corresponded to the 300 marginal grassland sample parcels we intended to survey. Google Earth images were available for every sample parcel in 2005 and 2018 but only for a selection of parcels in 2009 and 2015. Furthermore, even when an image was available for a given survey year, there were specific instances when it could not be used for a given sample parcel. For example, if the sample parcel had been mown, was shaded, covered in bare earth (e.g., temporary ground disturbance, such as ploughing) or there was low contrast between rush tussocks and the surrounding vegetation. Consequently, we used a different number of grassland sample parcels during each survey year (Table 1). Further information on image availability and usage is provided in the Supporting Information (Files 2 and 3).

A total of 205 high-resolution Google Earth images were downloaded (Table 2). All images were selected from an eye altitude of 1 km while all Google Earth layers were switched off. Also, before a Google Earth image was captured, the compass and tilt were reset, and the "Atmosphere," "Sun," and "Water surface" options from the "View" menu were also deselected. After an image was downloaded, it was imported into ArcGIS and then georeferenced. Google Earth images are orthorectified, but the original images are captured using different camera angles (Google, Inc.). Therefore, to enhance subsequent alignment, the images were planimetrically corrected. We began by georeferencing 2018 images to the Ordnance Survey Open Carto base map layer within ESRI ArcGIS 10.4 using four control points per image (e.g., building corners, road intersections, and field boundary intersections). We then aligned 2005, 2009, and 2015 images to the georeferenced 2018 images using between 4 and 35 control points per image, that is, we stopped adding control points once a reasonable alignment had been achieved. Root mean square (RMS) error is a measure of georeferencing accuracy because it calculates the distance between known locations and locations that have been georeferenced. Therefore, care was taken to ensure that the RMS error of each georeferenced image was <1 (Table 2). Additional information about the aerial images used in this study is contained

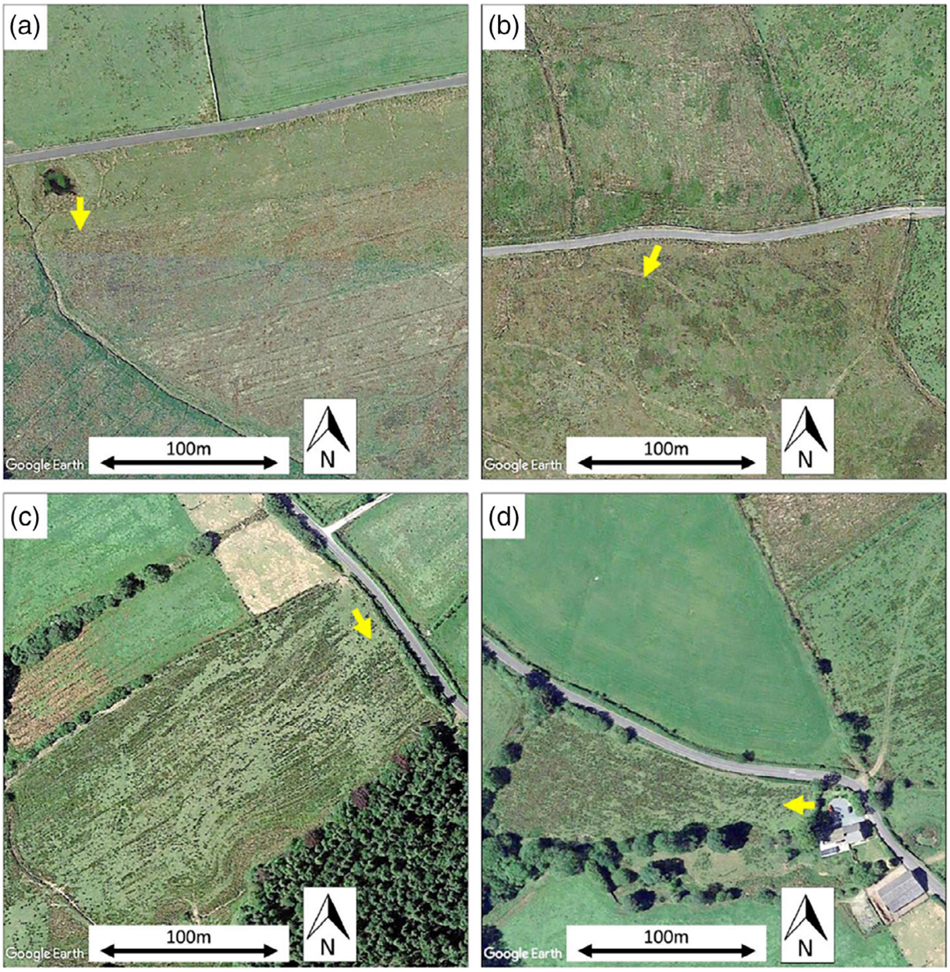

FIGURE 3 Modified Google Earth images corresponding to photographs (a–d) in Figure 2. The yellow arrow denotes the location and direction of the corresponding photograph. Note how rushes cannot be seen clearly within (a) Acid Grassland parcels and areas of (b) Heather Moorland, but they can be seen clearly within Marginal Grassland (c and d)

