Effects of litter on seedling establishment in natural and semi-natural grasslands: a meta-analysis

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Summary

1. Plant litter is a key component in terrestrial ecosystems. It plays a major role in nutrient cycles and community organization. Land use and climate change may change the accumulation of litter in herbaceous ecosystems and affect plant community dynamics. Additionally, the transfer of seeds containing plant material (i.e. litter) is a widespread technique in grassland restoration.

2. Ecosystem responses to litter represent the outcome of interactions, whose sign and strength will depend on many variables (e.g. litter amount, seed size). A previous meta-analysis (from 1999) reported that litter had an overall negative effect on seed germination and seedling establishment in different ecosystems. However, recent studies indicated that this might not be the case in grassland ecosystems.

3. We used 914 data from 46 independent studies to analyse the effects of litter on seedling (i) emergence, (ii) survival and (iii) biomass, employing meta-analytical techniques. Each data set was stratified according to methodology, grassland type, irrigation conditions, litter amount and seed size.

4. We found an overall neutral effect of litter presence on seedling emergence and survival and a positive effect on seedling biomass. However, whereas for field experiments the response remained neutral, it was positive for common garden studies. In glasshouse experiments, litter effects were negative for emergence and positive for biomass.

5. Litter may have a positive effect on seedling recruitment in dry grasslands or under water-limited conditions, or in the presence of low to medium litter amounts (< 500 g m^{-2}). However, high litter amounts (> 500 g m^{-2}) will inhibit seedling recruitment. Large seeds showed a more positive response to litter presence with respect to seedling emergence and survival, but not concerning biomass.

6. *Synthesis*. Under dry conditions (e.g. dry grasslands or dry periods) or with low to medium litter amounts, litter presence has a positive effect on seedling establishment. However, climate and land use change may promote litter accumulation and reduce seedling establishment, affecting grasslands composition and ecosystem functions.

Key-words: after-death interactions, facilitation, grassland restoration, Hedges' d, plant recruitment, plant–plant interactions, seedling biomass, seedling emergence, seedling survival, stress-gradient hypothesis

Introduction

Grasslands are areas dominated by herbaceous vegetation with little or no tree cover. While natural grasslands occur in regions where climatic or soil conditions, or a combination of both, prevent tree growth, semi-natural grasslands are maintained by continuous anthropogenic use (Veen *et al.* 2009).

Both types are among the most common and largest ecosystems in the world, with an estimated area of 52.5 million square kilometres (Suttie, Reynolds & Batello 2005). They also support plant communities of high diversity and conservation value (Hansson & Fogelfors 2000; Critchley, Burke & Stevens 2004; Hodgson *et al.* 2005). Land use changes (i.e. the lack of regular mowing or grazing after abandonment, Moog *et al.* 2002; Quétier *et al.* 2007; Galvánek & Lepš 2012) but also climate change (i.e. increasing biomass production, Parton *et al.* 1995; Owensby *et al.* 1999; Díaz *et al.*

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2007) may result in the accumulation of litter (i.e. dead plant tissues) especially in grassland ecosystems (Parry *et al.* 2007). This in turn may hamper recruitment and affect the structure, diversity and dynamics of plant communities (Fowler 1986; Bergelson 1990; Facelli & Pickett 1991a; Špačková & Lepš 2004; Sayer 2006; Rasran, Vogt & Jensen 2007; Ruprecht *et al.* 2010a; Eckstein *et al.* 2011). Analogously, these effects of litter are of interest for the restoration of grassland communities through the transfer of plant material (Donath *et al.* 2007; Kiehl *et al.* 2010; Török *et al.* 2010; Schmiede, Otte & Donath 2012).

Plant litter supplies large amounts of substrate for decomposition (Ajtay, Ketner & Duvigneaud 1979; Aber & Melillo 1991) and thus plays an important role in biogeochemical nutrient cycles (Aerts & Chapin 1999). Litter decomposition may influence ecosystem productivity and community composition (Aerts & Chapin 1999; Quested *et al.* 2005). However, the accumulation of a litter layer may also have important effects on vegetation (Facelli & Pickett 1991a). These after-death interactions of vegetation may carry over from one generation to the next (Bergelson 1990; Facelli & Facelli 1993), indicating the role of litter as a temporal (i.e. the effect of litter on recruitment of future cohorts) and a spatial (i.e. the effect of heterogeneous accumulation of litter) factor in community organization (Facelli & Facelli 1993).

Litter acts through different mechanisms. It can act as a mechanical barrier to seedling emergence, interfering with seedling development and growth (Facelli & Pickett 1991b; Donath & Eckstein 2008; Ruprecht & Szabo 2012) or change physical conditions such as soil temperature and moisture regime and light quantity and quality (Holmgren, Scheffer & Huston 1997). Litter can also release allelochemicals (Bosy & Reader 1995; Ruprecht *et al.* 2008, 2010b), which may be toxic or act through reduction in the soil water potential (Barritt & Facelli 2001; Ruprecht *et al.* 2008), diminishing seed germination.

In a meta-analysis concerning the effect of litter on seed germination and seedling establishment in different ecosystems, Xiong & Nilsson (1999) reported an overall negative effect of litter. However, in grasslands and with grass litter, the effects ranged from strongly negative to slightly positive. Similarly, recent studies showed that litter may also exert facilitative effects on germination and survival (Quested & Eriksson 2006; Donath & Eckstein 2008). Litter has been reported as the primary factor controlling species richness and evenness in a dry fescue grassland (Lamb 2008), and Hovstad & Ohlson (2008) showed that litter effects are also species- and habitat-specific.

The effect of litter depends on environmental conditions. Its effect may vary across gradients of physical stress (Bertness & Callaway 1994) and, as proposed by the stress-gradient hypothesis (SGH), will be more important under extreme environmental conditions (Maestre *et al.* 2009). The SGH predicts that facilitative effects are more frequent and more intense under high-stress conditions (Brooker *et al.* 2005; Lortie & Callaway 2006), whereas competitive interactions prevail under favourable environmental conditions. In dry environments, or during droughts, the presence of a litter layer may maintain soil moisture, reduce the intensity of desiccation (Fowler 1986; Boeken & Orenstein 2001) and thus facilitate seedling establishment. This may change the structure and dynamics of plant communities due to differential species-specific recruitment during these periods (Facelli & Pickett 1991a).

However, effects of litter also depend on litter amount (Gross 1984; Wilsey & Polley 2003). Moderate litter amounts may support vegetation development by improving microsite conditions, that is, attenuating extremes in moisture and temperature (Fowler 1986; Jensen & Gutekunst 2003; Eckstein & Donath 2005; Deutsch, Bork & Willms 2010; Eckstein *et al.* 2012), and thus facilitating the performance of living vegetation (Brooker *et al.* 2008). However, facilitative effects are reduced, or even cease, when litter amounts are too high (Goldberg & Werner 1983; Tilman 1993; Foster & Gross 1997, 1998; Wardle, Bonner & Nicholson 1997; Xiong & Nilsson 1999). A thick litter layer may reduce light quantity and quality to conditions representing deep shade or darkness (Jensen & Gutekunst 2003; Eckstein & Donath 2005). Additionally, it can also prevent seeds from reaching the soil (Rotundo & Aguiar 2005; Donath & Eckstein 2010) and may create an impenetrable physical barrier for seedlings (Facelli & Pickett 1991b). However, during dry periods, the presence of a thicker litter layer may have more positive effects than that of a thinner litter layer (Eckstein & Donath 2005; Ruprecht *et al.* 2010b) by reducing air temperatures and creating a barrier to water diffusion (Facelli & Pickett 1991a).

Plant species responses to litter depend on seed traits (Fenner & Thompson 2005). Seedling performance is related to seed size (Leishman *et al.* 2000; Moles *et al.* 2006), which in turn influences seeds' mobility (Bekker *et al.* 1998; Burmeier *et al.* 2010; Donath & Eckstein 2010). Large seeds are caught more persistently within a litter cover, while small-seeded species can percolate through it (Donath & Eckstein 2010) and may potentially be incorporated in the permanent seed bank (Funes *et al.* 1999; Schmiede, Donath & Otte 2009). Additionally, large-seeded species are more likely to germinate and establish from beneath a dense litter layer and rapidly escape low-light conditions (Everham, Myster & Van De Genachte 1996; Křenová & Lepš 1996). This suggests that large-seeded species may better cope with a thicker litter layer.

