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Patterns of variation in plant diversity vary over different spatial levels in seasonal coastal wetlands

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Abstract

Aim: To quantify the responses of alpha and beta diversity to multivariate gradients, incorporating variation in environmental and management variability in coastal dune slacks.

Location: United Kingdom dune slacks.

Methods: Plant community composition, plant nutrient status and soil characteristics were measured for 164 quadrats in 41 dune slacks across 12 coastal sand dune systems. Data were collated on climate and atmospheric deposition. Hydrological regimes at daily resolution were modelled and calibrated using daily-to-monthly site measurements, from which we calculated quadrat-level hydrological metrics. Alpha diversity (richness, Shannon diversity and Pielou's evenness) metrics and beta diversity (turnover and nestedness) for species and genera were calculated across three spatial levels from sand dune system (highest) to dune slack to quadrat (lowest).

Results: Diversity patterns depended on the spatial and taxonomic level considered. At smaller spatial levels (between dune slacks and between quadrats), alpha and beta diversity varied along gradients driven by soil characteristics, water table depth and atmospheric deposition. At larger spatial levels (between sand dune systems), patterns of beta diversity were a consequence of plant nutrient status. There was little variability in alpha diversity along this same gradient, with only small changes in Pielou's species evenness. Patterns at a coarser taxonomic level (genus) mirrored those at the species level.

Main conclusion: We show that patterns of variation in plant diversity are dependent on the spatial level considered, but taxonomic level made little difference in understanding these patterns. Therefore, if we do not consider patterns across different spatial levels, important environmental and management drivers could be missed. The high biodiversity value and degree of threat to these European protected habitats makes such understanding invaluable for their conservation.

KEYWORDS
alpha diversity, beta diversity, dune slacks, eco-hydrology, plants, spatial scale, wetland

1 | INTRODUCTION

Biodiversity is declining at an unprecedented rate (Díaz et al., 2019). This will have significant global impacts on ecosystem services, which are essential for human health and wellbeing (Dasgupta, 2021). To understand these changes, it requires determining which factors control biodiversity at different spatial, temporal and taxonomic scales (Chase et al., 2019; McGill et al., 2015; Sax & Gaines, 2003). The processes which control diversity—including extinction, extirpation (regional-level extinction), speciation and immigration—can operate at different scales. At a regional scale, climate, dispersal and biogeographic history can strongly control plant community diversity; at a local scale, species interactions, management and resources can exert stronger control (Harrison & Cornell, 2008; Lortie et al., 2004). These impacts are further complicated by species relatedness (Cavender-Bares et al., 2006). In general, more closely related species respond in more similar ways than less-related species (Burns & Strauss, 2011). Therefore, the responses of biodiversity metrics to environmental gradients at higher taxonomic resolutions (e.g. genus) may have high similarity to those at the species level. As such, exploring biodiversity at a range of spatial and taxonomic scales can provide key insights for understanding the drivers of diversity. This has important consequences for managing biodiversity loss, as different anthropogenic drivers will impact biodiversity at different scales (Vellend et al., 2017).

The importance of scale is difficult to disentangle because of the practical difficulties in obtaining comparative data at multiple scales (Chase et al., 2018). While there is a large body of literature highlighting the role that spatial scale can play in shaping biodiversity patterns, they tend to focus on a single driver of diversity change. This provides excellent understanding of how biodiversity is impacted by individual drivers such as along temperature, precipitation or latitudinal gradients (Fitzpatrick et al., 2013; Franklin et al., 2019; Ibanez et al., 2018). However, environmental gradients are multivariate; multiple drivers of biodiversity change operate together. If only individual drivers are explored, interactions between drivers of biodiversity change could be missed. Therefore, understanding of real-world patterns requires consideration of real-world gradients. This is essential if we are to scale up and/or down anthropogenic impacts on biodiversity.

Coastal sand dunes are one of the most at risk habitats in Europe and are important reservoirs of biodiversity (Janssen et al., 2017). Dune slacks are seasonal coastal wetlands, which in the UK support several species of conservation importance (JNCC, 2021). They are expected to be particularly sensitive to environmental changes due to complex interactions between hydrology, nutrient inputs and plant communities (Curreli et al., 2013; Rhymes et al., 2016). Depth to the water table, seasonal fluctuations and duration of drought or flood can alter species interactions and therefore community assembly (Dwyer, Millett, et al., 2021; Willis et al., 1959). The hydrological regime also influences nutrient levels within the dunes, with high water levels maintaining low nitrogen and phosphorus (Lammerts & Grootjans, 1997). Successional processes are also important in

structuring dune slack plant communities. Pioneer species establish on bare soil containing low or no nutrients. Over time, plants adapted to these low nutrients colonize, and a moss layer develops. In mature phases, the soil organic matter layer has developed and nitrogen mineralization increases. There is a decline of typical dune slack plants and increase in taller species as competition shifts from nutrients to light (Berendse et al., 1998; Grootjans et al., 2008; Lammerts et al., 1999). Soil organic matter can alter plant responses, as thicker organic matter layers (indicating older dune slacks) have a higher water holding capacity (Bordoloi et al., 2019). Management, such as grazing, may help to slow down successional processes and therefore alter the plant community composition (Millett & Edmondson, 2013). These complex interactions are disrupted by anthropogenic pressures such as climate change, with species that are already at risk being more likely to decline (Bartholomeus et al., 2011). Nitrogen deposition can also disrupt these interactions, with species richness being lowest in sites receiving high levels of nitrogen deposition (Field et al., 2014).

How each wetland will respond will depend on the geographic location (Jones et al., 2013), vertical elevation (Moeslund et al., 2013), hydrological regimes (Silvertown et al., 2015), successional processes (Dwyer, Millett, et al., 2021; Grootjans et al., 1991; Jones et al., 2008) and management (Pakeman et al., 2019). To fully understand these drivers of biodiversity variability requires that we disentangle impacts on both alpha and beta diversity. Drivers of alpha and beta diversity are related because beta diversity results from changes in plant communities in space and time, particularly along environmental gradients. However, they are not necessarily tightly coupled because changes in community composition does not always result in changes in alpha diversity. Therefore, to predict how dune slack plant diversity will respond to the various pressures, understanding is needed of how complex environmental interactions drive biodiversity patterns across different spatial and taxonomic levels. Determining how scale of measurement impacts the interpretation of the drivers of biodiversity is essential for a complete understanding of diversity patterns (Anderson, 2018). Without such understanding, it is difficult to determine the drivers of diversity, the impacts on biodiversity and potential ways to manage these impacts.

In this study, we investigated the spatial-scale dependence of environmental and management drivers of plant community diversity in coastal dune slacks across the UK, and how the measured response depends on the taxonomic resolution considered. Specifically, the aim was to quantify the responses of alpha and beta diversity to multivariate gradients, incorporating variation in environmental and management variability in UK dune slacks. To do this, three steps were followed: (1) We identified the key environmental gradients between dune slacks; (2) we explored the multivariate gradients associated with patterns of alpha diversity (diversity in an assemblage) across spatial (coastal sand dune system, dune slack and quadrat) and taxonomic (species and genus) levels; and (3) we explored the multivariate gradients driving beta diversity (the variation in composition of assemblages) across spatial and taxonomic levels.

As beta diversity can reflect turnover (replacement) and nestedness (loss), we explored changes in both turnover and nestedness over spatial and taxonomic levels. We also explored the spatial and multivariate environmental drivers of turnover, and how the rate and intensity of turnover differs along these multivariate environmental gradients.

2 | METHODS

2.1 | Coastal sand dune systems

Coastal sand dune systems were selected to represent geographic, climatic and hydrological variability around the UK (Figure 1a). Long-term hydrological recording was needed to fully understand plant responses to previous hydrological conditions (Silvertown et al., 2015), but only a subset of the sites had a history of hydrological recording (using a dipwell). Therefore, to address this gap, we installed dipwells in four sand dune systems to monitor water levels. Specifically, we installed dipwells in Coll Nature Reserve, Sands of Forvie, Tentsmuir and Winterton dunes between June and August 2017. In total, 41 dipwells (one dipwell per dune slack), within 12 coastal sand dune systems across the UK were surveyed.

2.2 | Community composition

Between June and September in 2017 and 2018, 164 quadrats across 41 dune slacks within 12 UK coastal sand dune systems were surveyed in the field (Figure 1a,b). In each dune slack, percentage cover of vascular and non-vascular plant species was recorded in, usually, four quadrats (1 m × 1 m) located 4 m north, east, south and west of a central point (the dipwell). This fixed approach around the dipwell ensured that data collection was consistent across the UK. The location and elevation of each dipwell (41) and each quadrat (164) were recorded using a differential GPS (DGPS) (R6 Trimble RTK-GPS), with vertical accuracy <10 mm (Trimble, 2013). These data were used to calculate quadrat-level hydrological metrics, described below.