TABLE 1 The number of grassland parcels used for each survey year

Survey year	Number of parcels used
2005	293
2009	106
2015	189
2018	283
All years	91

Note: The "All years" category refers to sample parcels for which data were available across all four survey years (i.e., continuous data).

within Supporting Information File 2 (image date, the number of georeferenced points used, and the RMS error per image).

2.5 | Sampling strategy

We used a stratified random sampling approach whereby we recorded rush frequency per grassland parcel within 10 randomly placed 2 m × 2 m quadrats sited in a 20 m × 20 m randomly located sample area. The same random quadrats were used during each survey year (2005, 2009, 2015, and 2018). To begin with, a negative 20 m buffer was applied to each of the 300 grassland parcels. This was performed to ensure that the randomly located sampling plots did not extend outside the grassland parcel boundary. We then created a single randomly located 20 m × 20 m sampling plot within each of the 300 marginal grassland parcels using the "Create Random Points" and "Buffer" tools within ArcGIS. After this, we used the same process as above to create 10 random 2 m × 2 m quadrats within each 20 m × 20 m sample plot. During this process, we set the "Minimum Allowed Distance" to 1.5 m to ensure that the quadrats did not overlap. Finally, we recorded whether rush tussocks were present or absent within each of the 10 quadrats for each available plot and survey year combination (see Supporting Information File 3 for raw frequency data). Figure 4 provides an illustrative example of how rush frequency was recorded across survey years.

2.6 | Accuracy and limitations of the method

We validated the accuracy of our rush detection method by ground truthing 45 (15%) of the 20 m × 20 m sample plots. Validation plots were selected using a convenience sample based on their proximity to roads and public footpaths. The first stage of the validation process involved visiting all 45 of the 20 m × 20 m validation plots and recording whether rush tussocks were present or absent. A shapefile containing all 45 of the 20 m × 20 m validation plots was loaded into Google Maps (Google, Inc.) so that they could be accurately located using a tablet in the field. It is important to note that we recorded rush as absent if individual stems of young rush plants were present, but rush tussocks were absent. We did this because individual rush stems are not visible on aerial imagery, but rush tussocks are. Consequently, our approach is likely to underestimate rush frequency. Ground truthing took place on the September 20, 2019.

During the second stage of the validation process, the most recent Google Earth images used during our survey (2018) were inspected to determine whether rush was present or absent within each of the 45 plots visited in the field. Unfortunately, because of the lack of site-specific field data, we could not validate rush presence within the plots during earlier study years (2005, 2009, and 2015). The field and 2018 aerial image data were then compared, and this indicated there was 100% agreement between the two datasets (see Supporting Information File 4 for raw validation data). Despite the complete agreement between aerial imagery and field

TABLE 2 Descriptive statistics for the georeferenced Google Earth images used for each survey year

		Georeference points		RMS error	
Survey year	No of images	Mean ± *SEM*	Min–Max	Mean ± *SEM*	Min–Max
2005	70	10.4 ± 0.7	4–30	0.4 ± 0.0	0.02–0.56
2009	19	8.0 ± 0.9	4–17	0.3 ± 0.0	0.07–0.51
2015	46	9.1 ± 0.8	4–35	0.3 ± 0.0	0.03–0.75
2018	70	4.0 ± 0.0	4–4	0.2 ± 0.0	0.02–0.36

Note: RMS error minimised using a first order polynomial (Affine) transformation. For further information about the Google Earth images used see Supporting Information File 2.

