Soil seed banks in plant invasions: promoting species invasiveness and long-term impact on plant community dynamics

Půdní semenná banka v rostlinných invazích: vliv na invazivnost druhů a dlouhodobou dynamiku společenstev

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Invasions by alien plant species significantly affect biodiversity and ecosystem functioning. Investigations of the soil seed banks of invasive plant species and changes in the composition and structure of resident seed banks following plant invasions can provide valuable insight into the long-term implications of plant invasions. Soil seed banks play a major role as reservoirs of species and genetic diversity and allow for the persistence of a species at a locality, buffering environmental changes that may occur over time. Despite the emerging body of literature on ecological impacts of invasive plants on the diversity of resident communities, the long-term implications of impoverished soil seed banks for vegetation dynamics and ecosystem functioning have only recently begun receiving attention. Evidence has so far indicated that there is a correlation between the invasiveness of a species and the characteristics of its seed bank, and that changes in the seed banks of resident communities associated with plant invasions affect their biotic resistance to primary and secondary invasions. To promote the study of soil seed banks in the context of invasive species, we (i) summarize the functional roles of soil seed banks; (ii) describe how the capacity to form a seed bank may contribute to a species’ invasiveness using data from the flora of the Czech Republic, showing an increasing representation of species capable of forming long-term persistent seed bank from casual to naturalized to invasion stage; (iii) assess the impact of invasive plants on seed banks of resident communities, including the potential creation of conditions that favour secondary invasions by other alien species or native weeds, and long-term implications of such impact; and (iv) describe the potential effects of climate change on the soil seed bank in the context of plant invasions. We conclude with highlighting promising avenues for future research on invaded soil seed banks, and emphasize the importance of this knowledge in the development of control programs and restoration strategies.

Keywords: climate change, control, community dynamics, impact, plant invasions, restoration, seed persistence, soil seed bank, species invasiveness

Introduction

by subsequently altering ecosystems via changes in e.g. primary productivity, hydrology, fire frequency and intensity, and nutrient cycling (Vitousek et al. 1987, Cronk & Fuller 2001, Ehrenfeld 2003, 2004, 2006, Wardle et al. 2011).

Ultimately, the long-term implications of plant invasions for ecosystem functioning depend on the persistence of an invader at a locality and on the buffering capacity of resident communities against the full or partial displacement of species in the standing vegetation (Thuiller et al. 2008, Gioria et al. 2011). Characterizing the impact of plant invasions on resident communities and subsequent ecosystem functioning requires an understanding of how invasive species affect resident plants over their entire life cycle, from seed development and seedling recruitment through reproduction (see Gioria & Osborne 2010, Gioria et al. 2011 and references therein). Depauperation of the soil seed bank and changes in vegetation associated with plant invasions, as reported by several studies (Holmes 2002, Seabloom et al. 2003, Turner et al. 2008, Fisher et al. 2009, Gioria & Osborne 2009a, b, 2010), can be considered as indicators of ecosystem degradation due to invasion (Gaertner et al. 2009, Catford et al. 2012).

Recent studies highlight the importance of evaluating changes in the seed bank of invaded communities (i) to predict the long-term impact of invasive species on vegetation (e.g. Brock 2003, Krinke et al. 2005, Fourie 2008, Vosse et al. 2008, Gioria & Osborne 2009a, 2010), (ii) to develop sustainable strategies aimed at controlling the spread of invasive species (e.g. Pyšek et al. 2007b, Richardson & Kluge 2008, Pardini et al. 2009, 2011, Pyšek & Richardson 2010), and (iii) to evaluate the restoration potential of a site after the removal of an invader (e.g. Holmes et al. 2000, Zavaleta et al. 2001, Wearne & Morgan 2006, Bossuyt et al. 2007, Fourie 2008, Gaertner et al. 2011, Marchante et al. 2011). While reproductive traits and the seed bank have been investigated for a range of invasive species (Table 1; Moravcová et al. 2010, see also Pyšek & Richardson 2007 for a review), the long-term effects of invasive species on ecosystem functioning, including the invasibility of an ecosystem via alterations in the seed bank, have only been little explored (Gaertner et al. 2009, 2011, Gioria et al. 2011).

Here, we aimed to (i) summarize the functional roles of seed banks; (ii) describe how the capacity to form a seed bank may contribute to a species’ invasiveness, and illustrate this phenomenon by using data from the alien flora of the Czech Republic; and (iii) describe the impact of invasive plants on the seed banks of resident communities, including potential facilitation of secondary invasions and implications of ongoing climate change. The ultimate goal of this paper is to encourage consideration of seed banks in studies on the impact of invasive species. Such information is central to the development of effective conservation, management and control strategies, and could provide valuable insight into the mechanisms underlying the invasiveness of a species and the invasibility of a community.

