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Linking functional traits and species preferences to species' abundance and occupancy trends through time to identify habitat changes in coastal ecosystems

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ABSTRACT

Coastal habitats are rich in biodiversity and provide highly valued ecosystem services. However, they are subject to many environmental drivers that can have severe impacts on these inherently fragile ecosystems. A resurvey approach was used to assess changes in species' abundances and occupancy on sand dunes and machair in Scotland, UK to assess how this could impact on this set of habitats. These were assessed to see if increasers and decreasers shared common trait values, if trends were similar to other terrestrial habitats and if responses to environmental drivers were modulated by traits. In general, there has been a shift towards taller species with more exploitative growth forms and an increase in indicators of unfavourable habitat condition according to criteria for assessing sites designated for nature protection as part of the EU Natura 2000 network, particularly tall grasses characteristic of nutrient-rich conditions exemplified by *Arrhenatherum elatius*. Coastal heathlands have been particularly affected by the increase in species such as *Betula* spp. and *Pteridium aquilinum* which can dominate and exclude other heathland species. On average, increasing species were both more common nationally and increasing nationally, suggesting increasing homogenisation between sand dunes/machair and other terrestrial habitats. Changes have been faster and more negative in conservation terms in cooler, drier and more polluted sites (mainly on the east coast of Scotland) and also in sites which had seen reductions in grazing. Reinstating grazing could counteract some of the negative impacts of eutrophication, but this could prove problematic to integrate with recreational activities and the largely arable based farming systems adjacent to these sites.

1. Introduction

Coastal ecosystems, such as sand dunes and machair (a species-rich habitat complex found on shell sands on exposed coasts in Scotland and Ireland), deliver highly valuable ecosystem services that are far more important to society than the limited area they cover would suggest (Jones et al., 2011). The service of coastal defence and the cultural services surrounding tourism and recreation are particularly valuable to society. They also provide habitats for many specialised and rare species (May, 1988). However, ecosystems on soft coasts are inherently fragile due to the juxtaposition of drivers such as sea level rise, increased storminess and changes in sediment supply, as well as more local drivers such as development, changing land use and pollution, and the lack of buffering capacity in the soil and poor soil structure that allows these drivers to have severe impacts. Thus, sand dunes have been seen to be negatively impacted by coastal reconfiguration, relocation and a reduction in area of intertidal and supratidal habitats (Orford et al., 2007), largely driven by falling sediment supply since the last glaciation (Hansom, 2001) and coastal squeeze as a result of climate driven sea level rise (Saye and Pye, 2007). These large-scale processes, coupled with increased coastal development (Jones et al., 2011), drive a loss in area of these coastal habitats, whilst climate change (Chen et al., 2011; Groom 2013), continued atmospheric deposition (Jones et al., 2004; Remke et al., 2009) and land use changes (Brunbjerg et al., 2014; Millett and Edmondson, 2013) impact more on the composition of vegetation and its ability to respond to changing environments.

In order to manage these fragile and valuable systems for a sustainable delivery of key ecosystem services, it is necessary to understand their dynamics, and in particular the dynamics of the species which make up these habitats (Milligan et al., 2015). If species' trends can be assessed, then it offers the potential to understand both what is driving the dynamics of the system and the potential impacts of those

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species' trends on the rest of the system based on the autecology of the species changing. These trends in individual species can be synthesised and made more general through analysing if those species increasing (i.e. 'winners') and those decreasing (i.e. 'losers') possess different attributes or different trait values (Lavorel and Garnier, 2002) or if their environmental preferences differ (Diekmann, 1995; Smart et al., 2003). These trends can be assessed as part of the overall change in habitat quality, but if drivers differ across space, then dividing this space up into regions characterised by different levels of drivers or driver combinations allows for a finer scale understanding of change (Pakeman et al., 2017) and a more precise ability to predict the impact of future changes on biodiversity and ecosystem services.

Coastal habitats make up only a small proportion of the land area of most countries and are usually distinct from those that occur inland. Given that some of the drivers operating are not important in inland systems (e.g. those relating to coastal processes), there is potential for species' trends in coastal habitats to be different from those of species characteristic of inland systems. Hence, an important check is to assess whether trends in coastal habitats are in parallel or in opposition to national trends (Ozinga et al., 2009). If similar, and if increasers are dominated by common species, it is possible that biotic homogenisation (McKinney and Lockwood, 1999; Smart et al., 2006) is occurring between coastal and inland systems.

Using a resurvey approach based on species composition data from quadrats, the aim of this paper was to understand how sand dune and machair habitats have changed by addressing the following questions: 1) which species in which habitats have increased and decreased? 2) did increasers, and in-turn decreasers, share common trait values, attributes or environmental preferences? 3) did species' trends within coastal systems match those across the rest of Great Britain? 4) were trends towards habitats in better condition? and 5) were the responses of species to environmental drivers modulated by their traits?

