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RESEARCH ARTICLE

Fine-scale hydrological niche segregation in coastal dune slacks

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Abstract

Questions: Hydrological niche segregation is widespread and has been found across a range of different habitats. Different plant species can occupy distinct hydrological niches, and as a result fine-scale variability in hydrology can structure plant communities. However, these patterns may not be as clear in habitats where differences in hydrology are more short-lived, such as coastal dune slacks. We explored the extent that the hydrological regime structures dune slack plant communities.

Location: Ainsdale Coastal Sand Dune National Nature Reserve, UK.

Methods: Six hundred quadrats were surveyed, 100 in each of six coastal dune slacks. Water table levels are recorded monthly in each slack. Metrics summarising hydrological regime were calculated and adjusted for each quadrat based on elevation. We tested the relationship between water table depth, plant communities and topography across and within dune slacks.

Results: Half (three) of the slacks showed a significant influence of hydrology on plant community composition. The three that did not were the ones that varied least topographically and contained less diverse plant communities. We also provide indirect evidence of niche segregation by modelling species-specific responses between mean water table depth and probability of species presence.

Conclusions: We demonstrate that hydrology is a dominant driver of plant community composition across dune slacks. However, plant communities are not always structured by hydrology, demonstrating the complexity of vegetation patterns. Topographic variation appears to impact plant community patterns, as do successional processes, highlighting the need to create diverse habitats for slack restoration and management.

KEYWORDS
coastal wetlands, dune slack, hydrology, microtopography, niche segregation, sand dunes, succession, topography

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1 | INTRODUCTION

Hydrological processes are important in structuring plant community diversity and composition (Silvertown et al., 2015). Hydrological regimes in lowland areas can vary spatially at small scales (cm to m) due to differences in topography. Small elevation differences can have important impacts on hydrological factors such as depth to the water table, periods of flooding and water availability (Silvertown et al., 1999; Økland et al., 2008; Moeslund et al., 2011, 2013a, 2013b). For instance, Vivian-Smith (1997) demonstrated that changes of 1–3 cm in height can segregate wetland plant species. Hydrological regimes can also vary temporally, such as differences in the duration and frequency of flooding. Species may have specific responses to these hydrological patterns, which promotes co-existence. For instance, closely related species can have different tolerance to water availability (Parolin et al., 2010; West et al., 2012; Craine et al., 2013). This specialisation may also be driven by temporal hydrological differences among years (temporal storage effect) (Chesson et al., 2004; Silvertown et al., 2015). Hydrological niche segregation is widespread, and has been found across a range of biodiversity-rich habitats including floodplain meadows, coastal heathlands, alpine and desert tundra, and coastal dune slacks (Dawson, 1990; Silvertown et al., 1999; Schachtschneider & February, 2010; Araya et al., 2011; Curreli et al., 2013; Letten et al., 2015; García-Baquero et al., 2016). Understanding how plant species and communities respond along local hydrological gradients has important implications for conservation management, as hydrologically driven biodiversity-rich habitats may be sensitive to climate change.

In complicated systems there is clear evidence that many species occupy distinct hydrological niches, and as a result, fine-scale variability in hydrology drives community composition and patterns of biodiversity (Silvertown et al., 2015). These differences of species preferences and therefore their segregation within the same habitat, can be studied along hydrological gradients. However, these patterns may not be as strong in habitats where differences in hydrology are more short-lived. Habitats where hydrological regimes vary significantly temporally and spatially, may respond differently to hydrological pressures, due to complex biotic and abiotic factors. Therefore, exploring plant–hydrology patterns in habitats with short-lived hydrological regimes, such as coastal dune slacks, can help us to understand to what extent hydrology is driving the distribution of vegetation patterns in these biodiversity-rich habitats.

Dune slacks are seasonal wetlands found between coastal sand dune ridges (Grootjans et al., 1998). They are typically nutrient-poor and support species of conservation importance including the natterjack toad (*Epidalea calamita*), fen orchid (*Liparis loeselii*) and petalwort (*Petalophyllum ralfsii*) (Houston, 2008). Dune slacks lie close to the water table, which varies seasonally and annually, causing periods of flooding-stress and drought-stress (Ranwell, 1959). Dune slack hydrology is complicated as they can be fed by different pathways of water movement such as from groundwater, surface water and precipitation (Grootjans et al., 2008; Rhymes et al., 2015). Depth to the water table, seasonal fluctuations and duration of drought or flood can alter species interactions, and therefore community patterns (Willis et al., 1959; Lammerts et al., 2001). These interactions are altered by climate-driven changes in groundwater, with species that are already at risk from climate change more likely to decline (Bartholomeus et al., 2011). Therefore, to predict how dune slack plant communities will respond to climate-driven changes in groundwater, it is essential to understand and explore the fine-scale hydrological drivers in these systems.

Vegetation composition in dune slacks is not only driven by hydrological conditions. For instance, successional processes can shape plant communities. In the pioneer phase, small species establish on limited soil. Over time a moss layer develops, and the depth of the soil organic matter and nitrogen mineralisation increases. Plant–plant interactions shift from competition for nutrients to competition for light, and a decrease in bare ground cover (Bossuyt et al., 2003; Sýkora et al., 2004; Grootjans et al., 2008). The depth of the soil organic matter indicates dune slack age (reflecting accumulation over time), but also impacts water-holding capacity (Minasny et al., 2015; Bordoloi et al., 2019). The presence of leaf litter (dead organic matter) increases water-holding capacity by reducing water loss from the soil surface (Li et al., 2014). Composition can also be altered by disturbance from grazing animals, which can be indicated by high bare ground cover and presence of dung (Plassmann et al., 2010; Millett & Edmondson, 2015). Dispersal limitations (Bossuyt et al., 2003) and priority effects (arrival and establishment of a certain species impacts later arrivals by taking key resources) may also be important drivers of variation in vegetation composition (Eriksson & Eriksson, 1998; Fukami, 2015; Vaughn & Young, 2015). To predict how plant communities will respond to climate change, we therefore need to understand how these complicated interactions drive community structure.

