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Effects of genetic impoverishment on plant community diversity

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Summary

1 Established individuals removed at random from populations of 11 long-lived herbaceous species coexisting in a local area of ancient limestone pasture at Cressbrookdale in North Derbyshire were subjected to clonal propagation to produce stocks of genetically identical individuals sufficient to create 36 model communities identical in species composition but widely contrasted in genetic diversity.
2 Three levels of genetic diversity were imposed. In one treatment, all individuals of each species were genetically unique. The second contained four randomly selected genotypes of each species. In the third, there was no genetic diversity in any of the species but each community contained a unique combination of genotypes.
3 Over a period of 5 years the communities were allowed to develop in microcosms containing natural rendzina soil and exposed to a standardized regime of simulated grazing and trampling. The treatments were maintained by the removal of flowers, immature seed-heads and seedlings originating from the seed-bank and seed rain. Point quadrat surveys were used to monitor changes in species composition and diversity in the three experimental treatments.
4 During the experiment a distinction rapidly developed between five canopy dominants and five subordinates, a process that caused the vegetation structure to closely resemble that occurring at Cressbrookdale.
5 A gradual loss of species diversity occurred in all three treatments but by the end of the fifth growing season species diversity was higher in the most genetically diverse communities.
6 Ordination of the 36 communities at intervals over a 5-year period revealed a gradual convergence in the species composition of the 4-genotype and 16-genotype communities and this effect was more strongly developed in the latter. A comparable process was not observed in the 1-genotype communities, suggesting that interaction between particular genotypes of different species in local neighbourhoods may be an essential part of the mechanism that determines the predictable composition of a mature pasture community.
7 It is concluded that, under the conditions of this experiment, genetic diversity within component species reduced the rate at which species diversity declined. The relative importance in this effect of factors such as greater disease resistance and moderated competitive interactions remains uncertain.

Key-words: calcareous grassland, genetic diversity, microcosms, model communities, species diversity

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Introduction

Plant ecologists are prominent among those who have recognized the theoretical possibility that genetic variation within populations plays an important part in the maintenance of biodiversity in communities. Antonovics (1976, p. 233) asserted that 'Forces maintaining species diversity and genetic diversity are similar. An understanding of community structure will come from considering how these kinds of diversity interact'. A year later Harper (1977, p. 707) wrote that 'Diversity of a plant community is inadequately described by the number and abundance of the species within it'

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and he contended that 'a major part of the community diversity exists at the intraspecific level'. More recently, Aarssen & Turkington (1983, p. 212) have supported this proposition stating that 'Changes in genetic constitution may have important consequences at the community level … irrespective of taxon'. This perspective allowed the same authors to construct a qualitative model (Aarssen & Turkington 1985) for community evolution in pastures in which the community is considered as a collection of genotypes with genetic and species diversity functioning as integral and interdependent components of community diversity. Evidence consistent with this model is available from studies documenting the existence of genetic variation within populations of established plants (Harberd 1957; Burdon & Harper 1980; Burdon 1980a,b) and comparing its extent in plant communities differing in antiquity but maintained under comparable conditions (Charles 1961; Aarssen & Turkington 1985).

So far, definitive measurements of the contribution of genetic diversity to species diversity have not been possible, although some progress has been achieved by conducting experiments with model communities of bacteria (Rosenzweig *et al*. 1994; Turner *et al*. 1996; Treves *et al*. 1998; Rozen & Lenski 2000). Here a difficulty arises from the genetically labile nature of bacterial populations; in order to recognize the genetic components in mechanisms of species coexistence it is desirable to hold the genetic composition of experimental populations constant for periods long enough to detect their effects. On this basis perennial plant communities may be more suitable subjects for investigation. The experiment described in this paper explores this possibility by using model communities of herbaceous plants composed of populations of long-lived individuals of known genetic identity. Although it is appropriate to describe the synthesized vegetation in this study as consisting of model communities, steps have been taken to ensure relevance to natural conditions. All the plants used are derived from vegetative individuals selected at random and coexisting within the same small local area within an ancient species-rich calcareous grassland. This ensured that the experiment employed materials that had survived the selective mechanisms operating in the field. Approximation to natural conditions was also achieved by using a natural rendzina soil, by including bryophytes from the same location and by subjecting the synthesized communities to treatments simulating grazing and trampling by sheep and cattle.

Because the experiment employed slow-growing plants subjected to mineral nutrient stress and regular defoliation it was necessary to allow a long period of time for the communities to assemble and for effects of treatment to appear. This paper presents results from the first 5 years of the experiment.

