



# Climate drives temporal replacement and nested-resultant richness patterns of Scottish coastal vegetation

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Beta diversity quantifies spatial and/or temporal variation in species composition. It is comprised of two distinct components, species replacement and nestedness, which derive from opposing ecological processes. Using Scotland as a case study and a  $\beta$ -diversity partitioning framework, we investigate temporal replacement and nestedness patterns of coastal grassland species over a 34-yr time period. We aim to 1) understand the influence of two potentially pivotal processes (climate and land-use changes) on landscape-scale ( $5 \times 5$  km) temporal replacement and nestedness patterns, and 2) investigate whether patterns from one  $\beta$ -diversity component can mask observable patterns in the other.

We summarised key aspects of climate driven macro-ecological variation as measures of variance, long-term trends, between-year similarity and extremes, for three important climatic predictors (minimum temperature, water-balance and growing degree-days). Shifts in landscape-scale heterogeneity, a proxy of land-use change, was summarised as a spatial multiple-site dissimilarity measure. Together, these climatic and spatial predictors were used in a multi-model inference framework to gauge the relative contribution of each on temporal replacement and nestedness patterns.

Temporal  $\beta$ -diversity patterns were reasonably well explained by climate change but weakly explained by changes in landscape-scale heterogeneity. Climate was shown to have a greater influence on temporal nestedness than replacement patterns over our study period, linking nestedness patterns, as a result of imbalanced gains and losses, to climatic warming and extremes respectively. Important climatic predictors (i.e. growing degree-days) of temporal  $\beta$ -diversity were also identified, and contrasting patterns between the two  $\beta$ -diversity components revealed.

Results suggest climate influences plant species recruitment and establishment processes of Scotland's coastal grasslands, and while species extinctions take time, they are likely to be facilitated by climatic perturbations. Our findings also highlight the importance of distinguishing between different components of  $\beta$ -diversity, disentangling contrasting patterns than can mask one another.

Over the last century shifts in climatic trends, namely global temperature gains and shifting precipitation patterns have been documented (Stocker et al. 2013), with several studies reporting associations between recent climatic patterns and temporal change in vegetation (Lenoir et al. 2008, Parolo and Rossi 2008, Gottfried et al. 2012). In the near to mid future (20–200 yr), systematic changes in climate are also forecast. Under the A1B scenario (IPCC 2007), mean annual temperatures are projected to rise, precipitation is to increase with latitude and spatial climatic patterns are to shift with varying velocities (Loarie et al. 2009). Consequently, climatic stability is expected to decline, as storm frequency and periods spent under climatic extremes relative to the norm increase (IPCC 2007). Understanding how these climatic changes might affect biological communities, especially vegetation patterns, has become a major challenge in contemporary ecology. Climatic variation, or indeed lack thereof, steep climatic trends and or climatic extremes are four antagonising processes with the potential to 1) increase or decrease establishment and extinction processes and 2) increase or decrease

abundance, particularly for species at the limit of their environmental space (Huntley et al. 2010).

Beyond the climatic filter, vegetation patterns at the landscape-scale are strongly influenced by local topography and parent material (Hodge 2005), among which spatial variability is positively linked to diversity (heterogeneity diversity relationship (HDR); Lundholm 2009, Tamme et al. 2010). However, like climate, notable changes in landscape scale heterogeneity (hereafter heterogeneity) have been documented over the last century. The patterns are most pronounced for human dominated regions where a large proportion of land-cover is agricultural. A common trend is for traditional agricultural practices, often associated with configurationally and compositional heterogeneity (sensu Fahrig et al. 2011) to be replaced with more intensive agriculture, typically characterized by large homogenous areas of crops. In line with HDR, loss of heterogeneity and associated community dissimilarity results in fewer beta niches (i.e. the region of a species' niche that corresponds to the habitat(s) where it is found; Silvertown et al. 2006), a reduction in the

number and or size of regional species pools (sensu Pärtel et al. 1996), and in turn, contributes strongly to landscape-scale temporal declines in gamma diversity.

Changes in heterogeneity and climate are therefore two potentially pivotal processes controlling the temporal dynamics of vegetation patterns; however an understanding of how change will manifest between the two theoretically antagonistic processes is not obvious a priori. On the one hand, with increasing landscape-scale homogenization we can expect a loss of diversity implying that site ( $\alpha$ -diversity) and landscape ( $\gamma$ -diversity) become smaller nested subsets of their former state (species loss without replacement). On the other hand changes in climatic trends can shift species realized niches. Assuming a time-lag response of 'trailing-edge' populations, i.e. those species that may lack dispersal capacities to successfully track climate (Svenning and Sandel 2013), diversity gains can be expected, however here former site ( $\alpha$ ) and landscape ( $\gamma$ ) diversities will be smaller nested subsets of their present state (species gain without replacement). Equally, changes in both heterogeneity and climate have the potential to facilitate balanced species losses and gains (i.e. species replacements), through abiotic process (e.g. extreme disturbance events) facilitating localized extinctions and freeing niche space for new populations, and through biotic processes (e.g. phenotypic exclusion) between newly established and extant populations.

