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*Research article*

# Two decades of dune slack restoration in North Wales: diversity, community and habitat specialists

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Humid dunes slacks are a highly threatened habitat, listed as vulnerable in the EU habitat red list. Accelerated successional processes in dune systems have resulted in the loss and degradation of ideal conditions for specialist dune slack species, hence the need for conservation management. We investigated the restoration of a dune slack in North Wales, UK, where vegetation and soil removal to 10 cm depth was undertaken to reinstate nutrient-poor, open and damp conditions. We assessed the outcomes of the management for dune slack communities over the 18 years since restoration. We also assessed the differences between restored and unrestored areas of dune slacks. The dunes were restored in the winter of 2004/2005, after which we conducted vegetation surveys in fixed quadrats for most years in the restored and adjacent, un-restored dune slacks. Species diversity and plant community composition changes over time were assessed using Shannon's index, multivariate analysis and indicator species analysis. Comparisons between the restored and unrestored areas of the dune slacks were also made. Ellenberg indicator values (EIVs) were examined to identify potential environmental drivers of post management successional changes. After 18 years the restored dune slacks developed a species-rich and diverse community. compared to the unrestored slacks. The establishment of species occurred rapidly in the first three years, followed by continued but slower increases in species richness and diversity. This is due to the addition of new species without losses of established species. EIVs show no significant difference over time suggesting the restored areas are still at an early stage of succession. Distinct stages of community change since restoration are characterised by different indicator species. Plants are likely to be largely recruited from an existing seed bank. Restoration by turf removal may be suitable for other low nutrient, species rich habitats dependent upon fluctuating groundwater levels.

Keywords: dune slacks, indicator species, plant communities, restoration, species diversity, succession

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## Introduction

Humid dune slacks are low-lying, low nutrient habitats in coastal sand dune systems with a fluctuating water table, typically flooding during the winter and drying out in summer. These conditions produce a species-rich and diverse flora that supports several rare and endangered species adapted to withstand the hydrological fluctuations (Dwyer et al. 2021). As well as being spatially restricted to coastal areas, they are also a highly threatened habitat, listed as vulnerable in the EU Red list of habitats (H2190) (Janssen et al. 2016). The UK has 14% of the European resource of dune slacks (Stratford et al. 2014) but they are generally considered to be in 'unfavourable – bad' condition (JNCC 2019).

Dune systems have long been central to understanding the process of natural succession (Prach et al. 2021). This is typically observed in zones from the mobile embryo dunes on the upper beach, through to foredunes colonised by a few hardy pioneer species, followed by yellow dunes which are more stabilised by increasing vegetation, then grey dunes which are more fixed and where vegetation has resulted in soil development and increasing nutrients. Beyond the grey dunes the soils have further developed, resulting in heath, scrub and woodland habitats. Dune slacks are typically formed in front of or behind the grey dunes due to the wind scouring away vegetation and sand and exposing the water table.

A reduction in traditional grazing, climate change, and increased nitrogen deposition have caused increased growth of vegetation on the UK's dune systems (Jones et al. 2010, Maskell et al. 2010). This has resulted in over-stabilisation of the dunes which prevents blow-outs and scouring which are critical in the creation of new embryo dune slacks (Houston 2008, Pye et al. 2014). This has accelerated the natural succession process in existing dune slacks leading to a loss of diversity (Bossuyt et al. 2003, JNCC 2004). As a result, the ideal conditions for many specialist species are being degraded and lost, leading to such species becoming increasingly rare (Van der Maarel and van der Maarel-Versluys 1996).

Indicator species are an important, widely used tool to help determine the classification of communities (e.g. National Vegetation Classification [NVC] communities; Rodwell 2006), through their association with environmental conditions such as soil type, ancientness of habitat or pollution levels, and to help monitor environmental change, for example in designated nature conservation areas (e.g. Joint Nature Conservation Committee Common Standards habitat monitoring, JNCC 2003). Certain species can indicate different successional stages which makes them useful tools in examining the stages of dune slack restoration. Assemblages of plants can also be used as environmental indicators by assessing their shared preferences for certain environmental conditions. EIVs (Hill et al. 1999) are a scoring system by which a plants' preference for light, temperature, pH, moisture, nutrients and salinity are given a score. Averaging these scores across species in a plant community or habitat can reveal information about the environmental conditions and changes at the site, informing site management decisions.

