

source of genetic variability, retaining a greater range of potential responses to environmental conditions or other factors than would be present in the standing vegetation (Venable and Brown 1988; Chesson *et al.* 2001).

In the context of plant invasions, soil seed banks may affect both the ‘invasiveness’ of certain alien plant species and the ‘invasibility’ of resident communities. While the role of the production of a large number of seeds and the formation of a soil seed bank in determining successful invasions by alien or weedy species has long been recognised (e.g. Williamson 1996; Fourie 2008; Gioria and Osborne 2008; 2009a), the effects of changes in the soil seed bank on the susceptibility of resident communities to invasions has only marginally been explored. Such changes may play a major role in determining the invasive success of an alien species and, in the long term, could provide the modified conditions that actually facilitate further colonisation by other alien or weedy species (Gioria 2007; Gioria and Osborne 2008; 2010) and contribute to what has been described as an ‘invasional meltdown’ (*sensu* Simberloff and von Holle 1999; Simberloff 2006).

Invasive species may affect the structure of seed bank of invaded communities directly, via the production of long-lived viable seeds (Gioria and Osborne 2008; 2009a). The formation of a soil seed bank by an invasive species can be viewed as a temporal dimension of propagule pressure (i.e. the number of separate introductions and the number of propagules introduced in an ecosystem at each point in time—see Colautti *et al.* 2006), which, so far, has been of the best predictors of successful invasions (Williamson 1996; Grime 2001; Lockwood *et al.* 2005). An alien plant, in fact, becomes invasive when, after being introduced and dispersed outside its native distribution range, succeeds in establishing self-sustaining populations and spreads into new areas (Richardson *et al.* 2000b; Richardson and Pyšek 2006; Davis 2009). As a store of suitable propagules, the seed bank of an alien species may be a major determinant of its invasive success by providing the genetic capability that is required to overcome any environmental or other barrier in its introduced range and by increasing the probability of finding a ‘window of opportunity’ (Richardson *et al.* 1992) for its establishment. Via their ‘storage effect’ (*sensu* Chesson *et al.* 2001 and references therein), soil seed banks may mitigate potential Allee effects (Stephens *et al.* 1999), which can substantially reduce the rate of invasion of certain species (Davis *et al.* 2004; Taylor and Hastings 2005), and the effects of density-dependent competition. The formation of a soil seed bank is particularly advantageous to the long-term persistence of a plant population

in highly variable environments (Thompson and Grime 1979; Thompson *et al.* 1998; Chesson *et al.* 2001), such as disturbed habitats, where invasive species have been shown to possess a strong colonising capacity (e.g. Planty-Tabacchi *et al.* 1996; Pyšek *et al.* 1998; Gioria and Osborne 2010). Finally, a large reservoir of seeds of an invader may lead to the saturation of available micro-sites for propagules establishment (Brown and Fridley 2003), thus reducing the recruitment of resident species from the seed bank.

In addition to the formation of a persistent reservoir of seeds, invasive plants may significantly affect resident soil seed banks via alterations that have been typically reported in the horizontal and vertical structure of the vegetation and in the biotic and abiotic conditions at a site (e.g. Vitousek *et al.* 1987; Mack *et al.* 2000; Ehrenfeld 2003; 2010; Davis 2009; Laungani and Knops 2009; Schweiger *et al.* 2010). Such alterations may in turn result in 1) changes in the amount and seasonality of seed rain; 2) changes in seed decay and mortality rates; 3) changes in seed germination and seedling establishment; and 4) physical limitations in seed dispersal (see Gioria 2007 and Gioria and Osborne 2010 for a review of these mechanisms). Previous investigations showed that invasions by large herbaceous species, such as the Japanese knotweed *Fallopia japonica* (Houtt.) Ronse Decraene and the giant hogweed *Heracleum mantegazzianum* Sommier & Levier, tend to promote a homogenisation of the soil seed bank, irrespective of the characteristics of the invaded habitat and of the reproductive strategy of the invaders (Gioria and Osborne 2010). Changes in the seed bank of resident communities associated with plant invasions may in turn have additive or multiplicative effects to any modification in the standing vegetation (Gioria and Osborne 2008; 2010). The disappearance of a species from both the vegetation and the seed bank will inevitably result in a permanent loss of this species in the absence of any introduction of propagules or dispersal events. Since a plant’s response to a stress factor is a function of its duration and severity (Grime 2001; Kranner *et al.* 2010), we can expect larger effects with increases in the duration of an invasion and in the number of introduced propagules. Changes in the soil seed bank will also inevitably impact on the genetic variability and evolutionary potential of invaded communities, with subsequent effects on their ability to respond to environmental variability (Venable and Brown 1988; Levin 1990) and, possibly, to respond to the introduction of propagules of other potential invasive species (Dukes 2002, but see Weltzin 2003).

Even though the importance of soil seed banks in determining plant community dynamics and as

reservoirs of biodiversity and genetic variability has long been recognised (Harper 1977; Templeton and Levin 1979; Thompson and Grime 1979; Chesson *et al.* 2001; Gioria and Osborne 2010), information on their role in secondary invasions is scarce. Here, we present the results of an investigation aimed at improving our understanding of the potential role of changes in the soil seed bank in successful secondary invasions. This study was conducted at a site experiencing a process of secondary invasion by *Fallopia japonica*, after being long colonised (over 50 years) by the giant rhubarb *Gunnera tinctoria* (Molina) Mirbel. These invaders are among the largest herbaceous species in the world (Bergman *et al.* 1992; Beerling *et al.* 1994). The particular conditions at this site, located in Achill Island, Ireland, provided a unique opportunity to investigate the characteristics of the soil seed bank of plant communities dominated by primary and secondary invaders and to improve our understanding of the potential long-term impact of these invaders on the vegetation. Specifically, we made a comprehensive assessment of the characteristics of the soil seed bank underneath each of these invaders and we tested the hypothesis that the structure (richness, abundance and composition) of the seed bank invaded by each of these species differs significantly, using a range of univariate and multivariate statistical procedures. Characterising the differences in the seed bank of sites subject to primary and secondary invasions allowed evaluation of whether these invaders differ in their impact on the soil seed bank, based on the plausible assumption that the seed bank invaded by *F. japonica* was similar to that invaded by *G. tinctoria* prior to the beginning of the process of secondary invasion. Secondly, we discussed plausible causes of secondary invasions by *F. japonica*, focusing on the potential role of niche and fitness differences, and that of changes in the seed bank of invaded communities, in determining the outcomes of competition between these giant herbaceous invaders. This information is critical to evaluating the magnitude of the impact of these herbaceous invaders over time and to improve our understanding of the conditions preceding successful processes of invasion. Ultimately, these findings provide information that is important to developing effective control and restoration strategies that account for the characteristics and regeneration potential of invaded plant communities and their vulnerability to secondary invasions by other alien or weedy species. To our knowledge, this is the first study that investigates and compares the soil seed bank of communities subject to processes of primary and secondary invasion.