One way to disentangle these processes and evaluate the relative contribution of deterministic drivers on biodiversity is to measure beta-diversity ( $\beta$ ). Here, we assess patterns of temporal taxonomic  $\beta$ -diversity among coastal vegetation systems of Scotland, UK. Many measures of  $\beta$ -diversity exist in which to assess taxonomic compositional change (see Tuomisto 2010a, b, and Anderson et al. 2011 for examples), most being monotonic transformations of Whittaker's ratio between  $\gamma$ - and  $\alpha$ -diversities (Whittaker 1960). However, many of these measures do not quantify explicitly compositional change resulting from either 1) an imbalance in recruitment and extinction processes (nested-resultant dissimilarity; Baselga 2010, 2012) and or 2) a substitution of one species with another (replacement; Lennon et al. 2001). Importantly, these two processes are antithetic yet captured together through 'broad-sense'  $\beta$ -diversity measures (i.e. Sørensen and Jaccard indices, sensu Lennon et al. 2001), resultant patterns can become confounded (Baselga et al. 2012). Consequently, support for the judicious use of multiple measure of  $\beta$ -diversity have emerged (Anderson et al. 2011), with particular attention focused on developing frameworks for partitioning  $\beta$ -diversity into richness differences (nested or otherwise), and replacement components (Baselga 2010, Podani and Schmera 2011, Carvalho et al. 2012). For the latest contribution to the debate dealing with the meaning and relative advantages of each method see Baselga and Leprieur (2015); for a review see Legendre (2014) and for examples see Baiser et al. (2012), Marini et al. (2013), Bishop et al. (2015) and Liggins et al. (2015).

In this study, we partition temporal  $\beta$ -diversity of inherently variable Scottish coastal grasslands into replacement and nested components. Using a national scale spatio-temporal dataset our aims are to understand the influence of both changes in climate and landscape-scale heterogeneity on temporal  $\beta$ -diversity patterns of plant species over a

34-yr period. We focus on four measurable components of temperature and precipitation related climatic variables (variance, stability, rate of change and extremes) in line with the A1B near to mid-term climate change scenario (IPCC 2007). We expect climatic variance, rate of change and extremes to be positively correlated with temporal  $\beta$ -diversity patterns. For climatic stability, (i.e. between-year climatic similarity), we predict the opposite relationship, that is a decay in dissimilarity with greater climatic stability.

Our study system is largely semi-natural and tightly coupled to human land-use. Traditional, low input rotational arable agriculture has meant heterogeneity was historically high, however these practices are no longer widespread. Grazing is now the commonest management practice over most of the area and, in places, some larger-scale more intensive farming (Pakeman et al. 2011). We, therefore, ask whether temporal shifts in heterogeneity have had an influence in driving temporal  $\beta$ -diversity patterns for these grassland systems. Our expectation is that heterogeneity will be positively correlated with temporal  $\beta$ -diversity. This expectation follows the HDR but also the species–time–area-relationship (Alder et al. 2005, White et al. 2006). The latter suggests that if species are placed randomly throughout the landscape, increased spatial turnover should promote an increase in temporal turnover and vice versa (Steiner and Leibold 2004). Finally, we hold no a priori expectations of how climate and heterogeneity will influence separate components of  $\beta$ -diversity. Rather we investigate the relative contribution of climate and land-use changes on nested-resultant dissimilarity and replacement patterns of Scotland's coastal grasslands. More generally, we ask whether patterns from one turnover component can mask observable patterns in the other?

## Methods

### Study area

The vegetation of Scotland's coastal grasslands, specifically Machair grasslands, and its associated landforms were used as a case study. The Machair ecosystem is a distinct and biodiverse coastal bio-type that includes all transient habitats from seaward embryo dunes to inland sand-affected peatlands, including low lying, biodiverse grasslands. Their distribution is confined globally to the north western fringe of Europe (25 000 ha). Their Scottish extent (17 500 ha) is limited to the western and northern coasts, and latitudinal distribution ranges ca 650 km. This gradient encompasses a transition from warmer, drier climes in the south to wetter, colder climes in the north. The plant communities of these Machair ecosystems have been described in detail by Kent et al. (1996) and Dargie (1998).

### Data collection

#### *Species data*

The Scottish Coastal Survey of 1975 to 1977 (Shaw et al. 1983), and a resurvey in 2009–2011 formed the raw data for this study; these will be referred to as the 1976 and 2010 surveys for brevity. Resurvey methodology followed the original

survey techniques detailed in Shaw et al. (1983), recording relative abundances of all higher plant species to the nearest 1% for 1548,  $5 \times 5$  m quadrats. Original quadrat coordinates (British National Grid) were relocated to within  $\pm 10$  m accuracy using a hand held global positioning system. The final location of the quadrat was selected using information from the original vegetation composition to ensure that spurious changes due to relocation error were minimised. Where there was uncertainty over the original quadrat location, it was omitted from the re-survey. This method of revisitation surveying for non-permanent vegetation sampling has been shown to be effective in detecting temporal change (Ross et al. 2010).

### **Climate data**

Climate was represented by three variables summarising key aspects of climate driven macro-ecological variation. These were: 1) annual minimum temperature (MinT°C); taken as the mean of the daily minimum temperature for the coldest month in each year. 2) Water-balance (standardised precipitation index; SPI) – calculated using the R package *spei* following methods outlined in Vicente-Serrano et al. (2010). 3) Growing degree-days (GDD°C), expressed as the total accumulated temperature across every day of the year above a threshold of 5.5°C.

