

Environmental drivers of *Limonium britannicum* subsp. *celticum* (Plumbaginaceae) demographics inform site-specific conservation

Jennifer H. Wilkinson^{1*}; Paul A. Ashton¹

¹Department of Biology, Edge Hill University, Ormskirk, UK

*Corresponding author: wilkinson.nif@gmail.com

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Abstract

Limonium britannicum subsp. *celticum* is a rare endemic of the Irish Sea coast, occurring in small, scattered populations across saltmarsh, dune slack, sandy shore and rocky habitats. Its conservation has been complicated by inconsistent taxonomic treatment, which has historically obscured its restricted distribution within broader aggregates. This study presents the first complete census of all known populations, providing a demographic baseline and examining how environmental variables influence population structure. Sixty-one populations were surveyed across nine sites in North Wales, the Wirral and Morecambe Bay, with abundance, life stage, stress status, substrate, elevation and tidal regime recorded for 180 quadrats.

Abundance and demographic composition differed significantly among sites and between substrates. Generalised linear mixed models indicated that substrate contributed to these patterns, although a substantial proportion of variation remained unexplained, consistent with the influence of additional local drivers. Recruitment emerged as a key bottleneck, with sandy soil microsites supporting seedling establishment but vulnerable to erosion and disturbance, whereas rocky habitats supported established plants but offered limited opportunities for regeneration.

By documenting population structure across its entire distribution, this study establishes a benchmark for future monitoring and adds fine-scale ecological and demographic resolution to conservation assessment. The results also provide evidence to inform site-specific management of this rare coastal plant.

Keywords: sea-lavender; coastal endemic; demography; recruitment; saltmarsh; substrate

Introduction

The *Limonium* (Sea-lavender) genus is widely distributed across temperate coasts worldwide and comprises only halophytic species. It is a taxonomically complex genus, with species estimates ranging from c.350 to 700 (Malekmohammadi *et al.*, 2024). High levels of endemism, aided by apomixis and polyploidy, have generated morphologically distinct but often genetically similar lineages, complicating species

delineation and contributing to inconsistent taxonomic interpretations (Cowan *et al.*, 1998; Koutroumpa *et al.*, 2021).

These challenges are exemplified in the *Limonium binervosum* (Rock Sea-lavender) aggregate, one of several species complexes within the genus (Ingrouille & Stace, 1986; Cortinhas *et al.*, 2015). It comprises *c.*45 taxa with reproductive strategies including both sexual diploids and apomictic polyploids (Ingrouille & Stace, 1986; Stace, 2019). In this paper, nomenclature follows Stace (2019).

Limonium britannicum subsp. *celticum* Ingr., known as Celtic sea-lavender (hereafter *celticum*) is one such taxon, representing an aneuploid tetraploid cytotype ($2n = 35, 36$) (Stace, 2019). It is a UK endemic confined to a highly restricted and disjunct range along the Irish Sea coasts of North Wales and Northwest England (Fig. 1).

Within its distribution, *celticum* occurs across a variety of coastal conditions, from saltmarshes and dune slacks to sandy shores and natural or artificial rock. These environments are characterised by strong gradients in salinity, inundation frequency and substrate, factors known to influence the distribution, recruitment and persistence of coastal plant populations (Pennings & Callaway, 1992; Allen, 2000; Dwyer *et al.*, 2021). Although broad habitat associations have been described for *Limonium* taxa, fine-scale ecological and demographic studies of British subspecies within the *L. binervosum* aggregate remain scarce (Rees, 2022).



Figure 1. Known distribution of *Limonium britannicum* subsp. *celticum* (map produced in QGIS 3.28.3)

Broad taxonomic aggregation can obscure ecologically significant variation and complicate conservation assessment, particularly for taxa with narrow ecological niches and fragmented distribution (Mace & Purvis, 2007). In the case of *celticum*, earlier Red Lists followed aggregate-based treatments of the *Limonium binervosum*

group and did not assess the taxon separately (Dines, 2008; Stroh *et al.*, 2014). The new vascular plant Red List for Great Britain adopts the treatment of Sell & Murrell (2018), recognising *Limonium celticum* at species rank and explicitly assessing it as Least Concern (Stroh *et al.*, 2025). That assessment is based primarily on distributional data, with limited information currently available on population demographics. As a result, *celticum* is now formally recognised within conservation frameworks, while fine-scale ecological and demographic evidence remains limited.

The combination of fragmented distribution and highly specific habitat requirements may increase the sensitivity of *celticum* populations to climate-related and anthropogenic coastal pressures. These include trampling from recreational or livestock use, erosion associated with sea-level rise, coastal squeeze from management interventions such as hard defences, and shifts in estuarine salinity and sediment regimes (Feagin *et al.*, 2005; Martone & Wasson, 2008; Pontee, 2013; Khojasteh *et al.*, 2021).

The case of *celticum* highlights the importance of conserving taxa within evolutionarily dynamic genera such as *Limonium* (Hollingsworth, 2003; Mace & Purvis, 2007). These taxa serve as model systems for studying speciation, adaptation, and persistence under environmental pressures (Ozias-Akins & Carman, 2006; Kinnison *et al.*, 2007). The subspecies also forms part of the wider saltmarsh flora, where conserving individual taxa contributes to maintaining species richness and associated below-ground processes such as nutrient capture and sediment stabilisation (Allen, 2000; Redelstein *et al.*, 2018).