MATERIAL AND METHODS

STUDY SPECIES

Gunnera tinctoria (Gunneraceae), a polycarpic perennial species native to South America (Molina 1978; Osborne *et al.* 1991), is one of the largest herbs in the world (Bergman *et al.* 1992). The geographic regions where *G. tinctoria* is naturalised or invasive, principally Ireland, the Azores, and New Zealand (Osborne *et al.* 1991; Williams *et al.* 2005), belong to the temperate zone and are typically characterised by mild winter temperatures and high levels of humidity (Osborne and Sprent 2002). *Gunnera tinctoria* is gynomonocious, having both hermaphrodite and female flowers (e.g. González and Bello 2009), and can reproduce asexually, via a large rhizomatous system, as well as sexually, by the production of thousands of seeds (Osborne *et al.* 1991; Silva *et al.* 1996; Gioria and Osborne 2009a). A description of the main features of *G. tinctoria* can be found in Osborne *et al.* (1991), Williams *et al.* (2005), Osborne and Bergman (2009) and González and Bello (2009). Recent investigations showed that this species has the potential to form a large and persistent soil seed bank (Gioria and Osborne 2009a; 2010).

Fallopia japonica (Polygonaceae), a perennial herbaceous native to Eastern Asia, is also among the tallest herbs in Europe (Beerling *et al.* 1994; Grime *et al.* 2007). This is an aggressive competitor and is thus listed among the top three invasive terrestrial plant species in the UK (Manchester and Bullock 2000) and the IUCN 100 worst invasive species (Lowe *et al.* 2000) due to its ecological and economic impacts. A review of this species can be found in Beerling *et al.* (1994). There is no evidence for the production of viable seeds in Britain and Ireland, where only male-sterile plants appear to occur (Hollingsworth and Bailey 2000). Vegetative regeneration can occur from small fragments of rhizomes in either water or soil (Child and Wade 2000).

SITE DESCRIPTION

The study site is located in Achill Sound, Achill Island, Co. Mayo (53°55' 9" N, 9°55' 46" W; altitude 4m a.s.l.), where annual rainfall is high (in excess of 1500mm) and temperatures range from 3.1°C (average minimum) to 8.2°C (average maximum) in January and from 11.1°C to 16.8°C in July (www.met.ie/recentweather/monthlydata.asp). The sampling area is located within a field surrounded on three sides by a stone wall and on one side is bounded by the ocean (Fig. 1). One wall is parallel to the main road that connects Achill Island to the mainland. A breach in this wall likely

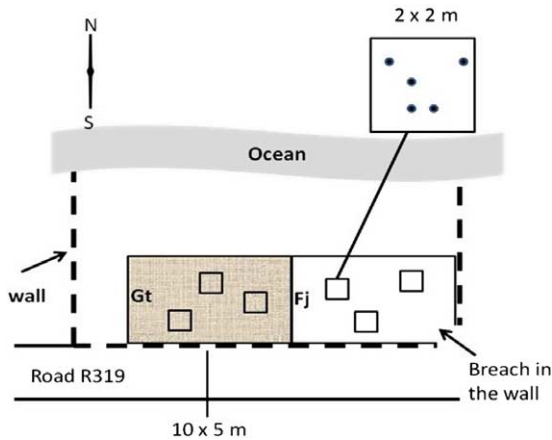


Fig. 1—Diagram illustrating the sampling protocol used in this study. Two adjacent areas (10m × 5m), one invaded by *Gunnera tinctoria* (Gt) and one, comparable, invaded by *Fallopia japonica* (Fj), were identified. Within each of these 50m² areas, three 4m² plots were randomly selected, and within each plot five random soil samples were selected. Each sample was divided into three depth categories (0–5cm; 5–10cm; 10–15cm). One side of the field side faces the ocean, while on three sides it is surrounded by a stone wall. A breach in this stonewall likely allowed the disposal of soil contaminated by fragments of *F. japonica* and subsequent invasion.

provided the opportunity to dispose of soil contaminated by fragments of *F. japonica* in this field, resulting in subsequent colonisation by this species. Based on anecdotal information, this site supported a typical *Festuca rubra* – *Plantago lanceolata* coastal grassland community (Rodwell 2000) prior to becoming invaded by *G. tinctoria* in the middle of the last century. In the standing vegetation, the presence of herbs such as *Bellis perennis* L., *Viola riviniana* Reichb., *Primula vulgaris* L., *Taraxacum officinale* L., and *Prunella vulgaris* L. as well as that of grasses such as *Poa trivialis* L., *Elytrigia repens* L., and *Holcus lanatus* L. was recorded under the dense canopy of *G. tinctoria* stands. Conversely, only *Urtica dioica* L. was recorded under the canopy of *F. japonica* over the summer months. Visual observations and anecdotal information indicate that secondary invasion by *F. japonica* and a process of displacement of *G. tinctoria* at the study site is only a recent phenomenon (three to five years at the time of sampling). There was no evidence of the presence of *G. tinctoria* individuals in stands of *F. japonica*. Visual observations at this site indicated that contaminated soil from one or more construction sites was the likely source of propagules for *F. japonica* colonisation.

SAMPLING DESIGN

Samples were collected from two comparable 50m² adjacent areas, one invaded by *G. tinctoria* (Gt) and one invaded by *F. japonica* (Fj) (Fig. 1). Five soil

cores (5cm diameter, 20cm depth) were collected randomly from three replicate 4m² plots that were randomly located within each 50m² area. The factor 'plot' was added to evaluate the differences between Gt and Fj invaded areas based on true replicates ($n = 3$) and to assess the spatial variability in the study area. Each soil core was divided into three depth categories (0–5cm; 5–10cm, and 10–15cm), for a total of 90 soil samples, equivalent to a surface area of 1767cm².

The basic assumption of this study is that the seed bank of plots currently invaded by *F. japonica* had a similar composition and abundance to that of plots invaded by *G. tinctoria* prior to secondary invasion by the former. The possibility that the seed bank in the area invaded by *F. japonica* differed from that of the area invaded by *G. tinctoria* was addressed (1) by selecting two adjacent areas, thus limiting any inherent habitat-related difference (see Gioria and Osborne 2010); (2) by limiting the size of the areas from which the two seed bank communities were sampled (50 m²); and (3) by carefully making use of anecdotal information from past and current land owners and local environmental officers.