Temperature and precipitation data were sourced from 5 km gridded monthly data covering the period 1970 to 2011, obtained from the UK Meteorological Office [[www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/](http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/)]. These three climatic measures were each expressed as four different predictors as follows: 1) climatic variance: the sample variance was calculated after detrending, as outlined in 2) below. 2) Climatic long-term trend: the rate of change of the variable along a timescale. Calculated by fitting a simple trendline using ordinary least squares regression to each 42-yr time series and using the regression coefficient as the measure of long-term trend. 3) Climatic stability (autocorrelation): the correlation in values between consecutive pairs of years (the lag-1 autocorrelation coefficient) was calculated; a measure of between-year climatic similarity. The variables were first detrended by simple regression, as described above for long-term trend. The autocorrelation coefficient was extracted from the residuals. 4) Climatic extremes (fat tail measure): the ratio of quantile differences (Q 0.975 – Q 0.025) / (Q 0.875 – Q 0.125). This measures the time the climatic (or other) variable spends in a portion of either tail (the numerator) relative to the time it spends in the central part of its distribution (the denominator; Schmid and Trede 2003).

## **Analysis**

### **Beta diversity**

Spatial  $\beta$ -diversity was measured as multiple site dissimilarity (MSD) in 1976 and 2010 for  $\beta_{\text{sne}}$  and  $\beta_{\text{sim}}$ . In contrast to average dissimilarity measures between pairs of sites (Izsák and Price 2001), multisite  $\beta$ -diversity provides information of identities of species shared across more than two sites (Baselga et al. 2007, Chao et al. 2012), and hence useful for evaluating landscape-scale heterogeneity patterns. Here, sites were taken as all quadrats within a single  $5 \times 5$  km grid.

For analyses, we used a sub-sample of the total spatio-temporal Scottish coastal data, selecting only quadrats ( $5 \times 5$  m) located within 5 km grids for which climatic data was available and where a minimum sample of 10 quadrats per grid were taken. In total the subset data used for turnover analyses included 52,  $5 \times 5$  km grids encompassing 1227 quadrats and spanning 10 distinct geographic regions. To avoid bias from dissimilarity in sample size within each 5 km grid, we randomly sampled sites to the minimum number of neighbours ( $n = 10$ ), using the command `beta.sample` in R package *betapart* (Baselga and Orme 2012). Temporal change in heterogeneity was measured as the absolute difference between MSD2010 – MSD1976.

We quantified temporal  $\beta$ -diversity at the landscape-scale comparing dissimilarity between all species recorded within each of the 52,  $5 \times 5$  km grids between 1976 and 2010. This temporal grain thus agreed with the spatial grain of climatic predictors. To disentangle patterns in species temporal compositional change we used the  $\beta$ -diversity partitioning framework of Baselga (2010), calculating two pairwise  $\beta$ -diversity indices. The first,  $\beta_{\text{sne}}$  captures only richness differences among nested assemblages, i.e. whereby a smaller assemblage equals a strict subset of a larger, focal assemblage (Ulrich et al. 2009). This is a measure of nested-resultant dissimilarity (Baselga 2010). Second,  $\beta_{\text{sim}}$  captures only compositional changes due to species replacements. This is Simpson dissimilarity (Simpson 1943), an extreme narrow sense index (Lennon et al. 2001) and invariant to any imbalance in species gains or losses. Importantly, the former  $\beta_{\text{sne}}$  is not a measure of nestedness per se, but the proportion of the fraction of total dissimilarity not related to replacement (i.e.  $\beta_{\text{Sørensen}} - \beta_{\text{sim}}$ ; Baselga 2012).  $\beta_{\text{sne}}$  thus forms a special-type of richness difference measure that can only be quantified when assemblages have, at the very minimum, one species in common. For our data, all temporal pairwise comparisons exhibited nested patterns, however for completely dissimilar communities,  $\beta_{\text{gl}}$  (Lennon et al. 2001) or  $\beta_{\text{rich}}$  (Carvalho et al. 2013) would prove a better alternative to  $\beta_{\text{sne}}$  in capturing patterns resultant from richness gradients. Spatial and temporal  $\beta$ -diversity, inclusive of both pairwise and multiple-site dissimilarity indices were calculated using the R package *betapart* (Baselga and Orme 2012).

### **Model selection**

A multi-model inference approach (Burnham and Anderson 2002) was used to evaluate evidence. In all cases the objective was to explain the variation in temporal turnover. For each measure of temporal  $\beta$ -diversity (i.e.  $\beta_{\text{sne}}$  and  $\beta_{\text{sim}}$ ), a set of separate statistical models were fitted, where temporal  $\beta$ -diversity (i.e. the response variables) and four climatic measures based of MinT, SPI and GDD were modelled as predictors and included as various subsets in accordance with our hypotheses (Table 1). Specifically models M2–M5 empirically test individual contributions of climatic processes (variance, similarity, trends and extremes) in controlling temporal biodiversity patterns. In addition to these, models M6–M11 explore varying contributions of pairs of climatic processes while M15 explores the contribution of all climatic predictors. These models test the assumption that multiple climatic processes drive temporal compositional change in vegetation. Finally models M12–M14

Table 1. Combinations of climatic predictors used to fit 15 varying regression models. Climatic measures include the variance, between-year similarity (autocorrelation), long-term trend (slope) and time spent in relatively uncharacteristic climatic conditions (fat-tail) for minimum temperature (T), water-balance (SPI) and growing degree-days (GDD).