Vascular and non-vascular plants were recorded to species level, nomenclature follows Paton (1999), Smith and Smith (2004) and Stace (2019). Vascular plant height was measured at 10 randomly located points within each quadrat. Plant community survey data were used to calculate three measures of alpha diversity: (1) species richness, (2) Shannon's diversity index and (3) Pielou's evenness index. These measures were calculated using the package "vegan" in R (Oksanen et al., 2015; R Core Team, 2022). Beta diversity was calculated using Bray–Curtis dissimilarity at the levels of sand
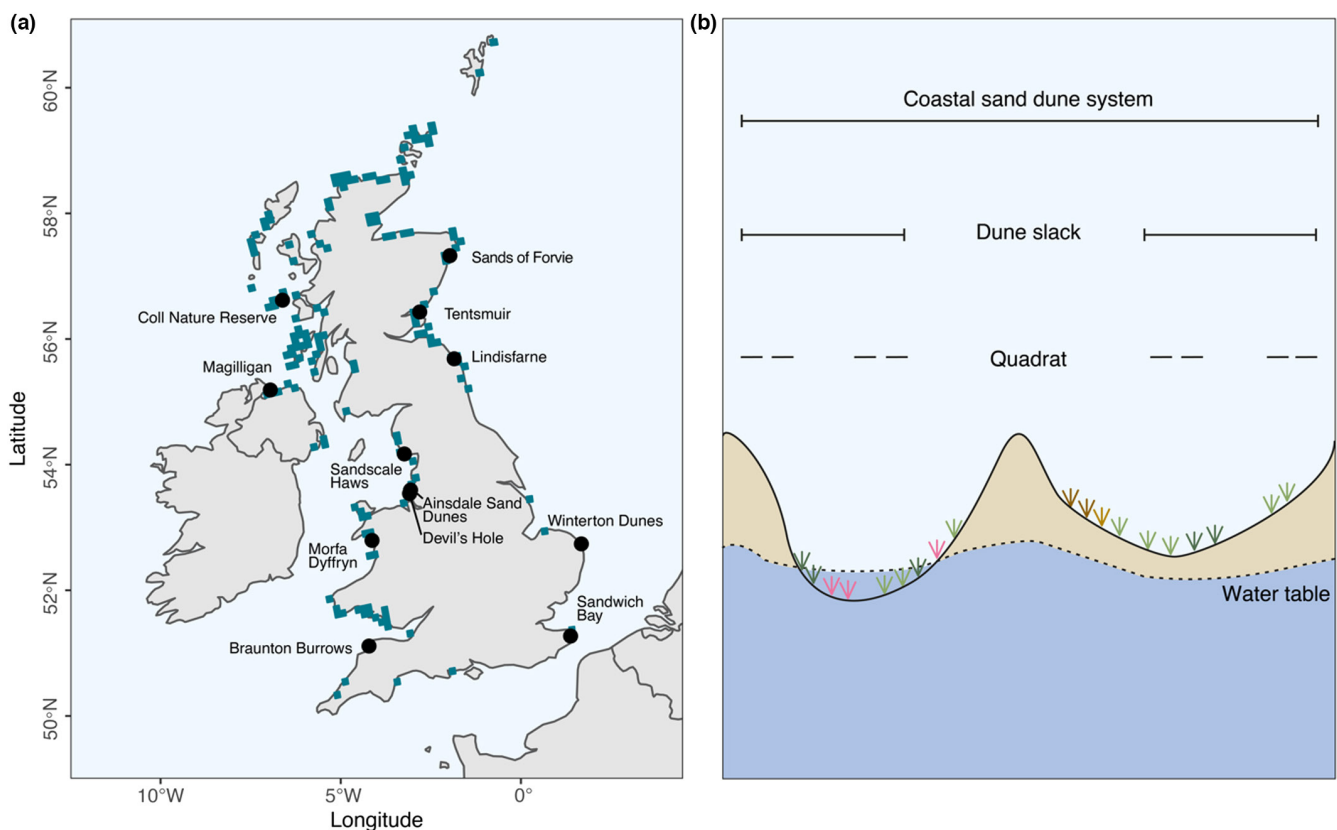
FIGURE 1 (a) Geographic locations of the 12 UK coastal sand dunes. The blue grids indicate locations based on 10 km presence of dune slacks in the UK (EU habitats directive annex I habitat—H2190) Data downloaded from Eionet central data repository (2020). Map image source: R package "rworldmap" (South, 2011). (b) Schematic diagram of the different spatial levels analysed (from largest to smallest level): Coastal sand dune system (*n* = 12), dune slack (*n* = 41) and quadrats (*n* = 164)

dune system, dune slack and quadrat (Figure 1b), using the package "BiodiversityR" (Kindt, 2018; R Core Team, 2022).

2.3 | Atmospheric deposition and climate data

Atmospheric deposition and climate data were collated to determine their potential environmental impacts on species diversity in dune slacks. Modelled atmospheric deposition data were downloaded from the Concentration Based Estimated Deposition (CBED) dataset (Smith et al., 2000). This consisted of 5 km×5 km gridded averages of oxidized nitrogen (NO_2/NO_3), reduced nitrogen (NH_3/NH_4), non-marine sulphur (SO_2/SO_4) and base cations (Ca and Mg). These were averaged over a 30-year period (1987–2017) because this has been shown to be the best predictor of plant community response to nitrogen (N) deposition (Payne et al., 2019). Climatic variables were extracted from the HadUK-Grid (Hollis et al., 2020). This consisted of 5 km×5 km gridded daily averages of mean, maximum and minimum annual temperature, and mean annual precipitation averaged over a 10-year period (2007–2017) (Britton et al., 2017).

2.4 | Harmonizing the hydrological data

Water table level for each dune slack was measured from a single dipwell, with depth from the ground surface to the water table recorded using data loggers or a water level sensor. The monitoring of water table level varied for each dune slack, with differences in the frequency of data collection (recorded daily, weekly or monthly) and length of data collection (the shortest monitoring period from 2017 to present and the longest from 1974 to present). To address these differences in recording frequency, fill any data gaps and to allow comparisons of water levels between dune slacks for a common monitoring period, there was a need to harmonize the water table data. To do this, water table levels were modelled using the time series analysis software MENYANTHES (Bartholomeus et al., 2008; KWR, 2020).

MENYANTHES uses daily climate data calibrated against measured water table depth from each dipwell to derive a daily time series model (von Asmuth et al., 2012). Daily climate data required was mean temperature (°C), precipitation (mm) and potential evapotranspiration (PET) (mm). PET was calculated using the Penman-Monteith formula for a reference vegetation (Allen et al., 1994), function "ET. PenmanMonteith" in the R package "Evapotranspiration" (Guo et al., 2016). Data required for PET included maximum, minimum and average temperature (°C), relative humidity (%) precipitation (mm), daily sunshine hours (h) and wind speed ($m\,s^{-1}$). Climate data were downloaded from coastal weather stations nearest to each sand dune system (MetOffice, 2022). A daily time series model was created for each dipwell for the period of measured water table depth, and the outputs (calibration statistics) were checked. Based on the daily time series models, the hydrological period could be extended by simulating the water table depths for each dipwell. For instance, hydrological data from 2017 to 2021 could be extended to

2014–2021. MENYANTHES provides guidelines on how far beyond the core data period it is appropriate to extend the simulation, depending also on the fit of the model. These simulations were particularly important for sand dune systems where the hydrological recording began in 2017, as the simulated water table depths from 2014 to 2018 were used for statistical analysis (see below). MENYANTHES was used to model each of the 41 dune slacks (41 dipwells), which reflects local sand dune system hydrology.

2.5 | Hydrological metrics

For each dune slack, mean and standard deviation of water table depth over a 4-year hydrological period—1 June 2014 to 30 May 2018—was calculated based on the daily values modelled in MENYANTHES. A 4-year average of water table depth is consistent with other studies in dune slacks (Curreli et al., 2013), and wet meadows (Gowing et al., 2002, 2005). Mean water table level gives a measure of the relative wetness of each plot, providing an understanding of overall prevailing conditions (Richter et al., 1996). At a given point in time, the water table may be higher or lower than this mean, and the extent of this variability will influence plants through drought or waterlogging. Standard deviation of water table level was calculated to give a measure of this variability, and so the extent to which the plant community experiences more extreme conditions.

Dune slacks can vary in size, shape and topography (Dwyer, Pakeman, et al., 2021). To account for differences in vertical elevation within the dune slack, quadrat-level hydrological metrics were calculated for all 164 quadrats. These metrics were based on the differences in elevation of each quadrat relative to the dipwell recorded using the DPGS.

2.6 | Soil characteristics

A soil core (5 cm diameter, 15 cm in depth) was sampled from the south-west corner of each quadrat. The thickness of the soil organic matter was measured in each sample. This was used as a proxy for the age of the dune slack, with older dune slacks having thicker organic matter layers (Grootjans et al., 2008). Organic and mineral horizons were separated. These samples were dried at 40°C, passed through a 2-mm sieve and weighed. Samples were dried at 105°C for 16 h to remove moisture. Loss on Ignition (LOI) at 550°C for 2 h in a furnace was used to provide an estimate of organic matter, and the difference between LOI at 550 and 950°C (for 4 h) to estimate carbonate content (LOC), respectively. Presented are the results for LOI and LOC for the organic horizon.

2.7 | Plant nutrient status (vascular leaf sample analysis)

Leaf samples of common dune slack species were collected. To keep the results as consistent as possible, species from four functional

groups (grass, sedge, herb or woody) were sampled. Groups sampled included grasses (*Agrostis stolonifera*, *Holcus lanatus*), sedges (*Carex arenaria*, *C. flacca*, *C. nigra*, *C. oederi* and *C. rostrata*), herbs (*Galium palustre*, *G. verum* and *Hydrocotyle vulgaris*), and a woody perennial (*Salix repens*). The species included in these samples varied because the same species were not present in every dune slack, and therefore, a random sample of species present in each group were taken. Plant samples were taken from the quadrats in each dune slack (total of 164 quadrats) for determination of nitrogen (N), phosphorous (P) and potassium (K) content. These values were used to provide a measure of plant nutrient status at each dune slack. Only leaves with no apparent damage were sampled. Leaves were dried in an oven at 60°C for 3 days and ground to a fine powder prior to analysis by an elemental analyser (Forest Research, 2021).

2.8 | Management

Management regimes can vary between coastal sand dune systems and may alter plant community composition (Millett & Edmondson, 2013). Vegetation height can be used as a proxy for the grazing regime in sand dune systems. For instance, shorter vegetation can indicate the presence of higher densities of grazing animals (Pakeman, 2004). To give an indication of grazing pressures for each quadrat, we used the average vegetation height (see earlier section), assuming that high grazing pressure will result in shorter vegetation.