Table 1. – Information on the size and type of seed bank for a range of invasive species, investigated in their invaded range. The values presented here are estimates obtained under invasive stands only. Seed bank density is expressed as seedlings/m$^2$, obtained by the seedling emergence approach; those estimates that were obtained by seed counting method are expressed as seeds/m$^2$ and indicated by the letter a. Some studies reported mean values only, others range values, that are shown below as minimum and maximum soil seed bank density. If mean±S. D. is given, the values refer to the lowest and highest means obtained from multiple sites, plots or habitats, or at different times in the season (see original studies for details). When only one value was given, it is indicated in the ‘Mean’ column. When explicitly indicated in the original study, information on the type of seed bank (sensu Thompson et al. 1997) is also shown: P – persistent, T – transient, STP – short-term persistent, LTP – long-term persistent. Life history (LH): af – annual forb, pf – perennial forb, ag – annual grass, pg – perennial grass, psucc – perennial succulent, s – shrub, t – tree.
<table>
<thead>
<tr>
<th>Species</th>
<th>LH</th>
<th>Region of origin</th>
<th>Invaded range</th>
<th>Habitat</th>
<th>Seed bank density (per m$^2$)</th>
<th>Type</th>
<th>Study</th>
</tr>
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<tr>
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<td>3600±279$^a$</td>
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<td>SW Australia</td>
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<td>Mean</td>
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<td>Ireland</td>
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<td>S and C America, Asia, Pacific Islands</td>
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<td>Solanum mauritianum</td>
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<td>S Africa</td>
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<td>66±32</td>
<td>554±228</td>
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<td>Vulpia myuros</td>
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<td>California</td>
<td>coastal sage scrub</td>
<td>4</td>
<td>506</td>
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</tbody>
</table>

b seedlings of all alien *Acacia* species under invasive *Acacia saligna* stands

cumulative number of seedlings collected from 20 × 20 × 20 cm samples (n = 16)
Functional roles of soil seed banks

Soil seed banks are a reserve of viable seed in the soil or on its surface (Roberts 1981) produced in the most recent reproductive period or over previous years (Dekker 1999). Seed banks thus represent a ‘memory’ of the past and recent vegetation (Templeton & Levin 1979). They are a major component of the life cycle of sexually reproducing species and an important source of plant diversity (Roberts 1981, Fenner 1985, Chesson et al. 2004) because they play a central role in species’ recruitment and establishment (Harper 1977, van der Valk & Davis 1978). Moreover, seed banks may facilitate the coexistence of potentially competing species and mitigate the effects of inter- and intraspecific competition (Rees & Long 1992, Pake & Venable 1995). This role has also been described as the ‘storage effect’ (e.g. Chesson 1994, Chesson et al. 2004), a mechanism of coexistence that allows many species to persist at the same locality because they have different means of responding to changing environmental conditions and of using resources.

Soil seed banks represent a form of dispersal in space and time, allowing the colonization of new localities (Thompson & Grime 1979, Baker 1989, Dekker 1999, Chesson et al. 2004). Thompson et al. (1997) classified seed banks as transient (<1 year), short-term persistent (1–5 years) or persistent (>5 years), based on their longevity. This classification provides useful information on the potential persistence of a species at a locality even in the absence of further introductions. Seed banks can be composed of both non-dormant and dormant seeds (Bell 1999, Thompson et al. 2001), which may enhance the probability of persistence of a species at a locality when conditions for germination are not favourable (Harper 1977, Thompson & Grime 1979, Venable & Brown 1988, Baker 1989) and/or in the absence of additional seed rain (Baskin & Baskin 1998). This is particularly important for the survival of rare species (Thompson 1993, Bakker et al. 1996, Thompson et al. 1997) and the persistence of plant populations in highly variable or disturbed environments (Cohen 1966, Livingston & Allessio 1968, Grime 1989, van der Valk & Pederson 1989, Hodgson & Grime 1990, Adams et al. 2005), where the formation of a seed bank provides a species with some degree of resilience and an improved ability to respond to unpredictable conditions, thus reducing its vulnerability to local extinctions (Houle & Phillips 1988, Venable & Brown 1988, Stöcklin & Fischer 1999).

Soil seed banks also represent a major source of genetic variability, enabling a range of responses to environmental variability (e.g. Templeton & Levin 1979, Venable & Brown 1988, Baker 1989, Levin 1990) and buffering populations against changes in genetic composition that may occur following severe fluctuations in population size. The formation of a seed bank may delay the rate of response to selection in juvenile or adult characteristics (Levin 1990) and affect evolutionary processes by biasing selection towards traits favoured in years of high seed yield (Templeton & Levin 1979, Brown & Venable 1991). Templeton & Levin (1979) showed that, for annual species, seed produced in ‘good’ years dominated the soil seed banks compared to those produced in unfavourable years. Since seed banks are formed by overlapping generations of seeds from individuals that reproduce periodically, they may serve as an ‘evolutionary filter’ that, over time, eliminates the selective impact of environmental conditions experienced in certain years (Templeton & Levin 1979).