Much of the global literature on the *Limonium* genus has focused on taxonomy and phylogenetics, particularly genetic relationships, polyploidy and reproductive strategies (Ingrouille & Stace, 1986; Koutroumpa *et al.*, 2018). Additional studies have examined morphological variation and broad habitat associations (Dawson & Ingrouille, 1995; Jarvis *et al.*, 2016). While this work provides valuable insights, systematic ecological and demographic studies of UK taxa, particularly subspecies of the *L. binervosum* aggregate such as *celticum*, remain scarce (Rees, 2022). As a result, evidence remains limited on how fine-scale environmental gradients and habitat conditions influence population persistence, constraining the development of locally informed conservation approaches (Stockwell *et al.*, 2003).

This study investigates how fine-scale environmental gradients shape the population ecology of *Limonium britannicum* subsp. *celticum*. It examines associations between substrate, elevation, and tidal inundation (frequency and duration) and population attributes, including demographic structure and indicators of stress. The study also tests whether site level differences persist after accounting for these gradients, indicating the influence of unmeasured local factors. In addition, it presents the first range-wide census of the subspecies, providing a baseline description of demographic structure and condition across all known extant populations.

Methods

Study Sites

Survey sites were identified from distribution records spanning the past 25 years. Records were sourced from the Botanical Society of Britain and Ireland (BSBI) Distribution Database, the North Wales Environmental Information Service (Cofnod), National Biodiversity Network (NBN) Atlas, and iNaturalist (BSBI, 2025; Cofnod,

2025; iNaturalist, 2025; NBN, 2025). All recorded locations were visited in summer 2025 to confirm presence or absence. Plants were identified according to Stace (2019). Extant populations were georeferenced, absences at historic sites were documented but excluded from analyses.

The nine study sites were distributed across the three regions: Arnside Beach, Bardsea, Plumpton Marsh and Knott End-on-Sea in Morecambe Bay; Hilbre Island and Red Rocks on the Wirral Peninsula; and Gronant Dunes, Lligwy Bay and near Rhoscolyn in North Wales. The majority lie within statutory protected areas, predominantly Sites of Special Scientific Interest (SSSI), with additional designations at some locations. Together these sites encompass the full current distribution of *celticum*.

Sampling Methods

Sampling was conducted during June–July 2025, when plants were most readily detectable and stress symptoms could be reliably assessed. Populations were defined as groups of individuals occurring within approximately 10 m of one another and were considered distinct if separated by more than 50 m or by clear physical breaks such as water channels or unvegetated ground (Rivers *et al.*, 2010).

Three 1 m² quadrats were placed per population to capture local variation in elevation and substrate within sites. In total 61 populations were sampled (20 in Morecambe Bay, 20 on the Wirral, and 21 in North Wales), yielding 180 quadrats. Sampling was reduced at two sites where plants were highly restricted.

Quadrats were placed only where *celticum* occurred and positioned to provide a representative sample of each population, and each quadrat was georeferenced. All individuals were counted and assigned to life stage categories based on rosette diameter: seedlings (<2 cm), juveniles (2–5 cm), mature plants (5–15 cm), and veterans (≥15 cm), with boundary values assigned to the higher class (Christman, 2000; Ramula *et al.*, 2009; Lindell *et al.*, 2022). As in other perennial *Limonium* taxa, *celticum* may reproduce clonally through woody rootstock; all rooted rosettes were therefore recorded as individuals (Ingrouille & Stace, 1986; Koutroumpa *et al.*, 2021).

Stress was recorded for each individual using a five-point scale: dead (no living tissue); severe stress (>75% discoloured, wilting, curling, poor turgor); moderate stress (~50% discoloured, recoverable); mild stress (>75% good colour, active growth, good turgor); and healthy (no visible stress, green, vigorous) (Bock *et al.*, 2020; Raposa *et al.*, 2020; Kutcher *et al.*, 2022).

Substrate was recorded as rock (natural outcrops or engineered embankments) or, where unconsolidated sediments occurred, by hand-feel texture (Richer-de-Forges *et al.*, 2022). Rock substrates comprised fissures and shallow sediment accumulations over exposed rock surfaces with insufficient material for hand texture assessment, whereas sandy soil substrates comprised deeper continuous sediments (Fig. 2). Only rock and sandy soil were observed in the field, so substrate was treated as a two-level factor in subsequent analyses.



Figure 2. Representative substrate types occupied by *Limonium britannicum* subsp. *celticum*. Plants growing in (A) sandy soil at Red Rocks and (B) shallow fissures on exposed rock at Hilbre Island

Elevation was extracted as metres above Ordnance Datum Newlyn (ODN) from national LiDAR datasets provided by the Environment Agency and Natural Resources Wales and processed in Google Earth Engine (GEE) (Gorelick *et al.*, 2017; Environment Agency, 2023; Natural Resources Wales, 2024).

