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Hodgson, J.G., Montserrat Marti, G., Šerá, B. et al. (17 more authors) (2020) Seed size, number and strategies in annual plants: a comparative functional analysis and synthesis. Annals of Botany, 126 (7). pp. 1109-1128. ISSN 0305-7364

https://doi.org/10.1093/aob/mcaa151

This is a pre-copyedited, author-produced version of an article accepted for publication in Annals of Botany following peer review. The version of record, John G Hodgson, Gabriel Montserrat Marti, Bozena Šerá, Glynis Jones, Amy Bogaard, Mike Charles, Xavier Font, Mohammed Ater, Abdelkader Taleb, Bianca A Santini, Younes Hmimsa, Carol Palmer, Peter J Wilson, Stuart R Band, Amy Styring, Charlotte Diffey, Laura Green, Erika Nitsch, Elizabeth Stroud, Gemma Warham, Seed size, number and strategies in annual plants: a comparative functional analysis and synthesis, Annals of Botany, Volume 126, Issue 7, 25 November 2020, Pages 1109–1128 is available online at: https://doi.org/10.1093/aob/mcaa151.

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

John G. Hodgson[1,2,*], Gabriel Montserrat Marti[3], Bozena Sera[4], Glynis Jones[2], Amy Bogaard[5], Mike Charles[5], Xavier Font[6], Mohammed Ater[7], Abdelkader Taleb[8], Bianca A. Santini[9,10], Younes Hmimsa[7], Carol Palmer[2], Peter J. Wilson[1], Stuart R. Band[1], Amy Styring[5], Charlotte Diffey[5], Laura Green[5], Erika Nitsch[5], Elizabeth Stroud[5], Gemma Warham[2]

[1]*Unit of Comparative Plant Ecology, The University, Sheffield S1 4ET, UK,* [2]*Department of Archaeology, The University, Sheffield S10 2TN, UK,* [3]*Dept. Ecología Funcional y Biodiversidad, Instituto Pirenaico de Ecología (CSIC) Aptdo. 202, E-30080 Zaragoza, Spain,* [4]*Comenius University in Bratislava, Faculty of Natural Sciences, Ilkovičova 6, Bratislava 842 48, Slovakia,* [5]*School of Archaeology, University of Oxford, 36 Beaumont Street, Oxford OX1 2PG, UK,* [6]*Department of Plant Biology, University of Barcelona, E-08028 Barcelona, Spain,* [7]*Laboratoire Diversité et Conservation des Systèmes Biologiques (LDICOSYB), Département de Biologie, Faculté des Sciences de Tétouan, Université Abdelmalek Essaâdi, BP 2062, 93030, Tétouan, Morocco,* [8]*Institut Agronomique et Vétérinaire Hassan II, Rabat, Morocco,* [9]*Department of Animal and Plant Sciences, The University, Sheffield S10 2TN, UK,*[10]*Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, C.P. 58190, Morelia, Michoacán, México*

* *For correspondence. Email j.hodgson@sheffield.ac.uk*

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

- **Background and Aims** Plants depend fundamentally on establishment from seed. However, protocols in trait-based ecology currently estimate seed size but not seed number. This can be rectified. For annuals, seed number should simply be a positive function of vegetative biomass and a negative one of seed size.
- **Methods** Using published values of comparative seed number as the 'golden standard' and a large functional database, comparative seed yield and number per plant and per m^2 were predicted by multiple regression. Subsequently, ecological variation in each was explored for English and Spanish habitats, newly-calculated CSR strategies and changed abundance in the British flora.
- **Key Results** As predicted, comparative seed mass yield per plant was consistently a positive function of plant size and competitive ability and largely independent of seed size. Regressions estimating comparative seed number included, additionally, seed size as a negative function. Relationships differed numerically between regions, habitats and CSR strategies. Moreover, some species differed in life history over their geographical range. Practically, comparative seed yield per 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 according to the 'golden standard' predictor used. Moreover, regressions estimating comparative seed yield m^{-2} achieved low precision.

- **Conclusions** For the first time, estimates of comparative seed yield and number for over 800 annuals and their predictor equations have been produced and the ecological importance of these regenerative traits has been illustrated. ‘Regenerative trait-based ecology’ remains in its infancy with work needed on determinate *versus* indeterminate flowering (‘bet-hedging’), C-S-R methodologies, phylogeny, comparative seed yield per m^2 and changing life-history. Nevertheless, this has been a positive start and readers are invited to use estimates for >800 annuals, in the Supplementary Data, to help advance ‘regenerative trait-based ecology’ to the next level.

Key words: allometry, bet-hedging, canopy structure, conservation status, C-S-R strategy, functional traits, inflorescence structure, life history, phylogeny, plant size, regenerative strategy, Seed−Phytomer−Leaf (SPL) theory, trade-offs.

INTRODUCTION

Although plants produce an abundance of seed, a plethora of risk factors impact upon subsequent seed dispersal and the development of new plants (Fenner and Thompson, 2005). In consequence, the exact ecological circumstances and location of establishment events are difficult to predict and even 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).

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). Relevantly, Barton and Hanley (2013) and Parmesan and Hanley (2015) strongly argue that, it is the primary 'life and death' factors relating to establishment from seed that fundamentally determine presence or absence. Nevertheless, the scientific literature focuses primarily upon the secondary selective forces operating, post-establishment, on vegetative plant performance. Regeneration remains largely neglected within trait-based ecology (Larson and Funk, 2016) and is poorly understood in weed science (Norris, 2007). The tools at our disposal to model ecological scenarios relating to climate change and the global destruction of habitats are fundamentally flawed. Accordingly, here, we will attempt to partially redress this imbalance between features of regeneration and those of the established vegetative plant.

Many complex ecological relationships can be understood using trait-based ecology (Kattge *et al.*, 2011) and we predict that the relationships between seed risk factors and plant establishment can be similarly integrated into a generalized theory using readily-measured plant functional traits. Nevertheless, at this early stage in synthesis, we will confine our efforts to one of the fundamentals, primary seed production. We will attempt to quantify the number and size of seeds produced by plants and to place findings in an ecological context. Moreover, for simplicity, we will restrict our attention to annuals. Perennials with vegetative organs of reproduction and/or perennation that might act as an additional sink for resources will be excluded.

Encouragingly, there are ecological foundations already established upon which to commence this building process.

Relationship 1: seed size versus seed number

This is described first not because it is necessarily the most important but because it has been the most widely studied. For a given allocation of resources a species may produce either many small seeds or fewer larger ones (Shipley and Dion, 1992; Aarssen and Jordan, 2001; Moles, 2018). The optimal strategy for the ‘colonisation–competition’ trade-off between few large seeds with potentially higher seedling survivorship and many small widely-dispersed seeds depends upon ecological circumstance (Grime, 2001; Westoby *et al.*, 2002; Moles and Westoby, 2006). Unfortunately, plants are phenotypically plastic and their size- and age-structure may vary between populations. As a result, the relationship between seed size and number continues to be difficult to quantify in all but the most general terms.

Relationship 2: resource allocation to seed, the key trait?

Seed production may be viewed simultaneously as the product of the vegetative and of the regenerative strategies of the plant. First, resource allocation to seed is a key regenerative processes, with seed allocation essentially defined as seed mass x seed number (Smith and Fretwell, 1974; Paul-Victor and Turnbull, 2009). It identifies the total 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 the vegetative plant, and, particularly for annuals, where resources are not diverted into long-lived vegetative structures, seed yield is likely to be quantitatively defined by size-related vegetative traits. Consistent with this, fecundity has been found to be positively correlated with vegetative biomass in monocarpic species both between and within species (Sugiyama and Bazzaz, 1998; Aarssen and Jordan, 2001; Chambers and Aarssen, 2009; Lutman *et al.*, 2011).

A general model incorporating relationships 1 and 2

Relationships between seed number and plant size have already been experimentally defined by Shipley and Dion (1992), for the rametes of 57 species, ranging from annuals to polycarpic herbaceous perennials (eqn 1a) and by Aarssen and Jordan (2001), for the whole vegetative shoots of 15 monocarpic species (eqn 1b)

$$\text{Predicted seeds per plant} = 1.4\,(\text{vegetative mass}_{\text{ramet}})^{0.93} \times (\text{individual seed mass})^{-0.78} \qquad (1a)$$

$$\text{Predicted seeds per plant} = 2.8\,(\text{vegetative mass}_{\text{shoot}})^{0.91} \times (\text{individual seed mass})^{-0.83} \qquad (1b)$$

These equations for species, with, additionally, the identification of similar relationships within species (Mohler and Callaway, 1995; Gallart *et al.*, 2010), provide a conceptual as well as, potentially, an arithmetic basis for routinely quantifying seed yield per plant in terms of *relationship 1*, the negative correlation between seed size *versus* seed number, and *relationship 2*, the positive one between vegetative and seed biomass.

Relationship 3: an ecological perspective – seed yield and CSR strategy theory

Since it is primarily a function of vegetative mass (*relationship 2*, eqns 1a-b), seed yield in annual plants is, by definition, regulated by the same fundamental rules that determine the success or failure of vegetative growth. Thus, arguably, it is in part defined by CSR strategy theory (Grime 1974, 2001), perhaps the most all-embracing set of ecological rules relating vegetative plant performance to environmental factors (Pierce *et al.*, 2017). In CSR strategy theory, it is argued 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. CSR strategy theory has been routinely measured using functional traits (Hodgson *et al.*, 1999; Pierce *et al.*, 2013, 2017; Novakovskiy *et* *al.*, 2016). Its inclusion here relates to (i) a methodological relevance, quantifying seed production, and (ii) a practical relevance, linking ‘regenerative functional ecology’ to theoretically key ecosystem processes and to important impacts of changing land use and climate on vegetation composition.

From precision to generality – methodological constraints

As part of an ongoing debate, Shipley *et al*. (2016) and Brodribb (2017) have questioned various theoretical fundamentals of trait-based plant ecology. In particular, in a provocative opinion piece entitled ‘*Progressing from ‘functional’ to ‘mechanistic’ traits*’, Brodribb (2017) argues ‘by ‘mechanistic traits’, I mean traits whose function can be clearly physiologically defined, as opposed to the more abstract ‘functional’ traits, such as leaf mass per area (LMA), that have been used to great effect in explaining plant economics over the last 15 years (Wright *et al*., 2004)’. While we share Brodribb’s misgivings about the use of LMA as a ‘flagship’ trait (Hodgson *et al*., 2011), we dispute the implication that ‘functional’ traits are of lesser value. Importantly, ‘mechanistic’ studies generate precision leading to an exact definition of key mechanisms. However, most involve time-consuming experimental/physiological measurements. As a result, global datasets of ‘mechanistic’ traits remain small, and difficult to integrate with other ‘mechanistic’ fields of study. They do not describe ‘the big picture’. They neither demonstrate the universality of mechanisms within whole floras nor do they directly identify how mechanisms complement, and integrate with, other specializations.

And this is where trait-based ecology offers synergy. True, as Brodribb points out, ‘functional’ traits are imprecise, both in measurement and in potential interpretation. Equally, with the current lack of easily-measured biochemical traits, the whole subject area is strongly and unhealthily skewed towards morphology. Nevertheless, imprecise but easily-measured ‘functional’ traits can be validated against a ‘gold standard’ derived from ‘mechanistic’ or related studies and large datasets can be generated with each species characterized with respect to many contrasted ecological dimensions. Subsequently, functional links between traits can be identified and floras functionally characterized. Trait-based ecology can add generality, and often greater utility to studies of ecological mechanisms. We believe that a balance between the two complementary methodologies can provide a powerful, and optimal, mix of precision and generality.

Unfortunately, in practice, ‘mechanistic’ and ‘functional’ studies are not always easy to integrate and, regrettably, neither Shipley and Dion (1992) nor Aarssen and Jordan (2001), the sources of eqns 1a and 1b, respectively, can be used as ‘gold standards’ in our functional studies. Each falls broadly into the mechanistic category of Brodribb (2017) with time-consuming measurements and relatively small datasets (only fifteen species in each usable to us). However, in this instance, progress is equally hampered by ‘functional’ problems. The only relevant ‘functional’ traits in regularly use identify plant height, leaf size and leaf construction costs. They provide an incomplete basis for estimating vegetative biomass.

Objectives

Despite the problems outlined above, our primary objective remains to generate ‘best estimates’ of seed yield for annual plant species and to present these values in an ecological context. And we are not totally data deficient. Medium-sized datasets for seed number per plant do exist for both the United Kingdom (Salisbury, 1942) and USA (Stevens, 1932, 1957), albeit without additional measurements of biomass. Furthermore, seed number per m^2 values are available for Slovenia (Šera and Šery, 2004). Assuming that standardized protocols were in place (i.e. seed number was measured using 'representatively-sized' individuals for each species), such values may be provisionally treated as best estimates, or a 'comparative gold standard' definition of regenerative potential. Equally, while it is not customary to directly measure biomass in trait-based ecology, the various components of biomass and performance routinely assessed may be augmented by other size-related traits. From these combined sources eqns 1a-b may be recast as:

Predicted seeds per plant $\cong f_1$ (plant size) x f_2 (leaf size) x f_3 (leaf construction costs) / f_4 (mass of an individual seed) (1c)

which may be in turn recast as

Predicted seed mass per plant = predicted seeds per plant x mass of an individual seed

$\cong f_1$ (plant size) x f_2 (leaf size) x f_3 (leaf construction costs) / f_4 (1d)

where the functional terms, f_1, f_2 and f_3, relate to different components of vegetative biomass production and with $f_1 - f_4$ all awaiting an exact arithmetic definition.

