OIKOS 104: 77–90, 2004

Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment

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Mouquet, N., Leadley, P., Mériguet, J. and Loreau, M. 2004. Immigration and local competition in herbaceous plant communities: a three-year seed-sowing experiment. – Oikos 104: 77–90.

Understanding the relative roles of local and regional processes in determining local species diversity is now of strong relevance in basic ecology. To address this question, we have tested the influence of immigration on species diversity dynamics in a three-year experiment using herbaceous plant communities. We manipulated the intensity of seed rain (i.e., immigration) and the relative contribution of each species to the seed rain. For each of three levels of intensity of immigration (seed rain), we considered three cases, in which immigration was either negatively correlated, positively correlated, or uncorrelated with local competitive ability. Our experiment illustrates how both immigration and local competition contribute to explaining species diversity in herbaceous plant communities. Communities were more diverse when they received more seeds and when immigration was inversely correlated or uncorrelated with local competitive ability. Only species of intermediate or low competitive ability responded positively to the seed-addition treatment. Community-level functional properties were not strongly modified by immigration: immigration treatments did not differ in total above-ground biomass and plant cover, soil surface occupation was higher at high immigration intensities. A comparison of our results with theoretical models of plant community structure suggests that the mechanisms underlying the species dynamics in our communities were probably a mixture of colonization-extinction and competitive weighted lottery.

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Whether coexistence between plant species is driven by local or regional processes is a classical question in community ecology (reviewed by Tilman and Pacala 1993, Bengtsson et al. 1997, Zobel 1997). Processes at these two scales probably act together to structure plant communities (Zobel 1997), and the degree to which each one contributes to local species diversity is now of considerable relevance in many aspects of community ecology (Ricklefs and Schluter 1993, Turnbull et al. 2000).

One way to explore the relative influence of the regional biota on the local scale is to ask what consequences immigration has for species diversity. For example, Loreau and Mouquet (1999) provided a formal and mechanistic model for the "mass-effect" hypothesis (Shmida and Ellner 1984, Shmida and Wilson 1985). Using a weighted lottery model (Chesson and Warner 1981), they studied the influence of immigration on the dynamics of local plant communities and showed that immigration could be a key factor defining local species diversity because it maintains a high diversity in communities in which a single species would dominate if they were closed (see also Mouquet and Loreau 2002). Local species richness was expected to increase when

Accepted 1 June 2003

ISSN 0030-1299

immigration intensity was higher than a threshold required for the successful individual's establishment. Immigration was also shown to have a large effect on species relative abundances and community-level functional properties, depending on whether its relation with local competitive ability was negative, positive, or null. For example, when the relationship between local competitive ability and immigration was negative, corresponding to the competition-colonization trade-off hypothesis (Levins and Culver 1971, Horn and MacArthur 1972, Hastings 1980, Tilman 1994), the model predicted a switch of dominance from species of high competitive ability to species of lower competitive ability as immigration intensity increased. Increasing immigration also caused total space occupation by the community to increase, but total biomass on average either decreased or stayed constant with increasing diversity, depending on the relationship between immigration and local competitive ability.

The influence of the regional biota on local species diversity has been tested experimentally in the plant community by manipulating immigration (Houle and Phillips 1989, Burke and Grime 1996, Tilman 1997, Turnbull et al. 1999, Zobel et al. 2000, Foster 2001). However, these experiments have not in general been designed to measure the relative importance of local competitive ability and immigration in shaping community properties as well as the consequences of varying the relationship between immigration and competition. The only two studies, to our knowledge, that have explored the consequences of immigration and local competition jointly have been performed by Turnbull et al. (1999) and Foster (2001). Turnbull et al. (1999) studied communities of annual plants and showed that immigration could drastically alter species composition in ways that were directly related to seed characteristics. At high seed-sowing density, large-seeded species excluded other species because they had the highest recruitment rate and higher competitive ability, indicating the potential for a competition colonization trade-off mechanism. Foster (2001) showed that species richness was enhanced by immigration only in low-productivity environments, where competition was not a major force in driving species richness. However, both studies used equal proportions of species in the propagule rain, so they could not fully address the relative importance of immigration and local competition.

Our study reports a three-year experimental approach to test the effects of immigration and competition and their interaction on plant community diversity. We focused on three major questions: (1) does immigration affect local species diversity and community-level functional properties such as total biomass or space occupation? (2) do the relative proportions of species in the seed rain affect the outcome of immigration experiments, and in what ways? (3) how much of the patterns of species abundances can be explained by local competition and immigration?

To address these questions, we manipulated the intensity of immigration and the relative proportion of species in the propagule rain into experimental plant communities consisting of both perennial and annual species. For each immigration intensity, we considered three cases: immigration was negatively correlated, positively correlated, and uncorrelated with local competitive ability, respectively. A negative correlation would result if species of low competitive ability have higher fecundity or dispersal ability and would therefore contribute more to the local seed rain (Hastings 1980, Tilman 1994) or have higher immigration rates (Levins and Culver 1971, Horn and MacArthur 1972). Positive correlation would occur if competitively dominant species (assuming that local abundance reflects competitive ability) made the greatest contribution to the seed rain. Lack of correlation corresponds to the null model. These three scenarios can also be interpreted without assumptions about competition-colonization trade-offs, if species are expected to differ in immigration rates because of differences in the spatial distributions of their populations at the regional level. We obtained the competitive hierarchy by analyzing the results of a one-year competition experiment performed under the same environmental conditions as the immigration experiment.

Methods

We performed two types of experiments. In a one-year experiment we measured species competitive abilities of eight plant species in a replacement-series experiment. In a second experiment we established communities with the same eight species and after one year of establishment started to add seeds at different intensities and with three different relationships between competitive ability and immigration during two years. The two experiment were performed in the same area; the competition experiment was done in the year we established the communities for the immigration experiment.

Study site and species used

The experiments were carried out at the biological field station of Foljuif, Saint-Pierre-les-Nemours, France. Plots were installed in an old meadow with a moderately acidic (pH = 6.1) sandy-loam soil. The climate is temperate; annual mean precipitation is 697 mm, and temperature ranges between monthly means of 2.2°C in January and 18.5°C in August. The experimental area was plowed to a depth of 20 cm and then rotovated in January 1998. Before plowing, the vegetation was cut to 2 cm and removed to limit burial of organic matter. From February to April 1998, a black plastic film covered the entire experimental area, to activate seed germination and the growth of vegetative fragments of perennial herbs or grasses. During this period, all vegetation was removed twice by hand. The experimental area was protected from vertebrate herbivores (rabbits and deer) by fencing.

Eight plant species were chosen for the experiment on the criterion that they belonged to the local flora, to ensure that they would be suited to the local environmental conditions. Plants were also chosen to have different life histories and growth forms. We give in Table 1 some general information from the literature about these eight species. We determined seed mass by weighing four groups of 50 seeds from the seed pool used in our experiment. The percentage of seed germination was measured in the field. For each species, we sowed 100 seeds on each of four replicate 50 × 50 cm plots under the same conditions as competition experiments. New seedlings were counted during the six weeks following seeding. These eight plant species were used in competition and immigration experiments.