Research strategy

In order to examine experimentally the contribution of genetic diversity to the maintenance of community diversity several conditions must be satisfied. It is clearly advisable to employ vegetation in which high genetic diversity, in addition to coinciding with high species richness, can be manipulated in the plant populations forming the bulk of the biomass. It is imperative that the populations used should consist of long-lived individuals with low rates of replacement by sexually derived progeny. Fast-growing species are easier to propagate but may not permit control of genetic composition over long periods of time. In order to meet these requirements the investigation focused on a 10×10 m area of ancient species-rich, calcareous pasture at Cressbrookdale in North Derbyshire. The site was occupied by a densely packed assemblage of out-breeding grasses, sedges, forbs and sub-shrubs and had been the subject of previous intensive studies (Furness 1980; Pearce 1987) that had established that these species were mainly represented by small, compact individuals randomly distributed in a short turf. This information provided important guidelines with respect to the method used to construct the model communities and allowed a convenient arrangement in which a standard number of similar-sized transplants of each species could be inserted through a planting grid in which each species and genotype was located at random.

To synthesize communities with controlled levels of genetic diversity it was necessary to draw upon a large stock of genetically identical individuals of each of the species and genotypes to be used in the experiment. This was created by systematic clonal propagation of 176 randomly selected cuttings (16 of each of 11 species) over the 3-year period immediately preceding the experiment.

In an attempt to increase the probability of detecting effects of genetic impoverishment comparisons were made between synthesized communities containing very contrasted degrees of genetic diversity and this was achieved by manipulating simultaneously and in parallel the levels of genetic diversity in each of the 11 component species. Three treatments were imposed. In the first treatment each of the 16 individuals of each of the species was genetically unique. In a second treatment each species was represented by four randomly selected genotypes. The third treatment contained no genetic diversity within any of the 11 species; here each replicate consisted of a unique combination of genotypes.

In order to maintain the integrity of the experimental treatments it was essential to prevent incursions by other species in the seed rain at the experimental site or present in the soil seed bank; this was addressed by regular weeding throughout the experiment. Genetic diversification by seedlings produced by the planted populations was prevented by removing all inflorescences, a procedure that in effect mimicked to a considerable extent the result of the grazing regime at Cressbrookdale.

Logistical and security problems made it impossible to locate the experiment in Cressbrookdale. The

Fig. 1 General view of the microcosms and experimental communities.

communities were assembled in microcosms in an experimental garden in an urban environment. However, as shown in Fig. 1, the 36 microcosms of the experiment described in this paper were, in fact, embedded at random within a matrix of 72 additional microcosms containing the same soil and plant species transplanted from Cressbrookdale and creating a local 'calcareous grassland enclave'.

The main technique employed to investigate the consequences of genetic impoverishment was to use point quadrats to record the abundance of each species in each of the communities over the course of the experiment. Ancillary data were collected but the most important objective was to monitor the rate of decline in community diversity using the point quadrat results.

Predictions

At the beginning of the experiment two main predictions were made with respect to the consequences of genetic impoverishment. The first was the expectation that, with increasing interaction between the species and the prevention of seedling recruitment, community diversity would decline gradually in all three treatments. However, it was predicted that the loss of diversity would proceed at a faster rate in the communities containing fewer genotypes. This was founded on the prediction (Miller & Fowler 1994; Prentice *et al*. 1995) that genetic diversity in local populations can sustain their abundance in a community either by moderating and diversifying the outcome of interspecific competition (Aarssen & Turkington 1983; Aarssen 1989) or by reducing vulnerability to pathogen attack (Thompson & Burdon 1992; Burdon 1993)

The second prediction refers specifically to the impact of genetic impoverishment on individual synthesized communities. Here it was forecast that it would not be possible to predict the identity of expanding and declining species in particular microcosms because this would vary idiosyncratically according to the different combination of genotypes representing the species in each community.

Materials and methods

MICROCOSMS

The communities were assembled in purpose-made, black polypropylene plastic microcosms (600 × 600 × 150 mm deep) situated in a fenced site located at Tapton Experimental Gardens, University of Sheffield, Sheffield. Each had welded corners and drainage holes in the base above which a layer of Terylene cloth retained the soil. The microcosms were arranged in a randomized block design and were raised to waist height on scaffolding supports (Fig. 1).

SOIL

Continuity of nutrient regime experienced by the experimental plants was assured by using natural rendzina soil brought from a site (Harpur Hill, Buxton) supporting a turf closely similar to that found in Cressbrookdale. The soil was extracted from the top 200 mm of the profile, cleaned of root debris and homogenized in a mechanical mixer and then distributed in aliquots to fill the microcosms, after which they were left to settle. The soil handling was carried out as swiftly as possible to maximize the survival of the natural soil flora and fauna and to encourage the rapid reconstruction of microbial and invertebrate food-webs.

