

# Impact of abundance weighting on the response of seed traits to climate and land use

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## Summary

1. Many studies have identified relationships between plant reproductive behaviour and environmental conditions. However, they have all been based on cross-species analysis and take no account of the relative abundance of species with vegetation.
2. Using two reproductive traits – seed mass and dispersal vector – as examples, a range of previously identified relationships were tested using both unweighted and weighted-by-abundance data collected from land-use transitions at 12 sites across Europe.
3. Seed mass was correlated positively with most measures of temperature (stronger relationships for unweighted data) and declined against measures of disturbance (stronger relationships with weighted data). It was not related consistently to measures of water availability.
4. There was some evidence that endozoochory was associated with damper environments, hoarding with drier ones and exozoochory with more fertile habitats.
5. Weighting reduced the slope of relationships between seed mass and environmental variables, possibly indicating that dominance within vegetation is determined by land use after the operation of a climatic filter. Fewer significant relationships were detected for weighted dispersal mechanisms compared to unweighted ones, indicating less difference of the dominants from other species with regard to this trait.
6. *Synthesis.* This analysis shows that weighting by abundance in the vegetation (compared to unweighted analysis) has a significant impact on the relationships between key species traits and a range of environmental parameters related to climate and land use, and that this impact was not consistent in its effects.

**Key-words:** agricultural abandonment, extensification, plant functional traits, seed dispersal agent, seed mass, species–environment relationships, weighted abundance

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## Introduction

An individual plant's fitness depends upon the production of offspring that in turn reproduce. Sexual reproduction that contributes to this fitness involves the production and dispersal of seeds, and life-history theory predicts that different environments should select for different optimal patterns of seed traits (e.g. Aarssen & Jordan 2001). Consequently, a wide range of studies have either identified relationships between reproductive traits and a range of environmental drivers or tested successfully for relationships between seed traits and factors such as climate, disturbance regime and management.

All these studies have been carried out using cross-species analysis; they have not been weighted by the abundance of the species within vegetation. In effect, the studies predict the seed traits for an 'average species' for the given conditions. However, because some plant traits (including some seed traits) are correlated with commonness/rarity within vegetation (Reader 1998; Pakeman & Queded 2007), these predictions may be limited in their predictive value for an 'average plant' and hence in their relevance and applicability to vegetation (Willson & Traveset 2000). Consequently, analyses based on species-level data may not be suitable to provide a functional understanding of vegetation (Grime 2006) and hence a quantitative approach at the assembly level is necessary to achieve this (Grime 1998).

Using data collected on largely herbaceous vegetation from a range of sites (12) and plots (194) that differed in climate, vegetation type and management (Garnier *et al.* 2007), we investigated the relationships between seed mass and dispersal mechanism with climate and habitat characters based on a range of expectations from the literature (set out in the following sections). Relationships were generated using both cross-species data and data weighted by abundance. The differences in the relationships produced from the two methods would then indicate the importance of weighting by abundance in understanding patterns in seed mass and dispersal in relationship to environmental controls.

### EXPECTATIONS RELATING SEED MASS TO CLIMATE, FERTILITY AND MANAGEMENT

Seed mass connects the ecology of reproduction with the ecology of vegetative growth – strategy sectors that are largely disconnected (Leishman *et al.* 2000; Díaz *et al.* 2004). Analysis has focused on the seed mass/seed number trade-off (Grime *et al.* 1997; Smith & Fretwell 1974; Venable 1992), phylogenetic relationships between species (e.g. Thompson *et al.* 1998; Moles *et al.* 2005) and the colonization/competition trade-off (e.g. Turnbull *et al.* 2004). It has been demonstrated that larger-seeded species have higher seedling survival rates (e.g. Westoby *et al.* 2002), but this does not make up for the numerical advantage of smaller-seeded species (Moles & Westoby 2004). Advantages accrue at later stages of the life cycle, through the production of either larger or more long-lived plants, such that lifetime seed production is not correlated to seed mass (Moles *et al.* 2004). In general, large seed masses should be

beneficial in situations where resources are limited, variable or are used up rapidly (Eriksson *et al.* 2000), but at the expense of being less able to respond through population growth when conditions are good (Coomes *et al.* 2002). The following 11 expectations formed the basis of the analysis.

#### ***Expectation 1: Seed mass increases in drier habitats***

It has been shown that larger seeds offer an advantage in drier conditions (e.g. Buckley 1982) or are more common in drier conditions (Wright & Westoby 1999), because the seedlings produced are more capable of resisting environmental hazards and reserves are needed for drought-resistance mechanisms (Leishman & Westoby 1994a). However, this relationship is not always present (Mazer 1989; Leishman & Westoby 1994a).

#### ***Expectation 2: Seed mass should increase with increasing temperature***

Analysis of a number of data sets has indicated a substantial negative relationship between seed mass and latitude (Moles & Westoby 2003; Moles *et al.* 2007) or temperature (Murray *et al.* 2004). Seed mass reduces tenfold with each 23° latitude shift towards the poles (Moles & Westoby 2003), but with a significant discontinuity at the edge of the tropics (Moles *et al.* 2007).

#### ***Expectation 3: Seed mass is independent of fertility***

There is conflicting evidence to suggest that seed mass is correlated with habitat fertility. It has been shown that larger reserve sizes are associated with species of both low fertility (e.g. Jurado & Westoby 1992; Parolin 2000) and high fertility (Fernández Alés *et al.* 1993; Maranon & Grubb 1993). A larger seed mass may be beneficial for rapid seedling growth in nutrient-rich environments where light competition is high, or to act as a buffer against poor environmental conditions. However, most studies of semi-natural vegetation have shown no effect at the assemblage level (Westoby *et al.* 1990; Hammond & Brown 1995; Wright & Westoby 1999; Pakeman 2004).

#### ***Expectation 4: Seed mass should be smaller where persistence is an advantage (i.e. in systems where disturbance is regular)***

Small-seeded species cannot bet hedge by being able to germinate across a wide range of conditions. Instead, they bet hedge through being able to persist in soil (Venable & Brown 1988; Lavorel *et al.* 1994; Rees 1996; Schippers *et al.* 2001). Small seeds are incorporated into soil easily and therefore escape surface predators (Leishman *et al.* 2000). Large seeds are not protected from predation by burial, so seed persistence is not a useful characteristic. Thompson (1987) and Kotorová & Lepš (1999) demonstrated experimentally that germination of large-seeded species is less suppressed by

competition of established vegetation than germination of small-seeded species in a meadow community. Also, large seed banks, dominated by persistent small-seeded species, build up in disturbed habitats in temperate climates (Thompson 2000; Fenner & Thompson 2005), but not where hard-seeded species dominate such as in Australia (Leishman & Westoby 1998; Moles *et al.* 2003) and these dominate the subsequent vegetation development after disturbance. Contingency table analysis of plants divided into those preferring arable, grassland or woodland habitats (Unit of Comparative Plant Ecology data, Grime *et al.* 1988) showed higher proportions of small-seeded species (lumped categories S and 1) and lower proportions of large-seeded species (lumped categories 5 and 6) in grassland than expected (categories 2, 3 and 4 not lumped, resulting in a  $3 \times 5$  contingency table). The opposite pattern is true of species found most commonly in woodland, with no departure from expectancy in arable species ( $\chi^2 = 27.7$ , d.f. = 8,  $P = 0.001$ ).

