

Research in context

Seed size, number and strategies in annual plants: a comparative functional analysis and synthesis

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Dedicated to Ferran Royo Pla 1969–2016: leader of Grup de Recerca Terres de l'Ebre, Catalonia, and friend.

Running headline: Seed size, number and strategies in annuals

Abstract

- *Background and Aims* Although ecologically important, the traits, seed yield and seed number, are not routinely studied. Nonetheless, for annuals at least, seed yield should primarily be a positive function of plant biomass and predictions of seed number should additionally include, negatively, seed mass. Demonstrating these relationships would allow a new regenerative dimension to be added to trait-based ecology.
- *Methods* Using published values of seed number as the ‘golden standard’ and a large functional database, seed yield and number plant⁻¹ and m⁻² were predicted by multiple regression. Subsequently, ecological variation in seed size and number was explored with respect to (a) English and Spanish habitat, (b) CSR strategy, from newly-calculated values, and (c) changed abundance in the British flora.
- *Key Results* As predicted, seed yield plant⁻¹ was consistently a positive function of plant size and competitive ability and largely independent of seed mass. Regressions estimating seed number included additionally seed mass as a negative function. However, relationships differed numerically between regions, habitats and CSR strategies. Practically, seed yield m⁻² was positively correlated with FAO crop yield, and increasing British annuals produced numerous seeds. Nevertheless, predicted values must be viewed as comparative rather than absolute: they varied with the ‘golden standard’ used. Moreover, regressions predicting seed yield m⁻² achieved low precision. Some ‘annuals’ had a different life-history over part of their range.
- *Conclusions* For the first time, estimates of seed yield and number for over 800 annuals and their predictor equations have been produced and the ecological importance of each trait has been illustrated. Nevertheless, many aspects require further work. These include determinate *versus* indeterminate flowering (i.e. ‘bet-hedging’), CSR methodologies, phylogeny, seed yield m⁻² and changing life-history. ‘Regenerative trait-based ecology’

remains in its infancy and readers are invited to use estimates, included as Supplementary Data Table S7, to advance studies to the next level.

Keywords: allometry, bet-hedging, canopy structure, conservation status, CSR strategy, functional traits, inflorescence structure, life history, phylogeny, plant size, regenerative strategy, seed mass, Seed–Phytomer–Leaf (SPL) theory, seed yield, trade-offs

INTRODUCTION

The world's flora is characterized by mass extinction and colonization events with the trajectory of change strongly influenced by the ability or failure of species to regenerate from seed (Walck *et al.*, 2011; Pimm *et al.*, 2014). Plants produce an abundance of seed. Nevertheless, a plethora of risk factors impact upon subsequent seed dispersal and the development of new plants (Chambers and MacMahon, 1994). In consequence, few seeds fulfil their potential and attain reproductive maturity. Thus, for example, a single oak tree (*Quercus robur*) may produce several million acorns during the course of its lifetime (Newbold and Goldsmith, 1981) yet oak is not a rapidly increasing species in the United Kingdom. Instead, the probability of any particular seed reaching reproductive maturity is close to zero. Establishment from seed should be viewed as an 'extreme event' and one where the exact ecological circumstances and location of its occurrence are difficult to predict.

As late as 1994, Chambers and MacMahon were complaining 'we do not have a balance sheet, in space or time, that permits us to account the seeds that a plant produces'. Despite impressive subsequent progress (e.g. Aarssen and Jordan, 2001; Forget *et al.*, 2005; Westerman *et al.*, 2008; Dalling *et al.*, 2011; Germain *et al.*, 2013; Crawley, 2014; Lustenhouwer *et al.*, 2017) the subject has been constrained by a shortage of data, the difficulty in generating general ecological rules and an insufficient integration between the subject area and other established disciplines within plant ecology (Larios *et al.*, 2017; Moles, 2018). Regeneration remains largely neglected within trait-based ecology (Larson and Funk, 2016).

So what of the future? We note that mineral nutrition, plant yield and herbivory, all individually complex processes, can be combined within a generalized, and extremely practically useful ecological concept, the leaf economics spectrum of Wright *et al.* (2004). We predict that the relationships between seed risk factors and plant establishment can be integrated into a similar generalized theory, again using 'trait-based ecology' *sensu* Shipley *et al.* (2016). Moreover, there are already established ecological foundations onto which to start this building process.

Seed size versus seed number

For a given allocation of resources a species may produce either many small seeds or fewer larger ones (Shiple and Dion, 1992; Greene and Johnson, 1994; Turnbull *et al.*, 1999; Jakobsson and Eriksson, 2000; Aarssen and Jordan, 2001; Henery and Westoby, 2001; Leishman, 2001; Moles, 2018).. The optimal strategy, few large seeds with potentially higher seedling survivorship, or many small seeds, depends upon ecological circumstance (Westoby *et al.*, 2002; Moles and Westoby, 2006; Grime, 2001). Unfortunately, this relationship is hard to quantify in any but the most generalized way. Annuals exhibit phenotypic plasticity with plants able to set seed even when small and stunted (Clauss and Aarssen 1994; Grime, 2001; Chambers and Aarssen, 2009; Tracey *et al.*, 2016). For example, in arid regions (e.g. north central Spain), where the incidence of rainfall is irregular, total regenerative failure is frequent and seed-set varies greatly from year to year (G. Montserrat Marti, field observations). Moreover, in contrast to the impressive quantity of seed mass measurements in the Seed Information Database (Royal Botanic Gardens Kew, 2015) and regional databases, few data are available for number of seeds produced. Equally, the expression of seed number is equally constrained by another important factor, the quantity of resources allocated by the plant to seed production.

Resource allocation to seed, the key trait?

As emphasized by Moles (2018), the trade-offs relating to seed production are complicated by numerous correlations between seed mass and life-history. Reproductive allocation to seed production varies both between species, and even between individuals within the same species (Aarssen and Jordan, 2001; Tracey *et al.*, 2016) and, significantly, from year to year particularly in arid regions (Venable and Brown, 1988; Pake and Venable, 1996; Metz, *et al.* 2010; Shriver, 2016; G. Montserrat Marti, field observations). Importantly, however, allocation to seed is catalysed by the transformation of vegetative meristems into reproductive ones. It can, therefore, be viewed as simultaneously a product of both the vegetative and regenerative strategies of the plant. First, it may

be defined in terms of key regenerative processes. Seed allocation approximates to seed mass x seed number (Smith and Fretwell, 1974; Paul-Victor and Turnbull, 2009). As such, it identifies the resources available to the ‘colonisation–competition’ trade-off between few large seeds with potentially higher seedling survivorship and many small widely-dispersed seeds (Westoby *et al.*, 2002; Moles and Westoby, 2006). Secondly, seed production is fuelled by, and quantitatively dependent upon, the vegetative plant. The strength of this association between regenerative strategy and the attributes of the mature plant varies between different ecological groupings (Hodgson *et al.*, 2017). However, the association is likely to be exceptionally strong in annuals, particularly in ‘well-grown’ specimens since resources are not channelled away from seeds and into long-lived vegetative structures. Thus, vegetative dry mass and fecundity in monocarpic species are positively related both between and within species (Aarssen and Jordan, 2001; Chambers and Aarssen, 2009). Moreover, increased competitive success may provide a ‘reproductive economy advantage’ even for small plants (Aarssen *et al.*, 2006; Aarssen, 2008, 2015).

Seed yield and CSR strategy theory

CSR strategy theory (Grime 1974, 2001) argues that two groups of external environmental factors vitally affect plant performance. The first, stress, includes factors that place prior restrictions on plant production. The most important of these are mineral nutrients, equivalent to the worldwide leaf economics spectrum of Wright *et al.* (2004). The converse, eutrophication, releases plants from nutrient stress. Other stresses include suboptimal temperatures and shortages of light and water. The second group of environmental factors, disturbance, results in the destruction of already-produced plant biomass. The group includes impacts of land use such as grazing, trampling, mowing and ploughing, and extreme climatic events including drought, fire, frost, soil erosion and wind-damage. In the third extreme scenario, where, stress and disturbance are both low, the distribution of species is determined by competition. Importantly, the abandonment or relaxation of land use intensity, dereliction, is associated with increased competition following a release from disturbance under

conditions of low stress. Thus, CSR strategy theory is relevant both to theoretically key ecosystem processes and to practically important impacts of changing land use. Moreover, CSR has an accepted and established role within ‘trait-based ecology’ (Pierce *et al.*, 2017) and, in view of the relationships between seed yield, biomass and competition described in the preceding section, we suspect that protocols for predicting strategy will, for annuals, also predict seed yield.

Objectives

As stated above, many risk factors impact upon regeneration by seed, too many to all be explored within a single paper. Here, we concentrate upon quantifying seed production. Moreover, for simplicity, we follow the lead of Aarssen and Jordan (2001) and restrict the study to annual plants, which lack the additional complication of perennation and regeneration by vegetative means.

Despite a general data shortage, medium-sized datasets on seed number plant⁻¹ do exist for both the United Kingdom (Salisbury, 1942) and USA (Stevens, 1932, 1957). Furthermore, seed yield m⁻² data have been collected in Slovenia (Šera and Šery, 2004). We shall treat these measurements as best estimates, or a ‘gold standard’ definition. Then, first, using a dataset with functional traits for over 800 annual species, we will generate multiple regression equations to predict both ‘reproductive allocation’ (seed mass x seed number) and seed number. Secondly, using extensive vegetation survey data from Spain and UK, we will illustrate how the resultant predictions of ‘reproductive allocation’ and the relationship between seed size and predicted seed number pattern in the field. Thirdly, we will consider the relevance of CSR strategy theory. As noted in Hodgson *et al.* (2017), the calculation of the R (ruderal) axis is in need of a radical revision and, accordingly, a new revised CSR classification will be produced specifically for annuals. Subsequently, the relationships between CSR strategy and seed production will be explored. Fourthly, we will consider commonness and rarity and show that seed number provides a better separation than seed size of increasing and decreased species in the UK flora. Fifthly, the problems and prospects of using a functional approach

to ‘reproductive functional ecology’ are discussed. Finally, our predictions of seed size and number for in excess of 800 annuals will be appended online to encourage further studies.

MATERIALS AND METHODS

Vegetation data and study sites

As described in Hodgson *et al.* (2017) a field context was provided by vegetation surveys of Central England (Grime *et al.*, 2007) and relevés from Tortosa, Catalonia, North-east Spain (Royo Pla, 2006) and Zaragoza, Aragon, North central Spain (Braun Blanquet and Bolós, 1953). Spanish data were abstracted from the SIVIM database (Font *et al.*, 2012). Intensity of land use was generally low in Zaragoza (survey predates arable intensification) but in Tortosa and England it was high except in areas difficult to cultivate. England → Tortosa → Zaragoza constituted a gradient from a cool wet (‘Atlantic’) to a ‘Mediterranean’ semi-arid climate (Hodgson *et al.*, 2017) with, in Zaragoza, the incidence of autumn-spring rainfall irregular and regenerative failure of annuals frequent (G. Montserrat Marti, field observations). Habitat classification relates to Grime *et al.* (2007) for English and Rivas-Martínez *et al.* (2002) for Spanish data. These surveys were used to assess the primary habitat with which each study species was associated in each region. In addition, species that had increased or decreased in UK were identified from the *Online Atlas of the British and Irish flora* (Botanical Society of Britain and Ireland and the Biological Records Centre, 2018). Also, in a conservation context, Status Index, $(\text{number of species}_{\text{increasing}} - \text{number of species}_{\text{decreasing}}) / (\text{number of species}_{\text{increasing}} + \text{number of species}_{\text{decreasing}})$ was calculated. A value of +1 indicated that all species had increased and one of –1 that all had decreased.

The dataset

Trait data were derived from a large functional dataset currently being prepared for publication (see Hodgson *et al.*, 2017). Most came from ‘in-house’ measurements but many other data sources were consulted including FIFTH database (Cerabolini *et al.*, 2010), *Flora Iberica* (Aedo *et al.*, 1980 onwards), *Flora Europaea* (Tutin *et al.*, 1964-1980), Hungarian seed bank data, (Csontos

et al., 2003, 2007; Török *et al.*, 2013), LEDA Traitbase (Kleyer *et al.*, 2008) and SID (Royal Botanic Gardens Kew, 2015). For reasons outlined in Hodgson *et al.* (2017) we have adopted the following protocols. First, values for both canopy and whole-plant dimensions have been generated. Secondly, three separate measures of leaf size have been used: (a) LA_{morph} (mm^2), the conventional ‘morphological’ unit, (b) LA_{devel} , the area of lamina produced by each phytomer, defined here as $LA_{\text{morph}} \times \text{number of leaves node}^{-1}$, which quantifies incremental growth more exactly than LA_{morph} , and (c) leaf width (LA_{funct}), which patterns with thickness of the boundary layer and efficiency of vascular transport within the lamina. Thirdly, seed mass (SeedM) has been preferentially measured for the germinule rather than the dispersule. Hemiparasites, which derive nutritional benefit for seed production from their host, and succulents, for which LDMC does not adequately define growth and soil fertility (Vendramini *et al.*, 2002) were excluded from the analyses. Although the study focusses upon annuals, the functional traits of the perennial species with which these annuals were growing was also briefly investigated.

Nomenclature follows The Plant List (2013).

Seed yield

Maximum values of seed number plant^{-1} ($\text{SeedNo}_{\text{Pl}}$) were abstracted from Stevens (1932, 1957) for USA and from Salisbury (1942) for UK. Data on maximum seed number m^{-2} ($\text{SeedNo}_{\text{m}^2}$; seed yield where vegetative cover of the subject species was 100%) derive from Šera and Šery (2004) for plants growing wild in Slovenia and FAO (2018) provides agricultural yield data for seed crops. Here, ‘maximum crop yield’, (SeedM_{ha}) expressed as hg ha^{-1} , was calculated arbitrarily as the 90 percentile of seed yield values since 2000 for all countries where the crop was grown.

The relationship between seed size and seed number plant^{-1} is first and fundamentally defined by seed mass yield (Stage 1). Stage 2 identifies how this seed yield is subsequently partitioned, few large seeds or many small ones. Therefore, Stages 1 and 2 have been analysed sequentially. Mass yield plant^{-1} (SeedM_{Pl}) and m^{-2} ($\text{SeedM}_{\text{m}^2}$) were routinely calculated in Stage 1 analyses by

multiplying values for seed number by those for seed mass (SeedM) and, subsequently at Stage 2 values were converted back to seed number.

Seed number is potentially a function of plant size and strategy. This makes the interpretation of trends difficult where floras contain a wide range of plant sizes and/or strategies. To partially offset this problem, species were assigned to size-related groupings based upon CSR strategy (see below). Within each grouping, species were ranked so that the lowest rank had a value of -1 (extremely low numbers of seed produced) and the highest a value of $+1$. Subsequently, values of this nonparametric Ranked Seed Number (RSN), independently calculated from the different 'size groupings', were combined to provide a more size-independent estimate of seed number.

Plant size

Canopy and plant height (Ht_{Can} , Ht_{Pl}) and canopy and plant diameter ($Diam_{Can}$, $Diam_{Pl}$) were subdivided into the following \log_2 classes: 1 = ≤ 20 mm; 2 = 21 – 40 mm 10 = > 5 m. From these, crude estimates of canopy and plant size ($Size_{Can}$, $Size_{Pl}$) were calculated as height x radius² (i.e. $Size_{Can} = Ht_{Can} + (2 \times (Diam_{Can} - 1))$ and $Size_{Pl} = Ht_{Pl} + (2 \times (Diam_{Pl} - 1))$. Shape was similarly assessed as height/diameter ($Shape_{Can} = Ht_{Can} - Diam_{Can}$; $Shape_{Pl} = Ht_{Pl} - Diam_{Pl}$). LA_{funct} was subdivided into the following \log_2 classes: 0 = ≤ 0.50 mm, 1 = 0.51 – 1.0 mm, 2 = 1.1 – 2.0 mm, 9 = > 128 . Leaf area values were converted to leaf mass (LM_{morph} , mg) and leaf mass node⁻¹ (LM_{devel}) using mean SLA values.