The ecological functions performed by soil seed banks make their management a critical component of any restoration programme (Bakker et al. 1996, Hölzel & Otte 2001,
Vecrin et al. 2006, Bossuyt & Honnay 2008, Fourie 2008, Gaertner et al. 2009). The characteristics of the seed banks of resident communities and their changes may play a major role in determining primary and secondary invasions (Gioria et al. 2011), while the seed bank of invasive species may be an important determinant of their invasiveness at a given locality (e.g. Richardson & Kluge 2008, Gioria & Osborne 2009a, 2010). The natural seed bank of only a few species has been comprehensively examined in their invasive range (Table 1). Extensive information has been generated on the seed bank of invasive *Acacia* species (Marchante et al. 2010, 2011, Gibson et al. 2011), particularly in the South African fynbos (e.g. Milton & Hall 1981, Pieterse & Cairns 1986, Holmes et al. 1987, Holmes 1988, 1989a, b, Holmes & Moll 1990, Morris 1997, Tozer 1998; see Richardson & Kludge 2008 for a review). For a few species only there has been a comparison of the size and type of seed bank formed in different ecosystem types, at different stages of invasion or under different climatic conditions (e.g. *Acacia longifolia*, *Heracleum mantegazzianum*, *Gunnera tinctoria*).

**Soil seed banks and species invasiveness**

Successful invasions occur when species introduced outside their native range by anthropogenic means establish self-sustaining populations and spread into new areas (Richardson et al. 2000b, Richardson & Pyšek 2006, Blackburn et al. 2011). A species’ colonization potential and its persistence at an invaded locality depend on its capacity to overcome dispersal and environmental barriers, which in turn depends upon its reproductive and dispersal characteristics (Richardson et al. 2000b, Moravcová et al. 2010).

The population growth of any species is dependent upon processes of emigration and immigration, survival, fecundity, and growth rates (Harper 1977), that are affected by abiotic conditions and biotic interactions, including competition and facilitation mechanisms (Seastedt & Pyšek 2011). Immigration rates of an invasive species are initially dependent upon propagule pressure (Colautti et al. 2006, Simberloff 2009), which has been commonly considered a good predictor of successful invasions (e.g. Williamson 1996, Lonsdale 1999, Levine 2000, Turnbull et al. 2000, D’Antonio & Thomsen 2004, Lockwood et al. 2005, 2009, Rejmánek et al. 2005, Richardson & Pyšek 2006, Pyšek et al. 2010b).

The seed bank of sexually reproducing alien plant species may be viewed as a source of propagules that enhance the probability of its establishment and persistence at a locality (Gioria & Osborne 2008, 2010). It may provide an alien species with a competitive advantage over native species due to differences in the timing of germination (Moravcová et al. 2005, Fisher et al. 2009) and/or seed persistence, and from the saturation of available microsites (Brown & Fridley 2003), which could subsequently limit the recruitment of native species (Thomsen et al. 2006, Ens & French 2008, Fisher et al. 2009, French et al. 2011).

The formation of a seed bank may also allow an alien species to overcome density-dependent effects and/or Allee effects (Allee 1931, Taylor & Hastings 2005), which may play a central role in the establishment of a species, particularly during the introduction phase and for self-incompatible founder populations (Elam et al. 2007). Recent studies showed the significance of Allee effects in determining the establishment of the invasive grass *Spartina alterniflora* (Davis et al. 2004a, b), as well as the maternal fitness of the self-incompatible invasive radish *Raphanus sativus* (Elam et al. 2007). Seed banks can
particularly favour the establishment and persistence of species introduced in disturbed habitats, such as riparian zones, or man-made corridors, such as railways and roadways (Vosse et al. 2008, Gioria & Osborne 2009b, 2010, Pyšek et al. 2010a, Albrecht et al. 2011).

Since a minimum threshold of seed density is a prerequisite for the successful establishment of a species (Brown & Fridley 2003), the time required to develop a large and/or persistent seed bank could, at least in part, explain why invasions are often characterized by a lag phase (i.e. the period between the introduction and the spread of an invasive species, prior to a rapid phase of colonization; Gioria & Osborne 2009b, 2011). As a genetic reservoir (Koch et al. 2003), the formation of a seed bank may also enhance the genetic variability of the invasive population and reduce the rate of genetic erosion (Thuiller et al. 2008). This could promote a species’ persistence at a locality by facilitating its response to environmental changes in space and time (Templeton & Levin 1979, Chesson 1994, Thuiller et al. 2008).