**Expectation 5: Seed mass should decline as grazing intensity increases**

Increased grazing led to an increase in plants with small seeds in many grazing experiments (e.g. Reader 1993; Eriksson & Eriksson 1997; Kahmen *et al.* 2002), although not in all (Pakeman 2004; Vesik *et al.* 2004). Large-seeded species with berries are associated with undisturbed/closed habitats with little grazing (Eriksson *et al.* 2000; Bolmgren & Eriksson 2005).

**Expectation 6: Seed mass should increase with increasing shade or vegetation height**

There is considerable evidence that seed mass increases with the shadiness of the habitat (Salisbury 1942; Leishman *et al.* 2000; Díaz *et al.* 2004). Smaller-seeded species suffer higher seed mortality in shaded conditions because the growth of smaller-seeded species is relatively more depressed than larger-seeded ones (Grime & Jeffrey 1965; Leishman & Westoby 1994b; Walters & Reich 2000). Larger seed reserves produce a taller, deeper-rooted and more long-lived seedling (Leishman *et al.* 2000) and confer a competitive advantage on seedlings competing with other seedlings (Leishman 2001) and existing plants (Black 1958). The same pattern is also associated with plant litter: smaller-seeded species germinate and establish better where litter is absent or disturbed, whilst larger-sized seeds can cope with deeper litter layers (Jensen & Gutekunst 2003; Lusk & Kelly 2003; Kostel-Hughes *et al.* 2005).

**EXPECTATIONS RELATING DISPERSAL MECHANISM TO CLIMATE, FERTILITY AND MANAGEMENT**

Seed dispersal is a process that increases fitness by reducing offspring competition with siblings and parent, by spreading offspring to take advantage of other resources, and is a means of risk spreading in unpredictable environments (e.g. Dieckmann *et al.* 1999; Kisdi 2002). It has been the subject

of considerable interest for many years and subject to many reviews (e.g. Willson & Traveset 2000; Levin *et al.* 2003). It is a trait that influences the dynamics and persistence of populations, the distribution and abundance of species, and community structure (Dieckmann *et al.* 1999). The tests of hypothesized relationships between seed-dispersal mechanisms and climate, fertility and management set out in the following sections focused only on broad categories, because refinement to very specialized categories results in very sparse data sets that are difficult to analyse. Therefore, the analysis focused on anemochory (wind dispersal), zoochory (animal dispersal, divided into endozoochory, exozoochory and hoarding) and species with no obvious dispersal mechanism. Hydrochory was not a major feature of species from the sites investigated.

**Expectation 7: Zoochory is more frequent on soils with a high water content or in sites with higher rainfall**

There is some evidence from Australia that vertebrate dispersal is higher on more moist soils (Willson *et al.* 1990). In general terms, climate does drive vegetation type, and hence different suites of dispersal attributes could occur under different climates.

**Expectation 8: Zoochory is more frequent in more fertile sites**

There is some evidence from Australia that vertebrate dispersal is more frequent on fertile soils (Willson *et al.* 1990). Also, more seeds are dispersed by endozoochory in fertile habitats than in infertile ones (Mouissie 2004).

**Expectation 9: Unassisted dispersal should be more common in disturbed habitats**

Comparison of the dispersal spectra of species with habitat across five floras showed that unassisted dispersal declined with increasing vertical diversity of vegetation structure, i.e. along a gradient from open to woodland habitats (Willson *et al.* 1990). Analysis of the Unit of Comparative Plant Ecology (UCPE) data (Grime *et al.* 1988) of species dispersed by animals, wind or with unassisted dispersal categorized by their most common habitat (arable, grassland, woodland) showed that species found most commonly in arable habitats had unassisted dispersal more often than expected. Species more abundant in woodland were less likely to have unassisted dispersal than expected ( $3 \times 3$  contingency table,  $\chi^2 = 10.63$ , d.f. = 4,  $P = 0.031$ ).

**Expectation 10: Zoochory should be more common in grazed habitats and in shorter vegetation**

Because dispersal by large vertebrates can only occur if they are present, zoochory should be more common in grazed habitats (e.g. Poschlod *et al.* 1998). This is the expected relationship for the largely open habitats in this study. In more closed

habitats with little grazing, bird-dispersed fruits are more common (Jakobsson & Eriksson 2002). The contingency-table analysis of the UCPE data (Expectation 9) also showed that zoochory was more common in species of grassland habitats than expected, and less common in woodland species.

**Expectation 11: Anemochory should be less common in sheltered habitats such as woodland and scrub**

Wind speeds are reduced under tree and shrub canopies, and hence wind dispersal should not be common in the ground-layer vegetation of woodland and scrub (Hughes *et al.* 1994). The contingency-table analysis of the UCPE data also showed that wind dispersal was less common in species of woodland habitats than expected.

## Methods

### DATA

Data were collected during 2003 and 2004 from 12 sites in nine countries from Scandinavia to the Mediterranean (Table 1). Within each site, a range of land uses was sampled to cover likely changes as a result of abandonment or extensification of agricultural use. Where possible, each stage of each land use change transition ('treatment') was replicated within a site ('plots'). Between the 12 sites, there were 194 plots selected to cover and replicate the range of land uses. Full information is given in Garnier *et al.* (2007).

Species abundance data were collected from random points during one survey of each plot. Only ground flora was considered when tall, woody vegetation was present. This standardized the analysis on herbaceous vegetation because plant size is correlated to a number of traits, including seed mass (Moles *et al.* 2005; Moles *et al.* 2007). Data were collected using biomass, point- or area-based quadrats, but were all standardized to percentage contribution to the total. Seed mass (always  $\log_{10}$ -transformed in all analyses) was collected from field material and observation. Where this was not available, it was supplemented by data from standard floras and databases. Dispersal data were collected from flora data and established databases such as Grime *et al.* (1988). Methods of data collection were standardized (Garnier *et al.* 2007). Plots were only entered into the analysis if trait information was available for species that totalled more than 80% of total abundance (mean 91.4%).

Monthly temperature and rainfall data were obtained from the meteorological stations closest to each site, and solar radiation from satellite data (<http://satel-light.com/>). Further climate indices to characterize the sites were calculated for both the whole year and, where appropriate, for the main growing season. Climate variables used in the analysis were rainfall, temperature, potential evapotranspiration (PET), the ratio between rainfall and PET (rainfall/PET), growing degree days (GDD), Thornwaite's Aridity Index (Thornwaite 1948), solar radiation and, as a further surrogate for temperature, latitude. Further details are in Garnier *et al.* (2007). Fertility was represented in the analysis by total soil nitrogen, extractable phosphorus, vegetation nitrogen content, maximum above-ground live biomass and annual net primary productivity (difference between minimum and maximum above-ground live biomass, NPP). Other variables were soil water-holding capacity, disturbance index (calculated as percentage biomass removed by management per year), presence of woodland cover, presence and intensity of grazing

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

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

**Table 2.** Significant ( $P < 0.05$ ) relationships (slope, Wald/d.f.,  $\chi^2$  probability and percentage variance explained for the site and site-treatment strata) between log mean seed mass weighted by abundance or unweighted and environmental and management variables from residual maximum likelihood analysis. Probabilities = 0.05 are shown in bold. Results of all analyses are shown in Appendix S1

