

REPORT

Invasion-resistance in experimental grassland communities: species richness or species identity?

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Abstract

The question as to why some communities are more invulnerable than others has profound implications for conservation biology and land management. The theoretical issues involved go right to the heart of our understanding of species coexistence and community assembly. The experiment reported here indicates that for productive, small-scale grassland plots, species identity matters more than species richness in determining both the number of invading species and the total biomass of invasives.

Keywords

Alopecurus, *Anthoxanthum*, *Arrhenatherum*, assembly, biodiversity, competition, *Festuca*, invasibility, methyl bromide, seeds.

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INTRODUCTION

The question as to why some communities are more invulnerable than others has profound implications for conservation biology and land management (Godfray & Crawley 1998). The most consistent correlates of invasibility are disturbance and propagule supply. The higher the rate of disturbance, the greater the number of invasive species likely to be found, and the greater the fraction of total biomass likely to be made up by invasive species (Crawley 1987; Burke & Grime 1996). The higher the number of introductions, and the greater the number of propagules per introduction, the greater the chance of successful invasion (Veltman *et al.* 1996). Suites of traits associated with the invasive potential of particular species have been identified from observational studies (e.g. seed production, seed size, dispersal adaptations, competitive ability as seedlings; Rejmanek 1989; Pysek & Prach 1993; Crawley *et al.* 1996) and from field experiments (e.g. larger-seeded species were less dependent on disturbance for successful invasion; Burke & Grime 1996).

Conventional wisdom (Elton 1958) was that species-rich communities were less invulnerable because (it was assumed) vacant niches were less common, and the intensity of interspecific competition was more severe (Lodge 1993; Robinson *et al.* 1995). However, in the small number of cases where the relationship between invasibility and species richness has been tested, it has been found that species-rich habitats may be just as prone to invasion by exotic species as species-poor habitats (Horvitz *et al.* 1998; Wiser *et al.* 1998). The issue of whether species richness or species identity is more

important in determining system-level function in biodiversity experiments is controversial (Naeem *et al.* 1996; Huston 1997; Tilman 1997; Tilman *et al.* 1997, 1998). Species differ, and it is *because* species differ that one might expect to observe effects in experiments where the number of species is varied.

Here, we argue that the relative importance of species richness and species identity is likely to be determined (among other things) by the resource supply rate and by the scale at which the experiment is carried out. In small scale experiments with a high rate of resource supply, it is likely that a single species will be best adapted. The attributes of the species that is the competitive dominant will determine the attributes of the community as a whole. In larger-scale experiments or where the resource supply is lower, spatial heterogeneity may be sufficient that different species perform best in different microhabitats. In low-productivity environments, fine-grained, small-scale patchiness may be sufficient to ensure that individuals rooted in their optimal microhabitats cannot grow so big that they exclude other species from a large neighbourhood. Under these circumstances, it is possible that system-level performance (e.g. biomass or productivity) will increase with the number of species sown because different niches are filled by different species (“complementarity”, see Hooper 1998). These two cases define the end points of a continuum from “identity matters” to “richness matters”. In most real communities, both richness and identity will matter, with their relative importance determined by resource supply, substrate heterogeneity, the size of the local and regional species pools, and the scale of the experiment.

In an experiment where communities are created by sowing different numbers of species, then we expect to observe trends in both mean biomass and biomass variance with species richness because of what is called the “sampling effect” (see Appendix A). The mechanism is extremely simple: the larger the sample of species sown, the more likely it is that the competitive dominant will be present on any given plot.

Here we report a 7-year experiment in which communities differing in species richness and identity were produced experimentally and then allowed to accumulate species by recruitment from the local seed rain. The question addressed is this: what attributes of the original, sown communities determine the number, identity, and success of invading species?

MATERIALS AND METHODS

There were 12 seed-sowing treatments: four perennial grass species (*Arrhenatherum elatius*, *Alopecurus pratensis*, *Festuca rubra*, and *Anthoxanthum odoratum*) were grown in monoculture (four plots), pairwise mixtures (six plots), and a four-species mixture (one plot), while a species-rich plot was sown with 80 species of dicots (“herbs”; see Appendix B), giving four levels of initial species richness (1, 2, 4, and 80). There were three liming treatments; lime was applied each January at a rate of 20 t ha⁻¹, or 5 t ha⁻¹, with an unlimed control. The species and lime treatments were selected because they matched parts of the Park Grass Experiment at Rothamsted (Williams 1978), the sister experiment to the Nash’s Field plots (Crawley 1990b). The whole design was replicated in six blocks (216 plots in all; see Fig. 1). Each of the 12 seed-sowing

treatments was allocated at random to 3 m × 3 m plots within each of the three liming treatments (a split-plot design) in 20 m × 20 m plots fenced against rabbits in Nash’s Field, Silwood Park (GR 41/945686).