2.9 | Data analysis

All data analysis was performed using R (v.4.0.3) (R Core Team, 2022). Four quadrats (across multiple sand dune systems) were removed from analysis due to missing soil characteristic data, resulting in 160 quadrats. For vascular plants, a total of 171 species were recorded, but nine species (across multiple sand dune systems) were removed from analysis as they were only identified to genus. As a result, in total 162 species distributed across 106 genera were analysed.

2.10 | Environmental gradients

To assess the co-linearity between the 16 environmental variables, we created a correlation matrix using the function "corr" in the package "boot" (Canty & Ripley, 2020). We visualized the data using the function "corrplot" from the package "corrplot" (Wei et al., 2017) (see Appendix S1). To account for these correlated variables and to reduce the dimensionality of the environmental data, we performed a Principal Components Analysis (PCA) of the 16 environmental variables using the function "prcomp" in the package "MASS" (Ripley et al., 2013). To ensure that the environmental variables had equal effect on the ordination, the data was standardized, so it has a mean of 0 and variance if 1 (scale = TRUE) using the function "prcomp" in the package "MASS" (Ripley et al., 2013).

A scree plot was used to determine how many principal components should be used (Holland, 2019, 2021). The first four PCA axes were chosen as they explained over 74% of the total variation in the data. There was a substantial drop in variation explained with the fifth axis. Loadings were calculated to understand how the environmental variables contribute to each principal component. A positive loading means the variable is positively correlated with the principal component, and a negative loading means the variable is negatively correlated with the principal component (Holland, 2019). As the principal components analysis was performed in a correlation matrix (Holland, 2019), we set the cut-off for associating variables to axes as the critical value for significance based on a two-tailed test using the Pearson's correlation coefficient ($df = 39$, $p = .05$, $r = .308$). Based on this approach, the cut-off value used was 0.308.

2.11 | Alpha diversity

To identify the multivariate environmental gradients (PCA axes) associated with patterns in alpha diversity at different spatial and taxonomic levels, we used linear models and linear mixed effects models. For sand dune systems, a linear model was used to predict alpha diversity as a function of the four PCA axes. A linear model was selected as there was no nesting at sand dune system level. Separate linear models were run for richness, Shannon diversity and Pielou's evenness for species and genus (six models in total). The full model was run using the function "lm" in the base package "stats" (R Core Team, 2022). To identify the most parsimonious model by AIC, backwards elimination was carried out using the function "step" in the package "lmerTest" (Kuznetsova et al., 2017).

Dune slacks and quadrats were analysed using linear mixed effects models (LMM) as they can partition the total variation into different levels, as quadrats were nested within dune slack, and dune slack within sand dune system. At a (i) dune slack level, sand dune system was included as a random effect and the four PCA axes were fixed effects. At the (ii) quadrat level, dune slack nested within sand dune system were included as random effects and the four PCA axes were fixed effects. The response variable were alpha diversity metrics (richness, Shannon diversity or Pielou's evenness), and therefore, separate models were run for each combination of spatial (dune slack and quadrat) and taxonomic level (species and genus) (12 combinations in total). We used a LMM using the function "lmer" in package "lme4," with a Gaussian distribution and the identity link function for (i) dune slack and (ii) quadrat (Bates et al., 2015). For each combination we compared four models, (a) a single level null model, (b) multilevel null model, (c) random intercept model (intercept of PCA axes to vary randomly with (i) dune slack or (ii) quadrat)), and (d) random slope and intercept model (intercept and slope of PCA axes to vary randomly with (i) dune slack or (ii) quadrat)). Models including a (d) random slope and intercept failed to converge for LMM, so results for only (c) random intercept models are presented. To identify the most parsimonious model, backwards elimination using maximum likelihood (REML = FALSE) was

carried out on non-significant fixed effects terms using the function "step" (with reduce. random = FALSE) in the package "lmerTest" (Kuznetsova et al., 2017). The model residuals were checked for overdispersion and heteroscedasticity. The final models were fitted with residual maximum likelihood (REML = TRUE) and presented in Table 1. Residual maximum likelihood results are presented as they compute the Satterthwaite degrees-of-freedom correction and give unbiased estimators. However, they can provide smaller p-values (Alday, 2021).

2.12 | Beta diversity (turnover and nestedness)

Beta diversity (the variation in composition of assemblages) may reflect turnover (replacement) and nestedness (loss). To identify how much of the plant composition variation is due to turnover or nestedness, and how it differs at spatial and taxonomic levels, we used the package "betapart" (Baselga & Orme, 2012). We partitioned the data into different spatial levels (mean of each sand dune system [$n = 12$], mean of each dune slack [$n = 41$] and quadrat level [$n = 160$]) and into taxonomic level (species [$n = 162$] and genus [$n = 106$]). For every combination of spatial and taxonomic level, we used the function "betapart.core" in the package "betapart" to create multiple-site beta diversity measures and pairwise dissimilarity matrices based on the composition data. We then used the "beta.multi.abund" with the family Bray–Curtis in the package "betapart" to partition this into nested and turnover components (Baselga & Orme, 2012; Franklin et al., 2018), which was presented as percentage of turnover.

To understand the spatial and environmental drivers of turnover, we used a generalized dissimilarity model (GDM) (Ferrier et al., 2007). GDM is a statistical method that analyses and predicts the spatial patterns of turnover across regions. It models the spatial turnover of composition between all samples as a function of the environmental differences between the locations (Ferrier et al., 2007). We used geographical distances (Latitude and Longitude) and environmental gradients (PCA axes) as predictors, and Bray–Curtis community distance matrix as response variables (Mokany et al., 2022b; Woolley et al., 2017). To prepare the data for GDM analysis, the "formatsitepair function" in the package "gdm" was used (Ferrier et al., 2007; Mokany et al., 2022a). To calculate the proportion of variance explained and the relative importance of each predictor by climate and geographic distance, two "formatesitepair" tables were created (1) geographical distances (predictor) and Bray–Curtis

TABLE 1 Environmental variables used in the principal components analysis (PCA)

Environmental variables	Code	Range
Climate		
Mean daily temperature (°C)	MeanTemp	8.5–11.3
Mean daily maximum temperature (°C)	MaxTemp	11.9–14.8
Mean daily minimum temperature (°C)	MinTemp	5.2–8.1
Mean daily precipitation (mm)	Rain	625.6–1631.2
Atmospheric deposition		
Total nitrogen deposition (oxidized nitrogen (NO_x) deposition and reduced nitrogen (NH_y) deposition (keq ha^{-1} year^{-1}) [kg N ha^{-1} year^{-1}]	TN	0.6–1.2 [8.4–16.8]
Non-marine sulphur (SO_2/SO_4) deposition (keq ha^{-1} year^{-1}) (g S ha^{-1} year^{-1})	NMS	0.4–1.1 [6.4–17.6]
Base cations (Ca and Mg) deposition (keq ha^{-1} year^{-1}) [kg Ca ha^{-1} year^{-1}]	Cation	0.4–1.2 [8–24]
Water table metrics		
Average water table level (4 years) (cm)[a]	AWL	−276.5 to 25.1
Standard deviation water table level (4 years) (cm)	SDWL	11.3–39.5
Soil characteristics		
Soil organic matter depth (cm)	SOM	0–15
Loss on ignition (%)	LOI	0–45
Loss of calcium carbonates (%)	LOC	0–53
Plant nutrient status (vascular leaf sample analysis) (%)		
Leaf nitrogen content	N	1.4–2.6
Leaf phosphorus content	P	0.1–0.4
Leaf potassium content	K	0.8–2.4
Management		
Mean vascular plant height (cm)	Height	2–76

[a]AWL—negative values are below ground surface, positive values are above ground surface.

community distance (response), and (2) environmental gradients (predictor) and Bray–Curtis community distance (response). Next, the function "gdm" in the package "gdm" (Ferrier et al., 2007; Mokany et al., 2022a), was used to compute three models: (model 1) environmental and geographic distances as predictors, (model 2) only environmental conditions as predictors and (model 3) only geographic distances as predictors (Legendre, 2008). The proportion of variance explained and the relative importance of each predictor of the three models was then compared following Franklin et al. (2018). This process was repeated for all combinations of spatial and taxonomic levels.

To understand how the rate and intensity of turnover differs along environmental gradients for spatial and taxonomic levels, we extracted the I-spline values from the GDM (GDM outputs from model 1) using the function "isplineExtract" in the "gdm" package (Ferrier et al., 2007; Fitzpatrick et al., 2013; Mokany et al., 2022a). This process was repeated for all combinations of spatial and taxonomic levels.

3 | RESULTS

3.1 | Environmental gradients

The first 4 axes of the PCA of environmental variables explained 74.1% of variation (26.5%, 22.1%, 13.8% and 11.7%, for axes 1–4 respectively) (Table 2). Axis 1 reflects the differences along a temperature, atmospheric deposition and water table gradient; high axis 1 scores indicated lower temperatures (MeanTemp, MaxTemp, MinTemp), lower non-marine sulphur deposition (NMS), and a less variable water table level (SDWL). Axis 2 reflects the differences along a precipitation, atmospheric deposition and soil characteristics gradient; high axis 2 scores indicated higher rainfall (Rain), higher base cation deposition (Cation), and higher organic matter content (LOI and LOC). Axis 3 is gradient of atmospheric deposition, soil characteristics and water table depth; high axis 3 scores indicate higher non-marine sulphur deposition (NMS) and wetter (AWL), older (SOM) dune slacks with taller vegetation (Height). Axis 4 reflects the differences along a plant nutrient status gradient; high scores indicate lower plant nutrient status (N, P and K). Total nitrogen deposition was not well correlated with any axis.