Weighting	Environmental variable	Slope	Wald/d.f.	P	% Variance explained	
					Site	Site treatment
Expectation 1						
Unweighted	Annual PET (mm)	0.00060	3.7	<b>0.028</b>	18.63	0.21
Expectation 2						
Weighted	Latitude (°)	-0.02695	4.62	<b>0.016</b>	24.84	0.29
	Annual solar radiation (MJ m <sup>-1</sup> year <sup>-1</sup> )	1.58E-05	5.44	<b>0.010</b>	26.70	0.32
	Growing-season solar radiation (MJ m <sup>-1</sup> year <sup>-1</sup> )	5.99E-05	5.15	<b>0.012</b>	30.16	0.18
Unweighted	Mean annual temperature (°C)	0.03128	2.8	<b>0.047</b>	12.80	0.19
	Annual GDD	0.00011	2.74	<b>0.049</b>	11.82	0.17
	Latitude (°)	-0.02486	6.86	<b>0.005</b>	35.39	0.25
	Annual solar radiation (MJ m <sup>-1</sup> year <sup>-1</sup> )	1.39E-05	7.01	<b>0.004</b>	34.09	0.19
	Growing-season solar radiation (MJ m <sup>-1</sup> year <sup>-1</sup> )	5.06E-05	5.74	<b>0.009</b>	32.90	0.14
Expectation 3						
Unweighted	Leaf N content (mg g <sup>-1</sup> )	-0.00623	4.76	<b>0.030</b>	4.92	5.15
Expectation 4						
Weighted	Disturbance index (% biomass removed)	-0.00545	9.01	<b>0.002</b>	6.38	16.90
Expectation 5						
Weighted	Grazing index (% biomass removed)	-0.00383	3.3	<b>0.035</b>	2.96	6.00
	Grazed (0/1)	*	8.87	<b>0.002</b>	11.16	15.12
Expectation 6						
Weighted	Vegetation height (cm)	0.00344	9.35	<b>0.001</b>	11.15	15.90
	Woodland (0/1)	*	6.95	<b>0.004</b>	0.00	17.43
Unweighted	Vegetation height (cm)	0.00193	5.34	<b>0.011</b>	10.47	8.77
	Woodland (0/1)	*	7.87	<b>0.003</b>	1.11	17.12

GDD, growing degree days; NPP, net primary productivity; PET, potential evapotranspiration.

\*, not applicable.

(calculated as percentage biomass removed each year by grazing) and vegetation height (weighted mean height of species within the vegetation). Further details on methodology have been presented by Garnier *et al.* (2007).

## STATISTICAL ANALYSIS

Statistical analysis was carried out using Residual Maximum Likelihood (Genstat, Rothamsted, UK; Lawes Agricultural Trust 2002), a form of linear mixed modelling. Because plot choice was restricted by site choice and land use change transitions (treatments) were replicated within sites (but not between sites), all analyses were carried out with treatment nested within site as a random factor and, individually, the climate, soil and management variables as fixed factors. When expectations were directional, a one-tailed test was used. Analysis was carried out on the mean of the species' log-seed mass (unweighted) and on the mean weighted by species abundance. The proportion of species possessing a certain dispersal mechanism (unweighted) or the weighted proportion of the vegetation with that dispersal mechanism were subject to analysis after arcsine square-root transformation. The following dispersal classes were included in the analysis: anemochory, endozoochory, exozoochory, dispersal by hoarding vertebrates and unassisted. A grouped mechanism, the sum of endozoochory, exozoochory and hoarding, was created to cover all vertebrate-dispersed seeds. The percentage of variance explained within each stratum of the analysis was calculated. Only significant relationships are shown in Tables 2 and 3. However, the results for all the tested relationships are shown in Appendix S1.

The slopes of the cross-species and abundance-weighted relationships (seed mass and dispersal mechanisms separately) were then compared using a linear regression (Ackerly 1999) after standardization. To allow comparison between relationships derived for environmental variables with different units, the regression coefficients were recalculated from the data after a transformation resulting in the minimum and maximum values on both axes being set to 0 and 1, respectively (i.e. subtraction of the minimum followed by division by their range). The relationship between these points was then compared to reduced major axis regression, because both variables were subject to sampling and measurement error and neither could be seen as the dependent variable (Bohonak & van der Linde 2004). The comparison for dispersal mechanisms excluded the synthesized total vertebrate-dispersed category because this was not independent of the categories summed to produce it.

## Results

### SEED MASS, CLIMATE, FERTILITY AND DISTURBANCE

#### *Expectation 1: Seed mass increases in drier habitats*

Weighted mean seed mass was unrelated to any measure of site dryness (rainfall, aridity, PET, ratio of rainfall to PET) over the growing season or over the whole year, whilst unweighted seed mass significantly increased as annual PET increased (slope = 0.0006 mm<sup>-1</sup>, site variance explained (SVE)

**Table 3.** Significant ( $P < 0.05$ ) relationships (slope, Wald/d.f.,  $\chi^2$  probability and percentage variance explained for the site and site-treatment strata) between arcsine square-root-transformed proportions of species displaying different dispersal mechanisms weighted by abundance or unweighted and environmental and management variables from residual maximum likelihood analysis. Probabilities = 0.05 are shown in bold. All analyses are shown in Appendix S1.

					% Variance explained	
		Slope	Wald/d.f.	P	Site	Site treatment
Expectation 7						
Exozoochory (weighted)	Soil WHC (cm <sup>3</sup> cm <sup>-3</sup> )	0.003249	4.03	<b>0.023</b>	20.09	0.00
Endozoochory (weighted)	Annual PET (mm)	-0.000349	3.28	<b>0.035</b>	15.84	0.42
Endozoochory (unweighted)	Soil WHC (cm <sup>3</sup> cm <sup>-3</sup> )	-0.00322	6.3	<b>0.006</b>	11.75	1.08
	Annual aridity index	-0.00262	3.99	<b>0.023</b>	20.49	0.00
	Annual PET (mm)	-0.00036	10.65	<b>&lt; 0.001</b>	47.52	0.00
	Annual rainfall/PET	0.08248	4.21	<b>0.020</b>	21.76	0.38
Hoarding (unweighted)	Annual aridity index	0.000778	3.36	<b>0.034</b>	11.75	1.84
	Growing-season aridity index	0.000983	3.67	<b>0.028</b>	14.21	1.81
	Annual PET (mm)	9.57E-05	5.64	<b>0.009</b>	27.66	1.30
	Growing-season PET (mm)	0.000247	8.53	<b>0.002</b>	44.48	0.00
	Annual rainfall/PET	-0.02807	5.2	<b>0.012</b>	27.18	0.52
Vertebrate dispersal (weighted)	Growing-season rainfall/PET	0.2461	3.95	<b>0.024</b>	23.21	0.00
Expectation 8						
Exozoochory (weighted)	Soil total N (mg g <sup>-1</sup> )	0.1512	2.71	<b>0.050</b>	22.57	0.00
	Standing live biomass (g m <sup>-2</sup> )	0.000393	3.49	<b>0.031</b>	36.86	6.99
	Above-ground NPP (g m <sup>-2</sup> d <sup>-1</sup> )	0.03733	8.06	<b>0.003</b>	39.92	14.07
Endozoochory (weighted)	Above-ground NPP (g m <sup>-2</sup> d <sup>-1</sup> )	-0.02489	3.55	<b>0.030</b>	34.60	4.74
Endozoochory (unweighted)	Leaf N content (mg g <sup>-1</sup> )	-0.0038	4.68	<b>0.030</b>	10.26	53.46
Vertebrate dispersal (weighted)	Soil total N (mg g <sup>-1</sup> )	0.2249	3.8	<b>0.026</b>	26.73	0.00
Vertebrate dispersal (unweighted)	Leaf N content (mg g <sup>-1</sup> )	-0.00522	12.71	<b>&lt; 0.001</b>	1.18	51.01
Expectation 9						
Unassisted dispersal (unweighted)	Disturbance index (% biomass removed)	0.002142	4.43	<b>0.018</b>	4.37	9.21
Expectation 10						
Endozoochory (unweighted)	Vegetation height (cm)	-0.00181	7.03	<b>0.004</b>	25.22	0.00
Hoarding (weighted)	Grazing index (% biomass removed)	0.001457	6.17	<b>0.007</b>	0.33	12.97
	Grazed (0/1)	*	5.31	<b>0.011</b>	0.00	12.48
Vertebrate dispersal (weighted)	Vegetation height (cm)	-0.002083	3.47	<b>0.032</b>	0.00	11.94
Vertebrate dispersal (unweighted)	Grazing index (% biomass removed)	-0.0014	4.75	<b>0.015</b>	0.00	7.36
	Grazed (0/1)	*	2.7	<b>0.050</b>	0.00	7.15

NPP, net primary productivity; PET, potential evapotranspiration; WHC, water-holding capacity.