In this study we investigated the extent to which hydrological regimes structure plant community composition in coastal dune slacks. Specifically, we addressed the following four questions: (1) is hydrology the dominant driver of community composition differences across dune slacks; (2) does hydrology control fine-scale spatial variability in community composition within dune slacks; (3) does the presence of a community–hydrology link relate to topographic variability; and (4) do species have consistent responses to hydrological gradients?

2 | METHODS

2.1 | Study site

The Sefton Coast is located in the northwest of England and is a designated Site of Special Scientific Interest (SSSI). It is the largest dune system in England, approximately 25 km long and 3 km wide (Dynamic Dunescapes, 2021). Within the Sefton Coast dunes lies Ainsdale Sand Dunes National Nature Reserve (NNR) which is also a Natura 2000 protected site. The site contains areas of plantation woodland, fixed dunes, and dune slacks. The site has a large rabbit population and some areas are grazed with livestock (Millett & Edmondson, 2013).

2.2 | Vegetation sampling

To measure fine-scale variability, plant communities in six dune slacks were surveyed between 09.2018 and 07.2019 (Figure 1; Appendix S1). Plant communities, which were co-located to a single dipwell (way to measure groundwater) in each dune slack, were surveyed using a stratified random sampling approach (Figure 2). Plant communities were surveyed within a 7-m radius of the dipwell, providing a robust measure of hydrological conditions for each quadrat (Curreli et al., 2013). Within the 7 m, the dune slack was sectioned into four quadrants (north, east, south and west). Within each quadrant, 25 random quadrats of 15 cm × 15 cm were sampled, totalling to 100 quadrats per dune slack. Species occurrences (vascular and non-vascular), bare ground, dead organic matter and dung were recorded as percentage cover values. Nomenclature for vascular plants follows Stace (2019) and non-vascular follows Atherton et al. (2010). Vascular plants identified to species were included in the analysis (six vascular species removed). From the vegetation data we calculated species richness, the Shannon diversity and Simpson diversity index for each dune slack in R (v.4.0.3) using the package *BiodiversityR* (Kindt, 2018; R Core Team, 2020).

2.3 | Hydrological data

Ainsdale NNR has an extensive hydrological monitoring network, where the water table depth (WTD) has been measured monthly since 1972 (Clarke & Ayutthaya 2010; Abesser et al., 2017). The names (numbers) used for dune slacks in this study follow the naming convention of the ongoing water table data collection. Differences in frequency (sampling interval) of the hydrological monitoring makes comparisons across slacks challenging (Bartholomeus et al., 2008). Therefore, daily hydrological time series models were created for each dune slack using the software Menyanthes (von Asmuth et al., 2002). Menyanthes uses the PIRFICT method (Predefined Impulse Response Functions In Continuous Time) which can handle different frequencies and time intervals (von Asmuth et al., 2012). The model requires WTD and climatic data as inputs. Climate data from Blackpool Squires Gates weather station were used for the models (Met Office, 2020). Data required included mean temperature (°C), precipitation (mm), and potential evapotranspiration (PET; mm). PET was calculated using the Penman–Monteith formula using the function "ET. PenmanMonteith" in the package *Evapotranspiration* (Allen et al., 1994; Guo et al., 2016). Data required included maximum, minimum and average temperature (°C), relative humidity (%), precipitation (mm), daily sunshine hours (hour) and wind speed (m/s).

2.4 | Calculating quadrat-level hydrological metrics

For use in the statistical analysis, the average of water table depth (AWTD) over a four-year hydrological period (01.06.2015–30.05.2019) was calculated based on modelled daily values for each slack. Previous hydrological studies in UK dune slacks have been based on one to three years of hydrological data (Ranwell, 1959; Jones et al., 2006; Rhymes et al., 2014). A four-year average extends current research, and is similar to another study in UK dune slacks (Curreli et al., 2013). Additionally, in UK wet meadows, hydrological variables over the preceding three to seven years explained shifts in plant communities (Gowing et al., 2002, 2005).

The location and elevation of the six dipwells and the 600 quadrats were recorded using a differential GPS (dGPS), with vertical accuracy <10 mm (Trimble R6 ; Trimble, 2013). Quadrat-level hydrological metrics were calculated based on the difference in elevation of each quadrat relative to the AWTD of the dipwell.

2.5 | Topographic variability

The shape and slack floor elevations of the dune slacks were often heterogenous, and dipwells were not always located in the centre of a dune slack. The dGSP measurements also provide a measure of the variation in topography of the dune slack (topographic roughness). The standard deviation for each dune slack was calculated based on



FIGURE 1 Ainsdale National Nature Reserve dune slack 49

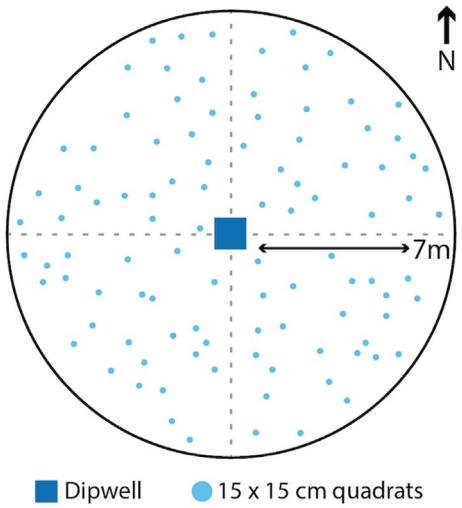


FIGURE 2 Schematic diagram of the stratified random sampling in a dune slack. A single dipwell is located within each dune slack. Within a 7 m radius from the dipwell, the dune slack is sectioned into four quadrants (north, east, south and west). Within each quadrant, 25 random quadrats of 15 cm × 15 cm are undertaken, totalling to 100 quadrats per slack

the quadrat-level elevation. The higher the standard deviation, the more topographically variable the dune slack. Standard deviation was calculated using the function "sd" in the base package *stats* (R Core Team, 2020).