3.2 | Alpha diversity

At a sand dune system level, the only measure of alpha diversity that the four PCA axes predicted was Pielou's species evenness which was lowest in older, wetter dune slacks, with taller vegetation and non-marine sulphur deposition (PC3), and when plant nutrient status (N, P and K) were lower (PC4) ($R^2 = .64$, $F_{2,9} = 7.92$, $p = .01$) (Table 3a and Figure 2). Pielou's genus evenness was also lowest in older, wetter dune slacks, with taller vegetation and non-marine sulphur deposition (PC3) ($R^2 = .40$, $F_{1,10} = 6.90$, $p = .03$) (Table 3 and Figure 2).

At a dune slack level and at quadrat level, species and genus richness, Shannon species and genus diversity, and Pielou's species evenness was lowest in older, wetter dune slacks, with taller vegetation and non-marine sulphur deposition (PC3) (Table 3b,c and Figure 2). Species richness was highest when there was higher rainfall, higher base cation deposition and higher organic matter content (PC2) (Table 3b,c and Figure 2). However, changes in species richness along PC2 were not significant but were retained in the final model as this produced the best model fit (Table 3b,c).

3.3 | Beta diversity (turnover and nestedness)

Essentially, all the variance in the composition dissimilarity matrix for sand dune system, dune slack and quadrat was due to turnover (replacement) rather than nestedness (species or genus loss) (Table 4).

The proportion of community composition variance explained by turnover was lowest at dune system level, and highest at quadrat level, and was consistently lower for genus than species (Figure 3). Between sand dune systems the total proportion of variance explaining turnover (environment, geographic distance, and shared environment and geographic distance) was 49% for species and 35% for genus; between dune slacks, the proportion of variance explaining turnover decreased to 27% for species and 20% for genus; between quadrats, the proportion of variance explaining turnover decreased further to 20% for species and 20% for genus (Figure 3). Additionally, across spatial and taxonomic level, there was a strong spatial structure (proportion of variance explained by shared environment and geographic distance, and geographic distance) (Figure 3).

The relative importance of the impact of each environmental gradient on turnover differed between spatial and taxonomic level (Figure 3). At the sand dune system level, PC4 explained the highest proportion of species and genus turnover. At a dune slack level and at quadrat level, PC3 explained the highest proportion of species and genus turnover (Figure 3).

The rate and intensity of turnover differed with spatial and taxonomic level, being strongest at quadrat and species level (Figure 4). Across all levels, the impact of distance between quadrat/dune slack/sand dune system on turnover plateaus is around 400 km. This indicates that with increasing distances up to 400 km the identity of species/genus in a dune slack changes, but over 400 km there is no further change. Across all spatial levels, the amount of composition turnover and rate of composition turnover was low for PC1 and PC2 (Figure 4). The most important variables in driving plant species and genus dissimilarities at quadrat and dune slack were PC3 (Figure 4). The highest variable in driving plant species and genus dissimilarities at sand dune system were PC4 (Figure 4).

4 | DISCUSSION

Patterns of plant biodiversity in dune slack communities varied depending on the spatial level at which data are collected and analysed,

TABLE 2 Results of the principal components analysis (PCA) of 16 environmental variables representing dune slack variability across the UK. The loadings for each variable on the first four axes are presented. Large loadings (>0.308) are highlighted in bold

Environmental variables	PC1	PC2	PC3	PC4
SDWL	**−0.365**	0.176	−0.047	0.119
MaxTemp	**−0.397**	−0.162	−0.096	−0.142
MinTemp	**−0.435**	0.168	−0.066	−0.051
MeanTemp	**−0.455**	0.016	−0.072	−0.113
NMS	**−0.325**	−0.128	**0.352**	−0.151
LOI	0.063	**0.409**	0.226	−0.168
Cation	−0.14	**0.442**	−0.165	0.07
Rain	−0.073	**0.445**	−0.074	0.211
LOC	0.062	**0.474**	0.158	−0.125
AWL	0.161	0.097	**0.353**	−0.062
Height	−0.099	0.012	**0.436**	−0.21
SOM	0.069	0.116	**0.453**	−0.137
K	0.221	−0.1	−0.023	**−0.367**
P	0.026	0.015	−0.291	**−0.525**
N	0.039	0.128	−0.263	**−0.591**
TN	−0.287	−0.251	0.269	−0.085

Abbreviations: AWL, average water table level; Cation, base cations; Height, mean vascular plant height; K, leaf potassium content; LOC, loss of calcium carbonates; LOI, loss on ignition; MaxTemp, maximum annual temperature; MeanTemp, mean annual temperature; MinTemp, minimum annual temperature; N, leaf nitrogen content; NMS, non-marine sulphur deposition; P, leaf phosphorous content; Rain, mean annual precipitation; SDWL, standard deviation water table level; SOM, soil organic matter depth; TN, total nitrogen deposition.

but not the taxonomic level. At smaller spatial levels (dune slack and quadrat), alpha and beta diversity varied along gradients driven by soil characteristics, water table depth and atmospheric deposition. At larger spatial levels (sand dune system), however, patterns of beta diversity were governed by plant nutrient status. Patterns of change in alpha diversity were only detected at some spatial levels, but not others. Indices of diversity (richness and Shannon's) varied at smaller spatial levels (slack and quadrat) while evenness varied mainly at the sand dune system level. The taxonomic level considered made little difference in understanding these patterns. These results have important consequences for understanding and managing biodiversity because patterns and drivers of biodiversity change can be missed by collecting and analysing data at only one spatial level.

The problem of pattern and scale in biodiversity measurement is well established (Levin, 1992). The environmental drivers of changes in diversity can operate at different scales (Sax & Gaines, 2003) because impacts on the key processes of colonization and extinction are expected to result in complex scale-dependant responses (Chase et al., 2019). Thus, the complex scale dependence of biodiversity patterns we have found is not surprising. The consequences of this problem, however, are rarely

quantified robustly using real biodiversity data. We found that if surveys were conducted at a sand dune system level (i.e. using a mean community composition per sand dune system) changes in evenness but not richness were detected, whereas if surveys were conducted within a sand dune system (i.e. dune slacks or quadrats) changes in richness but not evenness were detected. Similar differences were measured for beta diversity. At sand dune system level, turnover was driven along a plant nutrient status gradient, whereas within a sand dune system (i.e. dune slacks or quadrats), turnover was driven along an atmospheric deposition, soil characteristics and water table depth gradient. The consequence of this is that management or policy action taken based on data from one spatial level would not necessarily have resulted in optimal outcomes for the biodiversity of the system.

Diversity patterns across two taxonomic levels were explored to understand if species and genus have similar ecological responses. Phylogenetic correlations between species mean that genus level analyses might provide a fairer test for understanding diversity patterns along environmental gradients (Bonte et al., 2012). Our results show that simplifying the taxonomic resolution resulted in little information loss; the proportion of variation explained by species and genus was similar, largely because most genera were represented by a single species. These findings have an important applied management aspect to dune slacks and demonstrate that identification to a genus level still picks up similar patterns of community turnover as with species. This may save time and money, as in-depth surveys may not be required. However, this generalization may not apply to all habitats as some species-rich habitats contain genera with multiple species within which environmental niches may vary between species in the same genus.

This is the first time that the impact of multivariate environmental and management conditions on patterns of diversity in dune slacks have been explored at different spatial and taxonomic levels. The patterns of variation of plant community composition at smaller spatial levels (dune slack and quadrat) are consistent with some general findings in dune slacks—that diversity is lowest in dune slacks that are older (thicker soil organic matter) and have taller vegetation (lower grazing pressure) (Millett & Edmondson, 2013). Successional processes affect plant community structure. In general, pioneer species establish on bare sand, resulting in initial increases in diversity. Over time soil organic matter and nutrients accumulate, causing a shift towards shrubs and grasses and more intense competition, which results in the extinction of less-competitive species (Grootjans et al., 2008). In older soils with progressive leaching and decalcification, the soils also become more acidic (Berendse et al., 1998; Grootjans et al., 2008), resulting in conditions which support relatively low numbers of species. The grazing regime can also explain these patterns of variation (Millett & Edmondson, 2013). For instance, Plassmann et al.'s (2010) long-term monitoring on a coastal sand dune, demonstrated that extensive livestock grazing can increase plant diversity. It is possible that different grazing intensities caused the variation in alpha diversity in our study. Impacts of hydrology on plant communities

TABLE 3 (A) Linear model of mean Pielou's evenness at sand dune system level against mean principal components analysis (PCA) axis for sand dune systems. Presented is the final model, after model reduction. (B) Linear mixed effects models at dune slack level of richness, Shannon diversity and Pielou's evenness against environmental principal components analysis (PCA) axis. Presented is the final model, after model reduction. (C) Linear mixed effects models at quadrat level of richness, Shannon diversity and Pielou's evenness against environmental principal components analysis (PCA) axis. All presented models are the final model, after model reduction