\*, not applicable.

= 18.6%, Table 2) but was similarly not significantly related to other measures of site dryness (Appendix S1).

#### **Expectation 2: Seed mass should increase with increasing temperature**

Weighted seed mass was significantly negatively correlated with latitude (slope =  $-0.027^{\circ-1}$ , SVE = 24.8, Fig. 1a), positively correlated to solar radiation (either annual, slope =  $1.58 \times 10^{-5} \text{ MJ}^{-1}$ , SVE = 26.7; or across the growing season, slope =  $5.99 \times 10^{-5} \text{ MJ}^{-1}$ , SVE = 30.2, Table 2) and unrelated to mean temperature or GDD. Unweighted seed mass showed the same relationships (latitude slope =  $-0.025^{\circ-1}$ , SVE = 35.4; annual solar radiation slope =  $1.39 \times 10^{-5} \text{ MJ}^{-1}$ , SVE = 34.1; growing solar radiation season slope =  $5.06 \times 10^{-5} \text{ MJ}^{-1}$ , SVE = 32.9, Fig. 1b), but also increased with mean annual temperature (slope =  $0.031^{\circ-1}$ , SVE = 12.8) and annual growing degree days (slope =  $0.0001^{\circ-1}$ , SVE = 11.8). There was no significant relationship between unweighted seed mass and growing-

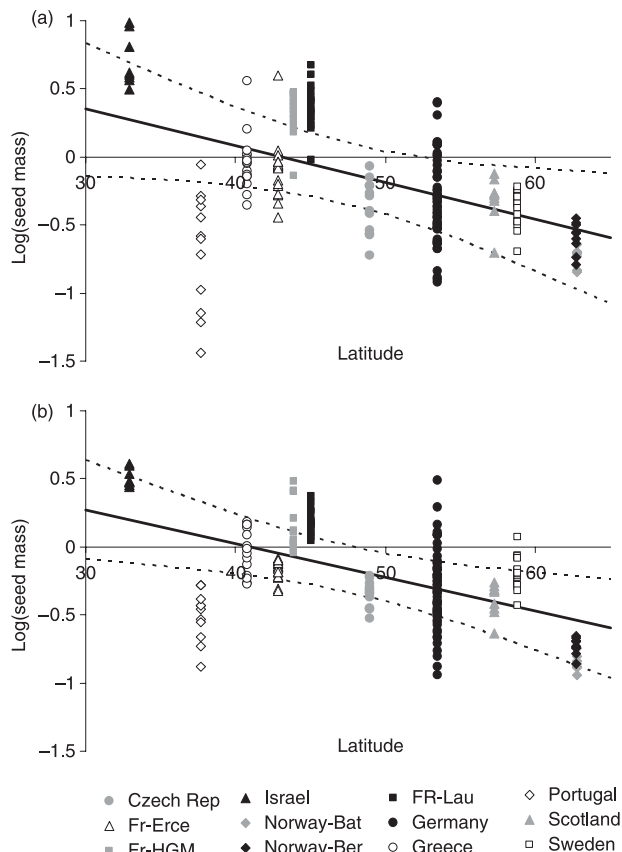
season mean temperature. Variance explained was consistently higher for the unweighted relationships.

#### **Expectation 3: No effect of fertility on seed mass**

There was no relationship between the available fertility measures (leaf nitrogen, soil nitrogen, soil phosphorus, above-ground biomass or productivity) and weighted mean seed mass. Unweighted seed mass declined with increased leaf nitrogen content (slope =  $-0.0062 \text{ mg}^{-1}$ , SVE = 4.9, site-treatment variance explained (STVE) = 5.2, Table 2), but was not significantly related to the other fertility measures (Appendix S1).

#### **Expectation 4: Seed mass should be smaller where persistence is an advantage (i.e. in systems where disturbance is regular)**

There was a significant, negative relationship between the intensity of management (disturbance index) and weighted



**Fig. 1.** Relationship between log seed mass (mg) and latitude (°) for (a) weighted and (b) unweighted data for the 12 sites. The fitted relationship from residual maximum likelihood (REML) is shown by an unbroken line, and its 95% confidence intervals by broken lines.

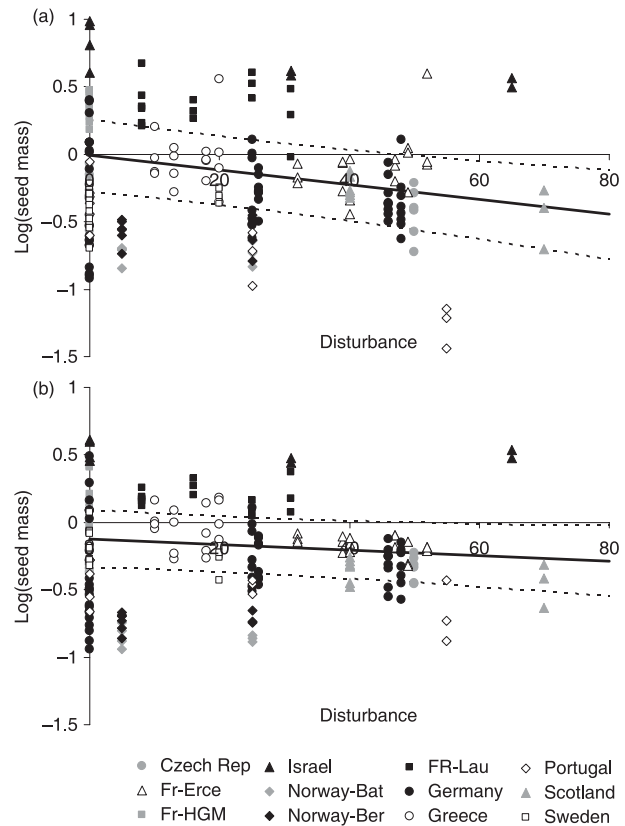
seed mass, which explained 17% of the variance at the site-treatment level (slope =  $-0.0055\%^{-1}$ , Table 2, Fig. 2a). This was not repeated in the analysis of the unweighted data (Fig. 2b, Appendix S1).

**Expectation 5: Seed mass should decline as grazing intensity increases**

Similarly, as grazing intensity increased weighted seed mass significantly declined (slope =  $-0.0038\%^{-1}$ , SVE = 3.0, STVE = 6.0) but there was no significant decline in unweighted seed mass (Table 2). Weighted seed mass was also significantly lower on sites subject to grazing ( $-0.227 \pm 0.131$  (1 SE),  $n = 106$ ) than on ungrazed sites ( $-0.0134 \pm 0.132$ ,  $n = 88$ ). Back-transformed, these values represent 0.593 mg and 0.969 mg, respectively.