It is widely recognised that intervention is needed to avoid large-scale loss of these already endangered dune slacks and associated losses of flora and fauna that depend upon them (Houston 2008, Pye et al. 2014, Stratford et al. 2014). Several management options are available to limit this accelerated succession and provide more open areas of habitat, including mowing or grazing regimes. Whist useful in the right circumstance, these techniques have their limitations, for example grazing requires consideration of public access and mowing does not prevent acidification of soils (Grootjans et al. 2002) and neither creates bare sand for early successional species (Pye et al. 2014). Furthermore, these techniques will not re-establish already lost dune slack communities (Lammerts et al. 1999), and some dune slacks may be too vegetated for these techniques to be effective. In these cases, restoration to reverse the process of succession by the removal of vegetation and topsoil (known as sod cutting, turf stripping or scraping) may be more effective. The build-up of nutrient-rich organic matter is removed, and the mineral substrate is revealed to allow early successional and characteristic dune slack species to re-establish in the nutrient-poor environment. The main aims of these types of dune slack restoration projects are typically to: 1) re-establish open, species rich dune slack plant communities, 2) to deliver dune slack habitats as part of a mosaic of dune habitats and 3) the conservation of specific plant and animal species at the site (Houston 2008).

There are many factors that can affect the successful re-establishment of dune slack communities and influence the types of community composition that emerge over time. For example, it has been found that increased acidification of soils can limit the lifespan of species rich dune communities (Lammerts and Grootjans 1998, Sýkora et al. 2004). Increased soil organic matter leading to enhanced growth of competitive species can cause the decline of early successional species due to subsequent competition for light (Berendse et al. 1998). Ground water levels and fluctuation can also influence the presence and composition of dune slack vegetation (Dwyer et al. 2021, Lammerts et al. 2001) and levels of groundwater nutrients can also affect dune slack plant assemblages (Rhymes et al. 2014). Research into how these factors can influence the outcomes of dune slack restoration is important to find the most effective ways of protecting and enhancing these endangered habitats. This is arguably becoming an even more important area of study given predictions that show dune slacks to be at serious risk from climate change (Curreli et al. 2013).

Much existing research on the outcomes of dune slack restoration projects and the factors affecting species and plant communities has been undertaken in mainland Europe, notably in the Netherlands and Belgium. This includes studies examining the role of seedbanks in restoration success (Bekker et al. 1999, Bakker et al. 2005, Plassmann et al. 2009) and the influence of hydrological factors (Lammerts and Grootjans 1998, Grootjans et al. 2001), nutrient limitation (Lammerts et al. 1999), soil conditions (Sýkora et al. 2004) and slack isolation (Grootjans et al. 2001, Bossuyt et al.

2005) on dune slack vegetation and communities. However little work has been done on long term community changes following slack recreation. This study aims to address that gap by looking at changes in diversity, community composition and indicator species following slack recreation.

This study investigated changes to dune slack plant communities over an 18-year period following restoration by topsoil scraping, in dune slacks on the North Wales coast, which is a designated site of special scientific interest (SSSI) and part of the Dee Estuary Ramsar Site, and Dee Estuary special area of conservation (SAC).

The aim of this research is to assess whether the dune slack management has restored dune slack species and communities. It specifically addresses the following questions: 1) how has species richness, diversity and community composition changed over time in the restored dune slacks? 2) How do species richness, diversity and community composition differ between restored and non-restored areas of dune slacks in 2022? 3) Does the restoration process result in distinct communities, identified by specific habitat indicator species?

## Material and methods

### Study site and design

The study site is situated within Gronant Dunes and Talacre Warren SSSI, located between Prestayn and Talacre on the North Wales coast (Fig. 1a). Talacre Warren forms the eastern part of the SSSI and contains a series of wet dune slacks between two main dune ridges. The site is owned and managed by ENI Liverpool Bay Operating Company Ltd and, in common with most UK dune systems, has become increasingly stabilised in the last half of the 20th century. The site has experienced a 41% decline in bare sand between the 1940–1950s and 2009 (Pye et al. 2014). By the early 2000s much of the former dune slack habitat on site had become overgrown with trees and scrub, and during the winter of 2004/2005 restoration work commenced within the dune slacks, aiming to return them to 'favourable condition'. The site's environmental regulator, Natural Resources Wales, have also articulated a further aim, which was to re-establish more open, species-rich communities as part of a mosaic of dune habitats across the SSSI and SAC (Smith pers. comm., 23 August 2022). Three neighbouring areas of over-stabilised, overgrown dune slack of approximately 200 $m^2$ in total were restored, with trees and scrub removed and 10 cm of nutrient rich topsoil scraped away to expose bare sand, and ten 2 × 2 m fixed quadrats were installed to allow surveys of the restored areas over time (Fig. 1b). These areas have since been allowed to naturally recover with no further documented intervention or management, except for quadrat 10 which was re-scraped in spring 2021.

