Review

Impact of invasions by alien plants on soil seed bank communities: Emerging patterns

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ABSTRACT

Much of our current understanding of the impact of invasive species on plant communities is based on patterns occurring in the above-ground vegetation, while only few studies have examined changes in soil seed banks associated with plant invasions, despite their important role as determinants of vegetation dynamics. Here, we reviewed the literature on the impact of plant invasions on the seed bank and we provide a quantitative synthesis using a meta-analysis approach. Specifically, (1) we quantified the impact of 18 invasive alien plants on (i) species richness and (ii) density of the seed banks of invaded communities, based on 58 pair-wise invaded-uninvaded comparisons (cases); we identified (2) the invasive taxa that are responsible for the largest changes in the seed bank; and (3) the habitats where substantial changes occur. Our study showed three major findings: (1) species richness (68% of cases) and density (58% of cases) were significantly lower in native seed banks invaded by alien plants; (2) species richness and density of native and alien species were remarkably lower in seed banks invaded by large, perennial herbs compared to uninvaded sites; and (3) invaded seed banks were often associated with a larger richness and/or abundance of alien species. This study indicates a need for additional seed bank data in invasion ecology to characterize species-specific and habitat-specific impacts of plant invasions, and to determine whether changes in the seed banks of native and alien species are a symptom of environmental degradation prior to a plant invasion or whether they are its direct result. The findings of this study help improve our capacity to predict the long-term implications of plant invasions, including limitations in the recruitment of native species from the seed bank and the potential for secondary invasions by seeds of other alien species.

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Introduction

Invasions by alien plant species are known to exert significant impacts on plant diversity, community dynamics, and ecosystems processes (e.g. Gordon, 1998; Levine et al., 2003; Ehrenfeld, 2010; Vilà et al., 2011; Simberloff, 2011; Pyšek et al., 2012). To date, extensive research has been conducted to characterize and predict the effects of invasive plants on resident communities, ecosystem functioning, and, more recently, on ecosystem services (e.g. Charles and Dukes, 2007; see Eviner et al., 2012 and references therein). Ultimately, the long-term implications of plant invasions will depend upon (i) the persistence of an invader at a locality, (ii) the type, magnitude, and time scale of the impact, and (iii) the capacity of resident communities to buffer against the full or partial displacement of resident species (Vilà and Weiner, 2004; Gioria et al., 2011, 2012).

In many ecosystems, the above factors are strongly dependent upon changes in the soil seed banks (hereafter termed seed bank) of invaded communities. Seed banks are reservoirs of viable seeds, either in the soil or on its surface, produced in the most recent reproductive period or over previous years (Templeton and Levin, 1979; Roberts, 1981) and fulfil several ecological functions in the structuring of many plant community types (Major and Pyott, 1966; Fenner and Thompson, 2005). Their potential role in contributing to species invasiveness and affecting community invasibility has been recently highlighted (Gioria et al., 2012), particularly in the naturalization and invasion stages of an invasion process (Richardson et al., 2000; Richardson and Pyšek, 2012). First, they may affect the successful establishment and spread as well as the persistence of sexually-reproducing and apomictic alien species by acting as a source of propagules (Pyšek and Richardson, 2007; Gioria and Osborne, 2009a; Gioria et al., 2012), particularly where alien species are capable of forming large, long-term persistent seed banks (*sensu* Thompson et al., 1997). As reservoirs of genetic variability (Templeton and Levin, 1979; Venable and Brown, 1988; McCue and Holtsford, 1998; Levin, 1990; Mandák et al., 2012), the formation of a seed bank will affect the response of alien plants to novel conditions experienced in their non-native range. For native species, seed banks will affect the probability of successful recruitment of native species from the seed bank as well as their capacity to respond to those sets of novel conditions that may follow the introduction of an invasive species (Gioria et al., 2012). Native seed banks may also mitigate the effects of competitive interactions with invasive species and buffer against changes in the vegetation, allowing native species to persist in an invaded community even after being displaced from the above-ground vegetation, at least for a short period of time.

The impact of invasive species on seed banks may differ substantially from that on the above-ground vegetation (e.g. Vilà and Gimeno, 2007; Gioria and Osborne, 2009a,b, 2010; Gaertner et al., 2011; Abella et al., 2012, 2013), since seeds buried in the seed bank may tolerate and escape environmental conditions that are unfavourable to adults (Templeton and Levin, 1979; Fenner and Thompson, 2005). Moreover, seed banks include some species possessing different, and often, contrasting ecological strategies to those present in the above-ground vegetation (Pickett and McDonnell, 1989), also potentially contributing to a differential

impact. Over the short term, plant invasions are likely to affect primarily the transient component of the seed bank (*sensu* Thompson et al., 1997), via alterations in the seed input associated with changes in the above-ground vegetation, while effects on the persistent component of the seed bank may not yet be evident (e.g. Marchante et al., 2011).

Since seed banks represent a source of propagules for both native and alien species (Gioria et al., 2012), knowledge of changes in the seed bank associated with plant invasions is essential to determining the persistence of an alien species at a locality and to developing cost-effective control and restoration measures (Holmes, 2002; Vilà and Gimeno, 2007; Richardson and Kluge, 2008; Abella et al., 2012). Any comprehensive characterization of the legacy of plant invasions on the resident vegetation should therefore include knowledge of changes in the seed bank of invaded communities. To date, however, our understanding of the effects of invasive species on plant communities is largely based on patterns occurring in the above-ground vegetation (e.g. Levine et al., 2003; Gaertner et al., 2009; Vilà et al., 2011; Pyšek et al., 2012), while comparatively few studies have examined directly the impact of plant invasions on the seed bank (see Gioria et al., 2012). Of those, some have reported significant differences in seed banks of invaded communities in various ecosystem types (e.g. Holmes and Cowling, 1997; Holmes, 2002; Gioria and Osborne, 2009a,b, 2010; French et al., 2011; Marchante et al., 2011; González-Muñoz et al., 2012), while others have failed to detect any significant impact (e.g. Wearne and Morgan, 2006; Vilà and Gimeno, 2007; Gaertner et al., 2011; Abella et al., 2012, 2013; see Gioria et al., 2012).

Here, we aim to review the literature on the impact of plant invasions on the seed bank and to provide a quantitative synthesis of those studies comparing species richness and density of seed banks in invaded and comparable uninvaded plant communities, in different habitat types, using a meta-analysis approach (Rosenberg et al., 2000). Specifically, we address three questions: (1) What is the impact of invasive alien plants on (i) species richness and (ii) density of the seed bank of invaded plant communities? (2) Which invasive species are responsible for the greatest changes in the seed bank? And (3) in which habitat types are these changes most pronounced? - Given that plant invasions often occur in disturbed areas, where other alien species may be present (e.g. Turner et al., 2008; Gaertner et al., 2011; Gioria et al., 2011, 2012; González-Muñoz et al., 2012), we examine the impact on the seed banks of all species, regardless of their native/alien status, that on native species only, and, indirectly, that on alien species. Finally, we discuss the significance of the results of this meta-analysis study, its limitations, and we offer future research directions.