Processed tidal data were obtained from the nearest gauges with available series in the UK National Tide Gauge Network (UKTGN), operated by the British Oceanographic Data Centre (BODC), namely Liverpool (Gladstone Dock), Heysham and Holyhead (BODC, 2025). For each quadrat, the assigned station provided a water level time series at 15-minute intervals from 16 June 2024 to 15 June 2025, referenced to ODN. A full year of data was used to capture seasonal and tidal variability (Krask *et al.*, 2022; Steinigeweg *et al.*, 2025). Inundation frequency was defined as the proportion of records exceeding quadrat elevation (metres ODN), and inundation duration as the cumulative hours above this threshold over the same period. These metrics represent flooding at the soil surface and therefore reflect root zone inundation rather than submergence of aerial parts.

Data Analysis

All analyses were conducted in R version 4.3.2 within RStudio (R Core Team, 2024; RStudio Team, 2024). Distributions and correlations among explanatory variables were examined, and model assumptions were evaluated using DHARMA. Where overdispersion was detected, models were refitted with a negative binomial error distribution.

Generalised linear mixed models (GLMMs) tested whether demographic structure and plant health varied with substrate, elevation and tidal inundation. Site was included as a random intercept to account for non-independence among quadrats from the same site. Counts of life stage and health class were modelled with a Poisson error distribution and log link in glmmTMB, refitted with negative binomial error distributions where overdispersion was detected. Total abundance was modelled using zero-truncated negative binomial GLMMs. Stress outcomes were compared between substrates using Wilcoxon rank-sum tests.

Inundation frequency and duration were highly correlated (Spearman $\rho = 0.958$, $n = 180$). To avoid collinearity, they were reduced to a single variable using principal components analysis. The first component (tidal PC1) explained all variance and was used as the inundation covariate in models. For descriptive analyses by life stage both metrics were retained.

To assess whether demographic composition differed between substrates, distance-based redundancy analysis (dbRDA) was carried out on Bray–Curtis dissimilarities using the vegan package. Models included substrate, standardised elevation and tidal PC1 as constraints, and significance was assessed by permutation.

Variance partitioning separated the unique and shared effects of substrate and site on demographic and stress composition using partial dbRDA. Adjusted R^2 values were partitioned into unique substrate, unique site, shared, and residual components. The significance of unique effects was tested using constrained ordination with the alternative factor partialled out.

Geographic confounding was assessed by testing for associations between substrate and spatial coordinates using Welch t-tests. Models were refitted with polynomial latitude and longitude terms plus standardised elevation to control for broad spatial patterns. Within site life stage GLMMs were restricted to sites containing both substrates and included substrate with site as a random intercept. Spatial autocorrelation in residuals was tested with Moran's I using the spdep package.

Model adequacy was assessed using variance inflation factors with values below 3 considered acceptable. AIC was used for model comparison. Statistical significance was assessed at $P < 0.05$, with Benjamini–Hochberg (BH) correction for multiple comparisons where appropriate.

Results

Population size varied among sites, with the largest at Gronant Dunes and the smallest at Bardsea. Mean plant density per quadrat was highest at Plumpton Marsh and Red Rocks, while Hilbre Island contributed the greatest number of quadrats but at lower mean densities. Across all sites, quadrats contained a median of 9.5 plants (IQR 3–25).

Model comparison of total abundance indicated that the model including elevation had the lowest AIC, although elevation was not a significant predictor (IRR = 1.40, 95% CI 0.93–2.11, $P = 0.11$). Mean abundance was higher on sandy soils than on rock (2.14× higher in raw quadrat means), although this difference was not significant in the mixed model (IRR = 1.67, 95% CI 0.79–3.57, $P = 0.18$). Abundance varied widely on both substrates and dense quadrats were more frequently observed on sandy soils. Several sandy quadrats contained more than 50 individuals, whereas fewer quadrats with high counts occurred on rock (Fig. 3A).

In the four sites where both substrates were present, seedlings, juveniles and mature plants were all significantly more abundant on sandy soil (seedlings: $z = 2.00$, $P = 0.046$; juveniles: $z = 2.48$, $P = 0.013$; mature: $z = 2.72$, $P = 0.0065$). Veterans were also more frequent on sandy soils, but this difference was not significant ($z = 1.71$, $P = 0.088$; Fig. 3B–C). Substrate effects were strongest for seedlings, juveniles and mature plants, but weaker for veterans. Life stage composition on sandy soils was dominated by mature plants, with juveniles forming the next largest group, whereas rock quadrats contained proportionally fewer juveniles and seedlings (Fig. 3B). Within site comparisons (Fig. 3C) indicated that the higher abundance on sandy soils was consistent across the four mixed substrate sites, although the magnitude of the difference varied between sites. Seedlings and juveniles were also more abundant in lower elevation quadrats, which are inundated more often, but neither elevation nor tidal PC1 were significant predictors overall (both $P > 0.2$). This pattern was evident in the raw elevation distributions, where lower elevation quadrats tended to contain more young plants, although overlap between occupied ranges was substantial.

