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

The interest in the relationship between biodiversity and ecosystem functioning has increased substantially in recent years (Naeem et al. 2009), particularly in the context of plant invasions (Tilman 1997, 2004, Petchey et al. 2009). Invasions by alien plants may permanently affect ecosystem functioning and structure by changing the diversity and composition of biotic communities (Naeem et al. 1994, Tilman 1997, Bakker & Wilson 2004, Gaertner et al. 2009, 2011, Hejda et al. 2009, Powell et al. 2011, Vilà et al. 2011) and 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.

Species	LH	Region of origin	Invaded range	Habitat	Seed bank density (per m^2)				Study
					Minimum	Mean	Maximum	Type	
Acacia cyclops	t	Australia	S Africa	fynbos	1370		5140	P	Holmes et al. 1987
Acacia paradoxa	s	Australia	S Africa	fynbos		1000[a]		P	Zenni et al. 2009
Acacia saligna	t	SW Australia	S Africa	fynbos	0		>2000[b]	P	Holmes 2002
Acacia saligna	t	SW Australia	S Africa	fynbos	7980		45,800	P	Holmes et al. 1987
Acacia saligna	t	SW Australia	New South Wales	dune coastal areas	1389±297[a]		3600±279[a]	P	Tozer 1998
Acacia saligna	t	SW Australia	S Africa	fynbos	2000		212,000	P	Morris 1997
Acacia saligna	t	SW Australia	S Africa	fynbos	391±303[a]		38,714±4006[a]	P	Jasson 2005
Acacia longifolia	t	Australia	S Africa	fynbos	3912±1217		4528±1075	P	Fourie 2008
Acacia longifolia	t	Australia	Portugal	coastal sand dune	500		1500	P	Marchante et al. 2010
Agropyrum desertorum	pg	W and C Asia, Europe	NW Utah	grassland	200		1600	T	Pyke 1990
Amaranthus albus	af	C America	California	coastal sage scrub	1		4		Cox & Allen 2008
Ambrosia artemisiifolia	pf	N America		cropland, set-asides, wastelands	23±12		292±62	P	Fumanal et al. 2008
Atriplex sagittata	af	Asia	Czech Republic	experimental site	4475		61,901	T, P	Mandák & Pyšek 2001
Avena barbata	ag, pg	Mediterranean Basin, C Asia	California	coastal sage scrub	0		93		Cox & Allen 2008
Bischofia javanica		Asia	Bonin Islands	natural mesic forest		203[c]		P	Yamashita et al. 2003
Bromus diandrus	ag	Chile	California	coastal sage scrub	4		1474		Cox & Allen 2008
Bromus hordeaceus	ag	Mediterranean Basin	California	coastal sage scrub	35		1976		Cox & Allen 2008
Bromus madritensis subsp. *rubens*	ag	S Europe, N Africa, S Asia	California	coastal sage scrub	65		4085		Cox & Allen 2008
Carpobrotus edulis	psuc	S Africa	California	dune scrub, grassland, coastal scrub	557		2229	STP	D'Antonio 1990
Centaurea solstitialis	af	Mediterranean Basin	California	grassland	65[a]		195[a]		Lortie et al. 2010
Eichhornia crassipes	pf	S America	S Africa	various aquatic ecosystems	0	2348	4428	LTP	Albano Perez et al. 2011
Elaeagnus angustifolia	s	S Europe, W Asia	Arizona	riparian habitats	336[a]		494[a]	STP	Brock 2003
Erodium brachycarpum	af	S Europe	California	coastal sage scrub	552		4344		Cox & Allen 2008
Erodium cicutarium	af	S Europe	California	coastal sage scrub	32		508		Cox & Allen 2008

Species	LH	Region of origin	Invaded range	Habitat	Seed bank density (per m^2)				Study
					Minimum	Mean	Maximum	Type	
Eupatorium adenophorum	pf	C Mexico	SW China	secondary forests, *Acacia*, *Leucaena* and *Eucalyptus* forests, shrubland, grassland	47		13,806		Shen et al. 2006
Fallopia japonica	pf	Japan	Belgium	semi-rural landscape	23±58		34±92	T	Tiébré et al. 2007
Fallopia japonica	pf	Japan	Ireland	lead mine, lake shore, roadside	0		0	N	Gioria & Osborne 2010
Filago gallica	af	Europe, N Africa	California	coastal sage scrub	0		30		Cox & Allen 2008
Gleditsia triacanthos	t	N America	Argentina	woodland	0		92	P	Ferreras & Galetto 2010
Gunnera tinctoria	pf	S America	Ireland	coastal cliff, coastal grassland, wet meadow	28,308±16,175		113,675±25,118	LTP	Gioria & Osborne 2009a
Heracleum mantegazzianum	pf	Caucasus, C Asia	Czech Republic	open areas	192±165		6719±4119	STP	Krinke et al. 2005
Heracleum mantegazzianum	pf	Caucasus, C Asia	Ireland	riparian grasslands	0	390	9762	T	Gioria & Osborne 2009b
Hirschfeldia incana	pf	Mediterranean Basin	California	coastal sage scrub	2		10		Cox & Allen 2008
Hordeum murinum	ag	Eurasia, N Africa	California	coastal sage scrub	0		9		Cox & Allen 2008
Hypochaeris glabra	af	Eurasia, N Africa	California	coastal sage scrub	4		84		Cox & Allen 2008
Lactuca serriola	af	Europe	California	coastal sage scrub	0		1		Cox & Allen 2008
Mimosa pigra	s	C America	Australia	floodplain	2000		12,000	P	Lonsdale et al. 1988
Piper aduncum	s	S and C America, Asia, Pacific Islands	Papua New Guinea	fallow vegetation	675		2578		Rogers & Hartemink 2000
Schismus barbatus	ag	Eurasia	California	coastal sage scrub	30		925		Cox & Allen 2008
Setaria faberi	ag	Asia	Indiana	cropland	19±4		151±22	P	Rothrock et al. 1993
Sisymbrium irio	af	S Europe	California	coastal sage scrub	7		197		Cox & Allen 2008
Solanum mauritianum	t	S America	S Africa	grassland high altitude and savanna low altitude	66±32		554±228		Witkowski & Garner 2008
Vulpia myuros	ag	Eurasia	California	coastal sage scrub	4		506		Cox & Allen 2008

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

[c] 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* (Radford & Cousens 2000), 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).