Dependent variable	Independent variable	Estimate	Standard error		*t*-value	Pr(>|t|)
(A) Linear model: Sand dune system level						
Pielou's species evenness	Intercept	0.70	0.02		43.71	<0.001
	PC3	−0.04	0.01		−3.28	<0.01
	PC4	−0.03	0.01		−2.45	<0.05
Pielou's genus evenness	Intercept	0.71	0.02		32.51	<0.001
	PC3	−0.05	0.02		−2.63	<0.04
Dependent variable	**Independent variable**	**Estimate**	**Standard error**	**df**	***t*-value**	**Pr(>|t|)**
(B) Linear mixed effects model: Dune slack level						
Species richness	Intercept	11.15	0.45	8.04	24.52	<0.001
	PC2	0.46	0.22	13.32	2.08	0.06
	PC3	−0.96	0.24	41.20	−4.03	<0.001
Genus richness	Intercept	10.36	0.51	8.57	20.57	<0.001
	PC3	−0.81	0.24	65.10	−3.37	<0.01
Shannon species diversity	Intercept	1.67	0.08	8.94	20.10	<0.001
	PC3	−0.09	0.03	103.21	−2.85	<0.01
Shannon genus diversity	Intercept	1.62	0.07	9.69	21.80	<0.001
	PC3	−0.09	0.03	85.65	−2.79	<0.01
Pielou's species evenness	Intercept	0.71	0.02	8.76	34.45	<0.001
	PC3	−0.02	0.01	63.03	−2.24	<0.05
(C) Linear mixed effects model: Quadrat level						
Species richness	Intercept	11.17	0.42	6.92	26.65	<0.001
	PC2	0.38	0.21	11.78	1.78	0.10
	PC3	−1.23	0.25	23.00	−5.00	<0.001
Genus richness	Intercept	10.41	0.45	8.80	23.14	<0.001
	PC3	−1.16	0.25	36.97	−4.67	<0.001
Shannon species diversity	Intercept	1.68	0.08	9.00	21.12	<0.001
	PC3	−0.12	0.03	70.41	−3.25	<0.01
Shannon genus diversity	Intercept	1.62	0.07	9.80	22.12	<0.001
	PC3	−0.10	0.03	62.55	−2.96	<0.01
Pielou's species evenness	Intercept	0.71	0.02	8.85	34.87	<0.001
	PC3	−0.02	0.01	48.03	−2.36	<0.05

appeared more complex as the hydrological regime influences plant community structure directly though disturbances such as periods of prolonged flooding, and indirectly through mechanisms such as nutrient levels (Grootjans et al., 2008; Jones et al., 2006; Lammerts & Grootjans, 1997). In wetter dune slacks, soil organic matter accumulation is faster (Jones et al., 2008). Along this same environmental gradient of wetter and older dune slack with taller plants, diversity measures were lowest when non-marine sulphur deposition was high. Sulphur emissions have decreased since the 1970s, and may no longer pose a long-term threat to diversity (Smith et al., 2001). Therefore, these results may be in part related

to the old legacy gradient of a much higher deposition (Guerrieri et al., 2011; Pakeman et al., 2016).

At higher spatial levels, patterns of beta diversity (turnover) were a consequence of plant nutrient status. Nutrients can alter plant diversity. For instance, in a long-term experiment Storkey et al. (2015) demonstrated that plant diversity increased with decreasing N fertilizer inputs and atmospheric deposition; Ceulemans et al. (2014) demonstrated across European grasslands that plant species richness was negatively related to soil phosphorous. Therefore, it was unsurprising that we observed turnover in dune slack plant communities along a gradient of high to low plant nutrient status. It is also
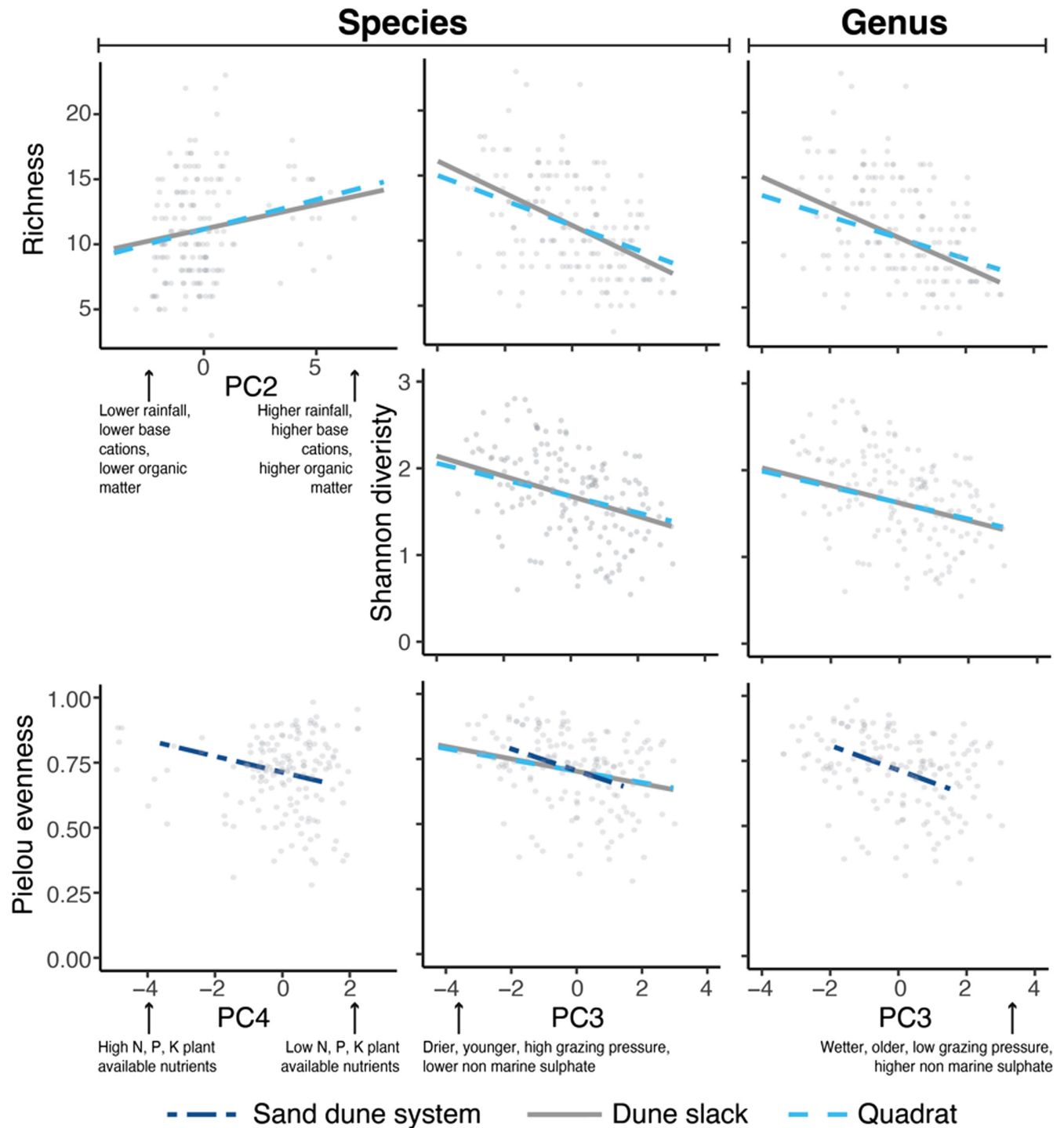
FIGURE 2 The relationship between alpha diversity metrics (richness, Shannon diversity and Pielou's evenness) and environmental gradients. Presented are changes in diversity indices along PCA axes 2 (precipitation, atmospheric deposition and soil characteristics), 3 (atmospheric deposition, soil characteristics and water table level) and 4 (plant nutrient status), for different spatial and taxonomic levels. The spatial levels are sand dune system, dune slack and quadrat, and the taxonomic levels are species and genus. We have presented the separate linear models and linear mixed effects models in one plot for visualization. The points (grey •) represent the 160 quadrats. For sand dune system, the fitted lines (dark blue - --- -) show the predictions from the linear models. For dune slack (grey -----) and quadrat (light blue - - - -), we have presented the partial plots of the random intercept linear mixed effects models. Changes in species richness along PC2 were not significant but were retained in the final model as this produced the best model fit

important to note that we sampled vascular plant leaves to indicate plant nutrient status within a dune slack, but the species sampled varied between dune slack. This gradient could, therefore, be an

artefact of the data collection, reflecting differences in leaf nutrient content between species rather than between dune slacks. However, for each dune slack we sampled from a range of plant species and

TABLE 4 Percentage community composition variance explained by only turnover in the compositional dissimilarity matrix based on Bray–Curtis dissimilarity abundance data using beta partitioning

	Species	Genus
Sand dune system	87.2	86.9
Dune slack	95.2	94.7
Quadrat	98.5	98.3

ensured that this sample covered the same plant functional groups. We are, therefore, confident that this represents a gradient of plant nutrient status.

Biogeography and the environment can play a key role in species diversity and community structure (Sax & Gaines, 2003). We found that there was a strong spatial signal at sand dune system, dune slack and quadrat level (proportion of variance explained by shared environment and geographic distance, and geographic distance). This suggests that spatially structured environmental factors within a sand dune system and within a dune slack have an important impact on determining community turnover. For instance, within a sand dune system, successional processes, hydrological variability and nutrients can vary considerably (Jones et al., 2006). Within a dune slack, spatial variation in topography means that the water table depth from ground surface varies as vertical elevation varies. Several authors have already noted that fine-scale change in hydrology and nutrient levels structure plant communities (Curreli et al., 2013; Rhymes et al., 2014, 2016; Silvertown et al., 2015). Community turnover may be also affected by the dispersal ability of different plant species (Bonte et al., 2012), and therefore, the priority effects (the order or the timing of species arrival may affect the growth, establishment or reproduction of a later arriving species) may also impact community structure (Weidlich et al., 2021).

