



## Research paper

# Long-term functional structure and functional diversity changes in Scottish grasslands



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## ARTICLE INFO

## Keywords:

Atmospheric deposition  
Functional richness  
Grazing  
Plant functional traits  
Resurvey

## ABSTRACT

Analysis of changes in functional traits and functional diversity offers a means of identifying the main environmental drivers of change, the impacts of that change on community assembly and the consequence of change on ecosystem function and service delivery. Changes in key traits and functional diversity in Scottish grasslands were analysed for a resurvey of 561 grasslands sampled an average of 40 years apart and these changes correlated with changes in environmental drivers. There were clear differences between the responses of different grassland habitats; more productive habitats showed evidence of increased agricultural utilisation, whereas more unproductive habitats showed evidence of reduced exploitation. This was echoed in an increase in Functional Richness in unproductive habitats and a decrease in productive ones; the latter indicating increased habitat filtering in the heavily utilised, productive habitats. There were also overall shifts to later-flowering species and less availability of resources for pollinators in less productive habitats. Models relating changes in traits to the environment had little power, but did indicate the importance of pollution and that recovery from the peak in livestock numbers between the surveys had not fully worked through. Similarly, changes in functional diversity were poorly explained by changes in environmental drivers, though increased rainfall had positive impacts on Functional Evenness and Richness. Functional Divergence (measured by Rao's Q) was, however, strongly linked to changes in species traits over time. Scottish grasslands have diverged in how they have been utilised; more productive grasslands have been exploited more, resulting in shifts towards species with more exploitative growth strategies, a narrower range of growth and investment strategies, but a reduction in competitive dominance. The less productive grasslands appear to be utilised less, with shifts towards more conservative growth strategies and reduced habitat filtering, and the potential to deliver greater ecosystem multifunctionality. Resource declines for pollinators appeared to be universal across all grassland habitats.

## 1. Introduction

As the response traits (Lavorel and Garnier, 2002) of plants within vegetation are determined by the environment, then if there are changes in the environment, whether that be management, climate or pollutant deposition, there should be changes in the community weighted means of these traits as the composition of vegetation responds to the altered environment. In fact, the responses of traits, as they integrate information across species, are a powerful method of understanding the impacts of drivers on vegetation (Pakeman et al., 2009) which complements analysis of changes in species composition; analysed in . However, most traits are impacted by many different drivers and as such they cannot be used to isolate the action of individual drivers. For instance, Leaf Dry Matter Content (LDMC) is

affected by both climate and management intensity, whereas Specific Leaf Area (SLA) is affected – amongst other drivers – by both soil fertility and management (Pakeman, 2013). Hence, plants integrate across drivers depending on the balance of, for example, selection for conservative versus exploitative growth strategies (Schellberg and Pontes, 2012). However, comparing patterns in trait responses over time with patterns of changes in drivers can help to identify which driver is having the greatest impact on vegetation change (Lewis et al., 2014).

A number of response traits are also effect traits (Lavorel and Garnier, 2002; Pakeman, 2011a) – they control other ecosystem processes. In addition, there is often strong correlation between response and effect traits, due to phylogenetic or ecological constraints (Pakeman, 2011a). As such, the driver producing a response and a

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linked change in an effect trait is immaterial, as it is the change in effect trait that propagates changes through a system. Whether a shift in leaf dry matter content is driven by climate or management intensity it will impact on diet quality for herbivores (Mládek et al., 2013) and on the dynamics of carbon return to the soil via litter (Fortunel et al., 2009). Understanding how changes in environmental drivers impact on ecosystem function is critical to understanding how these changes propagate through the system to impact on other trophic levels and on the services provided by it (Lavorel et al., 2013).

Much emphasis has been placed on understanding the shift in the mean value of traits in response to the environment (Garnier et al., 2007). However, changes in the distribution of abundances and ranges of traits in trait space can provide additional diagnostic information about the drivers operating in a situation. Changes in functional diversity can reveal as much about the drivers operating in the environment as do changes in mean trait values. In particular they reveal information about how the environment controls the assembly of communities (Laliberté et al., 2010). Increased disturbance, for instance, can reduce Functional Richness – the volume of niche space occupied by a community (Mouchet et al., 2010), but increase Functional Evenness – the evenness of abundance across niche space (Pakeman et al., 2011b). Putting together information on response traits and functional diversity, coupled with available information on environmental drivers, offers an analytical framework to understand how trait-mediated effects of environmental change can propagate through an ecosystem to affect other trophic levels and ecosystem services (Díaz et al., 2007).

Data from two surveys of grasslands within Scotland, UK, were used to assess if the trait composition and functional diversity of vegetation had changed over that period and if these could be linked to changes in the environment, specifically climate, grazing management and aerial deposition of pollutants. Four questions were addressed through the analysis of change: 1) Can drivers of vegetation change be identified from changes in response traits and their correlation with changes in the environment? 2) How do these changes in trait values propagate into changes in effect traits? 3) Do shifts in traits as a result of the action of these drivers have an impact on the range and distribution of these traits (FD); i.e. does community assembly change as a result of environmental change? 4) Are changes in functional diversity linked to shifts of mean position in trait space? For questions 1, 2 and 3, the differences between different types of grassland habitats were analysed to add precision in determining which grassland types had been most affected, as they differ in their conservation and agronomic value.