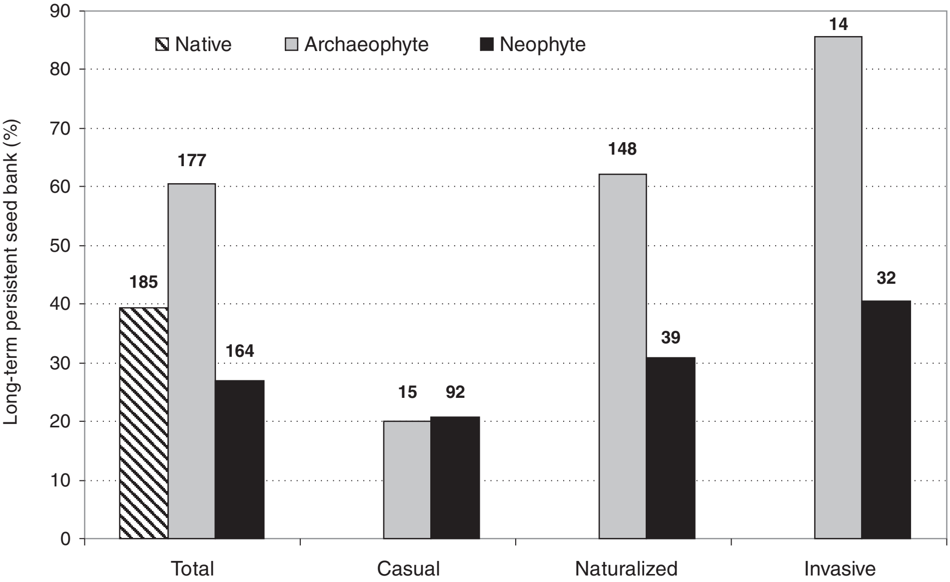

Fig. 1. – Percentage of species in the flora of the Czech Republic (Pyšek et al. 2002) capable of forming a long-term persistent seed bank, classified according to origin and invasion status, and residence times. Data on seed bank types were taken from LEDA database (Kleyer et al. 2008). If a species was reported as having a long-term persistent seed bank in an original study, it is considered as possessing the potential to form it. Alien archaeophytes and neophytes of different status (casual, naturalized invasive) significantly differed in the percentages of species, of the total number in the given group, capable of forming long-term persistent seed banks (G-test on contingency tables = 195.2, df = 7, $P < 0.001$). Numbers of species with data available in particular groups are indicated above bars.

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.

Invasive species	Native range	Invasive range	Study	Species richness	Abundance	Composition
Acacia spp.	Australia	S Africa	Gaertner et al. 2011	NS		
	Australia	S Africa	Holmes 2002	–	–	Δ
	Australia	S Africa	Holmes & Cowling 1997	–	–	Δ
Invasive alien trees	Australia	S Africa	Vosse et al. 2008	+ & –	–	Δ
Asparagus asparagoides	Tropical and S Africa	Australia	Turner et al. 2008	– nat	– nat	Δ
Chrysanthemoides subsp. *monilifera*	S Africa	Australia	French et al. 2011	– nat	–	Δ
Cytius scoparius	Europe	Australia	Wearne & Morgan 2006	NS 5/6	NS 4/6	NS
Erharta calcyna	S Africa	Australia	Fisher et al. 2009	SD	–	Δ
Gunnera tinctoria	S America	Ireland	Gioria & Osborne 2010	–	–	Δ
	S America	Ireland	Gioria & Osborne 2009a	–	–	Δ
Heracleum mantegazzianum	Caucasus, Europe, W Asia	Ireland	Gioria & Osborne 2009b	–	–	Δ
		Ireland	Gioria & Osborne 2010	–	–	Δ
Fallopia japonica	Asia	Ireland	Gioria & Osborne 2010	–	–	Δ
		Ireland	Gioria et al. 2011	–	–	Δ
Oxalis pes-caprae	Greece, S Africa	Spain	Vilà & Gimeno 2007	NS	NS	Δ
Pelargonium capitatum	S Africa	Australia	Fisher et al. 2009	–	–	Δ
Pennisetum clandestinum	Australia	S Africa	Gaertner et al. 2011	NS		
Multiple alien species	Eurasia	California	Cox & Allen 2008	–	–	Δ

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

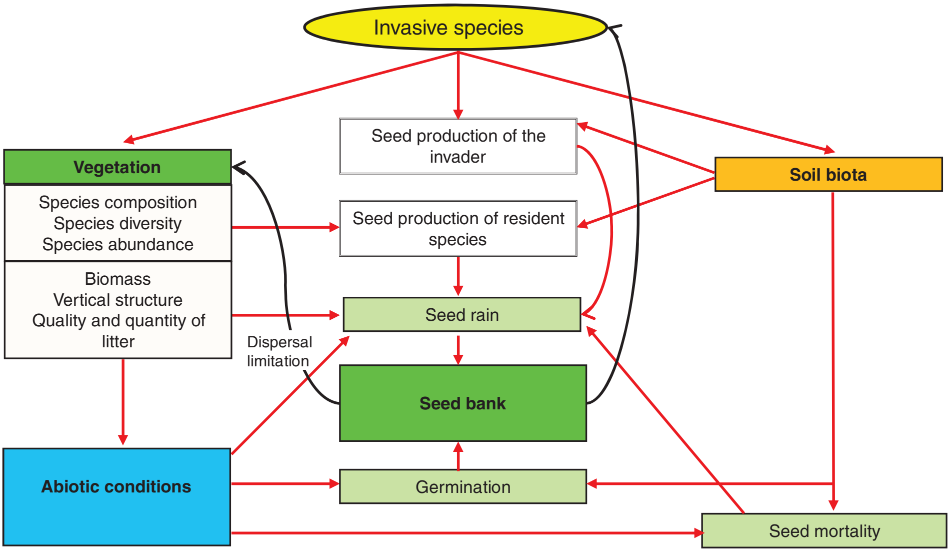

Fig. 2. – Theoretical framework of the mechanisms underlying the changes in soil seed banks of invaded communities. Invasive species may directly affect the seed bank by its own seed production and subsequent seed rain. Changes in the composition, species diversity and abundance of vegetation will affect the seed production by resident species. Since the biomass of vegetation dominated by the invading species typically increases, compared to the uninvaded community, the vertical structure of the vegetation and the amount and quality of the litter produced also change. These structural changes affect seed dispersal directly, by preventing seeds from reaching the soil and entering seed banks, or indirectly, because they alter abiotic conditions, which in turn affect seed production, germination and mortality. Increases in biomass and litter may also affect seed mortality and decay by altering the spectrum of predators and pathogens. Invasive species may also induce alterations in the soil fauna and pathogens, which affect seed germination and seed mortality and decay. Changes in the seed bank will in turn affect the vegetation, with effects that could be additive or even multiplicative.

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 Thomspon 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 non-target species (Cilliers et al. 2004, Gioria & Osborne 2008, 2010, Reinecke et al. 2008). However, despite the fact that weed managers have long recognized the need for more information describing the seed banks associated with unwanted species (Forcella & Burnside 1994), only few control and restoration programs have been based on extensive seed bank data (but see investigations on *Acacia* species in South African fynbos, e.g. Holmes & Richardson 1999, Richardson & Kluge 2008, Strydom et al. 2012 for reviews). In some cases, restoration programs were erroneously based on the assumption that native ecosystems would recover naturally after the invasive species' removal (Fourie 2008; see Richardson & Kluge 2008 and reference therein), thus they did not contemplate any additional intervention, such as seed additions and/or monitoring programs.