The six experimental plots were ploughed then rotovated to a fine tilth in July 1991. The seed bank, and any vegetative fragments of perennial herbs or grasses, were killed by methyl bromide treatment prior to sowing; plots were covered in transparent polythene sheeting and the gas was left for 6 days in August 1991. Seeds were sown at 2000 seeds m⁻² in September 1991, after any residual gas had time to clear. In the herb-sown plots, each of the 80 species was sown separately at ≈30 seeds m⁻². All seeds were supplied by John Chambers’ Wild Flowers Seeds, Kettering, NN15 5AJ, UK, and sown on moist filter paper in Petri dishes to check germination rate prior to sowing. All plots received 150 kg ha⁻¹ N, 35 kg ha⁻¹ P, and 225 kg ha⁻¹ K applied annually in April. Biomass samples measuring 25 cm × 50 cm were cut from the centre of each plot in early July each year from 1992 to 1998 (except 1993), sorted to species, and dried at 80°C. Plots were mown, and the hay removed, twice each year (in July and November). Cover data and plant species richness were taken for the entire 3 m × 3 m of all 216 plots in July 1998.

Species were selected on the sole criterion that they were British native mesic grassland plants; representing a mix of life histories (annuals, biennials, and perennials) and mature plant sizes (10 cm to 150 cm maximum height). Some of the species were present in Nash’s Field (residents), but most were not [nonresidents; see Crawley (1990b) for a description of the flora of Nash’s Field]. Seeds were sown separately for each species over the whole 3 m × 3 m area, with no gaps between adjacent plots. The first 0.5 m strip of each plot’s perimeter was treated as a guard row, leaving a central 2 m × 2 m experimental area, and 1 m walkways on the borders of each plot. The plots were weeded at 2-weekly intervals from germination in September 1991 until the end of the rapid growth phase in June 1992. Any gaps caused by patchy seedling recruitment were resown in October 1991, November 1991, or March 1992 as necessary. By June 1992 there was reasonably uniform cover of sown species on all the plots, and no bare patches larger than ≈3 cm diameter. Methyl bromide treatment was extremely effective in eliminating all the perennial species that would otherwise have regenerated from vegetative fragments (e.g. *Holcus mollis*, *Agrostis capillaris*, *Achillea millefolium*, *Rumex acetosella*), and killed most of the dormant seed-bank species (only three hard-seeded legume species survived the treatment; *Trifolium repens*, *T. dubium*, and *Lotus corniculatus*, and these in low numbers; Crawley 1990b).

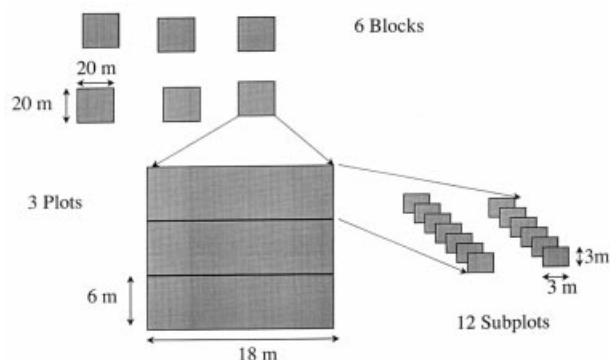


Figure 1 Experimental layout in Nash’s Field, Silwood Park. Six blocks (each 20 m × 20 m) were divided into three plots (18 × 6 m) to which one of three lime treatments was allocated at random [none, low (5 t ha⁻¹) and high (20 t ha⁻¹)]. Each plot was divided into 12 subplots each measuring 3 m × 3 m (in two rows of six), and 12 seed-sowing treatments (see text) were allocated at random to each subplot, independently for each plot and each block.

From July 1992 onwards, nonsown species were free to invade, either from seed production of sown species on adjacent plots, or by immigration of species from outside the experiment. For the purpose of this paper, an “invader” is simply a species that was not part of the original seed mixture on a given plot in September 1991; thus *Alopecurus* is an invader on a plot sown with a monoculture of *Anthoxanthum*, but a resident on a plot sown with the two-species mixture of *Alopecurus* and *Anthoxanthum*. The “invaders” are “nonsown species”, and not alien (exotic or nonindigenous) species. The key distinction is that invasion occurs one or more years after the communities were established, and involves competition between the invader’s seeds and established vegetation.

Statistical analysis involved log linear models with Poisson errors for counts of species richness (corrected for overdispersion where necessary), and ANOVA with normal errors following $\ln(y + 1)$ transformation for biomass data (Crawley 1993). Analyses were carried out separately, and standard errors presented separately, for each year of the experiment (excluding 1993 for which there are no data). There were 12 diversity/identity treatments nested within three lime treatments, and six blocks. Significance tests are presented in the figure legends.

RESULTS

For each of the four grass monocultures, biomass of the sown species was highest in the first year after sowing (Fig. 2a). Biomasses were either higher (*Festuca*) or broadly comparable (*Alopecurus*, *Arrhenatherum*, *Anthoxanthum*) with biomass of the same species on long-established plots on Park Grass (Williams 1978), indicating that the sown plots were reasonably well established by the time that invasion was allowed to begin. Subsequently *Anthoxanthum odoratum* declined rapidly, so that by 1995 it was all but extinct, and *Festuca rubra*, despite forming the highest biomass of any of the monocultures at the end of 1992, declined to very low levels by 1996. The other two grass monocultures fluctuated in biomass with the vagaries of spring rainfall (low in the drought years of 1995–97, and high in the wetter years of 1992, 1994, and 1998). Across the 7 years, total biomass (all species) was positively correlated with total rainfall in May and June ($r = 0.73$, $n = 7$, $P < 0.06$). The total number of species in the plots sown as monocultures (Fig. 2b) increased gradually over 7 years for *Alopecurus*, *Festuca*, and *Arrhenatherum*, but was high from the first year onwards for *Anthoxanthum*. The initial rate of invasion (in 1992) was inversely proportional to the biomass of the dominant, but subsequently, plots accumulated species at roughly equal rates (compare Fig. 2a, b). In the two- and four-species mixtures, where grass