Competition experiment

In our competition experiment, based on the de Wit (1960) replacement series (reviewed by Goldberg and Barton 1992), we measured the biomass of a species, grown alone or in a mixture, using a substitutive design with constant seed density. We used the ratio of Y_{ij}, the biomass of a focal species i when grown with an associate species j to Y_{ii}, the biomass of a focal species i grown in monoculture, as the measure of species relative yield. This measure allows us to distinguish two components in the competitive interactions: the competitive response and the competitive effect (Jacquard 1968, Goldberg and Werner 1983, Miller and Werner 1987). The competitive response corresponds to the ability to avoid or tolerate suppression. For a given focal species, it is equal to the mean of its relative yields when grown with the associate species. A low value for the competitive response indicates that the biomass of the focal species is higher when it grows alone. Competitive effect corresponds to the ability to suppress other species. For a given focal species, it is equal to the inverse of the mean of its associate species' relative yields when they grow with it. A high value for the competitive effect indicates that the biomasses of other species are lower when they grow with the focal species. A species with high competitive ability will have high competitive response and high competitive effect values. These measures include seedling and adult competitive abilities, germination ability, and species tolerance to density. This definition of local competitive ability is sufficiently broad to permit comparisons with our previous theoretical work (Loreau and Mouquet 1999).

The competition experiment was conducted from April through September 1998 for annuals and perennials and was continued through June 1999 for perennial species. Because competitive ability has been shown to be density dependent (Harper 1977), we used two seed-sowing densities (1 and 5 g m^{-2}). Species were grown alone or in two-species mixtures in 50 × 50 cm plots separated by 50 cm of bare soil and replicated four times (288 plots in total). Mixed-species plots received equal weights of seeds of the two species. We used equal weights rather than equal numbers of seeds because the species we used show a negative relationship between seed weight and germination probability (Baskin and Baskin 1998 and Table 1 with $r^2 = 0.70$). As a result, competing species had more equal numbers of seedlings than if we had used equal numbers of seeds (which would have advantaged species with large seeds). Plots were watered every day for three weeks after sowing and then every two or three days, depending on the weather, until one month before harvesting. Weeds were removed carefully by hand at emergence over the course of the whole experiment. A few plots were damaged by mole and small-rodent burrows and have been excluded from the statistical analysis. Ant repellent was applied around all plots every three days for three weeks after seed sowing to prevent seed predation by ants.

Plots were harvested between 15 and 25 September 1998. Because information at the individual scale was

Table 1. Characteristics of the eight species used in our experiments. Type: P = perennial, A = annual. Strategy (Grime 1977): C = competitor, S = stress tolerant, R = ruderal. Regenerative strategies (Regeneration): S = seeds, V = vegetative reproduction, B = seed bank. Seed mass (in milligrams per seed). Germination: percent of seed germination measured in the field. All seeds were supplied by Herbiseed (Wokingham, U.K.) except those of *Cerastium*, whose seeds were supplied by Arbiotech (Rennes, France).

Name	Type	Strategy	Regeneration	Seed mass	Germination
Anthoxantum odoratum	P	C-S-R	S-V-B	0.50 ± 0.047	38 ± 4
Arabidopsis thaliana	A	R	S-B	0.026 ± 0.002	21 ± 4
Cerastium glomeratum	A	R	S-B	0.06 ± 0.003	32 ± 12
Festuca rubra	P	C-S-R	S-V	0.94 ± 0.046	65 ± 3
Holcus lanatus	P	C-S-R	S-B-V	0.45 ± 0.024	61 ± 4
Lamium pupureum	A	R	S-B	0.85 ± 0.028	62 ± 6
Rumex acetosella	P	C-S-R	S-V	0.45 ± 0.034	27 ± 7
Veronica arvensis	A	S-R	S-B	0.095 ± 0.006	14 ± 7

needed, biomass per individual was estimated as well as population density. We estimated above-ground biomass by multiplying population densities by mean biomass per individual. We estimated population density by counting all individuals (or ramets) in small quadrats (15 × 15 cm) chosen at random in plots and replicated four times per plot. For estimates of mean biomass per individual, four groups of 20 individuals of the same species were taken arbitrarily from each plot, dried at 80°C for 24 hours, and weighed. When population density was too low, groups of only 10 individuals were collected. The plots with the four perennial species in mixture and in monoculture at the high sowing density were maintained in 1999. Vegetation on these plots was cut to 5 cm height with grass shears. These plots were weeded in March and April 1999 and harvested in June 1999 according to the same protocol used in 1998.

Using species with different life-history strategies always leads to difficult choices when it comes to outdoor experiments. We chose to start the competition experiment simultaneously for all species in early spring to ensure that all species could germinate. This might have penalised the winter annuals, but the seeds we bought had been previously treated to germinate all year (seeds were harvested in 1997 and once the moisture content had been reduced to 3–5% they were stored at −18°C to maintain germinability) and watering helped germination. Therefore we do not believe that this limitation resulted in underestimating the competitive ability of winter annuals. In any case, starting the competition experiment in autumn would have strongly penalised other species whose seedlings would have died during the winter.

Immigration experiment

The immigration experiment was conducted from April 1998 through June 2000. The communities were first established during one year and the immigration treatments were started during the second year. We used the eight species described in Table 1, mixed in 28 experimental communities established at the same time as the competition experiments. Plots of 1.5 × 1.5 m were surrounded by a vegetated border of 1.5 m wide to minimize border effects and fine mesh nets designed to prevent seed exchange among communities and immigration from outside. The vegetated border was initially sown with *Deschampsia flexuosa*, but because this species did not germinate well, it was replaced by *Festuca ovina* in the second year of the experiment. Nets were 1.30 m high, and their bases were buried 5 cm in the soil. The mesh was highly transparent (only 12% shading); mesh size was 0.6 mm (Texinov, tip 1000, St.-Didier-de-la-tour, France). The nets have been shown to be efficient against seed exchange between communities and immigration from outside (unpubl.). To establish the communities, we sowed a total of 5 g m^{-2} of seed equally distributed among the eight species. To prevent seed predation by ants, we applied ant repellent around all communities every three days for three weeks after sowing. To facilitate species establishment, we watered experimental plots every day for three weeks after sowing and then every two or three days, depending on the weather, until one month before harvesting in 1998. There was no watering in 1999 and 2000. Weeds, including their roots, were removed carefully by hand at emergence during all three years of the experiment. A few plots were damaged by moles and small rodent burrows, as well as ant nests, which were removed as soon as discovered. We noted their positions carefully to avoid making any population-density estimations in those locations.

