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Long-Term (37 Year) Changes in Coastal Dune Slack Plant Communities

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ABSTRACT

Questions: How did α-, β- and γ- plant diversity of coastal dune slack plant communities change over 37 years during a period of significant changes in conservation management practices?

Location: Ainsdale Sand Dunes National Nature Reserve, England.

Methods: We surveyed plant communities in dune slacks at Ainsdale Sand Dunes National Nature Reserve at two time points: in 1985 and in 2022. This period represents a time of significant change involving the introduction of conservation grazing in the context of declining natural rabbit populations and a changing environment.

Results: We show that over 37 years, α-diversity remained relatively stable, but γ-diversity increased, and β-diversity indicated shifts in community structure. Specifically, across the open dunes we observed a decline in positive dune slack indicator species (i.e., of conservation interest), an increase in *Salix repens* (frequency, cover and height) and a shift towards shade-tolerant and nitrogen-loving plants (as evidenced by Ellenberg values).

Conclusions: These findings suggest that despite the introduction of a conservation grazing programme, current grazing patterns (both wild and livestock) may not provide the level of disturbance required to maintain the open habitats and plant communities typical of healthy dune slacks.

1 | Introduction

Coastal sand dunes are biodiversity hotspots which support a variety of habitats, including open dunes, wet slacks, scrub and dune grassland (Doody 2005). These ecosystems are protected under legislation such as the EU Habitats Directive (Council Directive 92/43/EEC 1992) and the UK Wildlife and Countryside Act 1981 as they support species uniquely adapted to the strong within-site environmental gradients and extreme conditions (Bossuyt et al. 2003; P. H. Smith 2005; Grootjans et al. 2008; Dwyer, Millett, et al. 2021; Dynamic Dunescapes 2024; Smith and Lockford 2021). Dune slack plant communities play a key role in this biodiversity. These low-lying, typically nutrient-poor, seasonal wetlands contribute significantly to dune biodiversity through their high α- (within-slack) and β- (between-slack) diversity (Grootjans et al. 2008). Coastal dunes are under threat; for example, the extent of UK sand dunes has reduced by 30% since 1900 and most European dune systems are in unfavourable condition. There is, therefore, an urgent need to understand plant community change in these systems.

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Management of plant community succession is key for maintaining dune slack biodiversity (Johansen et al. 2024). Later successional communities are considered lower value due to the loss of important early successional species (Houston 2008; Hunt et al. 2019). A key threat in this context is the establishment of scrub and woodland. Historically, in Northwest Europe rabbits slowed succession on dunes through natural grazing (D. S. Ranwell 1959, 1960), maintaining the open habitats which are characteristic of this habitat. However, fluctuations in rabbit populations, due to myxomatosis in the 1950s, and rabbit calcivirus (RCV/RHD) more recently mean that conservation grazing is now widely used to maintain open dune habitats. Livestock grazing replaces the ecological role of wild grazing mammals, introducing disturbances that prevent the establishment of scrub and trees and creating habitat heterogeneity (Plassmann et al. 2010; Tälle et al. 2016; van der Hagen et al. 2017, 2020).

Repeat surveys of English dune slacks conducted between 1989 and 2012 indicate shifts in community composition over time (Stratford et al. 2014), and studies of slacks of different ages have shown the trajectory of soil and vegetation communities towards more stabilised habitats (Jones et al. 2008, 2010). However, long-term studies tracking dune slack plant communities over time remain rare (Ecological Continuity Trust 2015), particularly covering periods before and after significant changes in management such as the introduction of conservation grazing. Additionally, spatial variability and the resulting changes in β-diversity are often overlooked, which may fail to capture critical biodiversity change (Hillebrand et al. 2018) such as the loss of species of conservation importance.

We surveyed dune slack plant communities within a coastal sand dune system at Ainsdale Sand Dunes National Nature Reserve (Ainsdale NNR) in 1985 and repeated the survey 37 years later in 2022. We assessed changes in α-, β- and γ-diversity, including changes in notable species of conservation interest and indicators of habitat conditions. We knew from our own observations that changes in rabbit populations, particularly dramatic declines observed since c. 2010, had appeared to result in taller vegetation and a greater abundance of woody perennials, despite active management, including conservation grazing since 1991 covering a large proportion of the open dune area. We wanted to quantify some of these changes and predicted that they would result in some deterioration in habitat quality. Specifically, we expected to find evidence of decreased disturbance through increased cover of the dominant woody shrub *Salix repens*, resulting in decreased cover of dune specialist species, an overall decrease in α-diversity and a general homogenisation of plant communities (due to the absence of localised rabbit grazing and burrowing) resulting in decreased β-diversity.

2 | Methods

2.1 | Study Area

This study was conducted at Ainsdale Sand Dunes National Nature Reserve (hereafter 'Ainsdale NNR'), Merseyside, United Kingdom (Lat: 53.59° N, Long: 3.07° W). Ainsdale NNR is part of the Sefton Coast, England's largest open sand dune landscape (Jones et al. 2013), covering c. 500 ha with beach, open dune, wet slack, scrub and pine woodland habitat. It is designated as a Special Area of Conservation (SAC), Ramsar Site and Site of Special Scientific Interest (SSSI). Approximately 30% of the slacks are flooded to a depth of 0.1–0.3 m in the winter; in the summer, the slacks dry out as the water table drops to approximately 0.5 m below the surface (Clarke and Sanitwong Na Ayutthaya 2010).

Over the past 100 years, the Sefton Coast dunes have changed substantially. Cattle and sheep were grazed on commons in the dunes up until the 18th century, after which grazing was restricted due to concerns over wind-blown sand (P. Smith 2021). Rabbits (*Oryctolagus cuniculus*) were present in the dunes in warrens from at least the 15th century. Up until the 1950s, the dunes were characterised by blown sand on dune ridges and around dunes' slack edges (P. H. Smith 2009) and short vegetation, maintained by a large rabbit population. The 1953 myxomatosis outbreak caused a dramatic decline in rabbits and led to taller vegetation and shrub cover, resulting in 'fixed' dunes. The site was designated as an NNR in 1965, and a key management aim has been to conserve and restore open sand dune habitats (Gee 1998). Livestock grazing was reintroduced in 1991 for the purpose of nature recovery.

In 1991, approximately 200 Herdwick sheep were introduced, grazing from October to April each year. Herds of around 20 Hebridean sheep (2004), 10 Icelandic sheep (2010) and six Shetland cattle (2008) were introduced later. Grazing duration varies across enclosures, with the large enclosure grazed on average for 75 days a year between October and May, while grazing in the small and phase 1 enclosure was shorter, averaging 50 days/year. Grazing intensity was lower for the large enclosure (0.65 livestock units (LU) ha^{-1}) than for the small enclosure (1.5–2.5 LU ha^{-1}), where a sheep = 0.15 LU and cattle = 1.0 LU. Winter livestock is currently used because of concerns over the impacts of spring and summer grazing on flowering plants and Natterjack toads (*Epidalea calamita*) which are a priority species for conservation at the site. A detailed description of conservation grazing management at Ainsdale NNR is provided by Millett, van Soest, et al. (2025).

