Relative climatic, edaphic and management controls of plant functional trait signatures

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Abstract

Objective: To identify the relative roles of climatic, edaphic and management factors in controlling the weighted mean traits of vegetation.

Location: Eleven sites in Europe and one in Israel undergoing transitions in land use.

Material and Methods: Standardised methods were used to collect information on species traits and attributes from plots covering a range of land uses at each site. This was combined with abundance data to create a plot×trait matrix. Variance partitioning was used to identify the relative roles of climate, soil and management on the weighted and unweighted mean traits of the vegetation in the full data set, and the data set divided into vegetative traits (including life-form, clonality, defence and a range of leaf traits) and traits linked to regeneration via seeds (including seed mass, dispersal and pollination mechanism).

Results: Variance partitioning of the full data set showed that climate (18.7%), explained more variance in the weighted mean traits of the vegetation than climate and soil together (9.2), soil (6.9) and management (6.1). There was a similar distribution of variance explained for both vegetative and regeneration via seed traits, although more variance was explained for the latter. This restricted set of climatic, edaphic and management variables could explain 45-50% of the variance in the weighted mean traits of the vegetation between plots. There were only small differences between analyses of the weighted and unweighted data.

Conclusions: Despite large variations in climate and soils between sites, there was still a separate and recognisable impact of management on the mean weighted traits of the vegetation. There was also a degree of shared variation between the three groups of factors, indicating that the response of plant traits to one group of factors may not be predictable because they may be modulated by their response to other groups.

Key words: Disturbance; Environment-trait relationships; Land-use change; Variance partitioning.

Introduction

The relationship of individual plant traits with various environmental drivers has been a productive area of study for many years, from Raunkiaer's (1908) demonstration of the role of climate in determining the proportions of species with different life-forms to Moles et al. (2007) showing a decline in seed size with latitude, including a steep decline at the edge of the tropics. These studies of environment-trait relationships have largely attempted to correlate a trait or set of traits with a single or small group of environmental factors. These were recently summarised by Lavorel & Garnier (2002). However, only a small number of studies have shown how

traits may be influenced simultaneously by different environmental variables. Díaz et al. (1999) showed that the magnitude of disturbance response was dependent on the severity of the climate filtering effect on vegetation composition; a less dramatic response in composition was evident where the range of traits present is most constrained by climate. Similarly, de Bello et al. (2005) showed that traits well correlated to grazing did not show a strong repeatability across altitudes representing an aridity gradient, and thus that local scale relationships may not be generalisable. At regional scales, Kleyer (1999, 2002) showed that trait distributions in vegetation were a function on both site productivity and the level of disturbance, and Pakeman (2004) showed that the response of weighted mean traits of the vegetation to grazing was modified by the productivity of the grassland vegetation.

Recently, there have been attempts to link plant functional traits to a range of ecosystem processes. Processes investigated in this way include carbon cycling (Cornelissen et al. 2006), fire (Lavorel & Garnier 2002), nitrogen cycling (van der Krift & Berendse 2001; Eviner & Chapin 2005), primary productivity (Lavorel & Garnier 2002; Vile et al. 2006) and multiple processes (Eviner & Chapin 2003; Díaz et al. 2004; Garnier et al. 2004; Engelhardt 2006; Quétier et al. 2007). However, as these links depend on taking into account species abundance as well as presence in analyses (Grime 1998), analysis of unweighted (or species) data is not appropriate. Knowledge of the predictability of weighted mean trait responses to land-use and climate change is therefore vital in predicting the impacts of these changes on ecosystem processes and ecosystem services (Lavorel & Garnier 2002).

In order to ascertain the potential need to modulate trait-environment relationships by different types of environmental variables, the aim of the present study was to quantify the relative roles of different types of environmental drivers, climate that varies at large scales and management and edaphic variables that show variation at intermediate scales, in determining the traits displayed at the level of the vegetation (i.e. weighted mean traits). The specific objectives addressed in the study were: (1) to identify the relative contributions of climate, edaphic and disturbance factors in controlling the values of weighted mean plant traits in a data set collected across Europe to analyse the impact of land-use change on plant functional traits, ecosystem processes and services (Garnier et al. 2007). If there is considerable overlap between these contributions, then modulation of trait-management

relationships by climate and soil has to be taken into account when predicting the impact of land-use change on plant functional traits and ecosystem function; (2) to examine whether these relative contributions are conserved if the data set is split into traits associated with the vegetative (life-form, clonality, height and a range of leaf traits) and seed regeneration phases of the plant life cycle (including seed mass, dispersal and pollination mechanisms and timing of reproduction. These two major parts of the life cycle (Table 2), whilst not independent, are only relatively weakly coupled (Grime et al. 1997). The two groups of traits might be expected to show different relationships with environmental drivers, as traits linked to seed regeneration that are subject to divergent evolution (Grime 2006) may be less well correlated with environmental drivers than with vegetative traits that face convergent evolutionary pressures. As mean trait values can have different relationships with environmental variables to those of weighted mean values, the analysis was repeated with unweighted mean trait values to assess this impact (Cingolani et al. 2007; Pakeman et al. 2008). A final question (3) was whether any significant land-use-trait relationships could be identified if climate and soil were partialled out of the analysis.