The large amount of information gathered in recent years made it necessary to summarize these findings, with the aim to identify general global patterns in the response of grassland vegetation to the presence of litter. A deeper understanding of litter effects on the structure of grassland communities is crucial to predict possible consequences of land use change and climate change on plant diversity and composition in these ecosystems. Additionally, studying the effects of litter presence in grasslands and possible factors affecting their response will allow decision making for a correct management of these areas and also their biodiversity conservation and restoration.

In this work, we present the results of a meta-analysis testing the response of grassland plant species to litter accumulation. Three main questions were addressed:

1 Are there general patterns in the response of seedling (i) emergence, (ii) growth and (iii) survival of species to the presence of litter under different moisture conditions (i.e. different grassland types, different irrigation levels)?
2 Is there a tipping point with respect to the amount of litter where the sign of the litter effect changes?
3 Does the effect of litter vary in relation to seed size?

Materials and methods

DATA BASE AND SUITABILITY CRITERIA

We focused on published studies in grassland ecosystems or on grassland species, which explicitly manipulated litter cover and assessed the response of at least one of the following variables: seedling emergence, seedling survival or seedling above-ground biomass (hereafter denoted as emergence, survival and biomass). The available literature was screened using a search (search terms: 'plant litter' AND 'seed*' AND 'grassland') in the data base ISI Web of Science (© Thomson Reuters) for the period 1945–2012 (last search date: 01/08/2012). Additional studies were found using the reference lists of the sampled studies and in a previous meta-analysis on litter effects (Xiong & Nilsson 1999).

This primary search resulted in 387 papers. After carefully scanning through abstract, methods, figures and tables to decide whether these provided useful information, a total of 73 studies were retained. These were carefully read and selected for the present meta-analysis if they fulfilled the following criteria:

1 Plant litter was manipulated in herbaceous communities or under controlled conditions.
2 The response as compared to a control treatment without litter was reported in terms of at least one of the following stages of recruitment: (i) seedling emergence, (ii) seedling survival or (iii) seedling biomass.

Suitable studies should include mean values with some measure of dispersion and sample size, or include the raw data from which these could be calculated. In cases where not all information was available (e.g. lack of measure of dispersion), we contacted the authors of papers published within the last 15 years (i.e. from 1997 onwards) and asked for missing information or raw data. The same was done to gather additional information on covariates (see below). Studies that used artificial litter or simulated its presence through applying litter leachates or shade cloth were not included. As only one paper was conducted in germination chambers, it was discarded. If repeated measures over time were taken within a study, only a single measurement was included into the meta-analysis to assure independence of data (Gurevitch & Hedges 2001). In these cases, we used cumulated emergence or survival when available. Otherwise, the longer available period since the beginning of the study was used. If more than one publication presented results from the same experiment, the most recent paper was considered. For seedling survival and biomass, we also included data from seedlings transplants (i.e. individuals with 3–5 developed leaf). Finally, data from 46 studies were included into the present meta-analysis (see Appendix S1 in Supporting Information for details).

When available, we included multiple results from the same study. Although this may reduce overall heterogeneity, on the other hand exclusion of multiple results may underestimate effect size (Gurevitch & Hedges 1999). In cases where several species or litter types were used, or where the same experiment was carried out in different field sites, we treated these as separated data points. Likewise, when the litter manipulation was crossed with other treatments (e.g. irrigation levels, litter amount), each combination was treated as a separate data point. We included data where the only difference between control and treatment is the manipulation of litter. Several of these control vs. treatment comparisons shared the same control, which might increase data interdependence. However, not including this information may lead to a loss of information that would lead to more serious distortions of the effect size results (Gurevitch *et al.* 1992). A total of 914 data points were gathered: 66% on emergence, 8% on survival and 26% on biomass response.

In cases where data were only reported in graphical form, we used the software IMAGEJ (Abramoff, Magalhaes & Ram 2004) to extract the necessary information. To test the accuracy of the program, we performed a regression analysis between raw data from two of our own published papers (Donath & Eckstein 2008, 2010) and data extracted from these papers through IMAGEJ. A regression slope of 1.0013 ($R^2 = 0.9999$) demonstrates that extracting some data from graphs using IMAGEJ is a valid and accurate approach.

META-ANALYSIS PROCEDURE

We used Hedges' d (Rosenberg, Adams & Gurevitch 2000) as a measure of effect size. This index is calculated as the difference between means of treatment and control group, divided by the pooled standard deviation (SD) of the means and corrected for small sample size. If standard errors were reported, these were transformed to SDs. We considered samples without litter as control and samples with litter as treatment. Therefore, negative values of Hedges' d denote a negative effect of litter, whereas positive values indicate a positive effect. Coe (2002) pointed out that Hedges' g index, closely similar to Hedges' d used here (Rosenberg, Adams & Gurevitch 2000), is equivalent to a Z-score of a standard normal distribution. According to this work, an effect size of 2.5 corresponds to a probability of < 5% that a score sampled at random from the treatment group will be smaller than a score sampled from the control group (i.e. control and treatment are statistically different). Hedges' d was chosen to be able to compare our values with those of Xiong & Nilsson (1999). Hedges' d has some limitations (Gómez-Aparicio 2009), and another index, the response ratio, is considered to better estimate the difference in mean performance among treatments than Hedges' d. Consequently, we also calculated effect sizes for the complete data set (i.e. without covariates) using the natural log of response ratio index (lnRR) to test whether conclusions based on different indices deviate (see Appendix S2, Fig. S2).

We performed a random effect meta-analysis for each of the three data sets: (i) emergence, (ii) survival and (iii) biomass. In a random effect meta-analysis, for the calculation of the effect size, each data point effect size used is weighted according to their relative sampling error (i.e. variance) plus an estimate of the between-study variance (Rosenberg, Adams & Gurevitch 2000). In a first step, an overall effect size was calculated for each data set. Secondly, data sets were stratified according to three methodologies, that is, pot experiments, conducted either in glasshouse or in common gardens, or field experiments (except for survival data which only came from field studies). Analysis was performed when $n \geq 3$ data points. Finally,

data were further stratified according to four categorical grouping variables to address the specific questions outlined above. These categorical grouping variables were as follows:

1 grassland types (only field studies)
2 irrigation conditions (only common garden studies)
3 litter amount (all methodologies)
4 seed size (all methodologies)

Additionally, for litter amount and seed size, we performed meta-analysis without grouping according to the different methodologies employed (see Appendix S3, Figs S3-1 and S3-2) to compare the general response pattern with the pattern obtained for the different methodologies. Field studies were stratified according to the following grassland types: dry grassland, mesic grassland, flooded grassland and wetland. For common garden studies, irrigation conditions were stratified as low (pots were watered infrequently and fell intermittently dry) or high water availability (watered frequently to field capacity). Grassland type and irrigation treatment were used as proxies for moisture conditions. For litter amount, we only considered litter mass. Thus, studies reporting litter depth were omitted in this part of the analyses (e.g. Gross 1984). However, in some cases, we contacted the authors to be able to transform litter depth into litter mass (e.g. Donath, Hölzel & Otte 2006; Rasran, Vogt & Jensen 2007). Due to the nature of the information obtained, we considered litter amount as a categorical variable and not as quantitative. Consequently, we classified litter mass as low ($\leq$ 250 g m^{-2}), medium (250–500 g m^{-2}) and high (> 500 g m^{-2}), which corresponds to the amount of litter found in different grassland types (Tallowin 1999; Donath *et al.* 2004). Seed mass was stratified into species with small (< 1 mg) and large seeds (> 1 mg), which corresponds to mean seed size in different grassland types (Leishman, Westoby & Jurado 1995; Moles *et al.* 2006). We considered this a categorical variable, instead of continuous one, because the available information does not cover a continuous range of seed masses. Instead, > 80% of seed masses are below 3 mg and only very few species have larger seeds (3–15 mg), which will result in very poor meta-regression analyses (Cooper, Hedges & Valentine 2009). Information concerning all these covariates was extracted from the methods section of the respective studies. However, authors were contacted in case of doubt. If it was not reported, information about seed size was taken from the Seed Information Database (Royal Botanic Gardens Kew 2008). We also analysed the combinations of litter amount with grassland type or irrigation conditions. Unfortunately, further grouping with different covariates was not possible due to the lack or scarcity of data, which would make the results of such an analysis unreliable.