Despite the well-developed theoretical implications of the role of seed banks in plant invasions, quantitative evidence of seed banks actually promoting invasiveness and invasibility is rather scarce. Pyšek & Richardson (2007) reviewed available literature and found that out of 10 congeneric comparisons of alien and native species, or of alien species differing in invasiveness, six studies found significant differences in soil seed banks between the compared groups. Seed banks of alien species persisted longer than those of their native congeners in *Agropyron* (Pyke 1990) and *Polygonum* (Van Clef & Stiles 2001) and were larger in *Senecio* (Van Clef & Stiles 2001), although no difference was found for *Celastrus* and *Parthenocissus* (Van Clef & Stiles 2001). Invasive *Atriplex sagittata* was characterized by a pronounced dormancy while its non-invasive alien congener *A. hortensis* germinated immediately; a second congeneric pair studied within this genus did not differ (Mandák 2003). Neither of two invasive species, *Impatiens glandulifera* and *I. parviflora*, formed a seed bank, but the native *I. noli-tangere* formed one that is short-term persistent (Perglová et al. 2009). In a multi-species comparison of 211 invasive aliens and expanding native species, Thompson et al. (1995) found that the former were more likely to have a transient seed bank.

Unfortunately, comparative data on soil seed banks for a large number of alien species in their invasive range are lacking. Indirect predictors of a seed’s potential to persist in the soil and to form a seed bank are seed size (or mass) as well as seed shape and longevity. The fact that small and compact seeds persist longer in the soil has been illustrated with data from Britain (Thompson et al. 1993, 1998), Europe (Bekker et al. 1998, Peco et al. 2003), temperate Argentina (Funes et al. 1999) and northern China (Zhao et al. 2011). In Iran (Thompson et al. 2001) and semi-arid central China (Wang et al. 2011), only seed size was found to relate to seed persistence. Some studies associating seed characteristics with invasion success found small seed to be an advantage (Cadotte & Lovett-Doust 2001, Hamilton et al. 2005), but overall the results were ambiguous (see Pyšek & Richardson 2007 for a review). Some insight about the possible role of seed persistence in soil can be derived from a comparative study of naturalized aliens in the Czech Republic. Invasive species, compared to naturalized but non-invasive ones, had significantly lighter and more rounded seed, i.e. characteristics associated with seed persistence, although the former difference was significant only when controlling for phylogenetic relationships (Moravcová et al. 2010).
Some evidence on how seed longevity is distributed among invasive species and potentially associated with invasiveness can be obtained from data collated recently by the LEDA project (Kleyer et al. 2008) and here analysed in Fig. 1. It appears that when archaeophytes (aliens introduced until the year 1500 AD) are compared with neophytes (modern invaders introduced since that time; Pyšek et al. 2004) and with native species, they have a higher potential to form long-term persistent seed banks. This can be attributed to the fact that archaeophytes are often annual weeds of arable soil (Pyšek et al. 2005). However, separating the two groups of aliens according to the stage of invasion (sensu Richardson et al. 2000b, Blackburn et al. 2011) reveals a striking pattern, with the proportion of species reported to form long-term persistent seed banks increasing from casual to naturalized to invasive (Fig. 1). These results further suggest that successful neophytes do not have any obvious advantage over native species due to their potential to form a seed bank (the percentage of invasive neophytes with long-term persistent seed banks is similar to that of native species), but this characteristic may play a role in differentiating successful neophytes from less successful ones. A similar phenomenon has been observed for pollination patterns; the mode of pollination of central-European neophytes differed among species in particular phases of invasion but the invasive neophytes did not differ from native species (Pyšek et al. 2011).
Table 2. – List of studies addressing the effect of plant invasions on the seed banks of resident plant communities. The symbol – indicates negative effects (nat, on native species), + indicates positive effects, NS indicates that the effect was not significant (5/6, in five of six sites), SD indicates that the effect was site-dependent, while Δ indicates a variation in species composition.