The measured variables in this study only explain a proportion of the total variation, and there are various potential reasons for the unexplained variation. Firstly, we may have missed environmental, or management conditions experienced by plants that are important for explaining patterns of biodiversity. Secondly, it could be the type of hydrological metric used. We used a measure of water table depth which may not completely reflect the environment experienced by a plant. For instance, Bartholomeus et al. (2012) demonstrated that direct measures such as availability of water and oxygen in the root zone predicts vegetation better than measures such as mean spring groundwater level (average of March, April and May). However, our modelling picked out water table depth as a significant driver at both dune slack and quadrat level, suggesting that this proxy was adequate for the purpose. We used the software MENYANTHES to derive a daily time series model and extend the hydrological period for dune slacks where there was a no long-term hydrological data, and while the outputs for each model were checked to ensure they were robust, they remain predictions rather than actual measures. Thirdly, we found that unexplained variation is higher at the quadrat level compared with sand dune system level. It may be that measured environmental factors are perhaps better
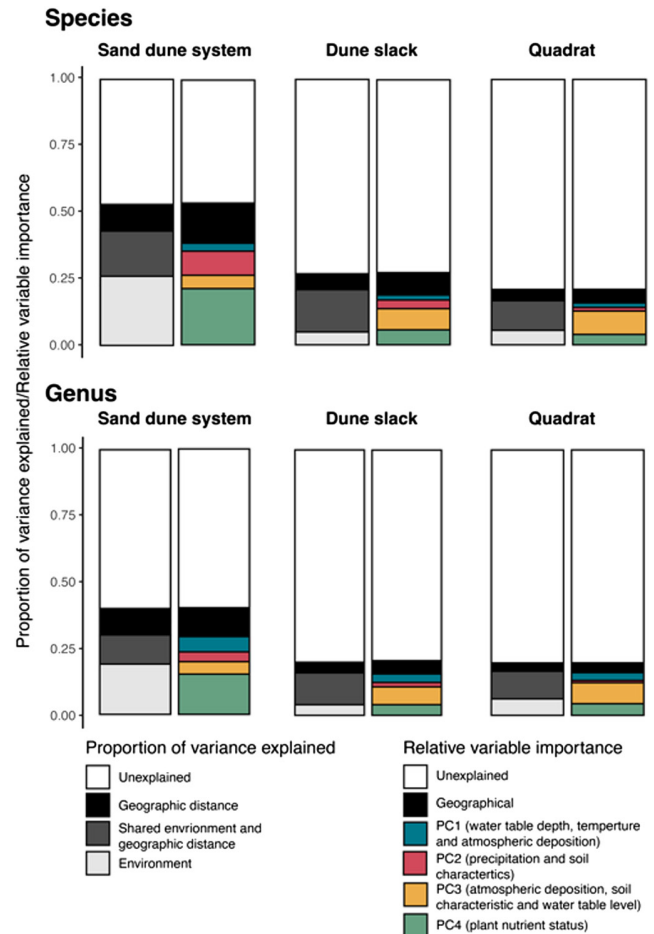

FIGURE 3 The taxonomic turnover along PCA environmental gradients using a generalized dissimilarity model (GDM) of Bray–Curtis distance matrix of abundance data for different taxonomic levels (species and genus) and for different spatial levels (sand dune system, dune slack and quadrat). Sand dune system level beta diversity is calculated from the mean composition of quadrats within the same sand dune system (n = 66), dune slack level beta diversity from the mean of quadrats located within the same dune slack (n = 820) and quadrat level beta diversity from all pairs of quadrats (n = 12,720). For taxonomic and spatial levels, the left-hand bar of each pair represents the proportion of variance explained by only environment, by only geographic distance, their shared variance and unexplained variance. Spatial structure is the combination of geographic distance (black), and shared environment and geographic distance (dark grey). Environmental variation is the combination of shared environment and geographic distance (dark grey), and the environment (light grey). The right-hand bar represents the relative importance of each of the PCA axes of the environmental variables. PC1 reflects the differences along a temperature, atmospheric deposition, and water table gradient. PC2 reflects the differences along a precipitation, atmospheric deposition, and soil characteristics gradient. PC3 is gradient of atmospheric deposition, soil characteristics and water table depth. PC4 reflects the differences along a plant nutrient status gradient

at explaining large-scale variation. In addition, potential stochastic effects on botanical composition are more likely to show up at smaller levels which could explain the higher unexplained variance at quadrat
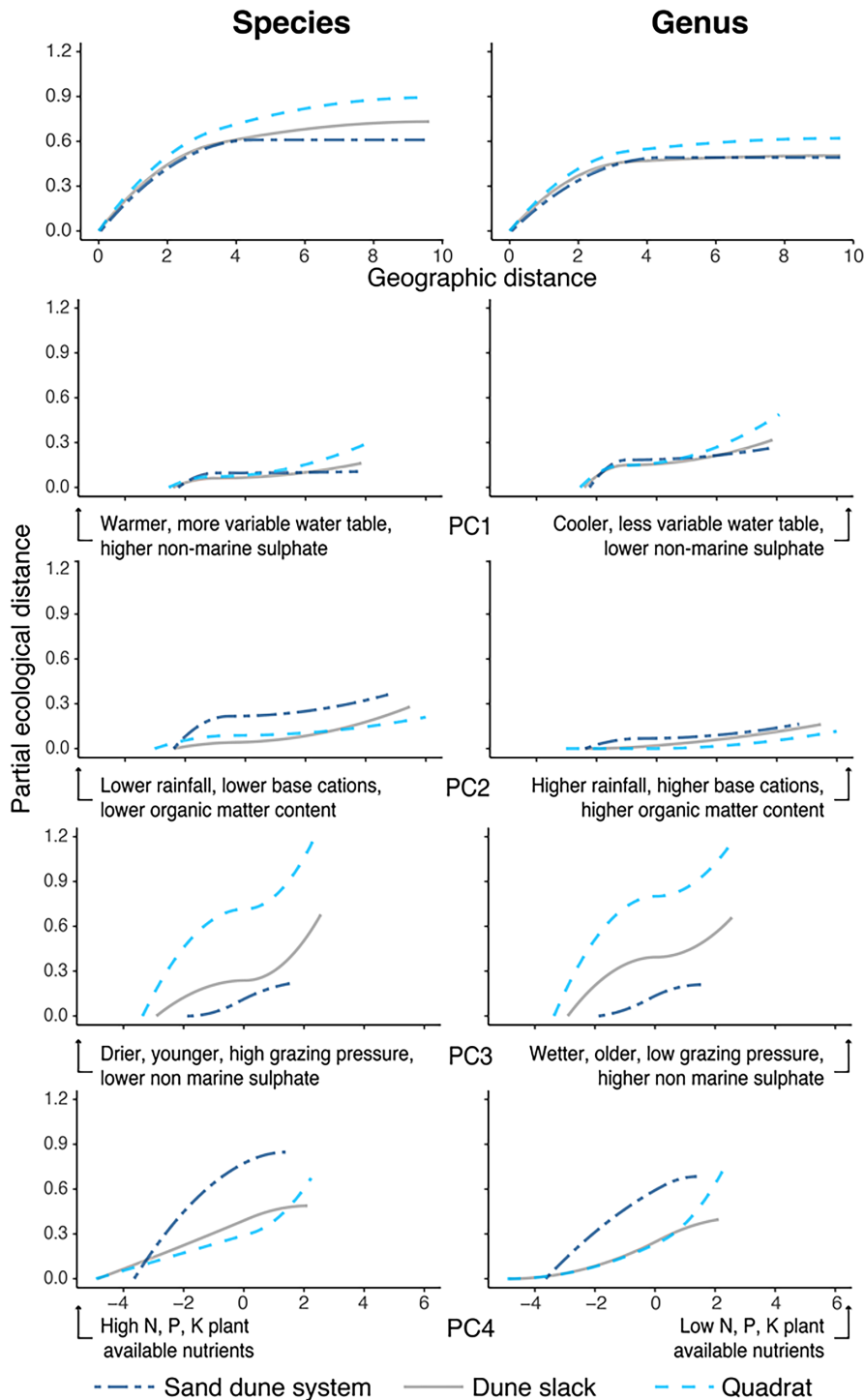
FIGURE 4 The taxonomic turnover (of species and genus) along PCA environmental gradients using generalized dissimilarity model (GDM) for spatial level (sand dune system, dune slack and quadrat). GDM models-fitted I-splines of Bray–Curtis distance matrix of abundance data for variables that are significantly associated with sand dune system, dune slack and quadrat. The height of the curve indicates the amount of composition turnover and the importance of the axis in explaining beta diversity. The shape of the curve indicates the rate of composition turnover along the PCA axis gradient. The length of the gradient depends on the data; that is, sand dune system is a mean of the 12 sand dunes. Geographic distance reflects the impact of distance. PC1 reflects the differences along a temperature, atmospheric deposition, and water table gradient. PC2 reflects the differences along a precipitation, atmospheric deposition, and soil characteristics gradient. PC3 is gradient of atmospheric deposition, soil characteristics and water table depth. PC4 reflects the differences along a plant nutrient status gradient

level (Bossuyt et al., 2003). Future studies should identify the extent to which this missed variation in the environmental conditions experienced by plants is important for understanding patterns of biodiversity.

5 | CONCLUSION

Our research demonstrates that diversity patterns in dune slack plant communities vary depending on the spatial level considered, but that the taxonomic resolution considered made little difference

in interpretation. Therefore, monitoring of biodiversity change and its drivers must consider variation due to the spatial level measured. If we do not consider patterns across different spatial levels, key environmental and management drivers could be missed. This could have important consequences for the conservation of these European protected habitats which are in decline. In addition, such scale dependence needs to be explored for other measures of biodiversity, such as genetic diversity. Overall, in the effort to understand global biodiversity loss, the importance of scale should take a higher priority than it currently does.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in figshare at https://doi.org/10.17028/rd.lboro.14212655

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REFERENCES

Alday, P. M. (2021). A brief introduction to mixed-effects models. https://phillipalday.com/stats/mixedmodels.html#fn2

Allen, R., Smith, M., Pereira, L., & Bulletin, A. P.-I. U. (1994). An update for the calculation of reference evapotranspiration. *CID Bulletin, 43*(2), 35–92.

Anderson, C. B. (2018). Biodiversity monitoring, earth observations and the ecology of scale. *Ecology Letters, 21*(10), 1572–1585. https://doi.org/10.1111/ELE.13106

Bartholomeus, R. P., Witte, J. P. M., Van Bodegom, P. M., & Aerts, R. (2008). The need of data harmonization to derive robust empirical relationships between soil conditions and vegetation. *Journal of Vegetation Science, 19*(6), 799–808. https://doi.org/10.3170/2008-8-18450

Bartholomeus, R. P., Witte, J. P. M., Van Bodegom, P. M., Van Dam, J. C., & Aerts, R. (2011). Climate change threatens endangered plant species by stronger and interacting water-related stresses. *Journal of Geophysical Research: Biogeosciences, 116*(G4). https://doi.org/10.1029/2011JG001693

Bartholomeus, R. P., Witte, J. P. M., van Bodegom, P. M., van Dam, J. C., de Becker, P., & Aerts, R. (2012). Process-based proxy of oxygen stress surpasses indirect ones in predicting vegetation characteristics. *Ecohydrology, 5*(6), 746–758. https://doi.org/10.1002/eco.261

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution, 3*(5), 808–812.