VASCULAR PLANTS

The 11 species used in the experiment were chosen from amongst those most commonly occurring in a 10 × 10 m area of the Cressbrookdale site. The frequency of each species in this area was determined by a survey

conducted on 100 turves located using random co-ordinates. *Festuca ovina*, *Koeleria macrantha*, *Helictotrichon pratense* and *Briza media* (grasses), *Carex flacca*, *C. panicea* and *C. caryophyllea* (sedges) and *Leontodon hispidus*, *Succisa pratensis*, *Campanula rotundifolia* and *Viola riviniana* (forbs) were selected. All species are winter-green except *L. hispidus*, which is deciduous, losing leaves and most root material and overwintering as a perennating organ. Nomenclature for vascular plants follows Stace (1991).

BRYOPHYTES

Bryophytes are a major component of damp, species-rich grasslands (Al-Mufti *et al*. 1977; van Tooren *et al*. 1988; During 1990) and contribute up to 30% of the above-ground biomass in Cressbrookdale (Furness 1980). For this reason an application of 25 g of mixed bryophyte was made to each of the 36 microcosms. The bryophyte shoots were removed directly from the Cressbrookdale site, teased apart and thoroughly mixed and introduced around the plants in two spring applications (14 g in 1998 and 11 g in 1999).

PROPAGATION

The plant material used in the experiment was created by intensive vegetative propagation, over a 3-year period, from 176 mature, established individuals (16 per species) randomly selected from the Cressbrookdale turves. In ongoing studies (R. Whitlock, personal communication), the genetic identity of each of the 16 propagated individuals in the 11 species is currently in process of determination by PCR analysis of genomic DNA using the ISSR marker method (Zietkiewics *et al*. 1994).

PLANTING

The complex planting operation extended over a period of 6 weeks and employed full-sized coded planting maps divided into equally spaced cells. The occupancy of each cell was randomly assigned, each species being allocated an identifying colour and an alpha-numeric code. The maps, varnished to withstand the outdoor conditions throughout the planting process, were placed over the soil surface of each microcosm. The roots of the propagated cuttings were washed free of compost, snipped to standard proportions and then inserted through slits made in the centre of each cell. Bundles of four tillers of the fine-leaved *Festuca ovina* were used as a single unit to ensure that the biomass was comparable with other species. Unhealthy plants were replaced until the maps were removed and the experiment began in May 1998.

GRAZING AND TRAMPLING TREATMENTS

Biannually, in June and October, throughout the experiment a clipping and simulated trampling regime was applied to the synthesized communities to mimic the occasional summer grazing by sheep and cattle that is used as a management procedure in Cressbrookdale National Nature Reserve. Shears, with Perspex side-plates designed to collect the clippings, were used to remove the layers of the canopy 25 mm above the soil surface. The simulation of trampling by sheep and cattle was applied to each community after the autumn clipping, using a tool made from a short length of angled steel attached to a length of quadrant beading. At 40 randomly located positions within each microcosm the tool was pushed into the soil surface and twisted slightly, exposing bare soil.

MAINTENANCE

Year-round weeding prevented recruitment from seed. Flowering was allowed but seed-heads were removed before ripening to prevent self-seeding.

Supplementary moisture as deionized water was applied during dry periods to avoid drought. This procedure was considered necessary because the soils at Cressbrookdale, although shallow and situated on fissured limestone, are subject to seepage and remain damp throughout most years.

EXPERIMENTAL DESIGN

Three levels of genetic diversity were imposed on 36 experimental communities of identical species composition. In the microcosms of high genetic diversity each of the 16 individuals representing each species was derived from a different mother plant. In an intermediate treatment the population of each species was composed of a unique combination of four individuals of each of four randomly selected genotypes and each genotype was used in either two or three communities. In a third treatment there was no genetic diversity in any of the 11 species, each species being represented by 16 individuals of the same genotype. High and intermediate diversity communities were replicated 10 times each whilst the treatment with no genetic diversity within each species had 16 communities each containing a unique combination of genotypes. Each community was created by planting 176 individuals (16 per species) in randomly allocated positions on a uniform planting grid and a different randomization was applied to each community.

This experimental design has several consequences, one of which is to call into question use of the term ‘replication’. Whilst the three treatments clearly represent different levels of genetic diversity, in two of them individual communities differ in genetic composition and for this reason cannot be regarded as true replicates. Even in the case of the 10 communities that contain the same 16 genotypes of each species some differences in community development may be expected to arise from the use of a unique planting pattern in each microcosm.