All meta-analyses were conducted using META-WIN 2.0 (Rosenberg, Adams & Gurevitch 2000). Differences in mean effect size among groups were calculated using random effect models (Borenstein *et al.* 2009). Confidence intervals (CI) for each effect size were calculated. If 95% CI do not overlap with zero, or the CI of other groups, differences between means are significant at $P < 0.05$. For every analysis, we calculated total heterogeneity of the analysis (Q_T) to test whether the variance in effect size is greater than expected by chance. Q_T is a weighted sum of squares (equivalent to total sum of squares in analysis of variance). The variance explained by the model (Q_M) was used to test differences among groups (equivalent to between-study variance in analysis of variance). Both are tested against a chi-square distributions with $n-1$ or $k-1$ degrees of freedom, respectively, where n is total number of data points and k is number of covariate groups. Information on heterogeneity, variance explained and statistical signif-

icance is reported in Appendix S3. The percentage of variation explained by covariates was estimated as Q_M/Q_T (Xiong & Nilsson 1999; Gómez-Aparicio 2009) and reported also in the main text.

PUBLICATION BIAS

We tested publication bias (i.e. higher possibility of publishing highly positive or negative results or not reporting non-significant effects) through graphical methods (shown in Appendix S4), such as weighted histograms and funnel plots (Rosenberg, Adams & Gurevitch 2000). Weighted histograms consist of the distribution of combined weight of data (weights = 1/effect size variance), rather than frequency, for different effect size categories. Funnel plots are scatter plots of effect size against sample size. It should show larger distributions of the effect size at smaller variance or sample size. Other publications bias tests (e.g. Rosenthal's fail-safe number) were not employed since their usefulness has been challenged (Borenstein *et al.* 2009). Weighted histogram for the complete data set of the three studied variables showed an approximately normal shape, indicating that there is no important bias in the data sets or missing values in the non-effect area (i.e. not published works with non-significant results; Fig. S4-1). However, there were some minor biases. While survival showed a slightly bias towards positive effect size, emergence and biomass showed a minor bias towards negative effect size. The same pattern can be observed in funnel plots (see Fig. S4-2).

For emergence data, we also performed a meta-analysis considering publications as a grouping variable, trying to find possible bias in results coming from the same paper (i.e. interdependence of data). This meta-analysis showed that there is a tendency towards narrower confidence interval when number of data increased (Fig. S4-3). Nonetheless, mean effect size for every study followed the same pattern as the results found for different methodologies (see Results section). This analysis explained 28% of the total variance. Unfortunately, for survival or biomass data, the data base was too small to perform such analyses.

Results

A total of 42 studies met the selection criteria for emergence data, yielding 602 suitable cases (Table S1). This data set includes field (30 studies), glasshouse (eight studies) and common garden (seven studies) experiments. Across all studies, litter had no effect on seedling emergence. However, when stratified according to different methodologies, field studies showed a non-significant effect of litter, whereas glasshouse studies showed a negative effect and common garden studies a positive effect of litter (Fig. 1a). These covariates explained 22% of the total variance. For survival, we obtained nine studies with 70 data, all under field conditions. The overall effect of litter was non-significant (Fig. 1b). Thirteen studies reported biomass across all considered methodologies. We found an overall positive mean effect size of litter on biomass. However, in field studies, there was no significant effect of litter on biomass, whereas glasshouse and common garden studies showed a positive effect of litter (Fig. 1c). These grouping variables explained 21% of the total variance. Calculations made with the lnRR index showed very similar results (see Fig. S2).
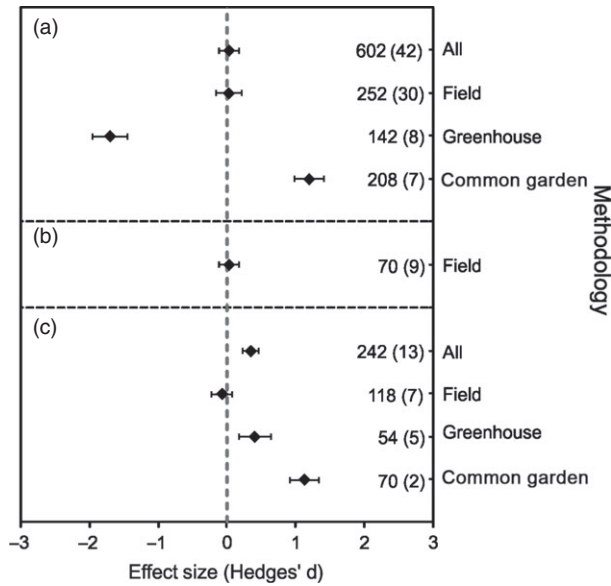
Fig. 1. Mean effect size for emergence (a), survival (b) and biomass (c) from field, glasshouse and common garden experiments. The number of cases is shown in the right inner part of the graph with number of studies in brackets. An effect size > 0 indicates a positive effect of the presence of litter, while values < 0 indicate negative effect. Error bars are 95% confidence intervals (CI). CIs that do not include 0 and do not overlap indicate a significant effect of litter and significant differences among groups, respectively. Additional details in Table S3-1.

EFFECT OF LITTER ON SEEDLING EMERGENCE

Considering the effect of litter under different conditions with respect to water availabilities, only dry grasslands showed a positive response to the presence of a litter layer (Fig. 2), explaining only 2% of the total variance. For common garden experiments, litter had a more positive effect under low water availability than under high water availability (Fig. 3), which explained 12% of the total variance. In general, high litter amounts (> 500 g m^{-2}) had more negative effects on seedling emergence than low and medium quantities (Fig. 4), although the analysis performed across methodologies suggested that medium litter amounts had more positive effects than low quantities (Fig. S3-1). In particular, dry grasslands showed a significant positive response to medium litter amounts [results not shown, Hedge's d (mean ± 95% CI) = 0.57 ± 0.36, based on 47 data points from eight independent studies]. Litter amount explained 8%, 1% and 5% of the total variance for glasshouse, common garden and field studies, respectively. In common garden experiments, medium litter amounts showed higher effect sizes in low water availability treatments, while for high water availability pots, litter had a positive effect only with low litter amounts (Fig. 3). Both variables together explained 22% of the total variance. In general, seedling emergence of large-seeded species (> 1 mg) was significantly less affected through the presence of a litter cover than that of small-seeded species (< 1 mg; Fig. 4), with small seeds showing a significantly negative response to litter presence, while large-seeded species
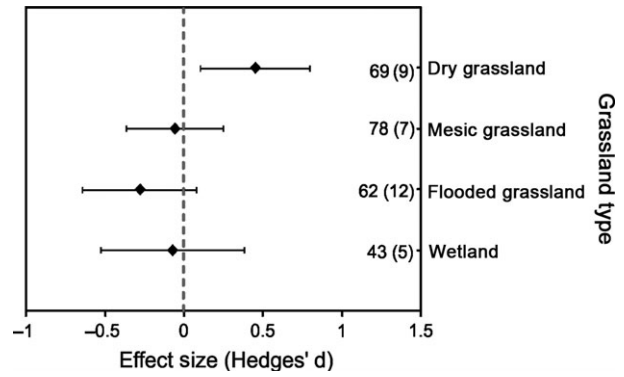