Four communities received no seed rain during the entire experiment. A factorial design with two treatments, "immigration scenario" and "immigration intensity," were applied in the other 24 communities. The "immigration scenarios" treatment included three scenarios of the relation between local competitive ability and immigration: positive correlation, negative correlation, and no correlation. The competitive hierarchy used was based on the results of the 1998 competition experiment. The treatment called "immigration intensity" consisted of low (4 g m^{-2}) and high (10 g m^{-2}) seed rains (Table 2). Each treatment combination was

Table 2. Total quantity (in grams) of seeds added to communities (plot size = 2.25 m^2) for each immigration intensity treatment (high, 10 g m^{-2}; low, 4 g m^{-2}) and combinations of immigration scenario (negative relation; no relation; positive relation between competitive ability and immigration). *Hol*, *Holcus lanatus*; *Rum*, *Rumex acetosella*; *Ant*, *Anthoxanthum odoratum*; *Fes*, *Festuca rubra*; *Cer*, *Cerastium glomeratum*; *Ara*, *Arabidopsis thaliana*; *Lam*, *Lamium purpureum*; *Ver*, *Veronica arvensis*.

Immigration intensity	Immigration scenarios	Species								Seed added (g/plot)
		Hol	*Rum*	*Ant*	*Fes*	*Cer*	*Ara*	*Lam*	*Ver*	
High	Negative	0.3	1	2.4	2.4	2.4	4.8	4.8	4.8	22.9
	None	2.81	2.81	2.81	2.81	2.81	2.81	2.81	2.81	22.5
	Positive	10	6	1.9	1.9	1.9	0.5	0.5	0.5	22.9
Low	Negative	0.1	0.5	1	1	1	1.9	1.9	1.9	9.3
	None	1.15	1.15	1.15	1.15	1.15	1.15	1.15	1.15	9.2
	Positive	4	2.5	0.7	0.7	0.7	0.2	0.2	0.2	9.2

replicated four times. Immigration was simulated (i.e. seeds were added) in March 1999, August 1999, and March 2000. The seed additions were not performed in August 1998 because results of the competition experiment were not available.

The competitive hierarchy, from results of the competition experiment in 1998, was *Holcus* > *Rumex* > *Anthoxanthum*, *Festuca*, *Cerastium* > *Arabidopsis*, *Lamium*, *Veronica*. We distributed seeds in such a way as to keep constant the quantity of seed added in each immigration scenario (Table 2). Because groups of similar competitive ability did not include equal numbers of species, we could not distribute the same quantity of seeds to equivalent groups when the relation between immigration and competitive ability was positive or negative. We understand that, because the different groups do not include the same number of species, the immigration scenarios can be confounded with diversity of seed added. We will address this point in our discussion.

Data were collected in September 1998, June 1999, and June 2000. Visual estimations of percentage of plant cover were performed by four different investigators. These investigators were first trained to standardize criteria for the estimation of plant cover. They then estimated population density by counting all individuals (or ramets for *Holcus*, *Festuca* and *Anthoxanthum*) present in small quadrats (15 × 15 cm) chosen at random in communities and replicated 12 times per plot. Individual plants that had several leaves, were flowering (for forbs), or were taller than 5 cm (for grasses) were considered to be adults (i.e. not seedlings). To estimate total above-ground biomass, we placed four replicate 50 × 50 cm quadrats randomly within each community and cut all plant biomass within the quadrats at 5 cm above the soil surface. This fresh biomass was dried at 80°C for 48 hours and weighed. Cutting the vegetation above 5 cm might take different proportions of the different species, but this was the only way to measure above-ground biomass without being too destructive for the community. The remaining vegetation was then cut at 5 cm just after data were collected. We chose to cut the vegetation once a year because the eight species we used in this experiment were found to coexist in neighbouring semi-natural communities where vegetation was cut once a year by human activity. After cutting, we estimated soil surface occupation: along a 1-m line, the percentage of area free of any plants was measured, and this operation was repeated six times in each community. Soil surface occupation gives a direct measure of the amount of space available for species recruitment.

We measured species diversity using the Shannon diversity index H, which incorporates both species richness and relative abundances. If p_i is species relative abundance, and a total of N species coexist,

$$H = -\sum_{i=1}^{N} p_i \ln(p_i) \qquad (1)$$

Finally, to determine which species showed the greatest response to seed addition, we developed an index of immigration success. This index is the proportion of successful immigration relative to the number of added seeds likely to have germinated. We considered for each species i, given a treatment of seed addition j, the difference in population density between 1999 and 2000, ΔD_{ij}. To separate the change in population density following seed addition from "natural" change in population density, we subtracted $\overline{\Delta D_{io}}$ (which is the mean change of species i population density in the four communities that did not received any seeds) from ΔD_{ij}. We then divided this difference by the number of seeds that potentially germinated in the field given the seed-addition treatment j. This last parameter depends on the number of seeds added I_{ij}/W_i (where I_{ij} is the quantity of seed added in g and W_i the seed mass in grams per seed), and germination rate G_i (as a proportion, see Table 1). The equation is

$$IS_{ij} = \frac{\Delta D_{ij} - \overline{\Delta D_{io}}}{\left(\frac{I_{ij}}{W_i}\right) \times G_i} \qquad (2)$$

Results

Competition experiment

Competitive hierarchy

Results of the competition experiment for 1998 are presented in the Table 3. At high density, species differed significantly in competitive responses (ANOVA, $F_{7,214} = 23.62$, $P < 0.0001$) and in competitive effects (ANOVA, $F_{7,214} = 14.30$, $P < 0.0001$). Similarly, at low density, species differed significantly in both competitive responses (ANOVA, $F_{7,211} = 19.79$, $P < 0.0001$) and competitive effects (ANOVA, $F_{7,211} = 19.08$, $P < 0.0001$). At both seed-sowing densities, *Holcus* was the best competitor in both competitive response and competitive effect. The very high competitive performance of *Holcus* (all its relative yields are > 1) suggests that it was strongly affected by intraspecific competition, i.e. it grows better with other species than alone; the large, significant difference between its competitive responses at the two seed-sowing densities supports this interpretation. *Rumex* was the second-best competitor at the two seed-sowing densities, in both competitive effect and competitive response. *Anthoxanthum*, *Festuca* and *Cerastium* had similar competitive effects and responses at the two seed-sowing densities. Finally, *Arabidopsis*, *Lamium* and *Veronica* constituted a fourth group of very poor competitors; *Veronica* was the poorest competitor. Finally, seed-sowing density did not influence

Table 3. Relative yields of the eight species grown in all pairwise combinations at two sowing densities (5 and 1 g m^{-2}). Note that we give inverse measures of competitive effects. Species of similar competitive responses and effects (Tukey's Studentized test, $P<0.05$) are denoted by common superscripts. Using the Mann-Whitney U test, we compared all related means in the two seed-sowing densities treatments (*$P<0.05$; **$P<0.01$). Species names are abbreviated as in Table 2.