**Expectation 6: Seed mass should increase with increasing shade or vegetation height**

Both weighted (slope =  $0.0034 \text{ cm}^{-1}$ , SVE = 11.2, STVE = 15.9) and unweighted (slope =  $0.0019 \text{ cm}^{-1}$ , SVE = 10.5, STVE = 8.8) seed mass significantly increased with increasing mean vegetation height (Table 2). As stated earlier, neither was related to



**Fig. 2.** Relationship between log seed mass (mg) and disturbance intensity (% biomass removed annually) for (a) weighted and (b) unweighted data for the 12 sites. The fitted relationship from residual maximum likelihood (REML) is shown by an unbroken line, and its 95% confidence intervals by broken lines.

above-ground biomass or productivity. Weighted mean seed mass was also significantly higher in woodland sites ( $0.0489 \pm 0.151$  (1 SE),  $n = 37$ ) than in open sites ( $-0.169 \pm 0.136$ ,  $n = 157$ ). Back-transformed, these values represent 1.119 mg and 0.678 mg, respectively. Unweighted seed mass was also significantly higher in woodland ( $-0.036 \pm 0.117$ ) than in the open ( $-0.196 \pm 0.108$ ). Back-transformed, these were 0.920 mg and 0.637 mg, respectively.

**DISPERSAL, CLIMATE, FERTILITY AND DISTURBANCE**

**Expectation 7: Zoochory is more frequent on soils with a high water content or in sites with higher rainfall**

Only three of the possible 36 relationships (four dispersal mechanisms – exozoochory and endozoochory, hoarding, vertebrate dispersal – by nine measures of water availability) were significant from the analysis of weighted data, and nine from the unweighted data (Table 3). Both of these proportions were in excess of the expected Type I error rate. The only relationship consistent for both weighted and unweighted data was the negative relationship between annual PET and the proportion of endozoochory (weighted slope =  $-0.00035 \text{ mm}^{-1}$ , SVE = 15.8; unweighted slope =  $-0.00036 \text{ mm}^{-1}$ , SVE = 47.5).

Exozoochory (weighted) was positively correlated to soil water-holding capacity (slope =  $0.0032 \text{ cm}^{-3}$ , SVE = 20.1), whilst endozoochory (unweighted) was negatively related (slope =  $-0.0032 \text{ cm}^{-3}$ , SVE = 11.8). There was also a positive relationship between vertebrate dispersal (weighted slope =  $-0.0025$ , SVE = 44.5) and endozoochory (unweighted slope =  $0.082$ , SVE = 21.8), with the ratio of rainfall to PET over the growing season and endozoochory (unweighted) negatively related to aridity (slope =  $-0.0026 \text{ cm}^{-3}$ , SVE = 20.5). The unweighted proportion of species dispersed by hoarding appeared to be related relatively consistently to drier sites: it had five significant relationships (annual aridity index slope =  $0.00078$ , SVE = 11.75; growing-season aridity index slope =  $0.00098$ , SVE = 14.21; annual PET slope =  $9.75 \times 10^{-5} \text{ mm}^{-1}$ , SVE = 27.7; growing-season PET slope =  $0.00025 \text{ mm}^{-1}$ , SVE = 44.5; annual rainfall/PET slope =  $-0.028$ , SVE = 27.2). Endozoochory was more common on wetter sites. All other relationships were not significant (Appendix S1).

#### Expectation 8: Zoochory is more frequent in more fertile sites

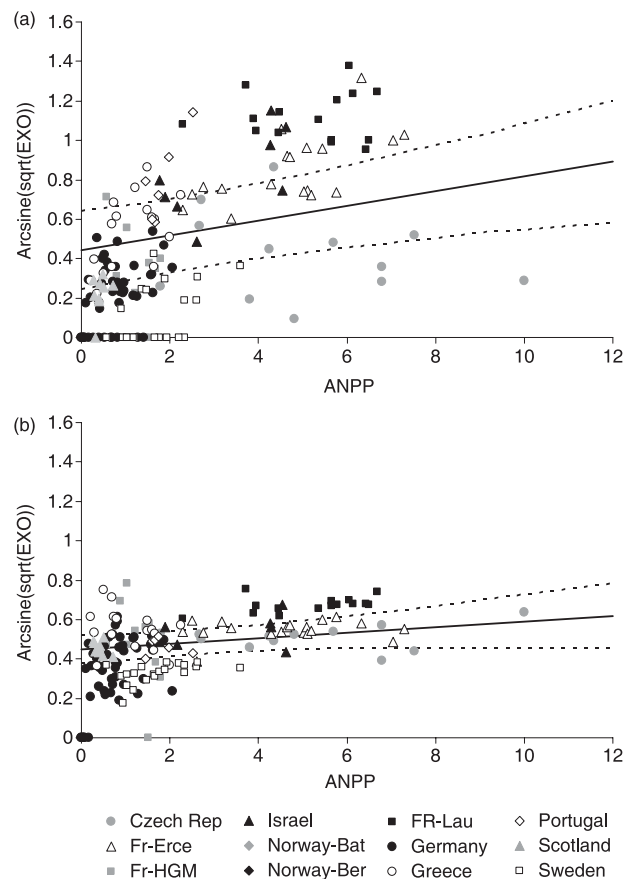
Of the 20 possible relationships between the dispersal mechanisms (four) and the measures of soil fertility (five), five were significant for the weighted data and two for the unweighted data (Table 3). Exozoochory (weighted) was positively related to soil nitrogen (slope =  $0.15 \text{ mg}^{-1}$ , SVE = 22.6), live biomass (slope =  $0.00039 \text{ g}^{-1}$ , SVE = 36.9, STVE = 7.0) and net primary productivity (slope =  $0.037 \text{ g}^{-1}$ , SVE = 39.9, STVE = 14.1, Fig. 3). Endozoochory was negatively related to leaf nitrogen (unweighted slope =  $-0.0038 \text{ mg}^{-1}$ , SVE = 10.3, STVE = 53.5) and to net primary productivity (weighted slope =  $-0.025 \text{ g}^{-1}$ , SVE = 34.6, STVE = 4.7). Following endozoochory, unweighted vertebrate dispersal was negatively related to leaf nitrogen (slope =  $-0.0052 \text{ mg}^{-1}$ , SVE = 1.2, STVE = 51.0), whilst weighted vertebrate dispersal followed exozoochory in being positively related to soil nitrogen (slope =  $0.22 \text{ mg}^{-1}$ , SVE = 26.7, STVE = 0). Other relationships between exozoochory, endozoochory and vertebrate dispersal with site fertility measures were not significant, and hoarding appeared completely unrelated to site fertility (all 10 relationships were non-significant, Appendix S1).

#### Expectation 9: Unassisted dispersal should be more common in disturbed habitats

There was a significant positive relationship between disturbance index and the proportion of the species showing unassisted dispersal (slope =  $0.0021\%^{-1}$ , SVE = 4.4, STVE = 9.2) but this was not replicated for the weighted data.