Soil fertility and shade

Traits commonly used were leaf dry matter content (LDMC, 100 x dry mass of leaf/saturated mass of leaf), which correlates positively with soil fertility and growth rate; leaf thickness (LThick, mm), negatively correlated with irradiance and positively with succulence and the more intermediate (Hodgson *et al.*, 2011) specific leaf area (SLA, leaf area (mm²)/leaf mass (mg)), positively with fertility and negatively with irradiance. Additionally, leaf nitrogen (LeafN (mg g⁻¹)) and leaf silica (LeafSi (percentage dry mass)) was considered with in-house measurements augmented, mainly by

Han *et al.* (2005), Hodson *et al.* (2005), and Stock *et al.* (2012). To assess the similarity of LDMC values between different taxonomic subsets of annual species, mean LDMC of associated annual species, weighted by abundance, was also calculated from both UK and Spanish field survey data.

Disturbance

Monocarpic species, and ephemeroids with a vernal phenology, are good indicators of high levels of temporal and/or spatial disturbance. Accordingly, as in Hodgson *et al.* (1999), mean ‘Annual Index’ value, ($\text{AnnIndex}, (\text{cover}_{\text{annuals}} + \text{cover}_{\text{ephemeroids}}) / \text{cover}_{\text{all_species}}$), was calculated for each species from field survey data. Flowering phenology, month of commencement (FIStart, negatively correlated with R axis) and duration (FIDuration, positively correlated) were abstracted from Clapham *et al.* (1987). They relate, parochially, to UK since scaling up of flowering phenology to the full study area is not yet feasible.

CSR strategy

First, the relationships between relevant functional traits were explored using Principal Component Analysis (PCA). However, because of problems with FIStart and FIDuration (see above) we have only indirect predictors for the R axis and for simplicity, just four functional traits were used. Two, LA_{Funct} , a key component of Dominance Index, and LM_{Devel} , which defines the size of each modular unit of growth (Hodgson *et al.*, 2017), positively contribute to competitive exclusion, and are negatively correlated with the ruderal (R) and stress (S) axes. Similarly, Size_{Can} is an integral of qualitative and quantitative aspects of the growth period and LDMC is inversely related to growth rate and soil fertility and positively correlated with the S axis. Subsequently, three ‘gold standard’ predictors were chosen to validate/interpret the PCA analysis. Competition may be defined as ‘the attempt by neighbours to capture the same unit of resource’ (Grime *et al.*, 2007). Moreover, the sequestering of resources into seeds is crucial for the survival of annual species into another generation. Thus, published values of SeedM_{Pl} , which defines the mass of seed produced by each plant, objectively predict the C axis. Secondly, LeafN, a key element of the worldwide leaf

economics spectrum (Wright *et al.*, 2004), correlates inversely with the S axis. Thirdly, as in Hodgson *et al.*, 1999, AnnIndex was utilized as the ‘gold standard’ for the R-dimension. Subsequently, the nature of the relationships between the three ‘gold standard’ predictors and PCA axes 1 and 2 was defined by multiple regression and ‘contour lines’ for each ‘gold standard’ predictor added to the PCA ordination diagram. The positions of CSR strategy types were then tentatively identified by reference to these contours, and to ecological theory (Grime 2001).

Other analyses

Prior to statistical analysis LDMC was square-root transformed and the remaining continuous trait variables log₁₀-transformed. To provide an estimate relevant to ecosystem properties, trait data weighted by abundance (rooted frequency/dominance scale) were routinely used to generate ‘functional averages’ for each vegetation sample.

Except for measured seed mass against predicted seed number, where the Ordinary Mean Squares method was preferred, linear regressions all relate to the Type II of Warton *et al.* (2006). Other statistical tests were performed with SPSS for Windows™ (Version 16.0). Correlation, χ^2 , multiple regression, Mann-Whitney U-tests and 1- and 2-way ANOVA were used to explore relationships within the dataset.

RESULTS

Range of values for plant traits

The range of values for each measured trait within our core dataset of 886 annuals is presented in Supplementary Data Table S1. There was a greater than 8-, 250-, 1000- and 10000-fold variation in untransformed variables relating to leaf structure, plant size, leaf size and seed mass and number respectively. However, in contrast to the wide ecological spectrum of species within our own dataset, the published datasets defining seed yield and leaf nitrogen related to a much narrower subset of species and there were significant differences in trait expression between them (Table 1).

Seed mass yield

SeedM_{PI} was similarly identified as a positive product of plant size, leaf/phytomer size and SeedM for both Stevens's 1932 and 1957 USA (eqn 1a) and Salisbury's 1942 British field measurements (eqn 1b).

$$\log_{10}\text{SeedM}_{\text{PIUSA}} = 1.460\log_{10}\text{LM}_{\text{morph}} + 0.076\text{Size}_{\text{Can}} - 1.147\log_{10}\text{LA}_{\text{devel}} + 0.229\log_{10}\text{SeedM} + 3.721 \quad (r^2 = 0.52^{***}, n = 56) \quad (1a)$$

$$\log_{10}\text{SeedM}_{\text{PIUK}} = 0.145\text{Size}_{\text{PI}} + 0.272\log_{10}\text{SeedM} + 0.118\text{LA}_{\text{funct}} + 0.145 \quad (r^2 = 0.77^{***}, n = 51) \quad (1b)$$

However, SeedM had relatively little impact on the expression of SeedM_{PI}. Its exclusion from the regression gave a reduction of only 0.04 and 0.02 respectively in r^2 (eqn 2).

$$\log_{10}\text{SeedM}_{\text{PIUSA}} = 0.095\text{Size}_{\text{Can}} + 1.445\log_{10}\text{LM}_{\text{morph}} - 1.044\log_{10}\text{LA}_{\text{devel}} + 3.143 \quad (r^2 = 0.48^{***}, n = 56) \quad (2a)$$

$$\log_{10}\text{SeedM}_{\text{PIUK}} = 0.176\text{Size}_{\text{PI}} + 0.141\text{LA}_{\text{funct}} - 0.522 \quad (r^2 = 0.75^{***}, n = 51) \quad (2b)$$

There was, however, no numerical correspondence between the two estimates. Predicted values for USA from eqn 2a were considerably higher than those predicted for UK from eqn 2b (eqn 3).

$$\log_{10}\text{SeedM}_{\text{PIUSApredicted}} = 0.936\log_{10}\text{SeedM}_{\text{PIUKpredicted}} + 0.835 \quad (95\% \text{ confidence intervals: slope } 0.90 - 0.97, \text{ constant } 0.74 - 0.93; r^2 = 0.72^{***}, n = 868; \text{ mean values } \pm \text{ s.d.: SeedM}_{\text{PIUSApredicted}} 3.43 \pm 0.73, \text{ SeedM}_{\text{PIUKpredicted}} 2.78 \pm 0.71; \text{ paired } t = 50.1^{***}, r^2 = 0.72^{***}, n = 868; \text{ similar results from eqn 1 not shown}). \quad (3)$$

In scaling up from SeedM_{PIpredicted}, (eqn 2) to SeedM_{m2}, traits relating to canopy and plant size were additionally accepted into the regression, (eqn 4).

$$\log_{10}\text{SeedM}_{\text{m2}} = 0.638\log_{10}\text{SeedM}_{\text{PIUSApredicted}} - 0.115\text{Size}_{\text{PI}} + 0.110\text{Size}_{\text{Can}} - 0.326\text{Shape}_{\text{PI}} + 0.248\text{Shape}_{\text{Can}} + 2.901 \quad (r^2 = 0.25^{***}, n = 120) \quad (4a)$$

$$\log_{10}\text{SeedM}_{\text{m2}} = 0.623\log_{10}\text{SeedM}_{\text{PIUKpredicted}} - 0.192\text{Size}_{\text{PI}} + 0.284\text{Size}_{\text{Can}} - 0.360 \text{Shape}_{\text{PI}} + 0.160 \text{Shape}_{\text{Can}} + 3.642 \quad (r^2 = 0.22^{***}, n = 121) \quad (4b)$$

Furthermore, estimates of SeedM_{m2} from eqn 4 predicted FAO-derived crop seed yield values (Fig. 1).

[For comparison, when SeedNo was estimated directly from traits, the regressions were as follows:

$$\log_{10}\text{SeedNo}_{\text{PIUSA}} = -0.739\log_{10}\text{SeedM} + 1.346\log_{10}\text{LM}_{\text{morph}} - 1.124\log_{10}\text{LA}_{\text{devel}} + 0.088\text{Size}_{\text{Pl}} + 3.498 \quad (r^2 = 0.55^{***}, n = 55) \quad (5a)$$

$$\log_{10}\text{SeedNo}_{\text{PIUK}} = 0.145\text{Size}_{\text{Pl}} - 0.737\log_{10}\text{SeedM} + 0.124 \log_{10}\text{LA}_{\text{funct}} + 0.147 \quad (r^2 = 0.58^{***}, n = 52) \quad (5b)$$

$$\log_{10}\text{SeedNo}_{\text{m2}} = -0.352\log_{10}\text{SeedM} + 4.959 \quad (r^2 = 0.13^{***}, n = 120) \quad (5c)]$$

C_RS_RR_R, providing an ecological context

PCA axis 1 of the ordination explained 54% of the variance and identified size and the C_R axis (Fig. 2A). PCA axis 2 (24%) scaled positively with LDMC and Size_{Can} (i.e. negatively with ruderality). These axes were defined by multiple regression as follows:

$$\text{PCA1} = 0.570\log_{10}\text{LM}_{\text{Devel}} - 0.288\sqrt{\text{LDMC}} + 0.104\text{Size}_{\text{Can}} - 0.218\text{LA}_{\text{Funct}} - 1.844 \quad (6)$$

$$\text{PCA2} = 0.199\log_{10}\text{LM}_{\text{Devel}} + 1.482\sqrt{\text{LDMC}} + 0.118\text{Size}_{\text{Can}} - 0.042\text{LA}_{\text{Funct}} - 7.807 \quad (7)$$

In addition, ‘gold standard’ variables patterned variously with the PCA axes (eqns 8-10).

$$\log_{10}\text{SeedM}_{\text{PIUSA}} = 0.538\text{PCA1} + 0.176\text{PCA2} + 3.195 \quad (r^2 = 0.38^{***}, n = 55) \quad (8a)$$

$$\log_{10}\text{SeedM}_{\text{PIUK}} = 0.606\text{PCA1} + 0.189\text{PCA2} + 2.567 \quad (r^2 = 0.73^{***}, n = 51) \quad (8b)$$

$$\log_{10}\text{LeafN} = 0.064\text{PCA1} - 0.065\text{PCA2} + 1.380 \quad (r^2 = 0.14^*, n = 55) \quad (9)$$

$$\text{AnnIndex}_{\text{XUK}} = -0.044\text{PCA2} + 0.522 \quad (r^2 = 0.06^{**}, n = 178) \quad (10a)$$

$$\text{AnnIndex}_{\text{XSIMIV}} = -0.014\text{PCA2} + 0.670 \quad (r^2 = 0.01^*, n = 734) \quad (10b)$$

$$(\text{AnnIndex}_{\text{XUK}} \text{ v } \text{AnnIndex}_{\text{XSIMIV}} \text{ } t = 7.7^{***}; r^2 = 0.65^{***}; \text{ mean difference } 0.09 \pm 0.16, n = 171)$$

SeedM_{PIUSA}, and, even more strongly, SeedM_{PIUK}, define the putative C_R axis with a relatively high r^2 (eqn 8). However, values of r^2 were low for the ‘gold standard’ variables predicted to define the S_R and R_R axes (eqns 9 and 10). Thus, in our ‘annuals-only’ analysis, FlStart and FlDuration, the ‘key ruderal traits’ in Hodgson *et al.* (1999), failed to pattern strongly with the R_R axis. FlDuration was

more centrally positioned within the C_R - S_R - R_R region and FlStart was, broadly, positively correlated with the C axis (Fig. 2Bi-ii). Instead, the key diagnostic element for identifying R_R -strategists appeared to be miniaturization. R_R -strategists were small with both precocious flowering and seed set (e.g. *Bellis annua*, *Limosella aquatica*). Moreover, many species, identified as R-strategists in Hodgson *et al.* (1999) and Grime *et al.* (2007), were classified as of intermediate strategy (e.g. *Poa annua*, CSR_R ; *Senecio vulgaris*, CR_R). Thus, our allocation to C_R - S_R - R_R strategies in Fig. 2 must still remain provisional. Nevertheless, less controversially, typical C_R -strategists included robust weeds (e.g. *Xanthium strumarium*) and crops (e.g. *Zea mays*) and S_R -strategists consisted of a small group of slower-growing, later-maturing annuals (e.g. *Crucianella patula*, *Minuartia campestris*) – Fig. 2.

The CSR analysis also allowed us to compare the ecological range of species included in the ‘gold standard’ datasets. Importantly and consistent with results in Table 1, Salisbury’s UK dataset exhibited a wider spread of values for PCA axes 1 and 2 than that associated with USA data (Fig. 2Biii). The UK dataset again appears to be the ‘more ecologically balanced’ and, for this reason, eqns 1b, 2b, 4b, 5b and 8b are to be preferred to eqns 1a, 2a, 4a, 5a and 8a.

Reproductive strategy patterns with $C_RS_RR_R$

As with measured data (Fig. 2A), predicted values for seed yield patterned with the C_R - S_R - R_R ordination (Fig. 3A). Seed mass yield, both plant^{-1} and m^{-2} , were highest for C_R -strategists and lowest for S_R , R_R and SR_R with intermediate strategies occupying an intermediate position (Fig. 3AI-II). Similarly, SeedM, could be ordered $R_R < S_R < C_R$ (Fig. 3AIII). C_R -strategists also had high SeedNo plant^{-1} (Fig. 3AIVi) while the estimate of SeedNo m^{-2} patterned least strongly with strategy (Fig. 3AIVii).

Despite these general relationships, data were extremely variable even within a single strategy. C_R -strategists included both the highly fecund small-seeded *Sisymbrium loeselii* (SeedM 0.09 mg, SeedNoPl 31894 (estimated), 37200 (measured)) and the few- but large-seeded *Vicia narbonensis* (136 mg, 60). Similarly, R_R -strategists included both *Limosella aquatica* (0.015 mg, 986

(estimated), 4236 (measured)) and *Montia fontana* subsp *chondrosperma* (0.26 mg, 47) and S_R-strategists both *Catapodium rigidum* (0.22 mg, 420) and *Brachypodium distachyon* (3.52 mg, 99). Thus, within each strategy there was additionally a strong negative correlation between SeedM, and predicted SeedNo plant⁻¹ (Fig. 3B). Regression equations for these relationships shared a common slope but differed significantly in intercept value. Small and/or slow-growing species (R_R- and S_R-strategists) had low intercept values and large plants (e.g. C_R-strategists) high ones (Fig. 3B).

Taxonomic variation in trait expression

Each family appeared to exploit a similar range of soil fertility: the mean LDMC of associated annual vegetation was similar for each of the three best-represented families, Asteraceae, Fabaceae and Poaceae (Supplementary Data Table S2). Nevertheless, familial trait averages, and values for the PCA axes themselves, tended to be significantly different (Supplementary Data Tables S2-S3, Fig. 2Biv). Although Asteraceae was widely distributed within the PCA ordination, Poaceae was largely confined to the upper end of PCA axis 2, and had highest LDMC, the key trait defining this axis. Fabaceae was intermediate. Moreover, the LDMC of species in Fabaceae and Poaceae was consistently higher than those of their associated annual vegetation (Supplementary Data Table S2). Nevertheless, these examples of trait expression do not simply identify specialization at the family level. Additionally, there were considerable differences in trait expression between different subfamilies and tribes within each major family (Supplementary Data Table S4).

In the case of annual Poaceae the high LDMC recorded might potentially have been attributable to the accumulation of silicon, which adds leaf mass at little metabolic cost (Raven 1983; Supplementary Data Table S3). However, such an increase in leaf dry mass would only have had a small direct impact on trait expression. For annual grasses recorded silicon values equate to silica content of on average 1.8% of leaf dry mass (Supplementary Data Table S3). Factoring out silica mass reduces estimates of LDMC by on average 0.4%. This ‘correction’ changed the mean LDMC of annual Poaceae only slightly from 22.1 to 21.7%. This is still much higher than the mean 16.2%

LDMC characteristic of other annuals. Moreover, ‘Si-corrected’ values for LDMC and LM_{devel} had a negligible impact when the PCA ordination was repeated (data not shown).