Focal species	Associate species								Comp. response
	Hol	*Rum*	*Ant*	*Fes*	*Cer*	*Ara*	*Lam*	*Ver*	
High-density treatment (5 g m^{-2})									
Hol	1	1.17	1.53*	1.44*	1.52*	1.67*	1.63*	1.43	1.49^{a**}
Rum	0.16	1	0.72	0.87	0.88	1.30	1.15*	0.96	0.86^{b*}
Ant	0.03	0.11	1	0.79	0.48	0.90	0.96	1.08*	0.62^{bc}
Fes	0.03	0.22	0.45	1	0.60	0.68	1.01	1.24*	0.60^{bc}
Cer	0.02	0.07	0.60	0.55	1	0.87	0.68	0.90	0.53^{c}
Ara	0.01*	0.17	0.25	0.30	0.22*	1	1.29	0.58	0.40^{cd}
Lam	0.01	0.15	0.52	0.48	0.27	0.48	1	0.60	0.36^{cd}
Ver	0	0.03	0.13	0.38	0.08	0.27	0.33	1	0.17^{d}
Inverse of comp. effect	0.03^{a}	0.27^{ab}	0.60^{bcd}	0.66^{bcd}	0.58^{bc}	0.88^{cde*}	1.01^{e*}	0.97^{de*}	
Low-density treatment (1 g m^{-2})									
Hol	1	0.76	0.97*	1.08*	0.96*	1.02*	1.09*	1.14	1.01^{a**}
Rum	0.24	1	0.71	0.59	0.61	0.75*	0.83*	0.85	0.65^{b*}
Cer	0.03	0.29	1	0.76	0.57	0.79	0.58	0.71	0.57^{bc}
Fes	0.04	0.18	0.57	1	0.55	0.75	0.74	0.79*	0.53^{bc}
Ant	0.10	0.18	0.48	0.78	1	0.46	0.71	0.63*	0.49^{bc}
Lam	0.01	0.30	0.33	0.34	0.52	1	0.56	0.72	0.42^{c}
Ara	0.08*	0.17	0.46*	0.37	0.37	0.51	1	0.82	0.42^{c}
Ver	0.05	0.10	0.20	0.06	0.16	0.45	0.11	1	0.18^{d}
Inverse of comp. effect	0.08^{a}	0.29^{b}	0.51^{c}	0.59^{c}	0.53^{c}	0.66^{cd*}	0.64^{cd*}	0.81^{d*}	

competitive hierarchies obtained in our experiment because competitive responses at the two seed-sowing densities were positively correlated ($r^2 = 0.89$, $P < 0.0001$, $n = 8$), as were the inverses of competitive effects $r^2 = 0.93$, $P < 0.0001$, $n = 8$).

In 1999, after the harvest of the four perennial species, we again found that *Holcus* was the best competitor in response and effect, but it had a significantly lower competitive response. *Rumex* had become the poorest competitor. The competitive rank of *Anthoxanthum* did not change, but its relation with other species did; it was less affected by *Rumex* in 1999 than in 1998 but more affected by *Festuca*. Finally *Festuca* was a significantly better competitor (in second place after *Holcus*).

Relation with species relative abundances in the immigration experiment

Fig. 1 shows populations densities obtained in 1998 and 2000 in the four communities that did not receive any seeds in the immigration experiment. *Holcus* was always very dominant, and other species (except *Veronica*) decreased significantly in abundance during those 3 years. The hierarchy of abundance was conserved over the course of the experiment except for *Veronica*, which moved from last to fifth place. In 1998, the log of population density was significantly positively correlated with competitive responses ($r^2 = 0.89$, $P < 0.0005$, $n = 8$) and negatively correlated with the inverses of competitive effects ($r^2 = 0.87$, $P < 0.0005$, $n = 8$) found at high seed density. This relation was conserved in population densities obtained in 2000 for both competitive response ($r^2 = 0.83$, $P < 0.001$, $n = 8$) and the inverses of competitive effects ($r^2 = 0.80$, $P < 0.005$, $n = 8$), suggesting that the competitive hierarchy found in the competition experiment after one year was a good predictor of the hierarchy of abundance in closed communities even after three years.

Immigration experiment

For clarity, we give results obtained in the last year of the experiment in 2000 after two seasons of immigra-

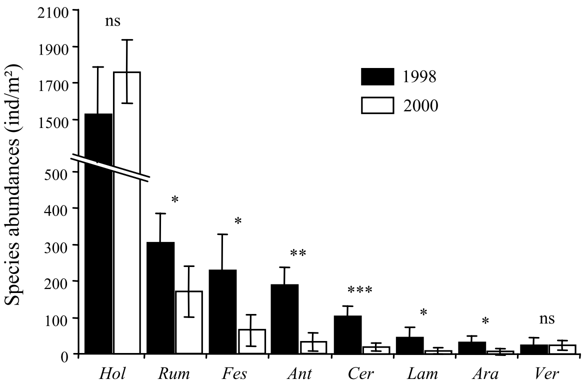

Fig. 1. Community composition (abundances) in 1998 (in black) and 2000 (in white) in the four communities that received no seed in the immigration experiment, expressed as mean and standard deviation $n = 4$). The difference between the means in 1998 and 2000 was tested with a Mann-Whitney non-parametric test (ns, non significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). Species names are abbreviated as in Table 2.

tion. Data obtained in 1999 are only used in the last part of the results section, where we discussed the differences in population density between 1999 and 2000 in multiple regressions.

Community-level responses

Species diversity was higher in communities that received high immigration intensity and where immigration was negatively correlated or uncorrelated with competitive ability (Fig. 2a, b).

Treatments did not differ in plant cover (Fig. 2c, d), whereas soil surface occupation was higher in communities that had received more seeds (Fig. 2c) and in the treatment where immigration was positively correlated with competitive ability (Fig. 2d). Plant cover and soil surface occupation were not correlated with the population density of any of the eight species or with the total population density, but soil surface occupation was positively correlated with the logarithm of *Holcus* seedling density ($r^2 = 0.38$, $P < 0.001$, $n = 28$). Note that estimates of soil surface occupation were higher than those of plant cover, but this difference was only due to the different techniques we used to obtain these estimates.

We did not find significant differences between the treatments in total above-ground biomass. Mean total above-ground biomass was on average 192.7 ± 64.8 g m^{-2}. Above-ground biomass was not correlated with the population density of any of the eight species used in this study, with the total population density, or with the sum of *Holcus* and *Rumex* (the two dominant species) population densities. Nevertheless, it was significantly positively correlated with plant cover ($r^2 = 0.53$, $P < 0.0001$, $n = 28$).

Species-level responses

Species showed different responses to immigration: *Holcus*, *Rumex* and *Lamium* showed no response, whereas the remaining species responded positively (Fig. 3). *Festuca* and *Cerastium* were more abundant when immigration and local competitive ability were uncorrelated (Fig. 3). *Arabidopsis* and *Veronica* were more abundant when immigration and local competitive ability were negative correlated (Fig. 3). abundances were equal in the two scenarios (Fig. 3). We also plotted population densities against the quantity (in grams) of seeds added (Fig. 4). *Anthoxanthum*, *Festuca*, *Cerastium* and *Arabidopsis* showed linear relations with immigration intensity, whereas *Veronica* showed a non-linear relation with an obvious plateau. Seedlings of *Holcus* recorded in March and April 2000 also showed a positive linear relation with immigration intensity.

