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SPECIAL FEATURE: VEGETATION RESURVEY

Drivers of species richness and compositional change in Scottish coastal vegetation

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Acidification; Eutrophication; Grazing; Machair; Sand dune; Scotland; Succession; Vegetation change

Nomenclature
Stace (2010) for plants

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Abstract

Question: What are the main drivers of vegetation change within coastal dune and machair habitats and are these amenable to action to protect biodiversity at a local and national scale?

Location: Coastal areas of Scotland.

Methods: A national-scale, quadrat-based re-visitation survey was used to assess where changes were occurring in terms of species richness and composition. Regression trees and linear mixed modelling were used to identify the main drivers of change between 1976 and 2010.

Results: There were losses of habitat to erosion (4.7% of previously visited quadrats) and development (2.3%). Species richness changes were largely positive where sand dune and machair habitats remain part of an agricultural management system in the Inner and southern part of the Outer Hebrides. Richness losses were driven by acidic deposition and reduced grazing. Compositional changes were less related to agricultural changes, climate change and pollutant deposition than species richness changes.

Conclusions: Reintroduction of grazing to coastal areas appears to be a policy that would have positive effects on biodiversity, as would continued efforts to reduce atmospheric deposition and coastal planning that allowed for realignment as sediment supply decreases and sea level rise continues.

Introduction

Coastal vegetation, both spatial and temporal, is inherently dynamic. This is partly driven by the balance of erosion and deposition of material by coastal currents, tides, waves and wind, and partly by early successional processes as the vegetation stabilizes coasts that are prograding. These coastal systems are especially valued for the ecosystem service of coastal defence and the cultural services surrounding tourism (Jones et al. 2011). Coastal habitats also support high levels of biodiversity, much of which is restricted to coastal areas. However, these systems are subject to a wide range of drivers that have the potential to affect the extent and quality of these habitats.

Many coastal systems are undergoing reconfiguration, relocation and a reduction in area of intertidal and supratidal habitats (Orford et al. 2007), partly due to a reduction in sediment supply since the early Holocene (Hansom 2001). Sea level rise is affecting the balance of erosion and deposition along the coast, contributing to 'coastal squeeze' (Saye & Pye 2007). In consequence, coastal habitats could be lost as a result of erosion. Losses of habitat area can also result from the direct impacts of building, the development of other infrastructure (often associated with tourism), afforestation and agricultural reclamation (Jones et al. 2011; Malavasi et al. 2013). Whilst unlikely to result in large-scale habitat loss, changing patterns of temperature and rainfall could influence species' ranges and dominance and have the potential to drive vegetation change (Chen et al. 2011; Groom 2013). Similarly, there is the potential for atmospheric deposition to impact both vegetation and ecosystem function (Jones et al. 2004; Remke et al. 2009) via acidification and eutrophication, as coastal habitats are usually nutrient-poor and often have low buffering capacities. Changes can also be driven by local disturbance associated with tourism, including trampling damage from people accessing beaches (Ciccarelli 2014). Finally, local management, principally grazing, has a direct

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impact on the structure and species composition of coastal habitats (Brunbjerg et al. 2014), and changes in grazing management impact directly on habitat structure and species composition (Millett & Edmondson 2013).

Together, these drivers fall along a continuum from those where no intervention is possible (sediment supply), via those that require global intervention (climate change and sea level rise), national intervention (atmospheric deposition, development) and local interventions (management). For effective decision-making concerning coastal conservation, an understanding of which drivers are the most important in shaping changes in the vegetation is necessary. This will ensure that efforts can be directed to changes in policy and to developing methods to mitigate the impact of drivers that cannot be directly controlled by local or national intervention.

This paper takes advantage of a large-scale re-visitation survey of Scottish coastal vegetation to address the overall question of what drivers have produced changes in coastal habitats. The analysis can be divided into two approaches. First, an analysis of the fate of quadrats between the two surveys to assess which drivers have impacted on the loss of area of habitat. Second, and where the main emphasis of the paper falls, analysing changes in species richness and vegetation composition to identify the drivers of vegetation change and assess if these are amenable to local or national modification. This second analysis required quadrat data from both surveys and was carried out on the full data set and three subsets: mobile habitats where the dominant changes may be due to succession, fixed habitats and samples where soil analysis provided additional information.

Methods

Survey data

Plant compositional data were available for the major dune and machair sites within Scotland from two periods; machair is a specific complex of habitats that occur on shell-sand deposits around the western coasts of Scotland and Ireland, and is typified by highly diverse grassland vegetation on free-draining, calcareous substrates (Angus 2001). Baseline data were taken from the Scottish Coastal Survey of 1975 to 1977 (Shaw et al. 1983); the bulk of the survey was carried out in 1976 so this year is used as shorthand for the first survey. A minimum of 30 quadrats (5 m × 5 m) were examined per site, with larger sites having additional quadrats to ensure a density of about 15 km^{-2} across the site. The second resurvey was carried out between 2009 and 2011 (Pakeman et al. 2015); with one site surveyed in 2013 due to issues with safe access (2010 is used as the shorthand for this survey). In total 89 out of the original 94 sites and 3862 out of 4079 quadrats were re-visited, with the fate of each quadrat between surveys recorded. Within sites, quadrats were re-visited in a random order to avoid bias in resampling different habitats. There was not time to resurvey all quadrats visited, and analysis of species richness and compositional change needed vegetation present in both surveys, so the analysis of vegetation change was restricted to 2408 quadrats.