The mean ± SD for annual mean, maximum and minimum daily temperature at Crosby (10.5 km from Ainsdale NNR) between 1984 and 2022 were, respectively, 10.4°C ± 0.71°C, 13.5°C ± 0.73°C and 7.4°C ± 0.71°C (Appendix S1) and increased over this period by, respectively, 1.6°C ± 0.31°C, 1.7°C ± 0.30°C and 1.3°C ± 0.34°C. Mean annual precipitation was 866 ± 119 mm yr.$^{-1}$ with no evidence of any trend of increase or decrease over the period 1984–2022, although between-year variability was high with annual precipitation varying between 642 and 1118 mm yr.$^{-1}$. Mean spring water table depth (WTD) in the indicator slack was on average 0.22 ± 0.33 m below the ground surface with no evidence of any increase or decrease between 1984 and 2022, but WTD varied year to year with a difference of 1.34 m between the highest and lowest spring WTD. Rabbit abundance increased until the mid-1990s and then decreased. In surveys of four slacks, rabbit droppings were found in slacks in 2009, but none were found in 2019 or 2021.

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2.2 | Plant Community Surveys

In 1985, 100 plots were randomly located across slacks in the open dunes at the northern end of Ainsdale NNR. Survey plots were selected randomly from within the entire area of open dunes at Ainsdale NNR using random number tables to generate coordinates and then accepting plots which fell in wet dune slack areas. In August/early September 1985, plant species cover was recorded in 1×1 m quadrats for each plot (Figure 1). The height of the frequent dune slack characteristic shrub *S. repens* was measured by placing a ruler at 10 points in each plot.

To relocate these plots in 2022, we aligned the original plot map (Figure S2) with an Ordnance Survey map in QGIS and digitised the locations. However, due to the lack of visible plot numbers on the map, we could not match specific survey data to individual plots. We resurveyed 50 of the original plot locations in June 2022 (Figure 1) (as 100 plots were not possible in the time available). Plots were relocated using a handheld GPS, and the cover of each plant species and *S. repens* height was measured in a 1×1 m quadrat. Plant community survey approaches were performed by different surveyors (both authors of this paper), both with high levels of plant community survey expertise; in 2022, we attempted to replicate as closely as possible the effort spent on surveys.

The survey plots in 1985 and 2022 include locations inside and outside the livestock enclosures. But because we do not know the identity of the plot location in 1985, it is not possible to determine which of these are inside or outside the enclosures. As such, this study cannot show the direct impact of livestock grazing per se. Instead, our resurvey data demonstrate plant community change across the entire open dune site and show the impact of livestock grazing on part of the site, in the context of changing wild rabbit numbers, environmental change and other site management.

2.3 | Data Analysis

In 1985, the distance of the 100 plots to the coast was measured on a paper map. Although distance to the coast data was available for each plot, the exact spatial location for the plot is unknown. In 2022, we measured the distance to the coast for each of the 50 resurveyed plots in ArcGIS by tracing the 1971 Ordnance Survey map's mean high water marks (Ordnance Survey 1971) and using the vector analysis tool to calculate perpendicular distances to mean high water. Although distance measurements were compiled for both 1985 and 2022, differences in measurement methods prevented direct comparisons.

Because precise spatial location for 1985 plots was unavailable, we used a coarser measure of spatial category. We examined the frequency distribution of plots by distance to the sea for 1985 and 2022 plots separately. This revealed two clear groups based on the clear demarcation in these frequency plots (Appendix S3)—seaward (closer to the coast) and landward (further from the coast) plots—covering a key geographic gradient (Figure 1).

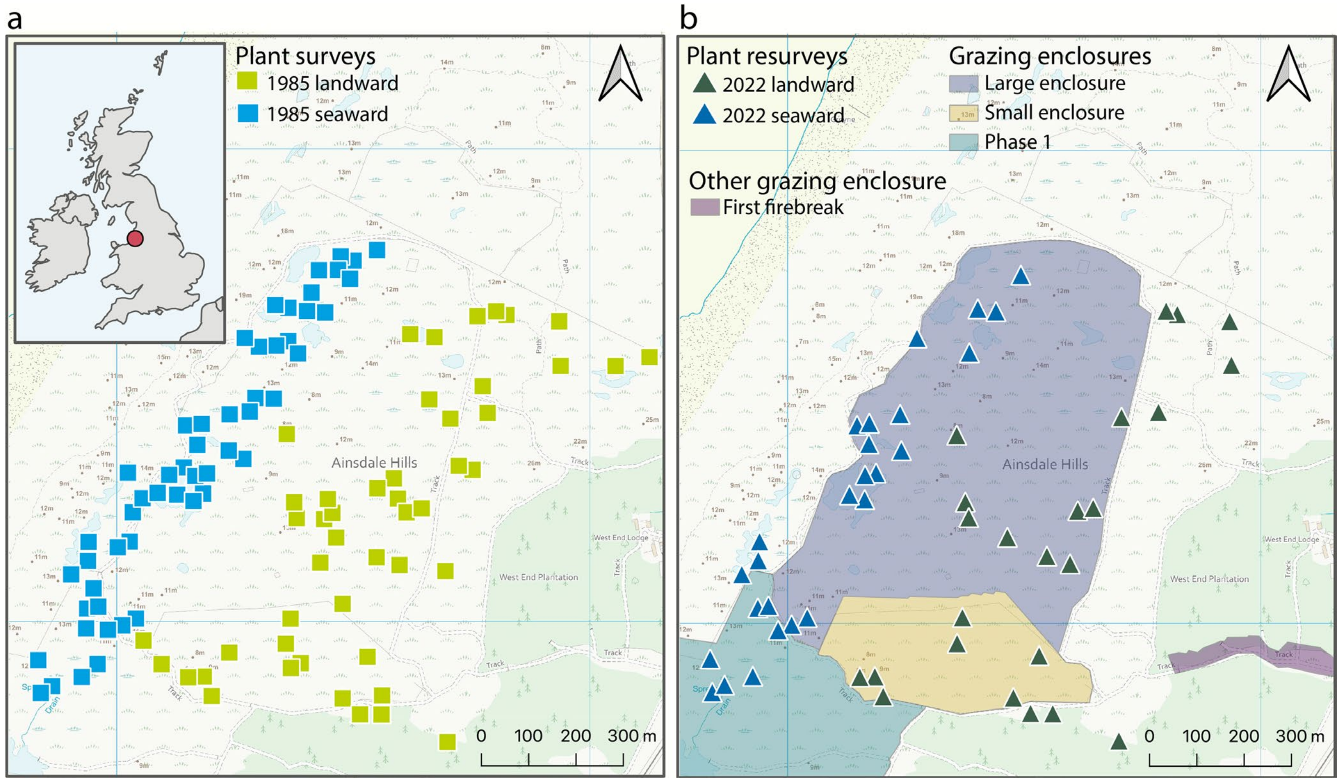

FIGURE 1 | Locations of (a) 100 sample points in 1985 (light blue and light green squares) and (b) 50 resurveyed points in 2022 (dark blue and dark green triangles) incorporating the grazing enclosures established in 1991 (grazing enclosures follow names used by site management: first fire break = dark purple, large enclosure = light purple, phase 1 = dark blue, small enclosure = yellow).

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2.4 | Statistical Analysis

All analyses were performed in R (v4.4.2.0; R Core Team 2024). For the 1985 surveys, 50 plots were randomly selected to standardise sample sizes for comparisons. A sensitivity analysis confirmed that a random subset of 50 samples reliably reproduces univariate diversity metrics and the multivariate structure of the 100-plot survey (Appendix S2). One plot was excluded as the plant community composition reflected that of a pond, with an 80% cover from a single species (*Chara* sp.).