Fig. 2. Mean effect size for seedling emergence in different grassland types. The number of cases is shown in the right inner part of the graph. Number of studies is indicated in brackets. For details on effect size interpretation, refer to Fig. 1. Additional details in Table S3-2.
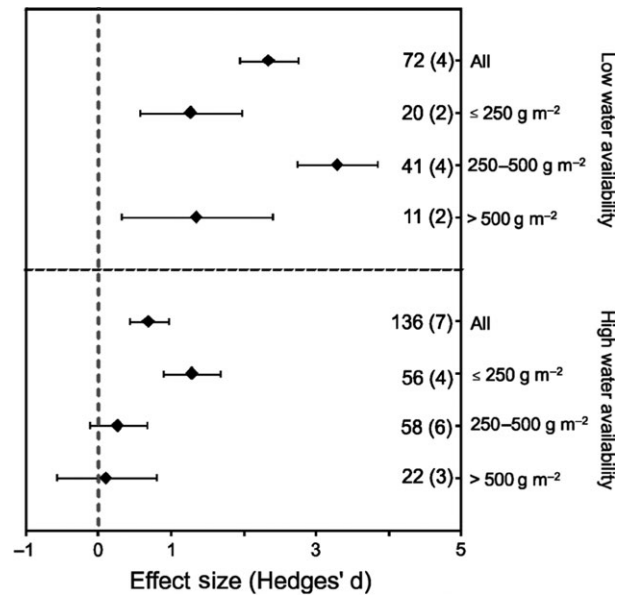

Fig. 3. Mean effect size for seedling emergence under different litter amounts and water availabilities for common garden studies. The number of cases is shown in the right inner part of the graph. Number of studies is indicated in brackets. For details on effect size interpretation, refer to Fig. 1. Additional details in Table S3-2.

exhibited a significant positive effect (Fig. S3-1). Seed size explained 8%, 6% and 1% of the total variance for glasshouse, pot and field studies, respectively.

EFFECT OF LITTER ON SEEDLING SURVIVAL

The presence of litter was positive in mesic grasslands and neutral in wetlands, while flooded grassland showed a negative effect of litter on survival (Fig. 5). Information for dry grasslands is lacking ($n < 3$). Litter amounting to < 250 g m^{-2} also showed positive effects on survival (Fig. 5). Effect size did not vary between different seed size classes (Fig. 5). Grassland type explained 31% of the total
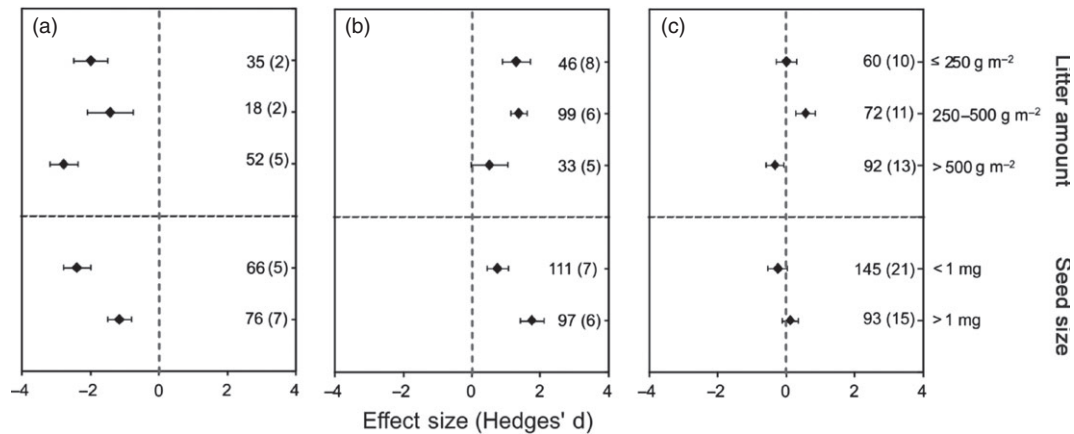
Fig. 4. Mean effect size for seedling emergence in relation to different litter amounts and seed sizes. (a) Glasshouse, (b) common garden and (c) field studies. The number of cases is shown in the right inner part of the graphs. Number of studies is indicated in brackets. For details on effect size interpretation, refer to Fig. 1. Additional details in Table S3-2.

Fig. 5. Mean effect size for seedling survival on field studies under different litter amounts, grassland types and seed size. The number of cases is shown in the right inner part of the graph. Number of studies is indicated in brackets. For details on effect size interpretation, refer to Fig. 1. Additional details in Table S3-3.
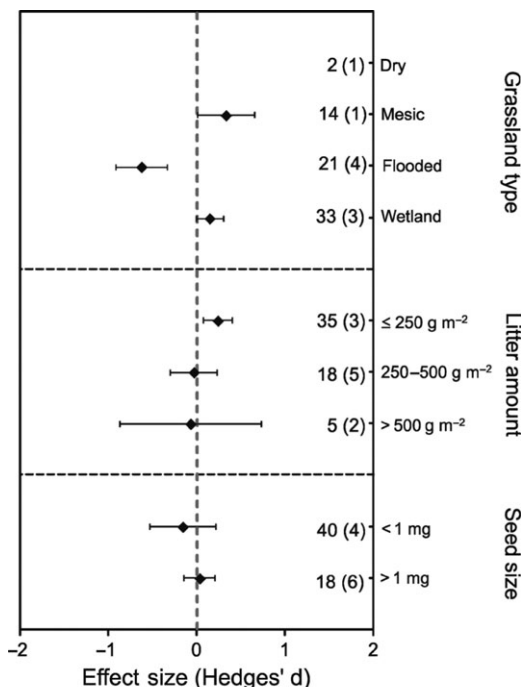
variance and litter amount explained 6%, while seed size explained only 1% of the variance.

EFFECT OF LITTER ON SEEDLING BIOMASS

There was no effect for any of the studied methodologies on seedling biomass stratified according to litter amount (Fig. 6), except for common garden studies where litter amount between 250 and 500 g m^{-2} leads to a significantly higher

seedling biomass (Fig. 6b). This variable explained 1%, 20% and 2% of the variance for glasshouse, common garden and field studies, respectively. When analysed across all methodologies, medium litter amounts also showed a positive effect on seedling biomass (Fig. S3-2). There were no differences in seedling biomass between small- and large-seeded species (Figs 6 and S3-2).

Discussion

Litter is an important factor influencing community structure (Grime 2001) and nutrient cycles (Wardle, Bonner & Nicholson 1997). As a form of an after-death, plant–plant interaction, it may affect the establishment of new individuals (Facelli & Pickett 1991a). According to Xiong & Nilsson (1999), negative effects of litter generally outweigh positive effects. However, these negative effects, which were supported by empirical studies in different ecosystems (Goldberg & Werner 1983; Bosy & Reader 1995; Tozer & Bradstock 1997; Scariot 2000; Barritt & Facelli 2001; Alexander & Schrag 2003), seem not to be as widespread as believed before. In the current meta-analysis, litter generally has a neutral or a slightly positive effect on recruitment in grasslands. However, a higher seedling emergence in the presence of litter with decreasing water availability (e.g. from wet to dry grasslands) generates interesting response patterns, which may have serious implications for plant community composition and diversity under ongoing land use and climate change but also for plant community restoration.