2.6 | Data analysis

Our analysis focussed on the four hypotheses exploring large and fine-scale community responses and species responses. All data analysis was performed using R (v.4.0.3) (R Core Team, 2020).

2.6.1 | Is hydrology the dominant driver of community composition differences across dune slacks?

The choice of multivariate analysis technique was informed by first running a Detrended Correspondence Analysis (DCA) using the "decorana" function in the package *vegan* (Oksanen et al., 2015; R Core Team, 2020). Four outlier quadrats were removed due to the presence of a species with high percentage cover (i.e., 90%) not recorded elsewhere, and two quadrats removed due to missing dGPS data. This resulted in a matrix of 594 quadrats by 69 species. The length of the first DCA axis was >4 (4.634) which indicates strong unimodality (Smilauer & Leps, 2014). Therefore canonical correspondence analysis (CCA) in the package *vegan* (Oksanen et al., 2020) was used for subsequent analyses to test the potential effects of the environmental parameters on the plant communities. CCA is a direct gradient analysis, where the ordination is constrained by the environmental variables. Variables such as dune slack identity can also be partialled out (Gardener, 2014). Environmental parameters were cover of non-vascular plants (NV; %), bare ground (BG; %), dead organic matter (DOM; %), dung (DU; %), and a four-year average water table (AWTD) (Table 1).

We first included all environmental variables in a global CCA model with dune slack identity as a dummy variable (model one). We used the function "cca" in the package *vegan* (Oksanen et al., 2020). To remove redundant variables and create a parsimonious model (model two), we used the "ordistep" function to select the minimum number of environmental factors that best explain community structure, with forward selection and R2scope = FALSE (Legendre & Gallagher, 2001; Oksanen et al., 2020). After this process, to determine the presence of multicollinearity between environmental factors, the variance inflation factor (VIF) was calculated using the "vif.cca" function. Variables with VIF values greater than 10 were subsequently dropped from the model. We then repeated this process but with slack identity included as explanatory variable using the function "Condition". We produced both a full model (model three) and a parsimonious model (model four). This enabled the environmental impacts on communities to be examined with dune slack-caused variability partialled out (the effects of the explanatory variable removed; Borcard et al., 2011). The significance of the models, for the entire model, each axis and each term, was assessed using an ANOVA using the "anova.cca" function (permutations = 1000).

2.6.2 | Does hydrology control fine-scale spatial variability in community composition within dune slacks?

We used non-metric multidimensional scaling (NMDS) to explore the relationship between hydrology and community composition for each dune slack. Matrix sizes (quadrats by species) were 99 cm × 26 (slack 3), 100 × 18 (slack 5), 99 × 44 (slack 6), 99 × 28 (slack 7), 98 × 22 (slack 11), and 99 × 24 (slack 49). NMDS is an indirect gradient analysis and was performed using Bray–Curtis dissimilarity (Borcard et al., 2011). The function "metaMDS" in the package *vegan* was used as it uses repeated random starts to find a stable solution (Oksanen et al., 2020). A maximum of 1,000 iterations for the distance matrix was run, and the NMDS was projected in $K = 2$ dimensions to minimise stress. The ordination was rotated using the function "MDSrotate",

TABLE 1 Environmental variables included in the canonical correspondence analysis (CCA)

Environmental variables	Code
Non-vascular (%)	NV
Bare ground (%)	BG
Dead organic matter (deadwood and litter) (%)	DOM
Dung (%)	DU
Average water table depth over four years (cm)	AWTD

to align the first dimension of the NMDS parallel with AWTD. The ordering of the relationships was assessed using a Shepard diagram, using the function "stressplot" (Borcard et al., 2011). The function "ordisurf" was then used to fit a quadratic trend surface corresponding to the AWTD for each slack (the results from the rotation), which was overlaid onto the NMDS ordination.

2.6.3 | Does the presence of a community–hydrology link relate to topographic variability?

We used linear models to determine the relationship between topographic variability within a slack and plant community diversity, and the composition–hydrology relationship. We tested relationships between topographic variability (roughness) and the dependent variables (1) species richness, (2) Shannon diversity, (3) Simpson diversity and (4) R^2-value from the NMDS trend surface. We used the function "lm" in the base package *stats* (R Core Team, 2020). Richness, Shannon and Simpson provided a measure of alpha diversity for each slack. R^2-value from the NMDS provided a measure of the strength of the hydrology–plant community relationship. For each model, we fitted and compared linear and logarithmic regression lines. Logarithm regression lines were the best fit (highest R^2) for all four models.

2.6.4 | Do species have consistent responses to hydrological gradients?

We modelled species-specific responses to the hydrology gradient (AWTD) using a generalised additive mixed models (GAMM) approach (Zuur et al. 2009). This approach allows for non-linear relationships between the response (species) and explanatory variable (AWTD) and can control for spatial autocorrelation. Models were created for species with more than 5% frequency across all slacks (present in 30 out of 596 quadrats). This reduced the number of species modelled from 69 to 20. Percentage cover data were converted to presence/absence data. A GAMM was fitted with presence of each species as the dependent variable and AWTD as the independent variable, using a cubic spline and the family binomial. The random effect of slack was included and spatial autocorrelation using latitude and longitude. The function "gamm" from the package *mgvc* was used (Wood, 2019).