The methods used in the second survey followed those used in the original survey (Shaw et al. 1983). Cover of all vascular plant species (nomenclature follows Stace 2010) was estimated visually, as well as the cover of other classes such as bryophytes, lichens, litter and bare ground within the quadrats. Relocation of quadrat positions was by GPS following the digitization of original sample points on 1:10 000 maps. Relocation was helped by a summary of the 1976 vegetation; a small number of quadrats (five) were not re-surveyed because surveyors were not convinced that vegetation change between the two dates was possible, and consequently a location error must have occurred during one or other survey (e.g. the 1976 survey relied on compass bearings to locate plots). Therefore, the degree of change reported here errs on the side of conservative, an approach shown to be effective for re-visitation studies of non-permanent quadrats (Ross et al. 2010; Kopecký & Macek 2015).

Land use and structure data

A number of simple measures of land use and vegetation structure were assessed in both surveys in the absence of other suitable data; agricultural census data are available at a level that is unrelated to the small sites considered here. The presence and absence of livestock species (cattle, horses and sheep) or their dung was noted; in the analysis this was converted to presence/absence of Livestock (1/0). Grazing was assessed as four categories: heavy (abundant dung, uniformly short vegetation, little sign of litter) = 3; moderate (less uniform sward, some dung and litter) = 2; light (some evidence of dung and removal of vegetation, larger mass of litter and much taller vegetation swards compared to moderate and heavy) = 1; and no grazing = 0. A final land-use driver was whether the site had been in the Environmentally Sensitive Area (ESA) scheme, an agri-environment scheme that was geographically restricted, started in 1987 and closed in 2000 (although some agreements ran up to 2009). The scheme aimed at maintaining extensive agricultural management based on traditional rotational cropping and grazing regimes (Department of Agriculture and Fisheries for Scotland 1989). With respect to this analysis, this scheme covered quadrats in the Inner Hebrides, the southern half of the Outer Hebrides and the Shetland Islands.

Vegetation structure was used as a proxy for the intensity of past management or land use. It was assessed

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separately for forbs, grasses, shrubs and trees in different height classes on a four-point scale; dense cover = 3, moderate cover = 2, light cover = 1, absent = 0. For forbs and grasses the height classes were: 0–20, 20–50, >50 cm, for shrubs 0–50, 50–200 and 200–500 cm, and for trees >500 cm. For analysis these data was aggregated into the following derived variables: Woody – the sum of structure scores for shrubs 50–200 cm, shrubs 200–500 cm and trees >500 cm (scale 0 – 9); Openness – the sum of grass 0–20 cm and herb 0–20 cm rescaled so that 0 represented closed ground vegetation and 3 open sand (i.e. 3 minus the sum of cover); and Density – as the sum of all herbaceous and short shrub layers (0–20, 20–50, 50–200 cm) with a maximum of three per layer (scale 0–9). The cover of Bare ground and Litter from the quadrat survey were also used as descriptors of vegetation structure.

Soil data

Soil parameters were assessed for one 5-cm diameter core of 5-cm depth taken from the centre of each quadrat. Measures assessed were soil pH (in water); soil inorganic and organic carbon (by acidification with phosphoric acid and heating to 720 °C, respectively, measuring with a non-dispersive infra-red detector; Shimadzu TOC-VCSH, Milton Keynes, UK); total N (Thermo FlashEA 1112 elemental analyser; Thermo-Fisher, Waltham, MA, US); and extractable Ca, Mg, K and P (using acetic acid extraction followed by inductively coupled plasma optical emission spectroscopy (ICP-OES). The C to N ratio was calculated as the ratio of organic C to total N. Due to cost, only a proportion of soils were analysed. The choice was randomized within sites and resulted in 1411 quadrats available for analysis.

Climate data

Climate data were taken from the UKCP09 5 km × 5 km gridded data (Perry & Hollis 2005) for 1960–2010. The monthly data were averaged (Mean temperature) or summed (Total precipitation) to give yearly values. To account for variable and changing climate, averages of annual values for the 15 yr prior to each survey period were calculated (1961–1975 for 1976, 1995–2009 for 2010). Fifteen years allowed for differences to occur between the sampling periods but reduced the influence of exceptional years. The gridded data were limited to grid cells with significant land present, so grid cells without data were assigned the average of adjacent coastal cells with values.

Pollution data

Modelled cumulative total N and SO_x deposition on a 5 km × 5 km grid for the period between 1850 and the surveys (1976–2010) were obtained from the CBED model (Smith et al. 2000) using historical scaling factors (Fowler et al. 2004) on a base year of 2005 (range 3.2–13.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$). As for climate, grid cells with little land present had no values for deposition and were assigned the average of adjacent coastal cells with values.