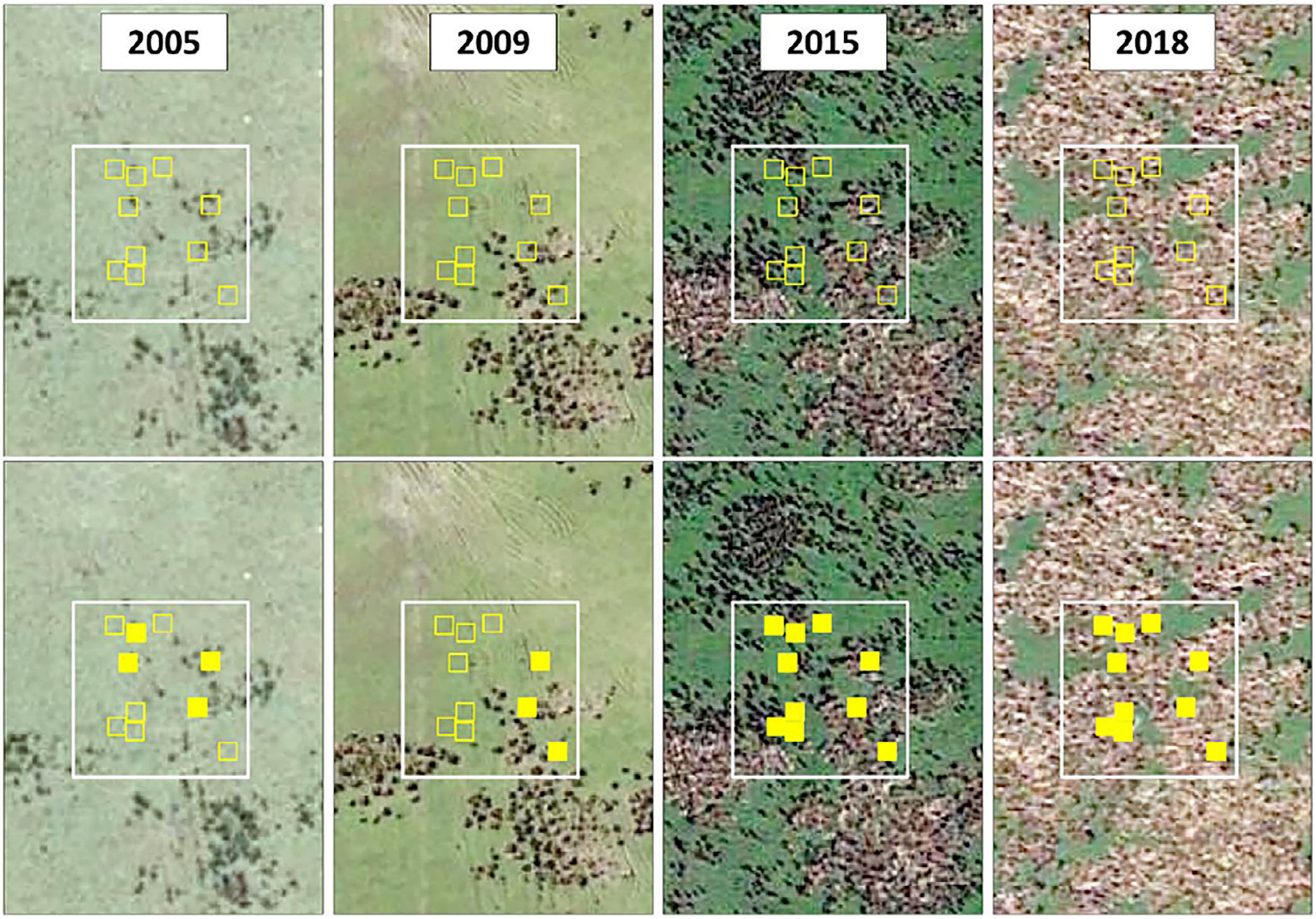

FIGURE 4 An illustrative example of recording rush frequency within the 10 quadrats (yellow squares) in the sample plots (white squares) across each sample year. Along the bottom row, quadrats are filled if rush is present and unfilled if rush is absent. Quadrats along the top row are left unfilled for comparison. We recorded rush as present if any part of a rush tussock (no matter how small) was within the quadrat boundary

data, the 2 m × 2 m quadrat polygons used during our survey are only likely to have sampled the same approximate (rather than exact) area within each grassland parcel between sample years. This is because Google Earth imagery is orthorectified, but the source images are captured using different camera angles, which means perfect alignment between survey years is impossible. Nevertheless, the RMS error of georeferenced images was extremely low during each survey year (Table 2). Furthermore, during the georeferencing process, care was taken to ensure that the field boundaries of the sample grassland parcels were aligned between survey years. Finally, it is also worth noting that other types of tall vegetation (e.g., thistles or nettles) may look similar to rushes on aerial imagery. However, such vegetation was rare within validation plots. In short, while our approach is not perfect, we believe that we have minimised error sufficiently to be confident that our approach is an accurate and valid technique for measuring rush frequency within marginal grasslands.

2.7 | Data analysis

All statistical tests were performed in R v.3.6.0 (R Core Team, 2019). Plot within study year served as a replicate during data analysis. For every plot-year combination (i.e., replicate), we summed the number of quadrats containing rush, which gave a rush frequency score of between 0 and 10. We subsequently examined temporal changes in rush frequency in two stages.