DATA COLLECTION AND ANALYSIS

It was essential that the methods of data collection did not compromise the procedures used to simulate the grassland management at Cressbrookdale. For this reason recording was mainly restricted to the use of point quadrats (60 points per community, randomly distributed and using a vertical 1.0 mm diameter pin) on four occasions during each growing season at the beginning of June, July, August and September. Throughout the 5 years of this survey, data were collected by the same two observers and involved recording the total number of pin contacts with the shoots of each plant species.

The total clippings resulting from the simulated grazing applied in June and September were dried at 80 °C and weighed. A more complete harvest of all above-ground vegetation was made in October 2000, when three randomly located, 75 mm diameter samples were removed from each microcosm and sorted into vascular plant material, bryophytes and litter components, which were then dried and weighed.

The point quadrat data provided a continuous record of the abundance of each plant species in each community over the 5-year period. For each stage of the experiment this allowed comparisons to be drawn between the three experimental treatments with respect to the Shannon-Weiner index of diversity. A repeated measures procedure was used to compare the trajectories of changing diversity in the later stages of the experiment. It was also possible to apply principal component analysis to the same data to recognize axes of variation in species composition over the recording period.

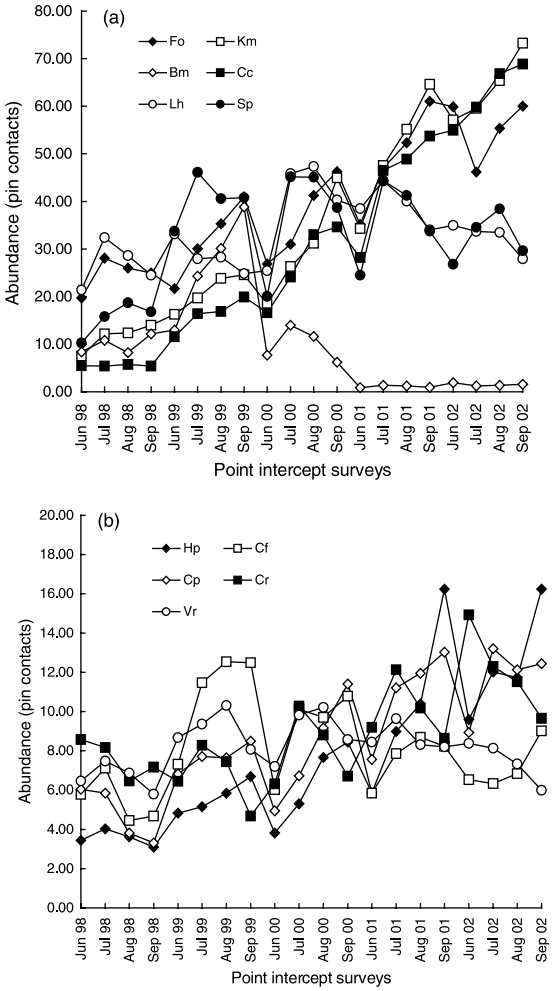

Fig. 2 Estimates of the abundance of (a) canopy species and (b) subordinate species expressed as the mean number of point quadrat contacts in all 36 communities, over the course of the experiment. See text for species abbreviations.

Results

PERFORMANCE OF SPECIES

In Fig. 2(a,b) the point quadrat scores for all the experimental communities, regardless of treatment, are brought together to provide mean values illustrating the changing abundances of the species. These data reveal that, with the exception of *Briza media* and *Viola riviniana*, all the species continued to increase in abundance over the course of the experiment. It is immediately apparent, however, that despite the close matching of species in weight of planted material, a dichotomy became apparent as early as the first growing season between five canopy dominants (*Festuca ovina*, *Koeleria macrantha*, *Briza media*, *Succisa pratensis* and *Leontodon hispidus*, Fig. 2a) and five subordinates (*Carex flacca*, *C. panicea*, *Helictotrichon pratense*, *Campanula rotundifolia* and *Viola riviniana*, Fig. 2b). The sedge, *Carex caryophyllea*, however, did not emerge from the ranks of the subordinates until the second year of the experiment, but subsequently rose to become the second most abundant species by the end of the fifth year (Fig. 2a).

In the third year a precipitous fall occurred in populations of the grass *Briza media*. This coincided with widespread symptoms of a rust disease in all three treatments and resulted in disappearance of the species from many of the communities.