Comparing traits of annuals in different floras

Mean SeedM of the annual vegetation and for the annual flora of each region was ordered Central England < North-east Spain < North central Spain and SeedNo_{PI} and RSN showed the converse relationship (Table 2A). The three regions also patterned in relation to strategy (Fig. 4A-B) with Central England (C_R, C_{RR} and R_R well represented) < North-east Spain < North central Spain (S_R, S_{RR} and S_{CR}). Equally, within regions, SeedM, SeedNo and RSN varied with respect to both habitat (Table 2B) and C_RS_RR_R strategy (data not shown). However, two-way ANOVAs identified strategy as the more consistently important determinant of seed size and number within all three regions (SeedM_{PI} – Central England (a) vegetation: strategy $F_{4,836} = 46.7^{***}$, habitat $F_{5,836} = 6.8^{***}$, interaction $F_{11,836} = 1.4$ ns; (b) species: strategy $F_{5,182} = 12.2^{***}$, habitat $F_{5,182} = 2.7^{***}$, interaction $F_{18,182} = 1.2$ ns; North-east Spain (a) vegetation: strategy $F_{4,454} = 9.5^{***}$, habitat $F_{4,454} = 3.5^{**}$, interaction $F_{9,454} = 1.5$ ns; (b) species: strategy $F_{7,331} = 9.8^{***}$, habitat $F_{6,331} = 1.4$ ns, interaction $F_{33,331} = 1.1$ ns; North central Spain (a) vegetation: strategy $F_{4,264} = 2.9^*$, habitat $F_{4,264} = 10.5^{***}$, interaction $F_{7,264} = 0.6$ ns; (b) species: strategy $F_{7,292} = 6.7^{***}$, habitat $F_{5,292} = 1.5$ ns, interaction $F_{28,292} = 0.9$ ns; SeedNo_{PI} – Central England (a) vegetation: strategy $F_{4,836} = 33.2^{***}$, habitat $F_{5,836} = 10.4^{***}$, interaction $F_{11,836} = 4.5$ ns; (b) species: strategy $F_{5,182} = 6.1^{***}$, habitat $F_{5,182} = 5.0^{***}$, interaction $F_{18,182} = 1.1$ ns; North-east Spain (a) vegetation: strategy $F_{4,454} = 6.1^{***}$, habitat $F_{4,454} = 4.4^{**}$, interaction $F_{9,454} = 1.0$ ns; (b) species: strategy $F_{7,331} = 6.9^{***}$, habitat $F_{6,331} = 2.2^*$, interaction $F_{33,331} = 1.0$ ns; North central Spain (a) vegetation: strategy $F_{4,264} = 0.6$ ns, habitat $F_{4,264} = 3.8^{**}$, interaction $F_{7,264} = 1.9$ $P > 0.1$; (b) species: strategy $F_{7,292} = 4.9^{***}$, habitat $F_{5,292} = 1.9$ $P > 0.1$, interaction $F_{28,292} = 0.5$ ns). In addition, when SeedNo_{PI} was replaced by RSN, habitat and interaction were generally statistically more and strategy statistically less significant (data not

shown). Equally, observations indicate that habitat range, and even life history of some species differs significantly between Spain and UK (Table 3).

Interrelationships between the annual and perennial components of vegetation

Functional traits of annuals patterned with those of co-occurring perennials. SeedM_{annual} was correlated positively with both SeedM_{peren} and DomI within each region (Table 4). Similarly, albeit less consistently, SeedNo_(annual) and RSN were correlated negatively with SeedM_{peren} and positively with DomI (Table 4) and broadly similar patterns were observed within individual habitats (Supplementary Data Table S5). In contrast, since large seeds occurred at both extremes of fertility (Fig. 3B), no clear and consistent trends were detected between annual seed traits and LDMC_{peren}. Instead, positive and negative correlations were variously recorded, according to ecological circumstance (Table 4, Supplementary Data Table S5).

The changed dynamics of C_RS_RR_R strategies and seed size v number in the British flora

Whether species have increased or decreased abundance depends strongly upon habitat and C_RS_RR_R strategies. Increased species were particularly associated with urban landscapes and with wasteland and spoil habitats (Supplementary Data Table S6). They also formed a slight majority within the C_RR strategy and were well represented in C_R (Fig. 4C). In contrast, declined species were characteristic of pastoral (upland) landscapes and wetland and arable habitats and more ‘stressed’ strategies (Fig. 4C; Supplementary Data Table S6). However, superimposed, there are additional reproductive differences. Increased species consistently produce greater SeedNo_{pl}, a relationship that appears largely independent of SeedM and plant size (Tables 2C, 5).

The database

Our predictions of seed number are inevitably rather imprecise and for some species (e.g. *Minuartia hamata*, where only three seeds plant⁻¹ are predicted) values may be out by several orders of magnitude. Accordingly, to encourage further work, data relating to SeedM, SeedM_{pl}, SeedM_{m2},

SeedNo_{PI} and SeedNo_{m2} and the PCA axes used to define C_RS_RR_R strategies for 842 annual taxa are included as Supplementary Data Table S7.

DISCUSSION

Painting on a blank canvas

Like all branches of science, functional trait ecology is dependent for its effectiveness upon the creation of general rules. Typically, these have been generated through major analyses of functional trait data abstracted from a geographically-diverse range of data sources (e.g. Wright *et al.*, 2004). However, restricted by the small number of widely-measured ‘traditional’ traits, the levels of novelty and utility in recent meta-analyses have failed to match those of this early study. Associated with these methodological constraints and other problems in merging and interpreting ecologically diverse datasets, there remain many gaps and ‘half-truths’ within trait-based ecology (Shipley *et al.*, 2016; Hodgson *et al.*, 2017; Moles, 2018).

Less mainstream, but still ‘big science’, is an ‘eco-taxonomic’ approach pioneered in Central Europe. The initial stage is a description and classification of vegetation. Subsequently, key ecological factors are identified and, from a working ecological knowledge of the flora under study, ‘ecological values’ for species within the flora can be generated on an industrial scale. Importantly, this procedure involves the assessment of all important ecological factors, not just those that are most easily measured. An historical illustration of the power and utility of this approach is provided by Ellenberg *et al.* (1992) with its phytosociologically-related Ellenberg habitat preference classes, ‘Ellenberg numbers’. We believe that a reliance upon a classification based upon where plants grow (‘Ellenberg numbers’) rather than how plants function (trait-based ecology) is outdated.

Nevertheless, Ellenberg included all ecosystem processes that he considered key in his classification of species. In this respect he was, and remains, ahead of much of trait-based ecology. We suggest that the way forward is not a reliance upon global analyses. Rather, like Ellenberg, studies in trait-based ecology should perhaps initially operate at a regional level with strong links to described

vegetation and the ecosystem processes shaping the flora (e.g. LEDA Traitbase; Kleyer *et al.*, 2008). At this more parochial focussed scale, additional important ecosystem processes can be more easily explored and new traits added to analyses. Positive outcomes will encourage the process of scaling up of both trait measurement and data analysis. We hope that this study will catalyse further work. Intensive land use and climate change are reshaping the floras both globally and within our study areas (Hodgson, 1986a; Pyke, 2003; Cirujeda *et al.*, 2011; Pimm *et al.*, 2014) and we urgently need more functional traits to investigate regenerative aspects of the processes involved.

Predicting SeedM_{PI} and SeedNo_{PI}

The large number of species (>800) and wide range of values of each functional trait give our own database the ecological breadth appropriate for broad comparisons of traits (Supplementary Data Table S1). In contrast, the species sets associated with the other (published) datasets used for SeedNo_{PI}, SeedNo_{m2} and LeafN are ecologically narrower (Table 1). Most importantly, the SeedNo_{PI} datasets for UK (Salisbury, 1942) and those for USA (Stevens, 1932, 1957) were strongly ecologically contrasted. The USA dataset relates primarily to weeds of agricultural concern in intensive productive arable landscapes whereas that from the UK, was drawn from the less productive British landscapes that preceded agricultural intensification. In consequence, large species predominate in the USA dataset whilst those from UK tended to be small- to medium-sized (Table 1). Although we have made predictions from each, we prefer the UK dataset. Its species appear to be the more representative of our own much larger functional database (Fig. 2Biii).

There is a further problem in data interpretation. Annuals exhibit phenotypic plasticity with plants able to set seed even when small and stunted (Clauss and Aarssen 1994; Grime, 2001; Chambers and Aarssen, 2009; Tracey *et al.*, 2016). This is likely to result in high intraspecific variability for seed yield particularly between ecologically-contrasted sites and climatically-contrasted regions and antilogged predictions of SeedM_{PI} for USA were on average three-times greater than those for UK (eqns 2-3). Nevertheless, the predicted UK and USA values are strongly

correlated, with an r^2 of 0.72. Moreover, although the terms accepted into the regression for 2a and 2b are not identical, the equation relating the two sets of predicted values has a slope close to 1:1. Thus, although they cannot be treated as absolute values, our estimates appear appropriate for ranking relatively well-grown examples of species in terms of seed yield. Furthermore, the predictor equations conform to theoretical expectations. They are consistent with relationships between size, flowering and yield observed by Gross (1981), Gross and Werner (1983) and Aarssen and Jordan (2001) for monocarpic species. Thus, for UK (eqn 2b; $r^2 = 0.75$), SeedM_{Pl} is essentially a positive function of plant size (Size_{Pl}) and performance (LA_{funct} , a key component of competitive ability, Keddy *et al.*, 2002; Hodgson *et al.*, 2017) with SeedM having only a marginal impact (compare eqns 1-2). SeedM_{Pl} may now be provisionally treated as a readily-estimated trait defined by vegetative attributes. Moreover, with so much SeedM data now available, $\text{SeedNo}_{\text{Pl}}$ may also be routinely assessed.

Scaling up to SeedM_{m2} and SeedNo_{m2}

Regressions predicting SeedM_{m2} from SeedM_{Pl} have a low r^2 (eqn 4). We suspect that two factors in particular contribute to this poor predictive ability. First, whether the inflorescence overtops the leaf canopy ($\text{Size}_{\text{Pl}} > \text{Size}_{\text{Can}}$) or not ($\text{Size}_{\text{Pl}} = \text{Size}_{\text{Can}}$), appears to impact upon seed yield (eqn 4). Our simple morphological traits may not be sufficiently precise to account for the dense interlocking structure of plants growing in monoculture. Secondly, vegetative dry mass and fecundity in monocarpic species are positively correlated within species (Aarssen and Jordan, 2001; Chambers and Aarssen, 2009). However, annual plants frequently, and perhaps usually, fail to attain their full potential either in terms of vegetative growth or seed production (Chambers and Aarssen, 2009; Tracey *et al.*, 2016). For example, this is particularly true in the more arid parts of our Zaragoza study region (G. Montserrat Marti, field observations). Our estimates of SeedM_{Pl} were derived using traits relating to large ‘well-grown’ plants. In contrast, SeedM_{m2} is measured under field conditions where the target species has close to a 100% cover. For most species, this is an unusual circumstance

with populations likely to exhibit a range of plant sizes. Furthermore, the proportion of maximum potential biomass achieved may vary between species. For these reasons the relationship between plant size and yield defined by eqn 2 may not be appropriate to scale up to 1 m². Nevertheless, SeedM_{m2} is the most viable ‘gold standard’ variable for extending predictions to seed yield in perennial species. And numerous values are already available (Šera and Šery, 2004). It remains a potentially crucial attribute albeit one in need of further study.

Scaling up to a global synthesis

In our study CSR strategy type, and their component traits, quantified SeedM_{PI} and SeedNo_{PI} (Fig 3) but, equally, were subject to phylogenetic constraints (Fig. 2Biv; Supplementary Data Table S2-4). This is not unexpected. Abundance within the flora of Central England and plant strategy are both strongly correlated with polyploidy (Hodgson, 1987), phylogenetic niche conservatism is very much a feature of the flora of Central Europe (Prinzing *et al.* (2001) and phylogeny identified commonness and rarity (Hodgson 1986b-c). We suspect that correlations between strategy and phylogeny stem, at least in part, from the shared recent evolutionary history of our study areas, from the Pleistocene (West, 1969). Importantly, this shared history has included episodes of climate change, the development and intensification of agriculture and the geographic spread and adaptive radiation of the flora from a common pool of founder species. However, our phylogenetic results were not confirmed by Edwards and Westoby (2000). Studies of SeedM_{PI} and SeedNo_{PI} in regions with a contrasted recent evolutionary history are required to robustly test the relationships identified here.

Bet-hedging, a missing dimension of trait-based ecology

With few easily measured functional traits, the R_R axis remains difficult to quantify (Hodgson *et al.*, 1999; Pérez-Harguindeguy *et al.*, 2012; Pierce *et al.*, 2017). The main problem probably relates to the nature of disturbance. The C_R and S_R axes are essentially simple axes of intensity. In contrast, the R_R axis is compound, defined by the intensity, frequency and predictability of

disturbance events. We envisage disturbance events broadly following one of two scenarios. In scenario 1, disturbance is to some extent seasonally unpredictable and variously weak and strong in different years (e.g. drought on very shallow soils, grazing, patchy shade, trampling and weeding). In scenario 2, disturbance is late, strong but seasonally predictable (e.g. crop harvesting, ploughing, shade caused by leafing-out of forest trees and summer drought on deeper soils). Shemesh and Novoplansky (2013) argue persuasively that there are important functional trade-offs that relate to the probability and severity of risks associated with these two scenarios. Species whose habitats or microsites are prone to less intense or intermittent disturbance (scenario 1) are predicted to exhibit deterministic bet-hedging (*sensu* Cohen, 1966). They flower at an early developmental stage. This ‘risk-averse’ pattern of growth mitigates in favour of ‘minimum fitness’ (i.e. the production of some seed) even in unfavourable years. Moreover, if there is no early catastrophic disturbance event, modular increments of vegetative growth, flowering and seed set continue. However, as a result of this continuing partial sequestration of resources into seed production, growth rates will remain relatively low in the event of conditions for remain good. For scenario 2, with prolonged opportunities for good growth, the better strategy will be a long period of purely vegetative growth followed by flowering. Annuals adapted to scenario 2 are potentially larger and with more structurally complex branch units. They are, therefore, less ruderal, and, important for estimating seed yield, they may be expected to produce more seed mass than comparable species adapted to scenario 1. We need to incorporate additional traits into future analyses so as to identify more precisely the greater potential seed production inherently associated with scenario 2.

Unfortunately, the current ‘gold standard’ ruderal variables, FIStart and FIDuration, are functionally ambiguous and fail to address bet-hedging. First, with respect to FIStart, most UK ruderal species flower precociously and early in the year. However, a few (e.g. *Elatine*) do not. *Elatine* exploits shallow water and mud that only becomes exposed as the water level falls in late summer. Thus, precocious flowering commences in August. Secondly, a long FIDuration may be

associated with two very different scenarios. A single individual flowering for a long time (e.g. *Veronica persica*, which may commence flowering from the second- or third-formed phytomer with additional flowers produced at each successive phytomer until growth ceases). Alternatively, the plant may be short-lived and may produce several generations of plants within a single growing season (e.g. *Senecio vulgaris*). Phytomer miniaturization and a reduction in the number of juvenile phytomers both promote early maturity (Hodgson *et al.*, 2017) and could replace FIStart. In addition, identifying the phytomer number at which flowering begins and ends may be a developmentally-appropriate trait to replace FIDuration.

Our attempts to redefine the R axis may also benefit from links to plant morphology, in particular, the ‘unifying inflorescence model’ of Prusinkiewicz *et al.* (2007). The model relates to the presence of a factor called ‘vegetativeness’ within the apical meristem. Variability in the expression of ‘vegetativeness’ in morphological space and developmental time impacts strongly on inflorescence structure. A greater understanding of the ecological risk factors may help morphologists to improve their models of inflorescence structure and ‘vegetativeness’. The studies such as Prusinkiewicz *et al.* (2007), Prusinkiewicz and Runions (2012), Bull-Hereñu and Claßen-Bockhoff (2013) and Harder and Prusinkiewicz (2013) may soon converge with those of Shemesh and Novoplansky (2013).