2.7.1 | Stage 1: Measuring rush frequency using the complete dataset

Initially, we used descriptive statistics to explore changes in mean rush frequency across all survey years using all the sample plots for which frequency data were available: 294 sample plots in 2005, 106 sample plots in 2009, 189 sample plots in 2015, and 283 sample plots in 2018. We also calculated and graphed the proportion of plots per study year in which rush frequency was: 0 (absent), 1–3, 4–6, 7–9, or 10 (dominant).

2.7.2 | Stage 2: Measuring rush frequency using only continuous data

During the second stage of analysis, we only used the 91 plots for which frequency data were available for 2005, 2009, 2015, and 2018 (the continuous dataset). Using these data, we tested for changes in rush frequency over time (2005, 2009, 2015, and 2018) using a Friedman's test. We used Friedman's test instead of a repeated-measures ANOVA because the data failed to meet several parametric assumptions, namely, normality and the homogeneity of variances. Friedman's test was followed up by post hoc comparisons between individual survey years using Wilcoxon signed-rank tests in which pairwise significance values were adjusted using the Bonferroni correction method.

Using the continuous frequency data, we then calculated and graphed three additional parameters. First, we calculated the average percent change in rush frequency per plot between 2005–2009, 2009–2015, and 2015–2018. Second, each of the 91 plots was assigned to one of three categories depending on whether rush frequency remained stable, increased or decreased between 2005 and 2018: "No change" (=), "Positive" (+), or "Negative" (–). Finally, we calculated the number of plots per study year in which rush frequency was: 0 (absent), 1–3, 4–6, 7–9, or 10 (dominant).

3 | RESULTS

3.1 | Examining rush frequency using the complete dataset

The complete dataset suggests that rush frequency has increased by 81.7% over the whole study period between 2005 and 2018 (Figure 5a). In line with these increases, rush absence decreased, and rush dominance increased within sample plots between 2005 and 2018 (Figure 5b). For example, rush was absent in 57.3% of the plots during 2005 but only absent in 35.3% of plots in 2018 (Figure 5b). Conversely, rush was dominant in only 6.8% of plots in 2005, but 16.3% of plots in 2018 (Figure 5b).

3.2 | Examining rush frequency using only continuous data

For the 91 plots for which we had continuous data, we recorded an increase in rush frequency during each consecutive study year (Figure 6a). Overall, mean rush frequency increased by 174.2% between 2005 and 2018. The Friedman test results indicated that the differences in rush frequency across all study years were significant ($df = 3$, $\chi^2 = 48.5$, $p < .001$). Furthermore, post hoc Wilcoxon signed-rank test comparisons suggested that there were significant differences in rush frequency between 2005–2018 ($p = .003$) and 2009–2018 ($p = .023$) (Figure 6a). Conversely, changes in rush frequency between 2005–2009, 2005–2015, and 2009–2015 and 2015–2018 were not significant.

The largest percentage increases in rush frequency within the WPM SSSI occurred between 2009–2015 and 2015–2018, with mean percentage increases in rush frequency per plot of 51.9 ± 17.2% and 53.8 ± 15.7% recorded during these periods, respectively (Figure 6b). Overall, between 2005 and 2018 rush frequency remained unchanged within 45 plots (49.5% of plots), increased within 39 plots (42.9% of plots), and decreased within seven plots (7.7% of plots) (Figure 6c). Finally, during each consecutive study year (2005, 2009, 2015, and 2018) the number of plots in which rush was absent decreased and the number of plots in which rush was dominant increased (Figure 6d).

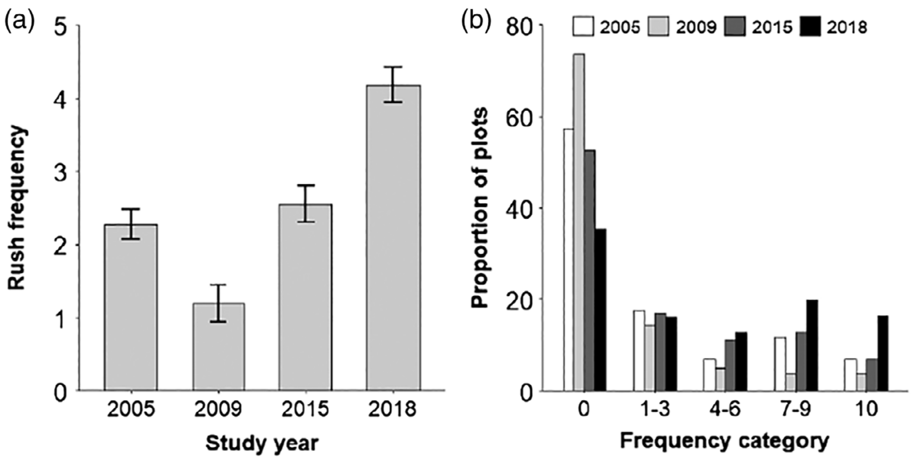

FIGURE 5 Results from the analysis of the complete dataset: (a) mean rush frequency per year (error bars are *SE* of the mean); and (b) the proportion of plots per year in which rush frequency was: 0 (absent), 1–3, 4–6, 7–9 or 10 (dominant). Rush frequency was measured within 10 quadrats per sample plot per year