SOIL SEED BANK ASSESSMENT

Soil samples were collected in May 2006, after a peak of germination of *G. tinctoria* seeds, which typically occurs in March (Hickey 2002) and in October 2006, after maturation of *G. tinctoria* seeds (Gioria and Osborne 2009a). The composition of the soil seed bank was estimated using a modified version of the seedling emergence approach (*sensu* Thompson and Grime 1979, see Gioria 2007; Gioria and Osborne 2008), expressed as the number of seedlings of each species per unit of soil surface (square metres). To expose the seeds to a wide range of temperatures, the soil samples (placed in 10cm-diameter pots) were located in unheated greenhouses. Control pots were randomly positioned among the sample pots at a 1:5 ratio, to detect and quantify any contamination caused by airborne seeds. Seedling emergence was recorded on a weekly basis for 52 weeks. Seed bank persistence was inferred from 1) the depth of viable seeds in the soil; 2) the size of the seed bank collected in May; and 3) from the relationship between the seed bank and the standing vegetation (see Thompson *et al.* 1997).

DATA ANALYSIS

Characterisation of the soil seed bank invaded by *G. tinctoria* and *F. japonica* was based on a combination of univariate, graphical/distributional, and multivariate techniques, which were recommended specifically for the analysis of soil seed bank data by Gioria and Osborne (2009b). Multivariate

analyses were based on a three-factorial hierarchical design: (1) invasive species (two levels: fixed), (2) plot (three levels: random, orthogonal), and (3) depth (three levels: fixed, crossed), with $n = 5$ observations per combination of factor levels.

Multi-species seed bank data was fourth-root transformed prior to multivariate data analyses, and a modified version of the Gower distance (Legendre and Legendre 1998) was used as the measure of dissimilarity between samples (see Gioria and Osborne 2009b). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was performed to test the differences in the structure (composition and relative abundance) between the seed bank invaded by *G. tinctoria* and *F. japonica* (9999 restricted permutations of raw data, with $\alpha = 0.5$). Permutational multivariate analysis of dispersion (PERMDISP; Anderson 2004) was used in combination with PERMANOVA to test for the variability of seed bank data within the two invaded seed bank communities (Gt and Fj). Multivariate patterns in species composition were visualised using non-metric multidimensional scaling (NMDS; Kruskal and Wish 1978). Similarity percentages analysis (SIMPER; Clarke 1993), based on Bray-Curtis similarities (Bray and Curtis 1957), was used to identify the species that contributed most to the average dissimilarity between the two seed bank communities (Gt and Fj), as well as those that contributed most to the average similarity within the two seed bank communities, using untransformed data. The degree of correspondence between the two communities was calculated using symmetric co-correspondence analysis (Co-CA) (ter Braak and Schaffers 2004). This ordination method was developed specifically to evaluate the degree of correspondence between two community data matrices (ter Braak and Schaffers 2004) and has been previously applied to evaluating the correlation between different taxonomic groups (ter Braak and Schaffers 2004; Gioria *et al.* 2010). Here, we used this method to evaluate the differences in two communities (belonging to the same taxonomic group) invaded by the two study invaders.

Differences in the abundance of the seed bank communities invaded by *F. japonica* and *G. tinctoria* were calculated using two-way analysis of variance (ANOVA), with invasive species (two levels: Gt and Fj) and depth (three levels, orthogonal) as factors. Seedling abundance data was fourth-root transformed and homogeneity of variance was tested using the Cochran C-test (Cochran 1951) prior to testing hypotheses concerning mean differences. When interactions were significant, *a posteriori* multiple comparison tests were conducted using the Student-Newman-Keuls (SNK) test (Day and Quinn 1989). ANOVAs were performed using the R software v. 2.10.1 (R Development Core Team

2010). The package ‘co-corresp’ of the R software (Simpson 2005) was used to perform Co-CA. PERMANOVA, PERMDISP, and dominance-diversity curves were performed using PRIMER v.6 and PERMANOVA Plus (Clarke and Warwick 2001; Anderson *et al.* 2008).

RESULTS

In total, 24 species were recorded from the seed bank invaded by *G. tinctoria*, while 18 species were recorded under *F. japonica* stands. *Fallopia japonica* did not set any viable seed at the study site, while *G. tinctoria* formed a large and persistent seed bank (*sensu* Thompson *et al.* 1997) (Table 1), representing 20% and 28% of the total seed flora collected under invasive *G. tinctoria* stands in May and October, respectively. The total seedling abundance of *G. tinctoria* was significantly lower in the area invaded by *F. japonica* ($F_{1,84} = 88.5$, $P < 0.001$ in May; $F_{1,84} = 97.0$, $P < 0.001$ in October) for each depth category, as indicated by pairwise *a posteriori* tests (Table 1). The relative abundance of *G. tinctoria* seedlings in the area invaded by *F. japonica* was higher in May (47%) than in October (11%), reflecting the contribution of the seed rain to the seed bank for many species prior to the October sample collection, although the actual number of *G. tinctoria* seedlings was similar. The majority of *G. tinctoria* seedlings germinated from the upper 0–5cm soil layer, and only a quarter emerged from the deepest (10–15cm) soil layer (Table 1).

Average species richness (aS) was higher in the seed bank invaded by *G. tinctoria*, particularly in the top 5cm soil layer (aS May = 8.07 ± 1.63 ; aS October = 8.33 ± 1.88), than in the seed bank invaded by *F. japonica* (aS May = 2.6 ± 1.30 ; aS October = 3.86 ± 1.35). Total seedling abundance was significantly lower in plots invaded by *F. japonica* ($F_{1,84} = 114.8$, $P < 0.001$ in May; $F_{1,84} = 118.5$, $P < 0.001$ in October). PERMANOVA analyses showed that the composition and relative abundance of the *G. tinctoria* soil seed bank were significantly different from those of plots invaded by *F. japonica* in May and in October (Table 2), both including and excluding seedlings of *G. tinctoria*. Differences in multivariate variability (measured using PERMDISP) were not significant in May, while in October the variability of the *G. tinctoria* seed bank was significantly higher than that of the *F. japonica* seed bank ($F_{1,88} = 4.935$, $P = 0.49$ without *G. tinctoria* seedlings; $F_{1,88} = 5.106$, $P < 0.001$ including *G. tinctoria* seedlings). This was evident in the NMDS plots (Fig. 2). The average dissimilarity between the two seed bank communities was high. Such dissimilarity was lower in October (71% and 70.5% including and excluding

Table 1—Mean number of seedlings $m^{-2} \pm SD$ (standard deviation) and percentage distribution of *Gunnera tinctoria* seedlings in the soil in areas invaded by *G. tinctoria* and *Fallopia japonica*, within each soil layer, in May and in October (one site, three plots, five observations). Superscripts summarise the results of ANOVAs and multiple SNK tests for two factors: 1) invasive species (small letters); 2) depth (capital letters), per each time of sampling. Values followed by the same small letter indicate that the differences between the seed bank under *G. tinctoria* and *F. japonica* stands are not significant, within each time of sampling, while those followed by the same capital letter indicate that the differences across depth of sampling were not significant.