Data analysis

First, the state of each quadrat in 1976 and 2010 (vegetated, not vegetated, inaccessible, development, cropped, below mean high water springs, etc.) was tabulated to show the overall picture of the loss of area of machair and sand dune between the two surveys; this could not be further analysed statistically.

The subsequent analysis focused on numeric changes in species richness (the number of vascular plant species recorded per 5 m × 5 m) and the change in the position of individual quadrats in ordination space between the two sampling dates (1976 and 2010). The latter was produced by ordination of the cover data in Decorana (Cornell University, Ithaca, NY, US) in the vegan package in R v 3.2.0 (R Foundation for Statistical Computing, Vienna, AT), with log transformation of abundances and rare species down-weighted (Pakeman et al. 2016). Different subsets of the data were analysed in addition to the full analysis (Full: 2408 quadrats), including data from: only non-mobile (i.e. fixed) habitats, as mobile habitats such as strandline and mobile dunes will show increased species richness as a result of succession following dune stabilization (Fixed: 2151); mobile habitats, to assess if only successional process are driving richness here (Mobile: 257); quadrats where relevant soil analysis had been undertaken (Soil: 1411).

Potential environmental drivers examined were of three types: the change in the level of a parameter between the two survey dates, cumulative values for the deposition data or a single value for the parameter. The last group was made up of values that were fixed, e.g. in the ESA scheme area, or were available at only one date, e.g. the soil data.

A regression tree approach was taken to separately analyse the species richness and the axes from the ordination. This non-parametric method allows for the possibility that different environmental drivers could have determined change in different subsets of the data (Jackson et al. 2012). Previous analysis suggested that some vegetation changes were highly restricted geographically (Pakeman et al. 2016), so this approach was selected because it gave the possibility of detecting the localized action of drivers. As the data were surveyed from specific sites and site-level changes may not be covered by the drivers analysed, this inherent structure in the data had to be accommodated in the analysis using a regression tree method that allowed

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for random factors: REEM-tree (Sela & Simonoff 2012) in R v 3.2.0. This uses a binary recursive splitting algorithm based on maximizing the reduction in sum of squares for a node. Splitting continued if a split decreased the overall lack of fit by a factor of cp (this complexity parameter was set to 0.001) and 20 samples were present at the node for splitting. This initial tree was then pruned based on tenfold cross-validation, with the final selected tree corresponding to the one with the largest cp value with a tenfold cross-validated error that was no more than 1 SE above the minimized value. The models were fitted with residual maximum likelihood, with the potential environmental drivers as fixed effects and site as a random effect. Error tolerance was set to 0.001 (convergence limit set as the difference between the likelihood of the linear models of two consecutive iterations), and the maximum number of iterations was set to 1000.

As a contrast to the parsimonious regression tree approach, the data were also subject to multi-model inference to investigate the weight of evidence surrounding individual drivers (Burnham & Anderson 2002). Mixed models with the same design as the regression tree analysis were fitted using nlme (http://CRAN.R-project.org/package=nlme), with the best supported models identified with the bias-corrected form of Akaike's information criteria (AICc) and multi-model inference carried out using MuMIn (http://CRAN.R-project.org/package=MuMIn) within R. This approach cannot deal with missing data as it means different models have different sample sizes, therefore the analysis was run separately for the full data set without the soil variables (Full) and for the quadrats where soils analysis had been done (Soil). Models within a ΔAICc < 4 were compared using model weights and model averaging carried out using the zero method – where a parameter estimate of zero is used in models where that parameter is absent in averaging over all models in the top model set so as to decrease the effect sizes of predictors that do not occur in all models (Burnham & Anderson 2002). The intention was to compare the importance of different drivers (Nakagawa & Freckleton 2010) rather than to select the single best performing model.

Results

Fate of quadrats

There was evidence of a role for coastal processes and development in the fate of vegetation on Scottish coasts (Table 1). First, a number of previously vegetated quadrats (176, 4.9%) were not recorded as they were below the high tide line, and of the small number of quadrats recorded as below the high tide line in 1976, 22.4% had developed vegetation (11 out of 49). There was a substantial increase in the number of quadrats where development had replaced the original vegetation (34–112); including replacement by new buildings, but the majority was associated with golf courses (e.g. fairways and greens). Some previously developed areas had revegetated after disturbance or due to a shift in the management of golf courses allowing unsown vegetation to develop. There was also a reduction in cropped area on the machair, which is in line with interview data from this region (Pakeman et al. 2011).

Vegetation change

The ordination showed clear, and long, gradients (Appendix S1). Axis 1 appeared to be a pH gradient (Appendix S1a); with species of acid soils such as *Calluna vulgaris* and *Potentilla erecta* at high values and species characteristic of lime-rich soils, such as *Daucus carota* and *Thalictrum minus*, at low values. Axis 2 appeared as a wetness gradient; species of damp areas (*Carex nigra* and *Plantago maritima*) showed low values and species of dry areas showed high ones (*Ammophila arenaria* and *Campanula rotundifolia*). Axis 3 represented a fertility gradient (Appendix S1b), species of infertile soils with high values (*Koeleria macrantha* and *Thymus polytrichus*), and species of richer soils with low values (*Arrhenatherum elatius* and *Ranunculus repens*). The gradient represented by Axis 4 was not interpretable and was not considered further (Pakeman et al. 2016). Axis 1 explained substantially more variation than the other axes: eigenvalues Axis 1 = 0.402, Axis 2 = 0.283, Axis 3 = 0.184, Axis 4 = 0.133.