2. Methods

2.1. Survey data

Trends in the commonness of species were assessed using species composition data from two surveys of the main dune and machair sites around Scotland (Shaw et al., 1983; Pakeman et al., 2015). The first survey was centred around 1976 (1975–1977) and the second around 2010 (2009–2011 with one site done in 2013 due to safe access restrictions). Quadrat locations in the first survey were selected using a restricted random approach for the majority of sites; larger sites (> 225 ha) sampling intensity was 2 samples per 15 ha, with sites less than 225 ha sampled at higher intensity to ensure a minimum of 30 quadrats per site (Shaw et al., 1983). Stratified random methods were trialled for the few (15) sites surveyed in 1975, but this approached was found to be unhelpful. Of the 94 sites and 3783 quadrats with vegetation records recorded in the first survey, the second survey visited 89 sites and repeated 2532 quadrats. As resources were not available to repeat every quadrat, within each site quadrats were surveyed at random to avoid bias in resampling.

Each survey followed the same methodology and was based on the visual estimation of percentage cover of all higher plant species (nomenclature follows Stace 2010) and other cover classes such as bryophytes, lichens, litter and bare ground within 5 m × 5 m plots. For the second survey, quadrats were relocated by digitising the original 1:10,000 mapped sampling points and using these points as target for GPS relocation. Testing against fixed landmarks (buildings etc) suggested an accuracy of ± 10 m for this process. The process was facilitated by summaries of the 1976 vegetation and quadrats were not resurveyed if there was any doubt in matching the two survey positons. This meant that measured change errs on the conservative, but it has been shown to be robust and effective for re-visitation surveys of non-permanent quadrats (Chytrý et al., 2014; Kopecký and Macek, 2015; Ross et al., 2010).

A number of simple measures of land use and vegetation structure were assessed in parallel to the vegetation composition in both surveys. The presence and absence of livestock species (cattle, horses and sheep) or their dung was noted; for use in the analysis this was converted to presence/absence of Livestock (1/0). Grazing was assessed into four categories: heavy (abundance of dung, together with a uniformly short vegetation sward and little sign of litter) = 3; moderate (less uniform sward, with some dung and some litter) = 2; light (some evidence of dung and removal of vegetation could be seen, with larger mass of litter and much taller vegetation swards compared to moderate and heavy grazed areas) = 1; and no grazing = 0. Vegetation structure was similarly scored on a four point scale; dense cover = 3, moderate cover = 2, light cover = 1, absent = 0. For forbs and grasses they were separately assessed for each of three height classes (0–20, 20–50, > 50 cm), for shrubs in three height classes (0–50, 50–200 and 200–500 cm) and trees in one height class (> 500 cm). For analysis this data was aggregated into the following derived variables: Woody − the sum of scores for shrubs 50–200, shrubs 200–500 and trees > 500 cm (scale 0–9); Openness − the sum of grass 0–20 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) with a maximum of 3 per layer (scale 0–9). The cover of Bare ground and Litter from the quadrat survey were also used as descriptors of vegetation structure. It was also noted if the site had been in the geographically targeted Environmentally Sensitive Area agri-environment scheme.

2.2. Species traits

Data on key functional traits for all tracheophytes were assembled from two sources (Table 1): BiolFlor (Klotz et al., 2002) and LEDA (Kleyer et al., 2008). Due to the nature of the analysis, life span, canopy structure, method of vegetative spread and pollen vector were assessed

Table 1
Traits used in the analysis with source and coding information.
Sources of data: [1]BiolFlor (Klotz et al., 2002), [2]LEDA (Kleyer et al., 2008), [3]PLANTATT (Hill et al., 2004).

Traits	Coding
Vegetative	
log Canopy height (m)[2]	continuous
Canopy structure − erosulate[1]	0/1
Canopy structure − hemirosette[1]	0/1
Canopy structure − rosette[1]	0/1
Leaf Dry Matter Content (mg g^{-1})[2]	continuous
log Leaf size (mm^2)[2]	continuous
Life-span − annual[1]	0/1
Specific Leaf Area (mm^2 mg^{-1})[2]	continuous
Vegetative spread − rhizome[1]	0/1
Vegetative spread − stolon[1]	0/1
Reproductive	
Flowering − start (month)[1]	1–12
Pollen vector − insect[1]	0/1
Pollen vector − self[1]	0/1
Pollen vector − wind[1]	0/1
log Seed mass (mg)[1]	continuous
Environmental preferences	
Ellenberg F (moisture)[3]	1 to 12, categorical
Ellenberg N (nitrogen)[3]	1 to 9, categorical
Ellenberg R (reaction)[3]	1 to 9, categorical
Mean precipitation[3]	continuous
Mean January temperature[3]	continuous
Mean July temperature[3]	continuous
Status	
Change index[3]	continuous
GB abundance − number of occupied 10 km × 10 km squares in Great Britain[3]	0–2048