The ten fixed quadrats were surveyed between May and July in: 2006, 2007, 2008, 2009, 2010, 2011, 2013, 2014, 2018, 2020, 2021 and 2022, to monitor botanical succession (Fig. 1b for locations).

An additional ten new 2 × 2 m quadrats in the non-restored areas of the dune slacks were also surveyed in July 2022 (Fig. 1b) to enable a comparison of botanical communities between the restored (hereafter termed 'scraped') and non-restored (hereafter termed 'unscraped') slacks.

### Data collection

The new unscraped quadrats were positioned using a random stratified sampling approach to ensure spread of unrestored dune slack close to restored is sampled. The original fixed quadrat markers were all successfully found and repeat surveys were carried out following the long-term monitoring vegetation protocol (Natural England 2016), as in previous years. For all quadrats, all vascular plants present were listed and their percentage cover was visually estimated as a proxy for abundance. Identifications were made using Rose (1989), Streeter et al. (2016) and Poland and Clement (2020).

Species data was collated from all previous survey years as follows: individual quadrat and abundance data (the DOMIN scale, a 1–10 scale for abundance (Rodwell 2006) was used in previous surveys) for 2006, 2007, 2008, 2018, 2020 and 2021 (hereafter termed 'full survey years'); total species list only for 2009, 2010, 2011, 2013 and 2014. Due to the nature of the vegetation – short with numerous very small plants – distinguishing between some closely related species can be difficult. This is likely to have resulted in differences in professional opinion between different surveyors over the years. Data was cleaned to account for these potential differences and enable analysis, see Supporting information for full details. Taxonomy follows Stace (2019) and previous survey lists have been updated to incorporate taxonomical changes in order to enable analysis. These changes are set out in the Supporting information.

### Data analysis

To be able to analyse comparable data, the DOMIN scores from previous full survey years were converted to percentage values using the mid-point percentage value of each DOMIN grouping. All analyses were performed using R ver. 4.2.1 (www.r-project.org), with packages for specific tests described below.

### Species, richness and diversity – scraped and unscraped quadrats

We assessed how species richness changed in scraped quadrats over time using Kruskal–Wallis and Tukey–Kramer–Nemenyi all-pairs tests. Kruskal–Wallis was carried out using the R package 'stats' ver. 4.2.1 (www.r-project.org), Nemenyi's tests used the 'PMCMRplus' package (Pohlert 2022). The data were normal and had homogenous variances. Mean species diversity was calculated for the scraped quadrats for each full survey year using Shannon's diversity index. To assess differences in mean species diversity between scraped quadrats in different years an ANOVA and Tukey post hoc tests were carried out using the R package 'stats'.


Figure 1. (a) Slack restoration site at Talacre, North East Wales (53°21’13“N, 03°19’56“W) and (b) position of scraped and unscraped quadrats at Talacre.

To assess differences in mean species richness between the 2022 scraped and unscraped quadrats, a t-tests was carried out. Mean Shannon's diversity index was calculated for both the unscraped and the 2022 scraped quadrats and compared with a t-test.

### Community composition – scraped and unscraped quadrats

The relationship between the plant communities in scraped quadrats over time and between unscraped and scraped quadrats was examined using nonmetric multidimensional scaling (NMDS) with a Bray distance matrix and Hellinger standardisation using the 'vegan' package ver. 2.6-2 (Oksanen et al. 2022).

Species of conservation importance in the quadrats were identified by comparison of the species list with those included in: the SSSI citation (Countryside Council for Wales 2022); the UK National Red Data Book (Cheffings et al. 2005), the Welsh National red data book (Dines 2008) and rare plants of Flintshire (Botanical Society of Britain and Ireland 2020).

Finer-scale changes in community composition, including presence/absence and losses/gains of species across all survey years a matrix of species was produced showing all species and all years. As with the scraped quadrats, a matrix of species was produced comparing species presence/absence between scraped and unscraped areas in 2022.