Model	Climatic Covars	Predictors											
		Variance (var)			Auto-correlation (cor)			Slope (sl)			Fat-tail (ft)		
		varT	varSPI	varGDD	corT	corSPI	corGDD	slT	slSPI	slGDD	ftT	ftSPI	ftGDD
m1	0												
m2	3	█	█	█									
m3	3				█	█	█						
m4	3							█	█	█			
m5	3										█	█	█
m6	6	█	█	█	█	█	█						
m7	6	█	█	█				█	█	█			
m8	6	█	█	█							█	█	█
m9	6	█	█	█	█	█	█						
m10	6	█	█	█	█	█	█	█	█	█	█	█	█
m11	6	█	█	█	█	█	█	█	█	█	█	█	█
m12	4	█			█			█			█		
m13	4		█			█			█			█	
m14	4			█			█			█			█
m15	12	█	█	█	█	█	█	█	█	█	█	█	█

evaluated the contribution of individual facets of climate (MinT, SPI, GDD) testing the assumption that MinT plays a more important role than GDD or SPI in controlling temporal  $\beta$ -diversity or vice versa.

To gauge the contribution of spatial turnover (i.e. a landscape-scale heterogeneity proxy), all models (M1:M15) were grouped into two model sets including and/or excluding spatial turnover as an additional model covariate:

$$\beta\text{-time} \sim \text{climatic co-variables} + \beta\text{-space} \quad (\text{set 1})$$

$$\beta\text{-time} \sim \text{climatic co-variables} \quad (\text{set 2})$$

Model M1 (Table 1) of model set 1 (S1M1), specifically evaluated the sole contribution of heterogeneity in controlling temporal  $\beta$ -diversity patterns. All other models within set 1 explored the spatial effect in conjunction with climate. Model set 2 excluded spatial  $\beta$ -diversity as a predictor; S2M1 modelled only the intercept.

To avoid violating the independent errors assumption caused by residual spatial autocorrelation (Cressie 1993, Beale et al. 2010), we used generalised least squares models with exponential spatially-structured random effects (residuals). For each model we extracted the standard regression coefficient and pseudo R-square. The 'best' models were identified using Akaike's information criterion (AIC; Burnham and Anderson 2002), the most parsimonious being the model with the lowest AIC value in each set.

Prior to analyses all model predictors were standardised to zero means and single unit variance. To assess associations of each predictor with temporal turnover, average model coefficients for each model set were calculated, (coefficients weighted by the Akaike model weights; Burnham and Anderson 2002). All statistical analyses were done in R ver. 3.1.3 (R Development Core Team), using the `gls` function in the R package `nlme` (Pinheiro et al. 2011).

## Results

### Climate drives temporal beta diversity

Results of the general least squares models identified climate to be an important explanatory predictor of temporal nested-resultant dissimilarity patterns among Scottish coastal grasslands. The 'best' model (i.e. the model with the lowest AIC) explained 37% of the variation in the data (pseudo  $R^2 = 0.37$ ; Table 2). This model (S2M11) modelled only climatic trends and periods of unusual climatic regimes relative to the norm (Table 1). Results showed climatic trends and extremes in GDD to have the largest model coefficients, both negatively correlated to temporal nested-resultant dissimilarity (Table 3). Equally parsimonious models (i.e. all models with a  $\Delta\text{AIC} < 2$ ; Burnham and Anderson 2002) also identified GDD and climatic extremes to be strong predictors of temporal nested-resultant dissimilarity in Scottish coastal

Table 2. Model results from the general least squares analysis. Presented are the top two parsimonious models (identified as having the lowest AIC), of each model set, where set 1 and set 2 includes and excludes a spatial heterogeneity predictor respectively. The best model (M) is denoted with \*. Pseudo R-square (square of the correlation of observed and predicted values), delta AIC ( $\Delta\text{AIC}$ ) and Akaike model weights ( $W_i$ ) are also shown. For models parameters see Table 1. For results of all models see Supplementary material Appendix 1.

Model	set	Model run	Pseudo $R^2$	AIC	$\Delta\text{AIC}$	$W_i$
$\beta\text{sne}$	Set 1	M11	0.37	103.92	0.00	0.37
		M14	0.32	104.65	0.72	0.26
	Set 2	M11*	0.37	102.04	0.00	0.37
		M14	0.32	102.69	0.65	0.26
$\beta\text{sim}$	Set 1	M5	0.16	38.61	0.00	0.31
		M1	0.03	39.55	0.94	0.19
	Set 2	M5	0.12	39.15	0.00	0.27
		M1	/	39.18	0.03	0.26

Table 3. Rank ordered model coefficients for models with  $\Delta AIC < 2$  for three indices of temporal turnover applied to 5 km gridded Scottish coastal vegetation ( $n = 52$ ): nested-resultant dissimilarity ( $\beta_{sne}$ ) and Simpsons ( $\beta_{sim}$ ). Four components of climate are presented: variance (var), between-year similarity (cor), long-term trend (sl), and climatic extremes (ft) for three climatic variables minimum temperature (T), water-balance (S) and growing degree-days (G). Spatial covariates include longitude (Long) and latitude (Lat) and spatial turnover ( $\beta$ -Space), measured as spatial  $\beta_{sne}$  and  $\beta_{sim}$  respectively. Model set (S) refers to the inclusion (S1) and exclusion (S2) of spatial turnover parameters. For models parameters see Table 1.