INDIRECT AND DIRECT EFFECTS OF WATER AVAILABILITY

We believe that indirect, often unintended, differences in soil moisture conditions caused strong variation in litter effects between the three methodologies. For seedling emergence, field studies showed neutral effects of litter presence, while glasshouse and common garden experiments showed
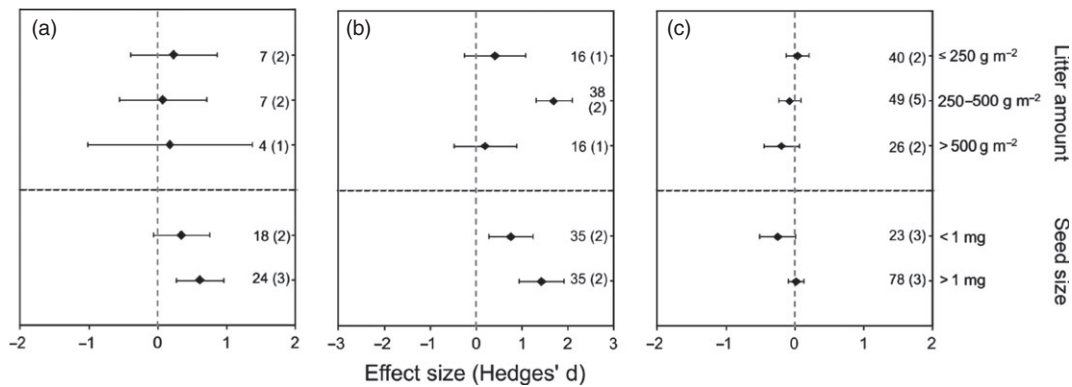
Fig. 6. Mean effect size for seedling biomass under different litter amounts and seed sizes. (a) Glasshouse, (b) common garden and (c) field studies. The number of cases is shown in the right inner part of the graph. Number of studies is indicated in brackets. For details on effect size interpretation, refer to Fig. 1. Additional details in Table S3-4.

diametrical negative and positive effects, respectively. Glasshouse experiments are conducted with optimal moisture and temperature conditions. Since positive effects of litter are more likely to be found under dry conditions, ample water availability in glasshouse studies may hide potential positive effects of litter (Gross 1984; but see Fowler 1986). However, in glasshouse studies, there were positive effects of litter on biomass. We suggest that this is probably related to density-dependent effects with lower plant density in litter-treated pots due to the lower emergence. However, Koorem, Price & Moora (2011), using woodland litter on forest species, found similar patterns even with equal seedling density per pot, suggesting that, additionally, nutrient release from litter may support seedling growth after emergence. On the other hand, the limited space for seedling development in pots (with < 2 L volume) will increase the probability of desiccation in control pots under outdoor conditions in a common garden at least in the upper layer of the substrate where germination and initial seedling growth take place (even when pots are frequently watered). Since litter reduces evaporation and thus desiccation of the substrate, the chance to detect positive litter effects increases in common garden pot studies.

However, the influence of plant litter may also vary directly with differences in moisture conditions, whether related to different ecosystem types or different experimentally manipulated irrigation levels. Thus, one of the most important effects of litter seems to be the maintenance of soil moisture and air humidity beneath the litter layer and the reduction in temperature fluctuations (Eckstein & Donath 2005; Deutsch, Bork & Willms 2010). This type of after-death interaction mediated by litter not only changes resource availability (i.e. water) but also non-resource conditions (i.e. temperature). Maestre *et al.* (2009) emphasized that when both resource and non-resource attributes are changed simultaneously, facilitation is expected to increase. Water limitations or high temperatures might affect seedling establishment (Boeken & Orenstein 2001; Noy-Meir & Briske 2002; Eckstein & Donath 2005; Ruprecht *et al.* 2010b; Wellstein 2012) and the positive effects of litter on soil moisture, air humidity and thermal amplitude may overcome its negative effects, such as mechanical impediment

of emergence (Amatangelo, Dukes & Field 2008) or liberation of allelochemicals on germination (Barritt & Facelli 2001; Hovstad & Ohlson 2008; Ruprecht *et al.* 2008). Usually, seed germination and seedling establishment occur when soil moisture is high, that is, above a certain threshold value (Welling, Pederson & Van der Valk 1988; Fenner & Thompson 2005; Padilla & Pugnaire 2007). Litter may maintain high soil moisture levels for longer periods of time, reduce soil evaporation and thus play a positive role for seed germination but also extend favourable conditions for seedling establishment under field conditions. However, if these conditions extend for a prolonged period, litter might also promote the development of pathogens, which may increase seedling mortality (Facelli *et al.* 1999).

Our results showed positive effect sizes for studies from different dry grasslands (e.g. temperate European dry grasslands, Israeli desert, Patagonian steppes, see Fig. S4-3). Litter in dry grasslands has higher lignin concentration than litter from mesic or wet areas and persists for longer periods (Díaz *et al.* 2004; Fortunel *et al.* 2009). Its composition also varies within a dry grassland type (e.g. temperate grasslands with shallow soils, semi-arid steppes or Mediterranean grasslands). Thus, positive effect size suggests that climatic conditions are one of the main drivers involved in the response of vegetation to litter accumulation. Thereby, the effect of litter on vegetation seems to depend more strongly on differences in climatic conditions than on different litter species composition, at least in several dry grassland types. In mesic and flooded grasslands, the effects of litter were neutral or even negative. However, these habitats may also benefit from the accumulation of a thin litter layer, since they are subject to recurrent drought periods (Tilman & Haddi 1992; Rosén 1995; Easterling *et al.* 2000; Schär *et al.* 2004; Loydi, Zalba & Distel 2012). The duration and frequency of dry periods, during which facilitative interactions are important (Gómez-Aparicio *et al.* 2004; Eckstein 2005), is predicted to increase in the present global change scenarios (Ciais *et al.* 2005; Parry *et al.* 2007). In these dry periods, the presence of a litter layer in herbaceous communities may play an important role for species establishment and biodiversity conservation (Tilman & Haddi

1992; Thuiller *et al.* 2005). Thus, litter acts as a modulator of the response of seeds and seedlings to different water availabilities. Idiosyncratic response of species to the presence of a litter layer may lead to a differential species establishment and thus changing community composition, structure, diversity and functionality, especially under conditions of increasing litter accumulation and changing environmental conditions in the course of global change.

LITTER AMOUNT

Litter amount is mentioned as one of the key drivers of litter effects (Hamrick & Lee 1987; Nash Suding & Goldberg 1999; Fenner & Thompson 2005). Xiong & Nilsson (1999) found positive effects of litter with amounts below 200 g m^{-2} and litter depths of 1.5 cm, meaning that the presence of litter promoted germination. Our meta-analysis showed positive effects of low and medium litter amount (< 500 g m^{-2}) on emergence in grassland ecosystems, while seedling survival increased with a low litter layer (< 250 g m^{-2}). This may have important implications for the establishment of individuals as a thin litter layer may provide better microclimatic conditions (Eckstein & Donath 2005; Deutsch, Bork & Willms 2010) that allow seedlings to survive for a longer period. On the other hand, when amounts increase above 500 g m^{-2}, litter has a negative effect on emergence. The latter litter amount corresponds to a litter layer of at least 4 cm thickness (Bosy & Reader 1995; Ruprecht & Szabo 2012), causing difficulties for seedling emergence simply because the limited seed reserves may be (almost) depleted while penetrating this mechanical barrier. Additionally, many studies (Goldberg & Werner 1983; Xiong *et al.* 2003; Schmiede *et al.* in press) showed that very high litter amounts (> 1000 g m^{-2}) completely inhibit seedling emergence. Unfortunately, it is not possible to incorporate this complete failure of emergence in a meta-analysis. Thus, a thin litter layer may facilitate seedling establishment, whereas the strength of the positive effect decreases with increasing litter amount (Nash Suding & Goldberg 1999). However, under dry experimental conditions, or in dry habitats, even high litter amounts seem to have a neutral (but no negative) effect on establishment (Hovstad & Ohlson 2009; Ruprecht *et al.* 2010a,b).

SEED SIZE EFFECTS

Seed size is a particularly good predictor for the effects of litter. We consistently found a stronger negative effect of litter on emergence of species with smaller seeds. Small-seeded species usually require light for germination (Hodkinson *et al.* 1998; Milberg, Andersson & Thompson 2000; Baskin & Baskin 2001; Burmeier *et al.* 2010), which explains in part the lower effect size found in these species. Additionally, Westoby *et al.* (1996) proposed other mechanisms that may partially help to explain this response: the reserve effect, the seedling size effect and the metabolic effect. The reserve effect determines survival in case of a carbon deficit. Small seeds contain less reserve tissue to support this deficit, diminishing emergence below a litter layer (Westoby *et al.* 1996; Leishman *et al.* 2000; Grime 2001; Fenner & Thompson 2005). In addition, species with smaller seeds produce smaller seedlings (seedling size effect) that have more difficulties to penetrate the litter layer (Carson & Peterson 1990; Everham, Myster & Van De Genachte 1996; Křenová & Lepš 1996). The metabolic effect, that is, large-seeded species tend to have slower RGR, will determine seedling size (Leishman *et al.* 2000). Thus, species with smaller seeds may compensate lower germination rates or survival by increased growth rates after the initial phase of seedling establishment (Westoby *et al.* 1996; Fenner & Thompson 2005), which is manifested in the positive effect size found for seedling biomass (Gross 1984).