Accordingly, first, using an unpublished database with functional traits for over 800 annual species from Europe, North Africa and the Middle East and published datasets for seed yield, we will attempt to validate and arithmetically define eqns 1c-d. We will generate multiple regression equations that predict both 'reproductive allocation' (seed mass x seed number) and seed number ('fecundity'). Secondly, we will explore how the resultant predictions of 'reproductive allocation' and the relationship between seed size and predicted seed number pattern in the field by reference to extensive vegetation surveys from Spain and UK. Here, we consider it essential to analyse seed yield and number in relation to ruderality and C-S-R strategy theory (Grime, 2001). Unfortunately, as noted in Hodgson *et al.* (2017), the calculation of the R (ruderal) axis is in need of a radical revision and this field analysis will utilize a new revised C-

S-R classification designed specifically for annuals. Thirdly, we will consider commonness and rarity and show that seed number effects a better separation of increasing and decreased species in the UK flora than seed size. Fourthly, the problems and prospects of using a functional approach to ‘reproductive functional ecology’ will be discussed. Finally, our predictions of seed size and number for in excess of 800 annuals will be appended online to encourage further studies.

A METHODOLOGICAL CAVEAT

Some key plant attributes are difficult to measure in an ecologically-relevant way. Vegetative biomass and seed yield achieved in the field are both very variable (Venable and Brown, 1988; Clauss and Aarssen 1994; Aarssen and Jordan, 2001; Lutman *et al.*, 2011; Shriver, 2016). For example, *Amaranthus retroflexus* routinely produces 200 - 500 seeds per (small) plant in one habitat but ca 100,000 seeds per (much larger) plant in another (Mohler and Callaway, 1995). Annual species are able to set seed even when small and stunted (Grime, 2001; Chambers and Aarssen, 2009; Tracey *et al.*, 2016) with, importantly, increased competitive success (i.e. increased vegetative biomass production) likely to provide a ‘reproductive economy advantage’ even for small plants (Aarssen *et al.*, 2006; Aarssen, 2008, 2015).

This innate plasticity, itself an important ecological attribute, makes the quantification and interpretation of growth-related processes difficult. Nevertheless, growth remains too important to ignore. One experimental option has been to standardize conditions and to make precise measurements of vegetative growth (Grime and Hunt, 1975). However, this approach is extremely time-consuming and the difficulties in exactly replicating growth conditions at other research establishments has further restricted the pool of species for which we have comparative values. In consequence, ecologist have been more reliant upon less precise but easily-measured surrogate traits generated within trait-based plant ecology (Pérez-Harguindeguy *et al.*, 2012). Using the theory and methodologies associated with the worldwide leaf economics spectrum (Wright *et al.*, 2004), potential growth rate has been routinely assessed indirectly, in comparative rather than in absolute quantitative terms, from specific leaf area (SLA) and leaf dry matter content (LDMC) and these comparative values subsequently used in ecological interpretation. Of necessity, our assessment of the equally variable, growth-related process, seed yield, will be similarly indirect and comparative. We hope that it will prove equally successful and that 'comparative regeneration' will stand with comparative estimates of the worldwide leaf economics spectrum of Wright *et al.* (2004) at the productive heart of trait-based plant ecology.

MATERIALS AND METHODS

Field 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 with the frequent regenerative failure of annuals. Indeed, climatic conditions and floristic composition are so variable in the Zaragoza region that a full complement of annual species is only present in many plant communities approximately every six years (G. Montserrat Marti, field observations).

Using the habitat classification of Grime *et al.* (2007) for English and Rivas-Martínez *et al.* (2002) for Spanish data, the above vegetation surveys were used to assess the primary habitat with which each study species was associated in each region. In addition, 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, (AnnIndex, (cover$_{\text{annuals}}$ + cover$_{\text{ephemeroids}}$)/cover$_{\text{all\_species}}$), was also calculated for each species from vegetation survey data. As described in the 'Phylogeny' section below, mean leaf dry matter content values were also calculated for each vegetation sample.

The *Online Atlas of the British and Irish flora* (Botanical Society of Britain and Ireland and the Biological Records Centre, 2018) separated species that had increased from those that had decreased in UK. From these data, Status Index (number of species$_{\text{increasing}}$ – number of species$_{\text{decreasing}}$)/(number of species$_{\text{increasing}}$ + number of species$_{\text{decreasing}}$) was calculated for vegetation samples. A value of +1 identified vegetation where all species had increased and one of –1 vegetation where all had decreased.

Nomenclature follows The Plant List (2013).

The trait dataset

Trait data were derived from a large functional dataset currently being prepared for publication. 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). Hemiparasites, which derive nutritional benefit for seed production from their host, and succulents, for which leaf dry matter content (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 perennial species with which these annuals were growing was also briefly investigated.

The key traits

The traits used to test eqns 1c-d, and their abbreviations, are listed in Table 1. Leaf nitrogen (LeafN, mg per g) and leaf silica (LeafSi (percentage dry mass)) were also considered with in-house measurements augmented mainly by Han *et al.* (2005), Hodson *et al.* (2005), and Stock *et al.* (2012). Additionally, in relation to flowering phenology, month of commencement (FlStart, negatively correlated with R axis in C-S-R strategy theory; Hodgson *et al.*, 1999) and duration (FlDuration, positively correlated) were abstracted from Clapham *et al.* (1987). These data relate to UK with the scaling-up of flowering phenology to include all study areas not yet feasible.

Sources of comparative seed yield data

The Canadian datasets of Shipley and Dion (1992) and of Aarssen and Jordan (2001), from which eqns 1a and 1b were calculated, both contained too few usable species to be directly utilized in our analyses. Thus, linked seed number/vegetative biomass data were unavailable to this study. Instead, comparative values of seed number per plant ($\mathrm{SeedNo_{Pl}}$) without vegetative biomass quantification were abstracted from Stevens (1932, 1957) for USA and from Salisbury (1942) for UK. Additionally, comparative data on maximum seed number per m^2 ($\mathrm{SeedNo_{m2}}$; seed yield where vegetative cover of the subject species was 100%) were derived from Šera and Šery (2004) for plants growing wild in Slovenia. Unfortunately, these three datasets are not expected to be exactly numerically equivalent: they originated from areas with contrasted climates and land use. Also FAO (2018) provided agricultural yield data for seed crops with 'maximum crop yield', ($\mathrm{SeedM}_{\mathrm{ha}}$) expressed as hg per ha, calculated arbitrarily as the 90 percentile of seed yield values since 2000 for all countries where the crop was grown.

In both Shipley and Dion (1992) and Aarssen and Jordan (2001), the statistically strongest relationship was between the vegetative and the seed mass of the plant ($\mathrm{SeedM}_{\mathrm{Pl}}$). Accordingly, prior to regression analysis, we converted our 'gold standard' values for comparative seed number ($\mathrm{SeedNo}_{\mathrm{PlUSA}}$ and $\mathrm{SeedNo}_{\mathrm{PlUK}}$) to seed mass per plant ($\mathrm{SeedM}_{\mathrm{PlUSA}}$ and $\mathrm{SeedM}_{\mathrm{PlUK}}$) by multiplying $\mathrm{SeedNo}_{\mathrm{Pl}}$ by SeedM. Subsequently, to identify how this comparative estimate of seed yield was partitioned, few large seeds or many small ones, predicted values of seed mass per plant were transformed back to seed number by dividing $\mathrm{SeedM}_{\mathrm{Pl}}$ by SeedM.

CSR strategy

Initially, relationships were explored with Principal Component Analysis (PCA) using, for simplicity, only four functional traits. Two, $\mathrm{LA}_{\mathrm{Funct}}$, a key component of Dominance Index, and $\mathrm{LM}_{\mathrm{Devel}}$, which defines the size of each modular unit of growth (Hodgson *et al.*, 2017), both contribute positively to competitive exclusion, and are negatively correlated with the ruderal (R) and stress (S) axes. Of the others one, $\mathrm{Size}_{\mathrm{Can}}$, is an integral of qualitative and quantitative aspects of the growth period whilst the other, LDMC, is inversely related to growth rate and soil fertility and positively correlated with the S axis. Regrettably, since, as described above, the dataset for FlStart and FlDuration included only UK species, we were unable to include direct predictors for the R 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, on theoretical grounds, published values of $\mathrm{SeedM_{Pl}}$, which defines the mass of seed produced by each plant, should objectively predict the C axis. Importantly, this first relationship has also been practically validated (Pierce *et al.*, 2014). For 371 annual and perennial species of the Italian flora, ‘total mass of seeds’ (i.e. $\mathrm{SeedM_{Pl}}$) was significantly positively correlated both with the degree of C-selection derived from the trade-off between vegetative traits, and with single size-related traits such as canopy height. Secondly, LeafN, a key element of the worldwide leaf economics spectrum (Wright *et al.*, 2004), correlates inversely with the S axis (Pierce *et al.*, 2014). Thirdly, as in Hodgson *et al.*, 1999, AnnIndex was utilized as the ‘gold standard’ for the R-dimension. Subsequently, the relationships between the three ‘gold standard’ predictors and PCA axes 1 and 2 were identified by multiple regression and ‘contour lines’ for each ‘gold standard’ predictor added to the PCA ordination diagram. The positions of C-S-R strategy types were then tentatively located by reference to these contours, and to ecological theory (Grime, 2001). Previous C-S-R classifications have additionally included a full range of perennial life histories. Therefore, to avoid confusion, our new designations are preceded by the prefix Ann_ with annual species with ‘competitive tendencies’ (CR in Grime’s classification) identified as Ann_C, those with ‘stress-tolerant tendencies’ (SR) as Ann_S and those with ‘ruderal tendencies’ (R) as Ann_R.

Phylogeny SeedM is an ecologically important trait that is conservatively expressed within major taxa, both within our flora (Hodgson and Mackey, 1986) and elsewhere (Westoby *et al.*, 1992; Moles *et al.*, 2005). Its expression and that of other important functional traits within our dataset is potentially constrained by two contrasted evolutionary processes. First and more anciently, some functions will be in part predefined by structures or processes that have originated from the integration of a whole suite of mechanistic features over evolutionary time. These functions, and attendant mechanistic features, have subsequently been retained simply because they are too developmentally complex to be readily modified (Stebbins, 1974; Hodgson and Mackey, 1986). Secondly and more recently, adaptive radiation of taxa, often involving hybridization and polyploidy (Ehrendorfer, 1980; Stebbins, 1985), provides an evolutionary mechanism enabling floras to rapidly adapt to altered ecological conditions. During episodes of climate change and the development and intensification of agriculture that has characterized the shared recent evolutionary history of our studied floras from the Pleistocene onwards, adaptive radiation of this type will have impacted upon the composition of our studied flora (West, 1969; Valentine, 1970; Hodgson, 1987).

These two contrasted evolutionary mechanisms will pattern differently with respect to phylogeny. Developmental constraints associated with complex structures are likely to result in conservatism in trait expression at deep ancestral levels of phylogeny. Such conservatism should be similarly evident in floras with contrasted recent evolutionary histories. Superimposed upon this, recent adaptive radiation will cause functional characteristics to be conservatively expressed at the uppermost branches of the phylogenetic tree. This ‘conservatism’ is simply a consequence of a shared recent evolutionary origin, not of trait immutability. Such phylogenetically-correlated similarities in trait expression are unlikely to be replicated in floras with contrasted recent evolutionary histories.

To explore these potential evolutionary dimensions, the expression of functional traits are compared between major families, tribes and subtribes. Additionally, for the CSR analysis, we provide an ecological-phylogenetic comparison for LDMC, a key element of the Ann_S axis. Mean LDMC of associated annual species, weighted by abundance, was calculated for different taxonomic subsets of annual species from both UK and Spanish field survey data.

Other analyses

Prior to statistical analysis, LDMC was square-root transformed and the remaining continuous trait variables $\log_{10}$-transformed. Two other transformations were applied less universally. First, to provide estimates relevant to ecosystem properties, trait data weighted by abundance (rooted frequency/domin scale) were used to generate ‘functional averages’ for vegetation samples. Second, since seed number is potentially a function of plant size and strategy, trends are difficult to interpret where a wide range of plant sizes and/or strategies are present. To partially offset this problem, species were assigned to Ann_C-S-R strategy groupings and within each grouping, species were ranked so that the lowest rank had a value of –1 (extremely small numbers of seed produced) and the highest a value of +1 (numerous seeds produced). Subsequently, values of this nonparametric Ranked Seed Number (RSN) were combined to provide a more size-independent comparative estimate of seed number.

Except for measured seed mass against predicted comparative 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^{TM} (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 comparative number respectively. However, in contrast to the wide ecological spectrum of species within our own dataset, the published datasets defining comparative seed yield and leaf nitrogen were from a much narrower subset of species and there were significant differences in trait ranges between each (Table 2).