Sample	May		October	
	Mean \pm SD	%	Mean \pm SD	%
<i>Gunnera tinctoria</i>				
GT 0–5cm	4380 \pm 1999 ^{aA}	61.14	4583 \pm 1886 ^{aA}	62.07
GT 5–10cm	1630 \pm 395 ^{aB}	22.75	1697 \pm 418 ^{aB}	22.98
GT 10–15cm	1154 \pm 302 ^{aC}	16.11	1103 \pm 344 ^{aC}	14.95
<i>Fallopia japonica</i>				
FJ 0–5cm	543 \pm 358 ^{bA}	57.14	713 \pm 258 ^{bA}	56.76
FJ 5–10cm	306 \pm 258 ^{bB}	32.14	407 \pm 211 ^{bB}	32.43
FJ 10–15cm	211 \pm 102 ^{bC}	10.72	233 \pm 136 ^{bC}	10.81

seedlings of *G. tinctoria*, respectively) than in May (86.5% and 94.4%, including and excluding seedlings of *G. tinctoria*, respectively), reflecting the contribution of the seed rain to the samples collected in October. The species that contributed most to the similarities within the two seed banks are presented in Table 3. The average similarity between samples collected from the seed bank invaded by *F. japonica* was very low (28.38%). Such a similarity was very low when seedlings of *G. tinctoria* (4%) were excluded, as shown by

NMDS and PERMDISP analyses, indicating that seeds of *G. tinctoria* also dominate the seed bank invaded by *F. japonica*. Conversely, the average percentage similarity between the two seed bank communities was comparable in October, although driven by different species. Co-correspondence analysis (Co-CA) showed that the correlation between the two seed banks was low and none of the Co-CA axes were significant, either including or excluding seedlings of *G. tinctoria*, independent of the time of sampling. Dominance-diversity

Table 2—Results of PERMANOVA analyses testing the effect of invasive species (*Gunnera tinctoria* vs *Fallopia japonica*), plot, and depth on the soil seed bank collected from areas invaded by *G. tinctoria* and *F. japonica* in May and October (three plots, five observations). Seedlings of *G. tinctoria* were excluded from the analysis.

Source	df	May				October			
		SS	MS	F	P	SS	MS	F	P
Species	1	144.99	144.99	32.67	0.001	44.82	44.82	13.54	0.001
Plot	2	6.56	3.28	0.90	0.546	5.84	2.92	1.00	0.442
Depth	2	23.77	11.88	3.51	0.001	23.14	11.57	4.71	0.001
Species \times Plot	2	8.88	4.44	1.22	0.258	6.62	3.31	1.14	0.288
Species \times Depth	2	25.73	12.86	3.87	0.001	16.72	8.36	3.06	0.009
Plot \times Depth	4	13.53	3.38	0.93	0.586	9.83	2.46	0.85	0.689
Species \times Plot \times Depth	4	13.29	3.32	0.91	0.601	10.91	2.73	0.94	0.545
Residuals	72	262.07	3.64			209.35	2.91		
Total	89	498.82				327.00			

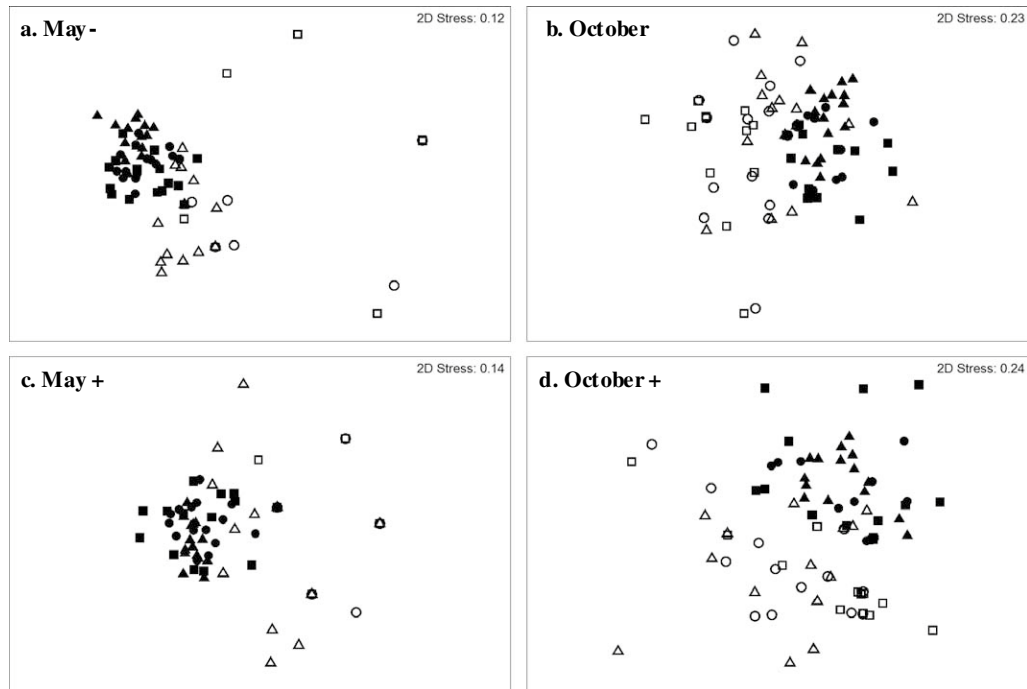


Fig. 2—Non-metric multidimensional scaling configurations showing soil seed bank assemblages collected beneath *Gunnera tinctoria* stands (full) and *Fallopia japonica* stands (empty) from three depth categories (triangle: 0–5cm; circle: 5–10cm; square: 10–15cm), excluding (a, b) and including (c, d) seedlings of *G. tinctoria*, in May (a, c) and in October (b, d).

curves showed that the seed bank of the area invaded by *G. tinctoria* was characterised by a higher dominance in May, due to the large contribution of seedlings of *Juncus effusus* L., while it was lower in October for most species, most likely due to the positive effect of the recent seed input (Fig. 3).