#### Expectation 10: Zoochory should be more common in grazed habitats

The weighted data suggested that hoarding was more common on grazed areas (2.44%) than on ungrazed plots (0.123%) but this pattern was not repeated with the unweighted data (Table 3). There was a reduction in unweighted, but not



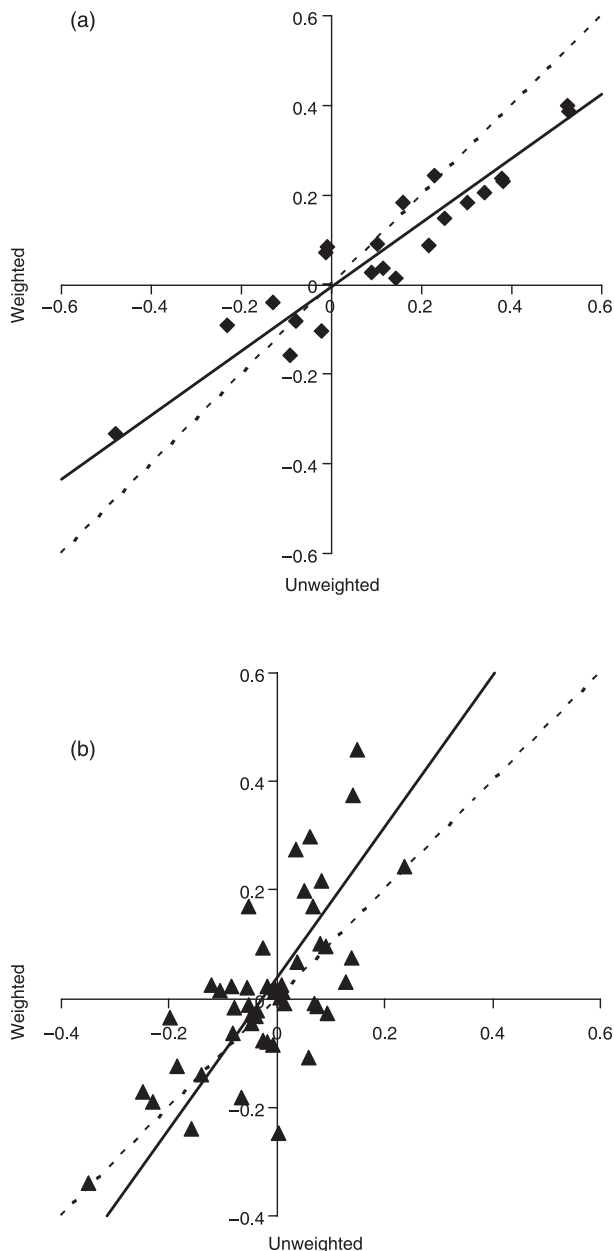
**Fig. 3.** Relationship between proportion of exozoochorous dispersed seeds and annual net above-ground primary productivity (ANPP,  $\text{g m}^{-2} \text{ day}^{-1}$ ) for (a) weighted and (b) unweighted data for the 12 sites. The fitted relationship from residual maximum likelihood (REML) is shown by an unbroken line, and its 95% confidence intervals by broken lines.

weighted, vertebrate dispersal with the intensity of grazing; it was lower on grazed plots (29.2%) than on ungrazed ones (32.6%). Presence of grazers had no significant effect on the proportion of seeds dispersed by endozoochory or exozoochory. Increased grazing resulted in more seed dispersed by hoarding (weighted slope =  $0.0015\%^{-1}$ , SVE = 0.3, STVE = 13.0; unweighted not significant), less by vertebrate dispersal overall (unweighted slope =  $-0.0014\%^{-1}$ , SVE = 0, STVE = 7.4; weighted not significant), and was not significantly related to endozoochory or exozoochory. The level of dispersal by endozoochory (unweighted slope =  $-0.0018 \text{ cm}^{-1}$ , SVE = 25.2, STVE = 0; weighted not significant) and vertebrate dispersal (weighted slope =  $-0.0008 \text{ cm}^{-1}$ , SVE = 0, STVE = 11.4; unweighted not significant) were negatively correlated with the height of the vegetation. Vegetation height was unrelated to the proportion of plants dispersed by exozoochory or hoarding.

#### Expectation 11: Anemochory should be less common in sheltered habitats such as woodland and scrub

There was no significant difference in the proportion of the vegetation with wind-dispersed seeds within and outside woodlands for both the weighted and unweighted analyses.





**Fig. 4.** Comparison of regression coefficients from relationships of (a) log seed mass and (b) dispersal by endozoochory, exozoochory and hoarding with environmental variables from the tests for expectations. The regression lines produced from reduced major axis regression are shown as unbroken lines, whilst the 1 : 1 line is shown by a broken line.

#### WEIGHTED AND UNWEIGHTED ANALYSES

There was a consistent relationship between the regression coefficients produced by the separate analyses of the weighted and unweighted seed-mass data (Fig. 4a;  $R^2 = 0.89$ ,  $P < 0.01$ ). The effect of weighting was to generally reduce the slope of the tested relationships (Table 2, Appendix S1) by a factor of  $0.714 (\pm 0.053, 1 \text{ SE})$ . In general, the impact of an environmental variable on seed mass was reduced after weighing the data by abundance. However, there was no difference in the

slopes for latitude (Fig. 1) and a substantially higher slope for the relationship between weighted seed mass and disturbance than that for unweighted seed mass (Fig. 2).

Similarly, there was a significant relationship between the regression coefficients produced from the analysis of regression coefficients from the weighted and unweighted dispersal data (Fig. 4b;  $R^2 = 0.48$ ,  $P < 0.01$ ). However, the effect of the weighting was generally to increase the slope of the tested relationship, in this case by an average of  $1.39 (\pm 0.105, 1 \text{ SE})$  (Table 3, Appendix S1, Fig. 3).

## Discussion

#### SEED MASS, CLIMATE, FERTILITY AND DISTURBANCE

There appeared to be little support for Expectation 1 (Table 2) – that seed mass was higher in drier climates – although the one significant relationship (unweighted seed mass with annual PET) was positive (cf. Leishman & Westoby 1994a; Wright & Westoby 1999). There was substantially more evidence that seed size was higher at warmer sites (Expectation 2), and with good explanatory power from a number of variables (Buckley 1982). However, Fig. 1 reveals a high degree of differences within site and substantial differences from expected findings for some sites – especially the Portuguese site, which had much smaller seeds than expected. This might indicate that the vegetation of the abandoned sites has a high degree of carry-over from the previous arable management. The relatively low number of significant results may be a result of the low statistical power available, and hence high Type 2 error possibilities (only 12 sites figured in the analysis).

There was little support for a relationship between fertility and seed mass (Expectation 3), with only one significant (negative) relationship between unweighted seed mass and leaf nitrogen content. Therefore, the analysis adds some weight to the evidence supporting the absence of an effect of fertility on seed mass (Westoby *et al.* 1990; Hammond & Brown 1995; Wright & Westoby 1999; Pakeman 2004).

Most of the tests carried out relating to Expectations 4–6 were confirmatory. A higher level of disturbance was associated with a decrease in mean seed mass (Expectation 4, weighted data only), indicating support for the link between seed mass and bet hedging through persistence in the soil – at least for the vegetation of Europe (Hodkinson *et al.* 1998; Thompson 1987, 2000; Venable & Brown 1988; Lavorel *et al.* 1994; Rees 1996; Leishman *et al.* 2000; Schippers *et al.* 2001). Seed mass did decrease with grazing intensity (Expectation 5, weighted data only) and was higher on sites that were ungrazed. This agrees with some experimental findings (Reader 1993; Eriksson & Eriksson 1997; Kahmen *et al.* 2002; Sternberg *et al.* 2003). Higher seed mass was also a feature of taller vegetation and woodland sites (weighted and unweighted). Thus, the vegetation-level data confirm observations based on cross-species analysis for many areas of the world (Leishman *et al.* 2000) and in many physiological studies (Expectation 6). Variances explained in the analyses for these expectations were generally low, indicating that fitting more complex models with climate involved might be profitable.