Methods

Literature search and data extraction

The effects of plant invasions on the seed bank were examined by performing a search of the published literature, up to February 2014, in the Web of Science (ISI) electronic database and Google Scholar. To maximize the number of studies identified by the search, we used multiple combinations of the keywords 'invas*', 'exotic', 'alien' 'seed bank', 'species richness', 'diversity',

'composition', 'plant community', 'density' and 'abundance'. A few additional studies were identified through screening the reference lists within the papers identified during the initial search as well as those papers citing the papers originally identified. We also conducted a search for grey literature, and experts in the field were contacted directly for potential unpublished material and dissertations.

Our meta-analysis was based on those studies examining the impacts of plant invasions on seed banks that met the following inclusion criteria:

(1) Studies focusing on the impact of individual alien species that are invasive in the study area(s) (*sensu* Richardson et al., 2000; Blackburn et al., 2011), while we excluded one study where more than one species were regarded as invasive at the study sites; the pair-wise invaded-uninvaded comparisons used in this meta-analysis thus refer to sites dominated by one invasive species only, although alien species that are often invasive elsewhere were also present;

(2) Studies examining the impact of plant invasions by testing for differences between invaded seed banks and comparable uninvaded seed banks at the same sites; we excluded studies assessing the seed bank under invasive stands and at reference sites that were not directly comparable;

(3) Replicated, observational field studies, examining the characteristics of the seed banks in sites invaded by an alien species and in comparable uninvaded sites; we excluded experimental studies comparing manipulated invaded and uninvaded seed banks;

(4) Studies quantifying one or both response variables: (i) species richness (defined as the number of species recorded per study plot), and (ii) density (expressed as the number of seeds/seedlings per square metre) in the seed banks of invaded and uninvaded sites. Seeds or seedlings of the invasive species under investigation were excluded from the analyses to assess the differences between invaded and uninvaded seed banks based on the characteristics of resident species only, as well as to allow for comparisons between the results of studies examining the impact of invasive alien species that form a seed bank and those that propagate exclusively vegetatively, or only form a transient, undetected seed bank;

(5) Studies for which information on (i) mean values, (ii) variances (standard variation or standard error), and (iii) sample sizes in invaded and uninvaded soil seed banks was available or can be retrieved. Where these data were not available in the respective publications, we contacted the authors directly and this information was calculated using the raw data when provided;

(6) Studies for which the rationale for the selection of the sampling sites was clear and all care had been taken by the authors to ensure that the conditions in invaded and uninvaded areas/plots were comparable.

In total, we identified 31 studies that examined seed banks at invaded and uninvaded sites. Some studies did not report the mean values and/or measures of variation, and had to be excluded when the authors did not provide the necessary information. The final dataset included 18 studies, for a total of 58 pair-wise invaded-uninvaded comparisons (hereafter called 'cases'), which examined directly the impact of 18 invasive alien plants (Table 1; Supporting Information S1, S2). Where possible, we separated the seed banks of native and alien species to analyze the impact of invasion on the (i) native and (ii) total seed bank (Supporting Information S1, S2). The studies were located in Europe (45%: Ireland, Spain), South Africa (26%), Australia and New Zealand (18%), South America (10%:

Argentina, Venezuela), and North America (3%: Arizona, Oklahoma) (Supporting Information S3).

The 18 invasive species (Table 1) are native to Africa (8 species), arid and semi-arid Africa and Asia (1), Asia (2), Australia (3), and South America (2). In relation to the invaded habitats, the majority of comparisons were conducted in shrubland (33%), broad-leaved forests (21%), and wetlands (19%). Only a few comparisons were available for ruderal habitats (a former lead mine and road banks), grasslands, and desert habitats (Table 1; Supporting Information S1, S2, S3, S4).

All studies included in our analysis estimated the seed bank using the seedling emergence approach (i.e. the collection of soil samples and the promotion of seed germination by placing the samples under relatively controlled glasshouse condition; Thompson and Grime, 1979) or some modifications (e.g. Gioria and Osborne, 2009a,b, 2010), thus ensuring that the impact of plant invasions was assessed only for the viable component of the seed bank. The emergence approach may underestimate seed bank richness and density, by failing to detect dormant seed whose germination requirements are not met under glasshouse conditions (Thompson and Grime, 1979), thus, it is possible that the studies used in our meta-analysis provide only a partial picture of the actual richness and density of the seed bank of the sampled plant communities. However, we expect that the effects of such underestimation would be similar in both invaded and uninvaded communities, thus not having any major effect on the assessment of the overall impact of invasions.

Meta-analysis

Analyses were conducted using 'meta-analysis', a statistical synthesis of separate, independent experiments (Hedges and Olkin, 1985). This method can largely alleviate the bias of favouring significant results in the literature, by weighing each case according to its sampling variance and size, and, as a result, can present a more robust synthesis than a traditional literature review. We used mixed effect meta-analytical models that are likely to conform to statistical assumptions in ecological research (Gurevitch and Hedges, 2001) and 95% bias-corrected bootstrap confidence intervals, based on 999 iterations and randomization tests in homogeneity statistics, to alleviate the assumption on normal distribution (Adams et al., 1997). Calculations were done in MetaWin v. 2 (Rosenberg et al., 2000).

The response variables obtained from primary studies were (i) average numbers of species present in seed banks (further termed 'seed bank richness') and (ii) average total number of seeds in seed banks (further termed 'seed bank density'). These variables were analyzed separately for (i) native seed banks and for (ii) total seed banks, to ascertain the effect of invasion on the native vegetation only as well as to obtain some information on the status of ecological degradation (Gaertner et al., 2011) of both invaded and uninvaded communities.

First, we examined whether the response variables differed significantly between invaded (I) and uninvaded (U) communities for each case study. For this purpose, we converted each I–U paired site into an effect size using Hedges' *d* (Hedges and Olkin, 1985), i.e. the weighted difference between I and U sites, which provide an estimate of the standardized mean difference that is not biased by sample size (Rosenberg et al., 2000). Publication bias (whether studies showing significant results are more likely to be published) and normality of data distribution were checked graphically by funnel plots (Light and Pillemer, 1984; Palmer, 1999) and normal quantile plots (Wang and Bushman, 1998), as well as, more formally, by rank correlation tests (Begg, 1994) and calculations of fail-safe numbers (Rosenberg, 2005), with the values of theoretical

Table 1

Studies, their grouping explanatory variables, and effect sizes and their variance for seed bank richness, S_d and Var(S_d), and seed bank density, D_d and Var(D_d), of all species. Blank cells are missing values.