Finally, we calculated the immigration success (Eq. 2) for the five species that responded to the seed-addition treatment (Fig. 5). *Festuca* showed the highest immigration success with 31.5% successful immigration, followed by *Anthoxanthum* with 12.4%. *Cerastium*, *Veronica* and *Arabidopsis* were not significantly different, showing 1.9, 1.6, and 1.0% immigration success, respectively. Within each species, we found no statistical differences in immigration success between the different scenarios used for the relation between local competitive ability and immigration.

Variables involved in species response

To elucidate the variables involved in species responses we have performed multiple regression for each species on both its population density in 2000 and the differ-

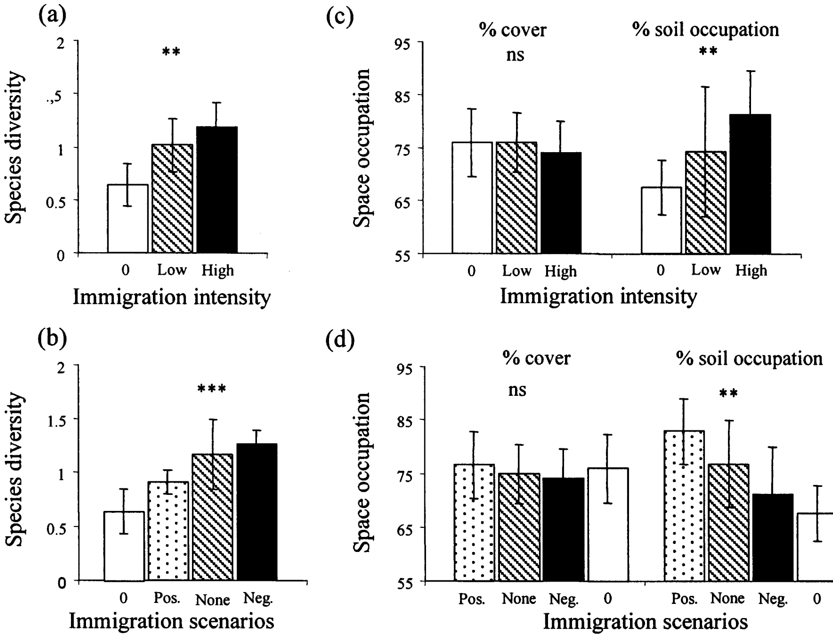

Fig. 2. Results of the immigration experiment. For immigration intensity, 0, no seeds; Low, 4 g m^{-2}; High, 10 g m^{-2}. For immigration scenarios, Pos, a positive relation between competitive ability and immigration; None, no relation; Neg, negative relation. In (a) and (b), we give results for the Shannon diversity index. In (c) and (d) we give results for the plant cover and soil surface occupation. Treatment effects were tested with a two-factor ANOVA ($n = 28$); ns, non-significant; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.005$. Interactions between the two treatments were always non-significant. In (b) and (d) we added no immigration ("0") for comparison, but it was not included in the ANOVA.

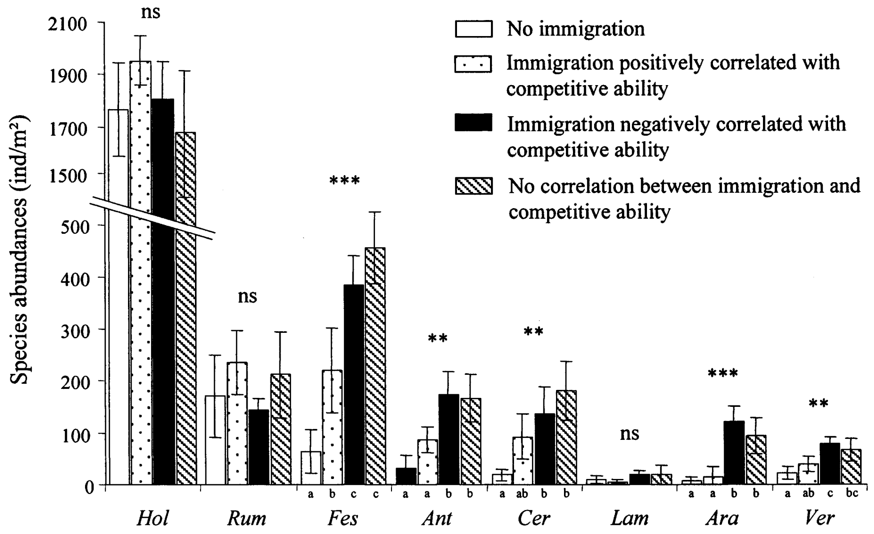

Fig. 3. Abundances for the eight species in 2000 in communities with no immigration and high immigration intensity (with positive, negative, or no correlation between immigration and local competitive ability). Differences between means were tested by one-factor ANOVA; ns, non-significant; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. We have clustered means in groups (Tukey's Studentized test, $P < 0.05$), denoted by common letters. Species names are abbreviated as in Table 2.