The resultant tree from the analysis of species richness of the Full data revealed a mix of large-scale and small-scale factors influencing the change in species richness (Fig. 1a). Species richness changes have largely been positive in the warmer sites, but only if they were in the area previously designated as ESA (compare Fig. 2a,b) and quadrats had not seen a substantial increase in the amount of bare ground. Richness changes in the left hand side of the tree were mixed, but generally negative where litter had increased, where bare ground had increased substantially and where livestock numbers had dropped. Where bare ground had substantially declined there were large increases in richness. Comparison of deviances of the root model and the fitted model give a pseudo-R^2 of 0.301 (McFadden 1974). Vegetation compositional change was not explained by any of the potential drivers included in the regression tree analysis for the three axes examined.

The initial divide in the analysis of species richness for the Fixed data was the same (Fig. 1b) and the pseudo-R^2 of 0.278 similar. However, richness changes were most positive for sites that showed only the lowest Mean temperature changes over the interval between surveys (Fig. 2c) and no increase in Openness. Where Mean temperature

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Table 1. Fate of the quadrats originally surveyed in 1976. 'Inaccessible' includes quadrats in dense forestry or gorse (*Ulex europaeus*), on tidal islands without safe access and within Ministry of Defence compounds; 'Cropped' areas were not entered to prevent damage to growing crops; MHWS mean high water spring; No reason was given for not recording on 15 of the original data sheets.

	Status 2010								
	Vegetated	Not Vegetated	Inaccessible	Development	Cropped	Below MHWS	Not Visited	Not Found	Total
Status 1976									
Vegetated	3167	15	84	86	44	176	206	5	3783
Not Vegetated	16			1		1			18
Inaccessible	15		19	1	5				40
Development	11			22		1			34
Cropped	86			1	47	1	5		140
Below MHWS	11					37	1		49
No Reason Given	13		1	1					15
Total	3319	15	104	112	96	216	212	5	