Predicting comparative seed yield per plant: a test of eqns 1c-d

Both $\mathrm{SeedM_{Pl}}$ and $\mathrm{SeedNo_{Pl}}$ were identified as a positive product of plant size, leaf/phytomer size and SeedM for both USA and UK datasets (Table 3A). Thus, save for the exclusion of traits relating to leaf construction cost, f_3, the results conform to the expectations of eqns 1a-d. Furthermore, consistent with the results of Shipley and Dion (1992) and Aarssen and Jordan (2001), SeedM, a key determinant of $\mathrm{SeedNo_{Pl}}$, had relatively little impact on the expression of $\mathrm{SeedM_{Pl}}$. Its exclusion from the regression gave a reduction of only 0.04 and 0.02 respectively in the value of r^2 (Table 3Ai). However, as expected (see 'A methodological caveat', above), the two regional estimates lacked an exact numerical correspondence (eqn 2). Predicted values derived using the USA regression (Table 3Aia) were considerably higher than those for UK (Table 3Aib).

$\log_{10}\mathrm{SeedM_{PlUSApredicted}} = 0.936\log_{10}\mathrm{SeedM_{PlUKpredicted}} + 0.835$ (95% confidence intervals: slope 0.90 – 0.97, constant 0.74 – 0.93; $r^2 = 0.72^{***}$, $n = 868$; mean values ± s.d.: $\mathrm{SeedM_{PlUSApredicted}}$ 3.43 ± 0.73, $\mathrm{SeedM_{PlUKpredicted}}$ 2.78 ± 0.71; paired $t = 50.1^{***}$, $r^2 = 0.72^{***}$, n

= 868: similar results relating to $\text{SeedNo}_{\text{Plpredicted}}$ not shown).

(2)

Predicting comparative seed yield per m²

SeedM_{m2} was a function of $\text{SeedM}_{\text{Plpredicted}}$, and traits defining canopy and plant size (Table 3Bi). However, values of r^2 (0.22 – 0.25) were low. Moreover, irrespective of the estimate of SeedM_{Pl} used, only SeedM contributed to the expression of $\text{SeedNo}_{\text{m2}}$ (Table 3Bii). Nevertheless, estimates of SeedM_{m2}, from Table 3Bi, predicted FAO-derived crop seed yield values (Fig. 1).

Ann_C-S-R, providing an ecological context

PCA axis 1 of the ordination explained 54% of the variance and identified size, and the Ann_C axis (Fig. 2A). PCA axis 2 (24%) scaled positively with LDMC and Size_{Can} (i.e. negatively with ruderality). The multiple regression equations defining these axes were as follows:

$$\text{PCA1} = 0.570\log_{10}\text{LM}_{\text{Devel}} - 0.288\sqrt{\text{LDMC}} + 0.104\text{Size}_{\text{Can}} - 0.218\text{LA}_{\text{Funct}} - 1.844 \quad (3)$$

$$\text{PCA2} = 0.199\log_{10}\text{LM}_{\text{Devel}} + 1.482\sqrt{\text{LDMC}} + 0.118\text{Size}_{\text{Can}} - 0.042\text{LA}_{\text{Funct}} - 7.807 \quad (4)$$

In addition, 'gold standard' variables patterned variously with the PCA axes (eqns 5-7).

$$\log_{10}\text{SeedM}_{\text{PlUSA}} = 0.538\text{PCA1} + 0.176\text{PCA2} + 3.195 \quad (r^2 = 0.38^{***}, n = 55) \quad (5a)$$

$$\log_{10}\text{SeedM}_{\text{PlUK}} = 0.606\text{PCA1} + 0.189\text{PCA2} + 2.567 \quad (r^2 = 0.73^{***}, n = 51) \quad (5b)$$

$$\log_{10}\text{LeafN} = 0.064\text{PCA1} - 0.065\text{PCA2} + 1.380 \quad (r^2 = 0.14^{*}, n = 55) \quad (6)$$

$$\text{AnnIndex}_{\text{UK}} = -0.044\text{PCA2} + 0.522 \quad (r^2 = 0.06^{**}, n = 178) \quad (7a)$$

$$\text{AnnIndex}_{\text{SIMIV}} = -0.014\text{PCA2} + 0.670 \quad (r^2 = 0.01^{*}, n = 734) \quad (7b)$$

(AnnIndex$_{\mathrm{UK}}$ *v* AnnIndex$_{\mathrm{SIMIV}}$ $t = 7.7$***; $r^2 = 0.65$***; mean difference 0.09 ± 0.16, $n = 171$) SeedM$_{\mathrm{PlUSA}}$, and even more strongly, SeedM$_{\mathrm{PlUK}}$, define the putative Ann_C axis with a relatively high r^2 (eqn 5). However, values of r^2 were much lower for the 'gold standard' variables expected to define the Ann_S and Ann_R axes (eqns 6 and 7). Furthermore, in our 'annuals-only' analysis, FlStart and FlDuration, the 'key ruderal traits' in Hodgson *et al.* (1999), failed to pattern strongly with the Ann_R axis. FlDuration was more centrally positioned within the Ann_CSR region and FlStart was, broadly, positively correlated with the Ann_C axis (Fig. 2Bi-ii). Instead, the key diagnostic specialization identifying Ann_R-strategists appeared to be miniaturization. Ann_R-strategists were small with both precocious flowering and precocious seed set (e.g. *Bellis annua*, *Limosella aquatica*). Moreover, many species, previously identified as R-strategists in Hodgson *et al.* (1999) and Grime *et al.* (2007), were classified here as of intermediate strategy (e.g. *Poa annua*, Ann_CSR, ≅ R-CSR in Grime's classification; *Senecio vulgaris*, Ann_CR, ≅ R-CR). Less controversially, typical Ann_C-strategists (≅ CR) included robust weeds (e.g. *Xanthium strumarium*) and crops (e.g. *Zea mays*) and Ann_S-strategists (≅ SR) consisted of a small group of slower-growing, later-maturing annuals (e.g. *Crucianella patula*, *Minuartia campestris*) – Fig. 2. In the absence of a reliable 'gold standard' measurement to define the Ann_R axis, our allocation to Ann_C-S-R strategies in Fig. 2 remains provisional.

The PCA ordination further illustrated a lack of ecological equivalence between the two 'gold standard' datasets defining SeedM$_{\mathrm{Pl}}$. Consistent with results in Table 2, the species in Salisbury's UK dataset exhibited a wider spread of values for PCA axes 1 and 2 than those from the USA (Fig. 2Biii).

Reproductive strategy patterns with Ann_C-S-R

As with measured data (Fig. 2A), predicted values for comparative seed yield patterned with the Ann_CSR ordination (Fig. 3A). Comparative seed mass yield, both per plant and per m^2, were highest for Ann_C-strategists and lowest for Ann_S, Ann_R and Ann_SR with intermediate strategies occupying an intermediate position (Fig. 3AI-II). Similarly, SeedM, could be ordered Ann_R < Ann_S < Ann_C (Fig. 3AIII). Ann_C-strategists were also characterized by high SeedNo$_{plant}$ (Fig. 3AIVi) while the estimate of SeedNo$_{m2}$ patterned least strongly with strategy (Fig. 3AIVii).

Despite the above tendency for comparative seed yield to pattern with strategy, there was still a wide range of values within each strategy class. Thus, Ann_C-strategists included both the highly fecund small-seeded *Sisymbrium loeselii* (SeedM 0.09 mg, SeedNo$_{Pl}$ 31894 (estimated), 37200 (measured)) and the few- but large-seeded *Vicia narbonensis* (136 mg, 60). Similarly, Ann_R-strategists included both *Limosella aquatica* (0.015 mg, 986 (estimated), 4236 (measured)) and *Montia fontana* subsp *chondrosperma* (0.26 mg, 47) and Ann_S-strategists both *Catapodium rigidum* (0.22 mg, 420) and *Brachypodium distachyon* (3.52 mg, 99). As a result, and associated with this wide range of values, there was also a strong negative correlation between SeedM, and predicted SeedNo per plant within each strategy grouping (Fig. 3B). Regression equations for these relationships shared a common slope but differed significantly in intercept value. Small and/or slow-growing species (Ann_R- and Ann_S-strategists) had low intercept values and large plants (e.g. Ann_C-strategists) high values (Fig. 3B).

Taxonomic variation in trait expression

All functional traits were to some extent conservatively expressed with respect to phylogeny. Statistically significant differences in trait expression were detected between (a) major families, (b) tribes within families and (c) subtribes within tribes and, in consequence, our predictions of comparative seed yield and the PCA axes defining the Ann_CSR similarly patterned with taxonomy (Supplementary Data Table S2, Fig. 2Biv). Despite these phylogenetically-related differences in trait expression, for LDMC, a key element of the worldwide leaf economics spectrum (Wright *et al*., 2004), mean values for associated annual vegetation was similar for Asteraceae, Fabaceae and Poaceae, the three best-represented families in the dataset (Supplementary Data Table S3). Moreover, the high values of LDMC in Poaceae did not appear attributable simply to silicon accumulation, which adds leaf mass to Poaceae at little metabolic cost (Raven, 1983; Hodson *et al*., 2005; Katz, 2019). We calculate, from published values, that silica content accounts for only ca 1.8% of leaf dry mass for annual grasses. Excluding silica content, reduces the mean LDMC of annual Poaceae only slightly from 22.1 to 21.7%. This is still much higher than the mean of 16.2% LDMC characteristic of other annuals. Equally, 'Si-corrected' values for LDMC and $\mathrm{LM_{devel}}$ 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 of the annual flora of each region was ordered Central England < North-east Spain < North central Spain with $\mathrm{SeedNo_{Pl}}$ and RSN showing the converse relationship (Table 4A). The three regions also patterned in relation to strategy (Fig. 4A-B) with Central England (Ann_C, Ann_CR and Ann_R well represented) < North-east Spain < North central Spain (Ann_S, Ann_SR and Ann_SC). Equally, within regions, SeedM, SeedNo and RSN varied with respect to both habitat (Table 4B) and Ann_C-S-R strategy (data not shown). Nevertheless, two-way ANOVAs identified strategy as the more consistently important determinant of seed size and comparative number than habitat within all three regions (Table 5). However, when RSN replaced $\mathrm{SeedNo_{Pl}}$, habitat and interaction terms showed generally greater statistical significance and strategy exhibited lesser significance (data not shown).

A further feature of the dataset and field observations was that some species varied ecologically between study areas. Habitat range, and even life history differed markedly between Spain and UK for some species (Table 6).

Interrelationships between the annual and perennial components of vegetation

Functional traits of annuals patterned with those of co-occurring perennials. $\mathrm{SeedM_{annual}}$ was correlated positively with both $\mathrm{SeedM_{peren}}$ and DomI within each region (Table 7). Similarly, albeit less consistently, $\mathrm{SeedNo_{annual}}$ and RSN were negatively correlated with $\mathrm{SeedM_{peren}}$ and positively with DomI (Table 7) with broadly similar patterns observed within individual habitats (Supplementary Data Table S4). 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 7, Supplementary Data Table S4).

The changed dynamics of Ann_C-S-R strategies and seed size v number in the British flora

Whether species have recently increased or decreased in abundance appears to depend strongly upon both habitat and Ann_C-S-R strategies. Increased species were particularly associated with urban landscapes and with wasteland and spoil habitats (Supplementary Data Table S5). They also formed a slight majority within the Ann_CR strategy and were well represented in Ann_C (Fig. 4C). In contrast, declined species were characteristic of pastural (upland) landscapes and wetland and arable habitats and with more ‘stressed’ strategies (Fig. 4C; Supplementary Data Table S5). However, 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 appended database

Our predictions of comparative seed number are inevitably rather imprecise and for some species (e.g. *Minuartia hamata*, where only three seeds per plant are predicted) values may be wrong by several orders of magnitude. Accordingly, to encourage further work, data relating to SeedM, $SeedM_{Pl}$, $SeedM_{m2}$, $SeedNo_{Pl}$ and $SeedNo_{m2}$ coupled with values for the PCA axes used to define Ann_CSR strategies are included in Supplementary Data Table S6 for 842 annual taxa.

DISCUSSION

Theoretically-expected traits predict $SeedM_{Pl}$ and $SeedNo_{Pl}$

The regression equations predicting $SeedM_{Pl}$ (Table 3) conformed to theoretical expectations. They were consistent with relationships between size, flowering and yield observed by Gross (1981), Gross and Werner (1983), Shipley and Dion (1992) and Aarssen and Jordan (2001). Thus, for UK with an r^2 of 0.75, $SeedM_{Pl}$ was 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 equations + and – SeedM in Table 3). The equation for the USA dataset included functionally similar, but not identical, terms (Table 3). Expectedly, since the two datasets came from different regions, and a contrasted set of growing conditions (see ‘A methodological caveat’, above), our two $SeedNo_{Pl}$ datasets for UK (Salisbury, 1942; from the less productive British landscapes prior to agricultural intensification) and for USA (Stevens, 1932, 1957; robust agricultural weeds collected from intensively productive arable landscapes) did not provide identical predictions (eqn 2). Nevertheless, the two sets of predicted values were strongly correlated, with an r^2 of 0.72, with a slope close to 1:1 (eqn 2). Our estimates appear appropriate for ranking relatively well-grown examples of species in terms of seed yield. $SeedM_{Pl}$ can now be viewed as a readily, albeit crudely, estimated comparative trait defined by vegetative attributes and suitable for use in ‘broad-brush’ ecological comparisons. As a result, $SeedNo_{Pl}$ can also be assessed in comparative although, again, not in exact quantitative terms and encouragingly, our predicted values of $SeedNo_{Pl}$ appear to have functional relevance to species distribution and floristic change (Figs 1, 3-4; Tables 3-4, 7-8).