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 indispensible for developing more effective control and restoration programs.

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Souhrn

Invaze nepůvodních rostlin významným způsobem ovlivňují biodiverzitu a fungování ekosystémů. Sledování skladby půdní banky zavlečených rostlin a jejích změn v průběhu invazního procesu představuje důležitý stupeň k pochopení dlouhodobých důsledků rostlinných invazí. Půdní semenná banka má důležitou funkci nejen jako prostá zásoba diaspor a genetické diverzity druhů na lokalitě, ale díky persistenci diaspor představuje také významnou pojistku proti změnám prostředí v čase. Vliv invazních rostlin na druhovou diverzitu původních rostlinných společenstev se začíná v poslední době intenzivně studovat, ale o dlouhodobých důsledcích ochuzování půdní semenné banky pro vegetační dynamiku a fungování ekosystémů toho víme zatím málo. Je známo, že vlastnosti půdní semenné banky nepůvodního druhu přispívají k jeho invazivnosti a že změny v půdní bance invadovaných společenstev ovlivňují jejich biotickou resistenci vůči primárním i sekundárním invazím. Článek shrnuje dosavadní literaturu o půdní semenné bance ve vztahu k invazím, rozebírá (i) ekologický význam a funkci půdní semenné banky, (ii) na datech z České republiky ukazuje, jak může schopnost vytvářet půdní semennou banku přispívat k invazivnosti druhu, (iii) hodnotí dlouhodobé důsledky invazí na půdní semennou banku invadovaných rostlinných společenstev a (iv) nastiňuje potenciální důsledky klimatických změn pro tvorbu půdní semenné banky v kontextu rostlinných invazí. Na závěr poukazujeme na důležitá témata, kterými by se měl výzkum půdní banky v souvislosti s invazemi zabývat a jejichž znalost je nezbytným předpokladem pro vytváření vhodné strategie kontroly zavlečených rostlin a obnovy původních společenstev.

References

Adams V. M., Marsh D. M. & Knox J. S. (2005): Importance of the seed bank for population viability and population monitoring in a threatened wetland herb. – Biol. Conserv. 124: 425–436.

Adler P. B. & HilleRisLambers J. (2008): The influence of climate and species composition on the population dynamics of ten prairie forbs. – Ecology 89: 3049–3060.

Albano Perez E., Coetzee J. A., Ruiz Tellez T. & Hill M. P. (2011): A first report of water hyacinth (*Eichhornia crassipes*) soil seed banks in South Africa. – S. Afr. J. Bot. 77: 795–800.

Albrecht H., Eder E., Langbehn T. & Tschiersch C. (2011): The soil seed bank and its relationship to the established vegetation in urban wastelands. – Landsc. Urb. Plan. 100: 87–97.

Allee W. (1931): Animal aggregations. A study in general sociology. – Univ. Chicago Press, Chicago.

Allison S. & Vitousek P. (2004): Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. – Oecologia 141: 612–619.

Baker H. (1989): Some aspects of the natural history of seed banks. – In: Leck M., Parker V. & Simpson R. (eds), Ecology of soil seed banks, p. 9–21, Academic Press, San Diego.

Bakker J. P., Poschlod P., Strykstra R., Bekker R. & Thompson K. (1996): Seed banks and seed dispersal: important topics in restoration ecology. – Acta Bot. Neerl. 45: 461–490.

Bakker J. D. & Wilson S. D. (2004): Using ecological restoration to constrain biological invasion. – J. Appl. Ecol. 41: 1058–1064.

Baruch Z. & Goldstein G. (1999): Leaf construction cost, nutrient concentration and net CO_2 assimilation of native and invasive species in Hawaii. – Oecologia 121: 183–192.

Baskin C. & Baskin J. (1998): Seeds: ecology, biogeography, and evolution of dormancy and germination. – Academic Press, San Diego.

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

Bell D. (1999): The process of germination in Australian species. – Australian J. Bot. 47: 475–517.

Blackburn T. M., Pyšek P., Bacher S., Carlton J. T., Duncan R. P., Jarošík V., Wilson J. R. U. & Richardson D. M. (2011): A proposed unified framework for biological invasions. – Trends Ecol. Evol. 26: 333–339.

Bossuyt B., Cosyns E. & Hoffmann M. (2007): The role of soil seed banks in the restoration of dry acidic dune grassland after the burning of *Ulex europaeus* scrub vegetation. – Appl. Veg. Sci. 10: 131–138.

Bossuyt B., Heyn M. & Hermy M. (2002): Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for ecological regeneration of ancient forest vegetation. – Plant Ecol. 162: 33–48.

Bossuyt B. & Honnay O. (2008): Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. – J. Veg. Sci. 19: 875–884.

Brock J. (2003): *Eleagnus angustifolia* (Russian olive) seed banks from invaded riparian habitats in northeastern Arizona. – In: Child L., Brock J., Brundu G., Prach K., Pyšek P., Wade M. & Williamson M. (eds), Plant invasions: ecological threats and management solutions, p. 267–76, Backhuys Publishers, Leiden.

Brown J. S. & Venable D. L. (1991): Life-history evolution of seed bank annuals in response to seed predation. – Evol. Ecol. 5: 12–29.

Brown R. & Fridley J. (2003): Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density. – Oikos 102: 15–24.

Cadotte M. W. & Lovett-Doust J. (2001): Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. – Ecoscience 8: 230–238.

Catford J., Vesk P., Richardson D. M. & Pyšek P. (2012): Quantifying invasion level: towards the objective classification of invaded and invasible ecosystems. – Glob. Change Biol. 18: 44–62.

Callaway R., Hierro J. & Thorpe A. (2005): Evolutionary trajectories in plant and soil microbial communities: plant invasions and the geographic mosaic of coevolution. – In: Sax D., Gaines S. & Stachowicz J. (eds), Exotic species bane to conservation and boon to understanding: ecology, evolution and biogeography, p. 342–63, Sinauer, Sunderland.

Chesson P. (1994): Multispecies competition in variable environments. – Theor. Pop. Biol. 45: 227–276.

Chesson P., Gebauer R. L. E., Schwinning S., Huntly N., Wiegand K., Ernest K., Sher S. K. M., Novoplansky A. & Weltzin J. F. (2004): Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. – Oecologia 141: 236–253.

Cilliers C. D., Esler K. J. & Boucher C. (2004): Effects of alien plant management and fire on soil seed banks and regeneration in the Cape Peninsula National Park, South Africa. – S. Afr. J. Bot. 70: 705–712.

Cintra R. (1997): A test of the Janzen-Connell model with two common tree species in Amazonian forest. – J. Trop. Ecol. 13: 641–658.

Cohen D. (1966): Optimizing reproduction in a randomly varying environment. – J. Theor. Biol. 12: 119–29.

Colautti R., Grigorovich I. & MacIsaac H. (2006): Propagule pressure: a null model for biological invasions. – Biol. Inv. 8: 1023–1037.

