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The plant traits that drive ecosystems: Evidence from three continents

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Abstract.
Question: A set of easily-measured ('soft') plant traits has been identified as potentially useful predictors of ecosystem functioning in previous studies. Here we aimed to discover whether the screening techniques remain operational in widely contrasted circumstances, to test for the existence of axes of variation in the particular sets of traits, and to test for their links with 'harder' traits of proven importance to ecosystem functioning.
Location: central-western Argentina, central England, northern upland Iran, and north-eastern Spain.
Recurrent patterns of ecological specialization: Through ordination of a matrix of 640 vascular plant taxa by 12 standardized traits, we detected similar patterns of specialization in the four floras. The first PCA axis was identified as an axis of resource capture, usage and release. PCA axis 2 appeared to be a size-related axis. Individual PCA for each country showed that the same traits remained valuable as predictors of resource capture and utilization in all of them, despite their major differences in climate, biogeography and land-use. The results were not significantly driven by particular taxa: the main traits determining PCA axis 1 were very similar in eudicotyledons and monocotyledons and Asteraceae, Fabaceae and Poaceae.
Links between recurrent suites of 'soft' traits and 'hard' traits: The validity of PCA axis 1 as a key predictor of resource capture and utilization was tested by comparisons between this axis and values of more rigorously established predictors ('hard' traits) for the floras of Argentina and England. PCA axis 1 was correlated with variation in relative growth rate, leaf nitrogen content, and litter decomposition rate. It also coincided with palatability to model generalist herbivores. Therefore, location on PCA axis 1 can be linked to major ecosystem processes in those habitats where the plants are dominant.
Conclusion: We confirm the existence at the global scale of a major axis of evolutionary specialization, previously recognised in several local floras. This axis reflects a fundamental trade-off between rapid acquisition of resources and conservation of resources within well-protected tissues. These major trends of specialization were maintained across different environmental situations (including differences in the proximate causes of low productivity, i.e. drought or mineral nutrient deficiency). The trends were also consistent across floras and major phylogenetic groups, and were linked with traits directly relevant to ecosystem processes.

Keywords: Argentina; Comparative ecology; England; Functional diversity; Iran; Plant functional types; Recurrent patterns of specialization; Spain; Specific leaf area.

Nomenclature: Bolòs et al. (1990); Flora Iranica (1963 onwards); Stace (1991); Zuloaga et al. (1994); Zuloaga & Morrone (1996, 1999).

Introduction

The photosynthetic activities of green plants provide the mechanism whereby resources enter ecosystems, and there has been gradual acceptance that in this process plants are not acting as a simple conduit. It is now widely accepted that differences between plants in the way they acquire, process and invest resources can have very large effects on the species composition and functioning of ecosystems (Chapin et al. 2000; Loreau et al. 2001).

At the present time many ecosystems are experiencing changes in land use and climate that are unprecedented in scale and rate (Vitousek et al. 1997). There is an urgent need to devise predictors of the impacts of such events and often this need arises in circumstances where there is no detailed knowledge of ecosystem properties. In recent years this problem has given extra impetus to the search for easily-measured, universally-applicable predictors of ecosystem function and responsiveness to change. Through investigations in various parts of the world (e.g. Chapin et al. 1996; Díaz & Cabido 1997; Grime et al. 1997; Reich et al. 1997; Wardle et al. 1998; Cunningham et al. 1999; Craine et al. 2001; Wright & Westoby 2002; Ackerly 2003), evidence is growing that such predictors do exist, and can be found in the form of single traits or sets of co-occurring traits of plants.

Why should screening of plant traits on a world basis lead to the discovery of universally applicable predictors of ecosystem properties? Superficial variety in plant life is deceptive and tends to obscure the presence of recurring constraints on the core functioning and evolutionary specialization available to plants. The evidence for this underlying constraint in the evolution and ecology of plants is to be found in a long series of investigations and reviews (Ramenskii 1938; Grime 1974, 2001; Chapin 1980; Lambers & Poorter 1992; Chapin et al. 1993; Westoby 1998; Aerts & Chapin 2000; Westoby et al. 2002). For the purposes of this paper, the key finding is that the core traits and trade-offs consistently identified in these publications (life history, growth rate, tissue life span, mineral nutrient concentrations, defence against generalist herbivores, resistance to decomposition), relate to aspects of plant functioning with unambiguous repercussions on ecosystem functioning.