In several of the species, but more conspicuously in canopy dominants such as *Festuca ovina*, *Koeleria macrantha* and *Succisa pratensis*, a temporary decline in abundance occurred in each year following the simulated grazing event in June. As we might expect this defoliation had less effect on some of the subordinate species such as *Viola riviniana*, which subtend many leaves close to the ground and beneath the height of clipping. A distinctive pattern is apparent in *Carex caryophyllea*, which, despite rising eventually to high abundance showed only weakly defined effects of each defoliation event.

YIELD AND CANOPY STRUCTURE

No statistically significant differences between the three treatments were detected when samples of all

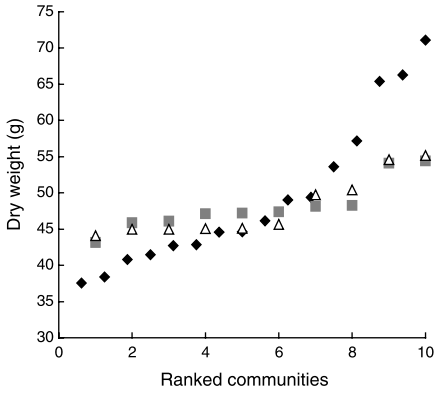

Fig. 3 Comparison of 36 communities with respect to the dry weight of material removed by clipping at a height of 25 mm in June 1999. The communities in each treatment are ranked in ascending order of dry weight. ■ = 4 genotypes; △ = 16 genotypes; ◆ = 1 genotype. The ranking of the 16 communities of the 1-genotype treatment has been compressed to occupy the spacing of the other two treatments. Variation in the 1-genotype communities is significantly greater ($P < 0.01$, Levine test of variance).

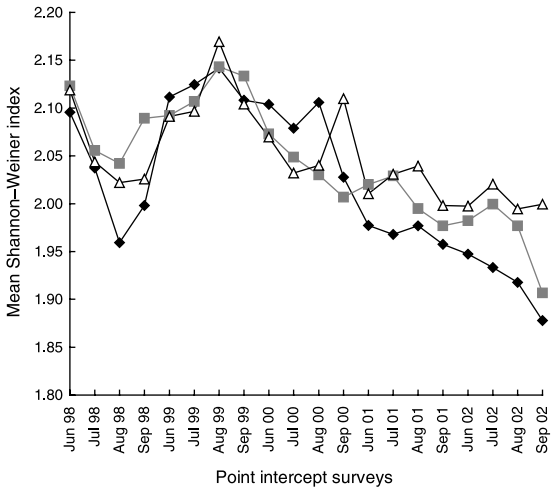

Fig. 4 Variation in species diversity, expressed as mean Shannon-Weiner index, for three sets of synthesized communities over a 5-year period (1998–2002). ■ = 4 genotypes; △ = 16 genotypes; ◆ = 1 genotype.

above-ground plant material were removed, sorted, dried and weighed in 2000. However, an effect coinciding with the most extreme level of genetic impoverishment was observed when comparisons were made with respect to the weight of clippings removed in the simulated grazing events. As illustrated in the specimen results for June 1999 (Fig. 3), all three treatments showed considerable variation in the weight of leaf canopy projecting above the height of clipping (25 mm) but this variation was much more pronounced in the communities lacking genetic diversity in component species, where it was significantly greater than in the two other experimental treatments ($P < 0.01$, Levene test of variance, SPSS, Version 11, SPSS, Chicago).

COMMUNITY DIVERSITY

In Fig. 4, estimates of the abundance of the vascular plant species in each microcosm have been used to calculate means for the Shannon-Weiner index of diversity in the three sets of synthesized communities representing different degrees of genetic impoverishment. A broadly similar pattern is evident in each treatment. Planting resulted in a fall in diversity in the first growing season, which was then followed by a recovery, itself then succeeded by a gradual decline in subsequent years. A divergence between the means became evident visually in June 2001 and persisted to the end of the period of recording. Application of a repeated measures procedure over the last 14 sampling occasions, which correspond to the phase during which all three treatments lost diversity, showed no statistically significant differences overall between the treatments, although significant differences ($F_{26,429} = 1.981$, $P = 0.003$) were detected between the three treatments with respect to the trajectories of change in diversity index with time.

COMMUNITY COMPOSITION

In an attempt to recognize the origins of the differences in community diversity detected in September 2002, principle component analyses were conducted on the species composition of the 36 synthesized communities measured at intervals throughout the experiment. The results (Fig. 5) show that, although the species compositions within each of the three treatments remained widely divergent for several years, a gradual convergence occurred in the 4-genotype and the 16-genotype communities and was more strongly developed in the latter. A similar convergence did not occur in the 1-genotype communities and in September 2002 half of the communities in this treatment had positions on the ordination diagram that were external to the area enclosing all the remaining communities in the experiment.