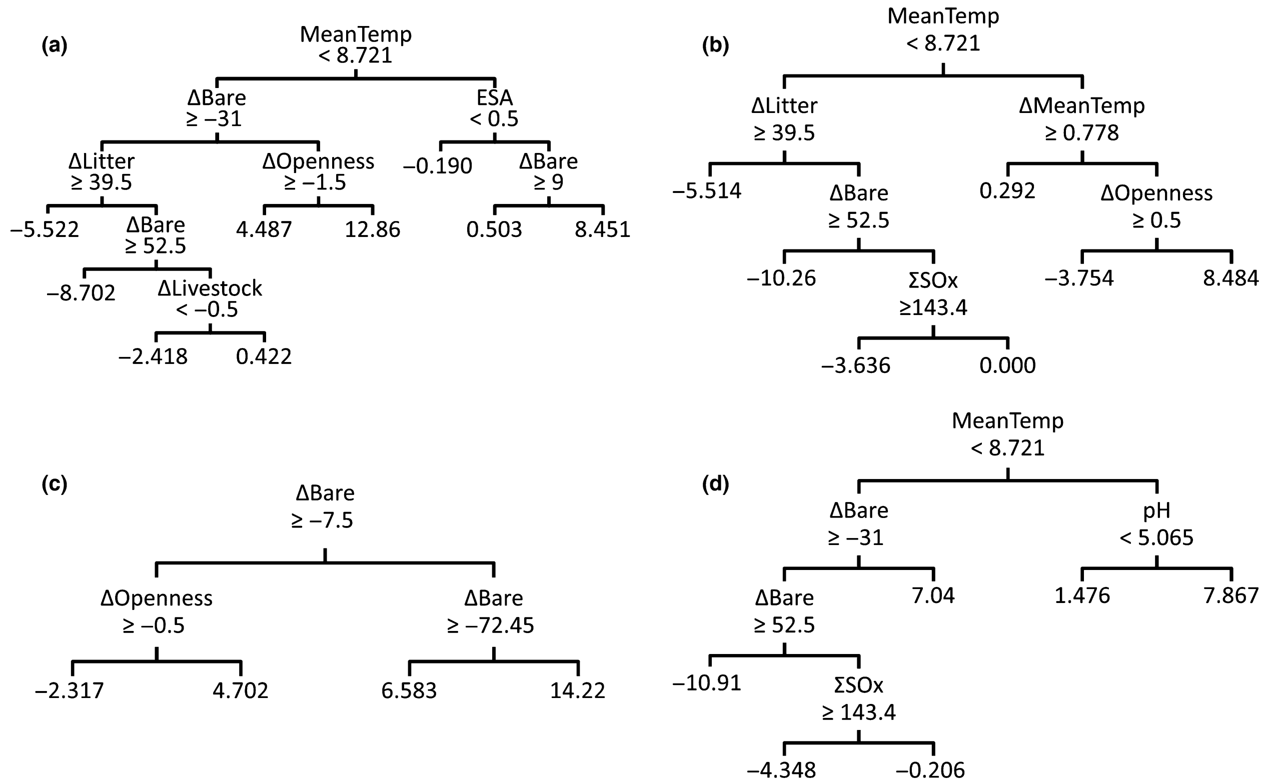

Fig. 1. Regression trees from the analysis of species richness for (**a**) the Full data set, (**b**) data from dune habitats that were considered as Fixed in 1976, (**c**) data from Mobile habitats in 1976, and (**d**) from quadrats with soil data available. If the condition given at each branch point is met, then the left hand branch is taken. Terminal numbers represent the change in mean species richness of the quadrats fulfilling the conditions leading to that terminal node. MeanTemp is mean annual temperature (°C), a positive Δ represents a positive change in a variable from 1976 to 2010, and Σ represents the cumulative amount of that variable between the two surveys.

changes were higher, only small average gains in species richness were made. For cooler sites (left hand side of the tree), species richness changes were negative except where Litter increases were small, Bare ground increases were small and where cumulative deposition of SO_x was low (Fig. 2d). Changes in species richness in the Mobile habitats were positive except in quadrats where the amount of bare ground had increased (wave or wind erosion) and the Openness of the vegetation had stayed the same or increased (Fig. 1c). The pseudo-R^2 was higher for this subset of the data, at 0.387. As for the full data set, compositional change was not explained by any of the

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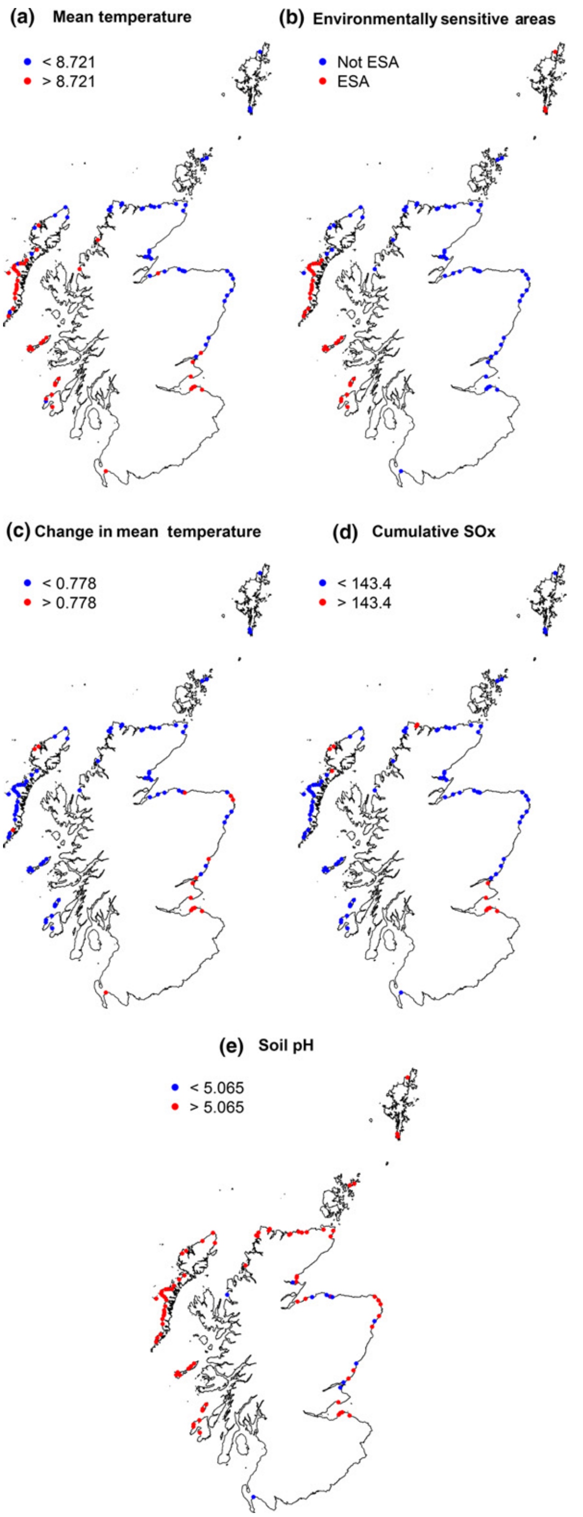

Fig. 2. Site means for the large-scale drivers of change: MeanTemp mean temperature °C, ESA Environmentally Sensitive Area, delMeanTemp change in mean temperature between 1961 to 1975 and 1995 to 2009, cumSO_x accumulated oxidized sulphur deposition between 1976 and 2010 and pH soil pH.

potential drivers included in the regression tree analysis for either the Fixed or Mobile data.