3 | RESULTS

A total of 69 species were recorded across the six dune slacks. Common species present in all slacks were *Agrostis stolonifera*, *Carex nigra*, *Galium palustre*, *Hydrocotyle vulgaris*, *Lotus corniculatus*, *Lotus pedunculatus*, *Rubus caesius* and *Salix repens* (Appendix S2). Across all slacks, *Salix repens*, *Hydrocotyle vulgaris* and *Rubus caesius* had the highest percentage cover recorded. The species richness within the slack varied from 22 to 44, Shannon diversity from 1.32 to 2.33 and Simpson diversity from 0.74 to 0.84 (Table 2).

3.1 | Is hydrology the dominant driver of community composition differences across dune slacks?

In the global CCA model (model one), the constrained variables (AWTD, NV, BG and DOM, and slack identity) explained 13.7% of the total variation. The first five axes were statistically significant, with axes 1 and 2 explaining respectively 30% and 23.5% of the explained variation. The constrained variables were all statistically significant except for DU. In the parsimonious model (model two), the constrained variables (AWTD, slack 3, 5, 6, 7 and 49 and NV) explained 13% of the total variation. Constrained variables DU, BG, DOM and slack 11 were dropped. The first seven axes were statistically significant, axes 1 and 2 explaining respectively 31.5% and 24.8% of the explained variance. The constrained variables were statistically significant.

In the full model, where slack identity was included as an explanatory variable (model three), the constrained variables (AWTD, NV, BG and DOM) explained 3.7% of the variance and slack identity explained 10%. Only the first axis was statistically significant, explaining 72% of the variation. The constrained variables AWTD and NV were statistically significant, but BG and DOM were not statistically significant. In the parsimonious model (model four), the constrained variables (AWTD, NV, BG and DOM) explained 3.6% of the variance and slack identity explained 10% (Figure 3). The constrained variable DU was dropped. Axes 1 and 3 explained respectively 74.7% and 9.7% of the explained variation. The constrained variables were statistically significant, but BG was not ($p = 0.078$), but was included in the final model as it was the best model fit.

3.2 | Is hydrology controlling community composition within each slack?

For three dune slacks (6, 7 and 49), plant community composition was strongly associated with the hydrological gradient (Figure 4). However, this was not the case for slacks 3, 5 and 11, where there was no clear structuring of the community by the hydrological gradient.

3.3 | How does the presence of a community–hydrology link relate to topographic variability?

There was good evidence that more topographically variable dune slacks contained greater plant species diversity (linear model: Richness: $F_{1,4} = 8$, Adj $R^2 = 0.58$, $p = 0.047$; Shannon: $F_{1,4} = 35.8$, Adj $R^2 = 0.87$, $p = 0.004$; Simpson: $F_{1,4} = 10.18$, Adj $R^2 = 0.65$, $p = 0.033$). There was evidence that more topographically variable dune slacks had significant water table depth

TABLE 2 Summary of the topography, water table depths, NMDS trend surface and alpha diversity for each slack

Slack	Topographic roughness	AWTD	NMDS trend surface			Alpha diversity		
	Standard deviation (cm)	Mean (cm)	*F* value	R^2	*p*-value	Total richness	Shannon diversity	Simpson diversity
3	4.9	−50.3	0.68	0.02	0.10	26	1.72	0.74
5	3.8	−28.9	0	0.01	0.67	18	1.49	0.68
6	36.4	−85.3	80.48	0.71	<0.001	44	2.33	0.84
7	5.1	−26.1	6.15	0.18	<0.001	28	1.9	0.78
11	2.2	−58.9	0	0	0.69	22	1.32	0.58
49	10	−22.6	26.11	0.44	<0.001	24	1.91	0.74

AWTD, average of water table depth; NMDS, non-metric multidimensional scaling.