Here it is also important to consider the importance of the inter-annual variability of climate. The inter-annual climate change is essential for the ecological competitiveness of many annuals. In places like the outskirts of Zaragoza where many annuals of very different sizes live, the different years provide opportunities for very different species. Some of them have opportunities to produce large quantities of seeds almost every year (*Galium parisiense*, *Helianthemum salicifolium*, *Polygala monspeliaca*) and others only in a few years, but they are not less successful. For example, this year has been bad for some annuals that I have not seen (*Chaenorhinum reyesii*, *Crucianella patula*, *Crucianella angustifolia*, ...) but, for others, such as *Ziziphora hispanica*, it has been a wonderful year. I have seen a lot of them in areas that I have visited very carefully during the last three springs. These plants are very successful in the few favorable years and in the rest of years they remain inactive in the seed bank. As they are annual plants, each year they complete their life cycle so they can be perfectly competitive, developing massively every year, or every 5 years, or every 50, etc. These are infrequent but sufficient episodes to recharge the seed bank. These species can persist perfectly if the habitat is not destroyed but the ecological function of both annual types can be very different. For example, annuals that bloom every year guarantee seeds for many species of insects that live on them.

Using SeedNo_{PI} in the interpretation of floristic change: a synthesis

The inclusion of SeedNo_{PI} in large-scale studies of floristic change is long overdue. Take the UK flora. Eutrophication and disturbance in managed habitats and abandonment of marginal habitats have fundamentally altered the nature of the landscape. Many tall species and those of fertile soils have increased, particularly those with low SeedM and high SeedNo (Table 5; Hodgson, 1986a; Hodgkinson and Thompson 1997). In contrast, low-growing species of infertile soils have generally decreased and many are now restricted to small isolated fragments of habitat (Hodgson, 1986a; Preston *et al.*, 2002; Hodgson *et al.*, 2014). However, the above description is an over-simplification. For reasons of convenience and practicality, we have, like many others, analyzed functional shifts in relation to species composition. However, key evolutionary processes impact upon trait expression at the level of the population (Harper, 1967; Moles, 2018) and extinction and range expansion are similarly defined by changes at the population level. Efforts to conserve individual rare species and control individual increasing ones will require an additional intraspecific focus.

Fortunately, a limited intraspecific dimension is available. First, differences in functional trait expression and habitat range have been recorded between study areas for several species (Table 3). Secondly, intraspecific variation in SeedM have been recorded. Populations of annuals from warm favourable climates tended to have smaller seeds than those from cool less favourable ones (McWilliams *et al.*, 1968; Montesinos-Navarro *et al.*, 2011; Burcu *et al.*, 2017). We assume that the ‘colonisation–competition’ trade-off between few large seeds with potentially higher seedling survivorship and many small widely-dispersed seeds (Westoby *et al.*, 2002; Moles and Westoby, 2006) routinely applies to populations in other ecological contexts. Thus, for populations of rare species in small isolated patches of habitat, larger seeds and potentially increased seedling survivorship may be advantageous. In contrast, the production of a larger number of smaller widely-dispersed seeds may facilitate the spread of increasing species. *In extremis*, changes in size and number may not be enough. As identified in Table 3, populations from less favoured habitats may either become extinct or may become less dependent upon regeneration by seed, becoming longer

lived – another type of bet-hedging. This potential range of scenarios for annuals, illustrated as Fig. 5, provides a possible focus for further regenerative studies in relation to land use. A similar diagram could perhaps, and more tentatively, be constructed to illustrate key ecosystem processes involved in climatically-induced floristic change.

CONCLUSIONS

Even for annuals, regeneration by seed is an extreme event with a plethora of risk factors including pre- and post-dispersal predation, plant competition and the perils of seed dispersal in time and space and seedling establishment all having an impact (Chambers and MacMahon, 1994). A key objective of this study was to, quantitatively and qualitatively, assess seed yield for annuals. And this we have achieved. Provisional data for >800 annuals are appended as Supplementary Data Table S7.

Hopefully, this dataset will provide suitable base-line data for the quantification of at least some of the risk factors and allow their interpretation within the context of today's changing landscapes and climates. In addition, further work is required on topics such as bet-hedging, phylogeny and the best way of scaling up from SeedM_{PI} to SeedM_{m2}. Nevertheless, it is clear that, for annuals, SeedM_{PI} is primarily a positive function of vegetative biomass. Its quantitative value will in turn constrain the 'colonisation–competition' trade-off between few large seeds with potentially higher seedling survivorship and many small widely-dispersed seeds (i.e. SeedM *versus* SeedN_{PI}). Moreover, in today's changing landscapes, survival of populations may depend upon reducing the dependence on regeneration by seed by adopting a more perennial life-history. Regenerative strategies will never conform to the linear elegance of the leaf economics spectrum of Wright *et al.* (2004). They are regulated by a complex network of factors *sensu* Messier *et al.* (2017). The challenge is to sufficiently distil the dimensions down so that we can emulate CSR strategy theory (Grime 1974, 2001) and provide a simple theoretically and practically useful multidimensional diagnostic system. Trait-based ecology is some way from this synthesis but we are making significant progress.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Table S1: range of trait values. Table S2: comparing LDMC between families and regions. Table S3: comparing traits between families. Table S4: comparing traits between tribes and subfamilies. Table S5: comparing traits of annuals with those of co-occurring perennials. Table S6: comparing Mean Status Index in different regions and habitats in Central England. Table S7: Functional estimates and measures of seed traits for >800 annuals.

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FIG. 1. Seed yield, estimated from eqn 4a, predicts FAO-derived crop seed yield values for annual crops. Values for x axis converted to hg ha⁻². $\text{Log}_{10}\text{SeedM}_{\text{ha}} = 0.699\text{log}_{10} \text{SeedM}_{\text{m2USApred}} + 1.429$ (95% confidence intervals – slope: 0.48 – 1.02; constant: 0.22 – 2.64; $r^2 = 0.38^{**}$, $n = 20$). [For UK data, eqn 4b: $\text{log}_{10}\text{SeedM}_{\text{ha}} = 0.766\text{log}_{10}\text{SeedM}_{\text{m2UKpred}} + 1.211$ (95% confidence intervals – slope: 0.52 – 1.13; constant: –0.12 – 2.54; $r^2 = 0.35^{**}$, $n = 20$)] Abbreviations for crops: *Avena* spp. (mainly *Avena sativa*, oats), *Brassica napus* var. *oleifera* (rapeseed), *Cannabis sativa* (hempseed), *Carthamus tinctorius* (Safflower seed), *Cicer arietinum* (chick peas, chickpea, Bengal gram, garbanzos), *Fagopyrum esculentum* (buckwheat), *Helianthus annuus* (sunflower seed), *Hordeum* spp. (two-row barley (*H. disticum*), six-row barley (*H. hexastichum*), four-row barley (*H. vulgare*); barley), *Lens esculenta* (*Ervum lens*, lentils), *Linum usitatissimum* (linseed), *Oryza* spp. (mainly *O. sativa*, paddy rice), *Papaver somniferum* (poppy seed), *Phalaris canariensis* (canary seed), *Pisum sativum* (garden pea + field pea (*P. arvense*); dry peas), *Secale cereale* (Rye), *Sorghum* spp. (*Sorghum*, guinea corn (*S. guineense*), common, milo, feterita, kaffir corn (*S. vulgare*); durra, jowar, kaoliang (*S. dura*)), *Triticum* spp. (common (*T. aestivum*) durum (*T. durum*) spelt (*T. spelta*) wheat, *Vicia faba* (broad beans, horse beans, dry), *Vicia sativa* (vetches, spring/common vetch), *Zea mays* (maize, corn, Indian corn, mealies).

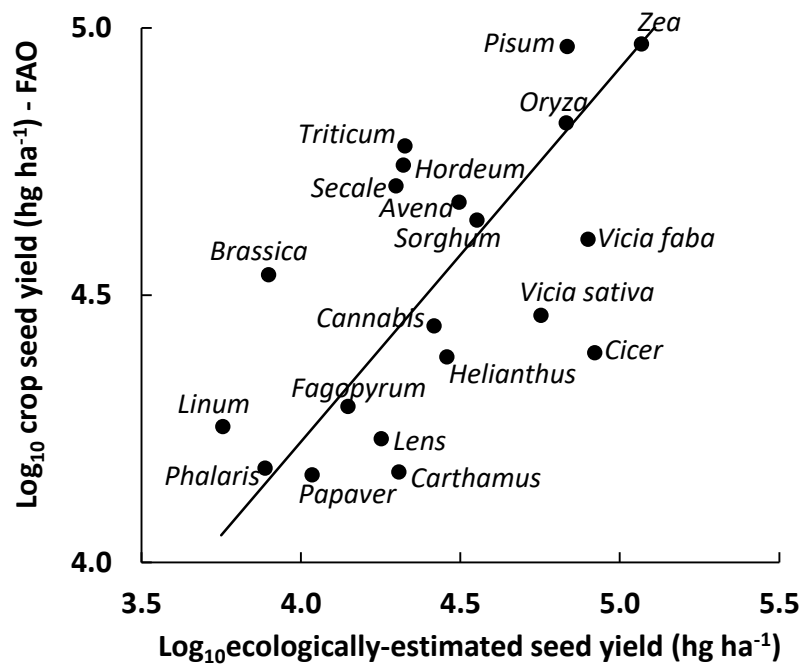
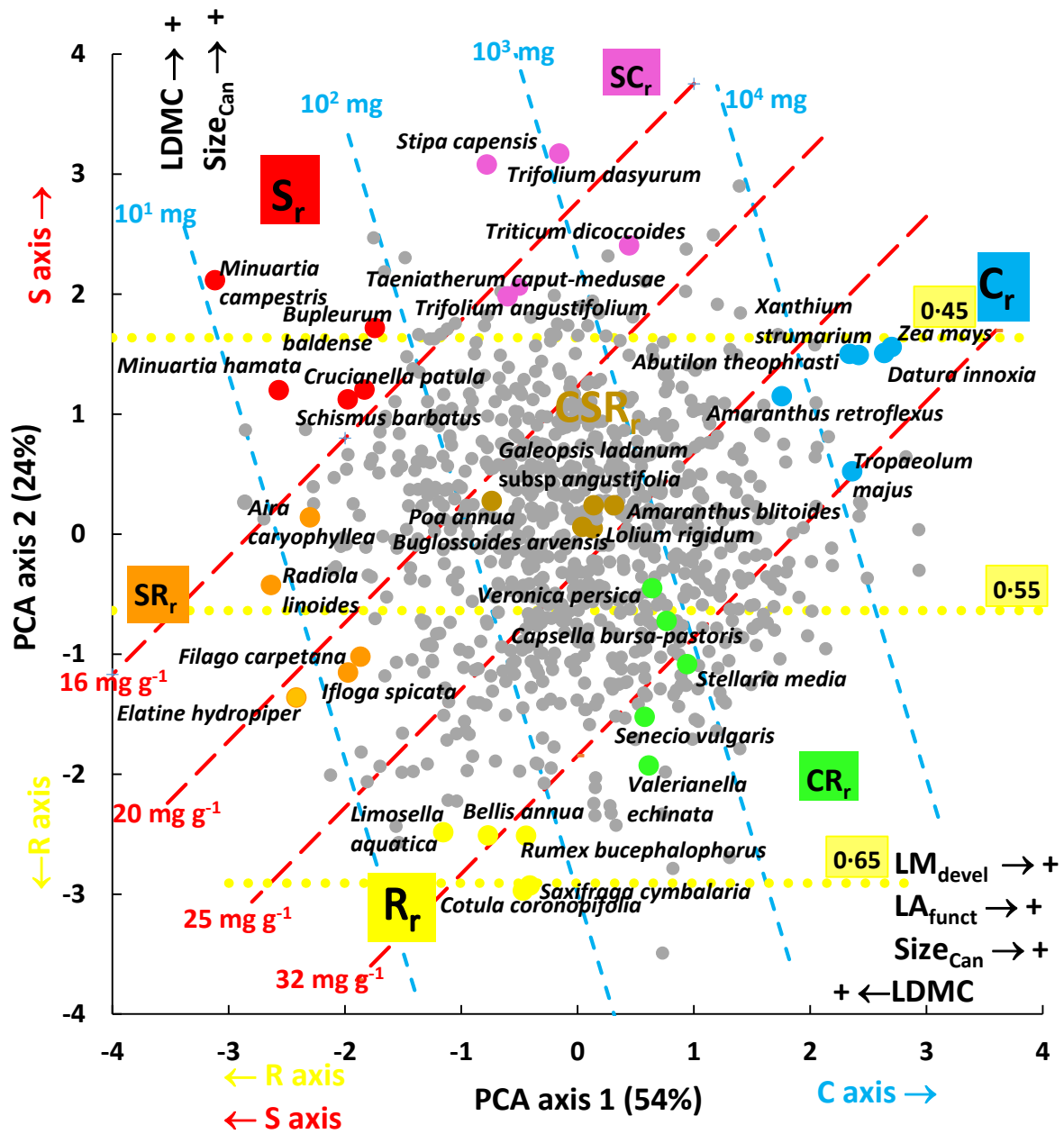
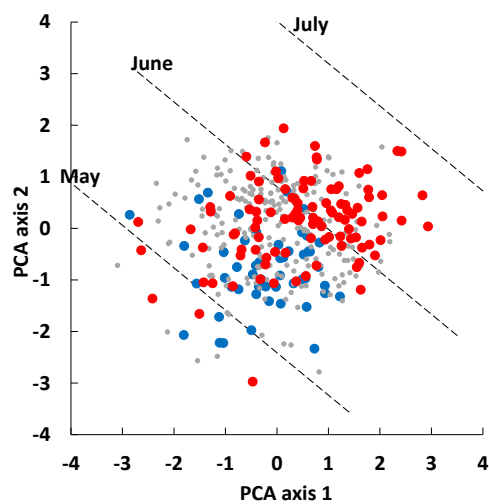


FIG. 2. PCA ordination of 868 annual angiosperm species on the basis of four functional traits, LA_{Funct} , LM_{Devel} and $Size_{Can}$. (A) An ecological classification of species. Labels display, in descending order of values, traits with the highest eigenvector scores on PCA axes 1 and 2. Eqns 8b and 9 from the Results section were used to add, as broken lines, contours for $SeedM_{PIUK}$ ('gold standard' for the C axis; blue, $mg\ plant^{-1}$) and $LeafN$ (negative 'gold standard' for the S axis; red, $mg\ g^{-1}$) and more tentatively, from eqn 10a for $AnnIndex_{UK}$ ('gold standard' for the R axis; yellow, proportion of ruderal species vegetative sample $^{-1}$) as dotted lines. Mindful of CSR theory (Grime 2001), these contours were used to locate putative positions for strategy types. Strategies are colour-coded, with named species examples. (B) Comparing traits and datasets. (i) Flowering Start Time (from Clapham *et al.*, 1987): April or earlier (blue dots), May to June (grey dots), July onwards (red dots). $FlStart = 0.256PCA1 + 0.311PCA2 + 5.750$ ($r^2 = 0.13***$, $n = 412$). (ii) Flowering Period in UK: 1-2 months (red dots), 3-5 months (grey dots), >5 months (blue dots). $Log_{10}FlDuration = 0.027PCA1 - 0.025PCA2 + 0.489$ ($r^2 = 0.03***$, $n = 372$). (iii) 'Gold standard' datasets for $SeedNo_{PI}$: mean values – PCA axis 1 UK (blue dots) 0.13 ± 1.12 , USA (red dots) 1.05 ± 0.71 $t = 5.0***$; PCA axis 2 UK -0.55 ± 0.91 , USA 0.10 ± 0.87 $t = 3.7***$. (iv) Major Families: Asteraceae (PCA axis 1^b 0.30 ± 1.02 , PCA axis 2^a 0.48 ± 0.94 , $n = 134$; blue dots), Fabaceae (mean \pm s.d.: PCA axis 1^b 0.05 ± 0.94 , PCA axis 2^b 0.57 ± 0.74 , $n = 119$; red dots), Poaceae (PCA axis 1^a -0.37 ± 0.95 , PCA axis 2^c 0.90 ± 0.71 , $n = 125$; green dots). PCA axis 1 ANOVA $F_{2,377} = 18.5***$; PCA axis 2 ANOVA $F_{2,377} = 103.6***$.