The next steps in 'regenerative trait-based ecology'?

Reshaping general approaches Intensive land use and climate change are reshaping our floras (Hodgson, 1986a; Pyke, 2003; Cirujeda *et al.*, 2011; Pimm *et al.*, 2014). An important element in understanding and moderating these effects is the ability to predict which species are capable of establishing, and which are not. To date, for methodological reasons, the only regenerative trait in regular use is SeedM and, as a result, trait-based ecology is failing to deliver. Like all branches of science, functional trait ecology is dependent for its effectiveness upon the creation of general rules. Initially, these tend to 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). Subsequently, generality can be improved by further increasing the geographical range over which a 'traditional' trait is measured. Unfortunately, this important validation process appears to have taken place almost to the exclusion of more exploratory studies into new ecological processes and traits. As a result, 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 provides 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 have been generated on an industrial scale. Importantly, the approach focuses upon all factors considered ecological important, not just those that are most easily measured. An historical illustration of its power and utility is provided by Ellenberg *et al*. (1992) and his phytosociologically-related habitat preference classes, 'Ellenberg numbers'. We believe that the reliance upon a classification based solely upon where plants grow ('Ellenberg numbers') rather than how plants function (trait-based ecology) is outdated. Nevertheless, Ellenberg attempted to include all key ecosystem processes in his scheme. Thus, arguably, in scope and scale, he remains ahead of much of trait-based ecology.

We suggest that the way forward is not directly through global analyses. Instead, like Ellenberg, studies in trait-based ecology should initially operate at a more local level where strong links can be maintained between measured traits and both vegetation descriptions and the observable ecosystem processes shaping the flora (e.g. LEDA Traitbase, Kleyer *et al.*, 2008; FIFTH database, Cerabolini *et al.*, 2010). At this more parochial but focussed scale, additional important ecosystem processes can be explored more readily and new traits added to analyses. Positive outcomes will encourage 'replicate' studies in other regions and ultimately global analyses, allowing trait-base plant ecology to grow and diversify.

The regional approach may also throw light on the currently intractable relationships between present-day ecosystem processes and past evolutionary events in trait expression. In this study, all functional traits and, in consequence, all predictions of reproductive allocation and strategy were conservatively expressed within families, tribes and subtribes (Supplementary Data Table S2-4 Fig. 2Biv). This apparent link between functional traits and phylogeny is not unexpected. Take, SeedM, a key element in comparative seed yield relationships whose expression appears to have been constrained through the evolutionary of the angiosperms (Westoby *et al*., 1992; Moles *et al*., 2005). Seed size may be subject to deep-seated evolutionary constraints associated with developmentally-complex structures and processes that are difficult to modify (Hodgson and Mackey, 1986). This has inevitable developmental impacts on plant size, particularly those with a short lifespan. Consistent with seed-phytomer-leaf strategy theory, all elements of vegetative plant size correlate positively with seed size (Hodgson *et al*., 2017), and, since it is a function of vegetative size (eqn 1, Table 3) so too will comparative seed yield. In addition, phylogeny is linked locally to commonness, rarity and plant strategy, and both are strongly correlated with polyploidy (Hodgson, 1986b-c, 1987). Such phylogenetic correlates were not identified in other regions (Edwards and Westoby, 2000). Nevertheless, phylogenetic niche conservatism is very much a feature of the flora of Central Europe (Prinzing *et al*. (2001). We suspect that, unlike the evolutionary factors constraining the expression of SeedM, some correlations (e.g. those relating to Ann_CSR) stem, at least in part, from the shared recent evolutionary history of our study areas, from the Pleistocene onwards (West, 1969) and an adaptive radiation of the flora from a common pool of founder species.

Broad replicate studies of comparative seed yield and its predictor traits are required in other regions to further explore the relationships identified in this paper. These should include new 'gold standard' datasets that include measurements of both seed yield and vegetative biomass. Moreover, the choice of species chosen should be such that separate predictor equations estimating SeedM_{Pl} can be generated for a contrasted range of phylogenetic groupings. Such work is important to confirm the generality of and refine the 'comparative precision' of the seed yield relationships identified here.

Adding new traits The Ann_R axis remains difficult to quantify (Hodgson *et al*., 1999; Pérez-Harguindeguy *et al*., 2012; Pierce *et al*., 2017) with, for annual species, the current 'gold standard' ruderal variables, FlStart and FlDuration, 'not fit for purpose'. First, FlStart does not consistently predict flowering precocity. Although most flower early, some equally precocious UK ruderals grow on mud exposed by summer drought and necessarily commence flowering in autumn (e.g. *Elatine*). Secondly, a long FlDuration may be associated with two very different strategies. A single individual may flower 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 both vegetative and reproductive growth ceases). Equally, individuals may be short-lived but produce several generations of plants within a single growing season (e.g. *Senecio vulgaris*). We suggest that, in accordance with seed–phytomer–leaf theory (Hodgson *et al*., 2017), phytomer miniaturization and a reduction in the number of juvenile phytomers, which both promote early maturity, could replace FlStart as an estimate of precocity. Equally, identifying the phytomer number at which flowering begins and ends may provide a developmentally-appropriate trait to replace FlDuration.

Consolidating regenerative theory The Ann_R axis is defined by the intensity, frequency and predictability of disturbance events. Disturbance may be seasonally unpredictable, variously weak and strong in different years (e.g. drought on very shallow soils or in regions where rainfall varies greatly from year to year, grazing, patchy shade, trampling and weeding). Alternatively, it may be late, severe but seasonally predictable (e.g. crop harvesting, ploughing, shade caused by leafing-out of forest trees and summer drought on deeper soils and in regions with predictable rainfall). Shemesh and Novoplansky (2013) argue persuasively that important functional trade-offs 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 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 the continuing partial sequestration of resources into seed production, growth rates inevitably remain relatively low. Alternatively, where the opportunity for growth is usually prolonged, the more productive strategy is a long period of purely vegetative growth before flowering. Annuals adapted to this latter scenario are potentially larger and have more structurally complex branch units. They are, therefore, less ruderal, and, important for estimating comparative seed yield, they may be expected to produce more seed mass relative to their vegetative size. Our attempts to factor these relationships into predictions of comparative seed mass yield may benefit from links to plant morphology and physiology (Prusinkiewicz *et al.*, 2007).

Comparative seed yield per m^2 Regressions predicting SeedM$_{m2}$ from SeedM$_{Pl}$ have a low r^2 (Table 3), and much lower predictive power. SeedM$_{m2}$ is measured under field conditions where the target species has close to a 100% cover. For most annual species, this is an unusual circumstance with populations likely to exhibit a range of plant sizes. Our estimates of SeedM$_{Pl}$ were derived using traits relating to large 'well-grown' plants. As a result, the relationship between plant size and yield per plant may not be wholly appropriate for scaling up to 1 m^2. Nevertheless, estimates of SeedM$_{m2}$ will be important for extending predictions to comparative seed yield in perennial species. And numerous values are already available (Šera and Šery, 2004). SeedNo$_{m2}$ remains a potentially crucial attribute albeit one in need of further study.

SeedNo$_{Pl}$, a valuable new regenerative dimension to trait-based studies of floristic change

In our most intensively studied region, Central England, eutrophication and disturbance in managed habitats and abandonment of marginal ones have fundamentally altered the nature of the landscape, and the flora. Many tall species and those of fertile soils have increased, particularly those with small seeds (Table 8; Hodgson, 1986a; Hodkinson 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).

Encouragingly, regeneration from seed adds an additional dimension to this well-established story. High $\text{SeedNo}_{\text{Pl}}$ is consistently a better predictor of increased abundance than low SeedM (Table 8). This relationship has important implications. Because key evolutionary processes impact upon survival and trait expression at the level of the population (Harper, 1967; Moles, 2018), populations of the same species may come to differ both in habitat and life history across their geographical range (Table 6). In particular, 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 operates at the population level. 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). On the basis of data from our study area, we predict that, there is likely to be selection for larger seeds and potentially increased seedling survivorship in populations of rare species confined to small isolated patches of habitat (Fig. 5). In contrast, the production of a larger number of smaller widely-dispersed seeds may facilitate the spread of increasing species. *In extremis*, since SeedM_{Pl} is a positive function of vegetative performance both theoretically (eqn 1a-d) and practically (Table 3), poor growth may consistently result in the occurrence of non-viable combinations of seed size and number. In this context, we provide regional examples of formerly-annual species that now tend to behave as perennials, less dependent upon regeneration by seed (Table 6). As illustrated here (Fig.5), the comparative regenerative traits devised in this paper complement the established set of vegetative traits routinely used in trait-based plant ecology and enhance their diagnostic capabilities.

CONCLUSIONS

With many seeds produced but few surviving, establishment from seed is a crucial but poorly understood 'extreme event' regulating species distribution. To date, within functional trait plant ecology, this process has only been studied within the context of seed size. Now, following this investigation, we have, additionally, comparative estimates for seed number including provisional values for >800 annuals, appended as Supplementary Data Table S6. Although, as emphasized in the Discussion, many methodological problems remain, for the first time, in addition to SeedM, we are in a position to routinely include comparative estimates of $\mathrm{SeedNo}_{\mathrm{Pl}}$. As a result, we can extend functional analyses to the fundamental '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 our analyses within the European flora illustrate the value of routinely including this additional regenerative element in trait-based plant ecology (Figs 1, 3-4; Tables 3-4, 7-8).

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), and some, like seed dispersal, we have yet to study. The challenge is to sufficiently distil down these dimensions of complexity so that we can emulate C-S-R 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. Importantly, our new regenerative dimension to trait-based plant ecology is already addressing key but poorly understood ecological processes, the establishment of ‘winners’ by seed, and the associated extinction of ‘losers’, during episodes of vegetation change (Fig. 5). We invite others to explore the potential of the appended database, to improve the methodology and to take ‘regenerative functional plant ecology’ to the next level.

ACKNOWLEDGEMENTS

We thank Philip Grime and other former colleagues for access to unpublished datasets from the Unit of Comparative Plant Ecology, past members of the Department of Archaeology, Sheffield and Instituto Pirenaico de Ecología, Zaragoza for their important early contributions to the database and Grup de Recerca Científica, Terres de l'Ebre and the Unita di Analisi e Gestione Biocenosi, Varese for their scientific guidance and hospitality during our many early trips to Catalonia and Lombardy. We are grateful to Simon Pierce, Mick Hanley and three anonymous reviewers for their constructive criticism of previous versions of the paper and the analyses of floristic change in UK would not have been possible without access to the data holdings and the interpretative information on the Botanical Society of the British Isles website (Botanical Society of Britain and Ireland and the Biological Records Centre, 2018), which is in the public domain.

John Hodgson participated in vegetation surveys, plant collection and the subsequent measurement of traits, curated the databases, carried out the analyses and wrote the various drafts of the paper. Gabriel Montserrat Marti[*] provided independently-collected functional data from Spain and participated in/led a number of collecting/measuring trips. Ferran Royo Pla provided field survey data and participated in/led some collecting/measuring trips. Bozena Sera[*] provided the dataset on seed yield m^{-2}. Glynis Jones[*], Amy Bogaard[*], Mike Charles[*], key archaeobotanical contributors since 1990's involved routinely in plant collecting and measurement. Xavier Font[*] provided Spanish field survey data. Mohammed Ater[*], Younes Hmimsa and Abdelkader Taleb organized and supervised several collecting trips to Morocco. Bianca Santini[*] provided independently-collected trait data. Carol Palmer[*], Peter Wilson, Stuart Band were historically major collectors of, as yet, unpublished functional data. Carol, additionally, had a major early role in the production of the archaeobotanist's version of the

database. The archaeobotanists, Amy Styring, Charlotte Diffey, Laura Green, Erika Nitsch, Elizabeth Stroud and Gemma Warham were involved in functional trait measurement on key recent field trips.Minor (and historically less recent) participants: Bruno Cerabolini organizing collecting trips in 2003–4 (and published FIFTH database, already acknowledged in paper), Alyson Hynd (unpublished trait data, 1996: little on annuals) Angel Romo-Dıėz and Lluis de Torres Espuny organizing collecting trip in 2004 and 2003, 2004 and 2006 respectively. [UCPE input acknowledged generally within paper.][*] paper sent directly to senior ecologists and archaeobotanists for comment.

FUNDING

A considerable quantity of the data used in this project was collected during projects funded by NERC (UK), Comisión Interministerial de Ciencia y Tecnología (Spain) and the European Research Council (AGRICURB project).