	Model	varT	varS	varG	corT	corS	corG	slT	slS	slG	ftT	ftS	ftG	$\beta$ -Space
$\beta_{sne}$	S2M11							0.21	-0.04	-0.30	0.13	-0.07	-0.27	
	S2M14			-0.08			0.12			-0.17			-0.25	
	S2M5										0.03	-0.06	-0.33	
$\beta_{sim}$	S1M5										0.01	0.00	0.12	-0.07
	S1M1													-0.06
	S1M14			-0.01			0.06			0.00			0.16	-0.08

grasslands (S2M14 and S2M5 Table 3; pseudo  $R^2 = 0.32$  and 0.21 Table 2 and Supplementary material Appendix 1).

The ‘best’ general least squares model modelling temporal replacement patterns among Scottish coastal grasslands also included climatic predictors (S1M5 Table 1 and 3) and explained 16% of the variation in the data (pseudo  $R^2 = 0.16$ ; Table 2). Like the nested-resultant dissimilarity models, parsimonious models of replacement identified GDD and extremes to be important climatic predictors, with model coefficients largest for extremes in GDD (Table 3). However, these were shown as positively correlated with temporal replacement, i.e. the converse of the relationship shown with nested-resultant dissimilarity.

### Landscape-scale heterogeneity drives temporal beta diversity

Our results provide little support for the expectation that temporal shifts in heterogeneity drive temporal compositional changes among Scottish coastal grasslands. ‘Best’ models for nested-resultant dissimilarity excluded spatial  $\beta_{sne}$  (Table 2 and 3), and even for those models where spatial  $\beta_{sne}$  was parameterized (i.e. models within set 1), its model coefficients were very small (supporting information). However, for temporal replacement patterns, spatial  $\beta_{sim}$  was included in the ‘best’ model (S1M5 Table 2 and 3). Furthermore, a  $\Delta AIC < 2$  was detected for model S1M1 that modelled only the contribution of spatial  $\beta_{sim}$ , however the variance explained by this model was low (pseudo  $R^2 = 0.03$  Table 2).

## Discussion

### Climate drives temporal beta diversity

The data analysis provides clear evidence that climate plays a substantial role in governing landscape-scale temporal  $\beta$ -diversity patterns of Scottish coastal grasslands. Furthermore, through use of a  $\beta$ -diversity partitioning framework our evidence suggests that climate has had a greater influence on temporal nested-resultant dissimilarity (i.e. temporal changes related to subset patterns) compared with temporal replacement patterns (i.e. temporal species substitutions) over the 34-yr period investigated.

Climatic trends and periods spent in unusual climatic regimes for GDD over the 34-yr survey period explained

temporal nested-resultant dissimilarity patterns in the data. Despite national-scale gains in species richness over the study period (Lewis et al. 2014a), measures of GDD were shown to negatively influence patterns of temporal nestedness (negative coefficients; Table 3) implying that identities of some species from 1976 were not preserved in 2010. Such patterns were visible among north-westerly regions (Fig. 1a, c). Here climatic conditions are described as ‘hyper-oceanic’ where humidity, wind speeds and precipitation are high and the annual temperature range is low. The climate here is partly responsible for increasing biodiversity, as the competitive ability of species common to low-lying grasslands are suppressed, facilitating the persistence of less-competitive species. In this study, we observed visible latitudinal gradients in temperature related changes and climatic instability in GDD (Fig. 2c and 3c), lowest among southern latitudes and highest among northern latitudes. Such a relaxation of the ‘harsh’ nature of the typical climatic environment has the potential to promote establishment, and or population gains of competitors and widespread generalists, and in turn, a concomitant demise in the presence or abundance of specialist stress-tolerant species. Indeed, north-westerly regions were not found to be void of replacement patterns (Fig. 1b). Replacement of specialists with generalists has important conservation implications. The result would be a tendency towards greater compositional similarity (i.e. biotic homogenisation, McKinney and Lockwood 1999), and overall lower biodiversity, a trend already linked to climatic warming (Ross et al. 2012) and reported for human-modified ecosystems across the UK (Smart et al. 2006).