Label	Study	Invader	Life history	Reproductive mode	Seed bank	Habitat	S_d	Var(S_d)	D_d	Var(D_d)
Gi1	Gioria et al. (2011)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Grassland	−2.446	1.165	−1.895	0.966
Gi2	Gioria et al. (2011)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Grassland	−0.673	0.704	0.265	0.673
Gi3	Gioria and Osborne (2009a)	*Heracleum mantegazzianum*	Perennial herb	Seed only	Short	Riparian or coastal	−8.199	4.702	−4.858	1.975
Gi4	Gioria and Osborne (2009a)	*Heracleum mantegazzianum*	Perennial herb	Seed only	Short	Riparian or coastal	−4.659	1.857	−4.134	1.568
Gi5	Gioria and Osborne (2009a)	*Heracleum mantegazzianum*	Perennial herb	Seed only	Short	Riparian or coastal	−12.883	10.873	−7.214	3.753
Gi6	Gioria and Osborne (2009a)	*Heracleum mantegazzianum*	Perennial herb	Seed only	Short	Riparian or coastal	−4.042	1.521	−5.610	2.467
Gi7	Gioria and Osborne (2009a)	*Heracleum mantegazzianum*	Perennial herb	Seed only	Short	Riparian or coastal	−9.491	6.130	−1.879	0.721
Gi8	Gioria and Osborne (2009a)	*Heracleum mantegazzianum*	Perennial herb	Seed only	Short	Riparian or coastal	−3.383	1.215	−1.363	0.616
Gi9	Gioria and Osborne (2009b)	*Gunnera tinctoria*	Perennial herb	Vegetative present	Long	Riparian or coastal	−8.040	4.540	−4.525	1.780
Gi10	Gioria and Osborne (2009b)	*Gunnera tinctoria*	Perennial herb	Vegetative present	Long	Riparian or coastal	−5.438	2.348	−4.149	1.576
Gi11	Gioria and Osborne (2009b)	*Gunnera tinctoria*	Perennial herb	Vegetative present	Long	Grassland	−1.763	0.694	−1.307	0.607
Gi12	Gioria and Osborne (2009b)	*Gunnera tinctoria*	Perennial herb	Vegetative present	Long	Grassland	−5.430	2.343	−22.051	30.889
Gi13	Gioria and Osborne (2009b)	*Gunnera tinctoria*	Perennial herb	Vegetative present	Long	Grassland	−2.551	0.907	−1.957	0.739
Gi14	Gioria and Osborne (2009b)	*Gunnera tinctoria*	Perennial herb	Vegetative present	Long	Grassland	−2.453	0.876	−2.644	0.937
Gi15	Gioria and Osborne (2010)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Ruderal	−5.048	2.093	−21.072	28.252
Gi16	Gioria and Osborne (2010)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Ruderal	−3.310	1.185	−4.306	1.659
Gi17	Gioria and Osborne (2010)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Riparian or coastal	−14.130	12.979	−18.183	21.163
Gi18	Gioria and Osborne (2010)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Riparian or coastal	−8.278	4.783	−6.768	3.363
Gi19	Gioria and Osborne (2010)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Ruderal	−19.680	24.706	−19.069	23.227
Gi20	Gioria and Osborne (2010)	*Fallopia japonica*	Perennial herb	Vegetative present	No	Ruderal	−5.883	2.663	−3.518	1.273
Vi21	Vilà and Gimeno (2007)	*Oxalis pes-caprae*	Annual herb	Vegetative present	No	Ruderal	0.194	0.251	−1.275	0.301
Vi22	Vilà and Gimeno (2007)	*Oxalis pes-caprae*	Annual herb	Vegetative present	No	Ruderal	−1.103	0.288	0.610	0.262
Vi23	Vilà and Gimeno (2007)	*Oxalis pes-caprae*	Annual herb	Vegetative present	No	Ruderal	−0.035	0.250	−0.215	0.251
We24	Wearne and Morgan (2006)	*Cytisus scoparius*	Shrub	Seed only	Short	Forest	0.000	0.125	0.325	0.127
We25	Wearne and Morgan (2006)	*Cytisus scoparius*	Shrub	Seed only	Short	Forest	0.276	0.126	0.523	0.129
We26	Wearne and Morgan (2006)	*Cytisus scoparius*	Shrub	Seed only	Short	Forest	0.323	0.127	−4.749	0.477
We27	Wearne and Morgan (2006)	*Cytisus scoparius*	Shrub	Seed only	Short	Forest	−0.689	0.132	−2.926	0.259
St28	Standish et al. (2001)	*Tradescantia fluminensis*	Perennial herb	Vegetative present	No	Forest			−0.181	0.223
St29	Standish et al. (2001)	*Tradescantia fluminensis*	Perennial herb	Vegetative present	No	Forest			0.565	0.231
Fi30	Fisher et al. (2009)	*Ehrharta calycina*	Perennial grass	Vegetative present	Long	Forest	−1.525	1.291	−1.344	1.226
Fi31	Fisher et al. (2009)	*Pelargonium capitatum*	Perennial herb	Seed only	Short	Forest	−3.465	2.501	−2.041	1.521
Ho32	Holmes and Cowling (1997)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−2.796	0.198	−1.643	0.098
Ho33	Holmes and Cowling (1997)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−3.494	0.253	−2.457	0.125
Ho34	Holmes and Cowling (1997)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−1.155	0.117	0.070	0.075
Ho35	Holmes and Cowling (1997)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−2.026	0.151	−0.226	0.075
Ho36	Holmes and Cowling (1997)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−0.439	0.082	−1.995	0.096
Ho37	Holmes and Cowling (1997)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−2.319	0.134	−1.968	0.095
Ho38	Holmes (2002)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−0.695	0.106	−0.564	0.104
Ho39	Holmes (2002)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−2.008	0.150	−0.011	0.100
Ho40	Holmes (2002)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	0.088	0.100	−0.536	0.104
Ho41	Holmes (2002)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−1.041	0.114	−0.660	0.105
Ho42	Holmes (2002)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−0.291	0.101	−0.582	0.104
Ho43	Holmes (2002)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	−0.851	0.109	−0.934	0.111
Tu44	Turner et al. (2008)	*Asparagus asparagoides*	Perennial vine	Vegetative present	No	Forest			−0.045	0.333
He45	Herrera and Nassar (2009)	*Kalanchoe daigremontiana*	Annual succulent	Vegetative present	Short	Shrubland	−0.146	0.201	1.173	0.234
He46	Herrera and Nassar (2009)	*Stapelia gigantea*	Perennial succulent	Vegetative present	Transient	Shrubland	0.444	0.205	0.625	0.210
Ga47	Gaertner et al. (2011)	*Acacia saligna*	Tree	Seed only	Long	Shrubland	0.643	0.140	0.554	0.139
Ga48	Gaertner et al. (2011)	*Eucalyptus cladocalyx*	Tree	Seed only	No	Shrubland	−0.211	0.134	−0.656	0.141
Ga49	Gaertner et al. (2011)	*Pennisetum clandestinum*	Perennial grass	Vegetative present	No	Shrubland	0.193	0.134	0.294	0.135
Ab50	Abella et al. (2012)	*Pennisetum ciliare*	Perennial grass	Vegetative present	Short	Desert	0.610	0.161	0.510	0.159
Gi51	Giantomasi et al. (2008)	*Pyracantha angustifolia*	Shrub	Seed only	Long	Shrubland	−0.005	0.125	−0.682	0.132
Gi52	Giantomasi et al. (2008)	*Pyracantha angustifolia*	Shrub	Seed only	Long	Shrubland	0.339	0.127	0.352	0.127
Ab53	Abella et al. (2013)	*Pennisetum ciliare*	Perennial grass	Vegetative present	Short	Desert			0.282	0.841
Go54	González-Muñoz et al. (2012)	*Acacia dealbata*	Tree	Seed only	Long	Forest	0.355	0.406	−0.056	0.400
Go55	González-Muñoz et al. (2012)	*Acacia dealbata*	Tree	Seed only	Long	Forest	−0.432	0.409	−1.330	0.488
Go56	González-Muñoz et al. (2012)	*Acacia dealbata*	Tree	Seed only	Long	Forest	−5.045	1.673	−5.771	2.065
Ma57	Mason et al. (2007)	*Chrysanthemoides monilifera*	Shrub	Seed only	Long	Riparian or coastal	−0.828	0.434	0.792	0.431