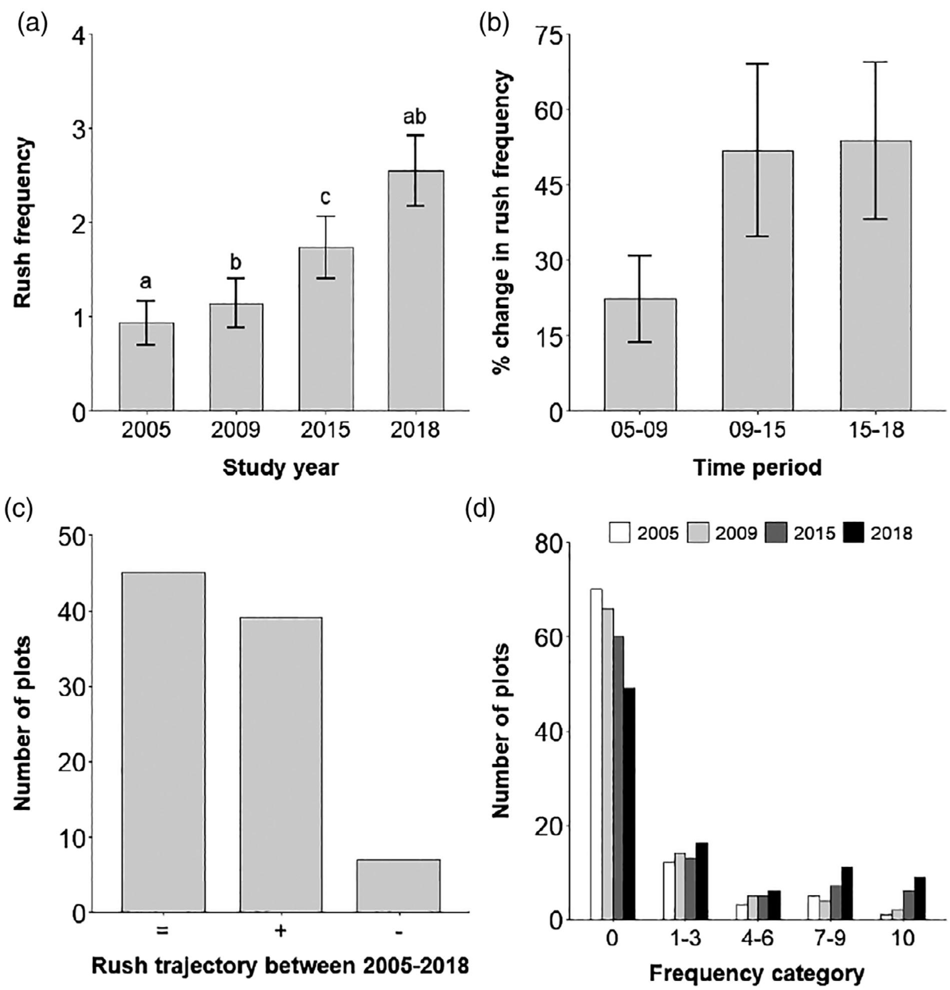

FIGURE 6 Results from the analysis of the continuous dataset: (a) mean rush frequency per year with bars marked with different letters being significantly different ($p < .05$) according to post hoc comparisons between individual survey years using Wilcoxon signed-rank tests adjusted using the Bonferroni correction method; (b) the mean percentage change in rush frequency per plot between 2005–2009, 2009–2015, and 2015–2018; (c) the number of continuous data plots in which rush frequencies displayed no change (=), were positive (+), or were negative (–) between 2005 and 2018; and (d) the proportion of plots per year in which rush frequency was: 0, 1–3, 4–6, 7–9, or 10. For figures (a) and (b) error bars are *SE* of the mean. Rush frequency was measured within 10 quadrats per sample plot per year