α-Diversity (plot-level) metrics, including species richness, Shannon diversity, Simpson diversity and Pielou evenness, were calculated for each plot based on the percentage cover of each species, using the functions *specnumber* and *diversity* in the package *vegan* (Oksanen et al. 2024). To test for differences in the diversity metrics between landward and seaward (referred to as location) plots in 1985 and 2022 (referred to as year), we used analysis of variance (ANOVA) using the function *aov* and the base package *stats* (R Core Team 2024).

Temporal and spatial β-diversity (between plots) was compared by visualising plant community differences between landward and seaward plots within 1985 and 2022 (four groups: 2× location and 2× year) using non-metric multidimensional scaling (NMDS) with 999 permutations and Bray–Curtis dissimilarity using the function *vegdist* in the package *vegan* (Oksanen et al. 2024). A scree plot indicated high dimensionality, so the first four axes ($k = 4$) were extracted to reduce the stress ~0.10. We used the function *metaMDS* in the *vegan package* (Oksanen et al. 2024) to run the NMDS analysis with $k = 4$. We used the function *envfit* to quantify the extent to which individual species cover is aligned with each axis score by calculating R^2 scores for each species × axis combination. The extent to which variation in species cover is associated with each species fit to the entire ordination (axes 1–4) was evaluated using a permutation test with 999 permutations. To help visualise the ecological patterns in these ordinations, we fitted community-weighted means (CWMs) of Ellenberg indicator values (L, F, R, N, S) for each plot to the four NMDS using *envfit* with 9999 permutations. Fits were done separately for NMDS 1–2 and NMDS 3–4. These comparisons were tested using a Gaussian many-response linear model with fixed effects of Year (1985 vs. 2022), Location (Landward vs. Seaward) and their interaction using *manylm* in the *mvabund* package (Wang et al. 2012). *p*-values were obtained by residual-based permutation tests of the Lawley–Hotelling trace (F-approximation) with 999 residual-based permutations, implemented in *mvabund*. This approach balances sensitivity to community changes with robustness to mild heteroscedasticity and non-normality. Percent data were converted to proportions and arcsine-square-root transformed before analysis. Multivariate homogeneity of group dispersions (β-diversity) was assessed using the function *betadisper* in the package *vegan* (Oksanen et al. 2024). Distances of plots to group centroids were compared with an ANOVA to enable Tukey HSD post hoc comparisons. To check robustness, we also ran a permutation test (999 permutations) of the ANOVA pseudo-F statistic with pairwise comparisons. We compared two groups (year) and separately the four groups (location and year). We measured the extent to which differences in community composition between plots within year and location are due to turnover (i.e., species replacement) and nestedness (i.e., species losses or gains) by using the function *beta.multi.abund* (specifying the Bray–Curtis dissimilarity) in the package *betapart* (Baselga et al. 2024).

γ-Diversity (across the sand dune system) was compared with rarefaction curves calculated using the function *iNext* in the *iNEXT* package (Hsieh et al. 2024). We used data from all 100 plots for 1985 and all 50 plots in 2022. Rarefaction curves were calculated separately for the whole site in each year and for landward and seaward plots in each year by fitting to the data up to the number of plots and then extrapolating up to the maximum number of plots. Differences between year and year × location were compared by assessing the overlap of 95% and 90% confidence intervals.

We collated a list of 36 notable dune slack species to evaluate the impacts of plant community change on species of conservation importance (Appendix S3). This list included positive (e.g., *Anagallis tenella*, *Hydrocotyle vulgaris*) and negative (e.g., *Arrhenatherum elatius*, *Senecio jacobaea*) indicator species of dune slack status (JNCC 2004; Dynamic Dunescapes 2024), alongside species listed as conservation priorities locally, nationally or internationally (Stroh et al. 2014). To determine how species of conservation interest have changed over time, we tested whether frequency and cover differed between 1985 and 2022. Fisher's exact test was used to evaluate frequency changes, whereas the Wilcoxon signed-rank test (function *wilcox.test* in package *stats*) assessed changes in species cover. For plots where *S. repens* was present, the height and cover of *S. repens* were compared using ANOVA for 1985 and 2022 (function *aov* in base package *stats*) (R Core Team 2024).

To evaluate indicators of changes in environmental conditions over time, Ellenberg values for light (L), water (F), pH (R), salinity (S) and nutrients (N) were used. Ellenberg values for each species were taken from PLANATT (Hill et al. 2004). These values were used to calculate both the mean (based on all species present in the plot) and CWM (including the abundance of each species) for each plot.

2.5 | Grazed Versus Ungrazed Plots

While the set-up of the study suggests a potential grazed versus ungrazed comparison, our study aimed to measure plant community changes across the entire open dune system. For completeness, we present a supplemental analysis comparing 2022 plots inside and outside enclosures, including effects on α- and β-diversity and *S. repens* frequency (Appendix S4). However, these results are limited by an unbalanced design and spatial autocorrelation of treatments.

3 | Results

3.1 | Plant Communities

In total, we found 98 plant species across plots in 1985 and 2022. In 1985, 69 species were identified and in 2022, 75 species were identified; of these, 46 species were present in both years. The most abundant species overall across 1985 and 2022 was

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the shrub *S. repens* (average cover = 58.0%), followed by the perennial forb *Hydrocotyle vulgaris* (12.8%), shrub *Rubus caesius* (8.8%) and graminoid *Agrostis stolonifera* (6.5%). For all other species, average cover was < 5%.

3.2 | α-Diversity

There was no overall change in α-diversity between 1985 and 2022 or between landward and seaward plots (Figure 2 and Table 1). For all α-diversity indices, there was no evidence of differences between year (1985 and 2022) and location (landward and seaward) (Table 1). However, there was moderate evidence that species cover within plots was more evenly distributed in seaward plots than in landward plots in 1985, a difference that was not present in 2022 (Table 1), due to a decrease in the evenness of communities in seaward plots and an increase in the evenness of landward plots over time. This suggests a homogenisation of seaward plant communities at the plot level over time.

3.3 | β-Diversity

The multivariate model explained a small but meaningful fraction of plant community variance (Hooper's R^2–0.0457). The Lawley–Hotelling trace for the full model was 151.9 ($p = 0.001$) providing strong evidence of plant community change. Specifically, there is strong evidence of differences in plant communities between landward and seaward plots (permutational ANOVA: Location effect—$F_{1,98} = 165.2$, $p = 0.002$) and of changes in plant communities between 1985 and 2022 (permutational ANOVA: Year effect—$F_{1,98} = 167.8$, $p = 0.002$). There is also moderate evidence that plant community differences between seaward and landward plots changed between 1985 and 2022 (permutational ANOVA: Year × Location interaction—$F_{1,98} = 119.0$, $p = 0.020$). Most community composition differences between plots were driven by turnover (i.e., species replacement). In 1985, turnover accounted for 93% of the variance in community composition across all plots, compared to 91% in 2022. In 1985, turnover accounted for 83% of community composition variance in landward plots and 91% in seaward plots. By 2022, turnover explained 85% of the variance in both landward and seaward plots (Appendix S3).