### Ellenberg indicator values (EIVs) – scraped and unscraped quadrats

Soil data was not collected as part of the previous surveys, therefore EIVs were used as a proxy measure to assess any changes in abiotic factors over time. Mean EIVs for light (L), moisture (F), reaction (R), nitrogen (N) and salt (S) (Hill et al. 1999) were calculated for all species on the total species list for all survey years to assess any changes in functional type over time. The EIV's were not weighted as the species lists contained no abundance data. To determine if there was any significant variation in Ellenberg values between the years a Kruskal–Wallis rank sum test was performed due to the data having a non-normal distribution. Mean EIVs for L, F, R, N and S were also calculated for all species in both the scraped and unscraped quadrats in 2022 as a proxy to assess differences in abiotic factors due to management.

### Habitat indicator species

To determine species which may be suitable for use as indicator species for stages of restored dune slack succession, the data was grouped into three categories ('young scrapes', defined as less than five years since restoration; 'older scrapes', 15 years or more since restoration, and 'unscraped'). A multilevel pattern analysis was then performed using the *multipatt()* function in the 'indicspecies' package (De Caceres and Legendre 2009) which assessed the association strength and significance of association between species and groupings of sites with the purpose of identifying those species which in either occurrence or abundance can be considered indicative of the site grouping .

## Results

### Species, richness and diversity – scraped and unscraped quadrats

A total of 87 species were recorded in the scraped quadrats between 2006 and 2022, with 14 of these (16%) considered to be of local or national conservation importance due to their scarcity, including *Centaurium littorale*, *Carex viridula* and *Dactylorhiza* species. Of the 13 vascular plants listed as typical humid dune slack species by JNCC (2004), 12 have been recorded in the quadrats (11 in 2022); full species list in the Supporting information.

The total number of species in the scraped quadrats in 2022 was 47, compared with 20 in 2006; an increase of 135% in 16 years, although most of this increase occurred in 2008 (91% increase between 2007 and 2008), three years after restoration.

The mean species richness per quadrat in 2022 was 22.8, compared with 11.0 in 2006. A Kruskal–Wallis rank sum test revealed a significant difference in mean species richness per quadrat between the full survey years ($\chi^2 = 40.701$, df = 6, $p < 0.001$). Pairwise comparisons using Tukey–Kramer–Nemenyi all-pairs test with Tukey-Dist approximation revealed significant differences in mean species richness between years (Fig. 2).

Mean species diversity calculated using the Shannon diversity index showed that diversity was highest in 2008. There is

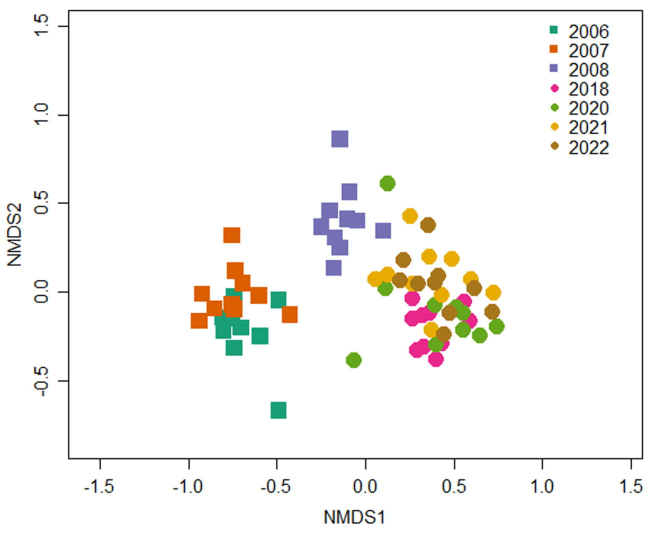


Figure 2. Nonmetric multidimensional scaling (NMDS) with a Bray distance matrix and Hellinger standardisation for the plant community composition in the scraped quadrats in the sand dunes at Talacre (Flintshire, North Wales) for all full survey years since restoration. Final stress = 0.15.

Table 1. Results of calculations showing total number of species, mean species richness per quadrat and Shannon diversity index per year for scraped quadrats. ( ) = SD. Surveys were not carried out in 2005, 2012, 2015, 2016, 2017 and 2019. Total species lists only were available for 2009, 2010, 2011, 2013 and 2014. The different letters adjacent to Species richness indicate a significant difference between the means of the years ($p < 0.05$) according to Tukey's test. The different letters adjacent to each Shannon score indicate a significant difference between the means of the years ($p < 0.05$) according to Tukey's test.