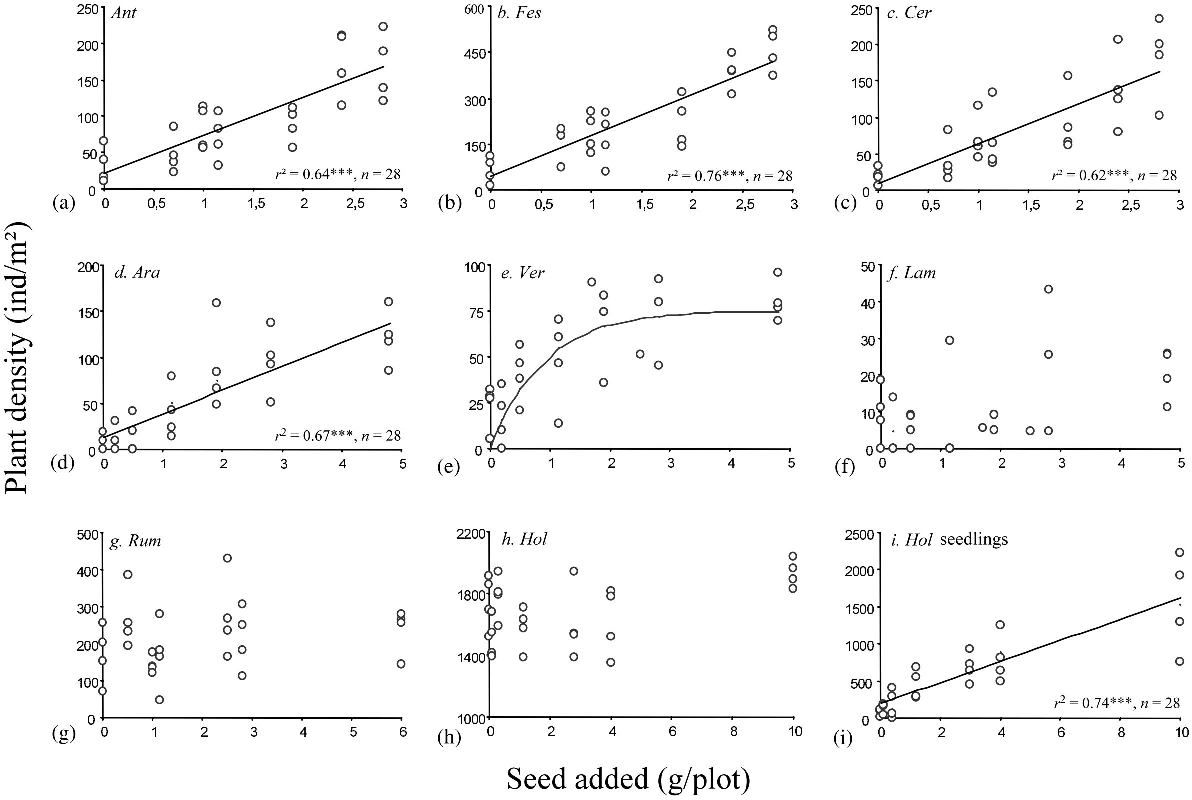

Fig. 4. Species density (in d m^{-2}) at each sowing intensity (a, b, c, d, e, f, g, h) recorded in June 2000. Panel (i) shows the number of *Holcus* seedlings recorded in March and April 2000 at each sowing intensity. When the relation is statistically significant ($P < 0.05$), we show the curve on the graph. *Anthoxantum, Cerastium, Arabidopsis* and *Holcus* seedlings show increasing variance with the quantity of seed added. For these species, we have also performed a log transformation and tested the relationship with the quantity of seeds added. We did not find any strong differences with the non-transformed data (regression with the log transformation: *Anthoxanthum* $r^2 = 0.62$, *Cerastium* $r^2 = 0.67$, *Arabidopsis* $r^2 = 0.52$ and *Holcus* seedling $r^2 = 0.39$). Accordingly, we present in the figure the results obtained without the log transformation to keep the Y axes the same for all species. For regression curves, r^2 is given directly on the graphs; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$ (a, b, and c, d, i). For *Veronica* (e), non-linear regression fitted the data better; the equation used is $y = \beta(1 - \exp(-\alpha x))$. Species names are abbreviated as in Table 2.

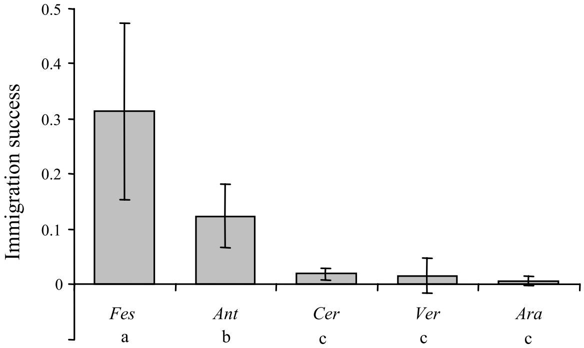

Fig. 5. Immigration success (Eq. 2) for the five species that responded to the immigration treatment (*Festuca*, *Anthoxanthum*, *Cerastium*, *Veronica* and *Arabidopsis*). Those means are significantly different (ANOVA, $F_{4,115} = 68.84$, $P < 0.0001$). We have clustered means in groups (Tukey's Studentized test, $P < 0.05$), denoted by common letters.

ence between its 1999 and 2000 densities, using variables potentially involved in species recruitment. To select those variables, we performed simple correlations between all the variables measured in our experiment and the two explanatory variables and retained those that were significantly correlated ($P < 0.05$); we selected the quantity of seed added, the population density in 1999, the soil surface occupation in 1999, and the population density of *Holcus* in 1999. Results are given in Table 4.

The difference in *Holcus* population density between 1999 and 2000 was negatively correlated with its population density in 1999, confirming the strong intraspecific competition suggested by the competition experiment. *Rumex* population density in 2000 was positively correlated with its population density in 1999 and inversely correlated with *Holcus* population density in 1999. Species of intermediate competitive ability (*Festuca*, *Anthoxanthum* and *Cerastium*) showed a strong positive relation with seed addition for both their population densities in 2000 and the difference in population density between 1999 and 2000. *Festuca* and *Anthoxanthum* also showed a positive relation between their population densities in 1999 and 2000. *Cerastium*, for both its population density in 2000 and the difference between its population densities in 1999 and 2000, showed a negative correlation with *Holcus* population density in 1999. For poor competitors (*Veronica*, *Arabidopsis* and *Lamium*), population densities in 2000 and the difference in population densities between 2000 and 1999 are positively correlated with seed addition. For *Veronica* and *Arabidopsis*, population density in 2000

Table 4. Multiple regression of the effect on population density in 2000 on difference in population density between 1999 and 2000 of the different variables potentially involved in species recruitment. For simplicity we give only the P and r^2 values of the global ANOVA and the P values for the t-test (H_0: each regression parameter differs from 0; ns = non-significant; $^*P<0.05$; $^{**}P<0.01$; $^{***}P<0.001$). For parameter estimates, we have added (−) when the parameter estimated is negative. We use the abbreviation abs. (absent) when the corresponding variable is not included in the model. Note that we did not consider *Lamium* population density in 1999 because it was zero. For all species n = 28. We have included between the lines species of the same relative competitive ability (Table 2). Species names are abbreviated as in Table 2.

	Population density in 2000 (Log)							
	Ver	*Lam*	*Ara*	*Fes*	*Cer*	*Ant*	*Rum*	*Hol*
(1) Analysis of variance								
P	**	*	***	**	***	***	ns	ns
r^2	0.48	0.29	0.58	0.64	0.64	0.70	0.27	
(2) Parameter estimates								
Variables								
Intercept	ns	ns	* (−)	ns	ns	ns	ns	
Seed added	**	*	*	***	***	***	ns	
Log 1999 population density	ns	abs.	ns	*	ns	**	*	
Log 1999 *Hol* population density	* (−)	*	* (−)	ns	* (−)	ns	* (−)	
Soil surface occupation in 1999	* (−)	ns	* (−)	ns	ns	ns	ns	

	Change in population density between 1999 and 2000 (Log)							
	Ver	*Lam*	*Ara*	*Fes*	*Cer*	*Ant*	*Rum*	*Hol*
(1) Analysis of variance								
P	**	*	***	**	***	***	ns	**
r^2	0.43	0.29	0.57	0.44	0.63	0.5		0.42
(2) Parameter estimates								
Variables								
Intercept	ns	ns	* (−)	ns	ns	ns		ns
Seed added	**	*	*	**	***	***		ns
Log 1999 population density	ns	abs.	ns	ns	ns	ns		** (−)
Log 1999 *Hol* population density	* (−)	*	* (−)	ns	* (−)	ns		abs.
Soil surface occupation in 1999	* (−)	ns	* (−)	ns	ns	ns		ns

and difference in population density between 1999 and 2000 were both negatively correlated with *Holcus* population density in 1999 and soil surface occupation in 1999.