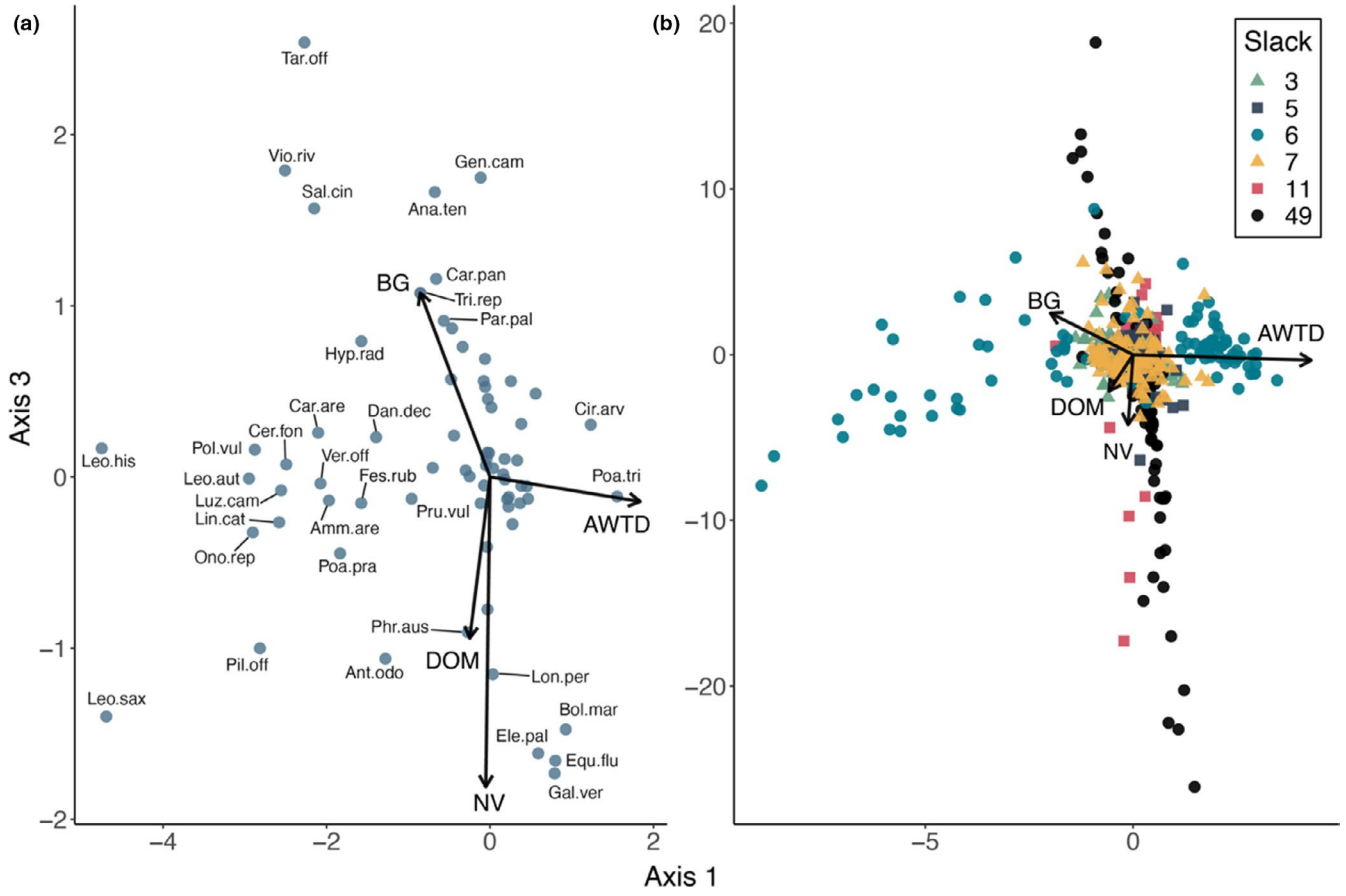


FIGURE 3 Canonical correspondence analysis (CCA) of the constrained parsimonious model (model four). (a) The plant species and the environmental factors. (b) The quadrats, the environmental factors and dune slack identity. Abbreviations for environmental variables are: NV, non-vascular plants; DOM, dead organic matter; BG, bare ground; and AWTD, average water table depth. Abbreviations for species are: Amm.are, *Ammophila arenaria*; Ana.ten, *Anagallis tenella*; Ant.odo, *Anthoxanthum odoratum*; Bol.mar, *Bolboschoenus maritimus*; Car.pan, *Cardamine pratensis*; Cer.fon, *Cerastium fontanum*; Cir.arv, *Cirsium arvense*; Dan.dec, *Danthonia decumbens*; Ele.pal, *Eleocharis palustris*; Equ.flu, *Equisetum fluviatile*; Fes.rub, *Festuca rubra*; Gal.ver, *Galium verum*; Gen.cam, *Gentianella campestris*; Hyp.rad, *Hypochaeris radicata*; Leo.his, *Leontodon hispidus*; Leo.sax, *Leontodon saxatilis*; Lin.cat, *Linum catharticum*; Lon.per, *Lonicera periclymenum*; Luz.cam,*Luzula campestris*; Lyt.sal, *Lythrum salicaria*; Ono.rep, *Ononis repens*; Par.pal, *Parnassia palustris*; Phr.aus, *Phragmites australis*; Pil.off, *Pilosella officinarum*; Poa.pra, *Poa pratensis*; Poa.tri, *Poa trivialis*; Pol.vul, *Polygala vulgaris*; Pru.vul, *Prunella vulgaris*; Sal.cin, *Salix cinerea*; Tar.off, *Taraxacum officinale*; Tri.rep, *Trifolium repens*; and Ver.off, *Veronica officinalis*

trends (linear model: NMDS R^2 trend surface: $F_{1,4} = 42.46$, Adj $R^2 = 0.89$, $p = 0.003$). Slack 6 was most topographically variable, contained most species and had the highest Shannon and Simpson diversity. Slack 11 was least topographically variable, had the second-lowest species richness, but lowest Shannon and Simpson diversity (Table 2; Figure 5).