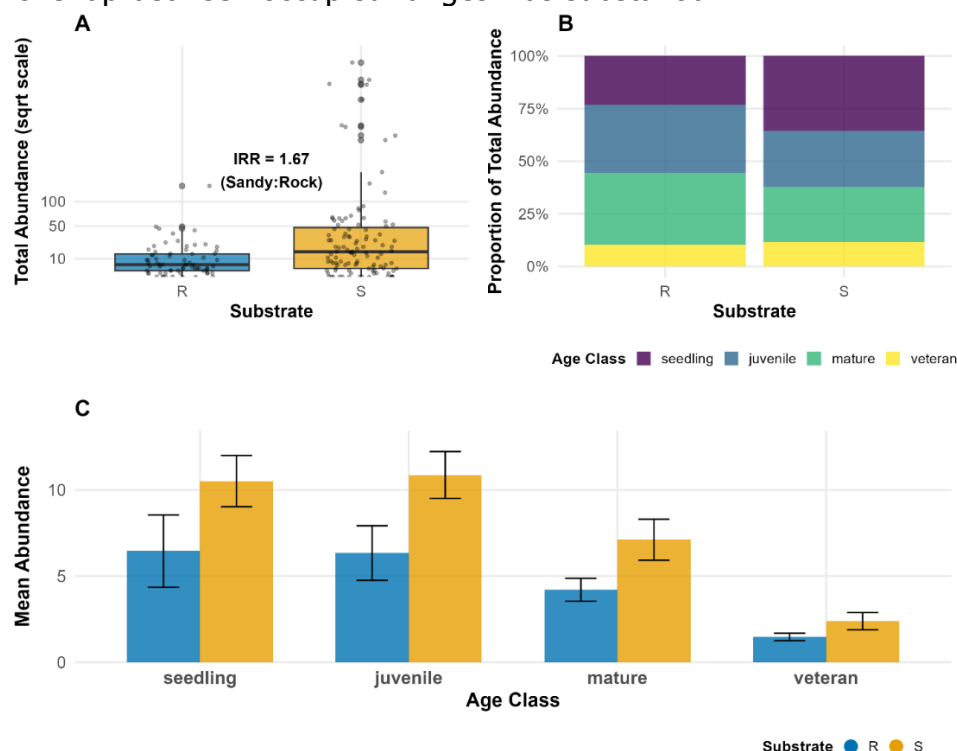


Figure 3. Abundance and demography by substrate. (A) Total abundance per quadrat on rock (R) and sandy soil (S). (B) Mean proportional life stage composition by substrate. (C) Within site comparisons at the four sites where both substrate types occurred, illustrating differences between substrates for each life stage

Substrates were unevenly distributed across the study area (Fig. 4A). Rock quadrats were further north (mean 53.81° vs 53.47°; Welch $t = 6.17$, $df = 117.4$, $P < 0.0001$) and further east (−3.19° vs −3.39°; $t = 2.90$, $df = 137.0$, $P = 0.0043$) than sandy quadrats, while elevation did not differ ($t = 0.91$, $df = 176.2$, $P = 0.37$). As a result, only four of the nine study sites contained both substrate types, while the others were dominated by either rock or sandy soil. Abundance also varied among sites (Kruskal–Wallis $\chi^2 = 27.68$, $df = 8$, $P = 0.0005$).

Ordination analyses revealed strong site level structuring of demographic composition. The NMDS ordination had a low stress value (0.050; Fig. 4B). Substrates differed significantly in the spread of quadrat values (PERMDISP $F = 18.70$, $P = 0.0003$), but not in their average position (dbRDA substrate: $F = 1.62$, $P = 0.082$). Elevation and tidal PC1 were also not significant predictors (both $P > 0.2$). In the dbRDA (Fig. 4C), quadrats from the same site clustered closely, while quadrats from different sites occupied distinct regions of ordination space. Site explained a greater proportion of demographic variation (adjusted $R^2 = 0.39$) than substrate (0.08) or tide (0.12).