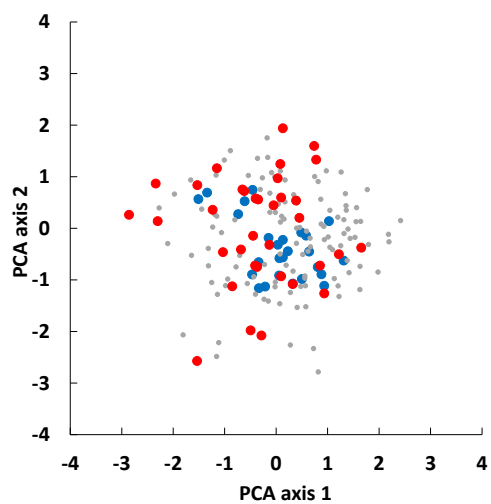
(A)



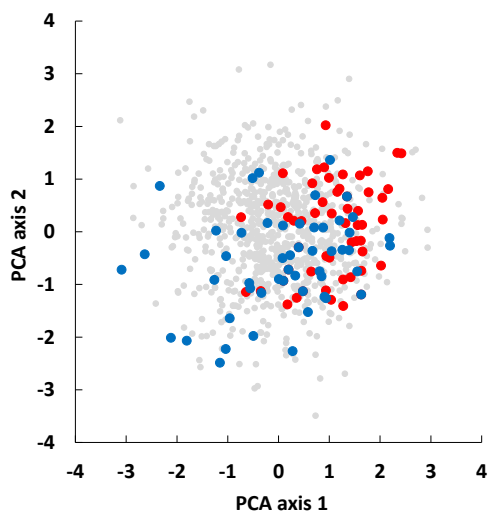
(B) i



ii



iii



iv

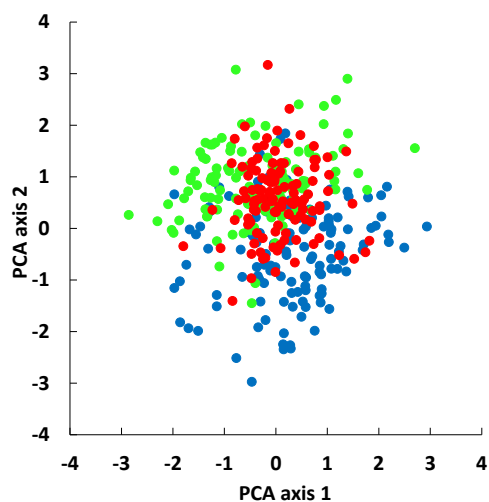


FIG. 3. Seed mass and number both pattern with C_R-S_R-R_R (A) and as a result the numerical relationship between seed mass and number varies with strategy (B). (AI) illustrates the basic geography of the CSR classification of plant functional types for annuals. In II-IV mean estimates \pm s.d. are provided for (IIi) total seed mass plant⁻¹ (one-way ANOVA $F = 213.6^{***}$) and (ii) m⁻² ($F = 122.7^{***}$), (III) mass of an individual seed ($F = 44.6^{***}$), (IVi) total number of seeds plant⁻¹ ($F = 19.7^{***}$) and (ii) m⁻² ($F = 8.0^{***}$). [Number of species: total 839, C_R 68, S_R 47, R_R 30, C_RR 90, S_CR 187, S_RR 74, C_SR 343. The putative direction of change from low to high values is illustrated with an arrow.] In (B) strategies are colour-coded (C, blue dots; S, red; R, yellow; other, grey) with the regions of the PCA ordination provisionally allocated to the three strategies illustrated within the inset. Equations \pm 95% confidence intervals:

$$\text{All species: } \log_{10}\text{SeedNo}_{All} = -0.459 \pm 0.043 \log_{10}\text{SeedM} + 2.783 \pm 0.036 \quad (r^2 = 0.35^{***})$$

$$\text{C}_R\text{-strategist: } \log_{10}\text{SeedNo}_C = -0.690 \pm 0.126 \log_{10}\text{SeedM} + 3.685 \pm 0.100 \quad (r^2 = 0.69^{***})$$

$$\text{R}_R\text{-strategist: } \log_{10}\text{SeedNo}_R = -0.654 \pm 0.257 \log_{10}\text{SeedM} + 2.043 \pm 0.300 \quad (r^2 = 0.49^{***})$$

$$\text{S}_R\text{-strategist: } \log_{10}\text{SeedNo}_S = -0.621 \pm 0.151 \log_{10}\text{SeedM} + 2.248 \pm 0.123 \quad (r^2 = 0.60^{***})$$

$$\text{C}_R\text{R-strategist: } \log_{10}\text{SeedNo}_{CR} = -0.586 \pm 0.105 \log_{10}\text{SeedM} + 3.287 \pm 0.093 \quad (r^2 = 0.59^{***})$$

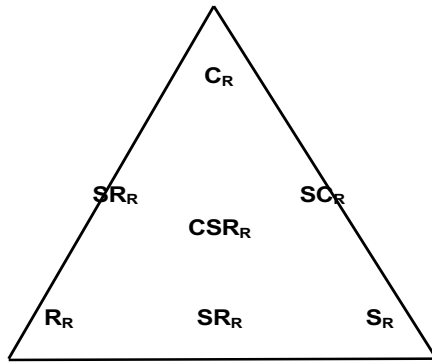
$$\text{S}_C\text{R-strategist: } \log_{10}\text{SeedNo}_{SC} = -0.679 \pm 0.070 \log_{10}\text{SeedM} + 2.877 \pm 0.058 \quad (r^2 = 0.67^{***})$$

$$\text{S}_R\text{R-strategist: } \log_{10}\text{SeedNo}_{SR} = -0.651 \pm 0.103 \log_{10}\text{SeedM} + 2.049 \pm 0.117 \quad (r^2 = 0.69^{***})$$

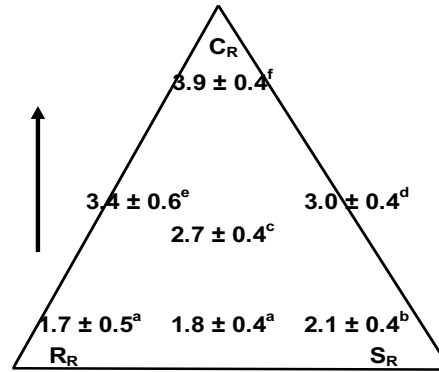
$$\text{C}_S\text{R}_R\text{-strategist: } \log_{10}\text{SeedNo}_{CSR} = -0.636 \pm 0.047 \log_{10}\text{SeedM} + 2.749 \pm 0.036 \quad (r^2 = 0.68^{***})$$

Test for common slope across groups $\chi^2 = 9150^{***}$; test for shifts along the common slope using WALD statistic 295^{***}.]

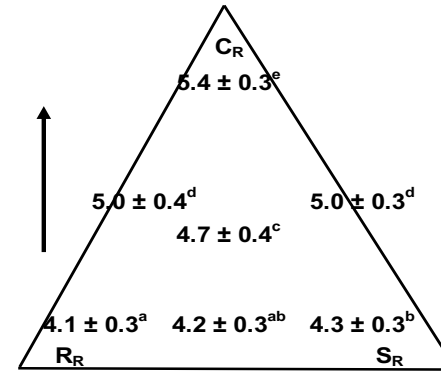
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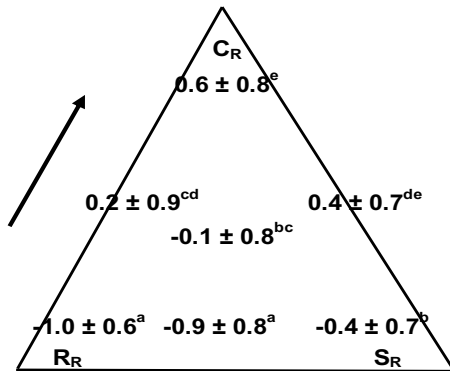
IIi



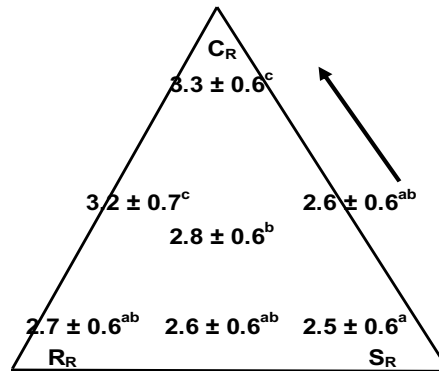
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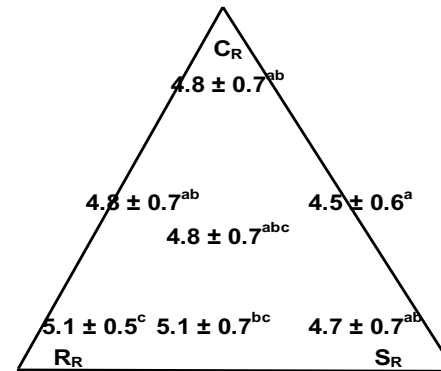
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IVi



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B.

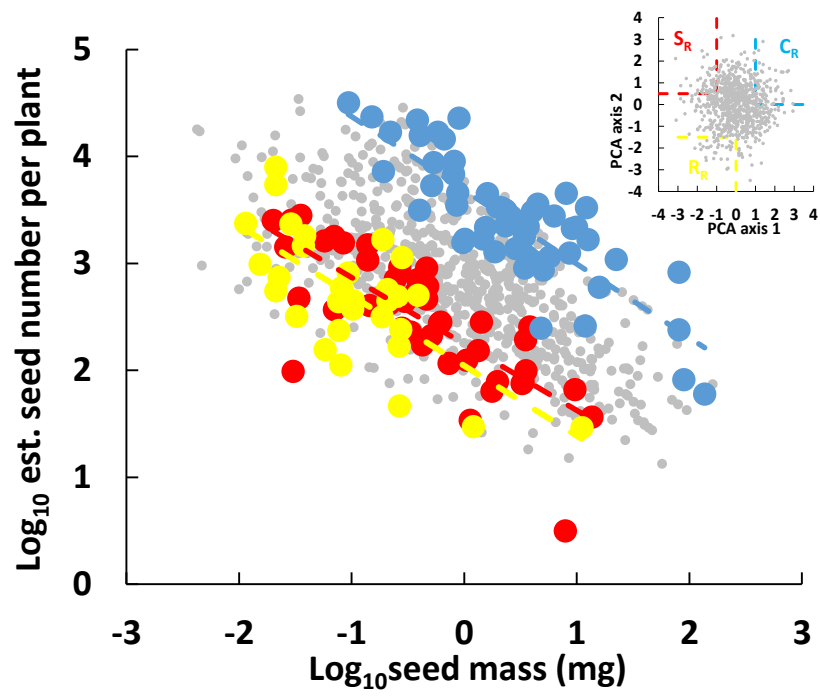
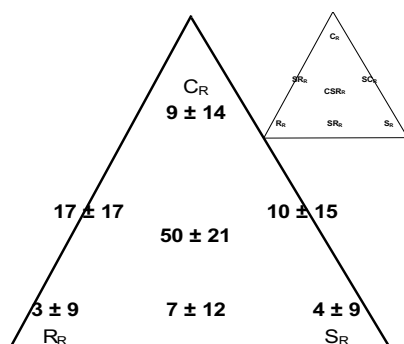
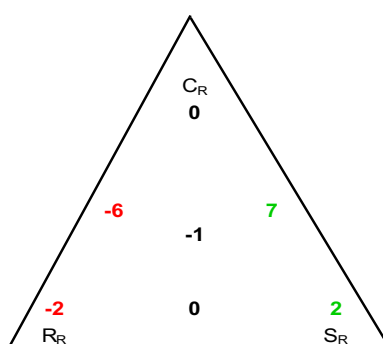


FIG. 4. Both with respect to (A) vegetation samples with ≥ 5 annual species and (B) the species recorded, our three study areas differ in their representation of C_R - S_R - R_R strategy types and (C) changed abundance within UK also patterns with strategy. In A_i (\pm s.d.), B_i and C_i values relate to Central England and are percentages. In the remainder of A and B values identify regional differences from Central England for (ii) North-east and (iii) North central Spain, respectively. Green indicates values higher and red lower than Central England. In (A) coloured values identify differences of $P < 0.05$ using the Mann-Whitney U-tests. In C_{ii} values relate to Status Index and are not calculated for strategies where $n < 10$.

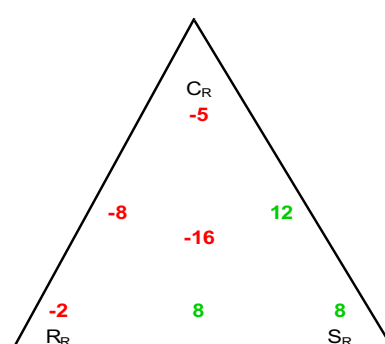
Ai



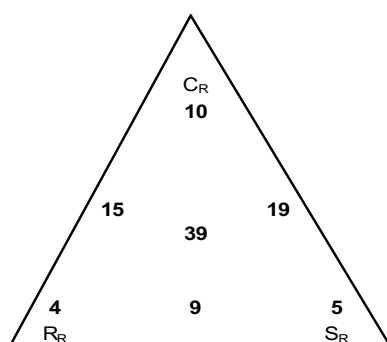
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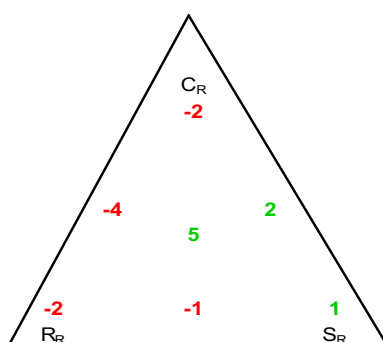
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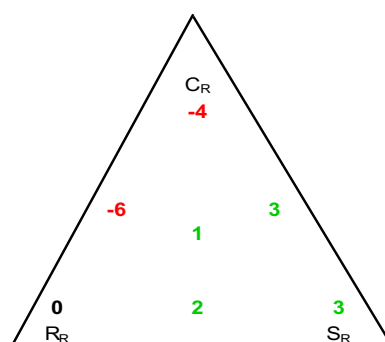
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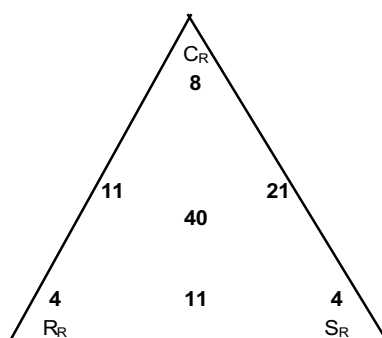
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iii



Ci



ii

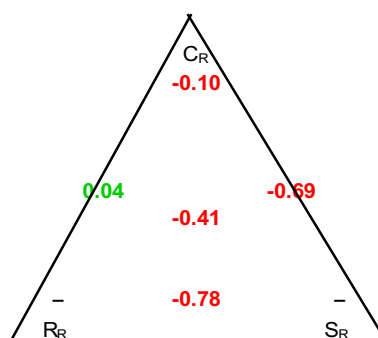
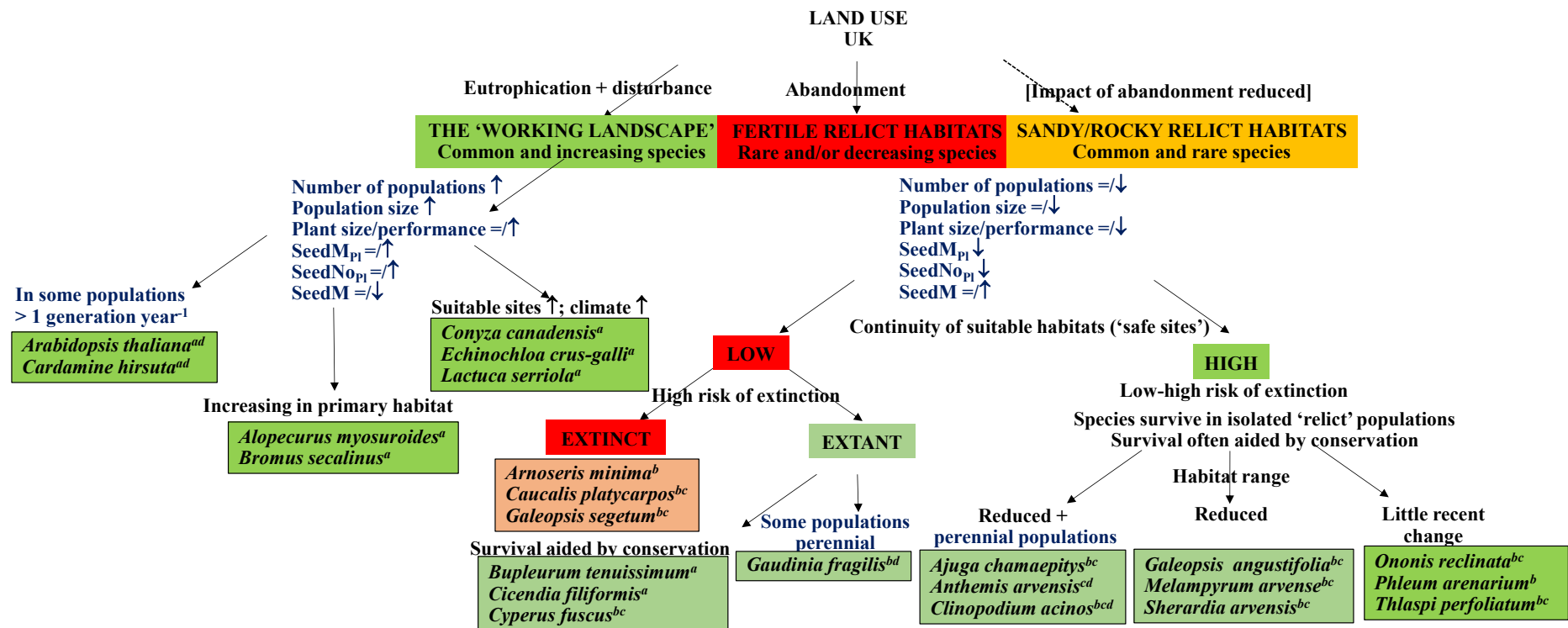