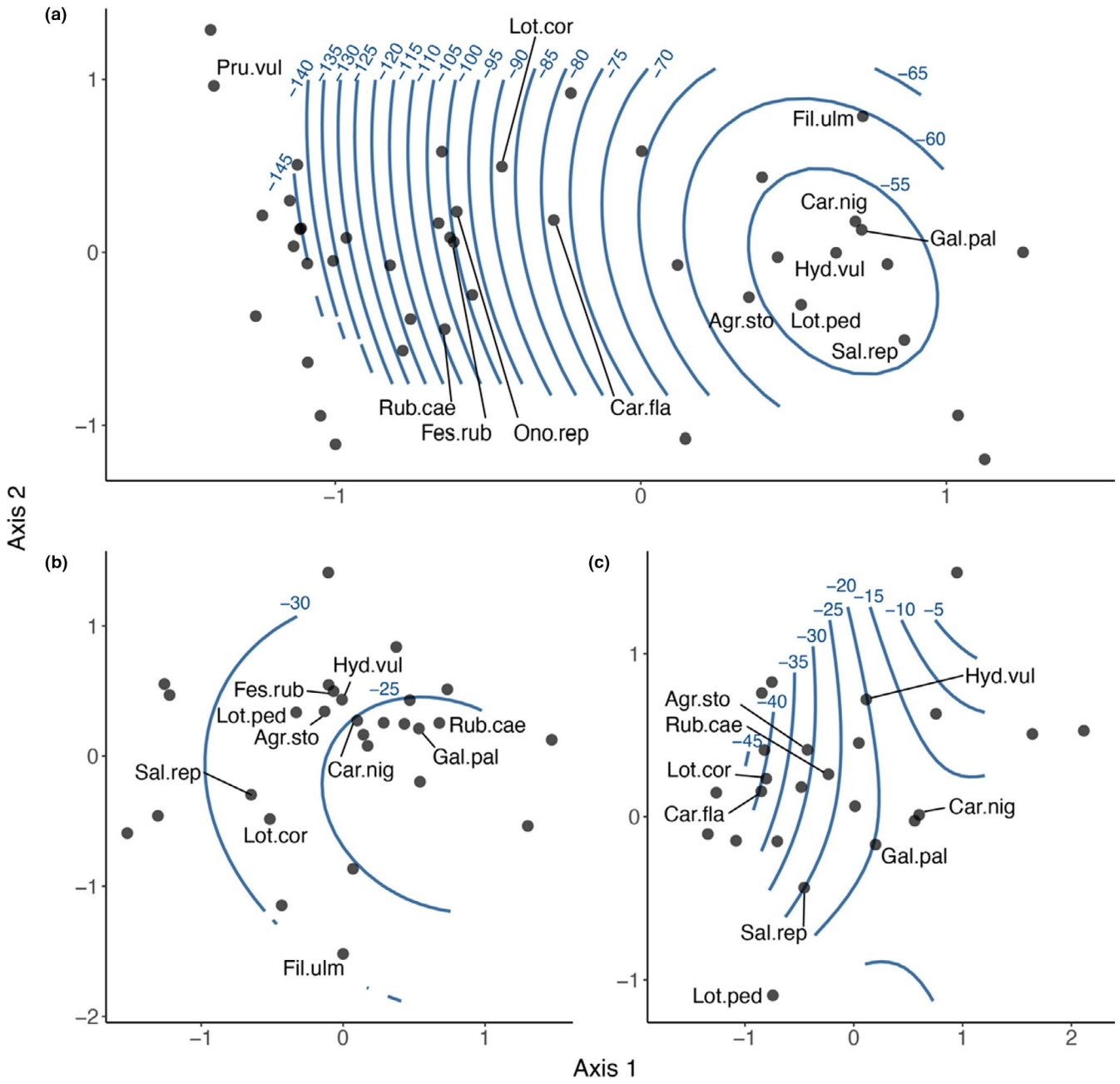


FIGURE 4 Main species gradients for: (a) slack 6; (b) slack 7; and (c) slack 49. Stress on the two-dimension non-metric multidimensional scaling (NMDS) was 0.13 (6), 0.18 (7), and 0.19 (49), an indication that ecological distances are well represented. Trend surface statistics for slack 6 were $R^2 = 0.71$, $F = 80.48$, e.d.f = 1.98, $p < 0.001$, $n = 99$; for slack 7 $R^2 = 0.18$, $F = 7.31$, e.d.f = 2.61, $p < 0.001$, $n = 99$; and for slack 49 were $R^2 = 0.44$, $F = 26.11$, e.d.f = 1.95, $p < 0.001$, $n = 99$. Contours depict ordination space representing the same hydrology (i.e., average water table depth [AWTD], with more negative meaning lower water level). Abbreviations for species are: Agr.sto, *Agrostis stolonifera* ; Car.fla, *Carex flacca* ; Car.nig, *Carex nigra* ; Fes.rub, *Festuca rubra* ; Fil.ulm, *Filipendula ulmaria* ; Gal.pal, *Galium palustre* ; Hyd.vul, *Hydrocotyle vulgaris* ; Lot.cor, *Lotus corniculatus* ; Lot.ped, *Lotus pedunculatus* ; Ono.rep, *Ononis repens* ; Pru.vul, *Prunella vulgaris* ; Rub.cae, *Rubus caesius*; and Sal.rep, *Salix repens*

3.4 | Do species have consistent responses to hydrological gradients?

Out of the 20 species investigated, for 12 the relationship between the depth to water table and probability of presence was statistically significant (Figure 6). Responses of species presence along a water table gradient from −171 cm (drier) to −4 cm (wetter) included hump-shaped (e.g., *Lotus pedunculatus*), curvilinear increasing (e.g., *Carex nigra*) and curvilinear decreasing (e.g., *Ononis repens*).

4 | DISCUSSION

We found that hydrology is a key driver of plant composition at a landscape scale because it explained variation in plant community

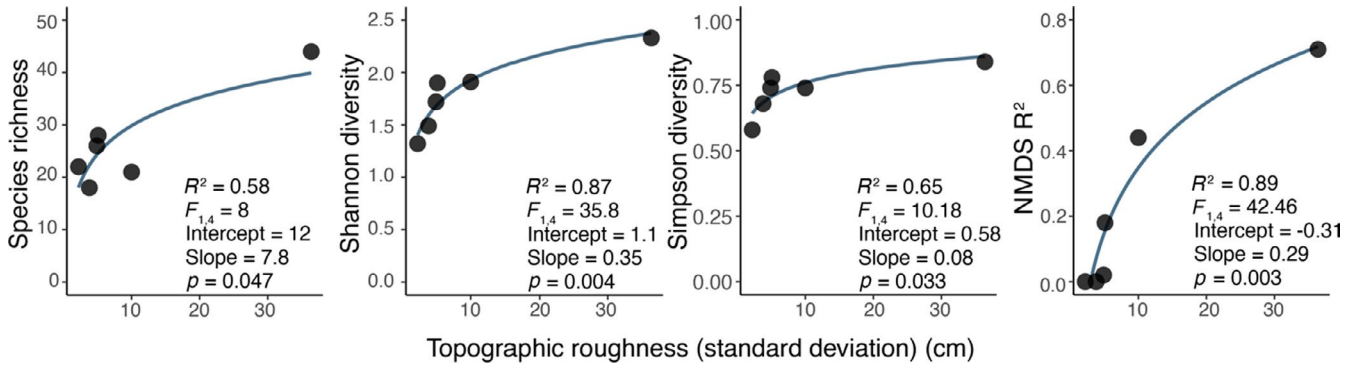


FIGURE 5 The relationship between topographic variability in a slack and measures of alpha diversity and the hydrology–plant community relationship. Presented are the surface roughness (standard deviation of between-quadrat variation in elevation) and dune slack (1) species richness, (2) Shannon diversity, (3) Simpson diversity and (4) non-metric multidimensional scaling (NMDS) R^2 trend surface. The fitted line is based on a logarithmic regression