The driver producing the initial divide for the Soil species richness data was the same as the Full and Fixed data (Fig. 1d), although the pseudo-R^2 was smaller at 0.259. Positive changes in species richness were a feature of warmer sites, particularly those with high pH soil (Fig. 2e), and cooler sites where Bare ground decreased most. Falls in species richness were particularly associated with sites where Bare ground had increased most and where cumulative SO_x deposition was higher. Similar to the other analyses, no trees were returned from the ordination data analysis for the three axes examined.

The multi-model averaging of the Full species richness data was restricted to seven models within an AICc of 4 of the best model (Table 2), with a mean pseudo-R^2 of 0.357. There was strong support for the inclusion of negative relationships between species richness and changes in Bare ground, Litter and Openness, and positive relationships between richness and changes in Grazing and Livestock, as well as for the sites having a higher level of Grazing in 1976 and being in the ESA. There was moderate support for negative changes in species richness where the vegetation was already dense or had a high percentage of woody cover in 1976. There was less support for the inclusion of changes in Density (positive impact on richness) and Woody cover (negative), as well as for quadrats that were from Tall vegetation (positive) and Open vegetation (negative). Species richness changes were also higher on warmer sites, but again with lower support.

The number of good candidate models explaining movement along both Axes 1 and 2 for the Full data set was high, 103 and 61, respectively, whilst those for Axis 3 were more consistent with only two models selected. For Axis 1 there was good support for increased woody vegetation driving the vegetation to be more characteristic of acid soils, while an increase in Bare Ground, higher cumulative SO_x deposition and being in the ESA drove vegetation to be more characteristic of basic soils (Table 2). Other drivers were less supported, but an increase in Litter and in Livestock were correlated to a movement towards vegetation more characteristic of acid soils. For Axis 2 there was good support for increases in Bare ground, Litter, vegetation Density and Openness in driving vegetation towards that more characteristic of wetter soils. There was less support for an increase in Woody vegetation driving quadrats towards wetter conditions, as well as for being in the ESA, a warmer climate and higher N deposition driving quadrats towards drier conditions. Increased Litter, Woody, Dense and Open vegetation, alongside cumulative SO_x deposition and warmer climate, drove the vegetation towards a less fertile type along Axis 3, while increased Grazing and higher rainfall drove the quadrats towards vegetation more

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Table 2. Summarized model averaging results for the multi-model inference of species richness and the movement of quadrats in ordination space for the Full data set. Estimates of parameter slopes are shown along with a summary of *P*-values, ***$P < 0.001$, **$0.001 \le P < 0.01$, *$0.01 \le P < 0.05$ and importance scores (sum of the Akaike weights over all of the models in which the term appears).

	Species Richness		Axis 1		Axis 2		Axis 3	
	Estimate	Importance	Estimate	Importance	Estimate	Importance	Estimate	Importance
Intercept	−0.810		0.198		0.213		0.353	
ΔLitter	−0.067	1	0.0004	0.42	0.002***	1	−0.002***	1
ΔBare	−0.096	1	−0.008***	1	0.004***	1		
ΔOpenness	−1.537	1	0.004	0.24	0.121***	1	−0.026	0.73
ESA	5.434	1	−0.123*	1	−0.040	0.58		
Mean Temp	0.090	1	0.010	0.23	−0.017	0.35	−0.068**	1
ΔWoody	−0.077	0.14	0.119***	1	0.008	0.37	−0.073***	1
ΔDensity	0.032	0.15	0.001	0.24	0.025***	1	−0.021***	1
ΣSO_x			−0.002*	0.98	0.00008	0.14	−0.001***	1
ΔGrazing	1.074	1	−0.000007	0.14	−0.0004	0.09	0.005	0.27
ΔLivestock	1.267	1	0.0010	0.34	−0.0007	0.09		
Total Rain			0.000004	0.15	−0.00005	0.18	0.0002***	1
Grazing	0.853	1						
ΣN			−0.00006	0.26	−0.0001	0.47		
Density	−0.199	0.71						
ΔMean Temp			−0.009	0.15	−0.052	0.23		
Woody	−0.463	0.27						
Tall veg	0.038	0.09						
Openness	−0.040	0.07						

characteristic of fertile sites. For all three axes the models explained only low levels of variance, with pseudo-R^2 of 0.128 for Axis 1, 0.076 for Axis 2 and 0.087 for Axis 3.

The multi-model averaging for the species richness data from the Soil data was restricted to eight models (Table 3) with a mean pseudo-R^2 of 0.349. A number of variables were consistently present in all models, Soil C:N and changes in Bare Ground and Litter (negative), and ESA, pH and changes in Livestock (positive). Four other drivers were selected for some models with varying degrees of importance: Soil C and Openness (negative), and changes in Vegetation density and Grazing (positive).