Materials and Methods

Data

The data were collected during 2003 and 2004 from 11 sites in eight countries in Europe, as well as from one site in Israel (Table 1). Sites were chosen to reflect typical land-use transitions taking place around the study sites and were not selected on the basis of their climate or soil type.

Abundance data of vascular plant species were collected during one survey near the mid-point of the growing season for each plot (an area with the same management and environmental conditions) within each site. Between the 12 sites, 194 plots were selected to cover a range of land-use intensities and vegetation cover types. Abundance data (based on point quadrat or frequency data) for each plot were recalculated to give relative abundance (see Garnier et al. 2007 for details).

Trait data (Table 2) were collected using standardised techniques supplemented by literature values where appropriate (Garnier et al. 2007). The matrix of plot×species data was multiplied by the matrix of species×trait data to provide a matrix of

Table 1. Position, climate, habitat and management history of the sites used in the analyses.

Country & Site	Latitude	Longitude	Altitude (m)	Climate	Habitat, management
Czech Republic – Ohrazeni	48°57N	14°36E	510	Central-European temperate	Meadow, mowing and fertiliser
France – Ercé	42°50N	1°17E	600-1000	Mountain humid	Grassland, grazing and mowing
France – Hautes Garrigues du Montpelliérais	43°51N	3°56E	100-160	Mediterranean sub-humid	Abandoned vineyard
France – Lautaret	45°02N	6°21E	1830-2050	Sub-alpine	Grassland. ploughing, mowing and grazing
Germany – Müritz National Park	53°27N	12°44E	65	Temperate	Grassland and woodland, grazing
Greece – Lagadas	40°47N	23°12E	450-550	Mediterranean semi-arid	Grassland and shrubland, grazing
Israel – Karei Deshe	32°55N	32°35E	60-280	Mediterranean semi-arid	Grassland, grazing
Norway – Båttjønndalen	62°47N	11°02E	800-1000	Alpine	Heathland, grazing
Norway – Berghøgda	62°42N	11°05E	800-1000	Alpine	Heathland, grazing
Portugal – Mértola Castro Verde	37°40N	8°00W	100-150	Mediterranean	Arable and grassland, grazing and ploughing
Scotland – South Uist	57°16N	7°24W	0-15	Oceanic	Arable, grassland, ploughing and grazing
Sweden – South East Baltic Sea	58°50N	17°24E	0-50	Cold temperate	Grassland and woodland, grazing

Table 2. Traits and their attributes used in the analyses.

Trait	Attribute
Vegetative traits:	
Raunkiaer (1908) life form	Chamaephyte, deciduous nanophanerophytes, deciduous phanerophytes, evergreen nanophanerophytes, geophytes, hemicryptophytes, unknown life form, therophyte
Clonality	Clonal aboveground, clonal belowground, non-clonal
Height from flora	-
Specific leaf area (SLA)	-
Leaf dry matter content (LDMC)	-
Leaf carbon content (LCC)	-
Leaf nitrogen content (LNC)	-
Leaf carbon:nitrogen (C:N)	-
Chemical/physical defence	Defended, not defended
Traits linked to regeneration via seeds:	
Flowering time	-
Log10 seed mass	-
Dispersal mechanism	Anemochory, ballistochory, bristles, endozoochory, exozoochory, hoarding, hydrochory, myrmechory, other mechanism, unknown mechanism, unassisted
Pollination mechanism	selfing, wind, insect

trait×plot, which formed the basis for all the analyses. Numerical traits such as Specific Leaf Area were described in one column of the species×trait matrix as their weighted mean, while categorical traits, such as dispersal, had one column for each attribute as their weighted proportion (e.g. dispersed by anemochory or endozoochory). The species within the species-trait matrix always made up at least 80% (mean 91.4%) of the vegetation composition, as it was not always feasible to collect trait information for every trait-species combination. This level (80%) is sufficient to give a robust estimate for weighted means of numerical (e.g. specific leaf area, leaf dry matter content) or the weighted proportions of each attribute of categorical traits (e.g. dispersal mechanism, method of clonal spread) where the weight corresponds to the proportion of individual species in the vegetation (Pakeman & Quested 2007). Original values for weighted means of numeric traits and their log10-transformed values were individually tested in separate RDAs to assess if transformation increased the variation explained. Only the transformation of seed mass increased the explained variation by more than 2%. A matrix of unweighted data was similarly created by multiplying a matrix of presence/absence of species×plot and the matrix of species×trait.