NMDS axis 1 appears to be a wetness gradient and differentiated plots particularly (Appendix S3, weightings > 0.4) by the abundance of *Eleocharis palustris* and *Equisetum palustre* and to a lesser extent (Appendix S3, weightings > 0.3) the abundance of *Chara* sp., *Eleocharis quinqueflora*, *Myosotis scorpioides*, *Mentha aquatica* and *S. repens*. NMDS axis 2 appears to be a gradient combining shade and nutrient availability differentiating plots particularly (Appendix S3, weightings > 0.4) by the abundance of *Holcus lanatus* and *S. repens* and to a lesser extent (Appendix S3, weightings > 0.3) the abundance of *Carex arenaria*, *Carex flacca*, *Cirsium arvense*, *Poa* sp., *Prunella vulgaris* and *Trifolium repens*. Seaward plots had lower scores than landward plots on NMDS1 in both years,

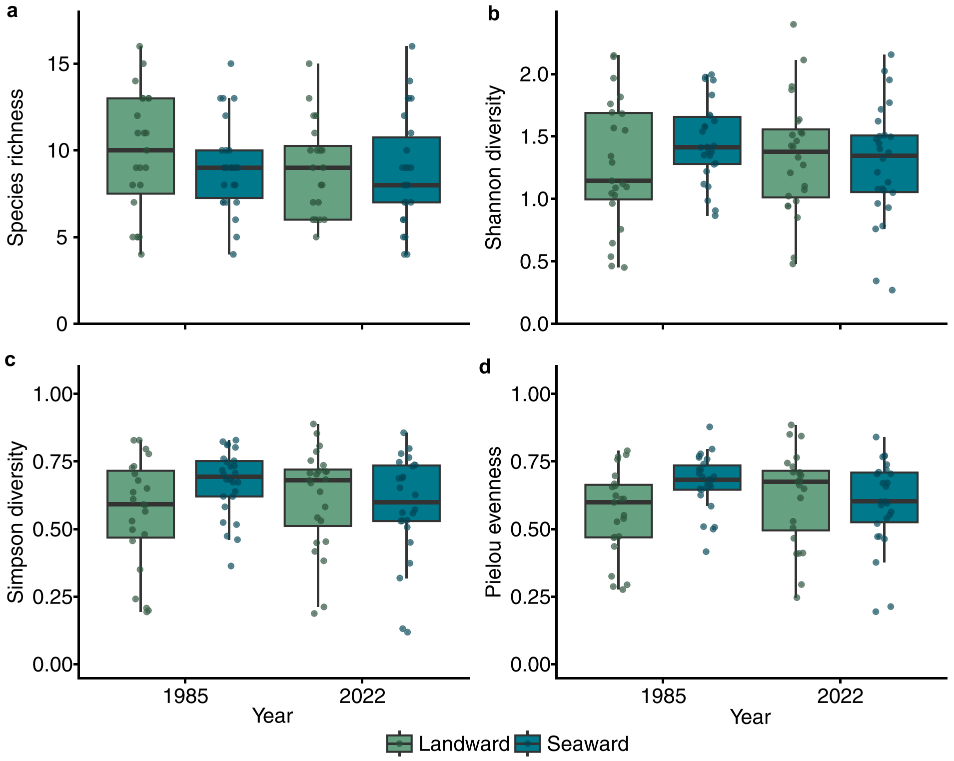

FIGURE 2 | α-Diversity of plant communities in plots in 2 years (1985 and 2022) and at two locations (landward or seaward). Presented are indices of diversity: (a) Species richness, (b) Shannon diversity, (c) Simpson diversity and (d) Pielou evenness. Boxplots present median, quartiles and 95%. Dots represent plot data. Statistical comparisons are in Table 1. There was weak evidence that Simpson diversity and Pielou evenness declined in seaward sites between 1985 and 2022 (post hoc pairwise comparisons using Tukey's HSD: $p = 0.084$ and $p = 0.072$, respectively), but no evidence of temporal change in landward sites for these metrics ($p = 0.271$ and $p = 0.173$, respectively).

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TABLE 1 | Results of statistical analysis (ANOVA) of the differences in α-diversity, *Salix repens* cover and height, and Ellenberg indicator values across 2 years (1985 and 2022) and two locations (landward and seaward), including their interaction effects.

Metric	df	Year (Y)		Location (L)		Y × L	
		F	***p***	***F***	***p***	***F***	***p***
α-diversity							
Species richness	1.95	0.821	0.367	0.539	0.465	0.314	0.577
Shannon–Wiener	1.95	0.421	0.518	0.485	0.488	1.718	0.193
Simpsons	1.95	0.266	0.607	1.197	0.288	4.022	0.048
Evenness (J)	1.95	0.151	0.699	2.033	0.157	5.059	0.027
Salix repens							
Cover	1.88	< 0.001	0.988	4.545	0.036	1.042	0.310
Height	1.88	23.855	< 0.001	0.429	0.514	0.008	0.927
Ellenberg values							
Mean light (L)	1.95	11.734	< 0.001	4.312	0.041	0.018	0.089
Mean moisture (F)	1.95	0.571	0.452	27.972	< 0.001	0.002	0.968
Mean pH (R)	1.95	2.342	0.129	0.438	0.510	0.356	0.552
Mean nutrients (N)	1.95	7.388	0.008	0.183	0.670	1.834	0.179
Mean salinity (S)	1.95	4.054	0.047	0.075	0.785	4.957	0.028
CWM light (L)	1.95	0.718	0.400	0.001	0.972	4.082	0.046
CWM moisture (F)	1.95	2.086	0.152	22.199	< 0.001	0.524	0.471
CWM pH (R)	1.95	5.218	0.025	0.254	0.615	0.059	0.081
CWM nutrients (N)	1.95	0.153	0.696	0.025	0.875	4.425	0.038
CWM salinity (S)	1.95	2.302	0.133	2.531	0.115	3.892	0.051

Abbreviations: CMW = community mean weight, F = moisture, L = light, Mean = mean weight, N = nutrients, R = pH, S = salinity.

but the difference was smaller in 2022. Plots in 2022 tended to have higher values on average on NMDS2 than those in 1985. Very little differentiation between year and/or location was present for NMDS axes 3 and 4 (Appendix S3). For NMDS 1 and 2, there was very strong evidence of alignment with the ordination for Ellenberg F (moisture) ($r^2 = 0.75$, $p = 0.0001$), N (nutrients) ($r^2 = 0.21$, $p = 0.0001$), L (light/openness) ($r^2 = 0.12$, $p = 0.0001$) and S (salinity) ($r^2 = 0.16$, $p = 0.0005$), with weak evidence for Ellenberg R (soil reaction/pH) ($r^2 = 0.05$, $p = 0.076$). For NMDS 3 and 4, there was very strong evidence of alignment with the ordination for Ellenberg N ($r^2 = 0.32$, $p = 0.0001$) and L ($r^2 = 0.21$, $p = 0.0001$), and strong evidence for S ($r^2 = 0.11$, $p = 0.0037$), and no evidence for R or *F* ($r^2 = 0.04$, $p = 0.121$; $r^2 = 0.04$, $p = 0.160$). Together, these results suggest that the plant communities differed between landward and seaward dune slacks with a reduction in abundance of species with higher Ellenberg *F*-values and that across the site there was a change in community composition between 1985 and 2022, with an increase in species with higher Ellenberg N-values and lower L-values.

There was strong evidence of differences in β-diversity between the four groups of plots (ANOVA: $F_{3,95} = 9.51$, $p < 0.001$, permutation test: $p < 0.001$). Post hoc tests indicated that seaward plots in 1985 were significantly more dispersed than all other groups, whereas by 2022 there was no difference between landward and seaward plots (Figure 3). This change indicates the homogenisation of seaward plant communities between plots. This can be visualised in Figure 4 through the narrowing of the centroid for seaward plots.