4 | DISCUSSION

Our results provide quantitative evidence of rush expansion within the marginal upland grasslands of the WPM SSSI between 2005 and 2018. Both datasets suggest that rush frequency has increased by 81.7% (all data) to 174.2% (continuous data) during the study period. Moreover, the continuous dataset indicates that between 2005 and 2018 rush frequency increased within 42.9% of plots, but only decreased within 7.7% of plots. The continuous data also shows that the largest increases in rush frequency occurred more recently between 2009–2015 (51.9%) and 2015–2018 (53.8%), with only moderate increases recorded between 2005 and 2009 (22.3%). These findings corroborate the results reported in the grey literature, which suggest that there have been significant increases in rush cover or frequency over time within the upland hay meadows of northern England (Hamilton et al., 2018; O'Reilly, 2011). However, our study differs in that: we measured rush expansion within marginal semi-improved upland grasslands (as opposed to upland hay meadows); we used a much greater number of sample fields and quadrats; we measured changes in rush frequency across a greater number of time periods (we used four time periods, whereas studies in the grey literature used two); and, more importantly, we used a consistent survey method across each time period.

Despite recording large and significant increases in rush cover, by 2018, there were still between 35.3% (all data) and 53.9% (continuous data) of plots in which rushes were absent. Furthermore, the continuous data also shows that within 42 of the 91 plots examined (46.2% of continuous data plots) rushes were absent throughout the entire duration of the study (i.e., during 2005, 2009, 2015, and 2018). Given that rush frequency did not increase within every grassland parcel and that the greatest increases in rush frequency happened after 2009, recent changes in field-level management appear to be the most likely cause of rush expansion within the WPM SSSI. Nevertheless, the drivers behind the recent expansion of rushes within upland grasslands are currently unknown.

4.1 | Factors controlling rush expansion within upland grasslands

4.1.1 | Field-level factors

One possible field-level factor driving the recent increase in rushes within upland grasslands is inadequate drainage. The gradual decline in the number of farmworkers combined with the low profitability of upland farming means that farmers do not have the time, labour, or money to maintain existing drains or install a new drainage system. Given the preference of rushes (especially *J. effusus*) for damp conditions (Hill et al., 2004; Richards & Clapham, 1941b, 1941c, 1941d), the recent decline in operational and efficient field drainage systems may have facilitated rush expansion. Surprisingly, Hamilton et al. (2018) found no evidence of a relationship between drainage and temporal changes in rush cover within the upland hay meadow sites they studied, but this could have been because of difficulties in relocating quadrat samples between repeat surveys and/or the assessment of hay meadow vegetation at the quadrat rather than field scale (e.g., two to three repeat quadrats per hay meadow).

Drainage capacity may have been further reduced in recent times by the increasing use of heavier farm machinery. For example, Hamilton et al. (2018) found that none of the upland hay meadow sites they studied had modern field drains, with many fields being described by farmers as having “old” or “Victorian” drainage systems (44.2% of farmers asked). Such old drainage systems are likely to have collapsed under the weight of heavier modern machinery and, because farmers are unable to repair or replace them, the soil in these fields will have become much wetter and thereby more favourable to rushes. The use of heavy farm machinery may have also caused soil compaction (Keller, Sandin, Colombi, Horn, & Or, 2019), which, in turn, may have facilitated rush expansion via increased soil surface wetness because of the creation of an impenetrable pan of soil preventing surface water from percolating down to the sub-soil and any existing field drains (Chyba, Kroulik, Krištof, & Misiewicz, 2017; Chyba, Kroulík, Krištof, Misiewicz, & Chaney, 2014).

During the headage era (1980–2005) hill farmers were paid a subsidy based on the number of sheep within their flock (Thomson, 2011). This policy led to the overstocking of sheep and may well have led to increased soil compaction and surface wetness (and thereby rush expansion) within marginal grasslands (Fuller & Gough, 1999; Sutherland, 2002; Wathern, Brown, Roberts, & Young, 1985). For example, sheep grazing can increase soil bulk density and reduce soil infiltration capacity within upland grasslands (Marshall et al., 2014). Overstocking of sheep may also lead to poaching, especially on undrained fields with wet soils (Bilotta, Brazier, & Haygarth, 2007). The creation of bare ground via poaching would facilitate the spread of rushes by providing the germination niches required by overwintering seeds lying dormant at the soil surface (Agnew, 1961; Cairns, 2013; McCarthy, 1971). Poaching induced rush germination may even occur at low stocking densities in rush dominated grasslands: because of the low palatability of rushes (Grant et al., 1984; Nielsen & Søegaard, 2000; Tweel & Bohlen, 2008), sheep may concentrate their feeding activity within the small patches of grass that remain. Thus, what should be a low stocking density in a rush-free grassland, becomes a high stocking density that causes localised poaching on the few remaining areas of productive grassland.