To date, most screening programmes that have suggested the existence of useful plant predictors of ecosystem properties and susceptibility to local or global change have concentrated on local floras and vegetation types. The main purpose of this paper is, when restricting attention to a set of easily measured ('soft') traits that have been identified as potentially useful predictors of ecosystem functioning in previous studies, to discover whether the screening techniques remain operational in widely contrasted circumstances, and to test for the existence of axes of variation in the particular sets of traits. Secondary objectives were to see how far these traits and axes of variation are aligned with phylogeny; and to relate them to 'harder' traits of proven importance to ecosystem functioning.

Table 1. A comparison of the study areas in four different countries.

	Argentina	England	Iran	Spain
Area (km^2)	ca. 40 000	ca. 3000	ca. 725	ca. 1000
Latitude (range)	31°25' - 32° S	53°05'-53°32' N	38°41' - 39°7' N	41°45'- 41°70' N
Longitude (range)	64°10' - 68°37' W	0°57' - 2°51' W	46°42' - 46°58' E	0°40' - 1°40' W
Altitude (range; m asl)	350 - 2155	2 - 636	350 - 2840	100 - 400
Mean annual rainfall (range; mm)	85 - 912	565 - 1800	316 - 686	300 - 350
Rainfall distribution	Confined to warm season	Throughout year but with winter maximum	Throughout year but with winter maximum	Mainly in spring and autumn
Mean annual temperature (range; °C)	8.1 - 19.6	9 - 11	5 - 14	6 - 24
No. frost-free months (range)	0 - 8	3 - 6	6	3 - 5
No. months in which evapotranspiration > precipitation (range)	1 - 12	0 - 2	2 - 4	6
Dominant vegetation types sampled	Halophytic shrubland Montane grassland Montane woodland Xerophytic woodland Xerophytic shrubland	Arable Broad-leaved woodland Coniferous plantation Grassland Heathland Wetland	Broad-leaved woodland Montane grassland Montane dwarf scrub	Arable Riverine habitats Xerophytic shrubland Xerophytic woodland
Land use in sampled areas	Extensive livestock (cattle, horses, goats and sheep) Ranching, with associated logging and burning Cultivation scattered and uncommon	Arable agriculture in lowland; grazing by sheep and cattle in uplands Some extensive coniferous plantations Much industrial and urban development in lowlands	Extensive livestock in summer (sheep and goats) Sites of cultivation now abandoned	Arable agriculture especially in lowlands; grazing by sheep much reduced and mainly confined to fallow arable land Some industrial and urban development in lowlands
Total number vascular plant species in the region studied	ca. 2100	ca. 950	ca. 1020	ca. 1000
Human population density	ca. 6 $ind.km^{-2}$	ca. 590 $ind.km^{-2}$	< 1 $ind.km^{-2}$; visited by nomads in summer	ca. 15 $ind.km^{-2}$

Methods

We constructed a data set comprising common vascular plant species from four countries differing greatly in climate, biogeography and land use: central-western Argentina, central England, northern upland Iran, and northeastern Spain (Table 1).

Species selection

The general criteria for species selection included: (1) a species had to be common; and (2) the collection had to cover a wide range of growth forms, families and habitats. Our species selection was not clade-based, but rather local assembly-based. This puts our trait selection strategy within the category of non-random taxon sampling (Ackerly 2000). This is the most appropriate sampling strategy considering that one of our major aims was to assess consistency of patterns across clades, species assemblies and ecosystems, and our questions were much more in the field of present-day community and ecosystem ecology, than in that of evolutionary ecology (Ackerly 2000; Westoby et al. 2002). We restricted our study to common species not only for practical reasons (considering all species in the four floras would have been unfeasible), but mainly because we wished to focus on species that (1) appeared well adapted to the local conditions; and (2) had a reasonably good chance of impacting upon major ecosystem processes. Only common species can ensure these goals (Grime 1998). We tried to cover the widest possible range of growth forms, families and habitats in an attempt to provide the strongest possible test for the patterns detected, and the widest possible scope for our generalizations.

The whole data set comprised 640 taxa belonging to 86 families (App. 1). The Argentine data set comprised the 207 most abundant species in 313 vegetation sample plots described in Díaz & Cabido (1997). The species set represented ca. 10% of the total number of species in the region, and included 51 plant families, numerous growth forms, and plants from pristine and from disturbed habitats. The 143 British species represented ca. 15% of the total number of species in the region, included 47 plant families, and were selected to ensure that all the major habitats and climatic regions (lowland and upland) were included. The 186 species from Iran (43 families, ca. 18% of the flora), and the 104 species from Spain (30 families, ca. 10% of the flora), were similarly representative. In total 49 species were common to two or more data sets; their measured trait values were similar in different countries, supporting the consistency and comparability of our methods, but sufficiently different to represent adapted portions of the local flora in each region, and therefore genuine unbiased contributors. The outcomes of the analyses were unaffected by whether they were considered or not; therefore we included them for completeness.