Comparison of the composition of the communities representing the three treatments (Fig. 6) reveals a tendency for genetic impoverishment to be associated with greater within-treatment variation in the relative abundance of species. In the communities lacking genetic diversity greater variation was most conspicuous in *Carex caryophyllea*, *Koeleria macrantha* and *Festuca ovina*, although this effect was confirmed statistically ($P < 0.001$, Levene test of homogeneity) in only the first of these species. Figure 6 also provides some pointers to the nature of the variation associated with axes 1 and 2. It would appear that as we move from right to left along axis 1 there is an increasing tendency for one or more of the species, particularly those of higher abundance, to show departures from their mean level of abundance in the experiment as a whole. This is illustrated in Fig. 7, where histograms describing the composition of the 16 communities lacking genetic diversity have been ranked according to the relative abundance of *Carex caryophyllea*. This figure reveals

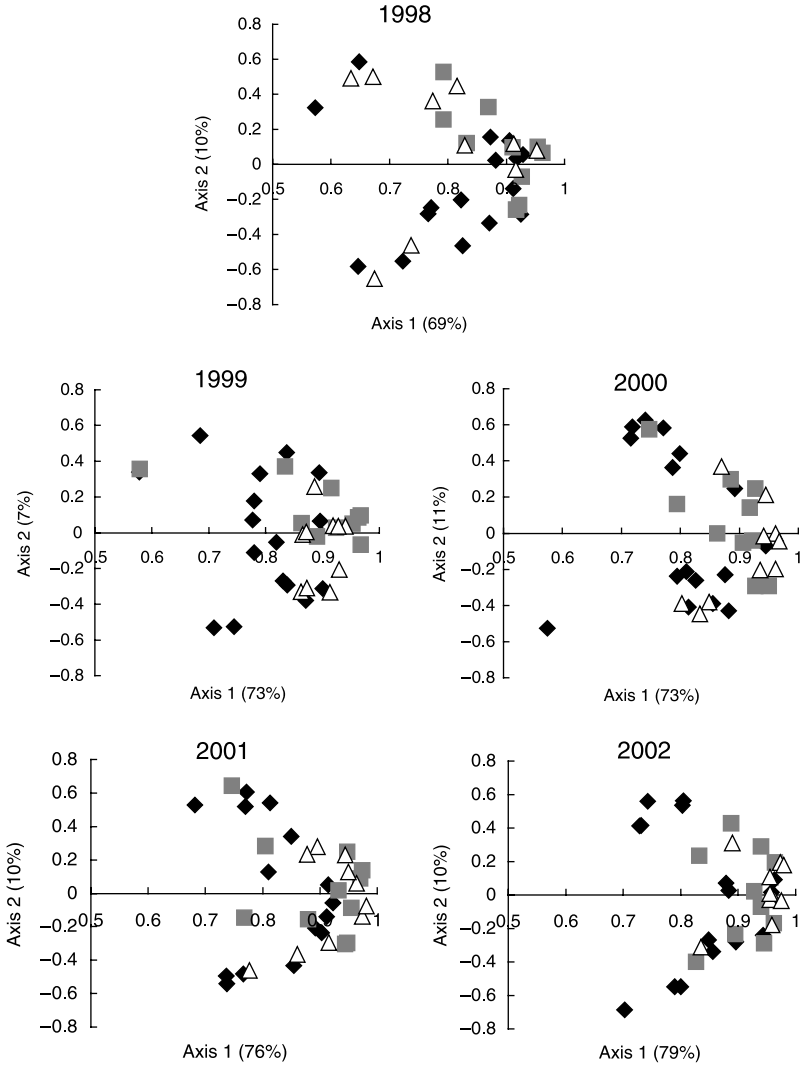

Fig. 5 Principal component analysis of variation in the species composition of 36 synthesized communities allowed to assemble over a period of 5 years. Each figure presents a PCA analysis of point quadrat data collected in September. ■ = 4 genotypes; △ = 16 genotypes; ◆ = 1 genotype.

that all of the eight outlying communities identified on the left of axis 1 have either unusually low or high relative abundances of *C. caryophyllea*. It is also interesting to observe that there is a remarkably consistent correlation between position on axis 2 and the ranking of the communities in Fig. 7. This strongly suggests that the extreme variability of *C. caryophyllea* acted as an influential factor in the development of the genetically depauperate communities and that variation in the identity of the dominant species (*K. macrantha*, *C. caryophyllea* or *F. ovina*) was implicated in axis 2.