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48.

Berendse, F., Lammerts, E. J., & Olff, H. (1998). Soil organic matter accumulation and its implications for nitrogen mineralization and plant species composition during succession in coastal dune slacks. *Plant Ecology, 137*(1), 71–78. https://doi.org/10.1023/A:1008051931963

Bonte, D., Breyne, P., Brys, R., De La Peña, E., D'Hondt, B., Ghyselen, C., Vandegehuchte, M. L., & Hoffmann, M. (2012). Landscape dynamics determine the small-scale genetic structure of an endangered dune slack plant species. *Journal of Coastal Research, 8*(4), 780–786.

Bordoloi, R., Das, B., Yam, G., Pandey, P. K., & Tripathi, O. P. (2019). Modeling of water holding capacity using readily available soil characteristics. *Agricultural Research, 8*(3), 347–355. https://doi.org/10.1007/s40003-018-0376-9

Bossuyt, B., Honnay, O., & Hermy, M. (2003). An Island biogeographical view of the successional pathway in wet dune slacks. *Journal of Vegetation Science, 14*(6), 781–788. https://doi.org/10.1111/j.1654-1103.2003.tb02210.x

Britton, A. J., Hewison, R. L., Mitchell, R. J., & Riach, D. (2017). Pollution and climate change drive long-term change in Scottish wetland vegetation composition. *Biological Conservation, 210*, 72–79. https://doi.org/10.1016/j.biocon.2017.04.005

Burns, J. H., & Strauss, S. Y. (2011). More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences of the USA, 108*(13), 5302–5307.

Canty, A., & Ripley, B. (2020). Boot: Bootstrap R (S-plus) functions. R package version 1.3-25. https://cran.r-project.org/web/packages/boot/index.html

Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology, 87*(sp7), S109–S122.

Ceulemans, T., Stevens, C. J., Duchateau, L., Jacquemyn, H., Gowing, D. J., Merckx, R., Wallace, H., Van Rooijen, N., Goethem, T., Bobbink, R., & Dorland, E. (2014). Soil phosphorus constrains biodiversity across European grasslands. *Global Change Biology, 20*(12), 3814–3822. https://doi.org/10.1111/gcb.12650

Chase, J. M., McGill, B. J., McGlinn, D. J., May, F., Blowes, S. A., Xiao, X., Knight, T. M., Purschke, O., & Gotelli, N. J. (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology Letters, 21*(11), 1737–1751.

Chase, J. M., McGill, B. J., Thompson, P. L., Antão, L. H., Bates, A. E., Blowes, S. A., Dornelas, M., Gonzalez, A., Magurran, A. E., Supp, S. R., Winter, M., Bjorkman, A. D., Bruelheide, H., Byrnes, J. E. K., Cabral, J. S., Elahi, R., Gomez, C., Guzman, H. M., Isbell, F., … O'Connor, M. (2019). Species richness change across spatial scales. *Oikos, 128*(8), 1079–1091.

Curreli, A., Wallace, H., Freeman, C., Hollingham, M., Stratford, C., Johnson, H., & Jones, L. (2013). Eco-hydrological requirements of dune slack vegetation and the implications of climate change.

Science of the Total Environment, *443*, 910–919. https://doi.org/10.1016/j.scitotenv.2012.11.035

Dasgupta, P. (2021). *The economics of biodiversity: The Dasgupta review.* HM Treasury.

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., … Zayas, C. N. (2019). *IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental Science-policy platform on biodiversity and ecosystem services.* IPBES Secretariat.

Dwyer, C., Millett, J., Pakeman, R. J., & Jones, L. (2021). Environmental modifiers of the relationship between water table depth and Ellenberg's indicator of soil moisture. *Ecological Indicators*, *132*, 108320. https://doi.org/10.1016/j.ecolind.2021.108320

Dwyer, C., Pakeman, R. J., Jones, L., Willegen, L., van Hunt, N., & Millett, J. (2021). Fine-scale hydrological niche segregation in coastal dune slacks. *Journal of Vegetation Science*, *32*, e13085. https://doi.org/10.1111/jvs.13085

Eionet. (2020). Habitats Directive Article 17 2019 submission UK - Redelivery. https://cdr.eionet.europa.eu/gb/eu/art17/envxuwt7a/

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*(3), 252–264.

Field, C. D., Dise, N. B., Payne, R. J., Britton, A. J., Emmett, B. A., Helliwell, R. C., Hughes, S., Jones, L., Lees, S., Leake, J. R., Leith, I. D., Phoenix, G. K., Power, S. A., Sheppard, L. J., Southon, G. E., Stevens, C. J., & Caporn, S. J. M. (2014). The role of nitrogen deposition in widespread plant community change across semi-natural habitats. *Ecosystems*, *17*(5), 864–877.

Fitzpatrick, M. C., Sanders, N. J., Normand, S., Svenning, J. C., Ferrier, S., Gove, A. D., & Dunn, R. R. (2013). Environmental and historical imprints on beta diversity: Insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1768), 20131201.

Forest Research. (2021). Plant analysis. https://www.forestresearch.gov.uk/services/plant-tree-soil-and-water-testing/plant-analysis/

Franklin, J., Andrade, R., Daniels, M. L., Fairbairn, P., Fandino, M. C., Gillespie, T. W., González, G., Gonzalez, O., Imbert, D., Kapos, V., Kelly, D. L., Marcano-Vega, H., Meléndez-Ackerman, E. J., McLaren, K. P., McDonald, M. A., Ripplinger, J., Rojas-Sandoval, J., Ross, M. S., Ruiz, J., … Vennetier, M. (2018). Geographical ecology of dry forest tree communities in the West Indies. *Journal of Biogeography*, *45*(5), 1168–1181.

Franklin, J., Majure, L. C., Encarnación, Y., Clase, T., Almonte-Espinosa, H., Landestoy, M., Kratter, A. W., Oswald, J. A., Soltis, D. E., Terrill, R. S., & Steadman, D. W. (2019). Changing ecological communities along an elevation gradient in seasonally dry tropical forest on Hispaniola (sierra Martín García, Dominican Republic). *Biotropica*, *51*(6), 802–816.

Gowing, D. J. G., Lawson, C. S., Youngs, E. G., Barber, K. R., Rodwell, J. S., Prosser, M. V., Wallace, H. L., Mountford, J. O., & Spoor, G. (2002). The water regime requirements and the response to hydrological change of grassland plant communities. DEFRA-commissioned project BD1310. Final report, Institute of Water and Environment, Silsoe, Bedfordshire.

Gowing, D. J. G., Lawson, C. S., Youngs, E. G., Barber, K. R., Rodwell, J. S., Prosser, M. V., Wallace, H. L., Mountford, J. O., & Spoor, G. (2005). Response of grassland plant communities to altered hydrological management. DEFRA-Commissioned Project BD1321. Final Report, Institute of Water and Environment, Silsoe, Bedfordshire.

Grootjans, A. P., Adema, E. B., Bekker, R. M., & Lammerts, E. J. (2008). Why coastal dune slacks sustain a high biodiversity. *Coastal Dunes*, *171*, 85–101. https://doi.org/10.1007/978-3-540-74002-5_6

Grootjans, A. P., Hartog, P. S., Fresco, L. F. M., Esselink, H., & Science, V. (1991). Succession and fluctuation in a wet dune slack in relation to hydrological changes. *Journal of Vegetation Science*, *2*(4), 545–554. https://doi.org/10.2307/3236037

Guerrieri, R., Mencuccini, M., Sheppard, L. J., Saurer, M., Perks, M. P., Levy, P., Sutton, M. A., Borghetti, M., & Grace, J. (2011). The legacy of enhanced N and S deposition as revealed by the combined analysis of δ13C, δ18O and δ15N in tree rings. *Global Change Biology*, *17*(5), 1946–1962. https://doi.org/10.1111/J.1365-2486.2010.02362.X

Guo, D., Westra, S., & Maier, H. R. (2016). An R package for modelling actual, potential and reference evapotranspiration. *Environmental Modelling and Software*, *78*, 216–224. https://doi.org/10.1016/j.envsoft.2015.12.019

Harrison, S., & Cornell, H. (2008). Toward a better understanding of the regional causes of local community richness. *Ecology Letters*, *11*(9), 969–979.

Holland, S. M. (2019). Principle components analysis (PCA). R package (Issue December).

Holland, S. M. (2021). Data analysis in the geosciences. http://strata.uga.edu/8370/lecturenotes/principalComponents.html

Hollis, D., McCarthy, M., Kendon, M., Legg, T., & Simpson, I. (2020). HadUK-grid gridded climate observations on a 5km grid over the UK, v1.0.2.1 (1862-2019). Centre for Environmental Data Analysis.

Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Culmsee, H., Cordell, S., Florens, F. B. V., Franklin, J., Giardina, C. P., Gillespie, T. W., Laidlaw, M., Litton, C. M., Martin, T. G., Ostertag, R., Parthasarathy, N., Randrianaivo, R., Randrianjanahary, M., Rajkumar, M., Rasingam, L., … Birnbaum, P. (2018). Regional forcing explains local species diversity and turnover on tropical islands. *Global Ecology and Biogeography*, *27*(4), 474–486.

Janssen, J. A. M., Rodwell, J. S., García Criado, M., Gubbay, S., Haynes, T., Nieto, A., Sanders, N., Landucci, F., Loidi, J., Ssymank, A., Tahvanainen, T., Valderrabano, M., Acosta, A., Aronsson, M., Arts, G., Attorre, F., Bergmeier, E., Bijlsma, R.-J., Bioret, F., … Valachovič, M. (2017). European red list of habitats. Part 2. Terrestrial and freshwater habitats. European Commission.