Trait selection and measurement

There is now sufficient published evidence pointing to a relatively short list of morphological and functional traits strongly linked to key aspects of both the established and regenerative phases of the life of plants (see Weiher et al. 1999; Lavorel & Garnier 2002 and Westoby et al. 2002 for recent reviews). Some of these traits have also been shown to influence ecosystem processes (Hobbie

Table 2. Traits measured on 640 vascular plant species from Argentina, England, Iran and Spain. See Cornelissen et al. (2003) and references therein for details on ecological meaning and measurement procedures. *1trait $\log_{10}$-transformed for analysis; *2categories follow Grime et al. (1988); *3maximum height of well grown individuals, but excluding small leaves above the height of the main canopy; *4seed size and shape were calculated for the whole dispersal unit (see Thompson et al. 1993 for details).

Trait	Type of variable
Leaf size	Continuous (mm^2)*1
Specific leaf area	Continuous (mm^2 leaf area / mg leaf mass)*1
Leaf toughness	Continuous (= leaf tensile strength; Newton mm leaf $width^{-1}$)*1
Inrolling of lamina	Continuous [1 – (inrolled width/expanded width)]
Leaf thickness	Continuous (mm)*1
Canopy height	Continuous (cm)*1*3
Woodiness	Ordinal: 0 = non-woody; 1 = semi-woody; 2 = soft wood ($\leq$ 0.6 $mg.mm^{-3}$); 3 = dense wood (> 0.6 $mg.mm^{-3}$)
Mean distance between ramets connected below ground or at ground level	Ordinal: 0 = no ramets; 1 = < 10 cm; 2 = 10 - 50; 3 = > 50
Shoot phenology	Ordinal for green biomass peak: 1 = no evident peak; 2 = winter, autumn, early spring peak; 3 = late spring, spring, spring-summer; 4 = late summer-early autumn; 5 = late spring-summer, summer*2
Life span	Ordinal: 1 = annual; 2 = biennial; 3 = perennial
Seed mass	Continuous (mg air-dry mass)*1*4
Seed shape	Continuous (variance among length, width and depth when length = 1; for a spherical seed, variance = 0)*1*4

1992; Berendse 1994; Aerts 1995; MacGillivray et al. 1995; Aerts & Chapin 2000), but many of these require procedures that are too laborious for large-scale screening purposes (i.e., 'hard' traits; see below). We aimed to employ only measurements of known importance to (1) the regenerative and established phases of the plant life cycle, (2) plant responses to the environment, and/or (3) plant effects on ecosystem processes. Measurements also had to be applied rapidly to large numbers of species, i.e. relatively 'soft' (Hodgson et al. 1999; Lavorel & Garnier 2002). We selected 12 continuous or ordinal traits (Table 2). These traits are known not to be trivially correlated among themselves, i.e. each trait is measuring a different plant property. All non-seed traits relate to healthy, sexually mature plants growing in unshaded habitats, and are the average of at least six replicates per species. See Hendry & Grime (1993), Díaz & Cabido (1997), Grime et al. (1997), Westoby (1998) and Cornelissen et al. (2003) for details on ecological interpretation and measurement of traits.

In order to test the links between these recurrent patterns of specialization and major ecosystem processes, we conducted additional screening of 'hard' traits on subsets of species from Argentina and England, selected to represent the whole range of habitats, growth forms, and taxa present in the main data bases (App. 1). These additional traits were relative growth rate, leaf nitrogen content, rate of litter decomposition, and preference by generalist invertebrate herbivores, all of proven value as predictors of ecosystem processes (Mooney 1972; Grime & Hunt 1975; Coley 1980; McNaughton et al. 1989; Herms & Mattson 1992; Hobbie 1992; Berendse 1994; Aerts 1995; Grime et al. 1996; Aerts & Chapin 2000; Lavorel & Garnier 2002). Relative growth rate was measured on seedlings growing under standard conditions (Grime & Hunt 1975; Hunt & Cornelissen 1997; F. Vendramini unpubl.). Leaf nitrogen content was measured on young, fully expanded sun leaves (Thompson et al. 1997; Vendramini et al. 2000). Potential decomposition rate was expressed as percentage of dry weight loss of 1 g litter in bags buried in a standard decomposition bed in an experimental garden under natural climatic conditions in the cities of Sheffield (England) and Córdoba (Argentina) (Cornelissen 1996; Pérez-Harguindeguy et al. 2000). Preference by model herbivores was determined as percentage of leaf area consumed by garden snails (*Helix aspersa*) in cafeteria experiments, involving ten 1-cm^2 replicates per species, randomly allocated to positions in a grid (Grime et al. 1996; Cornelissen et al. 1999; Pérez-Harguindeguy et al. 2003).