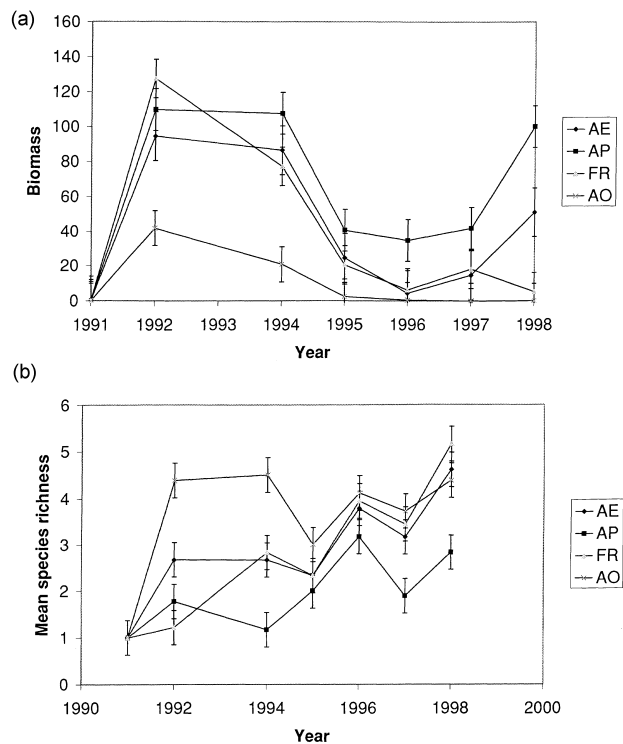


Figure 2 (a) Biomass of sown species on the unlimed grass-sown monoculture plots from 1992 to 1998. All of the sown grass species reached their peak mean biomass during the first growing season (i.e. while they were being weeded). *Festuca* produced the highest monoculture biomass in 1992 but declined steeply to virtual extinction by 1996. *Anthoxanthum* monocultures had the lowest initial mean biomass, and declined to virtual extinction by 1995. Note the overall depression of total biomass during the dry years 1995–97. Bars show 1 SE ($n = 6$). (b) Pattern of recruitment of invasive species on unlimed grass-sown monocultures from 1992 to 1998. Total species richness increased from one (sown) species in 1991, to an average of more than three species in 1998. *Anthoxanthum* accumulated nonsown species most rapidly during the first growing season postestablishment, and *Festuca* most slowly. By 1998, *Alopecurus*-sown plots supported significantly fewer species than plots sown with monocultures of the other three grass species. Note that species richness determined (as here) from sorted biomass samples (50 cm \times 25 cm) is lower than from the whole plot (3 m \times 3 m) survey carried out in 1998 (compare with Fig. 3b). Bars show 1 SE ($n = 6$).

species were sown together, the competitive ranking (based on total biomass in mixture) became clear: *Alopecurus* > *Arrhenatherum* > *Festuca* > *Anthoxanthum*. Surprisingly, the ranking was not affected by our soil pH treatments, presumably because our unlimed plots (pH 4.7) were not sufficiently acidic to give *Anthoxanthum* the competitive edge it obtains on nutrient-rich, acid plots in Park Grass data (Williams 1978).

The 18 plots sown originally with 80 species of herbs in 1991 (six replicates on each of three lime treatments) were very similar in 1992 with codominance by the annuals *Papaver rhoeas* and *Centaurea cyanus*. Subsequently they all showed a rapid decline in species richness as annuals were replaced by perennials. By 1998, the herb-sown plots were relatively similar in botanical composition, with most (11 of 18) plots dominated by sown *Tanacetum vulgare* (Asteraceae) or nonsown *Alopecurus* (seven of 18 plots). Averaged over the three lime treatments, mean species richness of sown herbs declined monotonically from 15.2 in 1992 to 5.1 in 1998. Very few of the sown herb species subsequently invaded plots sown originally to grass [only seven sown herb species were found on grass-sown plots in 1998, and then (except for *Tanacetum*) in very low numbers]. A total of 54 species was present on the 216 plots in 1998, of which 20 were sown (out of 84 originally), and 34 were invaders from other parts of Silwood Park (Appendix B). There was no evidence of neighbour effects causing local, seed-limited recruitment, and the likelihood of invasion of a given plot was not significantly affected by the sowing treatment on adjacent plots ($P > 0.05$).

The most successful, nonsown species were as follows, ranked by the percentage of plots invaded (out of 216): the grasses *Holcus lanatus* (38.0%), *Anisantha sterilis* (32.4%), *Agrostis capillaris* (14.8%), *Poa trivialis* (13.4%), and *Bromus hordeaceus* (6.0%), and the herbs *Stellaria media* (27.3%) and *Cirsium arvense* (9.7%). There were no significant associations between the probability of invasion by a given species and the identity of the sown species on the invaded plot, except in 1994 when there was a significant positive association between *Poa trivialis* and plots sown with *Anthoxanthum odoratum* (d.f. = 1, $P < 0.01$), and 1997 when there was a negative association between invasion by *Holcus lanatus* and presence of *Alopecurus pratensis* in the initial seed mixture (d.f. = 1, $P < 0.05$).