DISCUSSION

DIFFERENTIAL IMPACT OF *G. TINCTORIA* AND *F. JAPONICA* ON THE SOIL SEED BANK

Soil seed banks represent a major component of plant population dynamics (Harper 1977) and, as reservoirs of propagules and genetic diversity, they could contribute substantially to the biotic resistance of ecosystems to plant invasions (Gioria and Osborne 2010). Here, in a single site, soil seed banks associated with two large invasive herbaceous species, *G. tinctoria* and *F. japonica*, were similar in their being dominated by seeds of agricultural weeds, mostly *Urtica dioica*, and by seeds of *Juncus* species. This is consistent with the results of previous investigations in other regions and habitat types (Gioria and Osborne 2009a; 2009b; 2010), where a homogenisation of the seed flora following plant invasions has been reported (Gioria and Osborne 2010), in line with patterns traditionally observed in the standing vegetation (McKinney and Lookwood 1999; Mack *et al.* 2000).

Despite similarities in the composition (but not in the richness and abundance) of the seed bank invaded by these species, however, our results show that *G. tinctoria* and *F. japonica* clearly differ in their impact on the soil seed bank in the areas they have invaded in this site, although it was not possible to quantify such differences over the same time scale due to the lack of suitable control plots. More seeds and more species were found in the seed bank associated with the former, likely reflecting differences in the impact on the structure of the above ground vegetation and, possibly, additional changes at the ecosystem level. Due to the experimental design, we cannot rule out the possibility that differences between the seed banks were driven by factors other than the presence of the invaders (for example, proximity to a seed source, microclimatic differences, small scale changes in soil chemistry, microtopography etc.), but the likelihood of this was minimised by using small, adjacent areas and anecdotal information from past and present land owners, as well as local environmental officers, who indicated that both areas were similar in composition and land use prior to invasions. The differential impact was rather substantial considering that these species share many characteristics that have typically been used to explain their invasiveness, including a large stature, high biomass and persistent litter production, as well as a capacity for vegetative propagation (see Beerling *et al.* (1994) and Gioria

Table 3—Results of SIMPER analyses showing the contribution of the seedlings of each species to the average similarity between the communities invaded by *Gunnera tinctoria* and *Fallopia japonica* in a) May and b) October. Seedlings of *G. tinctoria* were excluded from the analysis.

a) May					
Species	Average abundance	Average similarity	Similarity/SD	Contribution%	Cumulative contribution%
GT: Average similarity: 39.04					
<i>Juncus effusus</i> L.	3847	20.67	1.32	52.94	52.94
<i>Urtica dioica</i> L.	1268	8.25	1.22	21.12	74.06
<i>Ranunculus repens</i> L.	2320	6.80	0.67	17.41	91.46
<i>Juncus bufonius</i> L.	441	1.34	0.41	3.43	94.90
<i>Rumex crispus</i> L.	238	0.45	0.29	1.15	96.04
<i>Stellaria media</i> (L.) Vill.	170	0.34	0.24	0.88	96.92
<i>Ranunculus acris</i> L.	362	0.30	0.20	0.78	97.71
<i>Lolium perenne</i> L.	215	0.25	0.20	0.64	98.34
<i>Persicaria maculosa</i> Gray	102	0.19	0.15	0.49	98.84
<i>Polygonum aviculare</i> L.	124	0.15	0.19	0.40	99.23
<i>Taraxacum officinale</i> agg.	79	0.14	0.14	0.36	99.59
<i>Rumex obtusifolius</i> L.	45	0.06	0.07	0.16	99.76
<i>Poa trivialis</i> L.	91	0.06	0.12	0.15	99.90
<i>Galium aparine</i> L.	34	0.02	0.05	0.05	99.95
<i>Cirsium arvense</i> (L.) Scop.	34	0.01	0.05	0.05	100
FJ: Average similarity: 4.34					
<i>Juncus effusus</i> L.	102	2.03	0.18	46.72	46.72
<i>Juncus bufonius</i> L.	57	0.78	0.10	18.02	64.74
<i>Lolium perenne</i> L.	68	0.67	0.11	15.43	80.18
<i>Urtica dioica</i> L.	79	0.56	0.11	12.93	93.11
<i>Rumex crispus</i> L.	57	0.16	0.06	3.66	96.77
<i>Ranunculus repens</i> L.	22	0.14	0.04	3.23	100

Table 3 (Continued)

<i>b) October</i>					
<i>Species</i>	<i>Average abundance</i>	<i>Average similarity</i>	<i>Similarity/SD</i>	<i>Contribution%</i>	<i>Cumulative contribution%</i>
GT: Average similarity: 41.98					
<i>Urtica dioica</i> L.	1675	17.05	1.85	40.61	40.61
<i>Ranunculus acris</i> L.	1245	10.97	1.17	26.12	66.73
<i>Juncus effusus</i> L.	1358	9.51	0.78	22.65	89.38
<i>Ranunculus repens</i> L.	407	1.59	0.42	3.79	93.17
<i>Juncus bufonius</i> L.	328	1.16	0.24	2.76	95.93
<i>Stellaria media</i> L.	317	0.60	0.25	1.42	97.36
<i>Rumex crispus</i> L.	283	0.54	0.26	1.29	98.65
<i>Galium aparine</i> L.	204	0.40	0.23	0.94	99.59
<i>Cirsium arvense</i> (L.) Scop.	57	0.07	0.10	0.17	99.77
<i>Taraxacum officinale</i> agg.	79	0.05	0.10	0.13	99.90
<i>Lolium perenne</i> L.	45	0.03	0.08	0.06	99.96
<i>Stachys sylvatica</i> L.	57	0.02	0.05	0.04	100
FJ: Average similarity: 37.20					
<i>Ranunculus acris</i> L.	905	20.32	1.29	54.62	54.62
<i>Juncus effusus</i> L.	747	12.18	0.79	32.75	87.36
<i>Juncus bufonius</i> L.	328	1.75	0.26	4.71	92.07
<i>Ranunculus repens</i> L.	170	1.55	0.28	4.16	96.23
<i>Rumex crispus</i> L.	124	0.59	0.19	1.58	97.81
<i>Urtica dioica</i> L.	91	0.50	0.17	1.35	99.16
<i>Cirsium arvense</i> (L.) Scop.	45	0.19	0.08	0.51	99.67
<i>Taraxacum officinale</i> agg.	34	0.05	0.05	0.14	99.81
<i>Rumex obtusifolius</i> L.	24	0.04	0.04	0.11	99.92
<i>Lolium perenne</i>	23	0.03	0.03	0.08	100