Sheep numbers within the British uplands have declined substantially since the outbreak of Foot and Mouth Disease in 2001 and the end of headage in 2005 (SAC, 2008; Thomson, 2011). Nevertheless, stocking densities may still be high enough to cause localised soil compaction and surface ponding in upland grasslands (e.g., Marshall et al., 2014). Therefore, current stocking levels may still be promoting rush expansion, especially in rush dominated fields where grazing is restricted to small areas of palatable grass.

Another possible field-level factor that has encouraged rush expansion is a reduction in management intensity. Many of the upland grassland agri-environment schemes available to farmers restrict the application of inorganic fertilisers or livestock manures and lime (Rural Payments Agency, 2019a, 2019b). Before the widespread adoption of such schemes, farmers would regularly fertilise their fields and increase the pH by liming, with both actions making the conditions more favourable to grasses and less favourable to rushes (Cairns, 2013; Hill et al., 2004). Such practices may have held back rush expansion within marginal grasslands (Cairns, 2013).

The cessation of traditional farming practices may have also created a series of field-level factors that may have contributed to the spread of rushes within upland grasslands. For example, upland farmers used to keep a much wider range of livestock than just sheep, including native cattle, and pony breeds (Fuller & Gough, 1999) that, unlike sheep, find rush more palatable (Coyle et al., 2018; Grant et al., 1984; O'Reilly, 2012). Native cattle and ponies may have been present in enough numbers to control rush expansion. Farmers also used to mow, bale, and remove grassland cuttings every year, which could have reduced rush seed fall and germination. Furthermore, the practice of burning rushes within marginal grasslands (i.e., swaling) has disappeared in upland areas across the United Kingdom. This practice would have had a negative effect on rush abundance via reductions in biomass and seed load (Ghantous & Sandker, 2015) and would have also increased the competitiveness of grass (in relation to rushes) via increases in soil nutrients and pH (e.g., Brockway, Gatewood, & Paris, 2002; Dudley & Lajtha, 1993; Niering & Dreyer, 1989).

To truly understand if and what field-level factors are contributing to rush expansion, we need to combine our satellite imagery approach with historical management data. Unfortunately, accurate historical data was not available for the grassland parcels used in this study, but such data is likely to be available in other areas.

4.1.2 | Climatic factors

North West England and North Wales (the climatic region in which this study took place) were 3% wetter between 2005 and 2018 than they were between 1981 and 2010, and 7% wetter than they were between 1961 and 1990 (Met Office, 2020b). Furthermore, recent increases in wetness during winter and summer have been even greater within the study region (Met Office, 2020b). For example, winters between 2005 and 2018 were 5% wetter than winters between 1981 and 2010 and 14% wetter than winters between 1961 and 1990 (Met Office, 2020b). Likewise, summers between 2005 and 2018 were 13% wetter than summers between 1981 and 2010 and 14% wetter than summers between 1961 and 1990 (Met Office, 2020b). By facilitating more favourable conditions for rushes (i.e., wetter and warmer), the recent increases in wetness may have compounded field-level drivers of rush expansion, such as inadequate drainage, soil compaction, and poaching.

Alongside the observed increases in precipitation, there has been a recent reduction in the number of days of air frost across the study region. For example, between 2005 and 2018, there have been 6% fewer days of air frost compared to the 1981–2010 average (Met Office, 2020a). Similarly, compared to the 1961–1990 average, there have been 16% fewer days of air frost between 2009 and 2018 (Met Office, 2020a). Several studies suggest that rush regrowth after cutting (or grazing) is reduced when plants are exposed to freezing temperatures (Folkestad, Østrem, & Netland, 2010; Østrem et al., 2018). Thus, combined with the cessation of traditional management (e.g., swaling, use of a wider range of native grazers or the cutting and removing grassland arisings), the recent reductions in the number of air frost days may have also contributed to grassland rush expansion.

4.2 | Implications of rush expansion within upland grasslands

The expansion of rushes within upland grasslands has several negative consequences. First and foremost, as rushes increase, palatable and productive grasses tend to be outcompeted. Consequently, rush infestations reduce farm productivity. For example, Cairns (2013) states that a "15% rush infestation in a productive grass sward, could reduce output by 1.25 t DM/ha/annum. If the field is cut for big bale silage on upland in-bye fields, the value of this lost production could be as high as £192 ha^{-1} (£78 $acre^{-1}$)". As Hamilton et al. (2018) note, such large losses are extremely significant on livestock farms in marginal upland areas within England where the average farm income is between £130 and £141 ha^{-1} (Rural Business Research, 2018 data from North West and North East England, respectively). Secondly, rush infestations lead to declines in plant and bird biodiversity. For instance, as more grassland area is taken up by rushes, there is less space for other grassland species. Also, while snipe and curlew may nest in rush dominated fields, redshank (*Tringa tetanus* L.) and lapwing prefer to nest in fields with a mixture of scattered rush tussocks (no more than 30% cover) and grassland patches in which to feed (Coyle et al., 2018; RSPB, 2017).