The effect of sown species richness (1, 2, 4, or 80) on the number of invasive species in 1998 is shown in Fig. 3(a). Taking all the data together ($n = 216$) there is no correlation between the number of species sown in 1991 and the number of nonsown species in 1998 ($r = 0.08$, $P > 0.2$). Taking account of the liming treatments reveals a more complicated picture. Unlimed plots sown with more than two species were invaded by a significantly greater mean number of nonsown species ($P < 0.05$). The pattern was different on the limed plots, where the plots sown with four grass species tended to show lower rates of invasion, and the herb-rich plots show a higher rate of invasion (Fig. 3a). For the experiment as a whole, there was a highly significant relationship between the presence of *Alopecurus* and the number of other species, whether the *Alopecurus* was a sown (Fig. 3b) or an unsown invader

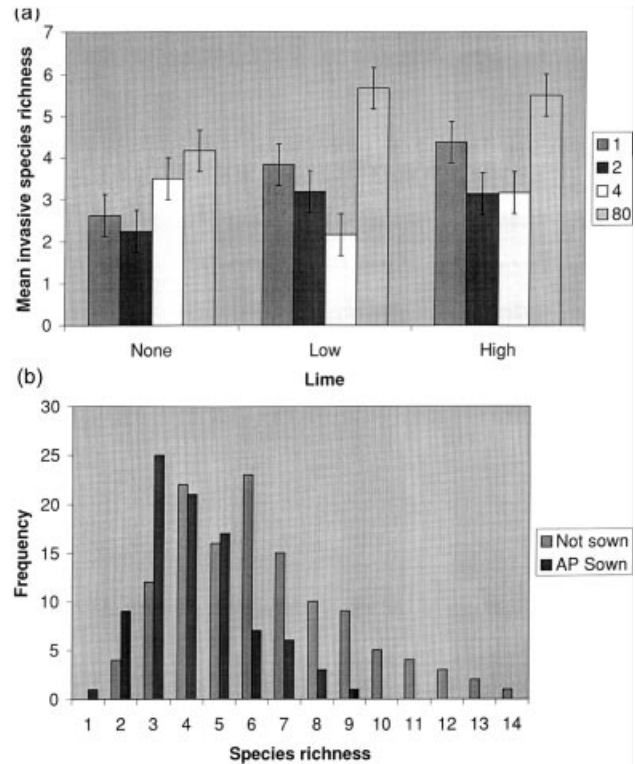


Figure 3 Species richness effects on invasion. (a) The mean number of invasive (nonsown) species for plots sown with 1, 2, 4, or 80 species for each of three liming treatments. Liming increased the mean number of invasive species. For a given lime treatment, the herb-sown plots were consistently more invasible than the grass-sown plots. There was no overall correlation between sown species richness and mean number of invasive species ($r = 0.08$, $n = 12$), but there was an increasing trend that was significant for the unlimed plots ($P < 0.05$, $n = 6$). (b) The impact of the presence of the superior competitor, *Alopecurus pratensis*, on total species richness (sown + nonsown species in $3 \text{ m} \times 3 \text{ m}$ plots) in 1998. Frequency of $3 \text{ m} \times 3 \text{ m}$ quadrants with a given species richness (total frequency = 216). Plots where *Alopecurus* was sown (AP Sown) were more likely to have low total species richness (one, two, or three species), and less likely to have high species richness (six or more species). No plots sown with *Alopecurus* supported more than nine species in 1998 ($\chi^2 = 47$, d.f. = 13, $P < 0.001$). On plots where *Alopecurus* was not sown, but invaded subsequently, there was a negative correlation between the biomass of *Alopecurus* and the number of species recorded in 1998 ($r = -0.216$, $n = 126$, $P < 0.02$).

($r = -0.216$, $n = 126$, $P < 0.02$). It is clear that the presence of *Alopecurus* in the mixture was the principal determinant of the variation in Fig. 3(a), rather than a response to species richness as such.

For each of the response variables (number of invading species, total biomass of invaders, etc.), the effects of initial community composition can be broken down into a number of *a priori* contrasts (e.g. number of species sown,

grasses vs. herbs, monocultures vs. polycultures, etc.). The only significant contrast, however, was species identity. Plots sown initially with *Alopecurus pratensis* as part (or all) of the seed-mix had significantly fewer invasive species, and significantly lower total abundance of invasives by 1998, than any other sowing mixtures (see Figs 4 and 5). For species richness, the total deviance for differences in species richness amongst the 11 grass-sowing treatments was $\chi^2 = 69.62$ (d.f. = 10), of which the *Alopecurus* contrast accounted for $\chi^2 = 52.64$ (d.f. = 1). For total biomass of invasive species, the total sum of squares attributable to sowing treatment was 21,004 (d.f. = 10), of which the *Alopecurus* contrast sum of squares accounted for 16,626 (d.f. = 1; $s^2 = 1363$). For the herb-sown plots, there was a significant negative correlation between the number of nonsown species and the abundance of *Alopecurus* that had established on the plots ($r = -0.47$, $n = 18$, $P = 0.05$). None of the other species' contrasts was significant. For this community, with its high resource supply rate, it is clear that identity matters more than species richness in determining invasibility.