| Year | Total number of species | Species richness | Shannon (H′) |
|---|---|---|---|
| 2006 | 20 | 11.0 (2.5)$^{a}$ | 1.92 (0.4)$^{b}$ |
| 2007 | 22 | 11.1 (2.3)$^{a}$ | 1.99 (0.3)$^{ab}$ |
| 2008 | 42 | 20.1 (6.7)$^{bc}$ | 2.77 (0.3)$^{c}$ |
| 2018 | 45 | 21.1 (4.3)$^{bc}$ | 2.37 (0.3)$^{acd}$ |
| 2020 | 48 | 17.5 (3.6)$^{b}$ | 2.29 (0.3)$^{abd}$ |
| 2021 | 42 | 20.6 (4.1)$^{bc}$ | 2.53 (0.2)$^{cd}$ |
| 2022 | 47 | 22.8 (4.3)$^{c}$ | 2.44 (0.3)$^{cd}$ |

a significant difference in mean species diversity between the years ($F_{6,63} = 9.8$, $p < 0.001$) (Table 1).

The total number of species in the scraped quadrats in 2022 was 47, compared with 39 species in the unscraped quadrats: a 20% difference. There were nine species of local or national importance in the scraped quadrats (19%) and two in the unscraped (5%), species list in the Supporting information.

The scraped quadrats have both a significantly greater mean species richness than the unscraped ($t = 5.5403$, $df = 18$, $p < 0.001$) and a significantly higher mean diversity ($t = 4.3231$, $df = 18$, $p < 0.001$) (Table 2).

## Community composition – scraped and unscraped quadrats

The NDMS ordination shows a distinct separation of plant communities in some years indicating there is a difference in community composition between these years. The plant communities in 2006 and 2007 are similar to one another and distinct from all other years; they form the most distinct group. The plant community in 2008 is also clearly distinct from all other years. After 2008 the community became more difficult to separate and the plant communities in 2018, 2020, 2021 and 2022 are similar to one another, and distinct from the earlier years. The 2020 community displays the most spread indicating that the species composition across quadrats were less similar to each other than in other years (Fig. 2).

Since restoration work was first undertaken in 2004, 87 new species have appeared. There have been 18 species recorded only once; some of these may be due to surveyor difficulty in identifying small species, and some may be present elsewhere on the slacks outside the quadrats.

The 2006/2007 community comprises several early pioneer species of basic open habitats, including *Blackstonia perfoliata*, *C. littorale* and *Lysimachia maritima*. Indicator species of humid dune slacks were present, (e.g. *Hydrocotyle vulgaris*, *Potentilla anserina* and *Salix repens*) and some of dry dune slacks (e.g. *Festuca rubra* and *Lotus corniculatus*). 2008 saw the establishment of several grass species and sedges, including *Agrostis* spp. and *C. viridula*, as well as *Mentha aquatica*, an indicator of wetter habitats. Forty of the 87 new species have been recorded since 2008 (22 of these since 2018). Aside from single-year records, there have been limited losses of established species. Therefore, the difference between the early and later communities is largely due to an increased richness of the community, rather than an exchange of species. This establishment process has resulted in a more mature species rich dune slack habitat between 2018 and 2022, but with all the early open-habitats pioneer species still present.

Table 2. Results of calculations showing total number of species, mean species richness and Shannon diversity index for scraped quadrats and unscraped quadrats in 2022. ( ) = SD.

| Management | Total number of species | Species richness | Shannon (H′) |
|---|---|---|---|
| Scraped | 47 | 22.8 (4.3) | 2.44 (0.3) |
| Unscraped | 39 | 13.0 (3.5) | 1.67 (0.3) |

When comparing the community composition of the scraped with the unscraped areas, the NDMS ordination shows a distinct separation of plant community assemblages. A comparison of species lists for the scraped and unscraped quadrats shows that the forb: graminoid ratio differs between the two areas, with the scraped quadrats list containing 19% graminoids and the unscraped areas 30%.

The unscraped areas were the most spread in ordination space which indicates that the species composition across these quadrats were less alike than those of the scraped quadrats (Fig. 3).