Cox G. (2004): Alien species and evolution: the evolutionary ecology of exotic plants, animals and microbes and interacting native species. – Island Press, Washington.

Cox R. D. & Allen E. B. (2008): Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. – Plant. Ecol. 198: 37–46.

Cronk Q. C. B. & Fuller J. L. (2001): Plant invaders: the threat to natural ecosystems. – Earthscan Publ., London.

D'Antonio C. M. (1990): Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* (*Aizoaceae*) in coastal strand communities of Central California. – J. Appl. Ecol. 27: 693–702.

D'Antonio C. (1993): Mechanisms controlling invasion of coastal plant communities by the alien succulent, *Carpobrotus edulis*. – Ecology 74: 83–95.

D'Antonio C. & Thomsen M. (2004): Ecological resistance in theory and practice. – Weed Technol. 18: 1572–1577.

Davis H., Taylor C., Civille J. & Strong D. (2004a): An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. – J. Ecol. 92: 321–327.

Davis H., Taylor C., Lambrinos J. & Strong D. (2004b): Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). – Proc. Natl. Acad. Sci. USA 101: 13804–13807.

Dekker J. (1999): Soil weed seed banks and weed management. – J. Crop Product. 2: 139–166.

de Witte L. C., Scherrer D. & Stöcklin J. (2011): Genet longevity and population age structure of the clonal pioneer species *Geum reptans* based on demographic field data and projection matrix modelling. – Preslia 83: 371–386.

Dukes J. (2002): Species composition and diversity affect grassland susceptibility and response to invasion. – Ecol. Appl. 12: 602–617.

Eckert C. (2002): The loss of sex in clonal plants. – Evol. Ecol. 15: 501–520.

Ehrenfeld J. G. (2003): Ecosystem effects and causes of exotic species invasions. – Ecosystems 6: 503–523.

Ehrenfeld J. G. (2004): Implications of invasive species for below-ground community and nutrient processes. – Weed Technol. 18: 1232–1235.

Ehrenfeld J. G. (2006): A potential novel source of information for screening and monitoring the impact of exotic plants on ecosystems. – Biol. Inv. 8: 1511–1521.

Elam D. R., Ridley C. E., Goodell K. & Ellstrand N. C. (2007): Population size and relatedness affect fitness of a self-incompatible invasive plant. – Proc. Natl. Acad. Sci. USA 104: 549–552.

Ens E.-J. & French K. (2008): Exotic woody invader limits the recruitment of three indigenous plant species. – Biol. Cons. 141: 590–595.

Essl F., Mang T., Dullinger S., Moser D. & Hulme P. E. (2011): Macroecological drivers of alien conifer naturalizations worldwide. – Ecography 34: 1076–1084.

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

Facelli J. & Picket S. (1991): Plant litter: its dynamics and effects on plant community structure. – Bot. Rev. 57: 2–32.

Fenner M. (1985): Seed ecology. – Chapman & Hall, London.

Fenner M. & Thompson K. (2005): The ecology of seeds. Ed. 2. – Cambridge Univ. Press, Cambridge.

Ferreras A. E. & Galetto L. (2010): From seed production to seedling establishment: important steps in an invasive process. – Acta Oecologica 36: 211–218.

Fisher J. L., Loneragan W. A., Dixon K. & Veneklaas E. J. (2009): Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. – Biol. Cons. 142: 256–269.

Forcella F. & Burnside O. C. (1994): Pest management – weeds. – In: Hatfield J. L. & Karlen D. L. (eds), Sustainable agriculture systems, p. 157–197, CRC Press, Boca Raton.

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

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

Fourie S. (2008): Composition of the soil seed bank in alien-invaded grassy fynbos: potential for recovery after clearing. – S. Afr. J. Bot. 74: 445–453.

French K., Mason T. J. & Sullivan N. (2011): Recruitment limitation of native species in invaded coastal dune communities. – Plant Ecol. 212: 601–609.

Fridley J. (2001): The influence of species diversity on ecosystem productivity: how, where, and why? – Oikos 93: 514–526.

Fumanal B., Gaudot I. & Bretagnolle F. (2008): Seed-bank dynamics in the invasive plant, *Ambrosia artemisiifolia* L. – Seed Sci. Res. 18: 101–114.

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

Gaertner M., Breeyen A. D., Hui C. & Richardson D. M. (2009): Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. – Progr. Phys. Geogr. 33: 319–338.

Gaertner M., Richardson D. M. & Privett S. D. J. (2011): Effects of alien plants on ecosystem structure and functioning and implications for restoration: insights from three degraded sites in South African Fynbos. – Env. Manage. 48: 57–69.

Gibson M. R., Richardson D. M., Marchante E., Marchante H., Rodger J. G., Stone G. N., Byrne M., Fuentes-Ramírez A., George N., Harris C., Johnson S. D., Le Roux J., Miller J. T., Murphy D. J., Pauw A., Prescott M. N., Wandrag E. M. & Wilson J. R. U. (2011): Reproductive biology of Australian acacias: important mediator of invasiveness? – Diversity Distrib. 17: 911–933.

Gioria M. (2007): The impact of three invasive species on soil seed bank communities. – PhD Thesis, Univ. College Dublin, Ireland.

Gioria M., Dieterich B. & Osborne B. (2011): Battle of the giants: primary and secondary invasions by large herbaceous species. – Biol. Env. 111: 177–193.

Gioria M. & Osborne B. (2008): Soil seed banks associated with two invasive species, *Gunnera tinctoria* and *Heracleum mantegazzianum*. – In: Tokarska-Guzik B., Brock J., Brundu G., Child L., Daehler C. & Pyšek P. (eds), Plant invasions: human perception, ecological impacts and management, p. 217–233, Backhuys Publishers, Leiden.

Gioria M. & Osborne B. (2009a): The impact of *Gunnera tinctoria* (Molina) Mirbel on soil seed bank communities. – J. Plant Ecol. 2: 153–167.

Gioria M. & Osborne B. (2009b): Assessing the impact of plant invasions on soil seed bank communities: use of univariate and multivariate statistical approaches. – J. Veg. Sci. 20: 547–556.

Gioria M. & Osborne B. (2010): Similarities in the impact of three large invasive plant species on soil seed bank communities. – Biol. Inv. 12: 1671–1683.

Grime J. (1989): The stress debate: symptom of impending synthesis? – Biol. J. Linn. Soc. 37: 3–17.

Grime J. (1998): Benefits of plant diversity to ecosystems: immediate, filter and founder effects. – J. Ecol. 86: 902–1010.

Grime J. (2001): Plant strategies, vegetation processes, and ecosystem properties. Ed. 2. – John Wiley & Sons, London.

Hamilton M. A., Murray B. R., Cadotte M. W., Hose G. C., Baker A. C., Harris C. J. & Licari D. (2005): Life-history correlates of plant invasiveness at regional and continental scales. – Ecol. Lett. 8: 1066–1074.

Harper J. (1977): The population biology of plants. – Academic Press, London.