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FIGURE CAPTIONS

FIG. 1. Comparative seed yield, estimated from Table 3Aiia, predicts FAO-derived crop seed yield values for annual crops. Values for *x* axis are converted to hg ha^{-2}. Log$_{10}$SeedM$_{ha}$ = 0.699log$_{10}$ SeedM$_{m2USApred}$ + 1.429 (95% confidence intervals – slope: 0.48 – 1.02; constant: 0.22 – 2.64; $r^2 = 0.38$**, $n = 20$). [For UK data, Table 3Aiib: log$_{10}$SeedM$_{ha}$ = 0.766log$_{10}$SeedM$_{m2UKpred}$ + 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. hexasticum*), 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 plus 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, LDMC, 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 5b and 6 from the Results section were used to add, as broken lines, contours for

$\text{SeedM}_{\text{PlUK}}$ (mg per plant; blue, 'gold standard' for the Ann_C axis) and LeafN (mg per g; red, negative 'gold standard' for the Ann_S axis;) and as dotted lines, more tentatively, from eqn 7a for $\text{AnnIndex}_{\text{UK}}$ (proportion of ruderal species per vegetative sample; yellow, 'gold standard' for the Ann_R axis). Mindful of CSR theory (Grime, 2001), these contours were used to locate putative positions for strategy types. Strategies were 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 $\text{SeedNo}_{\text{Pl}}$ PCA axis 1 (mean values ± s.d.): 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 PCA axis 1: Asteraceae (blue dots) 0.30 ± 1.02^{b}, $n = 134$; Fabaceae (red dots) 0.05 ± 0.94^{b}, $n = 119$; Poaceae (green dots) -0.37 ± 0.95^{a}, $n = 125$; ANOVA $F_{2, 377} = 18.5$***. PCA axis 2: Asteraceae 0.48 ± 0.94^{a}; Fabaceae 0.57 ± 0.74^{b}; Poaceae 0.90 ± 0.71^{c}; ANOVA $F_{2, 377} = 103.6$***.

FIG. 3. (A) Seed mass and comparative number both pattern with Ann_CSR and, as a result (B), the numerical relationship between seed mass and comparative number varies with strategy. (AI) illustrates the basic geography of the Ann_CSR classification of plant functional types for annuals. In II-IV mean estimates ± s.d. are provided for (IIi) SeedM_{pl} (one-way ANOVA $F = 213.6$***) and (ii) SeedM_{m2} ($F = 122.7$***), (III) SeedM ($F = 44.6$***), (IVi) $\text{SeedNo}_{\text{pl}}$ ($F = 19.7$***) and (ii) $\text{SeedNo}_{\text{m2}}$ ($F = 8.0$***). [Number of species: total 839, Ann_C 68, Ann_S 47,

Ann_R 30, Ann_CR 90, Ann_SC 187, Ann_SR 74, Ann_CSR 343. The putative direction of change from low to high values is illustrated with an arrow.] In (B) strategies are colour-coded (Ann_C, blue dots; Ann_S, red; Ann_R, yellow; other, grey) with the regions of the PCA ordination provisionally allocated to the three strategies illustrated within the inset. Equations ± 95% confidence intervals:

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

Ann_C-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_C} = -0.690 \pm 0.126\log_{10}\mathrm{SeedM} + 3.685 \pm 0.100$ ($r^2 = 0.69$***)

Ann_R-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_R} = -0.654 \pm 0.257\log_{10}\mathrm{SeedM} + 2.043 \pm 0.300$ ($r^2 = 0.49$***)

Ann_S-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_S} = -0.621 \pm 0.151\log_{10}\mathrm{SeedM} + 2.248 \pm 0.123$ ($r^2 = 0.60$***)

Ann_CR-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_CR} = -0.586 \pm 0.105\log_{10}\mathrm{SeedM} + 3.287 \pm 0.093$ ($\mathrm{r}^2 = 0.59$***)

Ann_SC-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_SC} = -0.679 \pm 0.070\log_{10}\mathrm{SeedM} + 2.877 \pm 0.058$ ($r^2 = 0.67$***)

Ann_SR-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_SR} = -0.651 \pm 0.103\log_{10}\mathrm{SeedM} + 2.049 \pm 0.117$ ($r^2 = 0.69$***)

Ann_CSR-strategists: $\log_{10}\mathrm{SeedNo}_{Ann\_CSR} = -0.636 \pm 0.047\log_{10}\mathrm{SeedM} + 2.749 \pm 0.036$ ($r^2 = 0.68$***)

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

FIG. 4. Both with respect to (A) vegetation samples with ≥ 5 annual species and (B) the species complement, our three study areas differed in their representation of Ann_CSR strategy types and in (C) changed abundance within UK also patterns with strategy. In Ai (± s.d.), Bi and Ci values relate to Central England and are percentages. In the remainder of A and B values identify regional differences between Central England and respectively (ii) North-east and (iii) North central Spain, respectively. Green identifies values higher and red lower than Central England. In (A) coloured values indicate statistically significant differences ($P < 0.05$ using the Mann-Whitney U-tests). In Cii values relate to Status Index and are not calculated for strategies where $n < 10$.

FIG. 5. Some predicted 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 since change is potentially buffered to some degree by a combination of lower soil fertility and summer drought. Predictions were based upon descriptions of the status of the flora (Hodgson, 1986a; Hodkinson 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 6). Arrows identify predicted direction of change. [A supplementary Spanish dimension. Consistent with Fig. 4, the relative abundance of relict (fertile) *versus* sandy/rocky habitats and their importance for annuals was considered to be: Central England > North-east > North central Spain. Putative differences in the Spanish

status of species was identified by the following suffices – habitat range: [a] similar, [b] wider habitat range, [c] arable still an important habitat; [d] life history different, Spanish populations typically annual. A number of potential impacts relating to the Mediterranean climate are not included (e.g. 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)).]

TABLE 1. *The functional traits potentially contributing to the expression of comparative number of seeds per plant in eqns 1c-d. Reasons for their use, are more fully described in Hodgson et al. (2017) and transformations of continuous trait variables prior to statistical analysis are identified in parentheses within 'Units' The suffices* $^+$, $^-$ and $^?$ *identify traits predicted to be expressed, respectively, positively, negatively and uncertainly in eqns 1c-d.*

Trait	Abbrev.	Units	Comments
(1) Plant size, potentially contributing positively to the f_1 term			
Canopy height$^+$	HtCan	$\log_2$ mm	1 ≤ 20 mm; 2 = 21 – 40 mm …… 10 = > 5 m.
Canopy diameter$^+$	DiamCan	$\log_2$ mm	1 ≤ 20 mm; 2 = 21 – 40 mm …… 10 = > 5 m.
Canopy size$^+$	SizeCan	$\log_2$ mm^2	Height x radius^2 [= HtCan + (2 x (DiamCan – 1)]
Canopy shape$^+$	ShapeCan		Height/diameter [= HtCan – DiamCan]
Plant height$^+$	HtPl	$\log_2$ mm	1 ≤ 20 mm; 2 = 21 – 40 mm …… 10 = > 5 m.
Plant diameter$^+$	DiamPl	$\log_2$ mm	1 ≤ 20 mm; 2 = 21 – 40 mm …… 10 = > 5 m.
Plant size$^+$	SizePl	$\log_2$ mm^2	Height x radius^2 [= HtPl + (2 x (DiamPl – 1)]
Plant shape$^+$	ShapePl		Height/diameter [= HtPl – DiamPl]
(2) Leaf size, potentially contributing positively to the f_2 term			
Leaf area$^+$	$\mathrm{LA}_{\mathrm{morph}}$	mm^2 ($\log_{10}$)	The conventional 'morphological' unit
Leaf area per node$^+$	$\mathrm{LA}_{\mathrm{devel}}$	mm^2 ($\log_{10}$)	$\mathrm{LA}_{\mathrm{morph}}$ x number of leaves per node; quantifies incremental growth more exactly than $\mathrm{LA}_{\mathrm{morph}}$
Leaf width$^+$	$\mathrm{LA}_{\mathrm{funct}}$	$\log_2$ mm	0 ≤ 0.5 mm; 1 = 0.51 – 1.0 mm, …… 9 = > 128; A 'competitive' attribute that patterns with thickness of the boundary layer and efficiency of vascular transport within the lamina

Leaf mass$^+$	$\mathrm{LM}_{\mathrm{morph}}$	mg (log$_{10}$)	Converted from $\mathrm{LA}_{\mathrm{morph}}$ using mean SLA values
Leaf mass per node$^+$	$\mathrm{LM}_{\mathrm{devel}}$	mg (log$_{10}$)	Converted from $\mathrm{LA}_{\mathrm{devel}}$ using mean SLA values
(3) Leaf construction costs, potentially contributing negatively to the f_3 term			
Leaf dry matter content$^-$	LDMC	% (square-root)	100 x dry mass of leaf/saturated mass of leaf; correlates positively with soil fertility and growth rate
Leaf thickness$^?$	Lthick	mm^2 (log$_{10}$)	Negatively correlated with irradiance and positively with succulence
Specific leaf area$^+$	SLA	mm^2 per mg (log$_{10}$)	Positively correlated with fertility and negatively with irradiance
(4) Mass of an individual seed contributing negatively as the f_4 term			
Seed mass of germinule$^-$	SeedM	mg (log$_{10}$)	Seed after investing structures that aid dispersal removed

TABLE 2. *Species in 'golden standard' 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 ± s.d.) 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)	*-0.04 ± 0.88*	30.8***	0.00 ± 0.73^{b}	-0.73 ± 0.76^{a}	-0.15 ± 0.72^{b}	1.47 ± 0.77^{c}	0.12 ± 0.83^{b}
(B) Plant size and shape							
Ht$_{Can}$ (log$_2$ scale)	*4.38 ± 1.44*	12.1***	5.63 ± 1.04^{b}	4.33 ± 1.53^{a}	5.23 ± 1.34^{b}	6.75 ± 0.91^{c}	5.44 ± 1.53^{b}
Ht$_{Pl}$ (log$_2$)	*5.22 ± 1.54*	10.1***	6.59 ± 1.09^{b}	5.37 ± 1.44^{a}	6.14 ± 1.34^{b}	7.40 ± 0.91^{c}	6.39 ± 1.40^{b}
Diam$_{Can}$ (log$_2$)	*4.90 ± 1.32*	4.6***	5.59 ± 1.16^{b}	4.68 ± 1.43^{a}	5.47 ± 1.05^{b}	5.80 ± 1.06^{b}	5.75 ± 1.35^{b}
Diam$_{Pl}$ (log$_2$)	*5.30 ± 1.20*	6.0***	6.16 ± 1.06^{b}	5.10 ± 1.33^{a}	5.93 ± 0.93^{b}	6.10 ± 0.79^{b}	6.18 ± 1.11^{b}
Size$_{Can}$ (log$_2$)	*12.20 ± 3.55*	8.3***	14.52 ± 3.63^{b}	12.04 ± 3.62^{a}	14.21 ± 2.87^{b}	16.35 ± 2.76^{c}	15.00 ± 3.72^{bc}
Size$_{Pl}$ (log$_2$)	*13.84 ± 3.32*	11.1***	15.45 ± 4.52^{b}	13.16 ± 3.69^{a}	16.03 ± 2.65^{b}	17.60 ± 2.30^{c}	16.80 ± 2.94^{bc}
Shape$_{Can}$ (log$_2$)	*-0.51 ± 1.39*	4.9***	0.04 ± 1.13^{a}	-0.36 ± 1.22^{a}	-0.19 ± 1.19^{a}	0.95 ± 0.89^{b}	-0.25 ± 1.35^{a}
Shape$_{Pl}$ (log$_2$)	*-0.07 ± 1.54*	3.1**	0.43 ± 1.20^{a}	0.26 ± 1.47^{a}	0.25 ± 1.20^{a}	1.30 ± 0.73^{b}	0.25 ± 1.50^{a}
(C) Leaf size							
Log$_{10}$LA$_{morph}$ (mm^2)	*2.66 ± 0.75*	6.8***	3.22 ± 0.60^{b}	2.60 ± 0.91^{a}	2.94 ± 0.64^{ab}	3.61 ± 0.54^{c}	3.05 ± 0.68^{ab}
Log$_{10}$LA$_{devel}$ (mm^2)	*2.74 ± 0.72*	5.6***	3.27 ± 0.60^{b}	2.84 ± 0.89^{a}	3.02 ± 0.64^{ab}	3.62 ± 0.55^{c}	3.15 ± 0.65^{ab}
LA$_{funct}$ (log$_2$)	*3.93 ± 1.72*	11.6***	6.55 ± 1.14^{c}	4.49 ± 1.69^{a}	4.94 ± 1.91^{ab}	5.60 ± 1.35^{b}	5.26 ± 1.86^{ab}
Log$_{10}$LM$_{morph}$ (mg)	*1.30 ± 0.75*	7.7***	1.81 ± 0.64^{b}	1.30 ± 0.95^{a}	1.52 ± 0.66^{ab}	2.24 ± 0.57^{c}	1.67 ± 0.71^{ab}
Log$_{10}$LM$_{devel}$ (mg)	*1.37 ± 0.72*	6.8***	1.86 ± 0.64^{b}	1.41 ± 0.91^{a}	1.59 ± 0.64^{ab}	2.25 ± 0.59^{c}	1.75 ± 0.67^{ab}
(D) Leaf structure							
√LDMC (%)	*4.15 ± 0.65*	4.7**	4.07 ± 0.49^{a}	3.88 ± 0.53^{a}	4.06 ± 0.49^{a}	4.42 ± 0.58^{b}	4.14 ± 0.53^{a}
Log$_{10}$SLA (mm^2 per mg)	*1.39 ± 0.15*	4.4**	1.40 ± 0.11^{ab}	1.43 ± 0.13^{b}	1.44 ± 0.10^{b}	1.37 ± 0.10^{a}	1.40 ± 0.12^{ab}
Log$_{10}$LThick (mm)	*-0.68 ± 0.22*	2.4^{+}	-0.64 ± 0.18^{a}	-0.63 ± 0.18^{a}	-0.72 ± 0.17^{a}	-0.72 ± 0.17^{a}	-0.70 ± 0.21^{a}
(E) Phenology							
Month of first flowering	*5.8 ± 1.1*	2.9*	6.2 ± 1.3^{a}	5.5 ± 1.1^{b}	5.8 ± 1.2^{ab}		6.1 ± 1.3^{a}
Summer annual (%)	*21*		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 3. *Functional traits identifying (I) plant size (f_1 in eqns 1c-d), (II) leaf size (f_2) and (IV) seed mass traits (f_4), but not (III) leaf construction costs (f_3), contribute in multiple regressions to the expression of (i) comparative seed mass (testing eqn 1d) and (ii) comparative seed number (eqn 1c) per plant. (A) includes regressions predicting comparative yield per plant from Stevens (1932, 1957) for USA (n = 56); and from Salisbury (1942; UK, n = 51).In (B) comparative yield per m^2 relates to Slovenia (Šera and Šery, 2004; n = 123). Only traits accepted into regressions (4 3, 0 and 1 respectively of types I, II, III and IV) are included here, with the numerical suffix after each coefficient identifying the order of acceptance into the regression. A full list of traits is included in Table 1.*