3.4 | γ-Diversity

In 1985, 58 species were recorded in landward plots ($n = 47$) and 63 species were recorded in seaward plots ($n = 53$). In 2022, 51 species were recorded in landward plots ($n = 24$) and 57 species were recorded in seaward plots ($n = 26$). When all plots were pooled within each year, total observed γ-richness was 72 species in 1985 (100 plots) and 75 species in 2022 (50 plots). Extrapolating the 2022 data to 100 plots to match the 1985 sampling effort increased predicted γ-richness to 82 species overall (landward = 71, seaward = 76), reflecting rare taxa likely missed by the smaller 2022 sampling effort. The 95% bootstrap confidence intervals do not overlap between 1985 and 2022 indicating an increase in γ-diversity. However, when examined separately for landward and seaward plots, the 90% confidence intervals overlap, suggesting little evidence of differences at this level of granularity (Figure 5 and Appendix S3).

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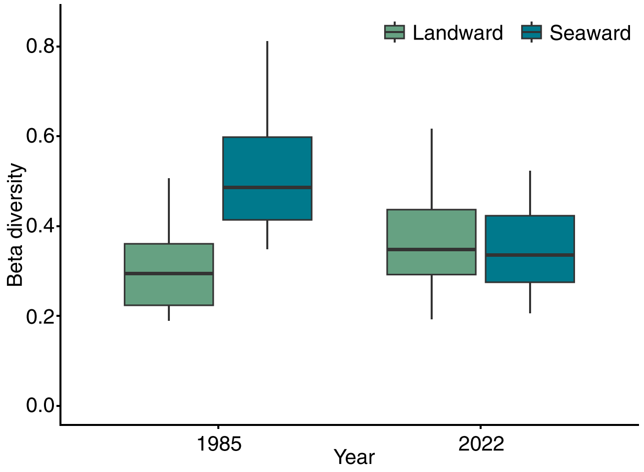

FIGURE 3 | β-Diversity (multivariate dispersion/distances to group centroids) for landward and seaward communities in 1985 and 2022. Groups with different letters have different dispersal based on Tukey HSD ($p < 0.001$). A permutation test of the ANOVA pseudo-F statistic (9999 permutations) gave consistently significant results.

3.5 | Dune Slack Notable Species

We identified 36 plant species as positive or negative indicators of dune slack status (Appendix S3) of which 33 (8 negative and 25 positive) were present in our survey data (Figure 6a,b). There was evidence of decline in the frequency of five positive indicator species between 1985 and 2022 surveys: *Prunella vulgaris* ($p = 0.006$), *Carex arenaria* ($p = 0.002$), *Carex flacca* ($p < 0.001$), *Equisetum variegatum* ($p < 0.001$) and *Carex panicea* ($p = 0.056$) (Figure 6a: orange); and evidence of increased frequency of three positive indicator species: *Carex nigra* ($p = 0.03$), *Galium palustre* ($p = 0.097$) and *S. repens* ($p = 0.005$). There was little evidence that the frequency of negative notable species declined between 1985 and 2022 surveys, and moderate evidence one species increased in frequency: *Arrhenatherum elatius* ($p = 0.015$) (Figure 6a: purple).

In the plots where positive notable species were present in both years, there was evidence of a decline in cover of three species: *Galium palustre* ($p = 0.022$), *Mentha aquatica* ($p = 0.003$) and *Lotus corniculatus* ($p = 0.005$); there was evidence that the cover of one positive indicator species increased: *Festuca rubra* ($p = 0.001$) (Figure 6b: orange). In the plots where negative notable species were present in both years, there was evidence in a decline in cover of one species—*Cirsium arvense* ($p = 0.026$)—and no evidence that any species increased in cover (Figure 6b: purple).

3.6 | *Salix repens* Changes

In 2022, *S. repens* was present in every plot assessed and was more frequent (due primarily to lower frequency in seaward plots in 1985) and taller than in 1985 (Table 1, Figure 7, Frequency: Fisher's exact test—$p = 0.002$). In the plots where it was present, *S. repens* cover did not differ between years but was consistently higher in landward than in seaward plots.

3.7 | Ellenberg Indicator Values

We present mean Ellenberg values here (Table 1, Figure 8), with CWM results shown in Figure S6, which were qualitatively similar. Mean Ellenberg light (L) values were lower in 2022 than in 1985 and were lower in landward plots in both years, aligning with the increased *S. repens* height—that is, taller plants creating more shade. Mean Ellenberg moisture (*F*) values were higher in seaward than in landward plots and did not vary significantly between years. There was little evidence of differences in mean Ellenberg pH (R) values across years or locations. Mean Ellenberg nutrient (N) values were higher in 2022 than in 1985, with little evidence of difference between locations. Mean salinity (S) values were lower in 2022 than in 1985, with an interaction with year and location.

4 | Discussion

The rediscovery of the 1985 plant community survey data for Ainsdale NNR provided a rare opportunity for a long-term resurvey of dune slack plant communities across 100 ha of open dune habitat—one of the rarest habitats in Europe and a nature recovery priority. This long-term study demonstrates that dune slack plant communities retained key characteristics of high conservation-value habitats. However, there was evidence of compositional shifts in the plant communities indicating an overall decline in habitat condition, with evidence of species homogenisation at the within- and between-plot level, declines in positive dune slack indicator species, an increase in *S. repens*, and a shift towards shade-tolerant and nitrogen-loving plants. The extent of these plant community changes varies along the landward–seaward gradient, with seaward communities changing more.

Our study measured changes in dune slack plant communities across the entirety of the open dune system at Ainsdale NNR, reflecting site-level management and environmental changes. Thus, our study measured the impact of site management in a holistic way, integrating the multifactorial changes over the very long timescales. Conservation grazing is a component of this, but the area under conservation grazing did not include the entire open dune habitat: 20% of our resurvey plots were in areas outside the conservation grazing areas, and 80% within them, reflecting the extent of this management intervention. In addition, other changes, for example rabbit numbers, climate and other dune management, have impacted plant communities over this time, and these impacts will be reflected in the plant community changes we have measured.

β-Diversity is rarely considered in studies of the effectiveness of habitat management interventions, especially across such long timescales. But within-site β-diversity is important (Elliott et al. 2024) because it provides information on the spatial and temporal patterns of biodiversity, such as species loss, gain and replacement within a protected area. Biotic homogenisation within a site can indicate declining habitat conditions, which will be signified by decreasing β-diversity. Differences in composition between plots across the site were primarily due to turnover (replacement of species) rather than