composition across all dune slacks. However, for variation in plant communities within a slack, hydrology was only an important control for half of the wetlands. We demonstrate that these differences in within-slack community–hydrology relationships are explained by the extent of within-slack variability in topography. In topographically variable slacks community composition is tightly coupled to hydrology; this is not the case in less variable slacks. Slack topographic variability was also a key driver of slack plant community diversity. We also demonstrate species-specific responses along hydrological gradients, providing evidence of hydrological niche segregation for some species at least. These patterns are important in demonstrating that, while the short-lived hydrological regimes can be very important drivers of plant community structure, they may not be the only factor responsible. We also demonstrate the key role that topography plays in structuring these biodiverse rich coastal wetlands. This will provide important information for coastal-site managers when considering dune slack restoration and emphasise the necessity of including topographical variability to support plant species diversity.

How species co-exist in spatially heterogenous environments depends on several criteria. One of the most important explanations for co-existence is that individual species have different responses to the environment (Chesson, 2000; Silvertown, 2004). We provide indirect evidence of hydrological niche segregation (due to being observational data) by modelling species-specific responses along a hydrological gradient (Silvertown, 2004). Evidence of species segregation along hydrological gradients has been noted in several habitats (Silvertown et al., 1999, 2015; Araya et al., 2011; Letten et al., 2015; García-Baquero et al., 2016).

Of the 20 species, 12 species were responding along the hydrological gradient; a lack of response for the remaining species may follow from priority effects. For instance, in a grassland system Damgaard et al. (2017) demonstrated that colonisation has a larger impact on species survival and success compared to survival of flooding.

Successional processes may also result in differences in plant communities that are not evidenced in current hydrological conditions (Pye & Saye, 2005; Davy et al., 2006). Successional processes may be altered by priority effects in young dune slacks, changing the trajectory of the plant community (Bossuyt et al., 2003). Extremely dry conditions can also delay the development towards older successional vegetation (Grootjans et al., 1991). Species co-existence and community structure may be affected by species dispersal and competition (Bossuyt et al., 2003). In addition, underlying mechanisms such as groundwater nitrogen that were not measured may be driving species-specific responses (Rhymes et al., 2016). Site management must, therefore, include recognition of other local factors in controlling vegetation composition other than water table depth.

In our study, within-slack topographic variability was the driver of differences in hydrology and plant community diversity. Less topographically varied dune slacks had the least variation in hydrology and had typically lower species diversity. The internal structuring of vegetation composition within flatter slacks is not determined by hydrology. Topographically controlled soil moisture plays an important role in structuring plant communities (Moeslund et al., 2013c). Vertical elevation is recognised as an important control of soil moisture in habitats that lie within a few metres of the water table (Moeslund et al., 2011, 2013a). For instance, as Moeslund et al. (2013b) demonstrated, at different spatial scales (2–250 m) across a range of lowland habitats in Denmark, elevation had the strongest impact on plant communities and topographically controlled soil moisture was the main determinant of habitat type. While only based on six dune slacks, our study demonstrates the potential for small-scale local topographic variability as a control over local plant diversity patterns. This is explained by the interaction between niche differentiation along the hydrological gradient, coupled with differences in niche diversity between habitats. This further demonstrates the importance of creating topographically variable dune slacks in restoration projects.

Across all dune slacks hydrology was a dominant driver of plant community composition. These findings are consistent with general trends in dune slacks (Willis et al., 1959; Grootjans et al., 1991, 2008; Lammerts et al., 2001). Our results also show that slack identity explained more variation than environmental variables. This could relate to differences in community composition within the