Predicted trait	r^2			(I) Plant size (f_1)				(II) Leaf size (f_2)			(IV) Seed size (f_4)	
		P	*SeedM$_{Pl}$*	SizeCan	ShapeCan	SizePl	ShapePl	LA$_{devel}$	LA$_{funct}$	LM$_{morph}$	SeedM	Constant
Ai SeedM$_{Pl}$												
a USA (+ SeedM)	0.52	***		0.076^{1}				-1.147^{3}		1.460^{2}	0.229^{4}	3.721
(– SeedM)	0.48	***		0.095^{1}				-1.044^{3}		1.445^{2}		3.143
b UK (+ SeedM)	0.77	***				0.145^{1}			0.118^{3}		0.272^{2}	0.145
(– SeedM)	0.75	***				0.176^{1}			0.141^{2}			– 0.522
ii SeedNo$_{Pl}$												
a USA	0.55	***				0.088^{4}		-1.124^{3}		1.346^{2}	-0.739^{1}	3.498
b UK	0.58	***				0.145^{1}			0.124^{3}		-0.737^{2}	0.147
Bi SeedM$_{m2}$												
a USA	0.25	***	*0.638^{1}*	0.110^{3}	0.248^{5}	-0.115^{2}	-0.326^{4}					2.901
b UK	0.22	***	*0.623^{1}*	0.284^{3}	0.160^{5}	-0.192^{2}	-0.360^{4}					3.642
ii SeedNo$_{m2}$	0.13	***									-0.352^{1}	4.959

TABLE 4. *The seed size, comparative number and RSN (± s.d.) of annuals differs between (A) regions, (B) habitats and (C) UK status relative to (i) vegetation samples and (ii) species. In (i) vegetation samples were categorized as 'decreased' if Status Index < -0.5 and 'increased' if 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 ± 0.33^{a}	3.21 ± 0.23^{c}	0.40 ± 0.17^{c}
North-east Spain	*465*	-0.23 ± 0.34^{b}	3.04 ± 0.33^{b}	0.25 ± 0.25^{b}
North central Spain	*275*	-0.15 ± 0.40^{c}	2.79 ± 0.31^{a}	0.06 ± 0.25^{a}
One-way ANOVA (*F*)		74.8***	323.2***	376.0***
(ii) Species				
Central England	*200*	-0.29 ± 0.71^{a}	3.10 ± 0.55^{b}	0.26 ± 0.49^{b}
North-east Spain	*323*	-0.07 ± 0.83^{b}	2.90 ± 0.66^{a}	0.10 ± 0.57^{a}
North central Spain	*284*	-0.03 ± 0.82^{b}	2.78 ± 0.67^{a}	0.02 ± 0.59^{a}
One-way ANOVA (*F*)		7.0***	13.9***	11.0***
(B) Habitats				
(i) Vegetation samples				
(a) Central England				
Wetland	*57*	-0.60 ± 0.32^{a}	3.52 ± 0.17^{d}	0.58 ± 0.13^{b}
Rocky	*136*	-0.65 ± 0.31^{a}	3.03 ± 0.16^{a}	0.36 ± 0.14^{a}
Pasture	*30*	-0.48 ± 0.41^{ab}	3.07 ± 0.17^{ab}	0.30 ± 0.15^{a}
Arable	*391*	-0.17 ± 0.29^{c}	3.20 ± 0.19^{bc}	0.33 ± 0.15^{a}
Spoil	*371*	-0.47 ± 0.28^{ab}	3.32 ± 0.20^{c}	0.50 ± 0.13^{b}
Wasteland	*499*	-0.38 ± 0.29^{b}	3.17 ± 0.25^{ab}	0.38 ± 0.17^{a}
Woodland	*8*	-0.05 ± 0.29^{c}	3.15 ± 0.18^{ab}	0.31 ± 0.21^{a}
One-way ANOVA (*F*)		66.0***	60.8***	58.3***
(b) North-east Spain				
Wetland	*23*	-0.58 ± 0.38^{a}	3.37 ± 0.23^{b}	0.52 ± 0.17^{c}
Artificial	*323*	-0.21 ± 0.32^{bc}	3.10 ± 0.31^{ab}	0.28 ± 0.23^{b}
Grassland	*80*	-0.19 ± 0.32^{bc}	2.77 ± 0.27^{a}	0.08 ± 0.24^{a}
Maritime/saline	*16*	-0.42 ± 0.37^{ab}	2.97 ± 0.30^{ab}	0.34 ± 0.24^{b}
Open habitats	*16*	-0.14 ± 0.38^{c}	2.85 ± 0.32^{a}	0.07 ± 0.24^{a}
Dwarf shrub	[*2*	-0.18 ± 0.37	2.77 ± 0.44	0.03 ± 0.38]
Woodland	[*5*	-0.07 ± 0.29	3.08 ± 0.15	0.34 ± 0.11]
One-way ANOVA (*F*)		8.2***	28.3***	23.2***
(c) North central Spain				
Wetland	[*2*	-0.74 ± 0.05	3.16 ± 0.24	0.48 ± 0.14]
Artificial	*121*	0.09 ± 0.29^{c}	2.92 ± 0.28^{c}	0.12 ± 0.23^{b}
Grassland	*94*	-0.21 ± 0.22^{b}	2.66 ± 0.32^{abc}	-0.01 ± 0.25^{ab}
Maritime/saline	*25*	-0.98 ± 0.23^{a}	2.90 ± 0.18^{bc}	0.17 ± 0.15^{b}
Open habitats	*12*	-0.29 ± 0.24^{b}	2.62 ± 0.18^{a}	0.01 ± 0.19^{ab}
Dwarf shrub	*13*	-0.15 ± 0.30^{bc}	2.43 ± 0.20^{a}	-0.19 ± 0.17^{a}
Woodland	*8*	-0.15 ± 0.35^{bc}	2.65 ± 0.19^{ab}	0.09 ± 0.22^{b}
One-way ANOVA (*F*)		72.6***	16.4***	7.6***
(ii) Species				

(a) Central England				
Wetland	*19*	-0.59 ± 0.74^{a}	3.09 ± 0.56	0.49 ± 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 ± 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 (*F*)		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 (*F*)		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 ± 0.68a^{b}	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 (*F*)		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}
t-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}
t-test		0.5 ns	3.8***	2.4*

TABLE 5. *Two-way ANOVAs identify strategy as more consistently important than habitat as a determinant of seed size and comparative number both for vegetation samples (veg) and for species (spp). High values for variance ratio (F), together with associated degrees of freedom (d of f) and P, are in bold.*

		n	Habitat			Strategy			Habitat x Strategy		
			d of f	*F*	*P*	*d of f*	*F*	*P*	*d of f*	*F*	*P*
(A) SeedM_{Pl}											
Central	veg	836	5	6.8	***	**4**	**46.7**	*******	11	1.4	ns
England	spp	182	5	2.7	***	**5**	**12.2**	*******	18	1.2	ns
North-east	veg	454	4	3.5	**	**4**	**9.5**	*******	9	1.5	ns
Spain	spp	331	6	1.4	ns	**7**	**9.8**	*******	33	1.1	ns
North central	veg	264	**4**	**10.5**	*******	4	2.9	*	7	0.6	ns
Spain	spp	292	5	1.5	ns	**7**	**6.7**	*******	28	0.9	ns
(B) $\text{SeedNo}_{\text{Pl}}$											
Central	veg	836	5	10.4	***	**4**	**33.2**	*******	11	4.5	ns
England	spp	182	5	5.0	***	**5**	**6.1**	*******	18	1.1	ns
North-east	veg	454	4	4.4	**	**4**	**6.1**	*******	9	1.0	ns
Spain	spp	331	6	2.2	*	**7**	**6.9**	*******	33	1.0	ns
North central	veg	264	**4**	**3.8**	******	4	0.6	ns	7	1.9	$^+$
Spain	spp	292	5	1.9	$^+$	**7**	**4.9**	*******	28	0.5	ns

TABLE 6. *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
(A) Habitat range		
Galeopsis angustifolia *Ononis reclinata* *Thlaspi perfoliatum*	Uncommon – very rare in UK. Now primarily confined to rocky sites with habitat continuity	Wide range of habitats including crop and/or fallow fields
Galeopsis segetum	Former arable weed, now extinct	Former arable weed, now largely restricted to open shaded sites with habitat continuity
(B) Life history		
Clinopodium acinos	Much reduced as an annual arable weed; increasingly a woody perennial of rocky sites with habitat continuity	Occupies a range of habitats but still characteristically an arable weed
Gaudinia fragilis	Primarily a tufted perennial of unimproved grassland	Typically an annual of disturbed habitats. [Seen in arable habitats in north Morocco.]

TABLE 7. *Seed traits of annuals correlate with the functional traits of coexisting perennials weighted by abundance. Values relate to Pearson r coefficients with number of releves in parentheses.*

	$\mathrm{SeedM_{peren}}$	$\mathrm{LDMC_{peren}}$	DomI
(A) $\mathrm{SeedM_{annual}}$			
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) $\mathrm{SeedNo_{annual}}$			
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 8. *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 ± 0.51;* $RSN_{Stable/increased}$ *0.25 ± 0.49; t = 3.0**.]*

	Mean $\log_{10}$SeedM ± s.d.					Mean $\log_{10}$SeedNo$_{Pl}$ ± s.d.		
	Decreased		Stable/increased		*t*	Decreased	Stable/increased	*t*
All	*172*	-0.22 ± 0.79	*165*	-0.31 ± 0.72	1.2 ns	2.87 ± 0.54	3.08 ± 0.60	3.5***
Ann_C	*11*	0.47 ± 0.33	*15*	0.20 ± 0.68	1.3 ns	3.22 ± 0.35	3.71 ± 0.47	2.9**
Ann_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*
Ann_CSR	*69*	-0.19 ± 0.63	*66*	-0.48 ± 0.66	2.6**	2.89 ± 0.52	3.12 ± 0.47	2.7**
Ann_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

Fig. 1

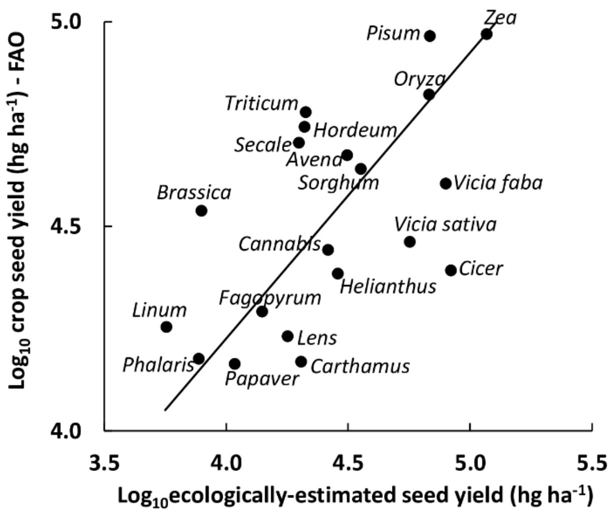

5.0
4.5
4.0
Log10 crop seed yield (hg ha-1) - FAO
3.5
4.0
4.5
5.0
5.5
Log10ecologically-estimated seed yield (hg ha-1)
Zea
Pisum
Oryza
Triticum
Hordeum
Secale
Avena
Sorghum
Vicia faba
Brassica
Vicia sativa
Cannabis
Cicer
Helianthus
Fagopyrum
Linum
Lens
Phalaris
Carthamus
Papaver