## DISPERSAL, CLIMATE, FERTILITY AND DISTURBANCE

There was conflicting evidence for Expectation 7. The results indicated that endozoochory was more common in wetter sites (as predicted), but that hoarding was more frequent on drier sites. This pattern, and the general lack of relationship between exozoochory and moisture, resulted in no significant relationship between zoochory and site moisture. Expectation 7 is therefore too general to be of use. There was confirmation for higher levels of exozoochory at higher fertility levels, but lower levels of endozoochory. Thus Expectation 8 may need further refining to cover different aspects of zoochory. As with the seed-mass analysis, the low number of significant results may be caused by the low statistical power available from the 12 sites in the analysis.

The proportion of the vegetation dispersed with no apparent adaptation was higher on disturbed sites (for the unweighted analysis), in part agreeing with Expectation 9. Anemochory was unrelated to the presence of woodland (Expectation 11); it was possible that the scrub and woodland communities surveyed were of too recent development to have fully acquired a ground flora characteristic of established woodland (Graae & Sunde 2000; Verheyen *et al.* 2003). Zoochory appeared little related to grazing, disturbance or vegetation height (Expectation 10), although hoarding was more common on grazed sites; it may be that grazing animals facilitate the trophic interactions between the plant species that produce seeds with this dispersal mechanism and the small mammals that hoard seeds. Where significant relationships existed (Table 3), it appeared that other types of zoochory were less common where land was managed by grazing, contrary to the predictions of Expectation 10 (cf. Eriksson *et al.* 2000). Exozoochory and endozoochory may only be viable dispersal mechanisms in vegetation where full seed/fruit development is allowed to take place, i.e. where grazing is not removing sufficient biomass to reduce reproductive output.

## IMPACT OF WEIGHTING BY ABUNDANCE ON SEED MASS AND DISPERSAL RELATIONSHIPS WITH THE ENVIRONMENT

The impact of weighting the analysis by abundance was, on average, to reduce the sensitivity of seed mass to the environment parameters tested: the regression had a slope significantly less than 1. This was not consistent for the climate or fertility indicators (Expectations 1–3), because points occurred both above and below the 1 : 1 line, but was consistent for indicators of land use (Expectations 4–6), where the points were all above the 1 : 1 line. The overall pattern suggests that, on average, differences in this trait between dominant species (i.e. those with a high weighting) along environmental gradients were smaller than between subordinate species, although the opposite appeared to be true only when land-use indicators were considered. The relatively small number of significant relationships must make any conclusions regarding the impacts of weighting seed mass tentative.

Conversely, the impact of weighting by abundance made the proportion of species displaying a different form of zoochory more sensitive to the environmental parameters tested: the slope of the regression was significantly steeper than 1. Differences in the dispersal traits of dominant species along the environmental gradients tested were greater than those for subordinate species. Again, there was considerable spread, so that many points lay below the 1 : 1 line. This and the relatively small number of significant relationships must make any conclusions regarding the impacts of weighting dispersal mechanisms by abundance similarly tentative.

This analysis adds further evidence to the correlation between seed mass and temperature (larger seeds at higher temperatures), and seed mass and management (smaller seeds with more disturbance). However, weighting by abundance reduced the number of significant relationships with climate, whilst it increased the number of significant management relationships. This, and the relative slopes of the weighted and unweighted relationship, may indicate that this trait is correlated with climate at the species level, but that dominance within a system is more associated with this trait's relationship with management. There was some evidence that endozoochory was associated with wetter sites, hoarding with drier sites and exozoochory with more fertile ones. Weighting by abundance reduced the number of significant relationships, which suggests that correlations between dispersal mechanism and climate and fertility might be relatively independent of dominance. However, the slope of the regression in Fig. 4b indicates that the dominant species might be more responsive than average to the environment.

The analysis described in this article clearly shows that weighting by species in abundance can produce different relationships between plant traits and environmental variables compared to unweighted analyses. The effect of weighting was different for the expectations related to seed mass compared to those for dispersal mechanisms, which indicates that the effects of weighting may not be universal or predictable. The impact of weighting increased the number of significant relationships with management variables and decreased those for climate variables, indicating that a choice of whether to opt for a weighted or an unweighted analysis depends on whether abundance in the vegetation, or just the occurrence of that particular plant, is important.

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## References

- Aarssen, L.W. & Jordan, C.Y. (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience*, **8**, 471–477.