Data analysis

To detect general specialization trends across the four floras, we organized the data into a single 12 trait × 640 species matrix. We submitted the matrix to a Principal Component Analysis (PCA) based on the correlation matrix of variables, in which data are centred and standardized by standard deviation, which is considered appropriate for mixed data (Jongman et al. 1987).

In order to assess whether trends detected in the whole data set were similar in different individual floras, we ran separate PCAs considering (1) only the species from each country; and (2) the species of all possible combinations of three countries (i.e. Argentina + England + Iran, Argentina + England + Spain, Argentina + Iran + Spain, and England + Iran + Spain). We then correlated the eigenvector scores of the 12 plant traits on PCA axes 1 and 2 obtained from analyses of each individual country against the eigenvector scores of the same traits from joint analyses of the three other countries.

In order to assess whether the general trends found in the analysis of the whole data set were consistent in different broad taxonomic groups, we ran separate PCAs for eudicotyledons (*sensu* Soltis et al. 1999), monocotyledons, and three major plant families, each represented by at least 50 species in the whole data set and at least 12 species in each individual country: *Asteraceae*, *Fabaceae* and *Poaceae*. We then correlated the eigenvector scores of 12 plant traits along Axis 1 and 2 obtained in separate PCAs (eudicotyledons against monocotyledons, *Asteraceae* against *Fabaceae*, *Asteraceae* against *Poaceae*, and *Fabaceae* against *Poaceae*). Only 11 traits (woodiness excluded) were considered in comparisons involving monocotyledons.

Table 3. Eigenvector scores of plant traits in three main PCA axes, obtained from a matrix of 12 traits × 640 species. Values are ranked in order of absolute magnitude along PCA 1. The four highest eigenvector scores for each PCA axis are indicated in bold. Values in parentheses indicate variance accounted for by each axis. See Table 2 for explanation of traits.

Trait	PCA 1 (23.87%)	PCA 2 (16.71%)	PCA 3 (13.16%)
Specific leaf area	**– 0.526**	– 0.020	0.063
Leaf thickness	**0.428**	0.137	– 0.224
Leaf size	**– 0.365**	**– 0.300**	0.222
Leaf tensile strength	**0.354**	0.202	**0.304**
Woodiness	0.285	**– 0.490**	– 0.132
Shoot phenology	– 0.265	– 0.201	0.233
Life span	0.219	– 0.199	**0.515**
Inrolling of lamina	0.158	0.193	**0.355**
Canopy height	0.152	**– 0.522**	– 0.056
Seed mass	0.148	**– 0.463**	– 0.120
Mean distance between ramets	0.086	– 0.068	**0.538**
Seed shape	0.067	0.030	0.186

We also compared the range of scores of species belonging to the *Asteraceae*, *Fabaceae* and *Poaceae* along axes 1 and 2 in the PCA ordination of the whole data set.

To evaluate whether the patterns of specialization detected on the basis of mostly 'soft' traits were consistent with traits of proven value as ecosystem predictors ('hard' traits), we correlated the scores of selected species from Argentina and England along PCA axis 1 obtained from the analysis of the whole data set against their relative growth rate, leaf nitrogen content, and rate of litter decomposition. In the case of consumption by generalist invertebrate herbivores, data distribution was markedly skewed due to the presence of many zero values; therefore we ran Mann-Whitney tests to compare the scores along PCA axis 1 (whole data set) of Argentine and British species that were eaten vs. those that were not eaten.

Results

Recurrent patterns of ecological specialization

Similar patterns of specialization were detected in the four floras (Fig. 1). The first PCA axis was identified as an axis of resource capture, usage and release, accounting for ca. 24% of the total variance, a remarkably high value considering the size and heterogeneity of the database. At the lower end of PCA axis 1 were species with large, thin, tender leaves of high specific leaf area, while at the higher end were species with small, thick, tough leaves of low specific leaf area. PCA axis 2 accounted for a further ca. 17% of the total variance and appeared to be a size-related axis. Tall species with dense wood, large leaves and large seeds (mainly trees) were found at low values while smaller, often herbaceous species with small leaves and seeds occurred at high values of PCA axis 2. Axis 3 appeared to be a life history/clonality axis (Table 3). Here attention is largely confined to the interpretation of axis 1.