Again, the number of good candidate models explaining the movement of quadrats in ordination space was high: 49, 89 and 103 for Axes 1, 2 and 3, respectively. There was good support for increased Bare ground and higher cumulative SO_x deposition being characteristic of movement towards more basic conditions on Axis 1, and this was associated with soils with high calcium content (Table 3). Increased Woody vegetation drove movement towards vegetation of more acid conditions, and this movement was more pronounced on soils with higher pH. There was also good support for increased Bare ground, Litter, vegetation Density and Openness being linked to vegetation becoming more characteristic of drier ground, and moderate support for a similar movement from quadrats on soil with high soil C:N ratio. There was moderate support for quadrats with a warmer climate, shifting composition to vegetation more characteristic of wetter sites. Quadrats shifting to more fertile conditions along Axis 3 were those with increased Woody and Dense vegetation, as well as those with increased Litter. There was also good support for sites with higher rainfall shifting towards wetter conditions. As for the analysis of the Full data set, all models explained low levels of variance, with pseudo-R^2 values for Axis 1 of 0.141, Axis 2 of 0.069 and Axis 3 of 0.099.

Discussion

Fate of quadrats

The re-visitation of a relatively small number of fixed points is not an ideal way to monitor the coastal processes of erosion and deposition, especially as quadrats were not sited deliberately in positions below the high tide line to assess coastal progression. However, over a 34-yr period, the surveys revealed considerable changes in the area of coastal habitats (Feagin et al. 2005; Schlacher et al. 2007). There has been a continued loss of land to development, and in particular golf courses, despite most of the sites surveyed being relatively remote from the main areas of population in Scotland. There has also been a loss of sample points to coastal erosion, in line with the outpacing of post-glacial uplift by sea level rise (Rennie & Hansom 2011).

Table 3. Summarized model averaging results for the multi-model inference of changes in species richness and the movement of quadrats in ordination space for the Soil data set. Estimates of parameter slopes are shown along with a summary of *P*-values, $***P < 0.001$, $**0.001 \le P < 0.01$, and importance scores (sum of the Akaike weights over all of the models in which the term appears).

	Species Richness		Axis 1		Axis 2		Axis 3	
	Estimate	Importance	Estimate	Importance	Estimate	Importance	Estimate	Importance
Intercept	−4.503		0.049		0.136		−0.028	
ΔBare	−0.095	1	−0.008***	1	0.004***	1	−0.00009	0.17
ΔLitter	−0.080	1	0.0003	0.26	0.001	0.81	−0.003***	1
ΔDensity	0.282	0.8	0.000005	0.06	0.022**	1	−0.019***	1
Soil pH	0.877	1	0.039	0.99	0.002	0.35	0.007	0.45
ΔWoody			0.157***	1	0.002	0.13	−0.078***	1
ΔOpenness	−0.852	0.8	0.003	0.12	0.095***	1	−0.0008	0.08
Soil C:N	−0.0168	1	−0.00003	0.12	0.0003	0.76	0.000004	0.06
ESA	5.358	1	−0.043	0.43	−0.003	0.08	0.019	0.25
ΔLivestock	1.434	1	0.009	0.23	−0.0002	0.03	0.022	0.12
ΣSO_x			−0.002	0.94	−0.000007	0.03	−0.0003	0.38
Soil Ca			−0.000001**	1	−0.00000008	0.16	−0.00000003	0.12
ΔGrazing	0.599	0.92	0.0007	0.08	−0.003	0.18	0.0005	0.08
Total Rain			0.000001	0.07	−0.000006	0.08	0.0002**	0.98
Soil C	−0.034	0.48	0.00009	0.07	−0.0008	0.34	0.0004	0.2
ΔMean Temp			−0.002	0.06	−0.260	0.63	−0.0132	0.1
Mean Temp			−0.0008	0.09	−0.0005	0.03	−0.028	0.48

Species richness changes

The regression tree analysis revealed a mixture of large-scale and small-scale drivers affecting species richness. The largest scale driver, Mean Temperature, was selected in all analyses except for the Mobile data. It largely separates the southeast, southwest and western sites from the eastern, northeastern, northwestern and northern sites. The next division on the right hand side of the trees (ESA, temperature change, soil pH) generally divided this region so that the area showing the largest increases in species richness were the southwest and western sites – i.e. the Inner Hebrides (Coll, Colonsay, Islay and Tiree) and the southern Outer Hebrides (Benbecula, North and South Uist). These islands comprise core areas for machair habitats with its high pH shell-sand substrate, have not shown the same temperature increases as the southeastern sites (Pakeman et al. 2015), and were previously part of the Argyll Islands and the Uist Machairs ESAs. The analysis also picked up that SO_x deposition, highest for the southeastern sites, had a negative impact on richness for some models. Small-scale drivers, i.e. those without a regional or national pattern, showed that richness increased with succession, i.e. less bare ground, but that it was reduced when grazing was reduced and litter was allowed to build up.

The linear mixed model analyses also highlighted the ESA and soil pH as positive, large-scale drivers of species richness. They also picked up similar small-scale drivers, i.e. increased litter and reduced grazing negatively affecting richness (competitive dominance, shading), and a reduction in bare ground (succession/colonisation) positively affecting richness. Overall, the regression tree models were more parsimonious than the LMM, but at the cost of explaining a little less variance: 0.301 vs 0.357 for the Full dataset and 0.259 vs 0.349 for the Soil dataset. However, the regression tree analysis should be more robust in dealing with potential correlation between the large-scale drivers such as temperature, pollutant deposition and the coverage of the ESAs.