Notwithstanding these arguments, compositional changes resulting from climate effects may not necessarily result in observable species losses. Many plant species, particularly long-lived species, possess high resistance to change, and are capable of persisting in a community as remnant populations under non-optimal environmental conditions (Diamond 1972, Eriksson 1996, Helm et al. 2006). As a result, species that disperse to and establish successfully in a given habitat can appear to have little influence on replacement mechanisms, as few species are immediately lost from the community. We found that gains in species richness were highest in the southwest (Fig. 1c), where also climatic extremes in MinT and GDD were low (Fig. 3). This indicates a relatively favourable and stable climate promotes species establishment without a concomitant loss of extant species. The result can be a colonisation credit that includes an extinction debt

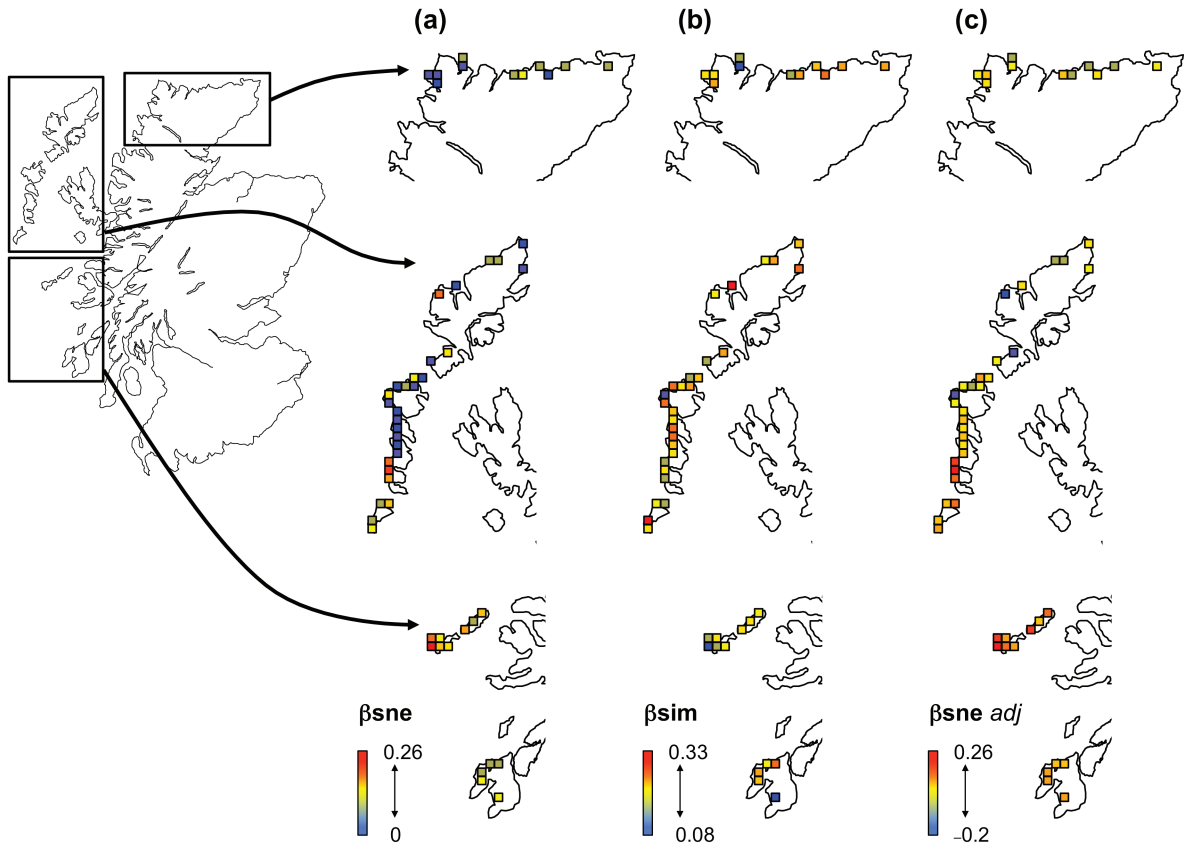


Figure 1. Extent of temporal turnover, mapped for (a) nested-resultant dissimilarity ( $\beta_{sne}$ ), (b) Simpsons ( $\beta_{sim}$ ) and (c) adjusted nested-resultant dissimilarity ( $adj \beta_{sne}$ ). The latter removes the ‘absolute’ from the equation:  $adj \beta_{sne} = ((b - c)/(2a + b + c)) \times (a/(a + \min(b, c)))$ . This permits the direction of temporal shifts in species richness gradients (i.e. species loss or species gain) to be visualized.