Unfortunately, for grassland ecosystems, most works deal with seedling emergence or establishment and not with the process of seed germination *per se* (but see Ruprecht *et al.* 2008). Therefore, it is unknown whether the mechanism behind the negative effect of litter under field conditions is the reduction in germination percentages (Bosy & Reader 1995; Ruprecht *et al.* 2008) or an increase in seedling mortality before emergence through the depletion of seed reserves (Fenner & Thompson 2005) or through pathogens (Facelli *et al.* 1999). Depending on the specific mechanism involved, seed size may have a differential bearing on this negative interaction. For example, if litter exerts negative effects by increasing seedling mortality before emergence, it may be expected that the response of species will depend on seed size, whereas negative effects of litter on the process of germination *per se* may be largely unrelated to seed size. More attention should be paid to this particular phase to assess a complete picture of the mechanisms involved.

META-ANALYSIS LIMITATIONS AND IMPLICATIONS FOR FUTURE RESEARCH

In order to find general patterns mediated through litter accumulation in plant communities, the present meta-analysis synthesizes research on the after-death effects of litter on recruitment in grassland ecosystems. Our review shows that there are still significant gaps in the published literature. The low number of independent studies for some estimators (e.g. Figs 5 and 6) may limit the strength of some of our findings. Data availability is high for some estimators (e.g. emergence), but not for others (e.g. survival, biomass). This also affects conclusions about different covariates by restricting statistical inference and power. Additionally, some effects of litter could not at all be assessed due to the lack of published studies, for example effects of different litter types (Boeken & Orenstein 2001; Quested & Eriksson 2006; Donath & Eckstein 2008), effect of litter on native vs. non-native species (Minchinton, Simpson & Bertness 2006; Brandt & Seabloom 2012), effects of conspecific vs. heterospecific litter (Jong & Klinkhamer 1985; Hovstad & Ohlson 2009) or response to litter in the presence of competitors (Lenz, Moyle-Croft & Facelli 2003; Donath, Hölzel & Otte

2006; Viard-Cretat *et al.* 2010), herbivores (Facelli 1994; Wilsey & Polley 2003; Donath & Eckstein 2012) or mowing (Nash Suding & Goldberg 1999; Stammel, Kiehl & Pfadenhauer 2006). Moreover, there is a bias of published papers in favour of North American and European grasslands and temperate biomes, whereas response patterns in African, Asian, Australian or South American regions or tropical and subtropical areas are poorly studied. The latter areas hold many of the most important natural and large grassland ecosystems in the world (Suttie, Reynolds & Batello 2005). More efforts should be undertaken to study the effects of litter in these ecosystems.

Conclusions

Climate change will increase net primary productivity, thereby potentially boosting litter accumulation (Smith *et al.* 2000) and change the dynamics of grasslands (Grime *et al.* 2000; Novick *et al.* 2004; Parry *et al.* 2007), whereas higher temperature will reduce soil moisture (Melillo *et al.* 1993). Additionally, the frequency and length of dry periods and fire frequency will increase (Parry *et al.* 2007). As soon as litter accumulation exceeds 500 g m^{-2}, changes in species composition and reduced species establishment can be anticipated since beyond this threshold litter reduces emergence and survival of seedlings. Consequently, through changes in species number and composition, ecosystem functions may be affected (Hooper & Vitousek 1997). However, quantities of < 500 g m^{-2} litter might help to mitigate the effects of droughts by reducing evaporation and temperature extremes and may represent a threshold value for the amount of plant material transferred in grassland restoration projects. A better understanding of the relationships between litter accumulation, plant diversity and climatic conditions, and a more complete comprehension of the mechanisms involved in this response, will allow us to incorporate litter-mediated mechanisms and processes in future scenarios of global change, land degradation and restoration ecology.

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References

Aber, J. & Melillo, J. (1991) *Terrestrial Ecosystems*. Saunders College Publishing, Philadelphia, PA.

Abramoff, M.D., Magalhaes, P.J. & Ram, S.J. (2004) Image processing with ImageJ. *Biophotonics International*, **11**, 36–42.

Aerts, R. & Chapin, F.S. (1999) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.

Ajtay, G.L., Ketner, P. & Duvigneaud, P. (1979) Terrestrial primary production and phytomass. *The Global Carbon Cycle* (eds B. Bolin, E. Degens & P. Ketner), pp. 129–181. Wiley, Chichester.

Alexander, H.M. & Schrag, A.M. (2003) Role of soil seed banks and newly dispersed seeds in population dynamics of the annual sunflower, *Helianthus annuus*. *Journal of Ecology*, **91**, 987–998.

Amatangelo, K.L., Dukes, J.S. & Field, C.B. (2008) Responses of a California annual grassland to litter manipulation. *Journal of Vegetation Science*, **19**, 605–612.

Barritt, A.R. & Facelli, J.M. (2001) Effects of *Casuarina pauper* litter and grove soil on emergence and growth of understorey species in arid lands of South Australia. *Journal of Arid Environments*, **49**, 569–579.

Baskin, C.C. & Baskin, J.M. (2001) *Seeds – Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.

Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. & Willems, J.H. (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology*, **12**, 834–842.

Bergelson, J. (1990) Life after death: site pre-emption by the remains of *Poa Annua*. *Ecology*, **71**, 2157–2165.

Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.

Boeken, B. & Orenstein, D. (2001) The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. *Journal of Vegetation Science*, **12**, 825–832.

Borenstein, M., Hedges, L.V., Higgins, J.P.T. & Rothstein, H.R. (2009) *Introduction to Meta-analysis*. Wiley & Sons, Chichester, UK.

Bosy, J.L. & Reader, R.J. (1995) Mechanisms underlying the suppression of forb seedlings by grass (*Poa pratensis*) litter. *Functional Ecology*, **9**, 635–639.

Brandt, A.J. & Seabloom, E.W. (2012) Seed and establishment limitation contribute to long-term native forb declines in California grasslands. *Ecology*, **93**, 1451–1462.

Brooker, R., Kikvidze, Z., Pugnaire, F.I., Callaway, R.M., Choler, P., Lortie, C.J. & Michalet, R. (2005) The importance of importance. *Oikos*, **109**, 63–70.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Burmeier, S., Donath, T.W., Otte, A. & Eckstein, R.L. (2010) Rapid burial has differential effects on germination and emergence of small-and large-seeded herbaceous plant species. *Seed Science Research*, **20**, 189.

Carson, W.P. & Peterson, C.J. (1990) The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia*, **85**, 8–13.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C. & Carrara, A. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Coe, R. (2002) *It's the Effect Size Stupid: What Effect Size is and Why it is Important*. Annual Conference of the British Educational Research Association, Exeter, UK, pp. 18.

Cooper, H.M., Hedges, L.V. & Valentine, J.C. (2009) *The Handbook of Research Synthesis and Meta-analysis*. Russell Sage Foundation, New York.

Critchley, C.N.R., Burke, M.J.W. & Stevens, D.P. (2004) Conservation of low land semi-natural grasslands in the UK: a review of botanical monitoring results from agri-environment schemes. *Biological Conservation*, **115**, 263–278.

Deutsch, E.S., Bork, E.W. & Willms, W.D. (2010) Separation of grassland litter and ecosite influences on seasonal soil moisture and plant growth dynamics. *Plant Ecology*, **209**, 135–145.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Marti, G., Grime, J.P., Zarrinkamar, F. & Asri, Y. (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684–20689.