The floras of Argentina and England showed the widest range and the most extreme types along PCA axis 1 (Fig. 1), with British aquatic plants and fast-growing, short-lived herbs of fertile soils representing one extreme, and desert succulents from Argentina representing the opposite extreme. Otherwise the four floras overlapped widely on the PCA ordination plane (scores ca. –1 to 4 along axis 1, and –4 to 2 along axis 2; Fig. 1). British plants from the most nutrient-deficient habitats, identified as extreme stress tolerators in an earlier functional comparison (e.g. *Festuca ovina*, *Koeleria macrantha*, *Deschampsia flexuosa*; Grime et al. 1997), occupied an intermediate position (scores ca. 1 to 2 along axis 1) in the ordination of the combined floras, very similar to that of plants typical of seasonally dry areas of Argentina and Spain. A separate PCA excluding desert succulents produced very similar results, including the same rank of eigenvector scores along both axes, indicating that the ordination was not strongly driven by these extreme plant

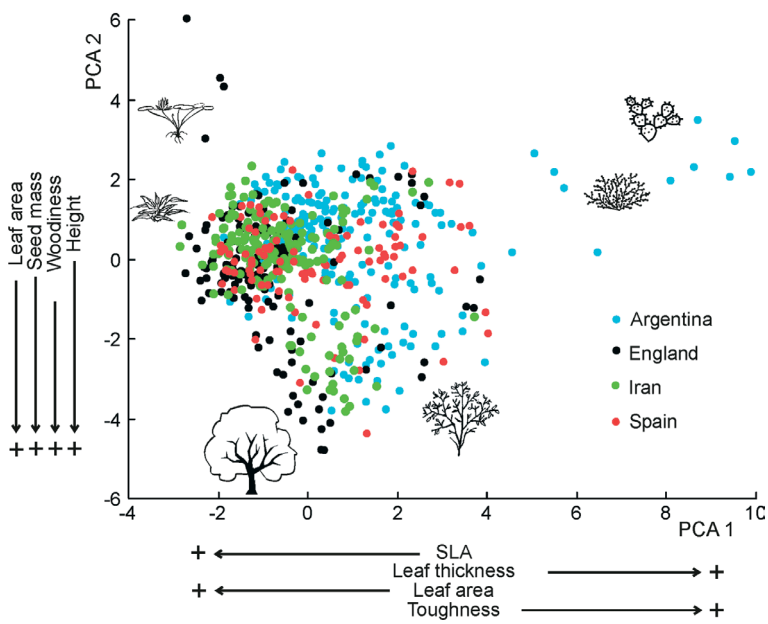

Fig. 1. PCA ordination of 640 plant species from Argentina, England, Iran and Spain, on the basis of 12 traits. Labels display traits with the highest eigenvector scores on PCA axes 1 and 2, with the label with the highest score presented nearest to the axis. Stylized figures indicate extreme types, such as aquatics and tender-leaved ephemerals at the lower end of PCA axis 1, *Cactaceae* at the higher end of PCA axis 1, and large-leaved deciduous trees and shrubs at the lower end of PCA axis 2. Eigenvector scores of all traits along PCA axes 1-3 are in Table 3. Locations of individual species on the ordination plane are available from the corresponding author.

Table 4. Correlations between the eigenvector scores of 12 plant traits (see Table 2) on PCA axes 1 and 2 from separate analyses of species from each individual country, and eigenvector scores of the same traits along PCA axes 1 and 2 from joint analyses of the three other countries. *r* = Spearman Rank Correlation Coefficient.

	PCA 1		PCA 2	
	r	*P*	*r*	*P*
Argentina	0.748	0.005	0.587	0.045
England	0.720	0.008	0.923	< 0.001
Iran	0.671	0.017	0.748	0.005
Spain	0.944	< 0.001	0.683	0.014

types (also see correlation between PCA of Argentine species against PCA of English + Iranian + Spanish species; Table 4). These results strongly imply the existence of suites of correlated traits, and consistent positive and negative associations between plant characteristics.

The patterns of ecological specialization detected along the first two PCA axes appear to be largely independent of geographical location. The eigenvector scores of different plant traits were very similar in separate PCAs of the data sets for individual countries (Table 4). The same traits remained valuable as predictors of resource capture and utilization despite major differences in the physical, chemical and biotic conditions of the four regions, and in particular, great variation in the proximate causes of low productivity (drought or mineral nutrient deficiency).