<table>
<thead>
<tr>
<th>Invasive species</th>
<th>Native range</th>
<th>Invasive range</th>
<th>Study</th>
<th>Species richness</th>
<th>Abundance</th>
<th>Composition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Acacia spp.</strong></td>
<td>Australia</td>
<td>S Africa</td>
<td>Gaertner et al. 2011</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Invasive alien trees</td>
<td>Australia</td>
<td>S Africa</td>
<td>Holmes 2002</td>
<td>–</td>
<td>–</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Chrysanthemoides subsp. monilifera</strong></td>
<td>S Africa</td>
<td>Australia</td>
<td>French et al. 2011</td>
<td>– nat</td>
<td>–</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Cytisus scoparius</strong></td>
<td>Europe</td>
<td>Australia</td>
<td>Wearne &amp; Morgan 2006</td>
<td>NS 5/6</td>
<td>NS 4/6</td>
<td>NS</td>
</tr>
<tr>
<td><strong>Erharta calcyna</strong></td>
<td>S Africa</td>
<td>Australia</td>
<td>Fisher et al. 2009</td>
<td>SD</td>
<td></td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Gunnera tinctoria</strong></td>
<td>S America</td>
<td>Ireland</td>
<td>Gioria &amp; Osborne 2010</td>
<td>–</td>
<td>–</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Heracleum mantegazzianum</strong></td>
<td>Caucasus</td>
<td>Ireland</td>
<td>Gioria &amp; Osborne 2009b</td>
<td>–</td>
<td>–</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Fallopia japonica</strong></td>
<td>Asia</td>
<td>Ireland</td>
<td>Gioria &amp; Osborne 2010</td>
<td>–</td>
<td>–</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Oxalis pes-caprae</strong></td>
<td>Greece, S Africa</td>
<td>Spain</td>
<td>Vilà &amp; Gimeno 2007</td>
<td>NS</td>
<td>NS</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Pelargonium capitatum</strong></td>
<td>S Africa</td>
<td>Australia</td>
<td>Fisher et al. 2009</td>
<td>–</td>
<td>–</td>
<td>Δ</td>
</tr>
<tr>
<td><strong>Pennisetum clandestinum</strong></td>
<td>Australia</td>
<td>S Africa</td>
<td>Gaertner et al. 2011</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Multiple alien species</strong></td>
<td>Eurasia</td>
<td>California</td>
<td>Cox &amp; Allen 2008</td>
<td>–</td>
<td>–</td>
<td>Δ</td>
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**Impacts of plant invasions on the soil seed banks of resident vegetation**

The effect of plant invasions on soil seed banks differs with the identity of the invading species and with the characteristics of invaded communities. Significant changes in composition, abundance and species richness were reported in several ecosystems, such as fynbos (Holmes & Cowling 1997, Holmes 2002, Fourie 2008, Gaertner et al. 2011), coastal dunes (French et al. 2011), Banksia woodlands (Fisher et al. 2009), river banks (Vosse et al. 2008), wet meadows, coastal cliffs and grasslands (Gioria & Osborne 2009a, b, 2010, Gioria et al. 2011). While effects on species composition have been reported in many studies (see Table 2), changes in the richness of native species are not always evident (see Wearne & Morgan 2006, Vilà & Gimeno 2007).

The magnitude of the impact of invading species on the soil seed banks generally increases with its residence time (Holmes 2002, Seabloom et al. 2003, Turner et al. 2008,
Fisher et al. 2009, Gioria & Osborne 2009a, b, 2010) and varies with the identity of the invader (Gioria & Osborne 2010, Gioria et al. 2011). For instance, *Fallopia japonica* has a capacity to alter the richness, composition, and abundance of resident seed banks, even at deep soil layers, within a short period of time (a few years only), an effect not observed for other large herbaceous species such as *Heracleum mantegazzianum* and *Gunnera tinctoria* (Gioria & Osborne 2010). In addition, where two invasive species grew together, *F. japonica* was capable of reducing the large, persistent seed bank of *G. tinctoria*, formed over 50 years of its documented invasion, by 84–88% in the top soil and by 77–79% in deep soil layers (5–15 cm), within a couple of years (despite not producing any viable seed at the study site; Gioria et al. 2011). These studies indicate that (i) certain invasive species have the potential to alter soil seed banks of plant communities within a short period of time and (ii) large invasive herbaceous species can suppress even the more persistent components of the soil seed banks.

Although different species have variable effects on soil seed banks, the scarce data available point to some generalities. Recently, Gioria & Osborne (2010) showed that invasions by large herbaceous species (*Fallopia japonica*, *Gunnera tinctoria* and *Heracleum mantegazzianum*) resulted in the homogenization of the seed banks of resident species, despite differences in the reproductive strategy and geographic distribution of these invaders as well as in the standing vegetation and habitat types examined. This suggests that some shared features of the invaders, such as a large standing biomass and extensive litter production, may create conditions that result in the survival and/or overrepresentation of persistent seeds of certain species or genera present in invaded seed banks (Gioria & Osborne 2010).

**Mechanisms affecting soil seed banks of resident plant communities**

Several mechanisms underlie the impacts of plant invasions on resident seed bank communities. Such impacts result from a complex interplay of changes in the seed rain of invading and resident species, changes in the production of both standing biomass and litter (and the associated alteration of the vertical structure of standing vegetation), and changes in the biotic and abiotic conditions that affect recruitment from the seed bank as well as seed mortality rates (Gioria & Osborne 2010; Fig. 2).