- Ackerly, D.D. (1999) Comparative plant ecology and the role of phylogenetic information. *Physiological Plant Ecology* (eds M.C. Press, J.D. Scholes & M.G. Barker), pp. 391–413. Blackwell Scientific Publications, Oxford.
- Black, H.G. (1958) Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum*) with particular reference to leaf area and the light microclimate. *Australian Journal of Agricultural Research*, **9**, 299–318.
- Bohonak, A.J. & van der Linde, K. (2004) *RMA: Software for Reduced Major Axis Regression, Java Version*, San Diego. <http://www.kimvdlinde.com/professional/index.html>.
- Bolmgren, K. & Eriksson, O. (2005) Fleshy fruits – origins, niche shifts, and diversification. *Oikos*, **109**, 255–272.
- Buckley, R.C. (1982) Seed size and seedling establishment in tropical arid dunecrest plants. *Biotropica*, **14**, 314–315.
- Coomes, D.A., Rees, M., Grubb, P.J. & Turnbull, L. (2002) Are differences in seed mass among species important in structuring plant communities? Evidence from analyses of spatial and temporal variation in dune-annual communities. *Oikos*, **96**, 421–432.
- Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Dieckmann, U., O'Hara, B. & Weisser, W. (1999) The evolutionary ecology of dispersal. *Trends in Ecology and Evolution*, **14**, 88–90.
- Eriksson, O., Friis, E.M. & Lofgren, P. (2000) Seed size, fruit size, and dispersal systems in angiosperms from the early cretaceous to the late tertiary. *American Naturalist*, **156**, 47–58.
- Eriksson, A. & Eriksson, O. (1997) Seedling recruitment in semi-natural pastures: the effects of disturbance, seed size, phenology and seed bank. *Nordic Journal of Botany*, **17**, 469–482.
- Fenner, M. & Thompson, K. (2005) *The Ecology of Seeds*. Cambridge University Press, Cambridge.
- Fernández Alés, R., Laffarga, J.M. & Ortega, F. (1993) Strategies in Mediterranean grassland annuals in relation to stress and disturbance. *Journal of Vegetation Science*, **4**, 313–322.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J. *et al.* (2007) A standardized methodology to assess the effects of land use change on plant traits, communities and ecosystem functioning in grasslands. *Annals of Botany*, **99**, 967–985.
- Graae, B.J. & Sunde, P.B. (2000) The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography*, **23**, 720–731.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–910.
- Grime, J.P. (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science*, **17**, 255–260.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology*. Unwin-Hyman, London.
- Grime, J.P. & Jeffrey, D.W. (1965) Seedling establishment in vertical gradients of sunlight. *Journal of Ecology*, **53**, 621–642.
- Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H. *et al.* (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259–281.
- Hammond, D.S. & Brown, V.K. (1995) Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. *Ecology*, **76**, 2544–2561.
- Hodkinson, D.J., Askew, A.P., Thompson, K., Hodgson, J.G., Bakker, J.P. & Bekker, R.M. (1998) Ecological correlates of seed size in the British Flora. *Functional Ecology*, **12**, 762–766.
- Hughes, L., Dunlop, M., French, K., Leishman, M.R., Rice, B., Rodgers, L. & Westoby, M. (1994) Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *Journal of Ecology*, **82**, 933–950.
- Jakobsson, A. & Eriksson, O. (2002) Seed size and frequency patterns of understory plants in Swedish deciduous forests. *Ecoscience*, **9**, 74–78.
- Jensen, K. & Gutekunst, K. (2003) Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic and Applied Ecology*, **4**, 579–587.
- Jurado, E. & Westoby, M. (1992) Seedling growth in relation to seed size among species of arid Australia. *Journal of Ecology*, **80**, 407–416.
- Kahmen, S., Poschlod, P. & Schreiber, K.-F. (2002) Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. *Biological Conservation*, **104**, 319–328.
- Kisdi, É. (2002) Dispersal: risk spreading versus local adaptation. *American Naturalist*, **159**, 579–596.
- Kostel-Hughes, F., Young, T.P. & Wehr, J.D. (2005) Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. *Journal of the Torrey Botanical Society*, **132**, 50–61.
- Kotorová, I. & Lepš, J. (1999) Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *Journal of Vegetation Science*, **10**, 175–186.
- Lavorel, S., O'Neill, R.V. & Gardner, R.H. (1994) Spatio-temporal dispersal strategies and annual plant species coexistence in a structure landscape. *Oikos*, **71**, 75–88.
- Lawes Agricultural Trust (2002) *Genstat® Release 6.1 Reference Manual*. Lawes Agricultural Trust, Rothamstead, UK.
- Leishman, M.R. (2001) Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos*, **93**, 294–302.
- Leishman, M.R. & Westoby, M. (1994a) The role of large seeds in seedling establishment in dry soil conditions – experimental evidence from semi-arid species. *Journal of Ecology*, **82**, 249–258.
- Leishman, M.R. & Westoby, M. (1994b) The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology*, **8**, 205–214.
- Leishman, M.R. & Westoby, M. (1998) Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Functional Ecology*, **12**, 480–485.
- Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. In: *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd edn (ed. M. Fenner), pp. 31–57. CABI Publishing, Wallingford, UK.
- Levin, S.A., Muller-Landau, H.C., Nathan, R. & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology and Systematics*, **34**, 575–604.
- Lusk, C.H. & Kelly, C.K. (2003) Interspecific variation in seed size and safe sites in a temperate rain forest. *New Phytologist*, **158**, 535–541.
- Maranon, T. & Grubb, P.J. (1993) Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Functional Ecology*, **7**, 591–599.
- Mazer, S.J. (1989) Ecological, taxonomic and life history correlates of seed mass among Indiana Dune angiosperms. *Ecological Monographs*, **59**, 153–175.
- Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A., Wood, J.T. & Westoby, M. (2007) Global patterns in seed size. *Global Ecology and Biogeography*, **16**, 109–116.
- Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B., Pitman, A.J. & Westoby, M. (2005) Factors that shape seed mass evolution. *Proceedings of the National Academy of Science*, **102**, 10540–10544.
- Moles, A.T., Falster, D.S., Leishman, M.R. & Westoby, M. (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology*, **92**, 384–396.
- Moles, A.T., Warton, D.I. & Westoby, M. (2003) Seed size and survival in the soil in arid Australia. *Austral Ecology*, **28**, 575–585.
- Moles, A.T. & Westoby, M. (2003) Latitude, seed predation and seed mass. *Journal of Biogeography*, **30**, 105–128.
- Moles, A.T. & Westoby, M. (2004) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, **92**, 372–383.
- Moussie, A.M. (2004) *Seed dispersal by large herbivores. Implications for the restoration of plant biodiversity*. PhD Thesis, Rijksuniversiteit Groningen, Groningen, The Netherlands.
- Murray, B.R., Brown, A.H.D., Dickman, C.R. & Crowther, M.S. (2004) Geographical gradients in seed mass in relation to climate. *Journal of Biogeography*, **31**, 379–388.
- Pakeman, R.J. (2004) Consistency of plant species and trait responses to grazing along a productivity gradient: a multi-site analysis. *Journal of Ecology*, **92**, 893–905.
- Pakeman, R.J. & Quested, H.M. (2007) Sampling plant functional traits: what proportion of the species need to be measured? *Applied Vegetation Science*, **10**, 91–96.
- Parolin, P. (2000) Seed mass in Amazonian floodplain forests with contrasting nutrient supplies. *Journal of Tropical Ecology*, **16**, 417–428.
- Poschlod, P., Kiefer, S., Trankle, U., Fischer, S. & Bonn, S. (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science*, **1**, 75–90.
- Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology*, **81**, 169–176.
- Reader, R.J. (1998) Relationship between species relative abundance and plant traits for an infertile habitat. *Plant Ecology*, **134**, 43–51.
- Rees, M. (1996) Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London – Series B*, **351**, 1299–1308.
- Salisbury, E.J. (1942) *The Reproductive Capacity of Plants*. G. Bell & Sons, London.
- Schippers, P., van Groenendaal, J., Vleeshouwers, L.M. & Hunt, R. (2001) Herbaceous plant strategies in disturbed habitats. *Oikos*, **95**, 198–210.

- Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506.
- Sternberg, M., Gutman, M., Perevolotsky, A. & Kigel, J. (2003) Effects of grazing on soil seed bank dynamics: an approach with functional groups. *Journal of Vegetation Science*, **14**, 375–386.
- Thompson, K. (1987) Seeds and seed banks. *New Phytologist*, **106** (Suppl.), 23–34.
- Thompson, K. (2000) The functional ecology of seed banks. *Seeds. The Ecology of Regeneration in Plant Communities*, 2nd edn (ed. M. Fenner), pp. 215–236. CABI Publishing, Wallingford, UK.
- Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology*, **86**, 163–169.
- Thornwaite, C.W. (1948) An approach towards a rational classification of climate. *Geographical Review*, **38**, 55–89.
- Turnbull, L.A., Coomes, D., Hector, A. & Rees, M. (2004) Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology*, **92**, 97–109.
- Venable, D.L. (1992) Size–number tradeoffs and the variation of seed size with plant resource status. *American Naturalist*, **140**, 287–304.
- Venable, D.L. & Brown, J.S. (1988) The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risks in variable environments. *American Naturalist*, **131**, 360–384.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M. & Foster, D.R. (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology*, **91**, 563–577.
- Vesk, P.A., Leishman, M.R. & Westoby, M. (2004) Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology*, **41**, 22–31.
- Walters, M.B. & Reich, P.B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology*, **81**, 1887–1901.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.
- Westoby, M., Rice, B. & Howell, J. (1990) Seed size and plant growth form as factors in dispersal spectra. *Ecology*, **71**, 1307–1315.
- Willson, M.F., Rice, B.L. & Westoby, M. (1990) Seed dispersal spectra: a comparison of temperate plant communities. *Journal of Vegetation Science*, **1**, 547–562.
- Willson, M.F. & Traveset, A. (2000) The ecology of seed dispersal. In: *Seeds. The Ecology of Regeneration in Plant Communities*, 2nd edn (ed. M. Fenner), pp. 85–110. CABI Publishing, Wallingford, UK.
- Wright, I.J. & Westoby, M. (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology*, **87**, 85–97.

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## Supplementary material

The following supplementary material is available for this article:

**Appendix S1.** Statistical information on all tested relationships between the environment, seed mass and seed-dispersal mechanisms.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01336.x>

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