Harper J. L. & Ogden J. (1970): The reproductive strategy of higher plants: 1. The concept of strategy with special reference to *Senecio vulgaris*. – J. Ecol. 58: 681–698.

Hejda M., Pyšek P. & Jarošík V. (2009): Impact of invasive plants on the species richness, diversity and composition of invaded communities. – J. Ecol. 97: 393–403.

Hodgson J. & Grime J. (1990): The role of dispersal mechanisms, regenerative strategies and seed banks in the vegetation dynamics of the British landscape. – In: Bunce R. & Howard D. (eds), Species dispersal in agricultural habitats, p. 65–81, Belhaven, London.

Holmes P. M. (1988): Implications of alien *Acacia* seed bank viability and germination for clearing. – S. Afr. J. Bot. 54: 281–284.

Holmes P. M. (1989a): Effect of different clearing treatments on seed-bank dynamics of invasive Australian shrub, *Acacia cyclops*, in the Southwestern Cape, South Africa. – For. Ecol. Manage 28: 33–46.

Holmes P. M. (1989b): Decay rates in buried alien *Acacia* seed populations of different density. – S. Afr. J. Bot 55: 299–303.

Holmes P. M. (2002): Depth distribution and composition of seed-banks in alien-invaded and uninvaded fynbos vegetation. – Austral Ecol. 27: 110–120.

Holmes P. M. & Cowling R. M. (1997): Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. – Plant Ecol. 133: 107–122.

Holmes P. M., Macdonald I. A. W. & Juritz J. J. (1987): Effects of clearing treatments on seed banks of the alien invasive shrubs *Acacia saligna* and *Acacia cyclops* in the southern and south-western Cape, South Africa. – J. Appl. Ecol. 24: 1045–1051.

Holmes P. M. & Moll E. J. (1990): Effect of depth and duration of burial on alien *Acacia saligna* and *Acacia cyclops* seeds. – S. Afr. J. Ecol. 1: 12–17.

Holmes P. M. & Richardson D. M. (1999): Protocols for restoration based on recruitment dynamics, community structure and ecosystem function: perspectives from South African fynbos. – Restor. Ecol. 7: 215–230.

Holmes P. M., Richardson D. M., van Wilgen B. W. & Gelderblom C. (2000): Recovery of South Africa fynbos vegetation following alien woody plant clearing and fire: implications for restoration. – Austral Ecol. 25: 631–639.

Hölzel N. & Otte A. (2001): The impact of flooding regime on the soil seed bank of flood meadows. – J. Veg. Sci. 12: 209–218.

Houle G. & Phillips D. L. (1988): The soil seed bank of granite outcrop plant communities. –Oikos 52: 87–93.

Hulme P. E. & Bremner E. T. (2006): Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. – J. Appl. Ecol. 43: 43–50.

Jasson R. (2005): Management of *Acacia* species seed banks in the Table Mountain National Park, Cape Peninsula, South Africa. – MSc Thesis, Univ. of Stellenbosch, South Africa.

Kays S. & Harper J. (1974): The regulation of plant and tiller density in a grass sward. – J. Ecol. 62: 97–105.

Kleyer M., Bekker R. M., Bakker J., Knevel I. C., Thompson K., Sonnenschein M., Poschlod P., Van Groenendael J. M., Klimeš L., Klimešová J., Klotz S., Rusch G., Hermy M., Adriaens D., Boedeltje G., Bossuyt B., Endels P., Götzenberger L., Hodgson J. G., Jackel A.-K., Dannemann A., Kühn I., Kunzmann D., Ozinga W., Römermann C., Stadler M., Schlegelmilch J., Steendam H. J., Tackenberg O., Wilmann B., Cornelissen J. H. C., Eriksson O., Garnier E., Fitter A. & Peco B. (2008): The LEDA traitbase: a database of plant life-history traits of North West Europe. – J. Ecol. 96: 1266–1274.

Klimešová J. & Pyšek P. (2011): Current topics in clonal plants research: editorial. – Preslia 83: 275–279.

Koch M., Huthmann M. & Bernhardt K. G. (2003): *Cardamine amara* L. (*Brassicaceae*) in dynamic habitats: genetic composition and diversity of seed bank and established populations. – Basic Appl. Ecol. 4: 339–348.

Krinke L., Moravcová L., Pyšek P., Jarošík V., Pergl J. & Perglová I. (2005): Seed bank in an invasive alien *Heracleum mantegazzianum* and its seasonal dynamics. – Seed Sci. Res. 15: 239–248.

Lavergne S., Mouquet N., Thuiller W. & Ronce O. (2010): Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. – Annu. Rev. Ecol. Evol. Syst. 41: 321–350.

Lehman C. L. & Tilman D. (2000): Biodiversity, stability, and productivity in competitive communities. – Am. Nat. 156: 534–532.

Levin D. (1990): The seed bank as a source of genetic novelty in plants. – Am. Nat. 135: 563–572.

Levine J. M. (2000): Species diversity and biological invasions: relating local process to community pattern. – Science 288: 852–854.

Levine J. M., Adler P. B. & HilleRisLambers J. (2008): On testing the role of niche differences in stabilizing coexistence. – Funct. Ecol. 22: 934–936.

Lichtenthaler H. K. (1996): Vegetation stress: an introduction to the stress concept in plants. – Plant Physiol. 148: 4–14.

Livingston R. & Allessio M. (1968): Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. – Bull. Torrey Bot. Club 95: 58–69.

Lockwood J. L., Cassey P. & Blackburn T. M. (2005): The role of propagule pressure in explaining species invasions. – Trends Ecol. Evol. 20: 223–228.

Lockwood J. L., Cassey P. & Blackburn T. M. (2009): The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. – Diversity Distrib. 15: 904–910.

Lonsdale W. M. (1993): Losses from the seed bank of *Mimosa pigra* soil microorganisms vs. temperature-fluctuations. – J. Appl. Ecol. 30: 654–660.

Lonsdale W. M. (1999): Global patterns of plant invasions and the concept of invasibility. – Ecology 80: 1522–1536.

Lonsdale W. M., Harley K. & Gillet J. (1988): Seed bank dynamics in *Mimosa pigra*, an invasive tropical shrub. – J. Appl. Ecol. 25: 963–976.

Loreau M., Mouquet N. & Gonzalez A. (2003): Biodiversity as spatial insurance in heterogeneous landscapes. – Proc. Natl. Acad. Sci. USA 22: 12765–12770.

Loreau M., Naeem S., Inchausti P., Bengtsson J., Grime J. P., Hector A., Hooper D. U., Huston M. A., Raffaelli D., Schmid B., Tilman D. & Wardle D. A. (2001): Biodiversity and ecosystem functioning: current knowledge and future challenges. – Science 294: 804–808.

Lortie C. J., Munshaw M., DiTomaso J. & Hierro J. (2010): The small-scale spatiotemporal pattern of the seedbank and vegetation of a highly invasive weed, *Centaurea solstitialis*: strength in numbers. – Oikos 119: 428–436.