Compositional changes

Modelling changes in vegetation composition was less successful and levels of explained variance were low, although there was a high degree of consistency between the modelling of the Full and Soil data sets as the main axes of the ordination largely represent abiotic environmental gradients. Land-use change, climate change and atmospheric deposition are unlikely to shift vegetation composition along these mainly soil-influenced gradients. Some relationships were interpretable, including the increased dominance of Woody species driving vegetation towards a more acidic type as a number of sites have seen increased dominance of planted and self-sown conifers (Pakeman et al. 2015). Also, the negative relationship between increasing bare ground and Axis 1 captures the acidification processes that occur during dune stabilization (Salisbury 1942). However, the negative relationship with cumulative SO_x deposition is opposite to the expected impact of acidification on the vegetation; this may be an

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artefact of the data, represent an underlying relationship between the spatial patterns of SO_x deposition and an unknown variable or it may represent recovery from acidification, as sites with the highest cumulative SO_x deposition have seen the largest falls in yearly deposition (Curtis & Simpson 2014). For Axis 3 the relationship between increased woody cover and more impoverished soils may also relate to the increased cover of conifers on some sites. Similarly, increased cover of Litter and higher levels of cumulative SO_x may also reduce site fertility. There were weak links between total N deposition and Axes 1 and 2 (Jones et al. 2004; Remke et al. 2009), but none with the expected Axis 3. Grazing changes appeared to have only a weak influence of driving vegetation change along the three major axes of the ordination, in contrast to the findings of Plassmann et al. (2010).

Drivers of change in Scottish sand dunes

Integrating across all the analysis a number of patterns can be identified:

1. As dune vegetation develops from an open strandline, through *Ammophila arenaria*-dominated mobile dunes into fixed dune and other vegetation types there is an accrual of species (Salisbury 1942). The reverse was true for quadrats where blow-outs or other erosion processes had occurred. Continued succession to shrub- and tree-dominated vegetation had a negative impact on species richness.
2. Sites still part of a farming system showed positive gains in diversity. These are concentrated in the Inner and southern parts of the Outer Hebrides (Pakeman et al. 2011) and were covered by the ESAs. The direct impact of the ESA scheme was short-lived, but the two areas were selected because of the link between traditional crofting/farming and the high nature value of the agricultural habitats, in contrast to the loss of integration of coastal habitats from agricultural management evident on the east coast of Scotland. The ESAs may have had a positive impact on land manager attitudes to conservation (Lewis et al. 2014), and have also been the focus of specific schemes targeted, for example, at corncrake and great yellow bumblebee conservation (Beaumont & Housden 2009).
3. Grazing appears beneficial to species richness. The direct measures, Grazing and Livestock, were both strongly correlated to increased species richness, while increased litter contributed to reduced diversity. Experimental studies of grazing at single sites show the same pattern (Plassmann et al. 2010; Millett & Edmondson 2013; Brunbjerg et al. 2014). Disturbance appears to be necessary to maintain diversity in dune systems (Brunbjerg et al. 2015).
4. A mixture of large-scale and small-scale drivers appeared to be affecting species richness and, to a lesser extent, vegetation composition change. Some are natural geomorphological processes driving succession and are hence difficult to modify. However, anthropogenic drivers include a regional scale: one representing continued agricultural management, as well as an impact of SO_x deposition. Small-scale drivers are linked to management; grazing is a positive driver of richness while succession to woody vegetation and litter build up in the absence of grazing was deleterious (Plassmann et al. 2010).

Conservation of coastal dunes

The analysis of the fate of quadrats revealed that the scale of fluxes is not trivial, and particularly negative as a result of development. The vegetation data revealed that the main positive driver for diversity was continued grazing management: machair and dune areas on the west coast islands provide essential winter grazing (Pakeman et al. 2011). On the east coast, many of the adjacent farms are engaged in arable agriculture and hence do not have the wherewithal or need to graze adjacent dunes. This also seems to be an increasing problem for sites on the north coast and the northern Outer Hebrides (Harris and Lewis). However, part of the increase in diversity could be due to the spread of generalist species at the expense of more specialist coastal species (Lewis et al. 2014).

Conservation of dune habitats could be enhanced by local or national policies to encourage appropriate grazing. Reductions in SO_x pollution have been considerable (RoTAP 2012), but it is unknown how long it will take for recovery to take place. Climate change and N deposition appear to be less important than management for diversity, the latter appears to affect ecosystem function rather than diversity at the levels experienced in Scotland (Pakeman et al. 2016), while climate change appears to increase species turnover (Lewis et al. 2015). Development pressures will continue for coastal areas (Jones et al. 2011), although on-going coastal realignment and sea level rise may reduce this pressure in the long-term as development is restricted in areas at risk of erosion and flooding. Policy decisions regarding the coastal zone will produce benefits for conservation if they focus on management, pollution reduction and providing space for coastal processes to realign the coast where possible.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Ordination biplots of plant species from Decorana analysis.