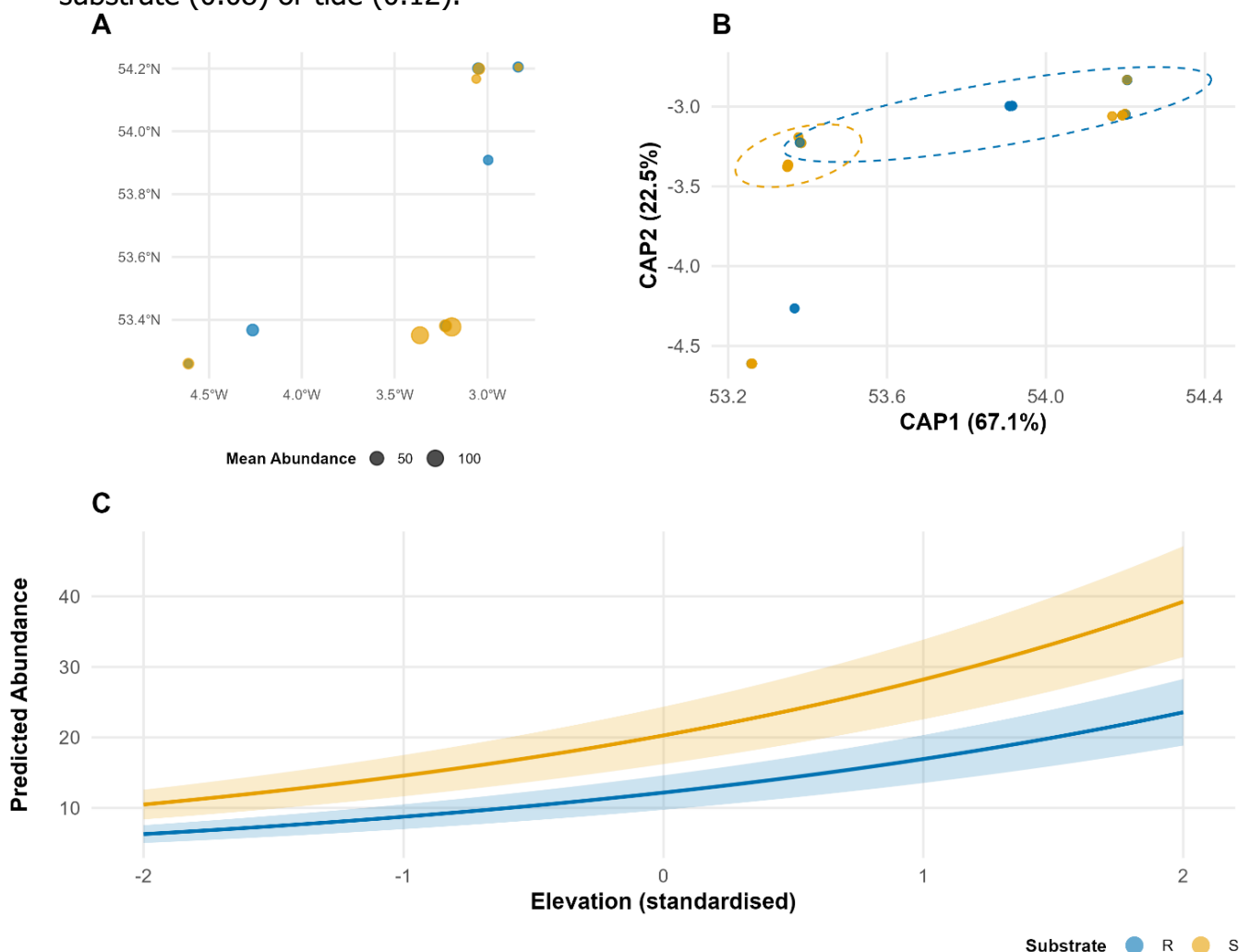


Figure 4. Geographic variation in population structure. (A) Location of quadrats by substrate across the nine study sites. (B) NMDS ordination of quadrats based on demographic composition. (C) dbRDA of quadrats constrained by substrate, elevation and tidal PC1

The proportions of plants in each stress category did not differ significantly between substrates after adjustment for multiple tests (all $P > 0.05$). Before correction, sandy soils had both more healthy individuals and more severely stressed individuals than rock, but these differences were not supported statistically (Fig. 5). Across both substrates, mildly stressed and healthy individuals were the most frequent categories, while dead and severely stressed plants were less common overall (Fig. 5A). Stress distributions were therefore broadly similar between substrates.

Predicted sandy to rock abundance ratios from the GLMMs showed higher abundance on sandy soils. After controlling for latitude, longitude and elevation, the ratio decreased from 2.11 to 1.67, a reduction of 20.7% (Fig. 5B). The sandy to rock ratio therefore decreased after geographic controls were applied.

Predictors were not strongly correlated (all VIF < 3). Residuals from the abundance models showed mild but significant spatial autocorrelation (Moran's $I = 0.098$, $P = 0.016$; model with geographic controls: $I = 0.089$, $P = 0.025$), indicating that the plants were locally clustered. This is reflected in several quadrats containing multiple individuals in close proximity, while other nearby quadrats were sparsely populated.