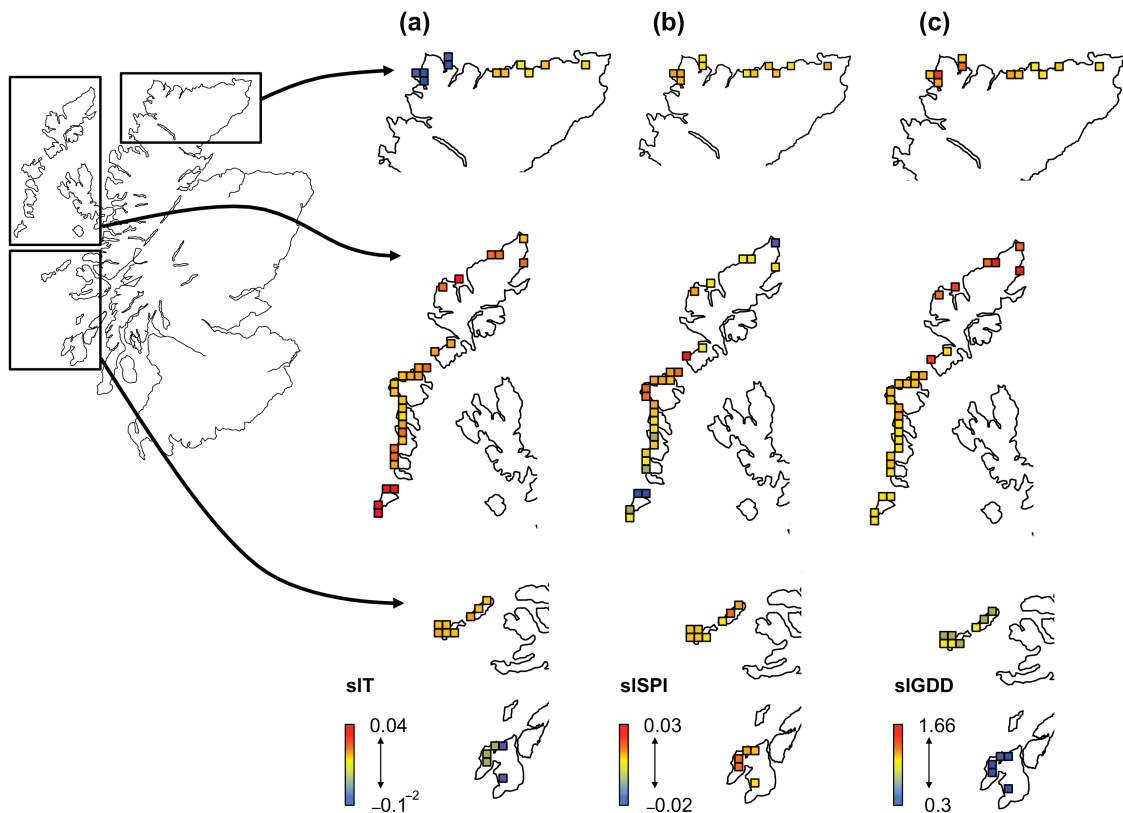


Figure 2. Spatial extent of climatic long-term trends (Slope) for (a) mean minimum temperature (T), (b) water balance (measured as SPI) and, (c) growing degree days (GDD) for Scottish coastal grasslands between years 1970–2011.

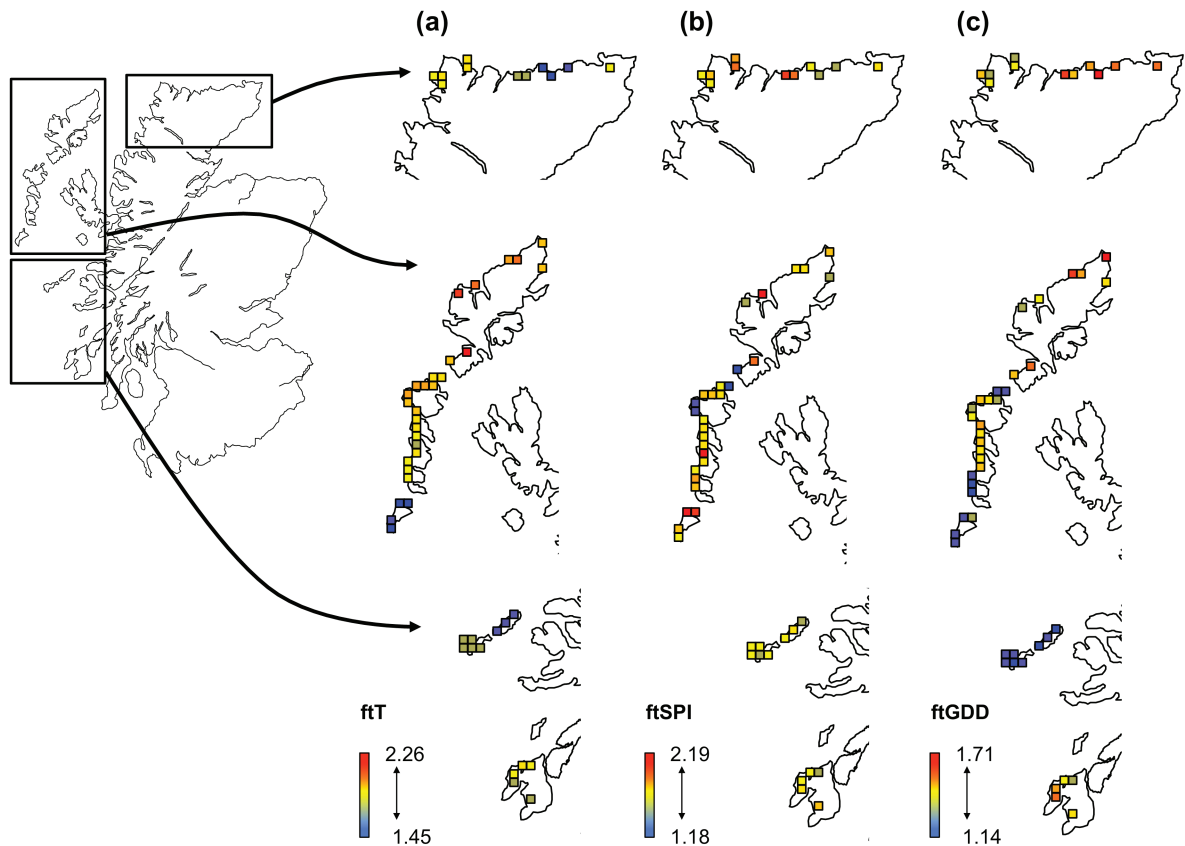


Figure 3. Spatial extent of time spent in uncharacteristic climatic periods relative to the norm (fat-tails) for (a) mean minimum temperature (T), (b) water balance (measured as SPI) and, (c) growing degree days (GDD) for Scottish coastal grasslands between years 1970–2011.