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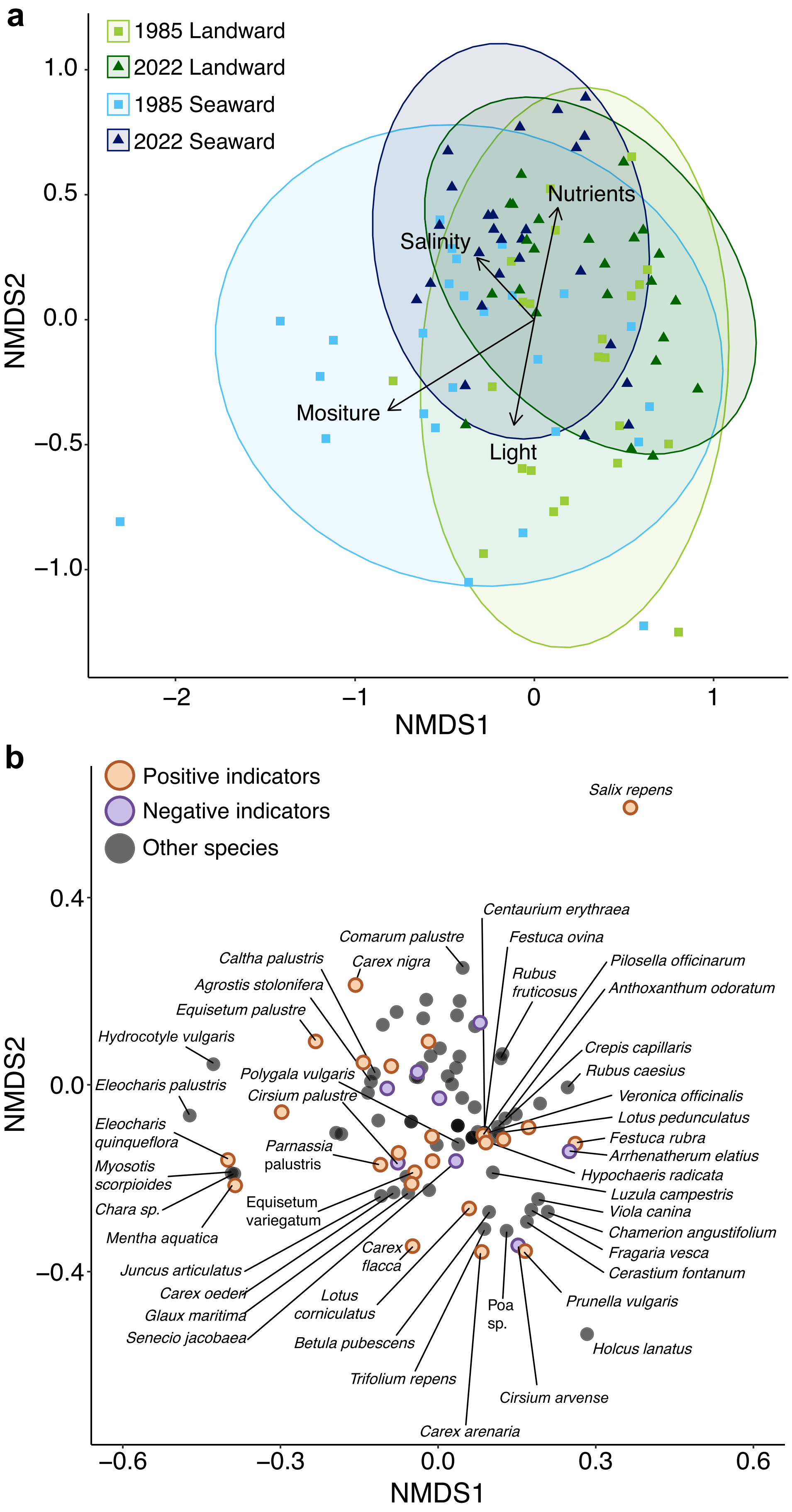

FIGURE 4 | Legend on next page.

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FIGURE 4 | β-Diversity: Non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity, presenting (a) individual plots and (b) species scores for NMDS axis 1 and NMDS axis 2. Plots in different locations (landward or seaward) are differentiated by colour (blue = seaward, green = landward) and different years (1985 or 2022) are differentiated by colour (1985 = square, 2022 = triangle). Ellipses represent a 95% confidence region for the mean of the data. Filled circles represent species. Species for which the p-value for the fit to the NMDS ordination < 0.10 are labelled. Stress value = 0.14 and $k = 4$. Arrows in (a) show envfit vectors for plot-level Ellenberg CWMs (permutation test, 9999 permutations); only variables with $p \leq 0.05$ are drawn. Arrow length is proportional to r^2. Arrows are scaled (×100) to aid visualisation. These CWMs are derived from species composition and are used for ecological interpretation rather than independent hypothesis testing.

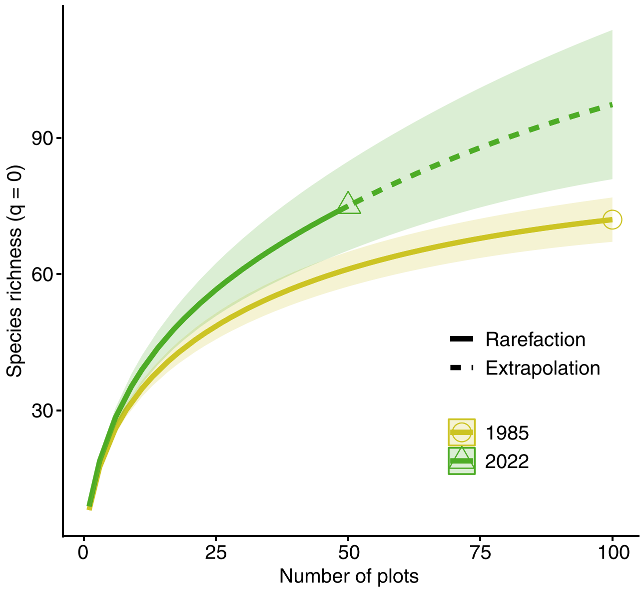

FIGURE 5 | γ-Diversity. Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) of species richness for dune slack vegetation in 1985 and 2022. Symbols indicate observed richness; shaded areas are 95% confidence intervals. Richness is expressed as hill numbers with $q - 0$, that is, the number of species irrespective of abundance.

nestedness (loss of species), which suggests that environmental filtering, the ability for a species to establish and persist, might be a key driver of β-diversity within the site (Kraft et al. 2015). Within dune slacks, differences in the seed bank (Bekker et al. 1999; Bossuyt and Hermy 2004), groundwater chemistry (Jones et al. 2006), hydrology and topography (Dwyer, Millett, et al. 2021; Dwyer, Pakeman, et al. 2021) might drive these between-slack differences. Across Ainsdale NNR, the hydrological regime varies between slacks (Clarke and Sanitwong Na Ayutthaya 2010; Abesser et al. 2017), and Ellenberg *F*-values confirm that the slacks where the seaward plots were located tended to be wetter. But successional processes are also key in determining plant community composition (Bossuyt et al. 2003). It might be the case that over the 37 years of this study, the increase in *S. repens* and consequent shading (as signified by decreased Ellenberg L-values) plus potentially nutrient enrichment has reduced environmental differences between slacks. This analysis of β-diversity, therefore, provides direction for considering management, which can increase variation across the site, for example, through mowing or turf stripping of focal dune slacks.

The total species pool (γ-diversity) increased from 1985 to 2022, reflecting both a slight rise in mean plot richness (α-diversity) and the addition of rare taxa predicted by extrapolation from the smaller 2022 sample. In contrast, β-diversity shows evidence of a modest decline over time, particularly in seaward plots, suggesting that communities have become more similar. The combination of relatively stable plot-level richness, modestly reduced turnover and a larger extrapolated species pool explains why overall γ-diversity has risen even though α-diversity remains unchanged. This pattern of species turnover without loss of local richness mirrors findings in other systems where species identities shift despite apparent stability (Hillebrand et al. 2018). Incorporating species indicator values (e.g., Ellenberg scores) and notable dune species can help link these compositional shifts to environmental drivers (Dwyer, Millett, et al. 2021; Dwyer, Pakeman, et al. 2021), providing managers with a practicable approach to monitoring environmental conditions and vegetation responses effectively (Diekmann 2003). Our results suggest that conservation grazing alone may not sustain open habitats which support slack specialists over multi-decadal timescales.