Environmental variables used in the analysis included site data on average climate values recorded locally, and plot data on a range of edaphic variables analysed as part of this project (listed in Table 3). The methods of collection are described in Garnier et al. (2007). Management data were used in two forms: a single index of disturbance that quantified the percentage removal of biomass each year (Pakeman et al. 2008), and a set of categorical variables describing the type of management. These were grazing (scaled 0 = no grazing, 1 = lightly grazed, 2 = heavy grazing), cutting (0 = no grazing, 1 = cut once per year, 2 = cut twice per year), ploughing as part of rotational arable (0, 1), fertiliser use (0, 1) and time since abandonment (scale 0 = in agricultural use, 1 = <5 years, 2 = 5-15 years, 3 = 15-60 years, 4 = >60 years since agricultural use ceased).

Analysis

The approach taken used a variance partitioning analysis (Borcard et al. 1992) of the plot×trait matrix (where each cell represents the weighted mean trait value or abundance of an attribute for a particular plot and trait/attribute combination) constrained by the plot×environment matrix. This approach has frequently been used to look at how different groups of environmental factors control species distributions (e.g. Ohmann & Spies 1998; Pakeman et al. 2006). Redundancy analysis (RDA) was used for all the analyses, as weighted mean trait values were assumed to be linearly, rather than unimodally, related to environmental variables. RDA is effectively a Principle Components Analysis (PCA) constrained so that the axes are linear combinations of the environmental variables (ter Braak & Šmilauer 2002) and is hence equivalent to a constrained multivariate multiple regression. Trait data were centred and standardised. All ordinations were carried out using CANOCO for Windows ver. 4.5 (ter Braak & Šmilauer 2002).

The variance partitioning (Borcard et al. 1992) was used to identify the contributions of climate (C), soil (S) and management (M), alone and in combination, to explaining the variation in traits and attributes across the surveyed plots and sites. Prior to partitioning, a stepwise ordination was carried out using each of the three groupings of variables in order to identify the most parsimonious set of explanatory variables, as advocated by Økland & Eilertsen (1994). As this involved multiple testing, Bonferroni adjustments were made at each stage of the stepwise addition of variables to prevent a too liberal list of explanatory variables being selected. The significance of these models and the other models developed was tested using an unrestricted Monte Carlo permutation (999 permutations). As climate varied between sites rather than between plots, this permutation test was too lax. A stricter test, using a permutation restricted by a split plot design with permutation between whole plots (sites), was not possible with this unbalanced data set. As a conservative test, five random subsets of data were created with only eight plots from each site (the minimum number of plots per site), and the significance checked against this split plot permutation test. After stepwise selection, the three sources of variation (climate, soil and management) were balanced in terms of their potential explanatory power by ensuring they each had the same number of variables going forward into the variance partitioning. This was achieved by replacing the later added variables in the grouping(s) with the most selected variables.

Table 3. Marginal effects (percentage variance explained) of including each climate, edaphic and management variable used in the analyses. Figures in normal text are from analysis of weighted mean data, figures in *italic* are from analysis of unweighted data. Superscripts in the complete trait column indicate the order of addition during the stepwise selection of variables.

Variables	Complete traits	Vegetative traits	Seed regeneration traits
Climate variables			
Mean annual temperature	9.4[1] (*14.2*)	11.3 (*15.7[1]*)	7.1 (*12.4*)
Growing degree-days (above local threshold)	8.1[7] (*13.5*)	10.1 (*15.0[7]*)	6.9 (*11.7*)
Total incident light	9.4[2] (*13.2*)	7.5 (*12.3[3]*)	11.7 (*14.3*)
Total rainfall	4.8[6] (*3.6*)	5.6 (*4.6[5]*)	3.9 (*2.3*)
Total potential evapotranspiration (PET)	8.6[4] (*13.5*)	9.4 (*14.0[4]*)	7.7 (*12.8*)
Ratio of rainfall to PET	6.1[5] (*7.4*)	8.3 (*8.9[6]*)	3.3 (*5.4*)
Aridity index (Thornwaite 1948)	7.8[3] (*11.8*)	9.0 (*13.7[2]*)	6.3 (*9.3*)
Edaphic variables			
Soil pH	3.7[5] (*4.5*)	3.0 (*3.5*)	4.6 (*5.7*)
Soil carbonate	2.8[4] (*3.2*)	2.6 (*1.1*)	3.1 (*5.7*)
Soil carbon content	5.3[2] (*6.2*)	6.7 (*7.7*)	3.6 (*4.4*)
Soil nitrogen content	5.6[3] (*5.4*)	6.4 (*7.2*)	4.6 (*3.3*)
Extractable phosphate	1.5[6] (*2.5*)	1.6 (*3.7*)	1.3 (*1.0*)
Soil water-holding capacity	5.7[1] (*2.4*)	4.7 (*1.4*)	6.9 (*3.6*)
Management variables			
Annual biomass removal (%)	3.1[3] (*3.4*)	4.2 (*3.9*)	1.9 (*2.8*)
Presence of grazing (none, light, heavy)	2.5[4] (*2.6*)	2.7 (*2.6*)	2.2 (*2.7*)
Cutting (none, once per year, twice per year)	3.5[1] (*2.4*)	3.3 (*2.8*)	3.9 (*1.8*)
Ploughing (none, regular)	1.7[5] (*1.1*)	1.6 (*1.2*)	1.8 (*1.0*)
Abandoned (five age categories)	3.3[2] (*4.8*)	3.4 (*3.8*)	3.2 (*6.1*)
Fertiliser (none, regular)	2.6[6] (*2.3*)	2.5 (*2.7*)	2.8 (*1.8*)