FIG. 5. Some potential changes in trait expression by annuals in response to changing land use in the United Kingdom. Fertile relict habitats include meadows, pastures, wetland and woodland and are very vulnerable to changes in land use. Rocky/sandy habitats are less vulnerable. Ecosystem processes are to some degree controlled by summer drought and their soils are less fertile. Predictions are based upon descriptions of the status of the flora (Hodgson, 1986a; Hodgkinson and Thompson 1997; Preston *et al.*, 2002; Cheffings and Farrell, 2005, Hodgson *et al.*, 2014; Botanical Society of Britain and Ireland and the Biological Records Centre, 2018), the ‘colonisation–competition’ trade-off between few large seeds with potentially higher seedling survivorship and many small widely-dispersed seeds (Westoby *et al.*, 2002; Moles and Westoby, 2006) and field observations (Table 5). Arrows identify predicted direction of change. Comparisons with Spain: consistent with Fig. 4, the relative abundance of relict (fertile) *versus* sandy/rocky habitats and their importance for annuals is identified as Central England > North-east > North central Spain. The putative difference in Spanish status of species is identified by the following suffices – habitat range: ^a similar, ^b wider habitat range, ^c arable still an important habitat; Spanish life history different: ^d typically annual. [Impacts of climate not superimposed here include– arid: dry years (large seeds) *versus* wet years (small) (Venable and Brown, 1988; Pake and Venable, 1996; Metz, *et al.* 2010; Shriver, 2016); cool less favourable (large) *versus* warm favourable (small) (McWilliams *et al.*, 1968; Montesinos-Navarro *et al.*, 2011; Burcu *et al.*, 2017).]



Eutrophication + disturbance

LAND USE
UK

Abandonment

[Impact of abandonment reduced]

THE 'WORKING LANDSCAPE'
Common and increasing species

FERTILE RELICT HABITATS
Rare and/or decreasing species

SANDY/ROCKY RELICT HABITATS
Common and rare species

Number of populations ↑
Population size ↑
Plant size/performance =/↑
SeedM_{PI} =/↑
SeedNo_{PI} =/↑
SeedM =/↓

In some populations
> 1 generation year⁻¹

Arabidopsis thaliana^{ad}
Cardamine hirsuta^{ad}

Increasing in primary habitat

Alopecurus myosuroides^a
Bromus secalinus^a

Suitable sites ↑; climate ↑
Conyza canadensis^a
Echinochloa crus-galli^a
Lactuca serriola^a

LOW

High risk of extinction

EXTINCT

Arnoseris minima^b
Caucalis platycarpus^{bc}
Galeopsis segetum^{bc}

Survival aided by conservation

Bupleurum tenuissimum^a
Cicendia filiformis^a
Cyperus fuscus^{bc}

Number of populations =/↓
Population size =/↓
Plant size/performance =/↓
SeedM_{PI} ↓
SeedNo_{PI} ↓
SeedM =/↑

Continuity of suitable habitats ('safe sites') ↓

HIGH

Low-high risk of extinction

Species survive in isolated 'relict' populations
Survival often aided by conservation

Habitat range

Reduced

Little recent
change

Reduced +
perennial populations

Ajuga chamaepitys^{bc}
Anthemis arvensis^{cd}
Clinopodium acinos^{bcd}

Galeopsis angustifolia^{bc}
Melampyrum arvense^{bc}
Sherardia arvensis^{bc}

Ononis reclinata^{bc}
Phleum arenarium^b
Thlaspi perfoliatum^{bc}

Some populations
perennial
Gaudinia fragilis^{bd}

TABLE 1. *Species in datasets measuring seed production (Stevens, 1932, 1957 (USA); Salisbury, 1942, UK; Šera and Šery, 2004 (Slovenia), FAO, 2018 (crops) and leaf nitrogen (composite database) show significant differences in trait expression. Values are average \pm standard deviation.) For comparison values for all species in the database were included in italics. For summer annuals statistical comparisons involved χ^2 using 2 x 2 contingency tables.*

	All annuals (n = 886)	One-way ANOVA (F value)	USA (n = 56)	UK (n = 51)	Slovenia (n = 123)	FAO - crops (n = 20)	Leaf N (n = 58)
(A) Log ₁₀ SeedM (mg)	<i>-0.04 \pm 0.88</i>	30.8***	0.00 \pm 0.73 ^b	-0.73 \pm 0.76 ^a	-0.15 \pm 0.72 ^b	1.47 \pm 0.77 ^c	0.12 \pm 0.83 ^b
(B) Plant size and shape							
Ht _{Can} (log ₂ scale)	<i>4.38 \pm 1.44</i>	12.1***	5.63 \pm 1.04 ^b	4.33 \pm 1.53 ^a	5.23 \pm 1.34 ^b	6.75 \pm 0.91 ^c	5.44 \pm 1.53 ^b
Ht _{Pl} (log ₂ scale)	<i>5.22 \pm 1.54</i>	10.1***	6.59 \pm 1.09 ^b	5.37 \pm 1.44 ^a	6.14 \pm 1.34 ^b	7.40 \pm 0.91 ^c	6.39 \pm 1.40 ^b
Diam _{Can} (log ₂ scale)	<i>4.90 \pm 1.32</i>	4.6***	5.59 \pm 1.16 ^b	4.68 \pm 1.43 ^a	5.47 \pm 1.05 ^b	5.80 \pm 1.06 ^b	5.75 \pm 1.35 ^b
Diam _{Pl} (log ₂ scale)	<i>5.30 \pm 1.20</i>	6.0***	6.16 \pm 1.06 ^b	5.10 \pm 1.33 ^a	5.93 \pm 0.93 ^b	6.10 \pm 0.79 ^b	6.18 \pm 1.11 ^b
Size _{Can} (log ₂ scale)	<i>12.20 \pm 3.55</i>	8.3***	14.52 \pm 3.63 ^b	12.04 \pm 3.62 ^a	14.21 \pm 2.87 ^b	16.35 \pm 2.76 ^c	15.00 \pm 3.72 ^{bc}
Size _{Pl} (log ₂ scale)	<i>13.84 \pm 3.32</i>	11.1***	15.45 \pm 4.52 ^b	13.16 \pm 3.69 ^a	16.03 \pm 2.65 ^b	17.60 \pm 2.30 ^c	16.80 \pm 2.94 ^{bc}
Shape _{Can} (log ₂ scale)	<i>-0.51 \pm 1.39</i>	4.9***	0.04 \pm 1.13 ^a	-0.36 \pm 1.22 ^a	-0.19 \pm 1.19 ^a	0.95 \pm 0.89 ^b	-0.25 \pm 1.35 ^a
Shape _{Pl} (log ₂ scale)	<i>-0.07 \pm 1.54</i>	3.1**	0.43 \pm 1.20 ^a	0.26 \pm 1.47 ^a	0.25 \pm 1.20 ^a	1.30 \pm 0.73 ^b	0.25 \pm 1.50 ^a
(C) Leaf size							
Log ₁₀ LA _{morph} (mm ²)	<i>2.66 \pm 0.75</i>	6.8***	3.22 \pm 0.60 ^b	2.60 \pm 0.91 ^a	2.94 \pm 0.64 ^{ab}	3.61 \pm 0.54 ^c	3.05 \pm 0.68 ^{ab}
Log ₁₀ LA _{devel} (mm ²)	<i>2.74 \pm 0.72</i>	5.6***	3.27 \pm 0.60 ^b	2.84 \pm 0.89 ^a	3.02 \pm 0.64 ^{ab}	3.62 \pm 0.55 ^c	3.15 \pm 0.65 ^{ab}
LA _{funct} (log ₂ scale)	<i>3.93 \pm 1.72</i>	11.6***	6.55 \pm 1.14 ^c	4.49 \pm 1.69 ^a	4.94 \pm 1.91 ^{ab}	5.60 \pm 1.35 ^b	5.26 \pm 1.86 ^{ab}
Log ₁₀ LM _{morph} (mg)	<i>1.30 \pm 0.75</i>	7.7***	1.81 \pm 0.64 ^b	1.30 \pm 0.95 ^a	1.52 \pm 0.66 ^{ab}	2.24 \pm 0.57 ^c	1.67 \pm 0.71 ^{ab}
Log ₁₀ LM _{devel} (mg)	<i>1.37 \pm 0.72</i>	6.8***	1.86 \pm 0.64 ^b	1.41 \pm 0.91 ^a	1.59 \pm 0.64 ^{ab}	2.25 \pm 0.59 ^c	1.75 \pm 0.67 ^{ab}
(D) Leaf structure							
$\sqrt{\text{LDMC}}$ (%)	<i>4.15 \pm 0.65</i>	4.7**	4.07 \pm 0.49 ^a	3.88 \pm 0.53 ^a	4.06 \pm 0.49 ^a	4.42 \pm 0.58 ^b	4.14 \pm 0.53 ^a
Log ₁₀ SLA (mm ² mg ⁻¹)	<i>1.39 \pm 0.15</i>	4.4**	1.40 \pm 0.11 ^{ab}	1.43 \pm 0.13 ^b	1.44 \pm 0.10 ^b	1.37 \pm 0.10 ^a	1.40 \pm 0.12 ^{ab}
Log ₁₀ LThick (mm)	<i>-0.68 \pm 0.22</i>	2.4 ⁺	-0.64 \pm 0.18 ^a	-0.63 \pm 0.18 ^a	-0.72 \pm 0.17 ^a	-0.72 \pm 0.17 ^a	-0.70 \pm 0.21 ^a
(E) Phenology							
Month of first flowering	<i>5.8 \pm 1.1</i>	2.9*	6.2 \pm 1.3 ^a	5.5 \pm 1.1 ^b	5.8 \pm 1.2 ^{ab}		6.1 \pm 1.3 ^a
Summer annual (%)	<i>21</i>		45 ^a	27 ^b	31 ^b		43 ^a

Here and in the remaining tables and figures ***, **, *, +, ns indicate $P < 0.001$, < 0.01 , < 0.05 , < 0.10 ; ns, not statistically significant and

groupings with the same superscript are not statistically significantly different at $P < 0.05$.

TABLE 2. *The seed size, number and RSN (\pm s.d.) of annuals differs between (A) regions, (B) habitats and (C) UK status for both (i) vegetation samples and (ii) species. In (C) ‘Decreased’, Status Index < -0.5; ‘Increased’, Status Index > +0.5.*

	n	Log ₁₀ seed mass	Log ₁₀ seed number	RSN
(A) Regions				
(i) Vegetation samples with ≥ 5 annual species				
Central England	1500	-0.38 \pm 0.33 ^a	3.21 \pm 0.23 ^c	0.40 \pm 0.17 ^c
North-east Spain	465	-0.23 \pm 0.34 ^b	3.04 \pm 0.33 ^b	0.25 \pm 0.25 ^b
North central Spain	275	-0.15 \pm 0.40 ^c	2.79 \pm 0.31 ^a	0.06 \pm 0.25 ^a
One-way ANOVA (<i>F</i>)		74.8***	323.2***	376.0***
(ii) Species				
Central England	200	-0.29 \pm 0.71 ^a	3.10 \pm 0.55 ^b	0.26 \pm 0.49 ^b
North-east Spain	323	-0.07 \pm 0.83 ^b	2.90 \pm 0.66 ^a	0.10 \pm 0.57 ^a
North central Spain	284	-0.03 \pm 0.82 ^b	2.78 \pm 0.67 ^a	0.02 \pm 0.59 ^a
One-way ANOVA (<i>F</i>)		7.0***	13.9***	11.0***
(B) Habitats				
(i) Vegetation samples				
(a) Central England				
Wetland	57	-0.60 \pm 0.32 ^a	3.52 \pm 0.17 ^d	0.58 \pm 0.13 ^b
Rocky	136	-0.65 \pm 0.31 ^a	3.03 \pm 0.16 ^a	0.36 \pm 0.14 ^a
Pasture	30	-0.48 \pm 0.41 ^{ab}	3.07 \pm 0.17 ^{ab}	0.30 \pm 0.15 ^a
Arable	391	-0.17 \pm 0.29 ^c	3.20 \pm 0.19 ^{bc}	0.33 \pm 0.15 ^a
Spoil	371	-0.47 \pm 0.28 ^{ab}	3.32 \pm 0.20 ^c	0.50 \pm 0.13 ^b
Wasteland	499	-0.38 \pm 0.29 ^b	3.17 \pm 0.25 ^{ab}	0.38 \pm 0.17 ^a
Woodland	8	-0.05 \pm 0.29 ^c	3.15 \pm 0.18 ^{ab}	0.31 \pm 0.21 ^a
One-way ANOVA (<i>F</i>)		66.0***	60.8***	58.3***
(b) North-east Spain				
Wetland	23	-0.58 \pm 0.38 ^a	3.37 \pm 0.23 ^b	0.52 \pm 0.17 ^c
Artificial	323	-0.21 \pm 0.32 ^{bc}	3.10 \pm 0.31 ^{ab}	0.28 \pm 0.23 ^b
Grassland	80	-0.19 \pm 0.32 ^{bc}	2.77 \pm 0.27 ^a	0.08 \pm 0.24 ^a
Maritime/saline	16	-0.42 \pm 0.37 ^{ab}	2.97 \pm 0.30 ^{ab}	0.34 \pm 0.24 ^b
Open habitats	16	-0.14 \pm 0.38 ^c	2.85 \pm 0.32 ^a	0.07 \pm 0.24 ^a
Dwarf shrub	[2	-0.18 \pm 0.37	2.77 \pm 0.44	0.03 \pm 0.38]
Woodland	[5	-0.07 \pm 0.29	3.08 \pm 0.15	0.34 \pm 0.11]
One-way ANOVA (<i>F</i>)		8.2***	28.3***	23.2***
(c) North central Spain				
Wetland	[2	-0.74 \pm 0.05	3.16 \pm 0.24	0.48 \pm 0.14]
Artificial	121	0.09 \pm 0.29 ^c	2.92 \pm 0.28 ^c	0.12 \pm 0.23 ^b
Grassland	94	-0.21 \pm 0.22 ^b	2.66 \pm 0.32 ^{abc}	-0.01 \pm 0.25 ^{ab}
Maritime/saline	25	-0.98 \pm 0.23 ^a	2.90 \pm 0.18 ^{bc}	0.17 \pm 0.15 ^b
Open habitats	12	-0.29 \pm 0.24 ^b	2.62 \pm 0.18 ^a	0.01 \pm 0.19 ^{ab}
Dwarf shrub	13	-0.15 \pm 0.30 ^{bc}	2.43 \pm 0.20 ^a	-0.19 \pm 0.17 ^a
Woodland	8	-0.15 \pm 0.35 ^{bc}	2.65 \pm 0.19 ^{ab}	0.09 \pm 0.22 ^b
One-way ANOVA (<i>F</i>)		72.6***	16.4***	7.6***
(ii) Species				
(a) Central England				
Wetland	19	-0.59 \pm 0.74 ^a	3.09 \pm 0.56	0.49 \pm 0.39 ^{ab}