DISCUSSION

At the end of the first growing season (1992) the patterns of total biomass were consistent with the predictions of the "sampling effect". Mean biomass was higher, and the variance in biomass was lower, in plots sown with more

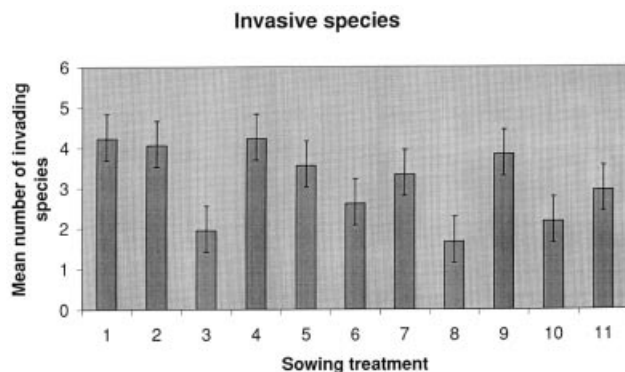


Figure 4 The number of invasive species in 1998 (3 m × 3 m plots) for each of the 11 treatments sown originally with grasses in 1991 (averaged over three lime treatments). The herb-sown plots (not shown in the figure) averaged 5.1 invasive species by 1998 (see Fig. 3a). Treatment codes are as follows (initials as in Appendix B): (1) AE monoculture; (2) FR monoculture; (3) AP monoculture; (4) AO monoculture; (5) two-species mix, AE and FR; (6) AE and AP; (7) AE and AO; (8) FR and AP; (9) FR and AO; (10) AP and AO; (11) four-species mix, AE, AP, FR, and AO. Error bars are back-transformed (+ 1 SE) from the log scale on which the modelling was carried out. There are significant differences amongst the means ($\chi^2 = 69.62$; d.f. = 10, Poisson errors).

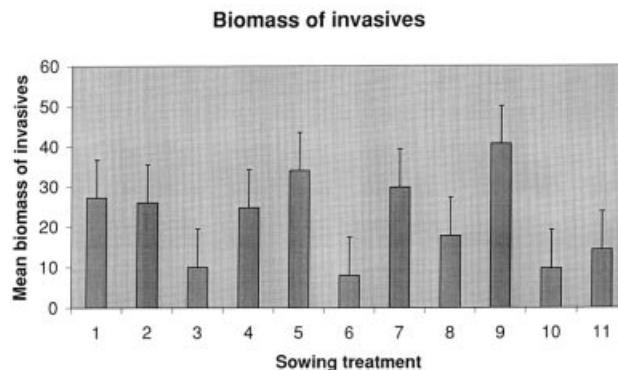


Figure 5 The biomass of invasive species in 1998 (50 cm × 25 cm plots) for each of the 11 treatments sown originally with grasses in 1991; sowing treatments as in Fig. 4. The herb-sown plots (not shown) averaged 11.7 g invasive biomass in 1998, not significantly different from the average of the grass-sown plots. Error bars (+ 1 SE) back-transformed from the $\ln(y + 1)$ scale on which the ANOVA (normal errors) was carried out. There are significant differences amongst the means ($F = 2.34$, $P < 0.05$, d.f. = 10, 187).

species, presumably because the competitive dominant, *Alopecurus pratensis*, was more likely to be present in species-rich mixtures. Note, however, that the magnitudes of the two effects were quite different; the sampling effect on total biomass was small (1.06-fold), while the effect on the variance in total biomass was pronounced (19.0-fold; see Appendix A). One important reason for this difference is that competitive exclusion did not occur, as required by the simple model underlying the sampling effect.

All experimental treatments were invaded by nonsown species. During the first growing season, the number of invasive species was inversely correlated with total biomass of sown species; lowest on the *Festuca*-sown plots and highest on the *Anthoxanthum*-sown plots. Subsequently, *Festuca* declined rapidly in abundance, perhaps as a result of the re-establishment of populations of soil pathogens following methyl bromide treatment in 1991 (see below). By 1998, mean species richness was significantly lower on the *Alopecurus*-sown than on the other three grass-sown monocultures (Fig. 3b). Both the biomass of invasive species and the number of invasive species were significantly lower on plots with *Alopecurus* in the seed mixture. No other sown species was involved in significant contrasts (Figs 4 and 5).

Overall, there was no correlation between species richness of the sown plots (1, 2, 4, or 80) and either the number of invasive species or the total biomass of invasive species, except in so far as *Alopecurus* was more likely to be part of the sown species mix on the higher-diversity plots (one of four for the monocultures, three of six for the two-species mixtures, and all of the four-species plots). There were significantly more invasive species on

the species rich, herb-sown plots, especially when lime was applied (Fig. 3b), but it is not possible to know whether this is a species-richness effect or a functional-types effect (i.e. that the plots were sown with herbs rather than grasses). The principal determinant of total species richness after 7 years was the presence of *Alopecurus* in the sown mixture (Fig. 3b). For the plots where *Alopecurus* was not sown, there was a significant negative correlation between species richness in 1998 and the biomass of invasive *Alopecurus* in the sorted biomass samples from 1998. Other species showed no such correlations.