Results

Complete trait set

All three sets of environmental data explained a significant proportion of the variation in weighted mean traits of the vegetation between plots (all $P < 0.001$). Testing the randomised subsets of data with the climate variables was always significant ($0.006 \leq P \leq 0.036$), indicating that it was justified to use the climate variables in the rest of the analyses. Stepwise selection of variables resulted in selection of all available variables being selected for each grouping (C, S, M). All variables were retained in the stepwise model at $P < 0.001$, except for Fertiliser (retained at $P = 0.006$) in the management selection (Table 3). Variance inflation factors ranged from 2.4 to 11.3 for soil factors, 1.8–7.4 for management variables and 4.9–14.7 for climate variables

except Growing Degree Days (GDD), where it equalled 30.6. Similar results emerged from analysis of the unweighted data. Consequently, GDD, as its removal reduced the variance least and because of its high variance inflation factor, was ignored for the rest of the analyses so that each grouping had six variables. The selected climate variables explained more (33.7%) of the variation than either the soil (19.5%) or the management (12.7%) variables. Light and mean annual temperature were the climate variables with highest explanatory power individually (Table 3), and, in general, individual climate variables were more powerful than edaphic or management variables. Soil water-holding capacity, carbon and nitrogen were important within the edaphic grouping, and cutting, abandonment and biomass removal in the management grouping. A similar picture emerged from the analysis of unweighted data, except that soil increased in explanatory power (22.7%) and management and climate declined slightly (12.5% and 33.1%, respectively). The power of most individual climatic and edaphic variables in explaining the variation present increased with the unweighted data (Table 3).

Ordination of the complete weighted mean trait data constrained by climate clearly showed that a number of the environmental variables were correlated – warm sites also had a long growing season, high light, high aridity, high evaporative demand and a low ratio of rainfall to evaporative demand (Fig. 1a). Nearly orthogonal to this axis was total rainfall. Sites with warmer climates on the right side of the biplot, such as those in France – Hautes Garrigues du Montpelliérais, Greece and Israel, were characterised by higher abundances of therophytes/ non-clonal species that were typically early flowering and insect-pollinated. Sites with wetter climates at the top of the biplot (France – Ercé, France – Lautaret, Scotland) had higher abundances of wind-pollinated, stoloniferous species and mean seed size

was high. Cold, dry climates (Germany, Sweden – lower left of the biplot) had higher abundances of rhizomatous and endozoochorous species. The ordination of the weighted mean trait data constrained by soil variables (Fig. 1b) showed that plots with high soil carbon usually had high soil nitrogen and high water-holding capacity, and orthogonal to this set of factors were soil pH and soil carbonate. Soils with high carbon, total nitrogen and water-holding capacity were typified by species with high leaf carbon content and leaf dry matter content and the species were more frequently hemicryptophytes and less frequently therophytes or insect-pollinated. Basic, lime-rich soils were typified by higher abundances of therophytes, bristle dispersal and non-clonal species.

Ordination of the data by the management variables showed a clear axis of variation between abandoned sites (top left, Fig. 1c) and grazed/disturbed sites (bottom right). Abandonment resulted in species with typically high leaf dry matter content, high leaf carbon-nitrogen ratios and were more frequently tall, evergreen and self-pollinated. Plots characterised by disturbance, including grazing, were typified by species with high leaf nitrogen content and low leaf dry matter content and seed mass. Ploughing, fertiliser application and cutting were weaker explanatory variables; possibly because they were the less common treatments in the data set, although cutting was associated with hemicryptophytes and species with wind pollination.