JNCC. (2021). 2190 Humid dune slacks. https://sac.jncc.gov.uk/habitat/H2190/

Jones, L., Garbutt, A., Hansom, J., & Angus, S. (2013). Impacts of climate change on coastal habitats. MCCIP Science review.

Jones, L., Reynolds, B., Brittain, S. A., Norris, D. A., Rhind, P. M., & Jones, R. E. (2006). Complex hydrological controls on wet dune slacks: The importance of local variability. *Science of the Total Environment*, *372*(1), 266–277. https://doi.org/10.1016/j.scitotenv.2006.08.040

Jones, L., Sowerby, A., Williams, D. L., & Jones, R. E. (2008). Factors controlling soil development in sand dunes: Evidence from a coastal dune soil chronosequence. *Plant and Soil*, *307*(1–2), 219–234. https://doi.org/10.1007/s11104-008-9601-9

Kindt, R. (2018). Package 'BiodiversityR'. Package for community ecology and suitability analysis. Version 1.10-1. 2018.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26.

KWR. (2020). MENYANTHES [Software]. https://www.kwrwater.nl/en/tools-producten/menyanthes/

Lammerts, E. J., & Grootjans, A. P. (1997). Nutrient deficiency in dune slack pioneer vegetation: A review. *Journal of Coastal Conservation*, *3*(1), 87–94. https://doi.org/10.1007/BF02908183

Lammerts, E. J., Pegtel, D. M., Grootjans, A. P., & Veen, A. (1999). Nutrient limitation and vegetation changes in a coastal dune slack. *Journal of Vegetation Science*, *10*(1), 111–122. https://doi.org/10.2307/3237166

Legendre, P. (2008). Studying beta diversity: Ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology*, 1(1), 3–8.

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73(6), 1943–1967. https://doi.org/10.2307/1941447

Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I., & Callaway, R. M. (2004). Rethinking plant community theory. *Oikos*, 107(2), 433–438.

McGill, B. J., Dornelas, M., Gotelli, N. J., & Magurran, A. E. (2015). Fifteen forms of biodiversity trend in the anthropocene. *Trends in Ecology and Evolution*, 30(2), 104–113. https://doi.org/10.1016/j.tree.2014.11.006

MetOffice. (2022). National Meteorological Library and Archive. https://www.metoffice.gov.uk/research/library-and-archive

Millett, J., & Edmondson, S. (2013). The impact of 36 years of grazing management on vegetation dynamics in dune slacks. *Journal of Applied Ecology*, 50(6), 1367–1376. https://doi.org/10.1111/1365-2664.12113

Moeslund, J. E., Arge, L., Bøcher, P. K., Dalgaard, T., & Svenning, J. C. (2013). Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany*, 31(2), 129–144. https://doi.org/10.1111/j.1756-1051.2013.00082.x

Mokany, K., Ware, C., Woolley, S., Ferrier, S., & Fitzpatrick, M. (2022a). Generalized dissimilarity modeling. Package version 1.5.0-3. https://cran.r-project.org/web/packages/gdm/gdm.pdf

Mokany, K., Ware, C., Woolley, S., Ferrier, S., & Fitzpatrick, M. (2022b). A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. *Global Ecology and Biogeography*, 31(4), 802–821. https://doi.org/10.1111/GEB.13459

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Maintainer, H. W. (2015). Vegan: Community ecology package. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. In R package version 2(0) (vol. 2, Issue 9, pp. 1–297). https://cran.r-project.org/web/packages/vegan/vegan.pdf

Pakeman, R. J. (2004). Consistency of plant species and trait responses to grazing along a productivity gradient: A multi-site analysis. *Journal of Ecology*, 92(5), 893–905. https://doi.org/10.1111/j.0022-0477.2004.00928.x

Pakeman, R. J., Alexander, J., Brooker, R., Cummins, R., Fielding, D., Gore, S., Hewison, R., Mitchell, R., Moore, E., Orford, K., Pemberton, C., Trinder, C., & Lewis, R. (2016). Long-term impacts of nitrogen deposition on coastal plant communities. *Environmental Pollution*, 212, 337–347.

Pakeman, R. J., Fielding, D. A., Everts, L., & Littlewood, N. A. (2019). Long-term impacts of changed grazing regimes on the vegetation of heterogeneous upland grasslands. *Journal of Applied Ecology*, 56(7), 1794–1805. https://doi.org/10.1111/1365-2664.13420

Paton, J. A. (1999). *The liverwort Flora of the British Isles*. Brill.

Payne, R. J., Campbell, C., Britton, A. J., Mitchell, R. J., Pakeman, R. J., Jones, L., Ross, L. C., Stevens, C. J., Field, C., Caporn, S. J. M., Carroll, J., Edmondson, J. L., Carnell, E. J., Tomlinson, S., Dore, A. J., Dise, N., & Dragosits, U. (2019). What is the most ecologically-meaningful metric of nitrogen deposition? *Environmental Pollution*, 247, 319–331. https://doi.org/10.1016/j.envpol.2019.01.059

Plassmann, K., Jones, M. L. M., & Edwards-Jones, G. (2010). Effects of long-term grazing management on sand dune vegetation of high conservation interest. *Applied Vegetation Science*, 13(1), 100–112. https://doi.org/10.1111/j.1654-109X.2009.01052.x

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rhymes, J., Jones, L., Wallace, H., Jones, T. G., Dunn, C., & Fenner, N. (2016). Small changes in water levels and groundwater nutrients alter nitrogen and carbon processing in dune slack soils. *Soil Biology and Biochemistry*, 99, 28–35. https://doi.org/10.1016/j.soilbio.2016.04.018

Rhymes, J., Wallace, H., Fenner, N., & Jones, L. (2014). Evidence for sensitivity of dune wetlands to groundwater nutrients. *Science of the Total Environment*, 490, 106–113. https://doi.org/10.1016/j.scitotenv.2014.04.029

Richter, B. D., Baumgartner, J. V., Powell, J., & Braun, D. P. (1996). A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, 10(4), 1163–1174. https://doi.org/10.1046/j.1523-1739.1996.10041163.x

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'MASS'. *Cran R*, 538, 113–120.

Sax, D. F., & Gaines, S. D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology and Evolution*, 18(11), 561–566. https://doi.org/10.1016/S0169-5347(03)00224-6

Silvertown, J., Araya, Y., & Gowing, D. (2015). Hydrological niches in terrestrial plant communities: A review. *Journal of Ecology*, 103(1), 93–108. https://doi.org/10.1111/1365-2745.12332

Smith, A. J. E., & Smith, R. (2004). *The Moss Flora of Britain and Ireland*. Cambridge University Press.

Smith, R. I., Fowler, D., Sutton, M. A., Flechard, C., & Coyle, M. (2000). Regional estimation of pollutant gas dry deposition in the UK: Model description, sensitivity analyses and outputs. *Atmospheric Environment*, 34(22), 3757–3777. https://doi.org/10.1016/S1352-2310(99)00517-8

Smith, S. J., Pitchera, H., & Wigley, T. M. L. (2001). Global and regional anthropogenic sulfur dioxide emissions. *Global and Planetary Change*, 29(1–2), 99–119. https://doi.org/10.1016/S0921-8181(00)00057-6

South, A. (2011). Rworldmap: A new R package for mapping global data. In R Journal (Vol. 3, Issue 1).

Stace, C. (2019). *New Flora of the British Isles* (4th ed.). Cambridge University Press.

Storkey, J., Macdonald, A. J., Poulton, P. R., Scott, T., Köhler, I. H., Schnyder, H., Goulding, K. W. T., & Crawley, M. J. (2015). Grassland biodiversity bounces back from long-term nitrogen addition. *Nature*, 528(7582), 401–404. https://doi.org/10.1038/nature16444

Trimble. (2013). R6 Trimble RTK-GPS [Apparatus]. https://www.trimble.com/en/

Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J. L., Messier, J., Myers-Smith, I. H., & Sax, D. F. (2017). Plant biodiversity change across scales during the anthropocene. *Annual Review of Plant Biology*, 68, 563–586.

von Asmuth, J. R., Maas, K., Knotters, M., Bierkens, M. F. P., Bakker, M., Olsthoorn, T. N., Cirkel, D. G., Leunk, I., Schaars, F., & von Asmuth, D. C. (2012). Software for hydrogeologic time series analysis, interfacing data with physical insight. *Environmental Modelling and Software*, 38, 178–190. https://doi.org/10.1016/j.envsoft.2012.06.003

Wei, T., Simko, V., Levy, M., Xie, Y., Jin, Y., & Zemla, J. (2017). R package "corrplot": Visualization of a correlation matrix.

Weidlich, E. W. A., Nelson, C. R., Maron, J. L., Callaway, R. M., Delory, B. M., & Temperton, V. M. (2021). Priority effects and ecological restoration. *Restoration Ecology*, 29(1), e13317. https://doi.org/10.1111/rec.13317

Willis, A. J., Folkes, B. F., Hope-Simpson, J. F., & Yemm, E. W. (1959). Braunton burrows: The dune system and its vegetation. *The Journal of Ecology*, 47(2), 249–288. https://doi.org/10.2307/2257366

Woolley, S. N. C., Foster, S. D., O'Hara, T. D., Wintle, B. A., & Dunstan, P. K. (2017). Characterising uncertainty in generalised dissimilarity models. *Methods in Ecology and Evolution*, *8*(8), 985–995. https://doi.org/10.1111/2041-210X.12710

BIOSKETCH

Ciara Dwyer is a plant ecologist, with an interest in linking plant community responses to environmental drivers. This research represents part of her PhD work, investigating the environmental and hydrological drivers of dune slack plant communities.

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SUPPORTING INFORMATION

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