The fact that the plot boundaries were still sharp after 7 years of invasion and competition draws attention to an important asymmetry that, until recently, has been ignored in theoretical models of coexistence (see Pacala & Rees 1998). The results of this experiment make clear that the outcome of seedling–seedling competition does not necessarily predict the outcome of seedling–adult competition. Seedlings of the superior competitor may not be able to invade a sward dominated by established adults of the inferior competitor. Many models (e.g. colonization/competitive ability trade-off; Tilman & Pacala 1993) are based on the implicit assumption that seedlings of the superior competitor can out-compete adults of the inferior competitor. If adult plants of the inferior competitor provide a refuge from competitive exclusion, this could represent a potentially powerful mechanism promoting coexistence (Chesson 1986; Pacala 1997).

The experimental protocol could be improved in a number of ways. It would have been better to weed the sown communities for several years, to ensure that they were thoroughly established, before allowing the process of invasion to begin. However, the fact that the biomasses of the sown communities were as high or higher than equivalent biomasses from the Park Grass experiment, where the plots are 140-years-old, suggests that this was not a major problem. The use of methyl bromide prior to sowing could be criticised for having such a massive impact on soil populations of invertebrate animals and fungi (both pathogenic and mycorrhizal), and for producing a large pulse of available nutrients in the first year. The extraordinarily high biomass of *Festuca rubra* during the first (1992) growing season suggests that it benefited disproportionately from methyl bromide treatment. This could have been because it suffers relatively more than the other grasses from soil pathogens (enemy release), or alternatively that the other grasses rely relatively heavily on their mycorrhizae (competitor release). Our decision to use methyl bromide was entirely pragmatic; we did not have enough labour to weed the plots sufficiently well to allow establishment from seed, in the face of competition from seed bank annuals and regeneration from vegetative fragments of vigorous perennials. The decision to use

such a high rate of fertilizer input was made, in part, to mask any initial pulse of nutrients following decomposition of material killed by the methyl bromide. In a parallel experiment reported elsewhere (Edwards & Crawley, manuscript) we describe seedling establishment in cultivated plots with and without methyl bromide. These results suggest that at sufficiently high seed densities, the sown species can outcompete seed bank recruitment and vegetative regeneration, and that with reasonable levels of hand-weeding, methyl bromide treatment could be avoided.

The herb-sown plots provide an interesting test of the predictability of community assembly. Conventional wisdom is that there is a major random component in species composition and relative abundance, but there is no assembly rule theory (other than competitive exclusion) to provide a useful null hypothesis about what to expect 7 years after sowing 80 species. In fact, the six replicate communities show a quite remarkable degree of similarity in species diversity, botanical composition, and relative abundance, in terms of both sown species (Table 1a) and invading species (Table 1b). Evidently, complete competitive exclusion has not occurred, although there has been massive species loss. The identities of the surviving and invading species seem to be highly predictable, giving us some hope that there may indeed be simple rules of assembly. The two species whose identities most strongly affect the outcome of this experiment show several similarities in growth form and life history. *Alopecurus pratensis* (Poaceae) and *Tanacetum vulgare* (Asteraceae) are both herbaceous perennials growing to a maximum 1.2 m in height and both are characteristic of nutrient-rich, well-watered conditions. The competitive ability of both species appears to involve long-term pre-emption of underground space by bulky roots, possession of winter-green leaves, rapid shoot growth in early spring, and a canopy that casts a dense shade at ground level.

The central result of this experiment is that identity matters more than species richness in determining invasibility by seed. While it is possible that the result is idiosyncratic to this grassland community and this high resource supply rate, only further experimental work will tell. The result is consistent with the prediction (Crawley 1990a) that interspecific competition is the most important process determining the likelihood of plant invasion. It also provides support for the view that adult–seedling competition needs to be considered along with seedling–seedling competition in models of invasion and coexistence (Pacala & Rees 1998).

ACKNOWLEDGEMENTS

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Table 1 Biomass and species richness in 1998 on the unlimed, herb-rich plots initially sown with 80 species. The (a) sown and (b) nonsown species in six replicate plots show a high degree of similarity. Biomass (g dry mass) sorted to species from 25 cm × 50 cm samples from the unlimed, control plots. +, Species present in the 3 m × 3 m quadrant but not found in the 50 cm × 25 cm sorted biomass sample; 0, absent from this block. Note that estimates of species richness are always higher in the larger quadrants.

	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
(a) Sown species						
<i>Tanacetum vulgare</i>	9.9	46.3	0.1	159.0	7.2	48.8
<i>Silene latifolia</i>	+	+	+	+	+	0.1
<i>Lotus corniculatus</i>	0	0	0.2	0	0	0
<i>Achillea millefolium</i>	0	0	1.8	0	0	+
<i>Cirsium vulgare</i>	0	0	0.7	0	0	0
Number of sown species 25 cm × 50 cm	1	1	4	1	1	2
Number of sown species at 3 m × 3 m	2	2	5	2	2	3
(b) Invading species						
<i>Alopecurus pratensis</i>	88.2	48.5	44.6	60.8	28.9	0
<i>Arrhenatherum elatius</i>	4.1	45.1	2.3	0.6	0	15.9
<i>Holcus lanatus</i>	0	0	0	0	25.6	113.1
<i>Anisantha sterilis</i>	0	0	+	+	0.6	0
<i>Bromus hordeaceus</i>	0	0	1.1	0	0	0
<i>Elytrigia repens</i>	0	+	22.3	0	0	0
<i>Deschampsia caespitosa</i>	0	5.7	0	0	0	0
<i>Festuca rubra</i>	+	0	0	0	0	0
<i>Poa trivialis</i>	+	+	0	0	0	+
<i>Holcus mollis</i>	0	0	+	0	0	0
<i>Rumex obtusifolius</i>	0	0	+	0	0	0
<i>Stellaria media</i>	0	0	+	0	0	0
<i>Agrostis capillaris</i>	0	0	+	0	0	0
Number of nonsown species in 25 cm × 50 cm	2	3	5	2	3	2
Number of nonsown species in 3 m × 3 m	4	5	9	3	3	3