Phylogeny was not the major factor in the expression of PCA axis 1, in the sense that the results were not significantly driven by particular taxa. The main traits determining PCA axis 1 were very similar in eudicotyledons and monocotyledons (Fig. 2a), and in the major families *Asteraceae*, *Fabaceae* and *Poaceae* (Fig. 2b-d). In all major taxa examined, PCA axis 1 differentiated between plants with large leaves, high specific leaf area, and peak production of new leaves strongly confined to the growing season, and evergreen plants with small, thick, tough leaves. Furthermore, when the full data set was considered (Fig. 1) the ranges of scores of *Asteraceae*, *Fabaceae* and *Poaceae* along PCA axis 1 overlapped to a very large extent (Fig. 3a). Despite differences between families that are apparent to all ecologists, and which have frequently led to the assumption that some families (e.g. legumes and grasses) represent distinct functional types in any ecological context, the same overriding trait trade-offs operate in each of these major taxa.

Phylogeny played a more important role in the determination of PCA axis 2 than Axis 1. Although the main traits determining PCA axis 2 were similar in eudicotyledons and monocotyledons ($r = -0.655$; $P = 0.029$), there were different trends for *Asteraceae*, *Fabaceae* and *Poaceae* (*Asteraceae* vs. *Fabaceae*: $r = 0.202$ and $P = 0.527$; *Asteraceae* vs. *Poaceae*: $r = 0.072$

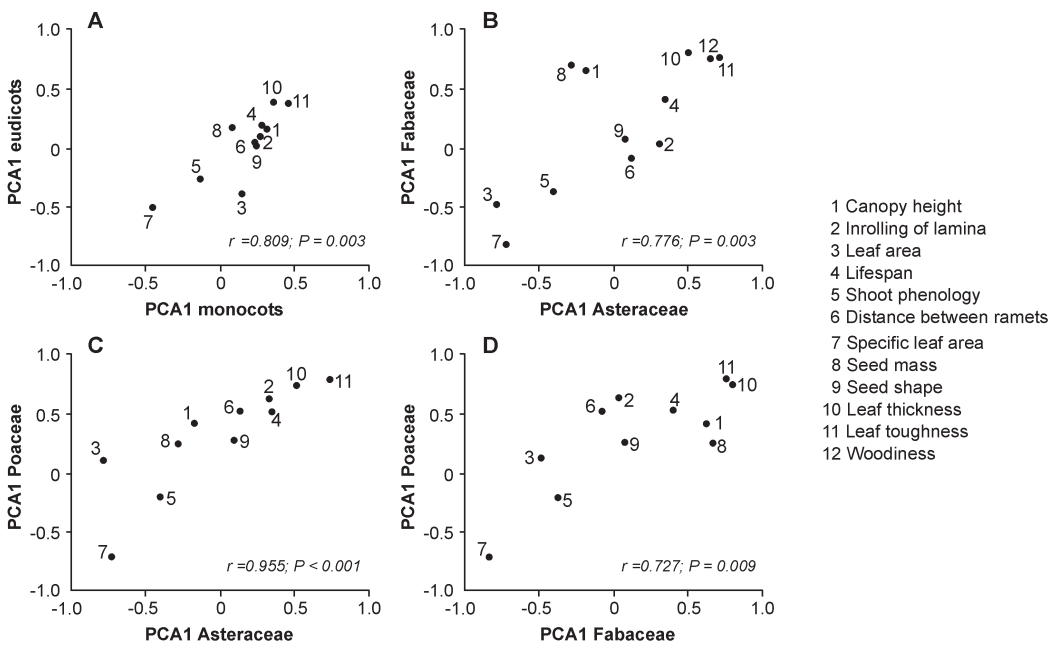

Fig. 2. Relationships between the eigenvector scores of 11-12 plant traits along Axis 1 of **(A)** separate PCA analyses of 150 monocotyledons and 490 eudicotyledons belonging to four different local floras (Argentina, England, Iran and Spain); and **(B-D)** separate PCA analyses of three major plant families with > 50 species in the database (*Asteraceae*: 87 species; *Fabaceae*: 51 species; *Poaceae*: 118 species). Only 11 traits (woodiness excluded) were considered in comparisons involving monocotyledons. *r* = Spearman Rank Correlation Coefficient.