Luna B. & Moreno J. M. (2010): Range-size, local abundance and germination niche-breadth in Mediterranean plants of two life-forms. – Plant. Ecol. 210: 85–95.

Mandák B. (2003): Germination requirements of invasive and non-invasive *Atriplex* species: a comparative study. – Flora 198: 45–54.

Mandák B. & Pyšek P. (2001): Fruit dispersal and seed banks in *Atriplex sagittata*: the role of heterocarpy. – J. Ecol. 89: 159–165.

Marchante H., Freitas H. & Hoffmann J. H. (2010): Seed ecology of an invasive alien species, *Acacia longifolia* (*Fabaceae*), in Portuguese dune ecosystems. – Am. J. Bot. 97: 1780–1790.

Marchante H., Freitas H. & Hoffmann J. H. (2011): The potential role of seed banks in the recovery of dune ecosystems after removal of invasive plant species. – Appl. Veg. Sci. 14: 107–119.

Milton S. J. & Hall A. V. (1981): Reproductive biology of Australian acacias in the south-western Cape Province, South Africa. – Trans. R. Soc. S. Afr. 44: 465–485.

Mooney H. & Cleland E. (2001): The evolutionary impact of invasive species. – Proc. Natl. Acad. Sci. USA 98: 5446–5451.

Moravcová L., Perglová I., Pyšek P., Jarošík V. & Pergl J. (2005): Effects of fruit position on fruit mass and seed germination in the alien species *Heracleum mantegazzianum* (*Apiaceae*) and the implications for its invasion. – Acta Oecol. 28: 1–10.

Moravcová L., Pyšek P., Jarošík V., Havlíčková V. & Zákravský P. (2010): Reproductive characteristics of neophytes in the Czech Republic: traits of invasive and non-invasive species. – Preslia 82: 365–390.

Moravcová L., Pyšek P., Krinke L., Pergl J., Perglová I. & Thompson K. (2007): Seed germination, dispersal and seed bank in *Heracleum mantegazzianum*. – In: Pyšek P., Cock M. J. W., Nentwig W. & Ravn H. P. (eds), Ecology and management of giant hogweed (*Heracleum mantegazzianum*), p. 74–91, CAB International, Wallingford, UK.

Moravcová L., Pyšek P., Pergl J., Perglová I. & Jarošík V. (2006): Seasonal pattern of germination and seed longevity in the invasive species *Heracleum mantegazzianum*. – Preslia 78: 287–301.

Morris M. J. (1997): Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa. – Biol. Contr. 10: 75–82.

Naeem S., Bunker D. E., Hector A., Loreau M. & Perrings C. (eds) (2009): Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. – Oxford Univ. Press, Oxford.

Naeem S., Thompson L. J., Lawler S. P., Lawton J. H. & Woodfin R. M. (1994): Declining biodiversity can alter the performance of ecosystems. – Nature 368: 734–737.

Ogden J. & Rejmánek M. (2005): Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: implications for management. – Biol. Cons. 125: 427–439.

Pake C. & Venable D. (1995): Is coexistence of Sonoran desert annuals mediated by temporal variability reproductive success. – Ecology 76: 246–261.

Pardini E. A., Drake J. M., Chase J. M. & Knight T. M. (2009): Complex population dynamics and control of the invasive biennial *Alliaria petiolata* (garlic mustard). – Ecol. Appl. 19: 387–397.

Pardini E. A., Drake J. M. & Knight T. M. (2011): On the utility of population models for invasive plant management: response to Evans and Davis. – Ecol. Appl. 21: 614–618.

Pauchard A. & Alaback P. B. (2004): In?uence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. – Cons. Biol. 18: 238–248.

Peco B., Traba J., Levassor C., Sanchez A. M. & Azcarate F. M. (2003): Seed size, shape and persistence in dry Mediterranean grass and scrublands. – Seed Sci. Res. 13: 87–95.

Perglová I., Pergl J., Skálová H., Moravcová L., Jarošík V. & Pyšek P. (2009): Differences in germination and seedling establishment of alien and native *Impatiens* species. – Preslia 81: 357–375.

Petchey O. L., Morin P. J. & Olff H. (2009): The topology of ecological interaction networks: the state of the art. – In: Verhoef H. A. & Morin P. J. (eds), Community ecology processes models and applications, p. 7–22, Oxford Univ. Press, Oxford.

Peterson C. & Facelli J. (1992): Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subject to various amounts and types of plant litter. – Am. J. Bot. 79: 1209–1216.

Pieterse P. J. & Cairns A. L. P. (1986): The effect of fire on an *Acacia longifolia* seed bank in the south-western Cape. – S. Afr. J. Bot. 52: 233–236.

Powell K. I., Chase J. M. & Knight T. M. (2011): A synthesis of plant invasion effects on biodiversity across spatial scales. – Am. J. Bot. 98: 539–548.

Probert R. (2000): The role of temperature in the regulation of seed dormancy and germination. – In: Fenner M. (ed.), Seeds: the ecology of regeneration in plant communities, Ed. 2, p. 261–292, CABI Publishing, Wallingford.

Pyke D. A. (1990): Comparative demography of co-occurring introduced and native tussock grasses: persistence and potential expansion. – Oecologia 82: 537–543

Pyšek P., Bacher S., Chytrý M., Jarošík V., Wild J., Celesti-Grapow L., Gassó N., Kenis M., Lambdon P. W., Nentwig W., Pergl J., Roques A., Sádlo J., Solarz W., Vilà M. & Hulme P. E. (2010a): Contrasting patterns in the invasions of European terrestrial and freshwater habitats by alien plants, insects and vertebrates. – Glob. Ecol. Biogeogr. 19: 317–331.

Pyšek P., Jarošík V., Chytrý M., Danihelka J., Kühn I., Pergl J., Tichý L., Biesmeijer J., Ellis W. N., Kunin W. E. & Settele J. (2011): Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time. – Ecol. Monogr. 81: 277–293.

Pyšek P., Jarošík V., Chytrý M., Kropáč Z., Tichý L. & Wild J. (2005): Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. – Ecology 86: 772–785.

Pyšek P., Jarošík V., Hulme P. E., Kühn I., Wild J., Arianoutsou M., Bacher S., Chiron F., Didžiulis V., Essl F., Genovesi P., Gherardi F., Hejda M., Kark S., Lambdon P. W., Desprez-Loustau A.-M., Nentwig W., Pergl J., Poboljšaj K., Rabitsch W., Roques A., Roy D. B., Shirley S., Solarz W., Vilà M. & Winter M. (2010b): Disentangling the role of environmental and human pressures on biological invasions across Europe. – Proc. Natl. Acad. Sci. USA 107: 12157–12162.

Pyšek P., Krinke L., Jarošík V., Perglová I., Pergl J. & Moravcová L. (2007a): Timing and extent of tissue removal affect reproduction characteristics of an invasive species Heracleum mantegazzianum. – Biol. Inv. 9: 335–351.