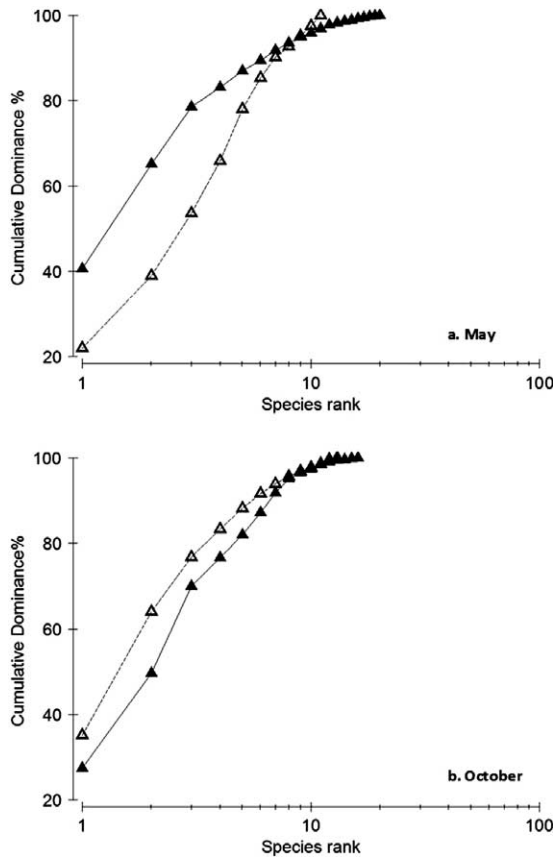


Fig. 3—Dominance–diversity curves calculated from seed bank data collected at one site invaded by *Gunnera tinctoria* (closed) and by *Fallopia japonica* (open) in May (a) and October (b). Seedlings of *G. tinctoria* were excluded from the analyses.

and Osborne (2009a) for a summary of these traits). Species richness and abundance were significantly lower in the seed bank of the area invaded by *F. japonica*. This is of particular significance, since we can expect that the seed bank invaded by *G. tinctoria* was already species-poor and small compared to its original structure prior to being invaded by this species a few decades ago, based on the results of previous investigations in Achill Island (Gioria and Osborne 2009a). Even the number of seedlings of *G. tinctoria* under the *F. japonica* stand was significantly lower than the number found under the canopy of *G. tinctoria*, at each depth category and time of sampling, despite the formation of a large and persistent seed bank by this species at the study site. It is plausible to assume that the seed bank of *G. tinctoria* was similar in both areas (that invaded by *G. tinctoria* and that invaded by *F. japonica*) prior to invasion by *F. japonica*, due to the relative homogeneity of the seed bank of the former across all the sampling plots.

Soil seed bank studies are complicated by a number of issues, including the processing of soil samples, space and time constraints, difficulties in

meeting the germination requirements for certain species (Thompson and Grime 1979; Thompson *et al.* 1997), as well as analytical difficulties associated with the high spatial and temporal variability of soil seed banks (Gioria and Osborne 2009b). In this study, we used a procedure that had been successful in promoting the germination of the majority of seeds in the soil (Gioria 2007; Gioria and Osborne 2010) as well as an analytical protocol that was specifically recommended to analyse soil seed bank data (Gioria 2007; Gioria and Osborne 2009b). Despite careful considerations made during the experimental design phase, it is possible that some species in the seed bank may have been missed. However, the magnitude of the differences in the structure of the seed bank of the communities collected under each invader allows us to state that the emergence of species with germination requirements that were not met under greenhouse conditions did not affect substantially the overall results.

Such a remarkable reduction in the abundance of the seed bank of *G. tinctoria* and that of other species in this site indicates that the effects of secondary invasion by *F. japonica* can exacerbate those already associated with primary invasion by *G. tinctoria*. Moreover, in this site, such an additional effect occurred within a period of few years only. This is consistent with the results of previous studies showing that, compared to other large herbaceous invasive species, *F. japonica* has a capacity to alter invaded soil seed banks at a faster pace (Gioria and Osborne 2010). Moreover, its detrimental impact on the seed bank is not limited to its transient component but also to the more persistent one, suggesting a capacity for this species to alter soil seed banks not only via changes in the seed rain and via mechanisms of dispersal limitation, but also via changes in seed decay and mortality rates. Since these two species are such problematic invaders, the generality of this finding needs to be verified in additional sites.

The differences in species richness and relative abundance of the seed bank associated with these invaders were significant both in May and in October, although such differences were higher in October. This is indicative of the importance of the contribution of the seed rain to the composition, richness, and abundance of the soil seed bank. In particular, this shows that the input of new seeds in October is critical to the maintenance of plant diversity and that the production of long-lived seeds is a necessary condition for the persistence of a species in areas invaded by large alien plants, as previously reported (Gioria and Osborne 2009a; 2010).

The displacement of resident species from the vegetation, through competition, the failure to reach reproductive maturity, and potential

decreases in fecundity associated with the novel conditions associated with these invaders were likely the major causes of the depletion and homogenisation of the soil seed bank in this site, consistent with previous investigations (Gioria and Osborne 2009a; 2010). Of the factors involved, shading effects, resulting from the replacement of a short-stature grassland community with tall herbs, and the production of extensive litter are probably of particular significance. These changes and subsequent alterations in other environmental conditions, including water availability, nutrient cycling, and microclimate, which have been commonly reported following invasions by *F. japonica* (Beerling *et al.* 1994; Vanderhoeven *et al.* 2005; Aguilera *et al.* 2010) and *G. tinctoria* (Hickey 2002; Gioria 2007), may have affected the soil seed bank by altering, for instance, seed recruitment and viability, seedling survival, growth rates, and the fecundity of the species recorded in the vegetation (see Gioria and Osborne 2010). Since the environmental conditions at a locality may substantially affect the balance between sexual and clonal reproduction for many species (Grime 2001), a number of resident species may have relied principally on vegetative propagation for reproduction and only rarely on regeneration by seeds in an adaptive response to the new biotic and abiotic conditions created by the introduction of these invaders, further contributing to changes in the seed rain.