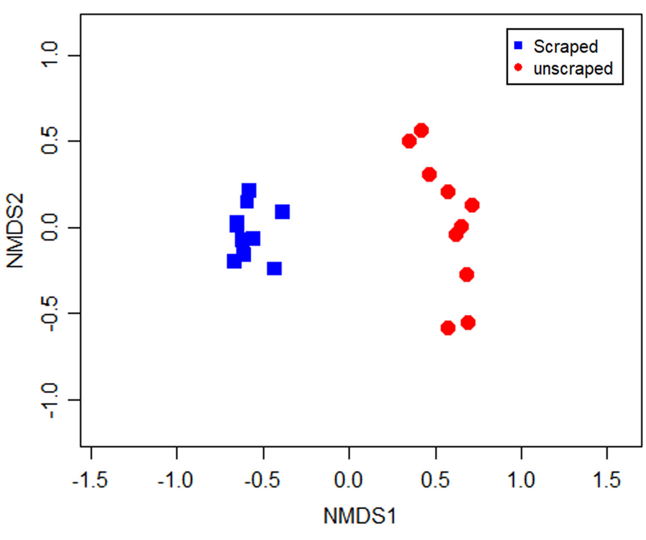


Figure 3. Nonmetric multidimensional scaling (NMDS) with a Bray distance matrix and Hellinger standardisation for the 2022 plant community composition in the scraped and unscraped quadrats in the sand dunes at Talacre (Flintshire, North Wales). Final stress = 0.098.

Table 3. Mean Ellenberg indicator values (EIVs) for scraped quadrats all years and mean EIVs Types for the scraped and unscraped quadrats in 2022. Eb L = light; Eb F = moisture; Eb R = reaction; Eb N = fertility; Eb S = salt.

| | Mean Ellenberg indicator (SD) | | | | |
|---|---|---|---|---|---|
| Year | Eb L | Eb F | Eb R | Eb N | Eb S |
| Scraped quadrats all years | 7.47 (0.61) | 6.15 (1.50) | 6.40 (0.87) | 4.24 (1.48) | 0.59 (1.12) |
| Scraped quadrats 2022 | 7.50 | 6.14 | 6.31 | 4.14 | 0.55 |
| Unscraped quadrats 2022 | 7.28 | 5.66 | 6.19 | 4.47 | 0.41 |

### Ellenberg indicator values (EIVs)

There was no significant difference between the years for any Ellenberg value (light $\chi^2 = 3.91$; moisture $\chi^2 = 2.95$; pH $\chi^2 = 3.25$; nitrate $\chi^2 = 2.77$, salt $\chi^2 = 1.53$; for all df = 11, $p > 0.90$) (Table 3).

There were higher mean EIV scores for light, moisture, reaction (pH) and salt in the scraped quadrats than the unscraped quadrats in 2022 (Table 3). The mean EIV score for nitrogen was higher in the unscraped quadrats than in the scraped quadrats. The greatest difference was observed in the mean EIV scores for moisture.

### Habitat indicator species

The plant community at the site has changed over the first 18 years since restoration. This is reflected in the indicator species analysis with several species having a significant association with young (< 5 year) restored slacks, including *B. perfoliata* and *Samolus valerandi*, with the former being found almost exclusively in the young slacks at Talacre. In the older restored slacks (> 15 year), there were a wider range of potential indicator species, including *Lysimachia tenella* and *Dactylorhiza* spp. which were found exclusively in the older slacks at Talacre, and *Lotus corniculatus*, *Carex flacca*, *Prunella vulgaris* and *M. aquatica* all of which are also considered typical indicator species for humid dunes slacks (JNCC 2004).

Of the 98 species recorded in this study, 34 species have a significant association with a specific class of scrape (Table 4); six species are associated with young scrapes, 13 species are associated with older scrapes and 15 species are associated with the unscraped slacks.

## Discussion

This research shows that species diversity has increased, and community composition of the slacks has changed over time, demonstrating succession. These stages of succession are identified by specific indicator species. Species richness and diversity were significantly higher in the restored areas of dune slacks than the unrestored areas in 2022. These findings have important implications for management because they demonstrate that such restoration projects can result in enhanced species diversity and a characteristic dune slack community.

### Changes in species richness, diversity, and community composition over time

Three main phases of vegetative development have occurred since the restoration: an initial colonisation of species in the first two years; followed by a rapid surge in species numbers by the time of the following survey with continued increase in the following years but at a much slower rate. These stages are characterised by specific indicator species and reflected in the NMDS (Fig. 2). More than half of the recorded species at the site established in the first three years following restoration.