fail-safe number established following Rosenthal (1979). We then examined whether the effect sizes, $\bar{E}$, significantly differed between the paired comparisons and whether there was significant heterogeneity between the paired comparisons. This was performed by calculating cumulative effect size $\bar{E}$ and total heterogeneity Q_T (Hedges and Olkin, 1985) and by plotting the effect sizes of individual cases with their confidence intervals (Rosenberg et al., 2000). Negative effect sizes signify a decrease in seed bank richness or seed bank density in invaded communities. Cumulative effect sizes are considered small (up to 0.2), medium (0.5), large (0.8) and very large (> 1), following Cohen (1969).

As a second step, in the case of significant total heterogeneity Q_T, we examined effect sizes for two categorical explanatory variables associated with each case, i.e. (i) identity of the invasive species ('invading species'), and (ii) habitat type in which invasion occurs, using a broad classification of habitats into seven groups ('habitat') (Table 1, Tables S1 and S2). We tested whether there were significant differences within each variable by calculating heterogeneity for its grouping factors, meaning e.g. for the invading species whether there are significant differences in effect sizes between individual invasive species. This was performed by calculating between group variability Q_B, mean effect size, and its 95% confidence interval for each grouping factor (Hedges and Olkin, 1985). Non-overlapping confidence intervals indicate that the grouping factors are significantly different (Rosenberg et al., 2000).

Publication BIAS

Data on seed bank richness indicated only slight or no publication bias. It is possible that there might be a bias against publishing negative results showing no significant difference in seed bank richness, and cases with larger sample size might have more power to detect significant differences between invaded and uninvaded sites. However, our analyses showed that these potential biases were quite unlikely to change the overall direction of the results of our separate analyses for native and total seed banks. Graphical checks by funnel plots (Figs. S1–S3) showed a skew only towards large effect sizes but did not indicate that cases with small effect or non-significance were omitted. Moreover, normal quantile plots (Figs. S1–S3) were indicative of normal distributions, thus conforming to the assumption on which most meta-analytical procedures are based. Standardized effect sizes of the total seed bank were negatively (Spearman's rank correlation $r_S = -0.27$) but only marginally significantly ($P = 0.05$) associated with sample size. This suggests that cases with small sample sizes could be slightly more likely to be published when large differences between invaded and uninvaded areas are found. No such tendency appeared for the native seed bank ($r_S = 0.16$; $P = 0.33$). Fail safe numbers, i.e. the numbers of cases that would have to be added to change the results of the meta-analyses of seed bank richness from significant to non-significant, were 5 268 and 5 301 for total and native seed banks, respectively, i.e. values much larger than their conservative theoretical assessments, 275 and 250, respectively.

Data on seed bank density did not indicate any publication bias. Graphical tests by funnel plots and normal quantile plots were consistent with results on seed bank richness (Figs. S4–S6). For native and total seed banks, standardized effect sizes were not significantly associated with sample sizes (Spearman's rank correlation for all and native species, respectively: $r_{ST} = 0.23$, $P = 0.09$; $r_{SN} = 0.09$, $P = 0.52$) and fail safe numbers were respectively 4287 and 4525, i.e. much larger than conservative theoretical assessments of these numbers, 295 and 255. We are thus quite confident that the observed results can be treated as reliable estimates of effect sizes. Similarly to patterns for species richness, rank

correlation tests and calculations of fail-safe numbers were not applied on alien species because their cumulative effect size was only medium ($\bar{E} = -0.242$) and, more importantly, non-significant (confidence interval CI = −0.563 to 0.031).

Results

Impact on seed bank species richness and density

Cumulative effect sizes for *native seed bank richness* were large ($\bar{E} = -1.868$; CI = −2.500 to −1.365). Of 47 cases for which this information was available, 32 indicated significant decreases in invaded sites, while the rest yielded non-significant results. None of the cases reported increases in native seed bank richness on invaded sites (Fig. S7a).
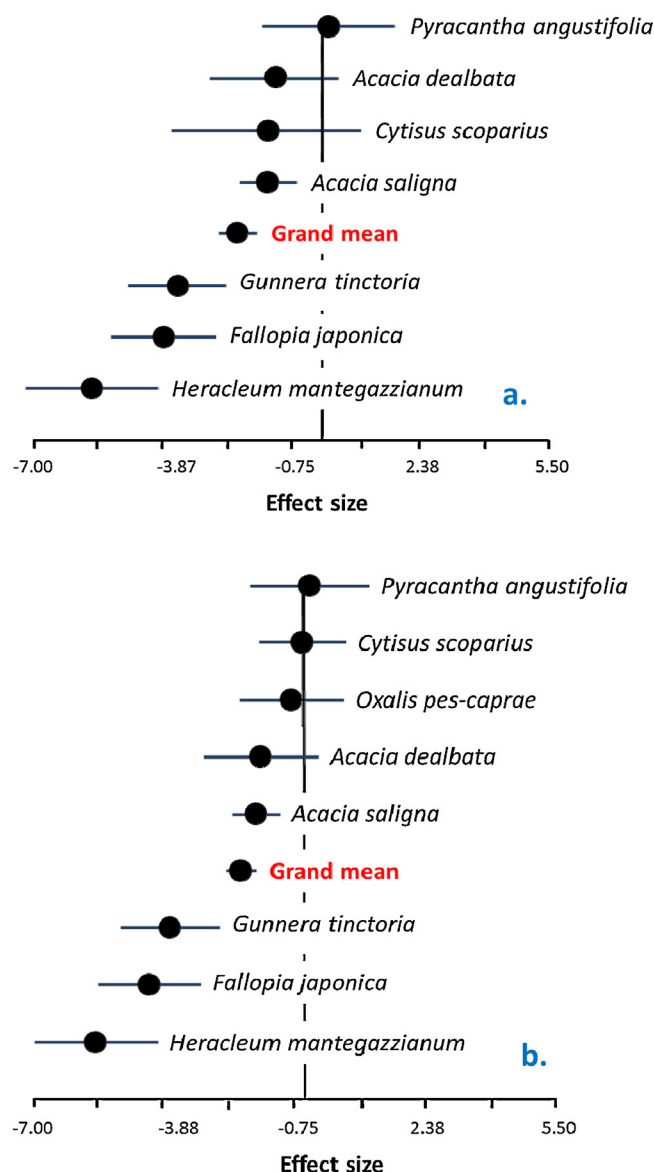