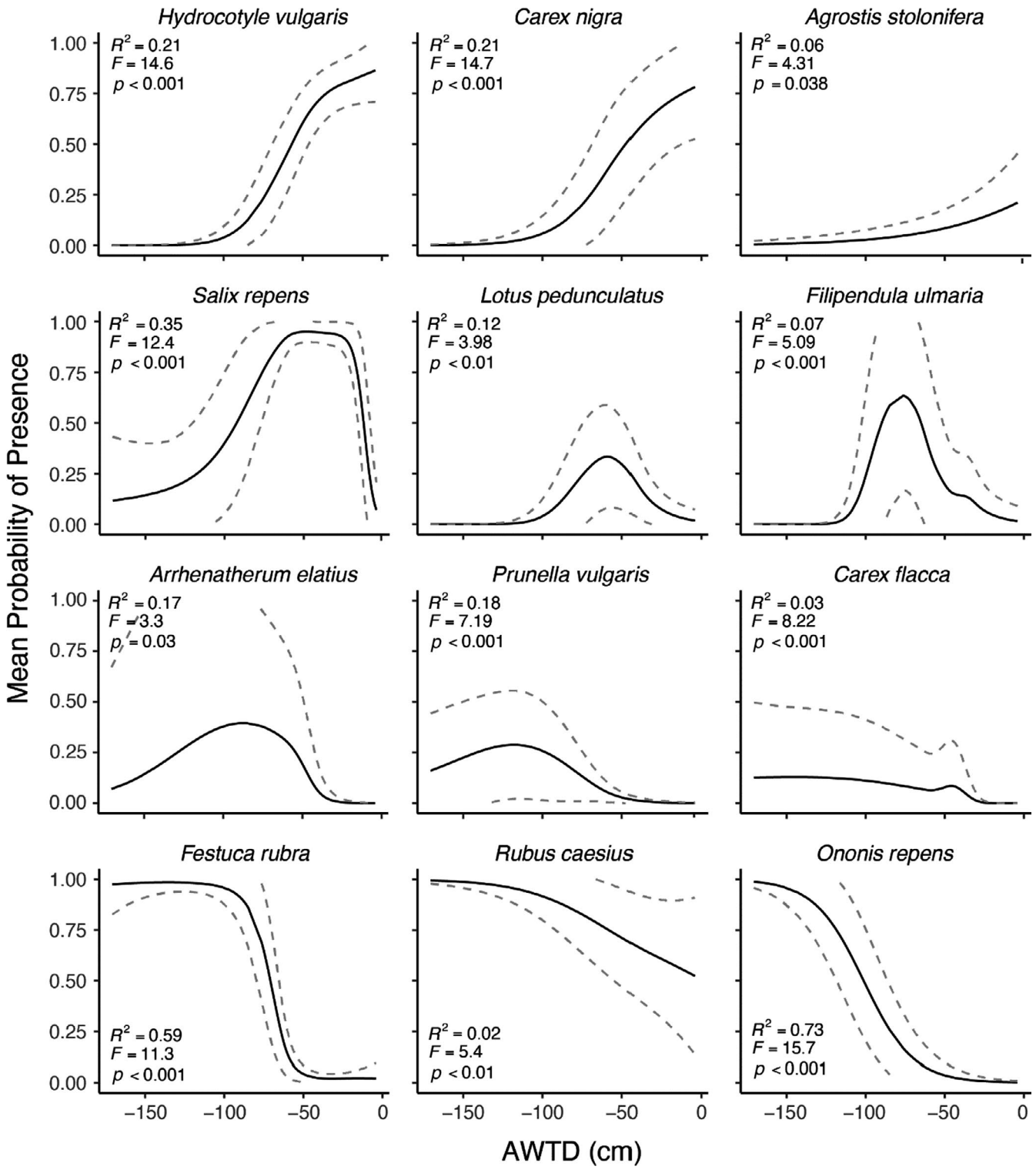


FIGURE 6 Fitted generalised additive mixed models (GAMM) for 12 species across all six dune slacks, accounting for spatial autocorrelation and random effect (of dune slack). The smoothers (—) and confidence bands (- - -) represent the mean probability of presence against average water table depth (AWTD in cm; $n = 594$)

slack, which could be driven by the difference in hydrological regime. For instance, fluctuations in the hydrological regime can alter intraspecific and interspecific interactions, and thus community composition (Bossuyt et al., 2003, 2005). Changes in the water table levels can also affect the removal of the nutrients, with high water levels maintaining a low nutrient status of nitrogen and phosphorus (Lammerts & Grootjans, 1997). Microbial communities and belowground interspecific competition can also be altered by the hydrological regime (Wolfe et al., 2006; Bartelheimer et al., 2010; Araya et al., 2013). These unmeasured effects driven by the hydrological

regime may be influencing the plant community structure differently within each slack. Plant species and community structure may also be affecting soil moisture dynamics (Leitinger et al., 2015; Zheng et al., 2015), and soil properties (Ehrenfeld et al., 2005; Fischer et al., 2014, 2015). For inst

ance, Fischer et al. (2019) demonstrated in a long-term grassland experiment that soil water content was affected by species richness and certain functional groups.

Water table depth provides a measure of the hydrological conditions of the slack. This metric is valuable for site managers, as it provides essential information on the seasonal and long-term hydrological changes, and can explain differences in community composition (Sterck et al., 2011; Curreli et al., 2013; Rhymes et al., 2014; Schietti et al., 2014; Earl, 2015). However, our choice of metric (four-year average) will not encompass all of the variability in hydrological regime. One of the challenges in interpreting plant responses along hydrological gradient is the role of water as both limiting resource and a stress when over-abundant. Silvertown et al. (1999) demonstrated that there is a trade-off of species tolerance between time spent in drought conditions and time spent waterlogged, which is measured as sum exceedance values (SEV). This is further supported by Araya et al. (2011), whereas Bartholomeus et al. (2012) suggest that direct measures such as availability of water and oxygen in the root zone predicts vegetation better than indirect measures such as mean spring groundwater or SEV. Consequently, our choice of metric may not have been sensitive enough to identify all the plant communities responding along hydrological gradients. Nonetheless, we found strong responses to the metric we used, indicating that we did characterise a component of slack hydrology which is important for plant communities.

Our results demonstrate the complexity of dune slacks, and the importance of exploring hydrological drivers in short-lived habitats. Across all dune slacks, hydrology was a key feature in structuring plant communities. However, communities in only half of the studied coastal wetlands were structed along a hydrological gradient. This relates to topographic variability within the slack. Even within the same sand dune system, plant communities may be controlled by different sets of environmental drivers. This has implications for understanding how the drivers of plant community change might impact communities and may result in idiosyncratic responses, where specific habitat-level controls are not fully understood. This research assists coastal dune management by demonstrating that to maximise habitat space for many species, topographically varied dune slacks need to be created and that successional processes and species interactions will play a role in determining final slack composition. Climate change will have a significant impact on dune slack hydrology and understanding how plants respond to hydrology is essential to protect these biodiversity-rich habitats.

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AUTHOR CONTRIBUTIONS

CD, LJ, JM and RJP conceived the ideas; CD, LV, NH and JM conducted the fieldwork, with help from collaborators; CD, RJP, LJ and JM analysed the data; CD led the writing with assistance from RJP, JM, LJ, NH and LV.

DATA AVAILABILITY STATEMENT

Data available from Dwyer et al. (2021) can be found at https://doi.org/10.17028/rd.lboro.15049908.v1

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Geographic location of the dune slacks in Ainsdale Sand Dunes National Nature Reserve

Appendix S2. Plant community data in Ainsdale Sand Dunes National Nature Reserve. Summary of the species found in the 594 quadrats

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