Pyšek P., Perglová I., Krinke L., Jarošík V., Pergl J. & Moravcová L. (2007b): Regeneration ability of *Heracleum mantegazzianum* and implications for control. – In: Pyšek P., Cock M. J. W., Nentwig W. & Ravn H. P. (eds), Ecology and management of giant hogweed (*Heracleum mantegazzianum*), p. 112–125, CABI Publishing, Wallingford.

Pyšek P. & Richardson D. M. (2007): Traits associated with invasiveness in alien plants: where do we stand? – In: Nentwig W. (ed.), Biological invasions, p. 97–125, Springer, Berlin.

Pyšek P. & Richardson D. M. (2010): Invasive species, environmental change and management, and health. – Annu. Rev. Env. Res. 35: 25–55.

Pyšek P., Richardson D. M., Rejmánek M., Webster G., Williamson M. & Kirschner J. (2004): Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. – Taxon 53: 131–143.

Pyšek P., Sádlo J. & Mandák B. (2002): Catalogue of alien plants of the Czech Republic. – Preslia 74: 97–186.

Radford I. J. & Cousens R. D. (2000): Invasiveness and comparative life history traits of exotic and indigenous *Senecio* species in Australia. – Oecologia 125: 531–542.

Rees M. & Long M. (1992): Germination biology and the ecology of annual plants. – Am. Nat. 139: 484–508.

Reinecke M. K., Pigot A. & King J. M. (2008): Spontaneous succession of riparian fynbos: is unassisted recovery a viable restoration strategy? – S. Afr. J. Bot. 74: 412–420.

Rejmánek M., Richardson D. M. & Pyšek P. (2005): Plant invasions and invasibility of plant communities. – In: van der Maarel E. (ed.), Vegetation ecology, p. 332–355, Blackwell, Oxford.

Richardson D. M., Allsopp N., D'Antonio C., Milton S. & Rejmánek M. (2000a): Plant invasions-the role of mutualisms. – Biol. Rev. 75: 65–93.

Richardson D. M. & Kluge R. L. (2008): Seed banks of invasive Australian *Acacia* species in South Africa: role in invasiveness and options for management. – Persp. Plant Ecol. Evol. Syst. 10: 161–177.

Richardson D. M. & Pyšek P. (2006): Plant invasions: merging the concepts of species invasiveness and community invasibility. – Progr. Phys. Geogr. 30: 409–431.

Richardson D., Pyšek P., Rejmánek M., Barbour M., Panetta F. & West C. (2000b): Naturalization and invasion of alien plants: concepts and definitions. – Diversity Distrib. 6: 93–107.

Richardson D. M. & Thuiller W. (2007): Home away from home: objective mapping of high-risk source areas for plant introductions. – Diversity Distrib. 13: 299–312.

Roberts H. (1981): Seed banks in soils. – Adv. Appl. Biol. 6: 1–54.

Roberts H. & Feast P. (1973): Emergence and longevity of seeds of annual weeds in cultivated and undisturbed soil. – J. Appl. Ecol. 10: 133–143.

Rogers H. & Hartemink A. (2000): Soil seed bank and growth rates of an invasive species, *Piper aduncum*, in the lowlands of Papua New Guinea. – J. Trop. Ecol. 16: 243–251.

Rothrock P. E., Squiers E. R. & Sheeley S. (1993): Heterogeneity and size of a persistent seed bank of *Ambrosia artemisiifolia* L. and *Setaria faberi* Herrm. – Bull. Torrey Bot. Club 120: 417–22.

Salisbury E. (1942): The reproductive capacity of plants: studies in quantitative biology. – G. Bell & Sons, London.

Schupp E. W. & Fuentes M. (1995): Spatial patterns of seed dispersal and the unification of plant population ecology. – Ecoscience 2: 267–275.

Seabloom E. W., Harpole W. S., Reichman O. J. & Tilman D. (2003): Invasion, competitive dominance, and resource use by exotic and native California grassland species. – Proc. Natl. Acad. Sci. USA 100: 13384–13389.

Seastedt T. S. & Pyšek P. (2011): Mechanisms of plant invasions of North American and European grasslands. – Annu. Rev. Ecol. Evol. Syst. 42: 133–153.

Shen Y., Liu W., Baskin J. M., Baskin C. C. & Cao M. (2006): Persistent soil seed banks of the globally significant invasive species *Eupatorium adenophorum*, in Yunnan Province, south-western China. – Seed Sci. Res. 16: 157–162.

Silvertown J., Dodd M., Gowing D. & Mountford J. (1999): Hydrologically defined niches reveal a basis for species richness in plant communities. – Nature 400: 61–63.

Simberloff D. (2009): The role of propagule pressure in biological invasions. – Annu. Rev. Ecol. Evol. Syst. 40: 81–102.

Stöcklin J. & Fischer M. (1999): Plants with longer-lived seeds have lower extinction rates in grassland remnants 1950–1985. – Oecologia 120: 539–543.

Strydom M., Esler K. J. & Wood A. R. (2012): *Acacia saligna* seed banks: sampling methods and dynamics, Western Cape, South Africa. – S. Afr. J. Bot. 79: 140–147.

Sydes C. & Grime J. (1981): Effect of tree litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. – J. Ecol. 69: 249–262.

Taylor M. & Hastings A. (2005): Allee effects in biological invasions. – Ecol. Lett. 8: 895–908.

Templeton A. & Levin D. (1979): Evolutionary consequences of seed pools. – Am. Nat. 114: 232–249.

Thompson K. (1993): Persistence in soil. – In: Hendry G. & Grime J. (eds), Methods in comparative plant ecology, a laboratory manual, p. 199–202, Chapman & Hall, London.

Thompson K., Bakker J. & Bekker R. (1997): The soil seed banks of North West Europe: methodology, density and longevity. – Cambridge Univ. Press, Cambridge.

Thompson K., Bakker J., Bekker R. & Hodgson J. (1998): Ecological correlates of seed persistence in soil in the north-west European flora. – J. Ecol. 86: 163–169.

Thompson K., Band S. R. & Hodgson J. G. (1993): Seed size and shape predict persistence in soil. – Funct. Ecol. 7: 236–241.

Thompson K. & Grime J. (1979): Seasonal variation in seed banks of herbaceous species in ten contrasting habitats. – J. Ecol. 67: 893–921.

Thompson K., Hodgson J. G. & Rich T. C. G. (1995): Native and alien invasive plants: more of the same? – Ecography 18: 390–402.

Thompson K., Jalili A., Hodgson J. G., Hamzeh'ee B., Asri Y., Shaw S., Shirvany A., Yazdani S., Khoshnevis M., Zarrinkamar F., Ghahramani M. & Safavi R. (2001): Seed size, shape and persistence in the soil in an Iranian flora. – Seed Sci. Res. 11: 345–355.