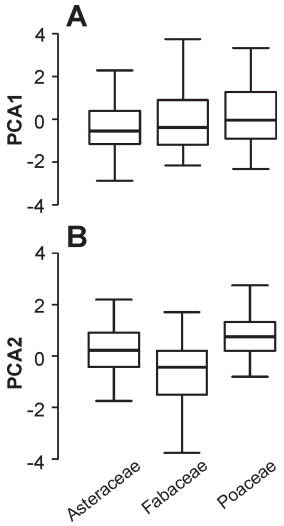

Fig. 3. Distribution of species belonging to plant families with > 50 species (*Asteraceae*: 87 species; *Fabaceae*: 51 species; *Poaceae*: 118 species) along PCA axes 1 **(A)** and 2 **(B)**. Values correspond to scores of species on axes 1 and 2 of a PCA ordination of 640 plant species from Argentina, England, Iran and Spain (Fig. 1). Box = interquartile range, containing 50% of values; line across box = median; whiskers = highest and lowest values, excluding outliers (i. e. cases with values > 1.5 box lengths from the upper or lower edge of the box). Two outliers were identified in **(A)**, representing less than 0.80% of the species considered in this analysis; these were the Argentine halophytes *Cyclolepis genistoides* (*Asteraceae*) and *Prosopis strombulifera* (*Fabaceae*). No outliers were identified in the case of **(B)**.

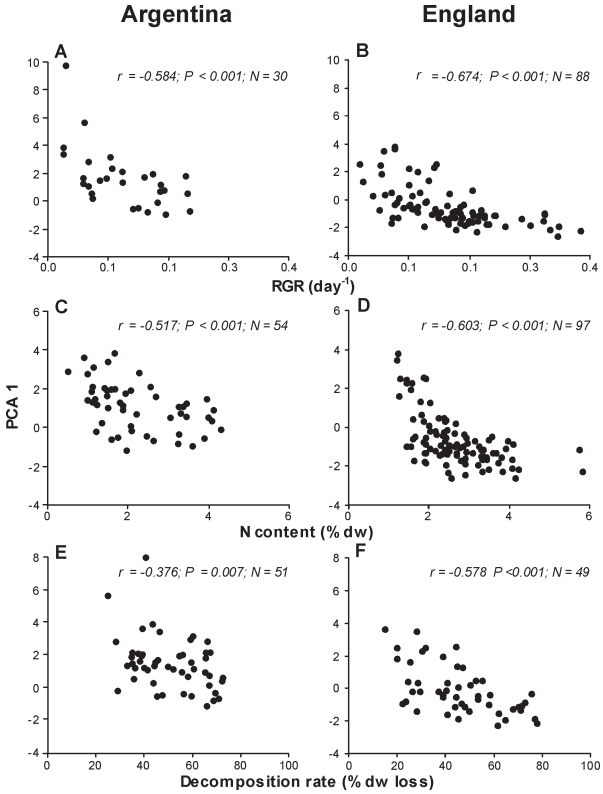

Fig. 4. Relationships between PCA axis 1 scores from Fig. 1 and relative growth rate **(A, B)**, leaf nitrogen content **(C, D)**, and potential decomposition rate **(E, F)** of subsets of species from Argentina and England, selected to represent the whole range of habitats, growth forms, and taxa present in the main database. dw = dry weight; r = Spearman Rank Correlation Coefficient. See App. 1 for list of Argentine and British species involved in this comparison.

and $P = 0.831$; *Fabaceae* vs. *Poaceae*: $r = 0.400$ and $P = 0.222$), and the ranges of scores of these taxa along axis 2 of the PCA ordination of the whole data set overlapped less than in the case of axis 1 (Fig. 3b). In particular, *Fabaceae* showed lower scores, associated with the large canopy height and seed size, and dense wood, that are typical of some of its member species.

Links between recurrent suites of 'soft' traits and 'hard' traits

The validity of PCA axis 1 as a key predictor of resource capture and utilization was confirmed by comparisons between this axis and values of more rigorously established predictors ('hard' traits) for the floras of Argentina and England (Fig. 4). PCA axis 1 was correlated with variation in relative growth rate (Fig. 4a, b), leaf nitrogen content (Fig. 4c, d), and litter decomposition rate (Fig. 4e, f). It also coincided with palatability to generalist herbivores in an analysis of preference by model herbivores (garden snails), with unpalatable plants being concentrated towards the higher end of PCA axis 1 for both countries (Mann-Whitney test; for Argentina, $N = 51$ species, $z = -2.124$; $P = 0.034$; for England, $N = 51$ species, $z = -3.532$; $P < 0.001$). These four attributes have clear links among themselves and with major aspects of ecosystem functioning, such as primary productivity, nutrient cycling and trophic transfers (see Introduction for references). Therefore, location on PCA axis 1 can be linked to major ecosystem processes.