Fig2a

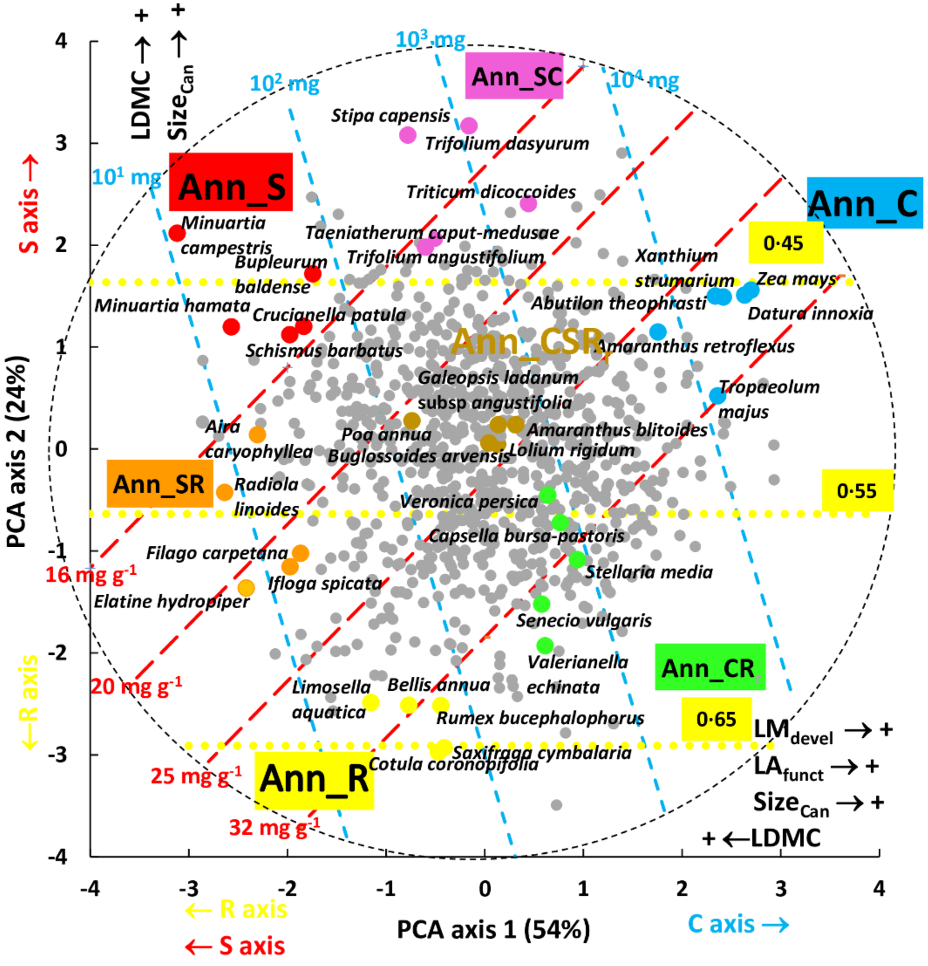

LDMC → +
Size$_{Can}$ → +
S axis →
←R axis
PCA axis 2 (24%)
PCA axis 1 (54%)
← R axis
← S axis
C axis →
4
3
2
1
0
-1
-2
-3
-4
10¹ mg
10² mg
10³ mg
10⁴ mg
16 mg g⁻¹
20 mg g⁻¹
25 mg g⁻¹
32 mg g⁻¹
0·45
0·55
0·65
Ann_S
Ann_SC
Ann_C
Ann_CSR
Ann_SR
Ann_CR
Ann_R
Stipa capensis
Trifolium dasyurum
Triticum dicoccoides
Minuartia campestris
Taeniatherum caput-medusae
Bupleurum baldense
Trifolium angustifolium
Xanthium strumarium
Zea mays
Minuartia hamata
Crucianella patula
Abutilon theophrasti
Datura innoxia
Schismus barbatus
Amaranthus retroflexus
Galeopsis ladanum subsp angustifolia
Tropaeolum majus
Aira caryophyllea
Poa annua
Amaranthus blitoides
Buglossoides arvensis
Lolium rigidum
Radiola linoides
Veronica persica
Capsella bursa-pastoris
Filago carpetana
Stellaria media
Ifloga spicata
Elatine hydropiper
Senecio vulgaris
Valerianella echinata
Limosella aquatica
Bellis annua
Rumex bucephalophorus
Saxifraga cymbalaria
Cotula coronopifolia
LM$_{devel}$ → +
LA$_{funct}$ → +
Size$_{Can}$ → +
+ ←LDMC

Fig2b

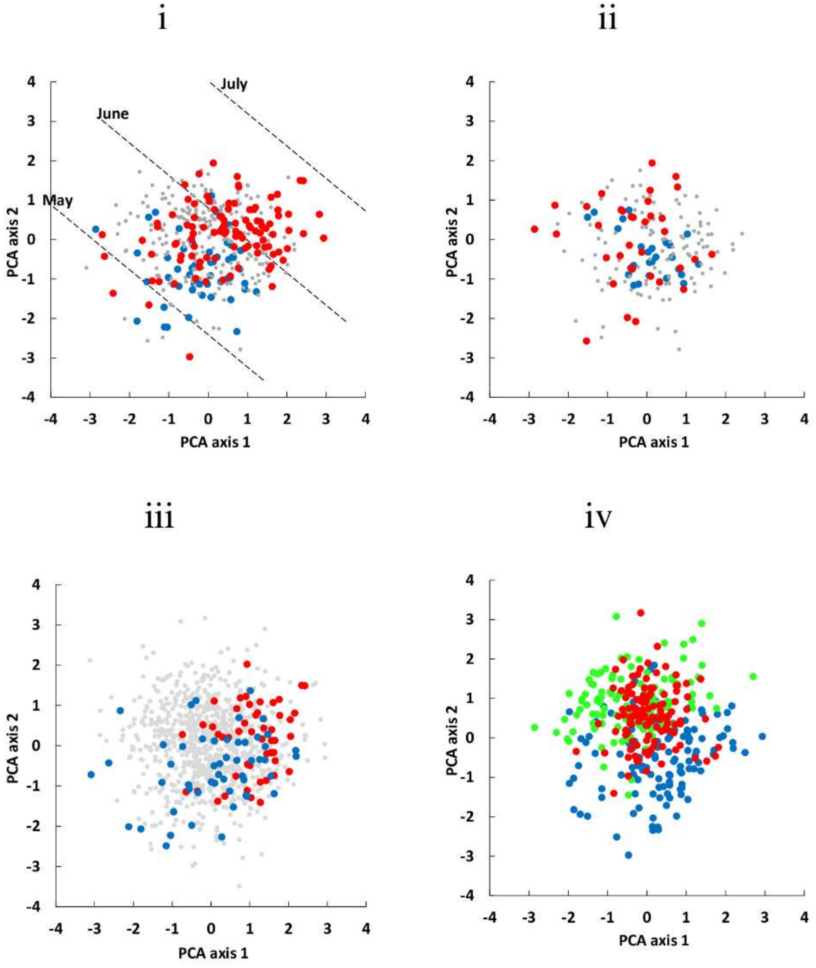


Fig 3A

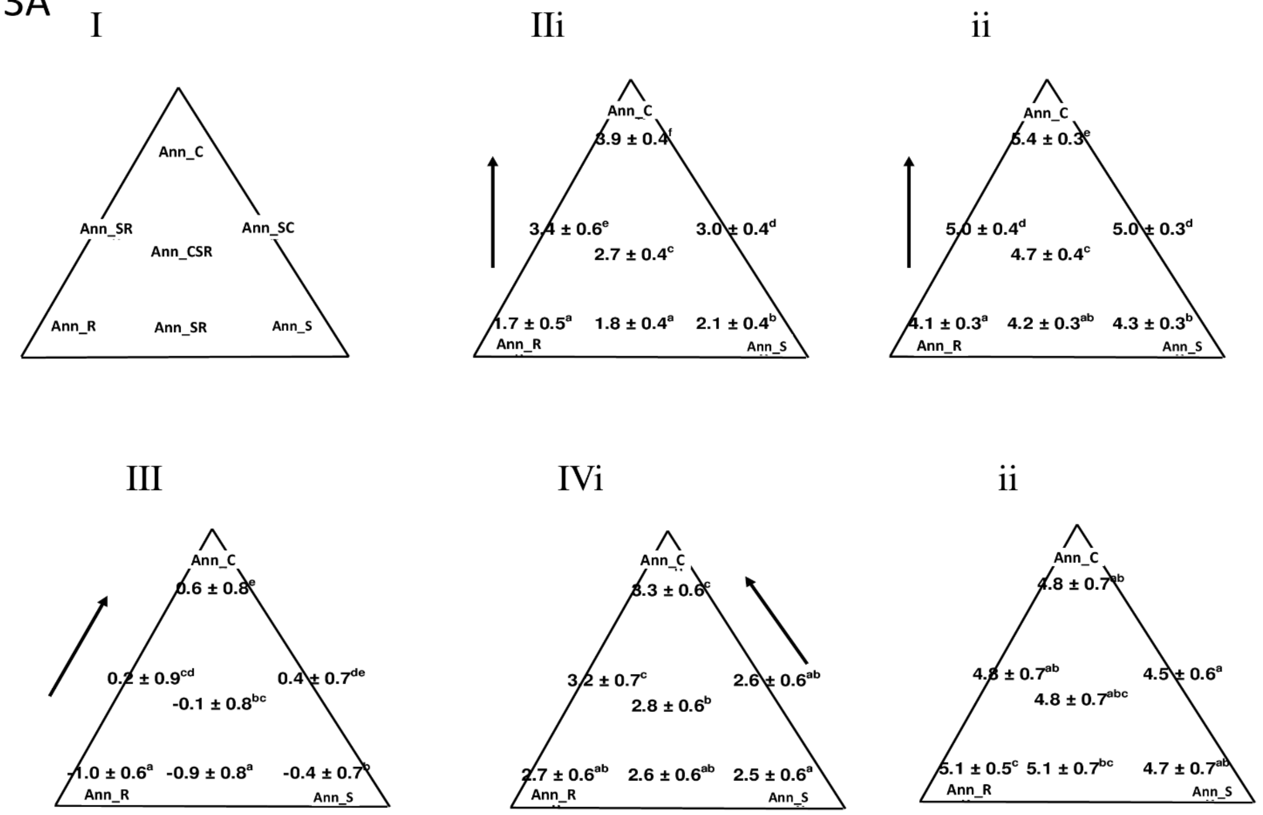
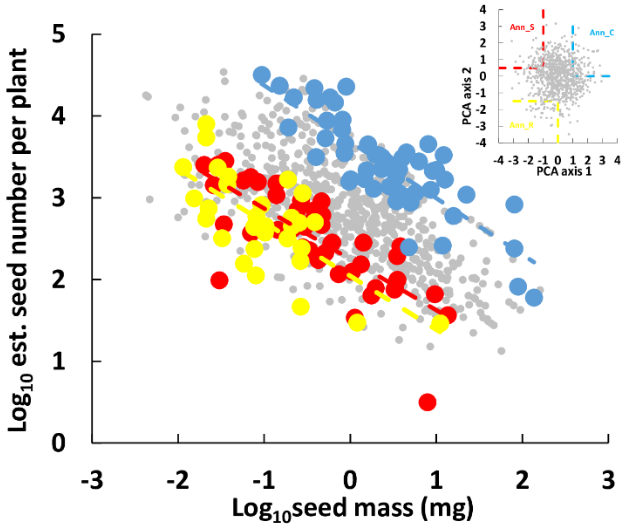
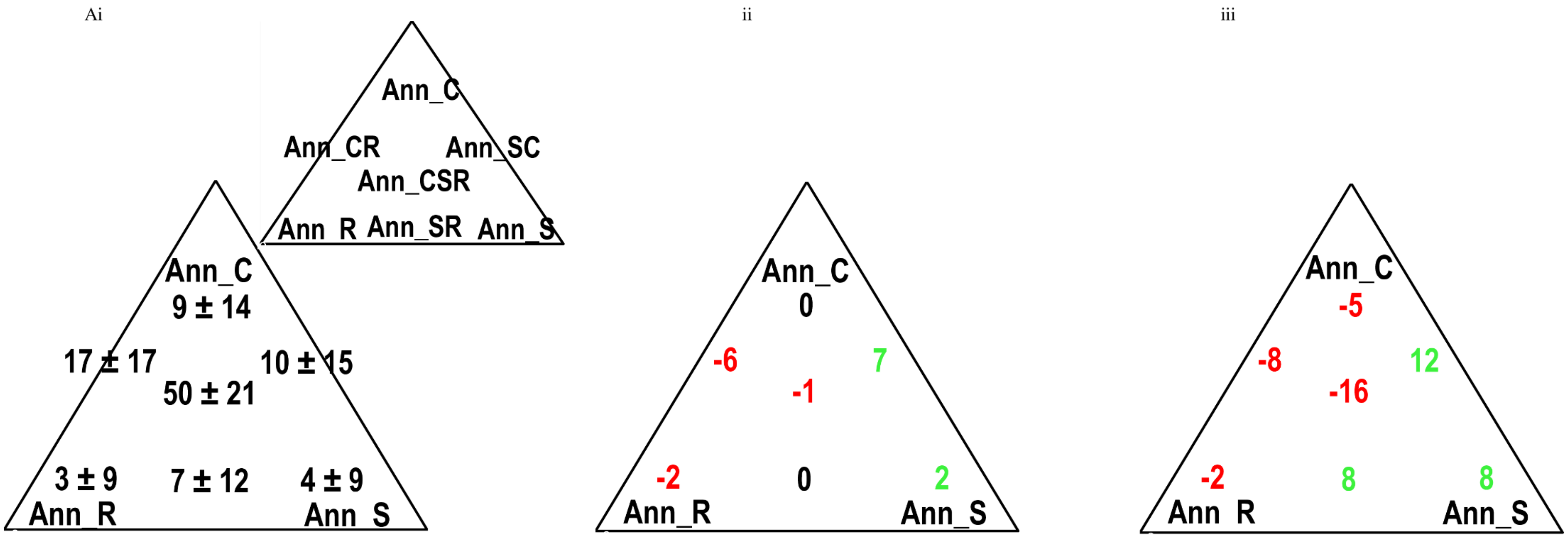
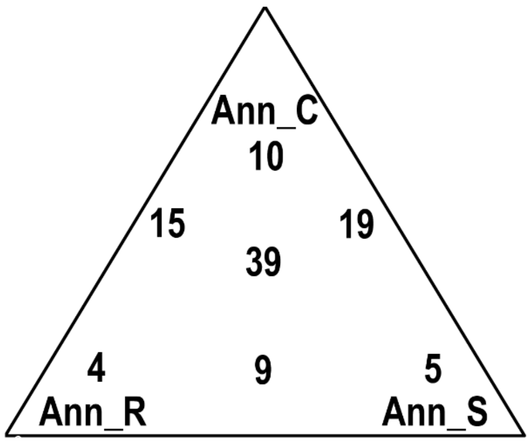