(i.e. extant species that are expected to go extinct because threshold conditions for their long term persistence are no longer satisfied; Tilman et al. 1994). Arguably therefore, temporal replacement patterns may be better explained, at least in part, by past environmental constraints (Gustavsson et al. 2007, Reitalu et al. 2010), perhaps explaining why replacement patterns were weakly explained relative to nestedness. However it might also be that replacement is driven more by biotic interactions (e.g. phenotypic exclusion) and or finer-scale disturbances (e.g. land-use) than macro-scale temporal shifts in climate. Ultimately, substantiating those process responsible for balanced species gains and losses (i.e. replacement) of Scotland's coastal grassland species requires further investigation.

Beyond identifying relevant measures and facets of climate that explain temporal compositional patterns (climatic long-term trends and extremes of GDD), results of this study also reveal confounding responses to climate of nestedness and replacement, as was detected for extremes in GDD (Table 2). The fact that extremes in GDD negatively impact temporal nestedness while positively influencing temporal replacement implies that extant species are losing out to newcomers – resulting in an imbalanced substitution that ultimately negatively changed the biodiversity. It is important to note that confounding patterns such as these can easily be overlooked if using broad-sense species turnover indices (e.g. Sørensen and Jaccard indices) which capture both richness gradients (nestedness or otherwise) and replacement patterns, indices that are well established in the literature

for species turnover analyses. Our results therefore highlight the utility of  $\beta$ -diversity partitioning frameworks for fully understanding drivers of temporal compositional changes, uncovering patterns that may otherwise be masked.

### Landscape-scale heterogeneity drives temporal beta diversity

Despite extant knowledge of shifting land-use patterns among our study system (Pakeman et al. 2011, Lewis et al. 2014a), we found little evidence to suggest temporal shifts in heterogeneity influence landscape scale compositions (i.e. 5 km<sup>2</sup>) of Scottish coastal grasslands over the last three decades. A possible explanation is that both the spatial grain and temporal extent at which our species compositional measurements were analysed were too coarse to reflect the dynamic processes inherent among these grasslands. For example, within a 5 km grid, pairs of sampled quadrats that were entirely dissimilar in 1976 can become identical in 2010. At the same time pairs of sampled quadrats that were identical in 1976 can become entirely dissimilar in 2010. In such a scenario, despite prevalent temporal change between local vegetation communities, the overall structure of landscape-scale heterogeneity remains unaltered. Therefore, among Scottish machair grasslands, although land-use disturbances (primarily linked to low-intensity rotational arable agriculture) significantly influences spatial variability (Lewis et al. 2014b), such may not necessarily translate to strong

patterns of temporal variability when assessed at landscape-scales, as contrasting changes within regions collapse one another. Alternatively, weakly linked heterogeneity patterns with temporal plant compositional change may be because of a time lag response of plant species to changing environmental conditions. As discussed above in relation to climate, communities can maintain an extinction debt, i.e. a suite of extant species maladapted to current conditions and therefore expected to be lost some time after an environmental perturbation (Hanski and Ovaskainen 2002). Despite the temporal extent of our study spanning three decades, for long-lived plant species, the relaxation time (i.e. the time required to reach new equilibrium; Kuussaari et al. 2009) may be longer, and therefore an even larger temporal extent may be required to link temporal compositional shifts with land-cover changes.

## Conclusions

Our analyses showed both temporal shifts in nested-resultant dissimilarity and replacement patterns of Scottish coastal grassland to be reasonably well explained by temporal changes in climate but only weakly explained by landscape-scale heterogeneity patterns over the last three decades. Links to climate were twice as strong for nestedness patterns compared to replacement patterns. Our results imply that climate moderately influences species recruitment and establishment processes, while species extinctions processes take time and are most likely a process governed more by biotic community assembly mechanisms. However, our analyses show some evidence to suggest that periods of non-typical climatic regimes (i.e. climatic extremes) may facilitate species losses. Studies addressing climate driven temporal shifts in plant compositions should therefore consider periods of past climate instability as well as time lag responses of vegetation to disturbance. The latter is also an important consideration when addressing temporal landscape-scale changes in heterogeneity, as is also the spatial grain and temporal extent relevant to the study area and taxa being investigated. Finally, our results demonstrate contrasting responses of temporal compositional change (i.e. nestedness and replacement) to the same aspects of climatic variation. Such patterns can be overlooked when using the many measures that conflate nestedness and replacement, whereas a  $\beta$ -diversity partitioning frameworks such as that applied here detects these contributions and so allows a deeper insight into processes that maintain biodiversity.

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Supplementary material (Appendix ECOG-01753 at <[www.ecography.org/readers/appendix](http://www.ecography.org/readers/appendix)>). Appendix 1.