Changes in the structure (species abundance, diversity, composition and patchiness) of standing vegetation associated with invasion (e.g. Tilman 1997, Levine 2000, Hejda et al. 2009, Gaertner et al. 2011, Vilà et al. 2011) inevitably result in changes in the seed rain. Increases in above-ground biomass and primary productivity and changes of the vertical structure of invaded communities have been reported for many species (Baruch & Goldstein 1999, Ehrenfeld 2003, 2004, 2006, Ogden & Rejmánek 2005, Gioria & Osborne 2010). These changes affect the balance between seed input and output by limiting the dispersal efficacy of resident species (Zobel 1997, Turnbull et al. 2000, Zobel et al. 2000, French et al. 2011). Increased production of litter also affects the dispersal efficacy of resident species (Tilman 1993, Foster & Gross 1998, Xiong et al. 2003, see Gioria & Osborne 2010 for a review). A high production of living biomass and/or litter may prevent seeds of resident species from reaching the soil (Facelli & Pickett 1991), leaving them exposed to the attack of predators (Cintra 1997) and/or pathogens, whose activities are
also likely to change during invasion processes (Lonsdale 1993, Richardson et al. 2000a, Callaway et al. 2005). Changes in the amount and quality of litter associated with plant invasions indirectly affect the number of seeds entering seed banks by potentially altering the growth conditions, and hence the fecundity, of resident species (Sydes & Grime 1981, Peterson & Facelli 1992, Foster & Gross 1997). In contrast, alterations in litter conditions may negatively affect seed germination rates (Peterson & Facelli 1992, Facelli 1994, Foster & Gross 1997) that are associated with changes in the amount and quality of light reaching the soil, soil moisture, temperature fluctuations and nutrient cycling (Facelli & Pickett 1991, Xiong & Nilsson 1997, Silvertown et al. 1999, Ehrenfeld 2003, 2004, 2006, Xiong et al. 2003, Allison & Vitousek 2004), thus limiting the output of seeds from the seed bank, although seed viability may also decrease.

The magnitude of the effects of seed limitation and dispersal limitation depend upon the dispersal ability of the resident species present in the standing vegetation (Schupp & Fuentes 1995, Gioria & Osborne 2010, Gioria et al. 2011). Although seeds of many species can survive in the soil for long periods of time, the seed bank of a species tends to decline over time at a rate that is a function of time since disappearance of a species from
the vegetation (Roberts & Feast 1973, Roberts 1981, Bakker et al. 1996). Thus, as invasion proceeds, fewer seeds of those species that are still present in the vegetation are added to the soil and the process of seed bank depletion may be rather rapid (Gioria & Osborne 2010, Gioria et al. 2011).

Finally, changes induced by invasion processes represent a source of stress (sensu Lichtenthaler 1996) to resident species (Gioria & Osborne 2010, see Gioria et al. 2011 and references therein). Many perennial species that reproduce both sexually and asexually exhibit adaptive responses to stressful conditions, resulting in increased vegetative propagation at the expense of sexual reproduction (Salisbury 1942, Harper & Ogden 1970, D’Antonio 1993, Watkinson & Powell 1993, Grime 2001, Eckert 2002). Changes in the balance between sexual reproduction and clonal regeneration may represent an indirect mechanism by which invasive species affect resident seed banks.

**Soil seed banks, invasive species and climate change**

Climate strongly regulates the distribution of alien plants (e.g. Thuiller et al. 2005, 2006, Richardson & Thuiller 2007, Essl et al. 2011) by affecting all developmental stages, from seed development to seedling recruitment (Probert 2000, Adler & HilleRisLambers 2008) and seedling survival, establishment and reproduction (e.g. Baskin & Baskin 1998, Walck et al. 2011). In recent years, there has been an increasing interest in predicting the long-term impact of climate change on vegetation processes and ecosystem functioning via alterations in plant community dynamics (e.g. Visser & Both 2005, Levine et al. 2008). In the context of plant invasions and soil seed banks, climatic changes may affect (i) seed germination rates, either directly, e.g. by reducing the germination niche-breadth of endemic species (Luna & Moreno 2010), or indirectly, by altering plant primary productivity, seed production, nutrient cycling, and decomposition rates of both resident and invasive species; (ii) seed germination requirements during seed development; and (iii) seed viability, either directly, or indirectly, via changes in the soil biota.

An indication that climate affects the capacity of an alien species to form a soil seed bank comes from comparisons of the same invasive species in climatically different regions. *Heracleum mantegazzianum*, which requires a period of cold stratification for germination, tends to form a short-term persistent seed bank (sensu Thomson et al. 1997) in the Czech Republic, where winters are cold (Krinke et al. 2005, Moravcová et al. 2006). In contrast, it forms a transient seed bank in Ireland, where winters are wet and relatively mild and seeds tend to lose their viability by May (Gioria & Osborne 2009b, 2010). Another invasive herb, *Gunnera tinctoria*, tends to form a large and persistent seed bank in various ecosystem types in Ireland, but only a minimal seed bank in invaded sites in New Zealand (Williams et al. 2005), where temperatures are warmer (Gioria & Osborne 2009a). The narrow temperature requirements for the germination of this species (Gioria 2007) suggest that even small changes in winter and summer temperatures can play a major role in the formation of a seed bank, thus affecting its capacity to colonize new areas.
Long-term implications of changes in the soil seed bank

Characterizing the changes in soil seed banks associated with an invasion is central to predicting the persistence of an invasive species at a locality, as well as the long-term implications of plant invasions for resident communities and ecosystem functioning. Even if a species disappears from the vegetation, its presence in the seed bank in a dormant state ensures its persistence, at least for a certain period of time. Conversely, the loss of a species from both the standing vegetation and the seed bank represents a permanent change in the absence of continued dispersal from the outside.