All the ordinations used in the construction of the partitioning on the weighted data were significant ($P < 0.001$). The partitioning (Fig. 2a) showed that climate alone explained the most variation (18.7%), with variation jointly explained by climate and soil (9.2%), soil alone (6.9%) and management alone (6.1%) next in importance. Only small amounts of variation were explained jointly by management and the other two sources of variation,

Fig. 1. Redundancy analysis of weighted mean trait values for each plot, with stepwise selected (**a**) climatic variables (traits shown are those that had fits of >20%), (**b**) edaphic variables (traits shown are those that had fits of >10%) and (**c**) management variables (traits shown are those that had fits of >10%). Variable abbreviations: *Abandon* time since abandonment, *Cut* frequency of cutting, *Disturb* annual percentage biomass removal, *Grazed* level of grazing, *Fert* addition of fertiliser, *MeanTemp* mean annual temperature, *Plough* regular ploughing *Soil_CO3* soil carbonate, *Soil_C* soil carbon content, *Soil_N* soil nitrogen content, *Soil_P* soil extractable phosphate, *Soil_WHC* soil water-holding capacity, *TotArid* aridity index, *TotGDD* growing degree-days, *TotLight* total incident light, *TotRain* total rainfall, *TotPET* total potential evapotranspiration, *TRainPET* ratio of rainfall to PET. Trait abbreviations: *Clon_abv*, *Clon_blw* clonal organ above- or belowground, respectively, *C:N* leaf carbon to nitrogen ratio, *Defend* leaf has physical or chemical defence, *Disp_brs*, *Disp_end*, *Disp_ex*, *Disp_hrd*, *Disp_oth*, *Disp_uns*, *Disp_wnd* dispersal by bristles, endozoochory, exozoochory, hoarding, other, unspecified or anemochory, *Eve_nano* evergreen nanophanerophyte, *Flora_ht* plant height from flora, *Flower_t* flowering time, *Geo* geophyte, *Hemicryp* hemicryptophyte, *LCC* leaf carbon content, *LDMC* leaf dry matter content, *log_sdms* log seed mass, *Nodefend* no leaf defences, *Non_clon* non-clonal, *Poll_ins*, *Poll_slf* and *Poll_wnd* insect, self- and wind pollinated, respectively, *Thero* therophyte.
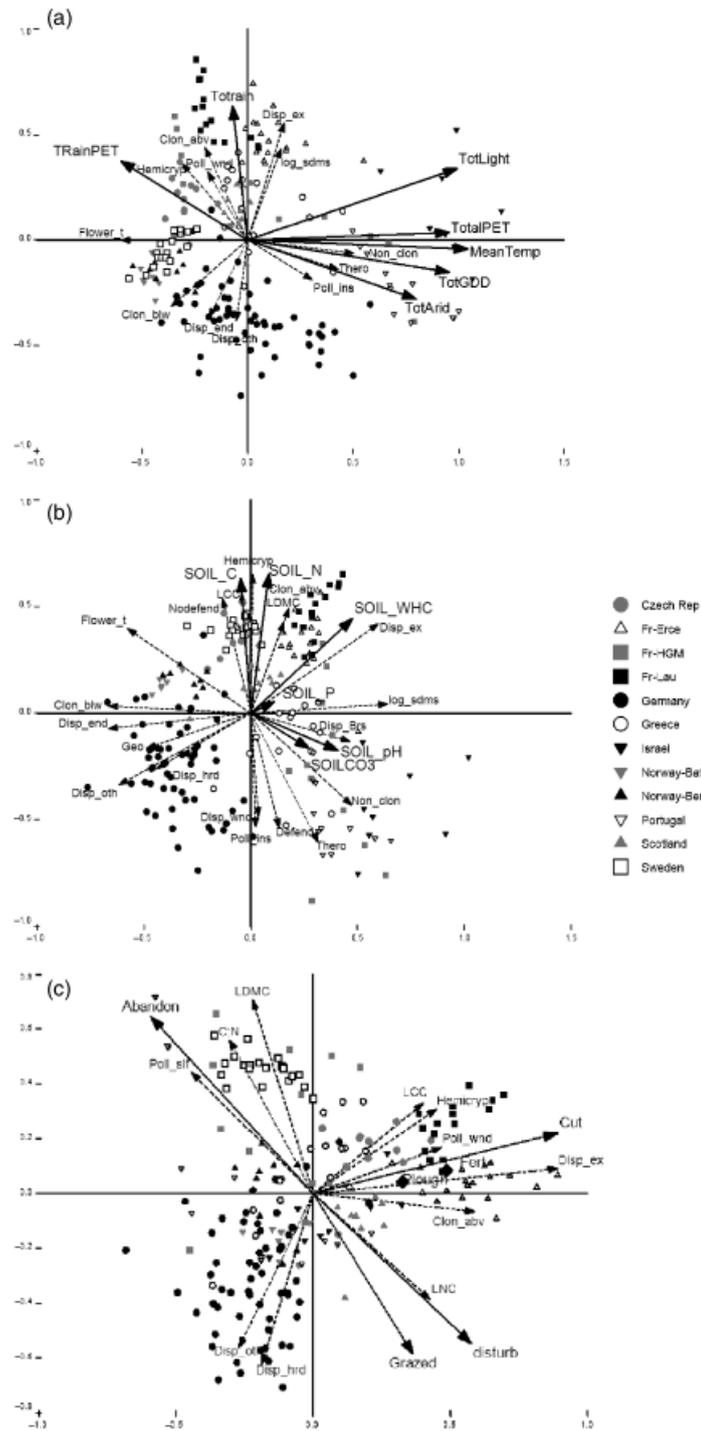
either singly or together (0.8–3.1%). Variation un-explained by the variables used in the analyses amounted to 52.6%. Very similar results were obtained by the same analyses of the unweighted data, except that the amounts of variation explained by soil alone and jointly by all three sources increased, while that explained by climate alone decreased.