APPENDIX A

Assume that under prevailing rates of resource supply the species can be ranked in terms of their competitive abilities: 1 is the least competitive and s is the most competitive. Now assume that when two or more species are grown together there is asymmetric competition leading to exclusion of all but the most competitive species (e.g. in the four-species mix 3, 7, 8, and 11, we would have a monoculture of species 11).

We are interested in the probability that species i is the largest in the sample of n species, so that species i will dominate a plot sown with that species mixture. When the sample $n > i$ there is no way that species i can be dominant, because there is bound to be at least one more competitive species on the plot (e.g. species 2 cannot be dominant on a three-species plot, because the least competitive mixture would be 1, 2, and 3). The probability that species 3 would dominate a three-species plot is just $6/[s(s-1)(s-2)]$.

Now there are $\binom{i}{n}$ ways of combining n species out of i , but not all of these sets contain species i . We need to constrain one species out of the set to be species i , so the number of combinations of n from i that contain species i is $\binom{i-1}{n-1}$. In general, therefore, the probability that a given species i will dominate a plot sown with n species is the probability that species i is the largest species in the subsample n out of the total species pool s . That is to say,

$$p(i) = \frac{\binom{i-1}{n-1}}{\binom{s}{n}}$$

Over replicated samples, therefore, the mean biomass, experiment-wide, for a given sown species richness n , will be

$$\bar{y}(n) = \sum_{i=n}^s w_i \cdot p(i)$$

where w_i is the mass of a monoculture of species i . We assume that competitive ability is proportional to shoot mass, so that $w_i > w_{i-1}$. The variance will be

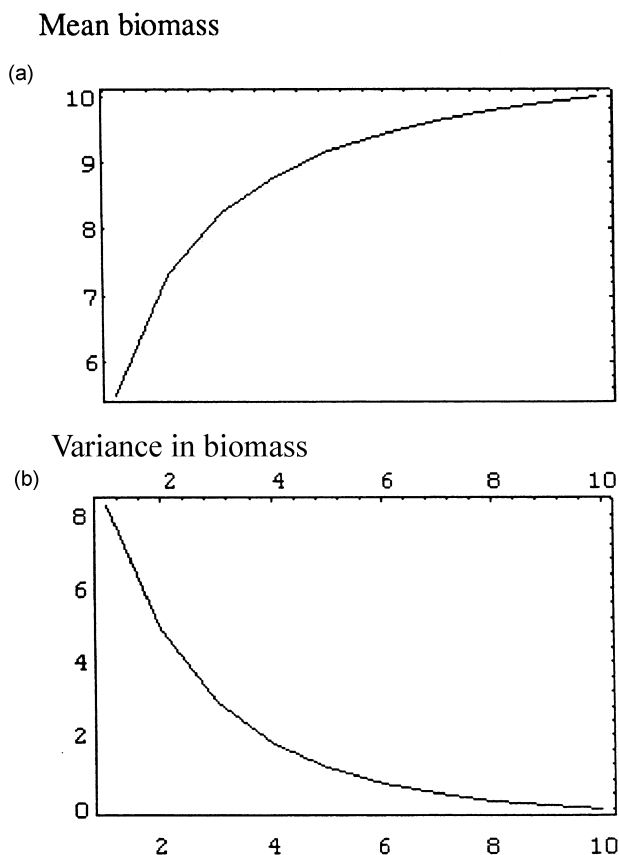


Figure 6 (a) Mean biomass increases monotonically with increasing numbers of species sown under the “sampling effect”. (b) Biomass variance declines monotonically with increasing numbers of species sown. Pattern for monocultures and mixtures of 10 species where, for simplicity, the biomass of each species $w_i = i$ and dominance is attained by the sown species with the largest w_i .

$$\sigma^2(n) = \sum_{i=1}^s w_i^2 \cdot p(i) - \bar{y}(n)^2$$

Thus, mean biomass increases monotonically with n , the number of species sown per plot, up to a maximum value of $\bar{y}(n) = w_s$, when $n = s$, and the variance decreases monotonically to zero when, with s species sown, all plots are dominated by species s (Fig. 6).

The data for the one-, two-, and four-species grass mixtures in 1992 at the end of the weeding period follow these patterns, but the magnitudes of the effects are different. The mean biomass increased as 118.0, 122.1, and 125.5 (only a 1.06-fold increase with species richness). Variance, however, declined steeply (424.7, 364.0, and 22.1 in the one-, two-, and four-species grass mixtures, a 19-fold decline based on variation between the 33 treatment means: three lime applications \times 11 grass-sowing treatments; data averaged over the six replicates). Clearly the sampling effect is not the only process

accounting for these patterns, but this experiment suggests that the impact of the sampling effect may be greater on the variance in biomass than on mean biomass.