Fig. 1. Group effect sizes for 'invading species' and 95% bias-corrected bootstrapped confidence intervals for *species richness* in the (a) native and (b) total seed bank. Grand Means are cumulative effect sizes. Groups with fewer than two studies were eliminated from the analyses. Confidence intervals that do not cross the zero *y*-axes are statistically significant. Negative effect sizes mean decrease of seed bank richness on invaded plots.

Native seed bank density also displayed large cumulative effect size ($\bar{E} = -0.935$; CI = -1.370 to -0.591). Twenty-five out of 49 applicable cases showed significant decreases in density of the native seed bank, one case an increase, while for the 23 remaining studies the effect of invasion was not significant (Fig. S7b).

The impact of invasions on *total seed bank richness* also yielded large a cumulative effect size ($\bar{E} = -1.501$; CI = -2.020 to -1.085); of 53 cases, 31 indicated significant decreases, 22 non-significant results, and none an increase (Fig. S8a). *Total seed bank density* exhibited a medium cumulative effect size ($\bar{E} = -0.660$; CI = -0.007 to -0.366), with 25 cases among the total of 57 displaying decreases in invaded sites, one increase, while the remaining were not significantly different between invaded and uninvaded plots (Fig. S8b).

Invading species causing the largest changes in the seed bank

Invasions by *Heracleum mantegazzianum*, *Fallopia japonica*, *Gunnera tinctoria*, and *Acacia saligna* significantly reduced native seed bank richness and density, with the first species having the largest impact on native (Fig. 1a) and total (Fig. 1b) seed bank richness, while *F. japonica* had the greatest impact on native (Fig. 2a) and total (Fig. 2b) seed bank density. Invasions by *Acacia dealbata* and *Cytisus scoparius* also resulted in a decrease in total seed bank density (Fig. 2b).

Habitats prone to the largest changes in the seed bank

For *native seed bank richness*, between-group variability indicated a significant effect of invading species and habitat (Table 2).
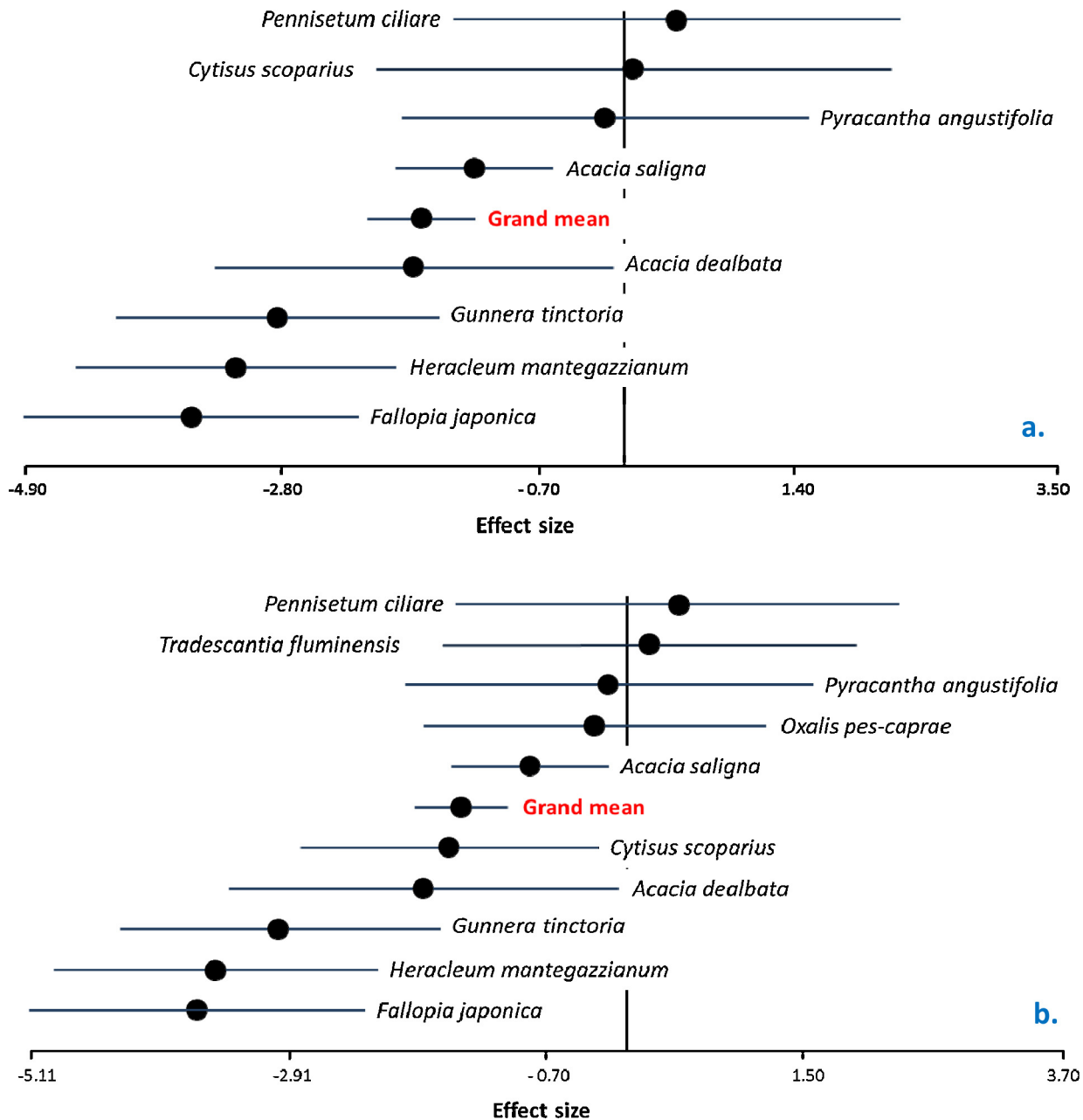

Fig. 2. Group effect sizes for 'invading species' and 95% bias-corrected bootstrapped confidence intervals for *density* of the (a) native and (b) total seed bank. Grand Means are cumulative effect sizes. Groups with fewer than two studies were eliminated from the analyses. Confidence intervals that do not cross the zero *y*-axes are statistically significant. Negative effect sizes mean decrease of seed bank richness on invaded plots.