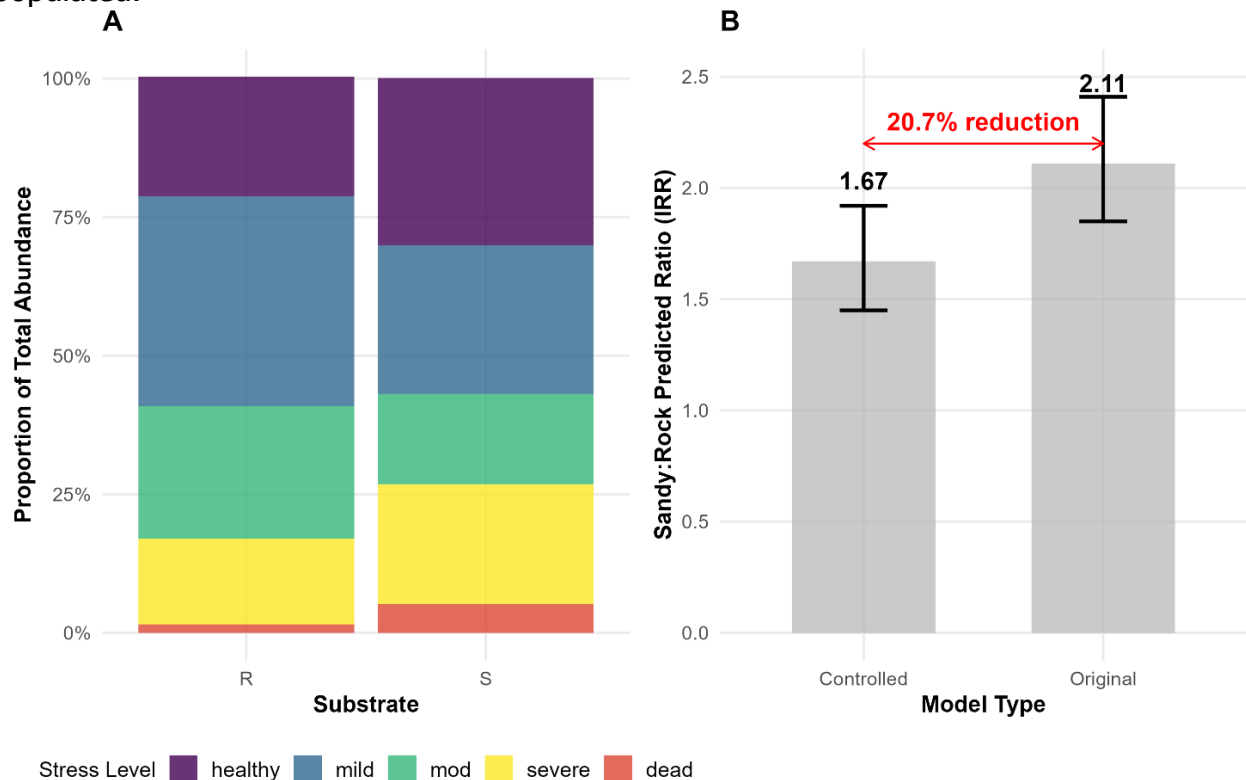


Figure 5. Stress categories and substrate effect adjustment. (A) Proportional distribution of stress categories on rock (R) and sandy soil (S). (B) Predicted sandy:rock abundance ratios from GLMMs with and without geographic controls, illustrating the reduction in substrate effect

Environmental variables explained 28.1% of the variation in total abundance (marginal R^2), increasing to 49.8% when site effects were included (conditional R^2). For demographic composition, the measured variables explained 10.4% of the variation, but this was not significant ($P = 0.28$).

Discussion

This study provides the first complete census of *Limonium britannicum* subsp. *celticum* and shows that demographic structure is shaped by both substrate and site-specific conditions. Fine-scale demographic data add ecological resolution to conservation assessments that are necessarily based on coarse distributional evidence. Recruitment emerged as a key bottleneck, with sandy soil microsites enabling establishment but remaining vulnerable to disturbance, while rocky habitats supported persistence but offered limited opportunities for regeneration. The results also support treating *celticum* as a distinct conservation unit by adding demographic and ecological resolution to its existing recognition within conservation frameworks. By establishing a demographic baseline, this study clarifies how underlying ecological processes constrain persistence and provides evidence to inform targeted management and future monitoring.

Substrate emerged as the most consistent predictor of population structure, with sandy soils supporting higher abundance across seedlings, juveniles and mature plants, while veteran abundance did not differ significantly between substrates. Elevation and tidal predictors explained less variation than substrate, although younger life stages showed a non-significant tendency to occur at lower tidal elevations. Substrate distribution was geographically structured, but site level effects remained substantially stronger than substrate alone, indicating the influence of unmeasured local drivers. Stress scores did not differ significantly between substrates after correction for multiple testing. Populations showed marked spatial clustering, with neighbouring quadrats tending to contain similar numbers of individuals.

Taken together, these findings indicate that while substrate influences recruitment, site-specific ecological processes are critical in shaping demographic outcomes. This highlights the importance of integrating fine-scale environmental variation with broader site level context when interpreting the ecology and conservation needs of *celticum*.

The 2025 Red List notes the absence of evidence for decline and limited information on population size and demographic structure, relying primarily on distributional data and inferred stability to assess *celticum* as Least Concern (Stroh *et al.*, 2025). The range-wide census and demographic analyses presented here therefore complement the assessment by filling recognised evidence gaps, rather than re-evaluating conservation status.

Substrate Effects

Higher abundances on sandy soils are likely linked to ecological differences between substrates. Sandy soils drain more rapidly and are better aerated than rock, reducing periods of anoxia following inundation and facilitating root development in seedlings (Colmer & Flowers, 2008; Allen, 2000). By contrast, plants on rock are confined to fissures with limited rooting volume, where water availability is variable and drainage is poor, constraining both moisture and oxygen supply. Salinity is also likely moderated on sandy soils through leaching, whereas salts can accumulate in rock fissures as pooled water evaporates (Bazihizina *et al.*, 2012; Veldhuis *et al.*, 2019). Although *celticum* is salt tolerant, elevated salinity commonly delays or reduces germination in halophytes, including other *Limonium* species, making salt

accumulation a plausible constraint on recruitment in rocky sites (Cardona *et al.*, 2021; Souid *et al.*, 2024; Dessì *et al.*, 2025).