Differences in the impact of these invaders on the soil seed bank may occur as the result of differences in their above-ground and below-ground architecture, in their phenology and physiology, in the quantity and quality of litter production, and in changes at the ecosystem level that are associated with their establishment. While *G. tinctoria* possesses few large leaves (100–150cm in diameter—see Molina (1978), Silva *et al.* (1996) and Gioria and Osborne (2009a)), *F. japonica* produces numerous small leaves and persistent tall shoots that possess a strong capacity to capture light (e.g. Beerling *et al.* 1994; Bradford *et al.* 2007). The differences in their light-interception capacity were evident in the differential impact of these species on the standing vegetation at this site. While only one species (*Urtica dioica*) coexisted under the dense summer canopy of *F. japonica*, a few species were recorded under the canopy of *G. tinctoria* invasive stands, consistent with observations reported in previous studies (Beerling *et al.* 1994; Bradford *et al.* 2007; see Gioria and Osborne 2009a; 2010 and references therein). A capacity for *F. japonica* to suppress the growth of resident species and limit their seed dispersal efficacy was suggested in the lower abundance and species richness of the seed bank invaded by this species in October (Grime 2001; Grime *et al.* 2007) compared to those

recorded underneath the *G. tinctoria* stand. A lower seed input from the seed rain in areas invaded by *F. japonica* is likely as a result of a higher impact of this species on the richness and abundance of the standing vegetation and of a higher capacity to limit the dispersal of seeds of other species, due to the formation of a denser canopy compared to that formed by *G. tinctoria*. A delay in flowering in *F. japonica*, coinciding with the arrival of winter at latitudes close to the northern limit of distribution (Beerling *et al.* 1994), resulting in a longer duration of the standing canopy of *F. japonica*, may also have led to a stronger impact of this species on the dispersal of seeds of resident species in this site.

Differences in the impact of these invaders on the soil seed bank may also have been dependent upon differences in the physiological traits of their leaves. These traits, in fact, affect directly the quality and decomposition of litter and thus impact on the germination rates of resident species by altering nutrient release from invasive litter and decomposition rates (Peterson and Facelli 1992; Ehrenfeld 2003; 2010), as well as seed mortality. Since litter limit substantially the dispersal of seeds of resident species (Facelli and Pickett 1991), differences in the quantity of litter produced by these invaders have also likely had a different impact on the seed bank via differences in the seed rain.

DIFFERENCES IN COMPETITIVE ABILITY AND NICHE DIFFERENCES

Gunnera tinctoria and *F. japonica* are considered to be good competitors, based on a classification of life strategies developed by Grime (1974); see Grime *et al.* (2007); Gioria and (unpublished), due to their ability to rapidly monopolise the resources within the invaded ecosystems (Beerling *et al.* 1994; Gioria and Osborne 2009a). Both species may expand clonally and are thought to outcompete native grassland communities via the rapid expansion of their foliage, which results in the interception of most available light (Manchester and Bullock 2000; Grime 2001; Gioria and Osborne 2009b; Aguilera *et al.* 2010).

The apparent competitive exclusion of *G. tinctoria* and the rapid depletion of the seed bank by *F. japonica* in this site raise a number of basic ecological questions and could be the result of a number of interacting factors, including: 1) fitness differences between these invaders; 2) the availability of empty niches created by the establishment and spread of *G. tinctoria*, which may have facilitated further invasions (e.g. changes in biodiversity and in nutrient cycling); and 3) niche differences between these species allowing the establishment and subsequent spread of *F. japonica*. Previous investigations have indicated that the outcome of biological invasions may largely depend

upon the relative strength of fitness differences (Chesson 2000; Levine *et al.* 2008). While niche differences can be seen as stabilising processes causing species to limit themselves and favour coexistence, fitness differences may drive ecosystems toward competitive exclusion (MacDougall *et al.* 2009). Thus, niche differences may allow the establishment of invasive species with a lower average fitness, while species with large average fitness may displace all competitors even in the absence of niche differences (Levine *et al.* 2008; MacDougall *et al.* 2009).

Differences in a range of traits including those in colonisation and dispersal ability, in longevity, as well as differences in propagule pressure may affect substantially the outcomes of competition among plants that rely on the same resource (Tilman 1994). *Gunnera tinctoria* and *F. japonica* differ in their average fitness, reflecting differences in their phenology, reproductive strategy, morphology, dispersal ability, longevity, or in phenotypic plasticity and their an ability to evolve and adapt to the new conditions experienced at a locality. Additional differences to those described above, and that may contribute to the success of *F. japonica* as a secondary invader, include their response to seasonal variation in daylight and temperature. In Ireland, both invaders germinate early in spring (Beerling *et al.* 1994; Gioria and Osborne 2009a; 2010 and references therein). Even if we assume that both species emerge at the same time early in the spring (March), the above mentioned differences in leaf and/or shoot dynamics and architecture inevitably affect their ability to capture light and resources. Since one of the major factors determining success in plant competition is the ability of a plant to extend leaves and roots and utilise the available resources before they are captured by neighbouring individuals (Campbell *et al.* 1992), differences in the morphology of these species likely contributed to the displacement of *G. tinctoria* by *F. japonica* in this site.

Gunnera tinctoria and *F. japonica* also differ in their strategies to maximise productivity in nitrogen-limited systems, as well as in their plant and litter chemistry and decomposition rates. *Gunnera tinctoria* is a nitrogen-fixing species, a trait that has been associated with successful in invasions elsewhere (e.g. Vitousek *et al.* 1987; Yelenik *et al.* 2007). In particular, invasions by nitrogen fixing invasive species tend to result in increases in the available N (Yelenik *et al.* 2007), although their long-term effects on soil nitrogen cycling may differ (see Ehrenfeld 2010 for a review). At our study site, high levels of available N may have facilitated secondary invasion by creating temporary new niches. Aguilera *et al.* (2009) showed a higher lignin:N ratios for *F. japonica* compared to that in dominant native canopy species, and that invaded

areas (five locations in Massachusetts) were characterised by greater above-ground biomass and standing N, while the cycling on nutrients was slower. These authors also suggested that inter-ramet access to stored nitrogen and photoassimilates may maximise stand level growth rates, facilitating the dominance by this species.

Differences in phenotypic plasticity, i.e. in their capacity to adapt to the conditions found in their introduced range, could also have affected their competitive ability and conferred a competitive advantage, as reported for other successful invaders (e.g. Williamson 1996; Richardson and Pyšek 2006). A high plasticity in salt tolerance traits for *F. japonica* (Richards *et al.* 2008) may have contributed to the invasive success of *F. japonica* at our study site, which represents a rather atypical habitat for this species. As for *G. tinctoria*, Gioria (2007) showed that saline conditions inhibit completely the germination of seeds of this invader and affect substantially its growth and fitness, although a large proportion of seeds buried in coastal habitats retain their viability. Since at the study site the vegetation is exposed to salt spray and grows on sandy soil, differences in their tolerance to saline conditions may have conferred *F. japonica* with a stronger competitive advantage.