Thomsen M., D'Antonio C., Suttle K. & Sousa W. (2006): Ecological resistance, seed density, and their interactions determine patterns of invasion in a California coastal grassland. – Ecol. Lett. 9: 160–170.

Thuiller W., Albert C. H., Araújo M. B., Berry P. M., Cabeza M., Guisan G., Hickler T., Midgley G. F., Paterson J., Schurr F. M., Sykes M. T. & Zimmermann N. E. (2008): Predicting global change impacts on plant species distributions: future challenges. – Persp. Plant Ecol. Evol. Syst. 9: 137–152.

Thuiller W., Richardson D. M., Pyšek P., Midgley G. F., Hughes G. O. & Rouget M. (2005): Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. – Glob. Change Biol. 11: 2234–2250.

Thuiller W., Richardson D. M., Rouget M., Procheş Ş. & Wilson J. R. U. (2006): Interactions between environment, species traits, and human uses describe patterns of plant invasions. – Ecology 87: 1755–1769.

Tiébré M.-S., Vanderhoeven S., Saad L. & Mahy G. (2007): Hybridization and sexual reproduction in the invasive alien *Fallopia* (*Polygonaceae*) complex in Belgium. – Ann. Bot. 99: 193–203.

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

Tilman D. (1997): Community invasibility, recruitment limitation, and grassland biodiversity. – Ecology 87: 81–92.

Tilman D. (2004): Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. – Proc. Natl. Acad. Sci. USA 101: 10854–10861.

Tilman D., Knops J., Wedin D., Reich P., Ritchie M. & Siemann E. (1997): The influence of functional diversity and composition on ecosystem processes. – Science 277: 1300–1302.

Tozer M. G. (1998): Distribution of the soil seed bank and influence of fire on seedling emergence in *Acacia saligna* growing on the central coast of New South Wales. – Austr. J. Bot 46: 743–755.

Turnbull L., Crawley M. & Rees M. (2000): Are plant populations seed-limited? A review of seed sowing experiments. – Oikos 52: 883–890.

Turner P. J., Scott J. K. & Spafford H. (2008): The ecological barriers to the recovery of bridal creeper (*Asparagus asparagoides* (L.) Druce) infested sites: impacts on vegetation and the potential increase in other exotic species. – Austral Ecol. 33: 713–22.

Van Clef M. & Stiles E. W. (2001): Seed longevity in three pairs of native and non-native congeners: assessing invasive potential. – Northeast. Natur. 8: 301–310.

van der Valk A. & Davis C. (1978): The role of seed banks in the vegetation dynamics of prairie glacial marshes. – Ecology 59: 322–335.

van der Valk E. & Pederson R. (1989): Seed banks and the management and restoration of natural vegetation. – In: Leck M., Parker V. & Simpson R. (eds), Ecology of soil seed banks, p. 329–344, Academic Press, San Diego.

Vecrin M. P., Grevilliot F. & Muller S. (2006): The contribution of persistent soil seed banks and flooding to the restoration of alluvial meadows. – J. Nature Cons. 15: 59–69.

Venable D. & Brown J. (1988): The selective interactions of dispersal, dormancy and seed size as adaptations for reducing risk in variable environments. – Am. Nat. 131: 360–384.

Vilà M., Espinar J. L., Hejda M., Hulme P. E., Jarošík V., Maron J. L., Pergl J., Schaffner U., Sun Y. & Pyšek P. (2011): Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. – Ecol. Lett. 14: 702–708.

Vilà M. & Gimeno I. (2007): Does invasion by an alien plant species affect the soil seed bank? – J. Veg. Sci. 18: 423–430.

Visser M. E. & Both C. (2005): Shifts in phenology due to global climate change: the need for a yardstick. – Proc. R. Soc. London B 272: 2561–2569.

Vitousek P., Walker L., Whiteaker L., Muellerdombois D. & Matson P. (1987): Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. – Science 238: 802–804.

Vosse S., Esler K. J., Richardson D. M. & Holmes P. M. (2008): Can riparian seed banks initiate restoration after alien plant invasion? Evidence from the Western Cape, South Africa. – S. Afr. J. Bot. 74: 432–444.

Walck J., Hidayati S. N., Dixon K. W., Thompson K. & Poschlod P. (2011): Climate change and plant regeneration from seed. – Glob. Change Biol. 17: 2145–2161.

Wang N., Jiao J., Jia Y. & Wang L. (2011): Seed persistence in the soil on eroded slopes in the hilly-gullied Loess Plateau region, China. – Seed Sci. Res. 21: 295–304.

Wardle D. A., Bardgett R. D., Callaway R. M. & Van der Putten W. H. (2011): Terrestrial ecosystem responses to species gains and losses. – Science 332: 1273–1277.

Watkinson A. & Powell J. (1993): Seedling recruitment and the maintenance of clonal diversity in plant populations: a computer simulation of *Ranunculus repens*. – J. Ecol. 81: 707–717.

Wearne L. J. & Morgan J. W. (2006): Shrub invasion into subalpine vegetation: implications for restoration of the native ecosystem. – Plant Ecol. 183: 361–376.

Williams P. A., Ogle C. C., Timmins S. M., La Cock G. D. & Clarkson J. (2005): Chilean rhubarb (*Gunnera tinctoria*): biology, ecology and conservation impacts in New Zealand. – Department of Conservation, Wellington, New Zealand.

Williamson M. (1996): Biological invasions. – Chapman & Hall, London, UK.

Witkowski E. T. F. & Garner R. D. (2008): Seed production, seed bank dynamics, resprouting and long-term response to clearing of the alien invasive *Solanum mauritianum* in a temperate to subtropical riparian ecosystem. – S. Afr. J. Bot. 74: 476–484.

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

Xiong S. & Nilsson C. (1997): Dynamics of litter accumulation and its effects on riparian vegetation: a review. – Bot. Rev. 63: 240–264.

Yachi S. & Loreau M. (1999): Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. – Proc. Natl. Acad. Sci. USA 96: 1463–1468.

Yamashita N., Tanaka N., Hoshi Y., Kushima H. & Kamo K. (2003): Seed and seedling demography of invasive and native trees of subtropical Pacific islands. – J. Veg. Sci. 14: 15–24.

Zavaleta E., Hobbs R. J. & Mooney H. A. (2001): Viewing invasive species removal in a whole-ecosystem context. –Trends Ecol. Evol. 16: 454–459.

Zenni R. D., Wilson J. R. U., Le Roux J. J. & Richardson D. M. (2009): Evaluating the invasiveness of *Acacia paradoxa* in South Africa. – S. Afr. J. Bot. 75: 485–496.

Zhao L. P., Wu G. L. & Cheng J. M. (2011): Seed mass and shape are related to persistence in sandy soil in northern China. – Seed Sci. Res. 21: 47–53.

Zobel M. (1997): The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? – Trends Ecol. Evol. 12: 266–269.

Zobel M., Otsus M., Liira J., Moora M. & Möls T. (2000): Is small-scale species richness limited by seed availability or microsite availability? – Ecology 81: 3274–3282.

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