Donath, T.W. & Eckstein, R.L. (2008) Grass and oak litter exert different effects on seedling emergence of herbaceous perennials from grasslands and woodlands. *Journal of Ecology*, **96**, 272–280.

Donath, T.W. & Eckstein, R.L. (2010) Effects of bryophytes and grass litter on seedling emergence vary by vertical seed position and seed size. *Plant Ecology*, **207**, 257–268.

Donath, T.W. & Eckstein, R.L. (2012) Litter effects on seedling establishment interact with seed position and earthworm activity. *Plant Biology*, **14**, 163–170.

Donath, T.W., Hölzel, N. & Otte, A. (2006) Influence of competition by sown grass, disturbance and litter on recruitment of rare flood-meadow species. *Biological Conservation*, **130**, 315–323.

Donath, T.W., Hölzel, N., Bissels, S. & Otte, A. (2004) Perspectives for incorporating biomass from non-intensively managed temperate flood-meadows into farming systems. *Agriculture, Ecosystems and Environment*, **104**, 439–451.

Donath, T.W., Bissels, S., Ho lzel, N. & Otte, A. (2007) Large scale application of diaspore transfer with plant material in restoration practice – impact of seed and microsite limitation. *Biological Conservation*, **138**, 224–234.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Eckstein, R.L. (2005) Differential effects of interspecific interactions and water availability on survival, growth and fecundity of three congeneric grassland herbs. *New Phytologist*, **166**, 525–536.

Eckstein, R.L. & Donath, T.W. (2005) Interactions between litter and water availability affect seedling emergence in four familial pairs of floodplain species. *Journal of Ecology*, **93**, 807–816.

Eckstein, R.L., Pereira, E., Milbau, A. & Graae, B.J. (2011) Predicted changes in vegetation structure affect the susceptibility to invasion of bryophyte-dominated subarctic heath. *Annals of Botany*, **108**, 177–183.

Eckstein, R.L., Ruch, D., Otte, A. & Donath, T.W. (2012) Invasibility of a nutrient-poor pasture through resident and non-resident herbs is controlled by litter, gap size and propagule pressure. *PLoS ONE*, **7**, e41887.

Everham, E.M., Myster, R.W. & Van De Genachte, E. (1996) Effect of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. *American Journal of Botany*, **83**, 1063–1068.

Facelli, J.M. (1994) Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology*, **75**, 1727–1735.

Facelli, J.M. & Facelli, E. (1993) Interactions after death: plant litter controls priority effects in a successional plant community. *Oecologia*, **95**, 277–282.

Facelli, J.M. & Pickett, S.T.A. (1991a) Plant litter: its dynamics and effects on plant community structure. *Botanical Review*, **57**, 1–32.

Facelli, J.M. & Pickett, S.T.A. (1991b) Plant litter: light interception and effects on an old-field plant community. *Ecology*, **72**, 1024–1031.

Facelli, J.M., Williams, R., Fricker, S. & Ladd, B. (1999) Establishment and growth of seedlings of *Eucalyptus obliqua*: interactive effects of litter, water, and pathogens. *Austral Ecology*, **24**, 484–494.

Fenner, M. & Thompson, K. (2005) *The Ecology of Seed*. Cambridge University Press, Cambridge, UK.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H. & Cruz, P. (2009) Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology*, **90**, 598–611.

Foster, B.L. & Gross, K.L. (1997) Partitioning the effects of plant biomass and litter on *Andropogon gerardi* in old-field vegetation. *Ecology*, **78**, 2091–2104.

Foster, B.L. & Gross, K.L. (1998) Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, **79**, 2593–2602.

Fowler, N.L. (1986) Microsite requirements for germination and establishment of three grass species. *American Midland Naturalist*, **115**, 131–145.

Funes, G., Basconcelo, S., Díaz, S. & Cabido, M. (1999) Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Science Research*, **9**, 341–345.

Galvánek, D. & Lepš, J. (2012) The effect of management on productivity, litter accumulation and seedling recruitment in a Carpathian mountain grassland. *Plant Ecology*, **213**, 523–533.

Goldberg, D.E. & Werner, P.A. (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia*, **60**, 149–155.

Gómez-Aparicio, L. (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, **97**, 1202–1214.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J. & Baraza, E. (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications*, **14**, 1128–1138.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. John Wiley and Sons, LTD, Chichester, UK.

Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I. P., Askew, A.P., Corker, D. & Kielty, J.P. (2000) The response of two contrasting limestone grasslands to simulated climate change. *Science*, **289**, 762.

Gross, K.L. (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology*, **72**, 369–387.

Gurevitch, J. & Hedges, L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142–1149.

Gurevitch, J. & Hedges, L.V. (2001) Meta-analysis: combining the results of independent experiments. *Design and Analysis of Ecological Experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 347–369. Chapman and Hall, New York.

Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992) A meta-analysis of competition in field experiments. *The American Naturalist*, **140**, 539–572.

Hamrick, J.L. & Lee, J.M. (1987) Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). *American Journal of Botany*, **74**, 451–457.

Hansson, M. & Fogelfors, H. (2000) Management of a semi-natural grassland: results from a 15-year-old experiment in southern Sweden. *Journal of Vegetation Science*, **11**, 31–38.

Hodgson, J.G., Montserrat-Martí, G., Tallowin, J., Thompson, K., Díaz, S., Cabido, M., Grime, J.P., Wilson, P.J., Band, S.R. & Bogard, A. (2005) How much will it cost to save grassland diversity? *Biological Conservation*, **122**, 263–273.

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.

Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. *Ecology*, **78**, 1966–1975.

Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.

Hovstad, K.A. & Ohlson, M. (2008) Physical and chemical effects of litter on plant establishment in semi-natural grasslands. *Plant Ecology*, **196**, 251–260.

Hovstad, K.A. & Ohlson, M. (2009) Conspecific versus heterospecific litter effects on seedling establishment. *Plant Ecology*, **204**, 33–42.

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.

Jong, T.J. & Klinkhamer, P.G.L. (1985) The negative effects of litter of parent plants of *Cirsium vulgare* on their offspring: autotoxicity or immobilization? *Oecologia*, **65**, 153–160.

Kiehl, K., Kirmer, A., Donath, T.W., Rasran, L. & Hölzel, N. (2010) Species introduction in restoration projects – evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology*, **11**, 285–299.

Koorem, K., Price, J.N. & Moora, M. (2011) Species-specific effects of woody litter on seedling emergence and growth of herbaceous plants. *PLoS ONE*, **6**, e26505.

Křenová, Z. & Lepš, J. (1996) Regeneration of a *Gentiana pneumonanthe* population in an oligotrophic wet meadow. *Journal of Vegetation Science*, **7**, 107–112.

Lamb, E.G. (2008) Direct and indirect control of grassland community structure by litter, resources, and biomass. *Ecology*, **89**, 216–225.

Leishman, M.R., Westoby, M. & Jurado, E. (1995) Correlates of seed size variation: a comparison among five temperate floras. *Journal of Ecology*, **83**, 517–529.

Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds: The Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 31–57. CAB International, Wallingford, UK.

Lenz, T.I., Moyle-Croft, J.L. & Facelli, J.M. (2003) Direct and indirect effects of exotic annual grasses on species composition of a South Australian grassland. *Austral Ecology*, **28**, 23–32.

Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology*, **94**, 7–16.

Loydi, A., Zalba, S.M. & Distel, R.A. (2012) Vegetation change in response to grazing exclusion in montane grasslands, Argentina. *Plant Ecology and Evolution*, **145**, 313–322.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J. & Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.

Milberg, P., Andersson, L. & Thompson, K. (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research*, **10**, 99–104.

Minchinton, T.E., Simpson, J.C. & Bertness, M.D. (2006) Mechanisms of exclusion of native coastal marsh plants by an invasive grass. *Journal of Ecology*, **94**, 342–354.

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. (2006) Global patterns in seed size. *Global Ecology and Biogeography*, **16**, 109–116.