The most notable shift in community composition and structure is increased *S. repens* frequency and height. *Salix repens* is a positive indicator of dune slacks, but its overabundance can be detrimental through suppression of forb and graminoid species (Sýkora et al. 2004). Experimental studies in the same dune system and our data from plots outside the conservation grazing enclosures demonstrate that livestock grazing does reduce woody perennial cover compared to ungrazed plots (Millett and Edmondson 2013, 2015). The increase in shrub cover that we observed, however, suggests that livestock grazing was not sufficient on its own to fully control shrub encroachment. The likely reason is a decrease in the rabbit population through the 2000s. After the devastating impact of myxomatosis in 1953, UK rabbit populations had recovered by the mid-1990s, but the emergence and spread of rabbit haemorrhagic disease (RHD) (Abrantes et al. 2012) has since reduced populations by around 70% (Aebischer 2019; Heywood et al. 2023). Rabbit numbers are not routinely monitored at Ainsdale NNR, but our measurements in four slacks showed that rabbits were present in 2009 and not in 2019 or 2021. The grazing regime over the period of our study, therefore, likely reflects a shift from rabbit to livestock (predominantly sheep) grazing.

This interaction between conservation grazing and rabbit population fluctuations has been demonstrated in other studies. For example, van der Hagen et al. (2023) showed that patterns of succession in a Dutch coastal dune system over 59 years were dependent on fluctuations in the rabbit population, driven by the decline due to myxomatosis, then recovery and subsequent decline due to RHD. Rabbits and livestock interact (Ford et al. 2012). Rabbits prefer short swards and will repeatedly

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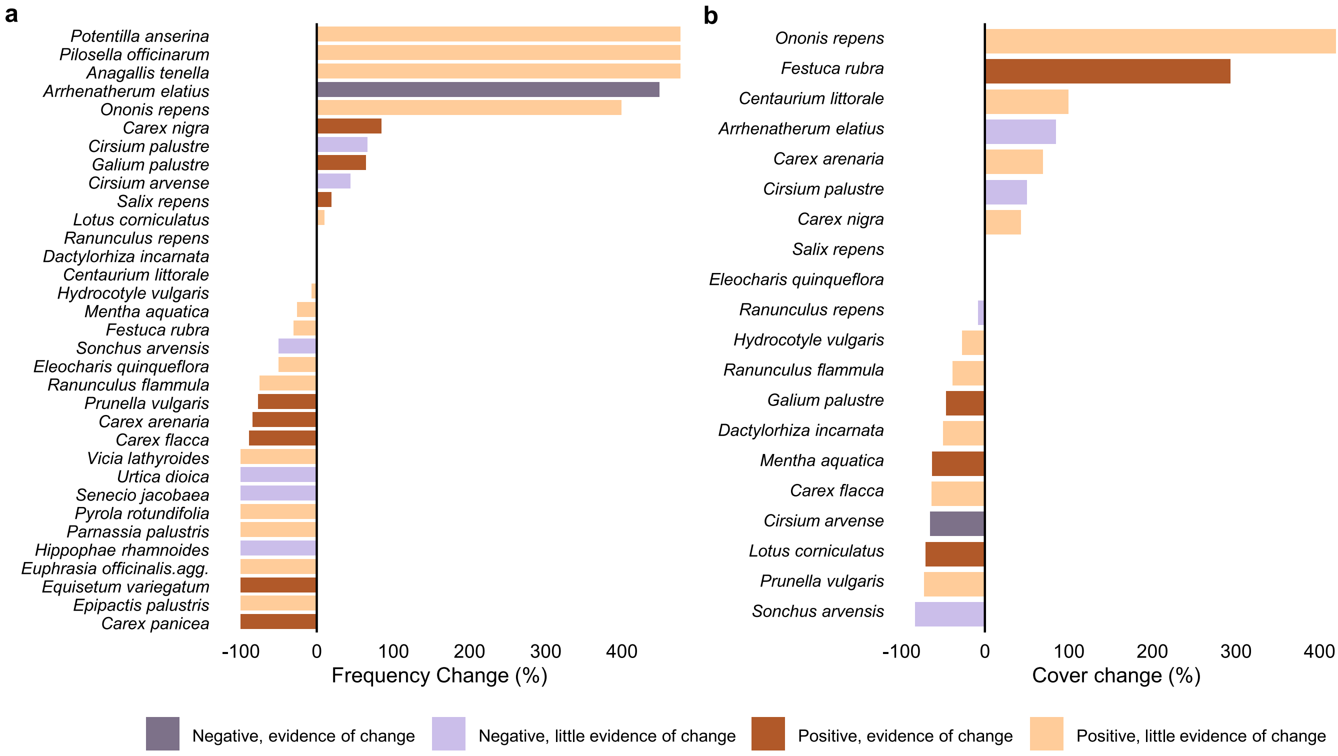

FIGURE 6 | Change in (a) frequency (number of plots in which species was present) and (b) cover (percentage cover in those plots where the species was present) for positive and negative dune slack notable species (see Table 1). Presented are the percentage changes between the surveys in 1985 and 2022. Dark bars indicate changes where $p < 0.1$, indicating evidence of change.

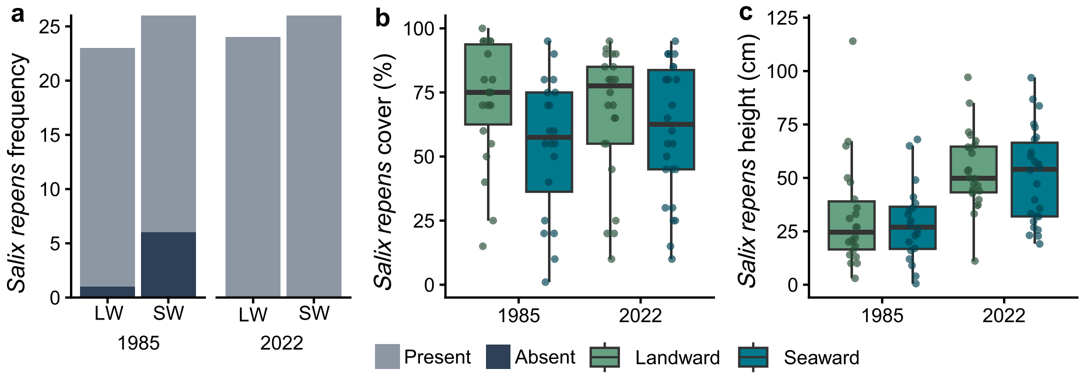

FIGURE 7 | Characteristics of *Salix repens* within dune slack plant communities in 1985 and 2022 in seaward and landward plots. Presented are (a) the proportion of occurrence (i.e., number of plots where *S. repens* is present), (b) mean cover within each plot (where present) and (c) mean height. Statistical comparisons are provided in Table 1. LW = landward plots, SW = seaward plots.

graze preferred patches; as such, rabbits intensify the impact of livestock, and livestock open patches of taller vegetation making them accessible to rabbits. Rabbits also demonstrate different behaviour to livestock due to their burrowing activities, so they cannot necessarily be directly replaced with livestock. Our findings demonstrate the challenges of managing grazing-dependent semi-natural habitats through livestock grazing alone, particularly where past ecology was dependent on rabbits Difficulties lie in achieving high enough stocking rates due to forage quality and replicating the digging and selective grazing behaviour of rabbits (Dolman and Sutherland 1992). Routine monitoring of rabbit populations would allow the interactions between wild and domestic grazing mammals to be fully understood to facilitate more effective livestock management. In addition, approaches for increasing rabbit populations might be important, such as the creation of brush piles (Bell et al. 2021), but evidence of their effectiveness is lacking.