Table 4. Multi-level pattern analysis of plant species found at Talacre. Significant association of a species with an age class suggests that the species may be an indicator species for that class. Age classes: Young scrape (< 5 year), Older scrape (> 15 year), Unscraped. Significance values: * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

| Age Class | Taxon | Indicator value |
|---|---|---|
| Young scrapes | *Blackstonia perfoliata* | 0.610*** |
| | *Samolus valerandi* | 0.549*** |
| | *Equisetum* sp. | 0.479*** |
| | *Epilobium parviflorum* | 0.359* |
| | *Equisetum arvense* | 0.329* |
| | *Jacobaea vulgaris* | 0.310* |
| Older scrapes | *Lotus corniculatus* | 0.610*** |
| | *Agrostis stolonifera* | 0.595*** |
| | *Carex flacca* | 0.589*** |
| | *Dactylorhiza* sp. | 0.573*** |
| | *Leontodon saxatilis* | 0.553*** |
| | *Prunella vulgaris* | 0.537*** |
| | *Mentha aquatica* | 0.494*** |
| | *Carex demissa* | 0.398** |
| | *Linum catharticum* | 0.342* |
| | *Carex viridula* | 0.330* |
| | *Pulicaria dysenterica* | 0.306* |
| | *Euphrasia* sp. | 0.300* |
| | *Lysimachia tenella* | 0.293* |
| Unscraped | *Rubus* c.f. *caesius* | 0.864*** |
| | *Arrhenatherum elatius* | 0.602*** |
| | *Ammophila arenaria* | 0.585*** |
| | *Juncus maritimus* | 0.579*** |
| | Graminaea sp. 1 | 0.555*** |
| | *Heracleum sphondylium* | 0.555*** |
| | *Ononis repens* | 0.490*** |
| | Graminaea sp. 2 | 0.471** |
| | *Populus nigra* | 0.420** |
| | *Festuca rubra agg.* | 0.401** |
| | *Centaurea nigra* | 0.378* |
| | *Betula pendula* | 0.350** |
| | *Angelica sylvestris* | 0.341** |
| | *Cirsium arvense* | 0.337* |
| | *Salix cinerea* | 0.328** |

The continuing increase in species diversity with additions of new species and few losses of species recorded indicates that the difference between the early and later communities is largely due to species enrichment of the community, rather than an exchange of species. This establishment process has resulted in a more mature species rich dune slack habitat after fifteen years, with all the early open-habitats pioneer species still present. This is akin to the natural process of dune slack succession as documented by Davy et al. (2006). This phase is thought to typically last between 20–30 years (Houston 2008). Thereafter accumulation of organic matter and nutrients facilitates more dominant species and causes the decline of the species-rich phase (Grootjans et al. 2002). However this is not a universal process in dune restoration. Berendse et al. (1998) and Grootjans et al. (2002) showed rapid establishment of rare slack species followed by a decline with 7–15 years. Other studies have reported early rapid increases in species establishment that have been subsequently sustained for much longer periods (Grootjans et al. 2002). Absence of regular flooding allied to inadequate supply of groundwater, leading to increased organic matter were considered to be the main cause of these short-lived successes. The environmental factors considered in this study determined wit EIVs showed no significant difference, although water table data was not investigated. However the scraped area at the study site has significantly flooded every year since the restoration, except for winter 2021/2022 which was a particularly dry year (Norman pers. comm., 31 August 2022). These wet conditions may have contributed to the successful establishment of the plant community and are reflected in the consistent Ellenberg moisture values over time.

The speed of species establishment and diversity of species in the early years suggests regeneration occurred mainly from the existing seedbank. Similar conclusions have been made in dune slack restoration studies elsewhere involving sod-cutting (Sival 1996, Berendse et al. 1998, Bekker et al. 1999), whereas later studies concluded that dispersal was the critical mechanism in the successful re-establishment of dune slack communities where the soil had been removed, as the seedbank was likely to also have been removed (Grootjans et al. 2001, Bossuyt and Hermy 2004, Bakker et al. 2005). At this site some dispersal is likely to have occurred due to flooding, and for some species by wind dispersal, however due to a lack of grazing and the isolated nature of the slack, other dispersal opportunities appear to be relatively limited. The depth of soil removal is likely to be an important and site-specific factor since it will be necessary to dig deep enough to uncover the seedbank of the former successional community (Jones et al. 2021), but not too deep so as to remove it. Current knowledge on dune slack seed banks is relatively limited and further research will be important to better understand their ecology (Plassmann et al. 2009). Such seed bank information can inform future management and restoration projects; and may have wider implications for other types of wetland restoration scheme.

The current species composition at the site, with all early pioneers still present, high species diversity, and continued increase in species richness indicates that the community has yet to move to the mature phase where more dominant and shrubby species outcompete the specialist slack species. The absence of change in mean EIVs between 2006 and 2022 provides further evidence that soil and nutrient conditions may not yet be supportive of more dominant species. Accumulation of organic matter and associated soil acidification have been found to be limiting factors for the longevity of species rich dune slack communities (Sýkora et al. 2004). Furthermore, dune slack fertilization studies have verified the importance of nutrient-poor conditions for the maintenance of these communities (Lammerts and Grootjans 1997) and this will be a key factor in sustaining this species-rich phase at the site for as long as possible.