Discussion

It was anticipated that effects of genetic impoverishment would be slow to appear under the conditions of low soil fertility and biomass removal applied in the experiment. This is confirmed in Fig. 4, which suggests that there were three phases in the development of the experimental communities. In the initial phase there was a sharp fall in diversity, presumably related to different sensitivities to transplanting shock among the species. This was followed by a phase of recovery of diversity, which reached a peak in August 1999 with the establishment of a closed turf. Finally, in a third phase there was a decline in diversity in all three treatments, coinciding (Fig. 2) with increasing disparities in abundance between the species. This process caused a progressive separation of the species into dominant and subordinate contributors to the canopy and brought the vegetation structure into close alignment with that described in the natural grassland at Cressbrookdale (Furness 1980).

It was only in the last 2 years of the study that differences in diversity began to distinguish between the treatments but it is interesting to note that, in the communities completely lacking in genetic diversity, an early sign of divergence was manifested as an increase in the variability of canopy structure (Fig. 3). This pattern is consistent with previous evidence of genetic variation in canopy height within populations of grassland plants (Bradshaw 1959; Mahmoud *et al*. 1975;

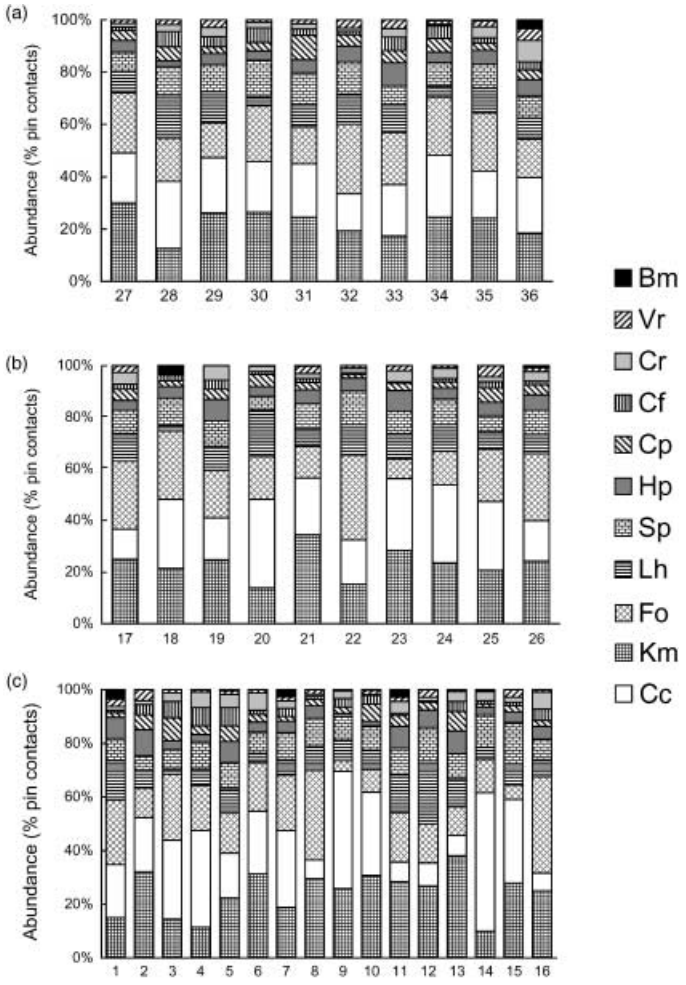

Fig. 6 Comparison of the species composition after 5 years of three sets of synthesized communities with contrasted levels of genetic diversity in component species. (a) 16 genotypes, (b) 4 genotypes, (c) 1 genotype.

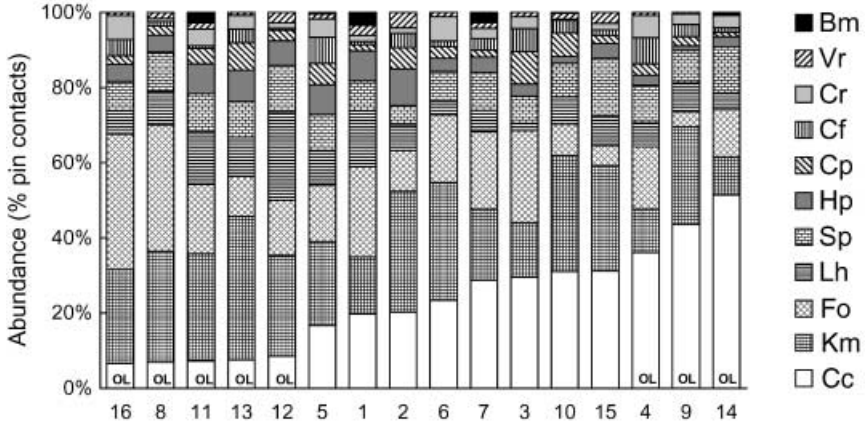

Fig. 7 Comparison of the species composition after 5 years of 16 communities, in each of which each species is represented by a different genotype. The communities are ranked in order of increasing relative abundance of *Carex caryophyllea*. Communities with outlying positions in the PCA (Fig. 5) are identified as OL.