Rocky	25	-0.54 ± 0.73^{ab}	3.34 ± 0.38^{bc}	0.15 ± 0.46^a
Pasture	[4	0.22 ± 0.45	2.80 ± 0.38	$0.23 \pm 0.15]$
Arable	77	-0.09 ± 0.61^{ab}	2.65 ± 0.21^a	0.18 ± 0.49^a
Spoil	32	-0.64 ± 0.69^a	3.08 ± 0.54^{abc}	0.63 ± 0.28^b
Wasteland	40	-0.21 ± 0.75^{ab}	3.49 ± 0.52^c	0.09 ± 0.54^a
Woodland	7	-0.10 ± 0.42^{ab}	2.90 ± 0.61^{abc}	0.11 ± 0.48^a
One-way ANOVA (<i>F</i>)		4.7***	7.2***	6.9***
(b) North-east Spain				
Wetland	38	-0.08 ± 0.84^{ab}	3.35 ± 0.54^b	0.46 ± 0.46^b
Artificial	123	-0.52 ± 0.90^a	2.93 ± 0.66^{ab}	0.08 ± 0.58^{ab}
Grassland	57	0.01 ± 0.81^{ab}	2.61 ± 0.57^a	-0.06 ± 0.55^a
Maritime/saline	27	-0.02 ± 0.91^{ab}	2.96 ± 0.58^{ab}	0.20 ± 0.56^{ab}
Open habitats	42	-0.13 ± 0.76^{ab}	2.80 ± 0.69^a	0.03 ± 0.64^a
Dwarf shrub	28	-0.06 ± 0.84^{ab}	2.75 ± 0.74^a	-0.02 ± 0.63^a
Woodland	17	-0.15 ± 0.71^{ab}	3.01 ± 0.47^{ab}	0.21 ± 0.44^{ab}
One-way ANOVA (<i>F</i>)		5.7***	5.9***	3.8**
(c) North central Spain				
Wetland	0			
Artificial	113	0.27 ± 0.76^c	2.85 ± 0.74	-0.01 ± 0.62
Grassland	74	-0.29 ± 0.83^{ab}	2.69 ± 0.67	-0.01 ± 0.59
Maritime/saline	18	-0.68 ± 0.87^a	2.91 ± 0.69	0.20 ± 0.60
Open habitats	27	-0.27 ± 0.68^{ab}	2.73 ± 0.54	0.06 ± 0.52
Dwarf shrub	33	-0.09 ± 0.68^{bc}	2.53 ± 0.64	-0.14 ± 0.14
Woodland	28	-0.01 ± 0.81^{bc}	2.93 ± 0.58	0.21 ± 0.51
One-way ANOVA (<i>F</i>)		8.2***	1.8 ns	1.4 ns
(C) UK status				
(i) Vegetation samples				
Decreased	418	-0.33 ± 0.38^b	3.14 ± 0.21^a	0.34 ± 0.16^a
Increased	450	-0.40 ± 0.30^a	3.29 ± 0.23^b	0.46 ± 0.17^a
<i>t</i> -test		3.0**	10.0***	11.8***
(ii) Species				
Decreased	172	-0.22 ± 0.79	2.87 ± 0.54^a	0.09 ± 0.51^a
Increased	71	-0.27 ± 0.70	3.17 ± 0.60^b	0.26 ± 0.50^b
<i>t</i> -test		0.5 ns	3.8***	2.4*

TABLE 3 *Examples of species whose populations were found to differ between the United Kingdom and Spain in (A) ecological range or (B) life history. Based upon field observations augmented by published records.*

Species	United Kingdom	Spain
(A) Habitat range		
<i>Galeopsis angustifolia</i> <i>Ononis reclinata</i> <i>Thlaspi perfoliatum</i>	Uncommon – very rare in UK. Now primarily confined to rocky sites with habitat continuity	Wide range of habitats including crop and/or fallow fields
<i>Galeopsis segetum</i>	Former arable weed, now extinct	Former arable weed, now largely restricted to open shaded sites with habitat continuity
(B) Life history		
<i>Clinopodium acinos</i>	Much reduced as an annual arable weed; increasingly a woody perennial of rocky sites with habitat continuity	Still characteristically an arable weed
<i>Gaudinia fragilis</i>	Primarily a tufted perennial of unimproved grassland	Typically an annual of disturbed habitats. [Seen in arable habitats in north Morocco.]

TABLE 4. *Seed traits of annuals correlate with the functional traits of coexisting perennials weighted by abundance. Values relate to Pearson r coefficients with number of relevés in parentheses.*

	SeedM _{peren}	LDMC _{peren}	DomI
(A) SeedM _{annual}			
Central England (1474)	0.269***	0.043 ⁺	0.256***
North-east Spain (427)	0.225***	0.086 ⁺	0.175***
North central Spain (255)	0.158*	-0.326***	0.293***
(B) SeedNo _{annual}			
Central England	-0.048 ⁺	-0.101***	0.219***
North-east Spain	-0.074	-0.061	0.141**
North central Spain	-0.297***	-0.305***	0.040
(C) RSN			
Central England	-0.095***	-0.048 ⁺	0.075**
North-east Spain	-0.099*	-0.103*	0.094 ⁺
North central Spain	-0.365***	-0.099	-0.067

TABLE 5. *Decreasing annual species in the United Kingdom produce significantly fewer seeds, but not significantly larger ones, than species with a stable or increasing distribution. Number of species are given in parenthesis and because of a shortage of data strategies with similar regression equations in Fig. 3B are combined. [For comparison: $RSN_{Decreased} 0.09 \pm 0.51$; $RSN_{Stable/increased} 0.25 \pm 0.49$; $t = 3.0^{**}$.]*

	Mean $\log_{10}SeedM \pm s.d.$					Mean $\log_{10}SeedNo_{pl} \pm s.d.$		
	Decreased		Stable/increased		<i>t</i>	Decreased	Stable/increased	<i>t</i>
All	172	-0.22 ± 0.79	165	-0.31 ± 0.72	1.2 ns	2.87 ± 0.54	3.08 ± 0.60	3.5^{***}
C	11	0.47 ± 0.33	15	0.20 ± 0.68	1.3 ns	3.22 ± 0.35	3.71 ± 0.47	2.9^{**}
CR/SC	55	0.19 ± 0.66	53	0.09 ± 0.53	0.9 ns	2.83 ± 0.57	3.07 ± 0.68	2.0^*
CSR	69	-0.19 ± 0.63	66	-0.48 ± 0.66	2.6^{**}	2.89 ± 0.52	3.12 ± 0.47	2.7^{**}
S/SR/R	35	-1.06 ± 0.62	28	-0.94 ± 0.61	0.8 ns	2.70 ± 0.47	2.72 ± 0.43	0.2 ns

TABLE 3 Examples of less common species whose populations were found to differ between the United Kingdom and Spain in (A) ecological range or (B) life history. Based upon field observations augmented by published records.

Species	United Kingdom	Spain
(C) Habitat range		
<i>Galeopsis angustifolia</i> <i>Ononis reclinata</i> <i>Thlaspi perfoliatum</i>	Uncommon – very rare in UK. Now primarily confined to rocky sites with habitat continuity.	Wide range of habitats including crop and/or fallow fields.
<i>Galeopsis segetum</i>	Former arable weed, now extinct.	Primarily restricted to open shaded sites with habitat continuity but also an arable weed.
(D) Life history		
<i>Clinopodium acinos</i>	Much reduced as an annual arable weed; increasingly a woody perennial of rocky sites with habitat continuity.	Typically an annual but in similar range of habitats and still an arable weed.
<i>Gaudinia fragilis</i>	Primarily a tufted perennial of unimproved grassland.	Typically an annual of rocky pastures and ruderal habitats. [Observed on arable land in north Morocco.]

TABLE S1. Range of trait values within the database.

	No. spp.	5th -95th percentiles	Lowest value	Highest value
(A) Seed				
SeedM (mg)	1038	0.03 – 30.1	0.004 <i>Lindernia procumbens</i> (wetland)	925.8 <i>Vicia faba</i> (crop)
SeedM _{PIUK} (mg plant ⁻¹)	52	9 – 8395	1 <i>Cicendia filiformis</i> (wetland)	22216 <i>Chenopodium polyspermum</i> (arable)
SeedM _{PIUSA} (mg plant ⁻¹)	56	7123 – 87627	92 <i>Veronica peregrina</i> (arable)	267788 <i>Hibiscus trionum</i> (arable)
SeedM _{m2} (mg m ⁻²)	123	2718 – 1629565	295 <i>Camelina microcarpa</i> (arable)	5724622 <i>Erodium cicutarium</i> (dry habitats)
SeedM _{ha} (hg ha ⁻¹)	20	14773 – 92393	14583 <i>Papaver somniferum</i> (crop)	93386 <i>Zea mays</i> (crop)
SeedNo _{PIUK}	52	138 – 26494	39 <i>Veronica hederifolia</i> (woodland, arable)	250000 <i>Chenopodium rubrum</i> (wetland)
SeedNo _{PIUSA}	56	250 – 176300	105 <i>Galium aparine</i> (woodland, arable)	842700 <i>Descurainia sophia</i> (arable)
SeedNo _{m2}	123	8370 – 2131361	969 <i>Camelina microcarpa</i> (arable)	12252500 <i>Chenopodium rubrum</i> (wetland)
(B) Plant size and shape				
Ht _{Can} (log ₂ scale)	1584	2 – 7	1 <i>Erophila verna</i> (dry habitats)	9 <i>Zea mays</i> (crop)
Ht _{Pl} (log ₂ scale)	1584	3 – 7	1 <i>Montia fontana</i> subsp <i>chondrosperma</i> (dry habitats)	9
Diam _{Can} (log ₂ scale)	1576	3 – 7	1 <i>Cicendia filiformis</i> (wetland)	10 <i>Citrullus lanatus</i> (crop)
Diam _{Pl} (log ₂ scale)	1576	3 – 7	2	10
Size _{Can} (log ₂ scale)	1576	6 – 18	1	24
Size _{Pl} (log ₂ scale)	1576	8 – 19	3	24
Shape _{Can} (log ₂ scale)	1576	-3 – 1	-5 <i>Euphorbia prostrata</i> (wasteland)	4 <i>Linum usitatissimum</i> (crop)
Shape _{Pl} (log ₂ scale)	1576	-3 – 1	-5	4 <i>Blackstonia perfoliata</i> (dry habitats)
(C) Leaf size				
LA _{morph} (mm ²)	973	23 – 7079	4 <i>Cicendia filiformis</i> (wetland)	87627 <i>Notobasis syriaca</i> (fallow land)
LA _{devel} (mm ²)	973	32 – 8511	8	87627
LA _{funct} (log ₂ scale)	1559	1 – 7	0 <i>Minuartia campestris</i> (dry habitats)	9 <i>Helianthus annuus</i> (crop)
LM _{morph} (mg)	931	0.9 – 343	0.1 <i>Cicendia filiformis</i> (wetland)	2163 <i>Notobasis syriaca</i> (fallow land)
LM _{devel} (mg)	931	1.4 – 352	0.2	2163
(D) Leaf structure				
LDMC (%)	929	9.9 – 27.0	4.9 <i>Sclerophylax spinescens</i> (waste land)	39.6 <i>Minuartia campestris</i> (dry habitats)
SLA (mm ² mg ⁻¹)	943	14.2 – 42.3	6.3 <i>Plantago ovata</i> (dry habitats)	102.3 <i>Ceratocarpus claviculata</i> (woodland)
LThick (mm)	875	0.10 – 0.46	0.04 <i>Trifolium micranthum</i> (lawn)	1.23 <i>Plantago phaeostoma</i> (dry habitats)

TABLE S2. Leaf dry matter content differed between families and regions. Paired *t*-tests assessed whether LDMC of species from target families were significantly different from mean values for co-occurring annual vegetation (excluding species from the three families under test). Two-way ANOVA: regions $F_{2,212} = 33.0^{***}$; families $F_{2,212} = 1.3$ ns; regions \times families $F_{4,212} = 0.9$ ns. Additionally, one-way ANOVAs compared the associated vegetation within each individual region and within each individual family.

Region	Asteraceae			Fabaceae			Poaceae			One-way ANOVA Families
	<i>n</i>	$\sqrt{\text{LDMC (spp - veg)}}$	<i>t</i>	<i>n</i>	$\sqrt{\text{LDMC (spp - veg)}}$	<i>t</i>	<i>n</i>	$\sqrt{\text{LDMC (spp - veg)}}$	<i>t</i>	
C England	26 ^a	-0.16	1.8	12 ^a	0.73	9.9***	19 ^a	0.84	14.7***	1.6 ns
NE Spain	33 ^c	-0.27	3.3**	23 ^{ab}	0.40	4.8***	29 ^{ab}	0.76	8.9***	0.4 ns
N C Spain	26 ^b	-0.48	5.4***	21 ^b	0.22	2.7*	23 ^b	0.71	10.6***	1.0 ns
One-way ANOVA Regions		22.1***			8.3***			6.6**		

TABLE S3. Traits entered in the CSR ordination, PCA axes and leaf silicon content differed between families. ANOVAs were carried out on both species and mean values for genera. Because of a shortage of published data for species submitted to the PCA, values for LeafSi included perennials and values where $n < 10$, in parenthesis, were excluded from the ANOVA.