APPENDIX B

(a) Grass species and their codes as sown in monocultures and mixtures: *Arrhenatherum elatius* (AE), *Anthoxanthum odoratum* (AO), *Alopecurus pratensis* (AP), *Festuca rubra* (FR).

(b) Species sown on the high-diversity, herb-sown plots. Nomenclature follows Stace (1997) where families and authorities can be found. *Achillea millefolium*, *Agrimonia eupatoria*, *A. procera*, *Anthriscus sylvestris*, *Anthyllis vulneraria*, *Bellis perennis*, *Campanula glomerata*, *Campanula rotundifolia*, *Centaurea cyanus*, *C. nigra*, *C. scabiosa*, *Cerastium fontanum*, *Chaerophyllum temulum*, *Cichorium intybus*, *Clinopodium vulgare*, *Daucus carota*, *Digitalis purpurea*, *Epilobium parviflorum*, *Filipendula ulmaria*, *F. vulgaris*, *Fragaria vesca*, *Galium verum*, *Genista tinctoria*, *Geranium pratense*, *Heracleum sphondylium*, *Hieracium pilosella*, *Hippocrepis comosa*, *Hypericum hirsutum*, *H. perforatum*, *Hypochaeris radicata*, *Knautia arvensis*, *Lathyrus pratensis*, *Leontodon autumnalis*, *Leontodon hispidus*, *Leucanthemum vulgare*, *Linaria vulgaris*, *Linum catharticum*, *Lotus corniculatus*, *Lotus uliginosus*, *Lychnis flos-cuculi*, *Malva moschata*, *Medicago lupulina*, *Ononis repens*, *O. spinosa*, *Onobrychis viciifolia*, *Origanum vulgare*, *Papaver rhoeas*, *Primula veris*, *P. vulgaris*, *Pimpinella saxifraga*, *Plantago lanceolata*, *Plantago media*, *Prunella vulgaris*, *Ranunculus acris*, *R. bulbosus*, *Reseda lutea*, *R. luteola*, *Rhinanthus minor*, *Rumex acetosa*, *Sanguisorba minor*, *Saxifraga granulata*, *Scabiosa columbaria*, *Silaum silaus*, *Silene conica*, *S. dioica*, *S. vulgaris*, *S. latifolia*, *Stachys officinalis*, *Stellaria graminea*, *Succisa pratensis*, *Tanacetum vulgare*, *Thymus praecox subsp. arcticus*, *Torilis japonica*, *Tragopogon pratensis*, *Trifolium dubium*, *Trifolium repens*, *Veronica chamaedrys*, *Vicia cracca*, *V. sativa* and *V. tetrasperma*.

(c) The frequency (%) of sown (S) and nonsown species in 1998 from 216 full-plot (3 m \times 3 m) cover surveys. Only 21 of the original 80 species sown were still present at the end of year 7, while 33 nonsown species had invaded. *Alopecurus pratensis* 92.6 (S), *Arrhenatherum elatius* 41.7 (S), *Holcus lanatus* 38.0, *Anisantha sterilis* 32.4, *Silene latifolia* 30.6 (S), *Achillea millefolium* 29.6 (S), *Stellaria media* 27.3, *Tanacetum vulgare* 20.8 (S), *Festuca rubra* 16.7 (S), *Agrostis capillaris* 14.8, *Poa trivialis* 13.4, *Cirsium arvense* 9.7, *Bromus hordeaceus* 6.0, *Geranium molle* 5.1, *Rumex acetosa* 5.1 (S), *Urtica dioica* 4.6, *Holcus mollis* 4.2, *Chamerion angustifolium* 4.2, *Trifolium pratense* 4.2 (S), *Vicia sativa* 3.7 (S), *Galium verum* 2.8 (S), *Anthoxanthum odoratum* 2.8 (S), *Galium aparine* 2.8, *Taraxacum officinale* 2.3, *Dactylis glomerata* 2.3, *Leucanthemum vulgare* 2.3 (S), *Silene dioica* 1.9 (S), *Heracleum sphondylium* 1.9, *Lotus corniculatus* 1.9

(S), *Papaver dubium* 1.4, *Centaurea cyanus* 1.4 (S), *Centaurea scabiosa* 1.4 (S), *Elytrigia repens* 1.4, *Galium saxatile* 1.4, *Onobrychis viciifolia* 1.4 (S), *Rumex crispus* 1.4, *Senecio jacobaea* 0.9, *Festuca pratensis* 0.9, *Myosotis arvensis* 0.9, *Poa pratensis* 0.9, *Rumex obtusifolius* 0.9, *Rumex acetosella* 0.9, *Trifolium dubium* 0.9, *Vulpia bromoides* 0.9, *Veronica persica* 0.5, *Agrostis gigantea* 0.5, *Capsella bursa-pastoris* 0.5, *Cirsium palustre* 0.5, *Centaurea nigra* 0.5 (S), *Geranium dissectum* 0.5, *Plantago lanceolata* 0.5 (S), *Reseda lutea* 0.5 (S), *Sonchus asper* 0.5, *Tragopogon pratensis* 0.1 (S).

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