Discussion

Competition experiment

Our results show that perennials were better than annuals both in their competitive effects and in their competitive responses in this experiment; *Holcus lanatus* was the best competitor and most abundant species. *Holcus* is a fast-growing perennial grass that forms big tufts with tall individuals that quickly suppress other species. It responds strongly to nitrogen and water addition (Grime et al. 1988) and probably benefited in our experiment from an increase in nutrient availability following plowing and from watering. All of these features confer on *Holcus* an exceptional competitive ability in moderately acid, fertile soils (Redosevich and Holt 1984, Grime et al. 1988, Thorhallsdottir 1990). *Rumex* also appears to have high competitive ability in our experiment. This species spreads strongly by vegetative rhizomes, which allow it to use empty space quickly (Putain and Harper 1970, Fowler 1981). Therefore, despite its low germination rate, it rapidly invaded plots by means of vegetative reproduction in 1998. It was a poorer competitor in 1999, however, probably because free space was much more limited, and it fared poorly in the face of strong competition from *Holcus*. *Festuca* was intermediate in competitive ability in 1998, but after two years its competitive ability increased considerably. This species appeared to become a better competitor as it slowly developed tufts. Data from the literature confirm the high potential competitive ability of *Festuca* (Goldsmith 1978). We found a similar response for *Anthoxanthum*, which has been show to be a good competitor under high-fertility treatments in other experiments (Fowler 1982).

In our study *Cerastium* was an intermediate competitor, whereas data from another competition experiment with perennials suggest that it is a very poor competitor (Fowler 1982). This result is a consequence of our using poorer competitors (other annuals) in the experiment, which allowed *Cerastium* to score relatively higher. Note, however, that the competitive ability of *Lamium* was probably underestimated because this species experienced high seed predation by ants.

We are aware that the substitutive (replacement) design we used in the experiment has been criticized in the plant-ecology literature (Goldberg and Barton 1992), but the competitive hierarchy observed in 1998 does a relatively good job in explaining species abundances in multispecies assemblages even after three years. The competitive hierarchy that we used to establish the seed quantities for the seed-rain experiment was therefore representative for at least the short- to mid-term competitive hierarchy and appropriate to the time scale of the immigration experiment. The competitive ranking of *Festuca*, however, improved in the second year of the competition experiment. Using the competitive hierarchy observed in year two would have slightly changed our experimental design, but these data were unavailable at the time we started the immigration experiment.

Local diversity and immigration

In 2000, communities were more diverse when they received more seeds and when immigration and competitive ability were negatively or uncorrelated. This increase in diversity was due to an increase in the population density of species of intermediate and poor competitive ability. After three years, the best competitors were very abundant and not influenced by immigration. The rarer species (poor competitors) experienced sufficient immigration to increase in abundance only in the scenarios where immigration and competitive ability were negatively correlated or uncorrelated, so diversity increased only in those scenarios. Diversity was not higher in the scenarios with negative correlation than in those without correlation because some poor competitors showed signs of saturation at high rates of immigration. Because the different groups of competitive species did not contain the same number of species, the higher diversity obtained where immigration was negatively correlated or uncorrelated with competitive ability could also reflect the higher diversity of seed added in the two treatments. Our results show clearly, however, that the best competitors (*Holcus* and *Rumex*) did not respond to immigration, ruling out the possibility of such a confounding effect.

For those species that responded to immigration, recruitment was controlled by four principal factors, the intensity of seed rain, the available soil surface, the abundance of the dominant species, and species competitive ability. These results are in agreement with those of previous studies on the influence of seed sowing on plant communities (reviewed by Turnbull et al. 2000). Space occupation has been shown to be one of the strongest limiting factors for species recruitment in herbaceous communities (Turnbull et al. 2000). In our communities, space was generally not saturated: 30% or more of ground surface was free of vegetation in 2000 in communities where no seeds were added. Moreover, our experiment had relatively low above-ground biomass which, according to Cantero et al. (1999), increases the potential for a positive influence of seed sowing on community diversity (Foster 2001). Competitive ability played an important role among species that had substantial recruitment in 2000, possibly indicating that, globally, intermediate competitors have found more suitable microsites for their establishment than poor competitors.

We also observed that the spatial distribution of *Holcus* tufts was strongly associated with space availability and thus with other species' recruitment. This species was strongly affected by intraspecific competition, so distances between *Holcus* tufts were large (pers. obs.). In addition, in 1998, available space between tufts was occupied by a mat of *Holcus* roots, which subsequently decomposed and left the soil surface free in late 1999. This result points out a possible indirect positive effect of *Holcus* on the recruitment of other species: the negative interaction between *Holcus* tufts created available space for other, poorer competitors. These openings between *Holcus* tufts were recolonized slowly by *Rumex* and then by *Holcus*, but new openings were formed elsewhere in the community (pers. obs.). More work is needed, however, before we can conclude on this potential indirect effect.

Species-level responses to immigration

Of the poor competitors, only *Arabidopsis* and *Veronica* responded positively to immigration. *Veronica* population density was more rapidly saturated than that of *Arabidopsis*, but given the immigration success (weighted by the number of seed added and species germination rate) these two species recruited equally. The positive response of *Veronica* to seed addition is consistent with the findings of Turnbull et al. (1999). *Lamium* showed no response, but this species suffered from seed predation by ants (pers. obs.), emphasizing the role of other factors such as seed predators in the regulation of plant community structure.

All of the intermediate competitors responded strongly to seed addition, especially *Festuca*, which had the highest immigration success. This finding confirms recent results in which this species has been shown to recruit strongly (Zobel et al. 2000) or moderately (Burke and Grime 1996) from added seed. *Anthoxanthum* responded intermediately, as reported by Peart (1989), who studied the colonization of vegetated sites in grasslands. *Cerastium* responded less than these two species, consistent with results from previous studies (Turnbull et al. 1999). Given its immigration success, this species was more similar to the two other annuals, *Arabidopsis* and *Veronica*.

Very good competitors were the most abundant but did not change in abundance with immigration intensity. Results for *Rumex* are consistent with those of other studies (Putain and Harper 1970), where, sown at up to 7.5 g m^{-2}, *Rumex* did not strongly recruit from seeds in undisturbed grassland. Results for *Holcus* are more difficult to interpret because it did not recruit substantially in our experiment, whereas previous studies have shown that it can recruit from seed addition at vegetated sites (Peart 1989, Burke and Grime 1996). Moreover, its seedling density was strongly positively correlated with immigration intensity. However, most of the seedlings were moribund or very small in June 2000 (at harvest) and were therefore not counted as adults. One might therefore conclude that the best competitors (*Holcus* and *Rumex*) became abundant very rapidly and might therefore have reached a saturating population density after which no extra recruitment could have occurred.

Turnbull et al. (1999) found that better competitors recruit more strongly from seed addition. We find different results because our study was not confined to annual species which are often seed limited. If we consider only the species that responded positively to immigration in our experiment, according to the prediction of Turnbull et al. (1999), (see Turnbull et al. 2000 for a review), large-seeded species are better competitors (*Festuca*, *Anthoxanthum*) and recruit more (Rees 1995, Burke and Grime 1996).