A potential competitive advantage of *G. tinctoria* over *F. japonica*, deriving from a potentially higher genetic variability associated with the formation of a large and persistent seed bank, may have been hampered by a large depth of seed burial and by a low recruitment from the seed bank after an initial phase of establishment, as indicated by a lack of *G. tinctoria* seedlings at the study site observed over a six-month period (April to October). This is consistent with observations from previous investigations showing that, once established, vegetative propagation prevails over recruitment from seeds (Hickey 2002; Gioria 2007; Gioria and Osborne 2009a), although the latter may play an important role in the long-distance dispersal of this invader (Fennel *et al.* 2010). If recruitment occurs principally from recently produced seeds found on or near the surface, the genetic and demographic role of the seed bank may be insignificant (Silvertown and Charlesworth 2001), with potential consequences on the average fitness of *G. tinctoria*. Moreover, density-dependent effects resulting from the large number of seeds produced by *G. tinctoria* could have contributed to reducing the survival, growth, and fecundity of this species, potentially destabilising its population dynamics at the study site, as reported for other species (see Ramula and Buckley 2010 and references therein).

The availability of empty niches and/or niche differences could have played a major role in determining secondary invasion by *F. japonica* at

the study site. Previous investigations showed that if a community does not occupy all the available niches and efficiently use the available resources, an opportunity for an alien competitor species to become invasive may become available, particularly after a disturbance event (Tilman 1997; Davis *et al.* 1998; 2000). There are at least two possibilities associated with a niche-based explanation for the establishment and secondary colonisation by *F. japonica*. Either *G. tinctoria* did not occupy all available niches or an alteration of the conditions through the primary invasion result in the creation of suitable niches for *F. japonica* colonisation. Empty niches could have arisen from a capacity for *G. tinctoria* to fix nitrogen (Osborne *et al.* 1991). Nitrogen-fixing invaders may increase the availability of soil N, through a reduction in the competition for any N present (N-sparing) or by a direct increase in N via plant root systems (Yelenik *et al.* 2007; Laungani and Knops 2005). Although for *G. tinctoria* there was no evidence for long term increases in soil nitrogen (Hickey 2002), N-sparing could be important in removing any potential nutrient constraints, allowing for secondary invasion by *F. japonica*. Empty niches could also have resulted of the absence of specific ‘enemies’ of *F. japonica* (e.g. Torchin *et al.* 2003). It is also possible that local herbivores, parasites or pathogens have evolved to attack *G. tinctoria*, due to its long-term presence on Achill Island (see Fennel *et al.* 2010).

Finally, a decline in the diversity of the standing vegetation and of the seed bank associated with the long-term dominance of *G. tinctoria* at the study site could have played a major role in facilitating a secondary invasion by *F. japonica*. Species losses from seed bank communities inevitably results in changes in their evolutionary potential (Thuiller *et al.* 2008) and in their storage effect (Chesson *et al.* 2001). There is increasing evidence that the loss of a species from an ecosystem alters ecosystem functioning (Loreau *et al.* 2001) and its susceptibility to biological invasions (Tilman *et al.* 1996; 1997; Naeem *et al.* 2000; see Naeem *et al.* 2009). In particular, the richness of an ecosystem may affect its capacity to respond to environmental changes (Lehman and Tilman 2000; Loreau *et al.* 2001; Cardinale *et al.* 2006), the availability of empty niches (Tilman *et al.* 1997; Tilman 2004), and a capacity for functional compensations between species or phenotypes in time (Norberg *et al.* 2001). 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, while the loss of transient species from a community will inevitably affect the probability of colonisation and establishment of new

functional types in a system after a disturbance event (‘founder effect’).

Changes in the genetic variability of the seed bank that directly follow those in the above- and below-ground vegetation (Gioria and Osborne 2008; 2010) may have also affected their role as ‘evolutionary filters’ (*sensu* Templeton and Levin 1979) and thus their capacity to respond to secondary invasions. Since environmental conditions may substantially affect the balance between sexual and clonal reproduction for many species (Salisbury 1942; Watkinson and Powell 1993; Grime 2001), it is possible that the novel conditions created by the invasion by *G. tinctoria* at this site may have further decreased the genetic variability of the seed bank via increases in the importance of vegetative propagation for those perennial species that reproduce both sexually and asexually (Gioria 2007; Gioria and Osborne 2010).

CONCLUSIONS

This study suggests that *Fallopia japonica* and *Gunnera tinctoria* have differing impacts on resident communities and ecosystems and that, during the process of invasion, *G. tinctoria* can create conditions that may facilitate secondary invasions by other alien species or native weeds. The seed bank associated with long-term stands of *G. tinctoria* was species-poor and mostly dominated by seeds of this primary invader or by seeds of other alien or weedy species. Such a depauperation of the soil seed bank may have facilitated secondary invasion by *Fallopia japonica* at this site. This species showed a capacity to rapidly and substantially alter both the vegetation and the seed flora in the area in which it has become invasive. This also suggests that the effects of this secondary invasion on resident communities may be even more detrimental than those caused by primary invader, but this may vary among invasive species. Another important conclusion that can be derived by this study is that the formation of a large soil seed bank by an invasive species is not sufficient in itself to guarantee its persistence at a locality and to prevent secondary invasions by other species. It is possible, however, that, via its storage effect, the formation of a large seed bank by *G. tinctoria* will in future play a significant role in its population dynamics. In particular, the formation of a large seed bank by this invader may become important following disturbance events that could promote the germination of its long-lived seeds (Gioria and Osborne 2009a), or fluctuations in available resources (see Williams 1996; Davis *et al.* 1998; 2000). It may also play an important role in adaptations to climatic changes (see Thuiller *et al.* 2008), which, in contrast, may constrain the performance of native and resident species that do

not form a viable seed bank. This study suggests that these invaders differ substantially in their competitive ability in this site. Although it was not possible to specifically test the role of niche and fitness differences in determining the outcomes of competition between these giant invaders, it is likely that fitness differences and/or the presence of unoccupied niches may play an important role in determining the success of *F. japonica* as a secondary invader. This information is central to a more predictive understanding of the potential long-term implications of plant invasions on ecosystems. Ultimately, an improved understanding of the impact of an invasive plant on the susceptibility of resident communities to processes of secondary invasion is indispensable to developing effective control and conservation strategies.

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