Moog, D., Poschlod, P., Kahmen, S. & Schreiber, K.F. (2002) Comparison of species composition between different grassland management treatments after 25 years. *Applied Vegetation Science*, **5**, 99–106.

Nash Suding, K. & Goldberg, D.E. (1999) Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology*, **87**, 436–449.

Novick, K., Stoy, P., Katul, G., Ellsworth, D., Siqueira, M., Juang, J. & Oren, R. (2004) Carbon dioxide and water vapor exchange in a warm temperate grassland. *Oecologia*, **138**, 259–274.

Noy-Meir, I. & Briske, D.D. (2002) Response of wild wheat populations to grazing in Mediterranean grasslands: the relative influence of defoliation, competition, mulch and genotype. *Journal of Applied Ecology*, **39**, 259–278.

Owensby, C.E., Ham, J.M., Knapp, A.K. & Auen, L.M. (1999) Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO2. *Global Change Biology*, **5**, 497–506.

Padilla, F.M. & Pugnaire, F.I. (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology*, **21**, 489–495.

Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. & Hanson, C. E. (2007) Contribution of working group II to the fourth assessment report of the intergovernmental panel on climate change. Cambridge, UK, 976.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Schimel, D.S. & Hall, D.O. (1995) Impact of climate change on grassland production and soil carbon worldwide. *Global Change Biology*, **1**, 13–22.

Quested, H. & Eriksson, O. (2006) Litter species composition influences the performance of seedlings of grassland herbs. *Functional Ecology*, **20**, 522–532.

Quested, H.M., Callaghan, T.V., Cornelissen, J. & Press, M.C. (2005) The impact of hemiparasitic plant litter on decomposition: direct, seasonal and litter mixing effects. *Journal of Ecology*, **93**, 87–98.

Quétier, F., Lavorel, S., Thuiller, W. & Davies, I. (2007) Plant-trait-based modeling assessment of ecosystem-service sensitivity to land-use change. *Ecological Applications*, **17**, 2377–2386.

Rasran, L., Vogt, K. & Jensen, K. (2007) Effects of litter removal and mowing on germination and establishment of two fen-grassland species along a productivity gradient. *Folia Geobotanica*, **42**, 271–288.

Rosén, E. (1995) Periodic droughts and long-term dynamics of alvar grassland vegetation on Öland, Sweden. *Folia Geobotanica*, **30**, 131–140.

Rosenberg, M.S., Adams, D.C. & Gurevitch, J. (2000) *MetaWin. Statistical Software for Meta-Analysis. Version 2.0*. Sinauer Associates, Sunderland, MA.

Rotundo, J.L. & Aguiar, M.R. (2005) Litter effects on plant regeneration in arid lands: a complex balance between seed retention, seed longevity and soil-seed contact. *Journal of Ecology*, **93**, 829–838.

Royal Botanic Gardens Kew (2008) Seed information database (SID). Version 7.1.

Ruprecht, E. & Szabo, A. (2012) Grass litter is a natural seed trap in long-term undisturbed grassland. *Journal of Vegetation Science*, **23**, 495–504.

Ruprecht, E., Donath, T.W., Otte, A. & Eckstein, R.L. (2008) Chemical effects of a dominant grass on seed germination of four familial pairs of dry grassland species. *Seed Science Research*, **18**, 239–248.

Ruprecht, E., Enyedi, M.Z., Eckstein, R.L. & Donath, T.W. (2010a) Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. *Biological Conservation*, **143**, 449–456.

Ruprecht, E., Józsa, J., Ölvedi, T.B. & Simon, J. (2010b) Differential effects of several "litter" types on the germination of dry grassland species. *Journal of Vegetation Science*, **21**, 1069–1081.

Sayer, E.J. (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*, **81**, 1–31.

Scariot, A. (2000) Seedling mortality by litterfall in Amazonian forest fragments. *Biotropica*, **32**, 662–669.

Schär, C., Vidale, P.L., Lüthi, D., Frei, C., Häberli, C., Liniger, M.A. & Appenzeller, C. (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Schmiede, R., Donath, T.W. & Otte, A. (2009) Seed bank development after the restoration of alluvial grassland via transfer of seed-containing plant material. *Biological Conservation*, **142**, 404–413.

Schmiede, R., Otte, A. & Donath, T.W. (2012) Enhancing plant biodiversity in species-poor grassland through plant material transfer – the impact of sward disturbance. *Applied Vegetation Science*, **15**, 290–298.

Schmiede, R., Ruprecht, E., Eckstein, R.L., Otte, A. & Donath, T.W. (in press) Establishment of rare flood meadow species by plant material transfer: experimental tests of threshold amounts and the effect of sowing position. *Biological Conservation*, doi:10.1016/j.biocon.2012.11.017.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermaker, L.K., Seemann, J.R. & Nowak, R.S. (2000) Elevated CO$_2$ increases productivity and invasive species success in an arid ecosystem. *Nature*, **408**, 79–81.

Špačková, I. & Lepš, J. (2004) Variability of seedling recruitment under dominant, moss, and litter removal over four years. *Folia Geobotanica*, **39**, 41–55.

Stammel, B., Kiehl, K. & Pfadenhauer, J. (2006) Effects of experimental and real land use on seedling recruitment of six fen species. *Basic and Applied Ecology*, **7**, 334–346.

Suttie, J.M., Reynolds, S.G. & Batello, C. (2005) Grasslands of the world. *Plant Production and Protection Series No. 34*, pp. 538. Food and agriculture organization of the United Nations (FAO), Rome.

Tallowin, J. (1999) Hay production from lowland semi-natural grasslands: a review of implications for ruminant livestock systems. *Grass and Forage Science*, **54**, 99–115.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245.

Tilman, D. (1993) Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology*, **74**, 2179–2191.

Tilman, D. & Haddi, A. (1992) Drought and biodiversity in grasslands. *Oecologia*, **89**, 257–264.

Török, P., Deák, B., Vida, E., Valkó, O., Lengyel, S. & Tóthmérész, B. (2010) Restoring grassland biodiversity: sowing low-diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation*, **143**, 806–812.

Tozer, M.G. & Bradstock, R.A. (1997) Factors influencing the establishment of seedlings of the Mallee, *Eucalyptus luehmanniana* (*Myrtaceae*). *Australian Journal of Botany*, **45**, 997–1008.

Veen, P., Jefferson, R., Smidt, J. & Straaten, J. (2009) *Grasslands in Europe of High Nature Value*. KNNV Publishing, Zeist, The Netherlands.

Viard-Cretat, F., Gross, N., Colace, M.P. & Lavorel, S. (2010) Litter and living plants have contrasting effects on seedling recruitment in subalpine grasslands. *Preslia*, **82**, 483–496.

Wardle, D.A., Bonner, K.I. & Nicholson, K.S. (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, **79**, 247–258.

Welling, C.H., Pederson, R.L. & Van der Valk, A.G. (1988) Recruitment from the seed bank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. *The Journal of Ecology*, **48**, 3–496.

Wellstein, C. (2012) Seed–litter–position drives seedling establishment in grassland species under recurrent drought. *Plant Biology*, **14**, 1006–1010.

Westoby, M., Leishman, M., Lord, J., Poorter, H. & Schoen, D.J. (1996) Comparative ecology of seed size and dispersal [and discussion]. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **351**, 1309–1318.

Wilsey, B.J. & Polley, H.W. (2003) Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands. *Ecology*, **84**, 920–931.

Xiong, S. & Nilsson, C. (1999) The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology*, **87**, 984–994.

Xiong, S., Johansson, M.E., Hughes, F.M.R., Hayes, A., Richards, K.S. & Nilsson, C. (2003) Interactive effects of soil moisture, vegetation canopy, plant litter and seed addition on plant diversity in a wetland community. *Journal of Ecology*, **91**, 976–986.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Data sources used in the meta-analysis.

Appendix S2. Effects size using response ratio index.

Appendix S3. Meta-analysis additional results and information.

Appendix S4. Publication Bias.