Disturbance from tides and waves interacts with these substrate conditions. Studies of coastal pioneer vegetation show that hydrodynamic forces can uproot young plants before they become securely anchored, with establishment depending on short periods of reduced wave energy (Balke *et al.*, 2011; Hu *et al.*, 2014). Such disturbance can limit recruitment in unconsolidated sediments, even where conditions otherwise favour establishment (Bouma *et al.*, 2016; Cao *et al.*, 2020). While sandy soils supported higher recruitment in *celticum*, studies of dynamic substrates show that seedling losses can be elevated under tidal disturbance (Balke *et al.*, 2013; Cao *et al.*, 2020).

By contrast, veteran abundance showed no significant difference between substrates, consistent with evidence that established perennials are less constrained by substrate than seedlings. Mature plants persist through extensive root systems and physiological adaptations that buffer against stress across a wider range of microhabitats (Colmer & Flowers, 2008). Similar demographic patterns are reported for *Limonium delicatulum* and other saltmarsh perennials, where recruitment is the critical bottleneck while adult survival is comparatively robust (Hegazy, 1992; Shumway & Bertness, 1992; Bouma *et al.*, 2016).

Stress categories add limited additional resolution to these patterns. Although not significant after correction, sandy soil quadrats included both more healthy and more severely stressed individuals. This pattern is consistent with higher recruitment but also greater exposure to variable stresses such as competition or disturbance, which were not measured here (Allen, 2000; Cao *et al.*, 2020). Rock quadrats supported fewer individuals, with stress scores clustered in intermediate categories. This suggests that while recruitment is restricted, some established plants persist in relatively stable microsites, defined as small-scale patches suitable for establishment and persistence (Eriksson & Ehrlén, 1992). Taken together, this aligns with a broader pattern in coastal plant systems, where recruitment is tightly linked to substrate and microhabitat conditions, while adult plants persist across a wider range of environments (Hegazy, 1992; Pennings & Callaway, 1992; Crain *et al.*, 2004).

Geographic Structure and Site Level Variation

The substrate effect persisted after accounting for geographic structuring, with sandy soils supporting higher abundance, indicating that both habitat and location contributed to demographic patterns. Site level differences were more influential than substrate, pointing to local ecological processes as stronger determinants of population outcomes than broad habitat categories. Roughly half of the variation in abundance was not explained by substrate, elevation or tidal exposure, suggesting the influence of unmeasured local drivers. These may include fine-scale hydrological conditions, soil properties, or management histories such as grazing or coastal defence works, which are recognised influences on saltmarsh vegetation (Bockelmann *et al.*, 2002; Kennish, 2021). More broadly, these drivers reflect the suite of abiotic and biotic processes known to shape saltmarsh demography, including sediment supply, hydrodynamics and vegetation interactions (Ladd, 2021).

Patterns of spatial clustering provide further evidence of localised processes. Spatial autocorrelation analyses confirmed significant clustering, with neighbouring

quadrats showing more similar abundances than expected under a random distribution. Comparison of field observations with previous records suggested that some colonies may persist for only a season or a few years before disappearing, while others had been consistently recorded for over 25 years in the same location with no apparent loss or expansion. Anecdotal reports from site managers and botanists echoed this pattern of short-lived colonies. At two such sites, excluded from analyses having lost their sole populations, loss was attributed to scrub encroachment, a recognised driver of change in coastal vegetation systems (Bockelmann *et al.*, 2002; Kennish, 2021).

Observations of short-lived colonies in some locations and long-term persistence in others, together with spatial clustering, are consistent with studies showing that fine-scale heterogeneity creates shifting mosaics of recruitment and mortality in coastal plants (Shumway & Bertness, 1992; Rand, 2000). This supports the interpretation that populations cannot be understood solely through broad environmental gradients. Their structure reflects a balance between colonisation opportunities and localised loss (Moffett *et al.*, 2010; Steinigeweg *et al.*, 2025).

Taken together, these patterns emphasise the importance of site-specific processes in shaping the demography of *celticum*. Substrate provides the broad framework for establishment, but the ecological realities at each site influence whether populations persist, expand, or contract (Crain *et al.*, 2004; Feagin *et al.*, 2005). This is consistent with broader patterns in coastal plant populations, which are shaped by the interaction of habitat-level gradients and fine-scale local drivers (Allen, 2000; Cao *et al.*, 2020). Recognising this interplay is important for conservation strategies that are both habitat appropriate and responsive to the distinctive conditions of individual sites (Burden *et al.*, 2020; Ladd, 2021).

Conservation Implications

The demographic findings indicate that *celticum* occupies a restricted realised ecological niche, with recruitment strongly shaped by substrate and site-specific processes. Although the 2025 Red List assesses the taxon as Least Concern, that assessment explicitly acknowledges limited information on population size and demographic structure (Stroh *et al.*, 2025). The results presented here therefore provide ecological and demographic resolution that complements the current assessment, without implying elevated extinction risk. The Red List evaluation necessarily relies on coarse-scale distributional evidence accumulated under mixed taxonomic concepts and does not resolve fine-scale demographic variation.