Discussion

Recurrent patterns of plant specialization and ecosystem processes: a good start for generalization in ecology?

Our results indicate a fundamental trade-off in plant design between a set of plant attributes that allow rapid acquisition of resources ('acquisitive type'), and another

set that permits conservation of resources within well protected tissues ('conservative/retentive types'). This confirms and extends the predictions of previous theoretical and empirical work based on more restricted databases (Mooney 1972; Grime 1974; Chapin 1980; Coley 1980; Lambers & Poorter 1992; Herms & Mattson 1992; Hobbie 1992; Chapin et al. 1993; Berendse 1994; Aerts 1995; Díaz & Cabido 1997; Grime et al. 1997; Reich et al. 1997; Aerts & Chapin 2000; Wright & Westoby 2002). On the basis of the largest and most diverse data set published so far, our findings suggest that this fundamental trade-off may be broadly applied to contrasting floras, environments, and growth forms. This trade-off appears to be largely independent of both geographical location and taxonomic affinity, and there is a close association between position in the trade-off and traits linked to major ecosystem processes.

Our findings suggest that water- and nutrient stress lead to convergent trait syndromes, a finding consistent with other recent empirical work (Cunningham et al. 1999; Lamont et al. 2002), and illustrate how, on the basis of different anatomical structures, plants from very different lineages address the same problem: the protection of photosynthetic tissue from external agents, especially desiccation and herbivory. Variation observed along PCA Axis 1, the fact that protection of photosynthetic tissue is achieved through slightly different mechanisms (e.g., fibrous, inrolling lamina in graminoids; thickened cuticle in succulents), and slight variations in the associations between some traits in different families (e.g. shoot phenology and seed mass, Fig. 2b-d) reconcile two different approaches in plant ecology, one that searches for general patterns of functional specialization, and another that emphasizes the fine-tuning of species and populations to particular abiotic and biotic habitat conditions (e.g., Harper 1982; Grubb 1985, 1998). Many traits, notably some aspects of the regeneration phase and phenology, with low association with the first PCA axes (Fig. 1, Table 3), appear to be relatively independent from the general trends described in this article, and thus provide ample scope for the exploration of patterns important at the local level, or important to certain populations in the face of particular sources of stress (e.g. pollution) or disturbance.

Particularly noteworthy was the close similarity in trait variation between *Fabaceae* and *Poaceae* (Figs. 2d and 3a), often separated as different functional types in ecosystem studies (Hooper & Vitousek 1997; Hector et al. 1999; Lepš et al. 2001; Spehn et al. 2000; Tilman et al. 2001). Our findings do not deny the fact that some members of these plant families can indeed act as distinct functional types in some situations. For example, the invasion of some nitrogen-poor systems by nitrogen-fixers (often, but not always, members of the *Fabaceae*), sometimes leads to dramatic increase of nitrogen availability in the soil (reviewed by Levine et al. 2003), and thus facilitates vegetational shifts from conservative to acquisitive traits. Rather, our results show that these three major families do not differ substantially in terms of the conservative-acquisite trade-off and thus in terms of their effects on major ecosystem processes mediated by these traits. This indicates that there is no evidence that justifies assuming *Fabaceae*, *Asteraceae* and *Poaceae* as different functional types *a priori* in every situation.

The existence of consistent links between 'soft' and 'hard' traits has been put forward as a promising way to connect plant traits with major ecosystem processes (Hodgson et al. 1999; Lavorel & Garnier 2002). Our results, based on extensive 'soft' and 'hard' trait information, show that those links are indeed present, and they are consistent across different environmental situations.

Perspectives and applications

The lesson from other sciences, such as physics and chemistry, is that genuine progress in understanding the diversity of the natural world comes from a recognition of its fundamental unity. In this paper we have shown that a major axis of evolutionary specialization, previously identified in several floras, can also be detected at the trans-regional scale, across floras exhibiting huge variation in phylogeny, and across areas of contrasting climates, land use regimes and biogeographical histories. Has this demonstration helped in the quest for the fundamental unity of ecology? We think it has, but there is still a long way to go. The strength of science may derive from the questioning and falsification of attempted generalizations, and from the search for exceptions, but this search is only truly meaningful against a solid background. For both theoretical and practical reasons, we need to know how the axes of ecological specialization identified here are distributed across heterogeneous landscapes, how they respond to global changes in climate and land use, and how far they predict key aspects of ecosystem functioning such as productivity, nutrient cycling, carbon storage, and resilience.

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