## 2. Materials and methods

### 2.1. Survey and re-survey data

Data on grassland composition were taken from a database of 1980 records of composition collected between 1958 and 1987, mean 1973 (Birse, 1980, 1984; Birse and Robertson, 1976). Sampled stands were homogeneous and representative of the plant community being described. Species' cover values (vascular plants, bryophytes and macrolichens) were recorded on the Domin scale in 2 m × 2 m plots, alongside location data (British National Grid to the nearest 100 m), elevation, slope, aspect, general vegetation cover and topographic position. The plots were not permanently marked. During 2012–2014, mean 2013, a sample of 561 (28%) of these plots, designed to cover all of the different grassland types, was revisited at as similar time of year to the original survey as possible and resurveyed following the methods of the first survey. Plot locations were identified using a combination of GPS and the original site description (altitude, slope, aspect etc). Where current stands were not homogeneous, final locations were selected to minimise change. A quadrat was not resurveyed if there was low confidence in relocation. This conservative approach to relocation does not overestimate the degree of compositional change (Ross et al., 2010).

Species' cover was recorded as percentages for values > 1% and as Domin categories for species with cover < 1% to ensure backwards data compatibility whilst maintaining maximum data quality for future use. The data were checked for consistency of species nomenclature between surveys; a small number of taxa had to be amalgamated as a result of taxonomic changes or inconsistencies in recording between the surveys. To ensure consistency in analysis, the re-survey cover data were converted to Domin categories, before both original and re-survey data were back-transformed to percentage cover, using the mid-point of each Domin category. To provide greater precision in the analysis, plots from the first survey were assigned to communities in the UK's National Vegetation Classification (NVC) (Rodwell, 1992) using TABLEFIT (Hill, 1996). The resulting communities were then amalgamated into broader Habitats: acidic (largely *Agrostis-Festuca* grasslands), calcareous, improved (*Lolium* spp. dominated), mesotrophic, *Nardus* (dominated by *N. stricta*) and wet grasslands. These are all largely managed as pastures, though some *Lolium*-dominated grasslands have been managed for silage. The communities making up each of the six broad habitat classes are detailed in Table S1.

### 2.2. Trait and environmental preference data

Trait data for all vascular plants were assembled from a range of sources (Table 1): BiolFlor (Klotz et al., 2002), LEDA (Kleyer et al., 2008) and Thompson et al. (1997). Life span, canopy structure and life-form were coded to reduce the number of attribute columns in the analysis. No coding was possible for traits such as pollen vector and flower colour. However, for the latter some categories were merged to reduce the number of categories (pink + red, brown + green, violet + purple) and the number of zeroes in the dataset. In addition to morphological traits, three independent measures of a plant's climatic affinity were taken from the PLANTATT database (Hill et al., 2004). These species' measures were the mean climate of the 10 km squares where they occur in Britain, Ireland and the Channel Islands based on their distribution records in the New Atlas of the British and Irish Flora (Preston et al., 2002). The values were Tjan – January mean temperature (°C), Tjul – July mean temperature (°C) and Prec – Annual precipitation (mm). There was a small proportion of missing trait information (< 2%), which was filled using information on congeners. In total 22 traits were used in the analysis.

### 2.3. Functional diversity metrics

Three measures of functional diversity (FD) were calculated to assess shifts in functional diversity over time. Functional Evenness (FEve) represents the regularity of distribution of species abundances in trait space, Functional richness (FRic) is an indicator of the range of trait values present (Cornwell et al., 2006), and Rao's (1982) measure of quadratic entropy (RaoQ) assesses trait dispersion in trait space (Botta-Dukát, 2005). Calculations were carried out using FD (Laliberté and Legendre, 2010; Laliberté and Shipley, 2011) in R version 3.2.0 (R Core Team, 2015), with the data subject to an initial principal coordinates analysis to reduce the dimensionality of the trait space. These metrics were chosen as they are largely orthogonal to each other; i.e. representing different aspects of functional diversity (Mouchet et al., 2010), and capable of discriminating the processes structuring biological communities. Attributes were weighted so that the total weight of each trait was set to one; e.g. the weight for each flower colour attribute was set to 1/6. Three sites were removed from the analysis due to low vascular plant species richness (less than four species).

To assess changes in assembly processes through time we compared the standardised effect size SES, (Gotelli and McCabe, 2002) of FRic and RaoQ as together these indices provide the power to test for changes in niche complementarity (Mason et al., 2013). These were calculated from 999 runs of a null model. For SESFRic the null model was created using a matrix-swap randomisation following the procedure of Gotelli

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