Long-term experiments are a 'gold standard' for evidence-based conservation but are limited in number and tend to be small scale (Ecological Continuity Trust 2015). For example, the Ainsdale Dune Slacks Long-Term Experiment (LTE) is co-located with the plots measured in the present study but only has survey plots located in four slacks and only in the landward part of the reserve (Millett and Edmondson 2013). Our results complement those of the LTE by demonstrating change across the whole area of open dunes and providing the potential to measure changes in spatial diversity patterns.

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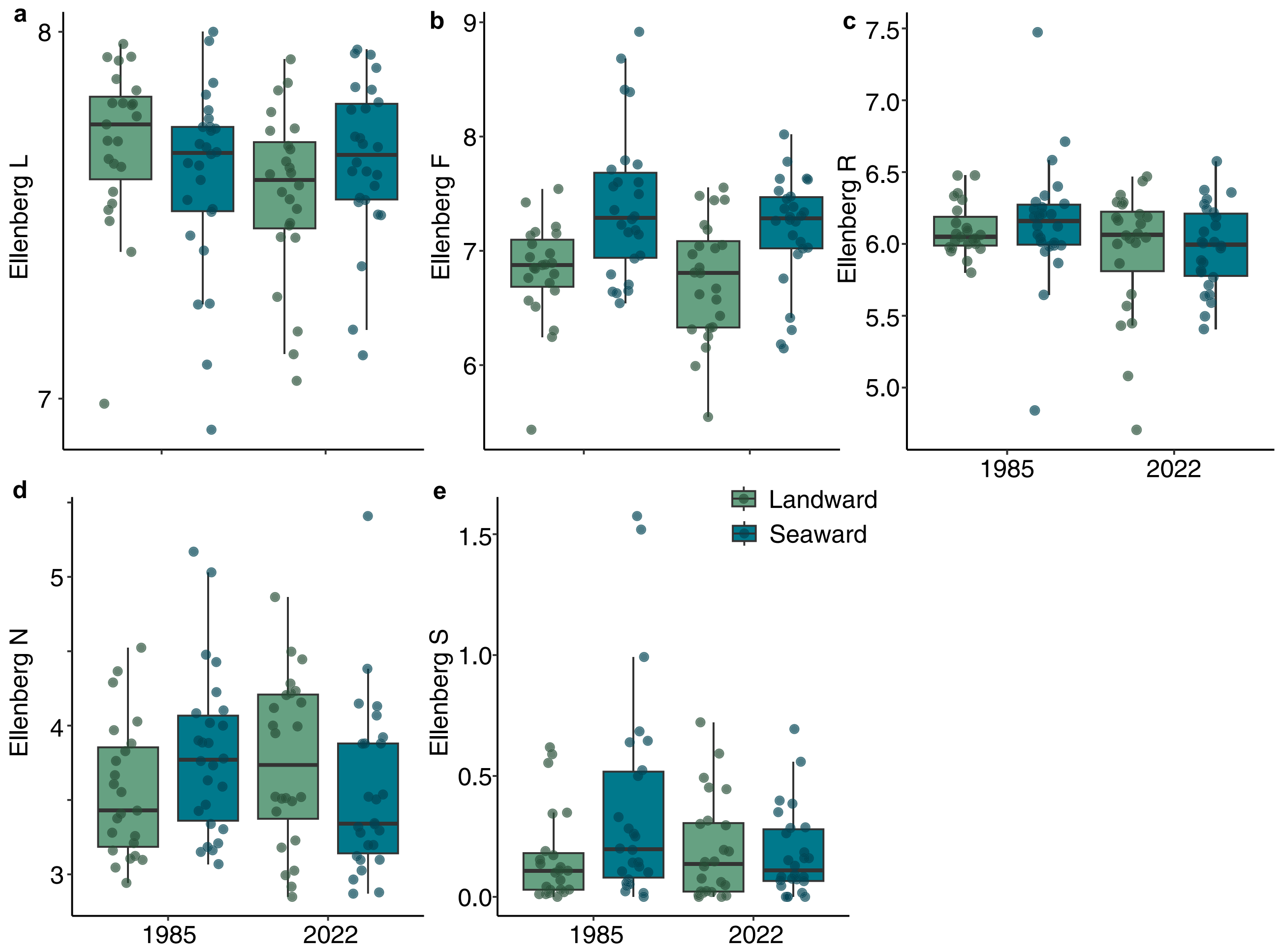

FIGURE 8 | Mean Ellenberg values for plant communities at Ainsdale NNR. Presented are mean values for plots in landward or seaward plots in 1985 and 2022 for Ellenberg values for (a) light (L), (b) water (*F*), (c) pH (R), (d) nitrogen (N) and (e)€ salinity (S). Statistical comparisons are in Table 1. There was moderate evidence that community-weighted mean light values decreased in landward sites between 1985 and 2022 (post hoc pairwise comparisons using Tukey's HSD; $p = 0.043$), and weak evidence that community-weighted mean nitrogen values increased in seaward sites between 1985 and 2022 ($p = 0.087$). There was no evidence of temporal change in seaward or landward sites ($p = 0.438$ and 0.212, respectively).

This demonstrates the benefits of a layered approach to developing the evidence base for conservation interventions. Resurvey studies such as ours, Plassmann et al. (2010), van der Hagen et al. (2023), Millett and Edmondson (2013) and Miao et al. (2022) provide valuable insights into plant community change at timescales which reflect the long-term horizon of nature recovery management. Setting up permanent monitoring plots in new nature recovery sites is essential and ensuring that plots can be relocated and that data will be accessible after decades should be a priority. The development of standardised protocols for data recording and storage would improve the ability of future researchers to use current surveys.

Author Contributions

Jonathan Millett: conceptualisation (equal); writing – original draft (equal); formal analysis (equal); writing – review and editing (equal); visualisation (supporting). **Ciara Dwyer:** conceptualisation (supporting); writing – original draft (equal); formal analysis (equal); writing – review and editing (equal); visualisation (lead). **Sally Edmondson:** conceptualisation (equal); investigation (equal); writing – review and editing (equal). **Ellen Jones:** writing – original draft (equal); investigation (equal); writing – review and editing (equal). **Ellen L. Fry:** supervision (lead); writing – review and editing (equal). **Laurence M. Jones:** writing – review and editing (equal). **Maud A. J. van Soest:** writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used to produce the analysis for this study are available in the Loughborough University Data Repository: https://doi.org/10.17028/rd.lboro.27927432 (Millett, van Soest, et al. 2025).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Details of environmental variables and long-term trends. **Appendix S2:** Methodological validation and sensitivity analysis. **Appendix S3:** Plant community composition, species information and diversity structure. **Appendix S4:** Details of comparison of plots inside and outside grazing enclosures.

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