Overall, the unexplained variation was also similar at 52.0%

Vegetative traits

Again, all three sets of environmental variables explained significant variation in weighted mean
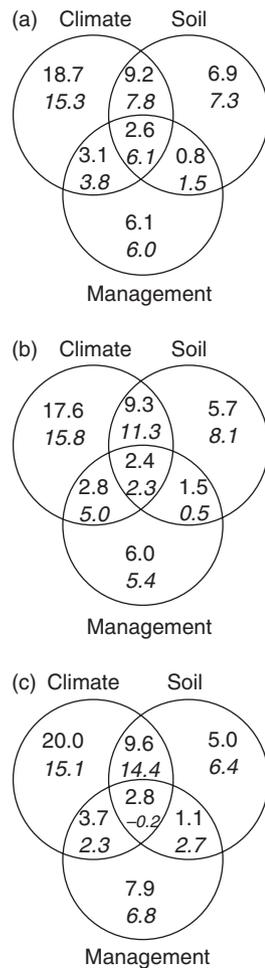
Fig. 2. Results of partitioning variance from climatic, edaphic and management sources for (**a**) all traits, (**b**) vegetative traits and (**c**) traits linked to regeneration via seeds. Figures in normal text refer to results from analysis of weighted mean data, figures in *italic* refer to results from analysis of unweighted data.

trait data ($P < 0.001$). The six climate variables together explained 31.7% (unweighted 34.4%) of the variation, the soil variables 17.9% (22.2%) and the management variables 12.7% (13.1%). The variables with the most explanatory power were the well-correlated mean temperature and growing degree-days, with light being less important than in the complete data set (Table 3). Again, individual climate variables were more powerful than edaphic or management variables. Soil carbon and nitrogen, and biomass removal, gave the highest proportion of variation explained by these latter two groupings.

All the ordinations used in constructing the partitioning were significant ($P < 0.001$, growing degree-days excluded, as in the full data set). The pattern of explained variation was similar to that for the full trait set, although with slightly less variation explained in all cases (Fig. 2b). Climate alone (17.6%), joint climate and soil (9.3%), management alone (6.0%) and soil alone (5.7%) explained the largest proportion of the variation. Taken together, the selected environmental variables explained 45.3% of the variation present. Analysis of the unweighted data gave very similar results, except the proportion of variation explained by soil variables alone and soil and climate together increased and that of climate decreased substantially. The environmental variables taken together explained 48.4% of the variation in the unweighted data.

Traits linked to regeneration via seeds

As in the previous two analyses, all three sets of variables explained significant variation in the weighted trait data (all $P < 0.001$). The six climate variables explained 36.2% (unweighted 31.6%) of the variation in the trait data, while soil variables (17.9%, unweighted 23.3%) and management (12.7%, unweighted 11.6%) explained less. Light was the most powerful climate variable in the analysis of seed regeneration traits, but generally the explanatory power was evenly spread across variables (Table 3). Soil water-holding capacity and cutting were the most powerful edaphic and management variables, respectively, for the weighted data, whereas for the unweighted data they were soil pH and carbonate and abandonment.

Again, all ordinations to construct the variance partitioning were significant (all $P < 0.001$, growing degree-days excluded as in the full data set, Fig. 2c). The pattern was also similar, except that the total proportion of variation explained was slightly higher (50.1%) for most parts of the partitioning. Analysis of the unweighted data was again similar in that it explained a similar proportion of the variation (47.5%). However, the proportion of variation explained by soil variables alone and soil and climate together increased and that of climate decreased substantially.