To fully understand the consequences of species being lost from the seed banks of invaded communities, it is useful to refer to a number of theories that have been proposed to explain the biodiversity-ecosystem functioning relationship. First, the loss of a species from the soil seed bank will inevitably alter the ‘insurance effect’ (Yachi & Loreau 1999) that the species provides to a community when changes in environmental conditions occur (Lehman & Tilman 2000, Loreau et al. 2001, 2003).

Grime (1998) suggested that the loss of subordinate species may affect community assembly via alterations in their ‘filter’ effect, i.e. their ability to control the recruitment of dominant species. Conversely, the loss of transient species from a community inevitably affects the probability of colonization and establishment of new functional types in a system after a disturbance event (‘founder effect’; Grime 1998). Previous studies have shown that invasions by large alien species resulted in a decrease in the absolute and relative abundance of subordinate and transient species in the seed bank, as well as in a concomitant increase in the abundance of dominant species (Gioria 2007, Gioria & Osborne 2009a, b, 2010, Gioria et al. 2011).

By altering the structure of resident seed bank communities, invasive plants may affect the biotic resistance of the vegetation and facilitate their own spread and/or that of other alien or weed species (Dukes 2002, Bakker & Wilson 2004, Turner et al. 2008, Gioria & Osborne 2009a). Invasibility can be strongly related to a low abundance of resident seeds, whose overall or species-specific decrease over time may affect species diversity (Brown & Fridley 2003). Seed limitation and, more generally, recruitment limitation have a major effect on a species’ population (Turnbull et al. 2000, Zobel et al. 2000, Xiong et al. 2003), and increases in seed limitation negatively affect plant diversity (Tilman 1997, Tilman et al. 1997, Fridley 2001).

Species losses from the seed bank or declines in seed abundances also alter the gene pool and evolutionary potential of a community (Gioria & Osborne 2008, 2010). Changes in genetic variation and ‘genetic erosion’ of resident species may confer an invading plant with additional advantages. Such advantages arise when resident species have a reduced ability to respond to selection pressures posed by invasion processes and other adverse events, such as natural and/or anthropogenic disturbances (e.g. Lavergne et al. 2010). This further affects the mechanisms of species coexistence in an ecosystem. A decline in the genetic variability stored in the seed bank may derive from a decreased number of species and/or their abundances, as well as from reduced seed production resulting from the aforementioned shifts towards vegetative propagation. In a computer simulation of Ranunculus repens population dynamics, Watkinson & Powell (1993) demonstrated a rapid loss of genets from populations in which there was no further seedling recruitment following an initial colonization event; this suggests a tendency for such populations to become increasingly dominated by a few large clones (see also Kays & Harper 1974, de Witte et al. 2011, Klimešová & Pyšek 2011).
Management and control strategies

Knowledge of the reproductive biology of invasive species, including seed production and seed persistence, is critical to the development of sustainable strategies aimed at controlling the spread of invasive plants and restoring previously invaded areas (Holmes 1988, 1989a, b, 2002, Holmes & Richardson 1999, Stöcklin & Fisher 1999, Bakker & Wilson 2004, Adams et al. 2005, Krinke et al. 2005, Fourie 2008, Gioria & Osborne 2008, 2010). Since the resilience of invasive species persisting in soil seed banks is a substantial impediment to their effective management, an evaluation of the type and size of the seed bank formed by an invader needs to become a central component of control and restoration programs (e.g. Holmes et al. 2000, Fourie 2008, Richardson & Kluge 2008, Gioria et al. 2011). Adams et al. (2005) recommended the use of information on the soil seed bank as a starting point to model the persistence of plant populations for conservation purposes. Information on the persistence of an invader can also be used to manipulate invaded soil seed banks and inhibit the germination of its seed (Bakker & Wilson 2004, Adams et al. 2005).

The ‘temporal’ classification of soil seed banks proposed by Thompson et al. (1997) is useful to predict the time required to substantially deplete the seed bank of an invasive species. If an invasive species does not form a seed bank, or only forms a transient one, its removal from the standing vegetation can be effectively used as a control strategy (Hulme & Bremner 2006, Gioria et al. 2009b). Conversely, controlling invasive species with a short- or long-term persistent seed bank is more complex and requires active management and monitoring for many years (Pyšek et al. 2007a, b, Gioria & Osborne 2009a, 2010, Strydom et al. 2012). Unfortunately, reliable information on how long the seeds persist is often not available, even for well-studied invasive species, since it requires long-term observation. *Heracleum mantegazzianum* can serve as an example of an invasive species for which seed longevity in seed banks has been seriously overestimated in the literature (see Moravcová et al. 2007).