Table 2
Between-group variability (Q_B) and its randomized probability for grouping variables of the tested explanatory variables of seed bank richness and density for total and native seed banks. Groups with fewer than two studies were eliminated from the analyses.

Measure	Factors	Total seed bank			Native seed bank		
		df	Q_B	Random probability	df	Q_B	Random probability
Species richness	Invading species	7	63.0899	0.001	6	43.83	0.001
	Habitat	4	46.2624	0.001	4	64.3251	0.001
Density	Invading species	9	38.0077	0.011	7	28.3857	0.017
	Habitat	5	26.6565	0.018	5	40.4912	0.001

Native seed bank richness was significantly reduced in all habitats, with the greatest effect in riparian, coastal or ruderal habitats, and lowest in forest and shrubland (Fig. 3a). Between-group variability indicated significant effects of invading species and habitat (Table 2) also for *native seed bank density*, which was significantly reduced in all habitats but desert, most so in ruderal or riparian habitats (Fig. 4a).

For *total seed bank richness*, between-group variability indicated a significant effect of invading species and habitat (Table 2), with patterns for the former factor similar to those found for native seed bank richness, but differing for habitats in forest or shrubland, which no longer were characterized by significantly reduced richness (Fig. 3b). Between-group variability indicated significant effects of invading species and habitat for *total seed bank density*,
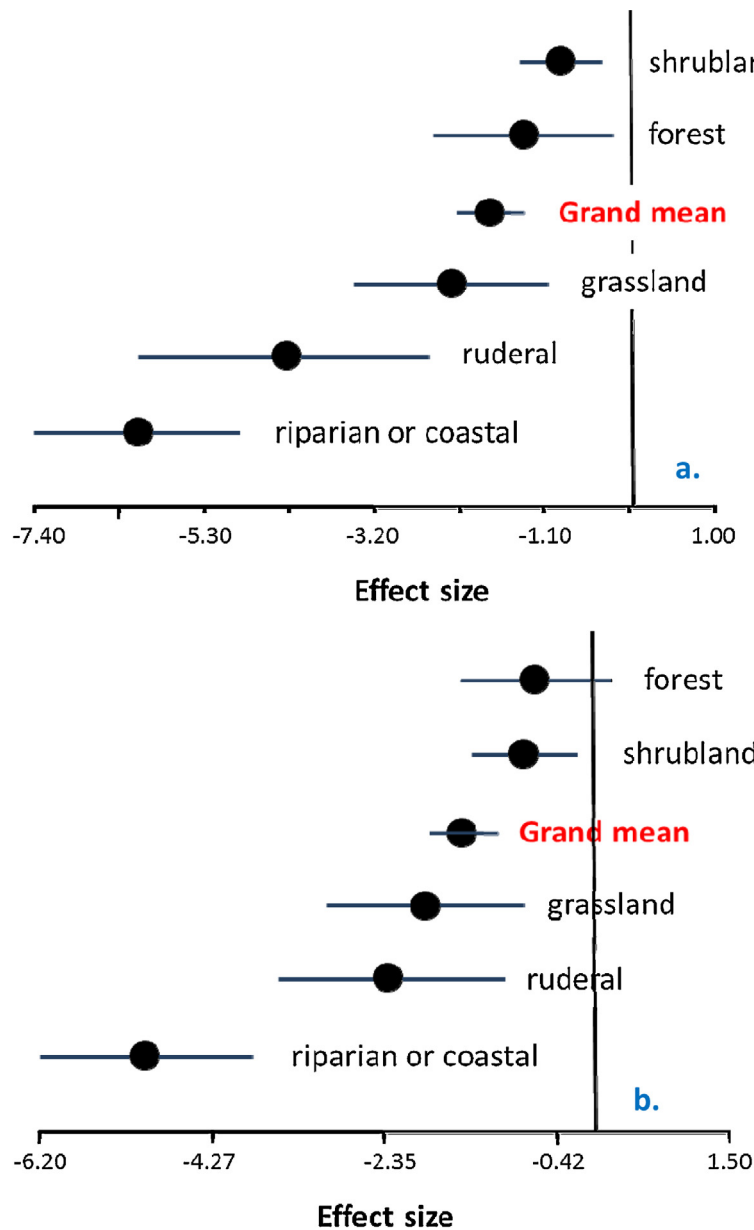

Fig. 3. Group effect sizes for 'habitats' and 95% bias-corrected bootstrapped confidence intervals for *species richness* in the (a) native and (b) total seed bank. Grand Means are cumulative effect sizes. Groups with fewer than two studies were eliminated from the analyses. Confidence intervals that do not cross the zero *y*-axes are statistically significant. Negative effect sizes mean decrease of seed bank richness on invaded plots.
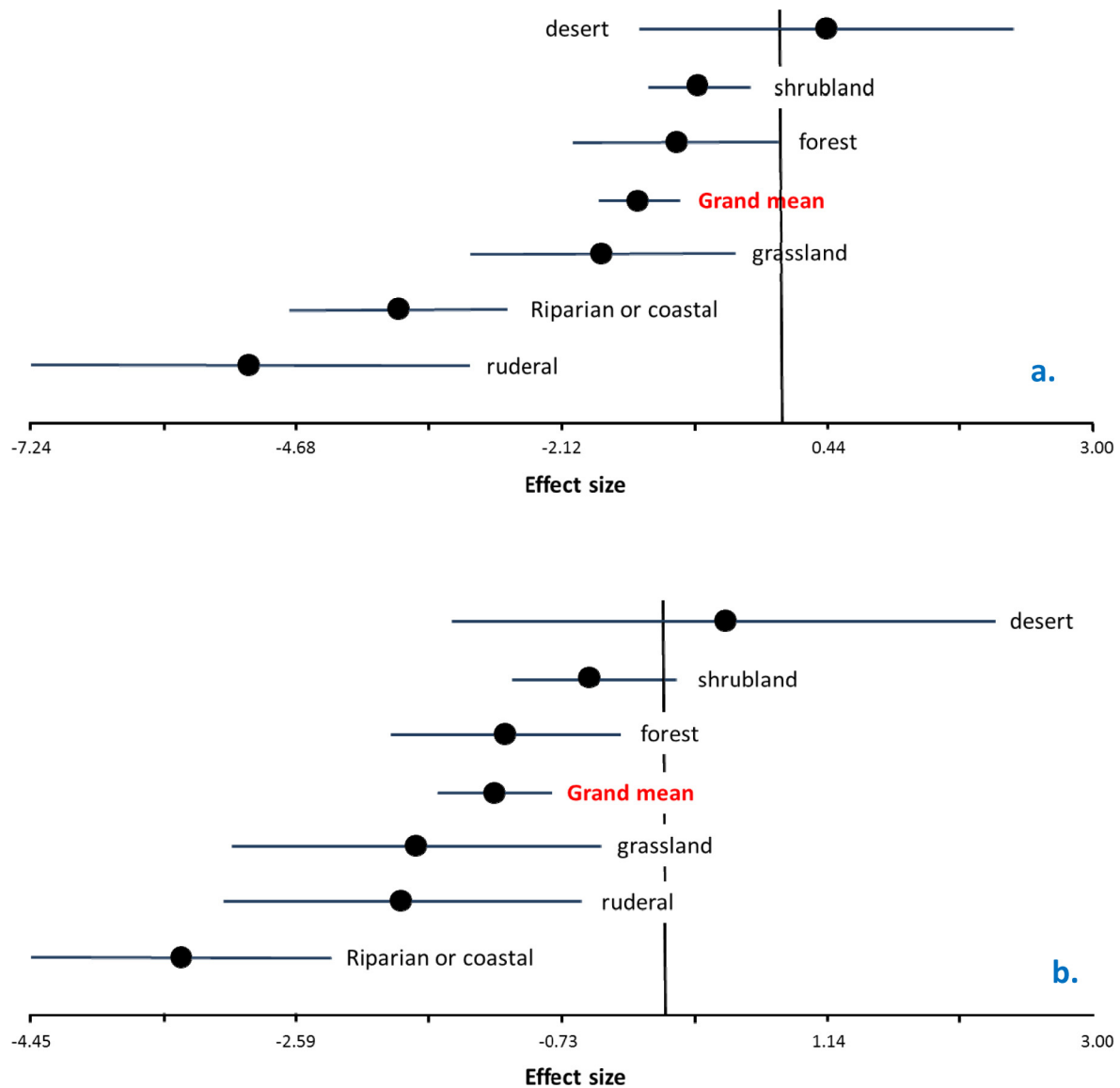
Fig. 4. Group effect sizes for 'habitats' and 95% bias-corrected bootstrapped confidence intervals for *density* of the (a) native and (b) total seed bank. Grand Means are cumulative effect sizes. Groups with fewer than two studies were eliminated from the analyses. Confidence intervals that do not cross the zero *y*-axes are statistically significant. Negative effect sizes mean decrease of seed bank richness on invaded plots.