Aarssen & Turkington 1985). Although the effects of genetic impoverishment were slow to develop and small in magnitude, it is interesting to observe that by the end of the period of observation the mean Shannon-Weiner indices for the three treatments had fallen into the order we had predicted.

Much more revealing insights into the consequences of genetic impoverishment became evident when the point quadrat data collected at the end of each growing season were subjected to principal component analysis (Fig. 5). This revealed that, over the course of the experiment, genetic diversity in the planted populations

was associated with a progressive convergence in the species composition of the communities and was most strongly developed in the 16-genotype treatment. In marked contrast, aggregation did not occur in the communities lacking genetic diversity. This suggests, following Aarssen & Turkington (1985), that the mechanisms responsible for the diversity, stability and predictable species composition of ancient, species-rich limestone pastures may depend upon contact and interaction between particular genotypes of different species. If this interpretation is correct, the delay in the process of convergence observed in Fig. 5 may be explained to some extent as the time necessary for lateral exploration of the microcosms by individual genotypes of species that are capable of clonal expansion. In current investigations this hypothesis is under test using molecular markers to measure the abundance of particular genotypes in the 4-genotype and 16-genotype communities.

As noted previously, half of the communities without genetic diversity were external to an area of the ordination diagram that enclosed all of the remaining communities. This suggested that reductions in genetic diversity had in some way eroded the mechanisms that maintain the distinctive composition of the Cressbrookdale community. As predicted, idiosyncratic expansions or contractions have occurred in the relative abundance of species, particularly in *C. caryophyllea*, and may be a symptom of such erosion. We presume that such excursions, whether up or down, are more likely where a species and its neighbours are represented by one or a few genotypes and we predict that eventually this loss of equitability in many of the genetically impoverished communities will lead to extinction of species; this hypothesis is relevant to the conservation and restoration of species-rich vegetation and will be tested in the next phase of the experiment.

Although both of the predicted consequences of genetic impoverishment have been confirmed, uncertainty remains with regard to their mechanisms. Further investigation will be necessary to assess the role, if any, of accentuated competition for resources or more virulent attack by pathogens in the observed losses of diversity. Severe fungal infections, leading in the case of *Briza media* to the death of many individuals, have occurred but there is no convincing evidence that these have been influenced by the experimental treatments.

The initial requirement in this investigation was to assemble model communities that resembled those at Cressbrookdale and to confirm that this was possible it was essential to monitor the synthesized communities for several years under a standard management regime. Constancy in management was also necessary in order to create circumstances in which even quite small effects of genetic impoverishment could be detected and interpreted. The advantages of this research strategy are evident in the effects of treatment that have appeared in Fig. 4. However, it may be important to recognize that the particular way in which effects of genetic impoverishment have been manifested in this experiment may have been conditioned by the particular and constant management conditions that were applied. Here it is interesting to note that a major factor implicated in the greater variation in species composition characterizing the 1-genotype communities (Fig. 5) is the extreme variability in the performance of *Carex caryophyllea*. The possibility must be considered that the decision to maintain a short turf by regular cutting over a period of 5 years resulted in strong discrimination between genotypes of this short, rhizomatous sedge. This interpretation is supported by field evidence (Lloyd 1972; Grime *et al*. 1988) that, in natural limestone pastures, *C. caryophyllea* is a consistent, minor component but does not attain the dominant status observed in some of the genetically impoverished communities of this experiment (Fig. 7). However, it would be premature to attribute such effects exclusively to genetic variation in *C. caryophyllea* as variation in the vigour of this species may be a more complex phenomenon involving modifying effects on the performance of *C. caryophyllea* due to interactions with the genotypes representing other species in the communities concerned.

Variable conditions, more nearly approaching those at Cressbrookdale, would be more likely to elicit responses in a wider range of species and genetically variable attributes but, because of the lags expected in the responses of communities of long-lived, slow-growing species, diagnosis of cause and effect will be complicated. Nevertheless, this step towards field reality is essential and will characterize the next phase of this experiment.

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