The depletion of soil seed banks, both in terms of species richness and seed density, represents a major challenge to the restoration of previously invaded ecosystems (Gioria & Osborne 2008, 2009a, Richardson & Kluge 2008, Fisher et al. 2009, Gaertner et al. 2011). In particular, previous investigations have shown that the seed banks of invaded communities were not sufficient to restore the pre-invasion vegetation (e.g. Vilà & Gimeno 2007, Fourie 2008, Vosse et al. 2008, Gioria & Osborne 2010, Gioria et al. 2011), indicating that, in many instances, the removal of an invasive plant should be followed by the reintroduction of seeds of target species (Seabloom et al. 2003, Gioria & Osborne 2008, 2010).

Knowledge of the composition of the post-invasion soil seed bank at a site is also important to avoid the germination and establishment of non-target species (Cilliers et al. 2004, Gioria & Osborne 2008, 2010). Seeds of weeds or alien species, which have been found to dominate invaded soil seed banks in grassland communities (Gioria & Osborne 2009b), may prevent the establishment of target species by interspecific competition (Bossuyt et al. 2002). The removal of an invader will inevitably bring about changes in the biotic and abiotic conditions as well as in the availability of empty niches in a community. This could trigger the germination of viable seeds of the invasive species as well as that of other unwanted alien or weedy species, which tend to dominate the seed bank of invaded areas (Cilliers et al. 2004, Pauchard & Alaback 2004, Gioria & Osborne 2009a, b, 2010, Pyšek et al. 2010a, Albrecht et al. 2011). The establishment of seeds of target species should then be monitored and actively managed to minimize the germination of seeds of
Conclusions: current gaps and future research avenues

Despite a strong appreciation of the ecological (Roberts 1981,Chesson 1994, Bakker et al. 1996, Fenner & Thompson 2005) and evolutionary (Levin 1990, Brown & Venable 1991) importance of soil seed banks, only a few invasive species (Acacia species in particular) have been subject to research in this area. As such, a solid understanding of the long-term implications of changes in soil seed banks of invaded communities is lacking. This is because the study of soil seed banks related to invasions is still in its infancy. The seed banks of invasive species in their introduced ranges have been studied for only a small fraction of invasive species worldwide (36 shown in Table 1) and most investigations have been confined to a few sites only. The majority of studies assessing the effect of invasions on the richness, density and composition of the seed bank of whole plant communities have been published in the last five years, and only 13 species, or groups of species of the same genus, were addressed (Table 2). This strongly suggests that future research should focus on screening invasive species in which seed banks are likely to be an important trait associated with their invasiveness, and should evaluate the effects their invasions have on seed banks of species in resident communities.

This situation currently appears to be a wasted opportunity. Studies on the soil seed bank have a great potential to provide an insight into the causes of species invasiveness as well as into the factors affecting susceptibility of resident communities to invasion. We suggest that the study of soil seed banks should become a central component of investigations on the potential causes and long-term implications of plant invasions. Future research should also be directed towards understanding how alterations in the seed bank communities affect their evolutionary potential (Mooney & Cleland 2001, Cox 2004).

The knowledge of seed banks may also enhance our capacity to predict how the probability of naturalization and invasion of particular species will be affected by future global changes, including climate change and nitrogen deposition. Additional research is required to evaluate the impact of interacting global changes, including plant invasions and climate change, on soil seed banks and vegetation dynamics.

Our study also highlighted some issues that limit our capacity to evaluate the effects of invasive species on invaded seed banks. Such difficulties are associated in general with differences in the methods used (i) to sample soil seed banks (e.g. different sampling depths, use of soil cores vs. trays) and (ii) to evaluate the size of the seed bank (e.g. seedling emergence approach vs. seed counting). This is further complicated by the fact that
some previous investigations on invaded soil seed banks have not clearly tested the effects of invasive plants on the structure (richness, density, and/or composition) of the soil seed bank and that some studies described the seed bank of invaded areas only, although we acknowledge the difficulties in finding suitable control sites. Differences in the statistical procedures used to test for differences in the richness, density, and composition of soil seed banks also affect our capacity to characterize the effects of invasive species on soil seed banks. We thus recommend the use of multivariate statistical procedures aimed at rigorously testing the effects on species composition, as previously suggested by Gioria & Osborne (2009b); this would allow the evaluation of species-specific and habitat-dependent effects. The use of common methodological and analytical procedures to characterize the impact of invasive species on soil seed banks would support systematic reviews that could provide further insights into the mechanisms underlying the invasiveness of certain species or the invasibility of certain ecosystems.

Finally, information on characteristics of the seed banks of particular invading species and of resident communities is indispensable for developing more effective control and restoration programs.

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References