Trait-management relationships

Despite the large variation in climate and soils across the study sites, there was still a recognisable effect of management on plant functional traits of the vegetation (Fig. 3). There was a major axis of variation between plots long abandoned (right hand side of the graph) to plots with a high degree of dis-
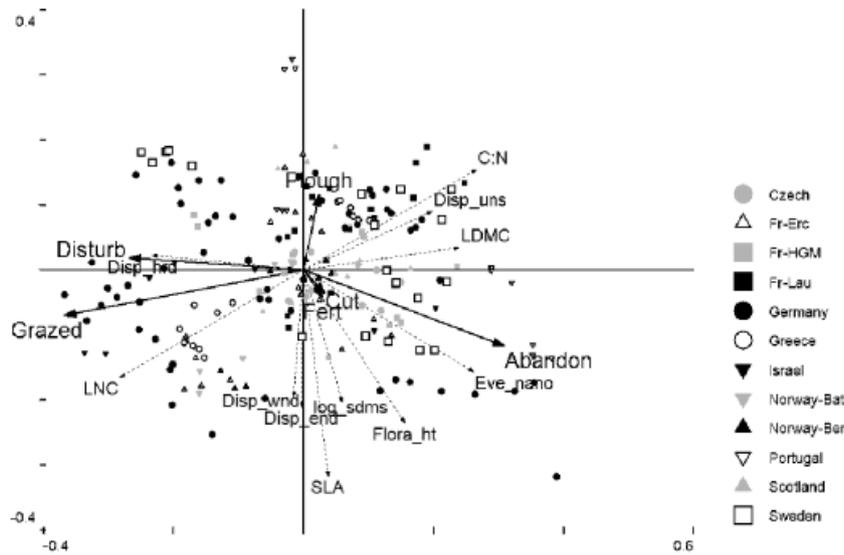
Fig. 3. Redundancy analysis of weighted mean trait values for each plot with management variables, with climatic and edaphic factors as covariables (traits shown are those that had fits of >3%.) Abbreviations as in Fig. 1, except *LNC* leaf nitrogen content and *SLA* specific leaf area.

turbance (left). Abandoned plots were characterised by higher cover of phanerophytes, taller species, plants with a high leaf dry matter content, high C:N ratios and low levels of leaf nitrogen, which is consistent with previous studies (e.g. Kahmen & Poschlod 2004), and analysis of this data set on a site-by-site basis (Garnier et al. 2007). Largely orthogonal to this gradient was an effect of ploughing that was associated with short, small-seeded species with low specific leaf areas. This latter relationship may be more a reflection of ploughing on low fertility sites (high fertility sites lie in the opposite direction), so that the leaf characteristics are more indicative of resource retentive strategies.

Discussion

Trait-environment relationships

The analyses showed that there were differences in the sensitivity of the different groupings of traits to the environmental gradients investigated. The initial stepwise ordinations clearly showed a strong filtering effect of climate on plant traits, as seen in the studies of Díaz et al. (1998) and Fonseca et al. (2000). For example, the balance between therophytes and herbaceous perennials generally changes with climate, because the former make a large contribution to the vegetation in warmer climates and the latter in colder ones (Raunkiaer 1908;

Crawley 1986). Similarly, pollination type was strongly related to climate; insect pollination was more frequent in hotter, drier climates, while wind pollination was more frequent in colder, wetter climates (Richards 1997).

As expected, plots with high soil carbon and high water-holding capacity had higher scores for traits associated for retentive characteristics (e.g. Grime 2006) such as high leaf carbon and leaf dry matter content. These plots were also associated with high total soil nitrogen, which is not a good predictor of available nitrogen as it is often associated with high organic matter content (Sprent 1987; Berendse et al. 1998; Sýkora et al. 2004). Management also produced the same effects; abandoned plots had higher values/frequencies of traits associated with resource-retentive life histories (e.g. evergreen leaves, high leaf dry matter content), whereas disturbed plots were more associated with acquisitive life histories (e.g. high leaf nitrogen content (Garnier et al. 2004; Kahmen & Poschlod 2004; Pakeman 2004; Louault et al. 2005; Vile et al. 2006). Disturbed plots were also characterised by small-seeded species (Lavorel et al. 1999; Schippers et al. 2001; Pakeman et al. 2008).