this being largely reduced in invaded riparian/coastal habitats and, to a lower extent, in forest or shrubland (Fig. 4b).

Discussion

Generalities and context-specific variation in the impact of plant invasions on soil seed banks

This study yielded three key findings. First, for the majority of invading taxa and in most habitat types, species richness and density in native seed banks associated with an invader are significantly lower than those occurring in uninvaded comparable areas (68% and 58% of case studies, respectively). Negative effects on seed banks are particularly pronounced for invasions by *F. japonica*, *G. tinctoria*, and *H. mantegazzianum*, which are among the largest herbaceous species in the world (Beerling et al., 1994; Tiley et al., 1996; Krinke et al., 2005; Gioria and Osborne, 2013). The fact that the seed banks of both native and alien species are remarkably reduced in areas invaded by these stout herbs, with the exception of

species that are capable of coexisting with the invader and setting persistent seed (e.g. *Urtica dioica*) largely reflects the changes in species composition in above-ground vegetation associated with invasions by those species and is indicative of the importance of dispersal limitation as a mechanism that prevents seeds of species from neighbouring communities to reach the soil at invaded sites. Previous investigations showed that the impact of these invaders on species composition is similar, resulting in impoverished communities overrepresented by weedy species (Gioria and Osborne, 2009a,b, 2010). However, the time scale of the impact may differ substantially.

Gioria and Osborne (2010) and Gioria et al. (2011) showed that the high invasiveness of *F. japonica* manifests below-ground by a strong impact on seed banks, although the species is only present as a female clone in Europe and does not normally produce seed (Hollingsworth and Bailey, 2000). The rapid above- and below-ground changes that occur immediately after the invasion of this species result in alteration of the long-term persistent seed banks of many species, including that of another effective invader in the

same community, such as *G. tinctoria*. This suggests that *F. japonica* may not only depauperate seed banks via alterations in the seed rain associated with the formation of virtually mono-specific and often dense stands, but also via alterations in seed viability and senescence, and in the structure of predators and/or pathogens (Gioria et al., 2011).

Invasions by *Acacia* species in fynbos ecosystems, mainly *A. saligna*, were also associated, in general, with a reduced species richness and density of the native seed bank, although the impact was smaller than that associated with invasions by large herbaceous species. This could be due to the fact that, despite the large canopy and litter produced by *Acacia* species, their overall capacity to limit the dispersal of seeds from surrounding areas might be lower than that of tall herbs (González-Muñoz et al., 2012) and/or it might act on a different temporal scale (Le Maître et al., 2011). Holmes and Cowling (1997) showed that *A. saligna* invasions had a negative effect on species richness and density in the seed bank as well as in the vegetation; however, changes in the seed bank were relatively small, suggesting that some fynbos species might form a long-term persistent seed bank. While uninvaded seed banks contained both short- and long-lived species, in particular long-lived ericoid shrubs, invaded seed banks contained relatively high densities of short-lived, wind-dispersed shrubs, with the seeds of the annual sedge, *Isolepis marginata*, present in large numbers. This is consistent with findings by Holmes (2002) in sand plain fynbos, where native seed banks were also of lower density and formed by a reduced number of species. There, invaded seed banks were dominated by ephemerals and short-lived species, confirming the long-term persistence of their propagules and their large number (e.g. Thompson et al., 1998), while persistent ericoids were better represented in uninvaded seed banks. Gaertner et al. (2011), who investigated the impact of *A. saligna* invasions in a natural fynbos community on the Agulhas Plain, South Africa, also found that native seed bank richness was similar under invaded and uninvaded *Acacia* stands, possibly reflecting the generally low species richness of fynbos seed banks as well as the fact that the cover of native species under *Acacia* stands did not differ significantly from that in uninvaded sites.

For some invasions, however, the impact on the total or native seed bank species richness and/or density was not significant, including invasions by *Oxalis pes-caprae* or *Pennisetum* species (e.g. Vilà and Gimeno, 2007; Gaertner et al., 2011; Abella et al., 2012, 2013). This was so despite substantial post-invasion changes in standing vegetation as well as in seed bank composition, indicating that the seed rain and seed persistence of some native species is likely to maintain the seed bank relatively unaltered, at least until major changes in the vegetation or other disturbances occur. Considerations on the time since the invasion, or residence time, at the time of sampling could provide additional insights into the velocity of the changes in the seed bank. Due to the scarcity of detailed information on residence times for many species, we could not quantify the effect of the duration of an invasion on changes in the seed bank. We can expect that, as an invasion process proceeds, changes in the composition of the above-ground vegetation will increasingly affect the seed bank, with overall effects on the vegetation additive or even multiplicative (Gioria and Osborne, 2010). Although seeds of many species can survive in the soil for long periods of time, the size of the seed bank of any species is a function of the period of time since it has disappeared from the vegetation (Roberts and Feast, 1973; Roberts, 1981; Bakker et al., 1996). Thus, in the long term, in the absence of or under reduced recruitment of seeds from the vegetation, natural seed senescence processes, and potential alterations in the viability of persistent seeds in the soil will almost inevitably result in substantial alterations in the seed bank (e.g. Marchante et al., 2011; González-Muñoz et al., 2012), including

its more persistent component (see Gioria and Osborne, 2009a,b, 2010; Gioria et al., 2011). Certain species, however, showed a capacity for altering the seed bank within few years only (e.g. *F. japonica*; Gioria and Osborne, 2010).