Maintenance of his community may thus require additional management in the coming years. Mowing regimes reduce growth of more dominant species and competition for light, but also support phosphorous limitation which may slow the growth of potentially dominant grasses (Lammerts and Grootjans 1997). Long term grazing has been shown to slow succession, reduce the growth of shrubby species and help sustain species rich dune slack communities (Millet and Edmondson 2013), as well as increasing water levels (Connor et al. 2021).

### Comparing species, richness, diversity, and community composition between restored and non-restored slacks

Comparing the scraped areas of the dune slacks with the non-scraped areas clearly highlights the impact of the restoration work on the plant communities present. This study found that both species richness and species diversity were significantly higher due to the restoration, with substantially more scarce, rare or vulnerable species of conservation concern present in the scraped areas. The ordination results reveal two distinct plant communities, with species lists showing that the scraped areas have more forbs and specialist species of low nutrient open habitats such as *B. perfoliata* and *L. maritima*, and of wetter habitats such as *L. tenella* and *H. vulgaris*. Whereas the unscraped areas have more grasses and more competitive forb species such as *Angelica sylvestris*, *Betula pendula*, *Cirsium arvense*, *Heracleum sphondylium* and *Salix cinerea*. Given that succession has proceeded unhindered in the unscraped areas of the slacks in the absence of management and because of the overall stability of the dune system, these results were expected. Other studies that have compared restored or young slacks with existing older vegetation have found similar results (Berendse et al. 1998, Lammerts and Grootjans 1998, Bossuyt et al. 2003).

Comparing mean EIVs between the restored and non-restored communities shows that the greatest difference occurs in the mean EIV for moisture, which is higher in the scraped area, indicating the more hydrophilic species in this area. The removal of trees and shrubby species which absorb greater amounts of water is a likely factor here, along with the lowering of ground levels towards the water table by scraping. Hydrological factors are key components in species composition of unrestored dune slacks (Rhymes et al. 2014, Dwyer et al. 2021).

The mean EIVs are also indicating a community of species with a greater preference for lighter conditions in the scraped areas. In the unscraped areas the process of succession is likely to have resulted in the build-up of nutrient rich organic matter, and under these conditions competition for nutrients is replaced by competition for light (Bossuyt et al. 2003). Early successional species are then shaded-out by the taller species (Berendse et al. 1998).

In this study no significant increase in the mean EIVs for reaction and nitrogen in the unscraped slacks was observed, indicating that acidification and eutrophication have not significantly progressed. Soil testing would provide clearer data on this, since EIVs offer a relatively crude indication of change and many of the pioneer species present in the scraped areas are known to be associated with base-rich and nutrient-poor conditions (Davy et al. 2006).

## Conclusion

This study showed that the restoration of dune slacks in North Wales has re-established typical dune slack species and plant communities during the first 18 years. A more stable species rich community has developed in recent years, in line with stages of dune slack community succession. Key success factors are likely to include adequate hydrological site conditions and successful removal of organic matter whilst retaining the seedbank.

Without the intervention of the restoration work, the whole of the former dune slack area, which represents most of the potential dune slacks at Talacre, would comprise habitat akin to that of the unscraped areas. Fifteen years post restoration, a range of species of both local and national conservation importance are now present on the site. These had previously been lost to the successional process. In addition, the wider dune system now comprises a more complete mosaic of habitats including dune slack communities. This shows the sustained effect of the dune scraping restoration technique.

Dune slacks are in decline and remain under threat, and there is a lack of long-term monitoring of dune slack restoration projects to inform decision-making. This research provides important information for evidenced-based management of dune slacks to enhance plant community diversity. There is a need for further long-term monitoring programmes to investigate dune slack communities in different localities since management needs to be tailored to local conditions.

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### Author contributions

**Nicola Johansen:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing – original draft (equal); Writing – review and editing (equal). **Michelle Davis:** Formal analysis (equal); Methodology (equal); Software (equal); Supervision (equal); Writing – review and editing (equal). **Paul Ashton:** Conceptualization (equal); Methodology (equal); Project administration (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

### Data availability statement

Data are available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.25148357 (Johansen et al. 2024).

### Supporting information

The Supporting information associated with this article is available with the online version.

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