Partitioned trait-environment relationships

The analyses clearly show that a substantial (45-50%) and significant proportion of both the weighted and unweighted mean traits of vegetation can be

explained by the environmental variables used in this analysis. As might have been expected, the grouping of variables that operated over the largest spatial scale, climate, explained most variation, despite the limited climatic variation between sites within Europe. However, once climate effects had been partialled out, soil explained a further 7.7% of the variation, and management explained a significant 6.1% of the variation in the data set (Fig. 2a). The high degree of overlap between climate and both soil and management is at least partly due to the dependence of both on climate: soil formation is influenced by climate and so is the range of realistic land management options. This is demonstrated from redundancy analysis of the soil variables as species showed that the six climate variables explained 55.5% of their variation. This was higher than the proportion of variation in management explained by climate, 32.3%, as expected from the higher degree of shared variation between soil and climate (Fig. 2a), or the variation in soil variables explained by management (16.6%) or vice versa (21.8%). The proportion of variation explained might be increased with variables that describe the vegetation's environment in a more appropriate fashion, e.g. nitrogen mineralization rate, nitrogen nutrition index (Lemaire & Gastal 1997), or an improved description of disturbance. The very similar results from analysis of unweighted data suggest that, however mean values are calculated, the proportion of variation that can be explained by simple environmental variables remains similar, despite potential changes in individual relationships between traits and the environment. There was some indication that climate was less powerful, and soil more powerful, in explaining the variation in unweighted traits across plots than in the weighted analysis, and that there was more variation shared between groups of variables.

It might have been expected that the proportion of explained variance would have been higher for the vegetative traits than the seed regeneration traits, because these should show a high degree of convergence as a result of a productivity filter selecting for a predictable range of traits related to resource acquisition and conservation (Grime 2006). Other filters related to disturbance produce divergence in traits related to phenology, seed and seedling traits. For example, seed size, which can vary over three to five orders of magnitude within a plant community (Leishman et al. 1995). Consequently, it is surprising that the explained proportion of variation was higher for seed regeneration traits. Hence, despite the evolutionary

pressures for divergence, such as different seed sizes within a community (Rees & Westoby 1997; Grime 2006), it appears that the weighted mean seed size and other weighted traits are predictable for an assemblage, although there is evolutionary pressure for variation in these traits. These patterns were conserved in the analysis of unweighted data, indicating that the conclusions are robust.

Partitioning of the whole trait set or its two parts (vegetative, seed regeneration) showed the proportion of variance explained was always highest for climate, followed by soil and then management. As a high proportion of the variance explained by soil and climate was shared, then the proportion explained by soil alone was similar to that explained by management alone. The precedence of climate agrees with previous studies that have shown a strong filtering effect on plant traits by climate (e.g. Díaz et al. 1998), but, unlike that study, the mean values of the seed regeneration traits were as strongly influenced by climate as the vegetative traits in this analysis. The exact balance was dependent on the traits chosen for study. All the climate variables available were always selected during the initial stepwise selection process, indicating that some variation in functional traits between plots was correlated to each of them, despite the high degree of covariance between some (Fig. 1a). This may reflect the scale at which the environmental filters operate on the species traits. Climate operates at the largest scale and hence should have the highest impact, while soil and management vary at smaller scales and should have less effect on explaining the variation in weighted mean traits.

The marginal explanatory power of the variables (Table 3) varied between the vegetative and the seed regeneration traits. Their individual power in explaining the variance in the complete trait set was usually midway between the values for the two parts of the data. Vegetative traits were better explained by mean temperature and growing degree-days, soil carbon and nitrogen and biomass removal. Traits linked to regeneration via seeds were better explained by light, soil water-holding capacity, abandonment and cutting. This suggests, as expected (Grime et al. 1997; Grime 2006), that different environmental factors have differing impacts on controlling the weighted mean traits of vegetation at different phases of the plant life cycle. However, the patterns in the total analysis and in that of vegetative traits were very similar, confirming that vegetative traits tend to overwhelm mixed analyses with regeneration traits (Shipley et al. 1989; Lavorel et al. 1997).

Three major conclusions can be drawn from this analysis. First, although there was a large variation in climate and soils across the study sites, there was still a recognisable effect of management on plant functional traits of vegetation (Fig. 3). This identification of variation attributable solely to management provided good evidence that repeatable trait-management relationships might be applied across large scales – although the generalisations based on climate are valid only within their range. Second, the strength of the controls on the weighted and unweighted mean traits associated with the vegetative and regeneration via seed stages of the plant life cycle are very similar (Fig. 2b and c). Traits that are associated with divergent evolution, and hence show a high degree of variation within communities, still have their mean value well predicted by the environment. Third, there is a lot of shared variation between climate and management, between soil and management, and between all three groups of variables. The weighted mean traits of the vegetation were impacted simultaneously by different groups of environmental variables in a complex manner. This indicated that these trait-management relationships may have to be modulated by information from climate (e.g. de Bello et al. 2005) or productivity (including both fertility and soil moisture effects, e.g. Pakeman 2004) in order to provide predictive capabilities when linking changes in management to vegetation dynamics or changes in ecosystem function.

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