I
Ann_C
Ann_SR
Ann_SC
Ann_CSR
Ann_R
Ann_SR
Ann_S
IIi
Ann_C
3.9 ± 0.4^{f}
3.4 ± 0.6^{e}
3.0 ± 0.4^{d}
2.7 ± 0.4^{c}
1.7 ± 0.5^{a}
1.8 ± 0.4^{a}
2.1 ± 0.4^{b}
Ann_R
Ann_S
ii
Ann_C
5.4 ± 0.3^{e}
5.0 ± 0.4^{d}
5.0 ± 0.3^{d}
4.7 ± 0.4^{c}
4.1 ± 0.3^{a}
4.2 ± 0.3^{ab}
4.3 ± 0.3^{b}
Ann_R
Ann_S
III
Ann_C
0.6 ± 0.8^{e}
0.2 ± 0.9^{cd}
0.4 ± 0.7^{de}
-0.1 ± 0.8^{bc}
-1.0 ± 0.6^{a}
-0.9 ± 0.8^{a}
-0.4 ± 0.7^{b}
Ann_R
Ann_S
IVi
Ann_C
3.3 ± 0.6^{c}
3.2 ± 0.7^{c}
2.6 ± 0.6^{ab}
2.8 ± 0.6^{b}
2.7 ± 0.6^{ab}
2.6 ± 0.6^{ab}
2.5 ± 0.6^{a}
Ann_R
Ann_S
ii
Ann_C
4.8 ± 0.7^{ab}
4.8 ± 0.7^{ab}
4.5 ± 0.6^{a}
4.8 ± 0.7^{abc}
5.1 ± 0.5^{c}
5.1 ± 0.7^{bc}
4.7 ± 0.7^{ab}
Ann_R
Ann_S

Fig 3B

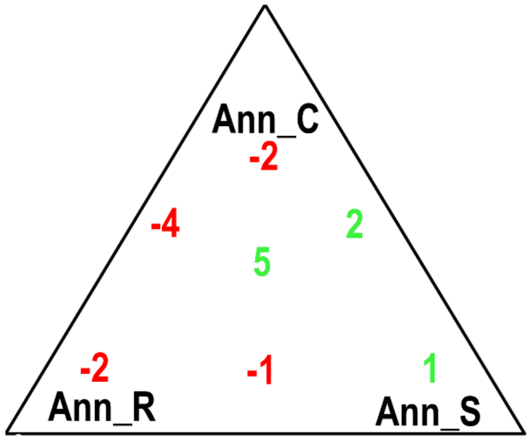

Log10 est. seed number per plant
0
1
2
3
4
5
-3
-2
-1
0
1
2
3
Log10seed mass (mg)
PCA axis 2
4
3
2
1
0
-1
-2
-3
-4
-4 -3 -2 -1 0 1 2 3 4
PCA axis 1
Ann_S
Ann_C
Ann_R
Ann_S


Ai
Ann_C
Ann_CR
Ann_SC
Ann_CSR
Ann_R
Ann_SR
Ann_S
Ann_C
9 ± 14
17 ± 17
10 ± 15
50 ± 21
3 ± 9
7 ± 12
4 ± 9
Ann_R
Ann_S
ii
Ann_C
0
-6
7
-1
-2
0
2
Ann_R
Ann_S
iii
Ann_C
-5
-8
12
-16
-2
8
8
Ann_R
Ann_S

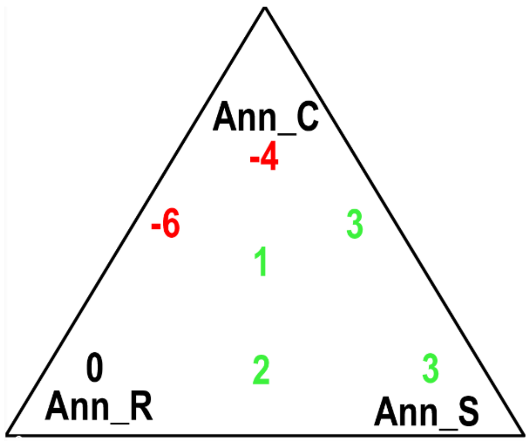
Bi


Ann_C
10
15
19
39
4
9
5
Ann_R
Ann_S

ii


Ann_C
-2
-4
2
5
-2
-1
1
Ann_R
Ann_S

iii


Ann_C
-4
-6
3
1
0
2
3
Ann_R
Ann_S

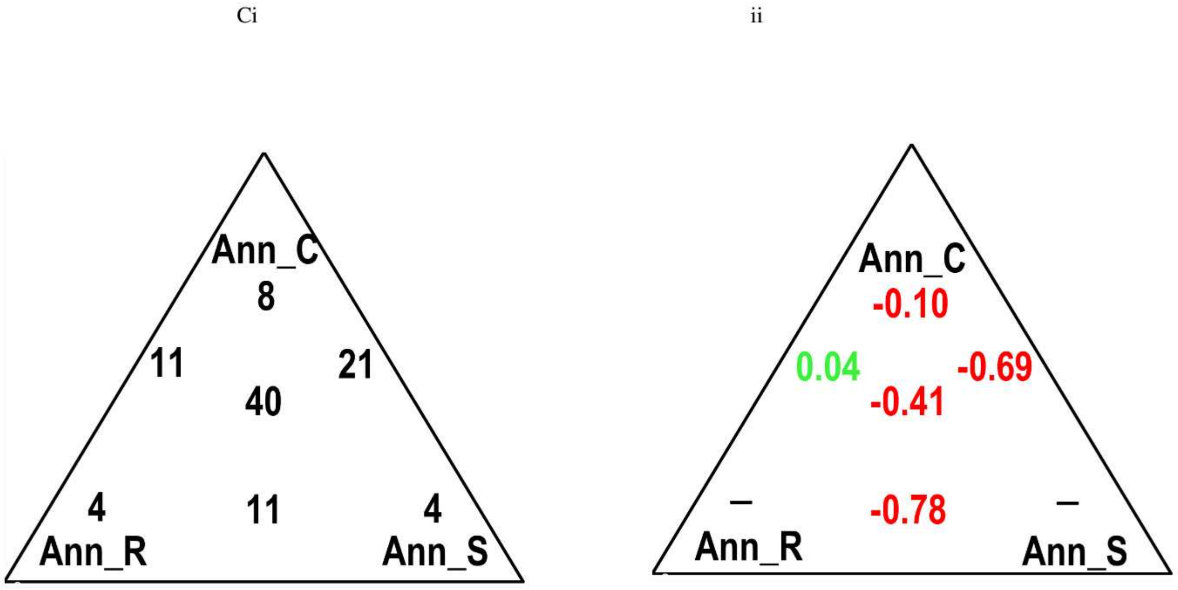
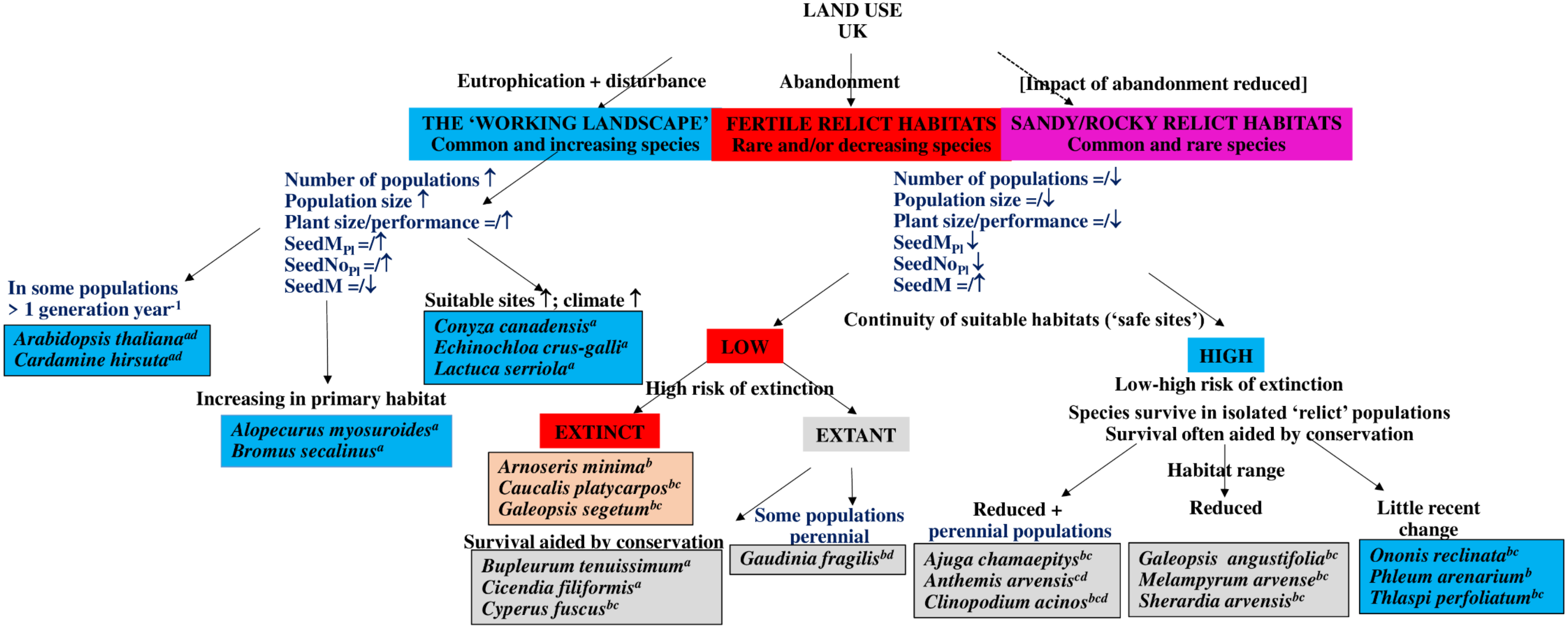

Ci
Ann_C
8
11
21
40
4
11
4
Ann_R
Ann_S
ii
Ann_C
-0.10
0.04
-0.69
-0.41
–
-0.78
–
Ann_R
Ann_S

Figure 5


LAND USE
UK
Eutrophication + disturbance
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$_{Pl}$ =/↑
SeedNo$_{Pl}$ =/↑
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}
Number of populations =/↓
Population size =/↓
Plant size/performance =/↓
SeedM$_{Pl}$ ↓
SeedNo$_{Pl}$ ↓
SeedM =/↑
Continuity of suitable habitats ('safe sites')
LOW
High risk of extinction
EXTINCT
Arnoseris minima^{b}
Caucalis platycarpos^{bc}
Galeopsis segetum^{bc}
Survival aided by conservation
Bupleurum tenuissimum^{a}
Cicendia filiformis^{a}
Cyperus fuscus^{bc}
EXTANT
Some populations
perennial
Gaudinia fragilis^{bd}
HIGH
Low-high risk of extinction
Species survive in isolated 'relict' populations
Survival often aided by conservation
Habitat range
Reduced +
perennial populations
Ajuga chamaepitys^{bc}
Anthemis arvensis^{cd}
Clinopodium acinos^{bcd}
Reduced
Galeopsis angustifolia^{bc}
Melampyrum arvense^{bc}
Sherardia arvensis^{bc}
Little recent
change
Ononis reclinata^{bc}
Phleum arenarium^{b}
Thlaspi perfoliatum^{bc}