Clearly, the paucity of studies assessing directly the impact of plant invasions on the seed bank does not allow us to reach robust conclusions on whether the magnitude and direction of this type of impact is dependent on the traits of the invader or those of the species found in invaded communities, whether it is strongly habitat-specific or a combination of those. The patterns reported here are to a large extent driven by several species whose impact on seed banks has been most intensively studied and by a skew towards habitats and ecosystems that are naturally disturbed or to which alien species have been intentionally or unintentionally introduced, while studies on invaded seed banks in formerly pristine areas are rare. The lack of reliable information on the duration of the invasion at the time of sampling for the majority of cases, also does not allow us to draw many conclusions about the time frame of changes in the seed bank. These limitations must be accounted for when attempting to generalize the impact of plant invasions on such a highly variable component of many plant community types in space and time.

The role of seed banks in secondary invasions

Our study reveals that areas identified by the original authors as uninvaded, based on the assessment of above-ground vegetation, already contain alien seed banks of varying richness and density that are further modified when the site becomes invaded. A larger total seed bank density and species richness, reflecting a larger seed bank for alien species in a few studies included in our meta-analysis, could be a symptom of environmental degradation prior to invasion (Turner et al., 2008; Gioria and Osborne, 2010; Gaertner et al., 2011) associated with the intentional or unintentional introduction of alien species. Alien seed bank richness and/or densities were typically higher in areas invaded by *Acacia* species (Gaertner et al., 2011) compared to uninvaded ones. Invasions by *A. dealbata* Link in native *Quercus robur* L. forests in north-western Spain also showed a higher relative density of alien species in invaded seed banks, mainly belonging to the genus *Conyza* (65%), i.e. annual, wind-dispersed, nitrophilous herbaceous species that could be favoured by increases in available nitrogen by *A. dealbata* at the study sites (González-Muñoz et al., 2012). These patterns are similar to those reported by Holmes and Cowling (1997) and Holmes (2002) in South-African fynbos invaded by *A. saligna*, as well as with findings by Marchante et al. (2011) in Portuguese coastal sand dunes invaded by *Acacia longifolia*, where *Acacia* invasion severely impoverished the invaded seed bank, which were associated with increases in the presence of wind-dispersed species, and were dominated by seeds of alien species, also including *Conyza* species.

The invasion by *Pennisetum clandestinum* in fynbos ecosystems (Gaertner et al., 2011) also had a positive, though marginally significant, effect on species richness and density of the alien seed bank. A higher species richness and density of the seed bank of alien species were reported by Turner et al. (2008) in *Banksia* woodland invaded by *Asparagus asparagoides* (L.) Druce, where seeds of long-lived native species had been replaced with those of short-lived species and with seeds of alien species. In their examination of the impact of the invasive shrub *Pyracantha angustifolia* on the seed bank in a montane shrubland (Córdoba, Argentina), Giantomasi et al. (2008) also reported a dominance of alien species in the seed bank of both invaded and uninvaded areas, with seed density of alien forbs being significantly higher below *P. angustifolia* stands compared to that below the native shrub *Condalia montana*. This could be indicative of some form of ecological degradation prior to

an invasion, which could have resulted in the intentional or unintentional introduction of alien species, rather than of a positive effect of *P. angustifolia* on the dispersal of alien species (Giantomasi et al., 2008).

Turner et al. (2008) pointed out that seeds of alien species may be regarded as 'sleeper cells' that, under changing environmental or biotic conditions, may exhibit their invasive potential by replacement of long-lived native species with short-lived alien species. For instance, changes in the seed bank could represent at least one of the mechanisms playing some role in invasions of grassland communities by annuals, such as invasions in tussock temperate grasslands in North America by Eurasian annuals (see Seastedt and Pyšek, 2011). Depauperation of seed banks of native species, combined with large numbers of alien seeds present at invaded sites, could ultimately promote 'secondary' invasion by alien species or native weeds (Gioria et al., 2012), i.e. invasions at sites that had been previously invaded by other invasive alien species. This may have major consequences for the resilience of a community to invasions by lowering (1) the potential for recruitment of a population from the seed bank; (2) the 'bet hedging' (*sensu* Venable, 1989) potential of the species in a community, i.e. the capacity of the species in a community to respond to environmental variability; and (3) the number of functional groups and traits in a community. In summary, a decline in either species richness and/or seed density will likely undermine the biotic resistance of native communities to invasions. Moreover, seed diversity and density of resident species are important determinants of ecological resistance, or community invasibility, because they buffer the effects of the displacement of species from and changes in their abundance in vegetation (Pugnaire and Lazaro, 2000; Brown and Fridley, 2003).

Given the observational nature of studies used in our analyses, however, it is not possible to establish whether invasions by alien species can promote the establishment and spread of other alien species by alterations in the seed bank of invaded communities, in agreement with the 'invasional meltdown hypothesis' (Simberloff and von Holle, 1999); nor can we disentangle the effects of alien species on the native ecosystems from the effects of the disturbance that led to the initial plant invasion (Gurevitch and Padilla, 2004; Turner et al., 2008; Gaertner et al., 2011). This limitation points to the lack of studies on the topic and calls for experiments carefully designed to disentangle the role seed bank could play in secondary invasions.

Conclusions

To the best of our knowledge, this is the first study attempting to quantify the impact of plant invasions on soil seed banks for multiple invading species, at the community level, and in a variety of habitat types. We showed that invasions ultimately result in some form of impact on seed banks, either on species richness, seed density, or both, with the seed bank of alien species being often richer or larger in invaded communities. The effects of invasive species appear to be remarkable where the invader is a large herbaceous perennial species. Changes in the seed bank may be directly associated with an invasion and/or be a symptom of environmental degradation, although the majority of studies used in this meta-analysis could not be used to test this hypothesis. Despite the limitations of our study resulting from the paucity of studies examining this type of impact, our findings represent a starting point to improve our understanding of the long-term implications for plant community dynamics following the introduction of invasive alien plants, by providing a robust assessment of the impact of different invasive species, often with contrasting reproductive strategies, as well as indication of habitats that are more prone to

become strongly impacted by plant invasions. This study provides information that is important for developing sustainable restoration strategies, which should include the control of the seed bank of those alien species that can potentially become invasive after the accumulation of large seed banks and should account for the depletion of the seed bank of native species. Our study also emphasizes the need for more comprehensive information on the impacts of plant invasions on soil seed banks that would improve our understanding and ability to predict the magnitude and direction of the impacts as well as to reveal to what extent they are correlated with traits of the invading species and invading habitat.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2014.03.003.

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