Populations occur largely within existing protected areas, most within SSSIs and many overlapping with other designations. However, Least Concern status and the absence of site-specific demographic information mean that *celticum* is rarely an explicit management focus. Active measures are likely confined to a few sites, while most populations benefit only indirectly from broader habitat protection. Observations of local clustering and the apparent short-lived nature of some colonies suggest that population persistence may be unstable in parts of the range. Recolonisation capacity remains unknown, but evidence from related *Limonium* species suggests dispersal may be limited (Palop-Esteban *et al.*, 2007; Róis *et al.*, 2018). Maintaining extant populations at currently occupied sites should therefore be prioritised.

At the site scale, conservation should prioritise sandy soil microsites, which are critical for recruitment but also vulnerable to erosion and disturbance (Balke *et al.*, 2011; Cao *et al.*, 2020). Rocky substrates can support established individuals but contribute less to regeneration and may be limiting where plants are confined to fissures where weathering can reduce rooting stability. Management should therefore focus on maintaining recruitment opportunities in sandy habitats while safeguarding existing colonies. Because factors influencing persistence vary, monitoring should extend beyond abundance to include life stage composition, providing an evidence base to guide responsive management (Raposa *et al.*, 2020; Kutcher *et al.*, 2022). The largest population observed in the field, at Gronant Dunes, illustrates these dynamics. Plants occupied sandy soil within an intertidal marsh sheltered by a foredune ridge, where reduced tidal disturbance likely sustained recruitment at larger scales than in more exposed sandy sites. This highlights the need for conservation measures to consider geomorphological context alongside substrate.

At regional scale, effective conservation requires safeguarding a network of sites across the current range. This portfolio approach reduces the risk of range contraction and spreads management across different habitat types and histories (Pressey *et al.*, 2007; Baker *et al.*, 2025). Such strategies depend on treating *celticum* as a distinct management unit, informed by its fragmented distribution and site-specific ecological requirements. Earlier aggregate-based treatments obscured these patterns at coarse scales, but recent taxonomic clarification has enabled more explicit consideration of its ecology within conservation planning (Ely *et al.*, 2017). This reflects the wider debate about how taxonomy shapes conservation outcomes (Mace, 2004; Garnett & Christidis, 2017).

Conserving *celticum* has importance beyond its limited range. At the evolutionary scale, it represents an important component of diversity and offers opportunities to explore adaptive potential in a taxonomically complex genus dominated by apomictic polyploids (Ennos *et al.*, 2005; Mace & Purvis, 2007). At the ecosystem scale, it contributes to the taxonomic richness that supports saltmarsh resilience, as diverse assemblages promote root development, nutrient capture and sediment stabilisation, processes that strengthen carbon storage and coastal protection (Allen, 2000; Redelstein *et al.*, 2018; Burden *et al.*, 2020). At the policy scale, these findings illustrate the vulnerability of coastal endemics with narrow distributions to pressures such as erosion, sea-level rise and land-use change. Explicit consideration within conservation frameworks, such as Shoreline Management Plans, is important for supporting long term persistence (Feagin *et al.*, 2005; Martone & Wasson, 2008; Pontee, 2013).

Taken together, these arguments underline the need for conservation strategies that integrate site-specific management, regional networks, and taxonomically informed management units to safeguard *celticum* within the dynamic coastal landscape it inhabits.

Future Research

While this study accounted for the major gradients of substrate, elevation, and tidal exposure, approximately half of the variation in abundance, and most of the variation in demographic composition, remained unexplained. This indicates the influence of additional unmeasured drivers. Likely site-specific contributors include

biotic pressures such as grazing, trampling and scrub encroachment, together with abiotic influences including shoreline management interventions, nutrient enrichment, local hydrology, wind exposure and erosion. These pressures are recognised influences on saltmarsh vegetation but were not quantified here (Bockelmann *et al.*, 2002; Ladd, 2021).

The study represents a single year, which may have influenced recruitment, stress status or phenology. The lower proportional abundance of seedlings relative to juveniles may partly reflect seasonal timing, as the demographic structure reported here represents a single temporal snapshot rather than repeated seasonal sampling. Multi-year monitoring will be required to establish whether the patterns reported here are consistent under contrasting seasonal and climatic conditions. Comparable demographic studies across contrasting coastal settings in other *Limonium binervosum* aggregate taxa would also help determine how widely these patterns apply.

A priority for future work is to quantify unmeasured biotic and abiotic pressures alongside demographic monitoring, to clarify their contribution to population outcomes. Incorporating finer-resolution environmental data, including sediment chemistry, porewater salinity and hydrodynamic exposure, would provide a more complete picture of the abiotic context shaping recruitment and persistence (Ladd, 2021).

The dispersal ecology of *celticum* remains unstudied, despite its importance for persistence in a fragmented range. Evidence from congeners indicates limited seed movement and strong local structuring, consistent with broader saltmarsh studies showing dispersal constrained by tidal gradients (Shumway & Bertness, 1992; Rand, 2000; Palop-Esteban *et al.*, 2007; Róis *et al.*, 2018). Empirical seed fate and colonisation studies are needed to clarify the potential for natural recolonisation.

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