Rush dominated fields, particularly bordering heather moorland, could also be a significant, but currently unidentified, wildfire risk, especially given that we know rushes are combustible (e.g., as highlighted by the historical practice of swaling, but also see Ghantous & Sandker, 2015). Furthermore, fields in which rush cover exceeds 50% will have a significant amount of biomass that is likely to become very dry (and thereby more combustible) during summer. To date, the wildfire risk posed by moorland edge rush infestation has not been investigated. If rush infestations *do* pose a significant wildfire risk, we would need to reduce rush cover at and just below the moorland line. Such a task would be difficult, given that we still do not know the most effective way to control rush infestations within grassland habitats (Coyle et al., 2018; O'Reilly, 2012).

4.3 | Research priorities

Our protocol for measuring rush frequency is subjective and restricted to grassland habitats where there is a clear height, colour, or tone differential between rush tussocks and the surrounding vegetation. Therefore, an obvious next step would be to develop a more objective and automated protocol for quantifying rush abundance across multiple habitats. One approach would be to use light detection and ranging (LiDAR) data to differentiate rush tussocks from the surrounding grassland vegetation in the same way tree canopies can be differentiated from the understory vegetation and the forest floor (e.g., Hamraz, Contreras, & Zhang, 2017; Latifi et al., 2015). Rush tussocks are generally less than 1 m wide (see Supporting Information File 4), which means that LiDAR with a spatial resolution of 1 m or less would be the most appropriate for mapping soft rush. However, in other habitats (e.g., acid grassland, heather moorland, or blanket bog) where there is less of a height differential between rushes and the surrounding vegetation, LiDAR may have to be replaced by or supplemented with spectral band analysis using satellite images, such as SENTINEL-2 or LANDSAT 8 (Davidson et al., 2016; Erinjery, Singh, & Kent, 2018; Forkuor, Dimobe, Serme, & Tondoh, 2018). Notwithstanding the points above, the development and implementation of an automated protocol for measuring rush abundance in upland grasslands across the United Kingdom is currently hampered by the limited coverage of high-resolution LiDAR data (spatial resolutions of ≤1 m).

In addition to the above, we have identified four further research gaps that need to be addressed. Firstly, we need to replicate our satellite imagery approach across different areas of the United Kingdom and further validate the method by using both contemporary and historical field data. Secondly, we need to determine the drivers behind the recent expansion in rushes within upland grasslands across the United Kingdom. This could be achieved by mapping changes in rush frequency over time and exploring how different management and environmental factors have influenced these changes. Potential drivers of rush expansion to explore are historical changes in management (e.g., changes in drainage efficiency, reduction in stocking levels, and restricted fertiliser inputs), changes in climate (e.g., changes in rainfall and temperature), and environmental factors (e.g., slope, aspect, and proximity to standing water). Climatic and topographical data for the United Kingdom are freely available online (e.g., Met Office and Ordnance Survey), and historical management data could be obtained by interview or questionnaire.

Thirdly, we need to establish the most effective rush control techniques to give land managers the tools to reduce rush dominance. The effectiveness of several rush control techniques have been explored within several studies (see Coyle et al., 2018; O'Reilly, 2012 and references therein), but not in any depth or within an experimental framework that compares the efficacy of different control methods across different farms with varying environmental and management contexts (i.e., in a way that provides practical knowledge to farmers and land managers).

Finally, we need to quantify the fundamental niche of soft rush, hard rush, and compact rush. Knowledge of the environmental tolerances of these invasive rush species will enable us to better understand the drivers behind the recent expansion in rushes within upland grasslands and allow us to reduce rushes where they have become dominant.

5 | CONCLUSIONS

This is the first peer-reviewed study to document the recent increases in rush abundance within upland grasslands. Our data suggest that the frequency of rushes within the marginal grasslands of the WPM SSSI has increased by 81.7–174.2% between 2005 and 2018. It is not clear why such increases may have occurred. However, they may be because of changes in field-level management, which have been further compounded by recent increases in rainfall and reductions in the number of air frost days. Future research into rush ecology, expansion, and management is urgently required to determine the broader extent of the problem in England and to combat the negative consequences of grassland rush infestations on the upland farm economy and grassland biodiversity.

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CONFLICT OF INTEREST

M. Ashby has provided independent ecological advice and evidence synthesis services to the Moorland Association since April 2019 and the Game & Wildlife Conservation Trust since October 2019.

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SUPPORTING INFORMATION

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

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