The ability of annuals to compete with perennials when they are all sown together (as in the competition experiment) might be different from their ability to invade a community of established perennials. The germination of the small-seeded annuals species might have been inhibited by shade in the immigration experiment, distorting the index of immigration success which was based on germination in bare soil. This might explain why *Cerastium* immigration success was less strong that would have been expected based on its competitive ability. Unfortunately, we do not have any measure of germination of annuals in established communities to appreciate the extent of this distortion. Despite this limitation, we believe that the conclusion that annuals have a low immigration success compared with intermediate competitors to be robust since the differences were very high (for example, *Festuca* has an index of immigration success that is 30 times higher than that of *Arabidopsis*).

Coexistence mechanism and immigration

Our results do not correspond fully to the prediction we had obtained from our previous model (Loreau and Mouquet 1999). Although the model predicted a complete shift in species dominance at high immigration, we found that the best competitors were still the more abundant species after three years at high immigration intensity in the scenario where local competitive ability and immigration were negatively correlated.

Our modeling results are valid given that local dynamics were governed by a weighted lottery (probabilities of establishment of species at free sites depended on the relative proportion of propagules, Chesson and Warner 1981), but other rules for species establishment could alter predictions about the influence of immigration. For example, if competitive ability rather than propagule density determines species establishment, coexistence can be promoted by niche differentiation (MacArthur and Levins 1967, Tilman 1982). In that case, the effect of immigration on species richness and abundances will depend on whether open niches are available. Local coexistence can also be viewed as promoted by appropriate trade-offs between competition and species fecundity (colonization) at the local scale (Tilman 1994). In that case, qualitative (Turnbull et al. 1999) and quantitative models have shown that diversity should generally decrease (Pacala and Rees 1998) or show a unimodal relation (Mouquet et al. 2002) with increasing immigration. This decline occurs because, after a threshold, increasing immigration will progressively allow the most competitive species to occupy all sites, and less competitive species will eventually be excluded. Again, the influence of immigration will be different depending on whether its relation with competitive ability is negative, positive, or null. We might expect a strong decrease in species diversity when immigration is positively correlated or uncorrelated with local competitive ability and an increase if it is negatively correlated with local competitive ability.

The results on species richness we have found in our experiment might thus shed light on the rules underlying species establishment and, in turn, species coexistence rules (Pacala and Rees 1998, Turnbull et al. 1999) in the community we have studied. First, the predictions based on the competition-colonization trade-off model are not supported, because we found an increase of species diversity even when competitive ability was positively correlated with immigration. Second, exclusion was nearly complete in closed communities, indicating that competition was acting to limit local diversity and that species niches were probably overlapping. Therefore, because despite the strong local competition, species richness was shown to increase in the three scenarios linking competitive ability to immigration, a kind of lottery weighted by species competitive ability may have been acting.

However, the finding that species responded differently to immigration and that one species (*Holcus lanatus*) had a very strong influence on other species responses, suggests that a more complex mechanism was acting to structure species diversity. We speculate that the mechanism behind species coexistence involved, first, a kind of colonization-extinction process (Horn and MacArthur 1972, Hastings 1980, Tilman 1994) between *Holcus* and other species. Negative interactions between *Holcus* tufts created openings that were colonized by other species. *Holcus* then recolonized these openings, but new ones were created elsewhere. Poorer competitors were therefore fugitive and coexisted with the strong competitor in a mosaic habitat because of this extinction-recolonization processes. Second, in competition for the space available between *Holcus* tufts, intermediate competitors had greater immigration success than did poor competitors because the probability of establishment was a function of both species competitive ability and propagule densities, and abundances were therefore related to both immigration and local competitive abilities.

Immigration and community-level functional properties

Previous theoretical studies (Loreau and Mouquet 1999, Mouquet et al. 2002) have produced a few predictions about the relationship between immigration and some community-level functional properties, such as total biomass or space occupation. It has been shown that the mechanisms underlying species coexistence were a key factor in determining this relationship (Mouquet et al. 2002). Space occupation should increase with immigration intensity regardless of the coexistence mechanisms, but the results for productivity differ. A weighted lottery should lead to no change or a decrease in productivity with increasing immigration, depending on whether immigration is positively or negatively correlated with competitive ability. If niche differentiation is acting, the result should be no change or an increase in productivity (depending on whether species had or had not yet occupied all of their available niche space) with immigration intensity. Finally, if the competition-colonization trade-off is acting, productivity should increase in all scenarios relating immigration to competition but more strongly if immigration is positively correlated with competitive ability.

Predictions about space occupation are supported by our experiment; we found that soil occupation was higher in communities that received immigration, but total above-ground biomass did not show any tendencies with immigration. This result is due to the strong dominance of *Holcus*, which, with Rumex, constituted the majority of total above-ground biomass in communities and did not respond to immigration. Even if the contribution of other species to community biomass increased with immigration, it was not sufficiently strong to change total above-ground biomass. Three species (*Festuca*, *Anthoxanthum* and *Cerastium*) did not show any population density saturation at high immigration intensity. If the experiment had continued for additional years, we would have expected the population density of these species to increase more, especially that of the two perennials (*Festuca* and *Anthoxanthum*). Therefore, the potential for long-term changes in total above-ground biomass with immigration cannot be completely rejected, even though we did not observe short-term responses to immigration.

Conclusions

We found that immigration can affect community composition by being a strong force in structuring local species dynamics but has less effect on community-level functional properties. Species did not show the same response to seed addition. Species establishment rules were a function of both local competition and immigration, but in varying degrees for each species; the intermediate competitors were the species that responded most strongly to immigration. Given that some seeds were available through immigration, coexistence was possible at this small scale even though species differed strongly in local competitive ability and the potential for competitive exclusion if the community were closed. In this scenario, seeds could either be produced locally (if weaker competitors have enough time to reproduce) or immigrate from other communities (Horn and MacArthur 1972, Chesson 1985, Holt 1993, Mouquet and Loreau 2002). On the basis of this and other studies (reviewed by Zobel 1997 and Turnbull et al. 2000) we emphasize that the composition and properties of plant communities must be considered as a combination of local (competition) and regional (immigration) processes.

Acknowledgements – We thank Isabelle Dajoz, Gérard Lacroix, Thomas Miller, and Martin Zobel for comments on the manuscript. A. B. Thistle kindly edited the manuscript. Many thanks are due to Jean Claude and Ghislaine Loyau from the station at Foljuif and students Bertrand Liatard, Eric Lenoble, Amanda Osuch, Ethel Gauthier, Guenolé Le Moaligou, Nicolas Rousset, and Pierre Barthelemy. Thanks to Nicolas Mouquet's family (Bernard, Lucile, Sylvain and Sarah) and some of his friends (Bertrand, Bruno, Cecile, Claire, Florence, Julien, Lucile and Tanguy), who helped in the field. Nicolas Mouquet was supported by a grant from the French Ministry of Research and Education. This research was supported by the CNRS, Programme populations fragmentées, extinctions, sélection d'habitat et biologie de la conservation.

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