Family	<i>n</i>	$\sqrt{\text{LDMC}}$	<i>n</i>	$\text{Log}_{10}\text{LM}_{\text{level}}$	<i>n</i>	Size_{Can}	<i>n</i>	LA_{funct}	<i>n</i>	PCA 1	<i>n</i>	PCA 2	<i>n</i>	$\text{Log}_{10}\text{LeafSi}$
1Amaranthaceae	32 ^{abc(1,2)}	4.02 ± 0.52	32 ^{cd(1,2)}	1.66 ± 0.66	54 ^{cd(2)}	15.6 ± 2.5	50 ^{cd(4)}	5.7 ± 1.7	32 ^{d(2)}	0.97 ± 0.73	32 ^{efg(1-4)}	0.16 ± 0.81	13 ^a	-1.16 ± 0.59
2Apiaceae	38 ^{def(1,2,3)}	4.47 ± 0.55	38 ^{cd(1,2)}	1.69 ± 0.71	58 ^{abc(1,2)}	11.7 ± 3.0	58 ^{a(1,2)}	2.6 ± 1.6	38 ^{abc(1,2)}	-0.29 ± 0.76	38 ^{gh(1-4)}	0.48 ± 0.86	3	-1.16 ± 0.38
3Asteraceae	137 ^{ab(1,2)}	3.78 ± 0.54	138 ^{cd(1,2)}	1.57 ± 0.74	205 ^{cd(1,2)}	12.8 ± 3.4	201 ^{bcd(2-4)}	4.3 ± 1.9	134 ^{cd(1,2)}	0.30 ± 1.02	134 ^{abcd(1-3)}	0.48 ± 0.94	23 ^b	-0.70 ± 0.46
4Boraginaceae	24 ^{a(1)}	3.70 ± 0.47	24 ^{cd(1,2)}	1.43 ± 0.57	50 ^{abc(1,2)}	11.3 ± 3.0	48 ^{cd(3-4)}	4.8 ± 1.2	24 ^{bc(1,2)}	0.16 ± 0.85	24 ^{a(1)}	-0.92 ± 0.74	0	
5Brassicaceae	79 ^{ab(1,2)}	3.82 ± 0.40	79 ^{cd(1,2)}	1.51 ± 0.78	127 ^{abc(1)}	11.1 ± 2.8	124 ^{cd(3-4)}	4.9 ± 1.6	77 ^{c(1,2)}	0.22 ± 0.99	77 ^{ab(1,2)}	-0.71 ± 0.67	4	-0.67 ± 0.60
6Caryophyllaceae	63 ^{bcd(1,2)}	4.09 ± 0.64	62 ^{ab(1)}	0.88 ± 0.79	117 ^{a(1)}	10.0 ± 2.5	114 ^{a(1-3)}	2.9 ± 1.7	60 ^{a(1)}	-0.65 ± 1.03	60 ^{abcde(1-3)}	-0.44 ± 0.88	2	-0.90 ± 0.46
7Euphorbiaceae	19 ^{ef(2,3)}	4.49 ± 0.38	20 ^{a(1,2)}	0.77 ± 0.50	32 ^{bcd(1,2)}	12.1 ± 2.4	32 ^{bcd(3-4)}	4.0 ± 1.2	19 ^{ab(1,2)}	-0.53 ± 0.73	19 ^{figh(2-4)}	0.30 ± 0.61	1	-0.96
8Fabaceae	120 ^{def(2,3)}	4.44 ± 0.48	120 ^{abcd(1,2)}	1.27 ± 0.46	208 ^{bcd(1,2)}	14.4 ± 2.1	208 ^{bcd(1-4)}	4.2 ± 0.9	119 ^{bcd(1,2)}	0.05 ± 0.61	119 ^{gh(3,4)}	0.57 ± 0.74	12 ^{ab}	-0.88 ± 0.56
9Lamiaceae	21 ^{cde(2,3)}	4.30 ± 0.39	21 ^{cd(1,2)}	1.66 ± 0.45	308 ^{cd(1)}	12.2 ± 2.4	30 ^{d(1-4)}	5.0 ± 1.4	21 ^{c(1,2)}	0.24 ± 0.78	21 ^{defg(1-4)}	0.14 ± 0.52	7	-0.33 ± 0.41
10Papaveraceae	22 ^{ab(1,2)}	3.90 ± 0.33	22 ^{d(2)}	1.78 ± 0.64	40 ^{c(1,2)}	15.5 ± 2.5	40 ^{a(1-4)}	2.7 ± 1.3	22 ^{c(1,2)}	0.25 ± 0.65	22 ^{cdefg(1-4)}	-0.05 ± 0.54	1	-0.24
11Plantaginaceae	31 ^{ab(1,2)}	3.86 ± 0.44	31 ^{abc(1,2)}	1.21 ± 0.44	66 ^{ab(1)}	10.5 ± 2.8	66 ^{ab(1-4)}	3.5 ± 1.3	30 ^{abc(1,2)}	-0.13 ± 0.60	30 ^{abc(1-3)}	-0.63 ± 0.71	3	-0.81 ± 0.36
12Poaceae	128 ^{f(3)}	4.81 ± 0.42	135 ^{bcd(1,2)}	1.30 ± 0.67	213 ^{abc(1)}	11.5 ± 3.6	211 ^{ab(1-4)}	3.4 ± 1.3	125 ^{abc(1)}	-0.37 ± 0.95	125 ^{gh(4)}	0.90 ± 0.71	76 ^c	-0.04 ± 0.27
13Ranunculaceae	25 ^{ab(12)}	3.91 ± 0.42	25 ^{bcd(1,2)}	1.34 ± 0.48	37 ^{abc(1)}	11.4 ± 2.5	41 ^{a(1)}	2.9 ± 1.8	21 ^{abc(1)}	-0.31 ± 0.62	21 ^{bcd(1-3)}	-0.29 ± 0.75	0	
One-way ANOVA														
Species		39.3***		8.6***		31.7***		29.3***		11.3***		36.7***		49.8***
[Genus		18.0***		3.7***		4.5***		7.5***		5.7***		12.8***		-]

Groupings with the same superscript letters (species) and numbers (mean values for genus) were not statistically significantly different at $P < 0.05$ in Tukey (*post hoc*) tests for one-way ANOVA.

TABLE S4. Traits entered in the CSR ordination differed between tribes and subfamilies of (A) Asteraceae, (B) Fabaceae and (C) Poaceae. Groupings where $n \leq 5$, in parenthesis, were excluded from statistical analyses.

(A)

Grouping	<i>n</i>	$\sqrt{\text{LDMC}}$	$\text{Log}_{10}\text{LM}_{\text{devel}}$	Size_{Can}	LA_{funct}	PCA 1	PCA 2
Asteroideae	74	$3.78 \pm 0.54^{1,2}$	1.27 ± 0.75^1	13.5 ± 3.6	3.6 ± 2.1^1	-0.03 ± 1.07^1	-0.51 ± 0.93^1
Anthemideae	28	$3.57 \pm 0.44^{\text{ab}}$	$1.16 \pm 0.41^{\text{b}}$	$14.5 \pm 3.4^{\text{bc}}$	$1.9 \pm 1.3^{\text{a}}$	$-0.29 \pm 0.62^{\text{a}}$	$-0.65 \pm 0.96^{\text{ab}}$
Astereae	6	$3.89 \pm 0.56^{\text{bc}}$	$1.36 \pm 0.58^{\text{bc}}$	$12.1 \pm 3.0^{\text{ab}}$	$5.5 \pm 1.0^{\text{cd}}$	$0.28 \pm 0.59^{\text{bc}}$	$-0.56 \pm 1.16^{\text{ab}}$
Calenduleae	3	3.31 ± 0.15	1.15 ± 0.15	14.3 ± 0.6	5.3 ± 0.6	0.51 ± 0.08	1.20 ± 0.24
Coreopsidaeae	5	3.91 ± 0.18	2.27 ± 0.43	15.8 ± 1.1	5.6 ± 1.8	1.18 ± 0.67	0.08 ± 0.40
Gnaphalieae	14	$4.40 \pm 0.39^{\text{c}}$	$0.26 \pm 0.40^{\text{a}}$	$9.3 \pm 2.3^{\text{a}}$	$2.7 \pm 0.6^{\text{ab}}$	$-1.40 \pm 0.47^{\text{a}}$	$-0.25 \pm 0.76^{\text{b}}$
Heliantheae alliance	7	$3.93 \pm 0.39^{\text{bc}}$	$2.29 \pm 0.61^{\text{d}}$	$18.0 \pm 2.3^{\text{c}}$	$7.3 \pm 1.1^{\text{e}}$	$1.79 \pm 0.75^{\text{d}}$	$0.29 \pm 0.71^{\text{b}}$
Inuleae	4	4.00 ± 0.18	1.51 ± 0.39	13.3 ± 2.5	4.8 ± 1.0	0.28 ± 0.56	-0.21 ± 0.57
Senecioneae	7	$3.11 \pm 0.30^{\text{a}}$	$1.73 \pm 0.46^{\text{bcd}}$	$12.7 \pm 1.6^{\text{ab}}$	$4.0 \pm 0.6^{\text{bc}}$	$0.44 \pm 0.39^{\text{bc}}$	$-1.52 \pm 0.66^{\text{a}}$
Carduoideae	26	4.01 ± 0.55^2	1.94 ± 0.63^2	13.4 ± 2.9	4.9 ± 1.6^2	0.57 ± 0.87^2	-0.10 ± 0.84^2
Cardueae	26	$4.01 \pm 0.55^{\text{bc}}$	$1.94 \pm 0.63^{\text{cd}}$	$13.4 \pm 2.9^{\text{b}}$	$4.9 \pm 1.6^{\text{cd}}$	$0.57 \pm 0.87^{\text{bc}}$	$-0.10 \pm 0.84^{\text{b}}$
Cichorioideae	34	3.66 ± 0.47^1	1.91 ± 0.45^2	13.2 ± 3.2	5.7 ± 1.4^2	0.80 ± 0.72^2	-0.69 ± 0.96^{12}
Cichorieae	34	$3.66 \pm 0.47^{\text{ab}}$	$1.91 \pm 0.45^{\text{cd}}$	$13.2 \pm 3.2^{\text{b}}$	$5.7 \pm 1.4^{\text{de}}$	$0.80 \pm 0.72^{\text{c}}$	$-0.69 \pm 0.96^{\text{ab}}$
One-way ANOVA							
Subfamily	134	3.3*	16.1***	0.1 <i>ns</i>	16.7***	10.1***	3.1*
Tribe	122	8.9***	26.7***	8.1***	35.2***	26.6***	3.8**

(B)

Family	<i>n</i>	$\sqrt{\text{LDMC}}$	$\text{Log}_{10}\text{LM}_{\text{devel}}$	Size_{Can}	LA_{funct}	PCA 1	PCA 2
Faboideae	74	3.78 ± 0.54	1.27 ± 0.75	13.5 ± 3.6	3.6 ± 2.1	-0.03 ± 1.07	-0.51 ± 0.93
Cicereae	1	5.03	2.17	16.0	4.0	0.47	1.81
Fabeae	35	$4.40 \pm 0.37^{\text{ab}}$	$1.48 \pm 0.43^{\text{b}}$	$15.7 \pm 1.8^{\text{b}}$	$4.3 \pm 1.2^{\text{b}}$	$0.31 \pm 0.61^{\text{b}}$	$0.69 \pm 0.59^{\text{b}}$
Galegeae	6	$4.39 \pm 0.50^{\text{ab}}$	$1.34 \pm 0.23^{\text{ab}}$	$12.7 \pm 0.8^{\text{a}}$	$3.3 \pm 0.5^{\text{a}}$	$-0.30 \pm 0.35^{\text{a}}$	$0.32 \pm 0.67^{\text{ab}}$
Genisteae	3	3.56 ± 0.43	2.31 ± 0.45	17.3 ± 2.1	5.0 ± 0.0	1.34 ± 0.59	-0.23 ± 0.36
Hedysareae	1	5.24	1.67	15.0	4.0	0.03	1.90
Loteae	16	$4.04 \pm 0.36^{\text{a}}$	$1.30 \pm 0.38^{\text{ab}}$	$14.2 \pm 1.5^{\text{ab}}$	$4.2 \pm 1.0^{\text{ab}}$	$0.12 \pm 0.58^{\text{ab}}$	$-0.06 \pm 0.51^{\text{a}}$
Trifolieae	57	$4.60 \pm 0.45^{\text{b}}$	$1.04 \pm 0.37^{\text{a}}$	$14.1 \pm 2.2^{\text{ab}}$	$4.4 \pm 0.7^{\text{b}}$	$-0.17 \pm 0.48^{\text{ab}}$	$0.69 \pm 0.76^{\text{b}}$
One-way ANOVA							
Tribe	115	7.9***	10.0***	7.4***	2.3 ⁺	6.8***	5.9***

(C)

Family	<i>n</i>	$\sqrt{\text{LDMC}}$	$\text{Log}_{10}\text{LM}_{\text{devel}}$	Size _{Can}	LA _{funct}	PCA 1	PCA 2
Pooideae	106	4.83 ± 0.41^1	1.27 ± 0.61^1	9.3 ± 2.1^1	3.7 ± 1.1^1	-0.49 ± 0.85^1	0.84 ± 0.69
Brachypodieae	1	5.53	0.90	8.0	3.0	1.23	1.63
Bromeae	20	4.85 ± 0.44^b	1.45 ± 0.31^{ab}	9.5 ± 1.4^a	4.0 ± 0.6^a	-0.34 ± 0.44^b	0.90 ± 0.73^{ab}
Poeae	54	4.76 ± 0.38^{ab}	1.01 ± 0.64^a	8.7 ± 2.1^a	3.4 ± 1.4^a	-0.75 ± 0.94^b	0.60 ± 0.56^a
Stipeae	1	6.19	1.48	10.0	3.0	-0.78	3.08
Triticeae	30	4.86 ± 0.38^b	1.64 ± 0.50^b	10.2 ± 2.1^a	3.9 ± 0.9^a	-0.09 ± 0.74^b	1.12 ± 0.63^b
Chloridoideae	5	5.15 ± 0.32	0.81 ± 0.47	8.6 ± 1.1	3.2 ± 0.4	-0.92 ± 0.52	1.27 ± 0.37
Cynodonteae	2	5.04 ± 0.49	0.86 ± 0.68	9.5 ± 0.7	3.5 ± 0.7	-0.64 ± 0.75	1.29 ± 0.53
Eragrostideae	2	5.08 ± 0.14	1.03 ± 0.21	8.0 ± 1.4	3.0 ± 0.0	-0.98 ± 0.38	1.05 ± 0.08
Zoysieae	1	5.48	0.27	8.0	3.0	-1.37	1.66
Danthonioideae	1	5.38	0.83	6.0	1.0	-1.98	1.12
Danthonieae	1	5.38	0.83	6.0	1.0	-1.98	1.12
Oryzoideae	1	5.21	2.13	14.0	5.0	0.93	2.38
Oryzeae	1	5.21	2.13	14.0	5.0	0.93	2.38
Panicoideae	12	4.55 ± 0.401^2	2.03 ± 0.70^2	12.8 ± 1.9^2	5.4 ± 1.4^2	0.97 ± 0.81^2	1.15 ± 0.84
Andropogoneae	2	4.91 ± 0.68	3.08 ± 0.34	15.5 ± 0.7	6.5 ± 2.1	2.05 ± 0.93	2.23 ± 0.95
Paniceae	10	4.48 ± 0.33^a	1.82 ± 0.54^b	12.2 ± 1.5^b	5.2 ± 1.3^b	0.76 ± 0.63^b	0.94 ± 0.68^{ab}
One-way ANOVA							
Subfamily	134	4.8*	16.0***	37.0***	24.3***	32.3***	2.2 <i>ns</i>
Tribe	114	2.8*	12.1***	12.7***	6.9***	12.0***	4.9**

TABLE S5. *Seed traits of annuals correlate differently with functional traits of co-occurring perennials. (A) regions, (B) habitats and (C) UK status for both (i) vegetation samples and (ii) species. In (C) ‘Decreased’, Status Index < -0.5; ‘Increased’, Status Index > +0.5. Values relate to Pearson r coefficients using, for each releve, mean functional traits weighted by abundance component of the vegetation for annuals and coexisting perennials.*

	SeedM _{peren}	LDMC _{peren}	DomI
(A) SeedM _{annual}			
Central England			
Wetland (57)	0.225 ⁺	0.290 [*]	0.095
Rocky (136)	0.224 ^{**}	-0.218 [*]	0.360 ^{***}
Arable (370)	0.214 ^{***}	0.129 [*]	0.050
Spoil (368)	0.247 ^{***}	0.114 [*]	0.166 ^{**}
Wasteland (498)	0.318 ^{***}	0.109 [*]	0.281 ^{***}
North-east Spain			
Artificial (296)	0.175 ^{**}	0.047	0.203 ^{***}
Grassland (80)	0.392 ^{***}	0.093	0.060
North central Spain			
Artificial (117)	0.160 ⁺	-0.266 ^{**}	0.227 [*]
Grassland (94)	-0.038	0.051	0.086
(B) SeedNo _{annual}			
Central England			
Wetland	-0.252 ⁺	-0.098	0.071
Rocky	0.152 ⁺	-0.164 ⁺	0.322 ^{***}
Arable	0.022	-0.081	0.158 ^{**}
Spoil	-0.053	-0.033	0.185 ^{***}
Wasteland	0.091 [*]	0.009	0.241 ^{***}
North-east Spain			
Artificial	-0.041	0.036	0.095
Grassland	-0.235 [*]	-0.059	0.115
North central Spain			
Artificial	-0.184 [*]	0.244 ^{**}	0.088
Grassland	-0.455 ^{***}	-0.469 ^{**}	-0.374 ^{***}
(C) RSN			
Central England			
Wetland	-0.249 ⁺	-0.308 [*]	-0.080
Rocky	0.140	-0.120	0.247 ^{**}
Arable	-0.047	0.035	0.027
Spoil	-0.136 ^{**}	-0.044	0.005
Wasteland	0.020	0.026	0.111 [*]
North-east Spain			
Artificial	-0.060	0.004	0.057
Grassland	-0.273 [*]	-0.172	0.129
North central Spain			
Artificial	-0.337 ^{***}	0.379 ^{***}	0.107
Grassland	-0.494 ^{***}	-0.572 ^{***}	-0.511 ^{***}

TABLE S6. *Mean Status Index differs according to (A) regional land use and (B) habitat in Central England.*

	Number of quadrats	Status Index
(A) Region		
Urban	379	0.47
Arable	159	-0.22
Pastural	330	-0.33
χ^2	126.0***	
(B) Habitat		
Wetland	25	-0.44
Rocky	80	-0.35
Pasture	16	0.00
Arable	242	-0.43
Spoil	233	0.55
Wasteland	272	0.17
χ^2	137.5***	