Journal of Ecology 2007
95, 895–907

The role of genotypic diversity in determining grassland community structure under constant environmental conditions

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Summary

1. A recent experiment varied the genetic diversity of model grassland communities under standardized soil and management conditions and at constant initial species diversity. After 5 years' growth, genetically diverse communities retained more species diversity and became more similar in species composition than genetically impoverished communities.

2. Here we present the results of further investigation within this experimental system. We proposed that two mechanisms – the first invoking genetically determined and constant differences in plant phenotypes and the second invoking genotype–environment interactions – could each underpin these results. This mechanistic framework was used as a tool to interpret our findings.

3. We used inter-simple sequence repeat (ISSR) DNA markers to confirm which of the individuals of six study species initially included in the model communities were unique genotypes. We then used the molecular markers to assess the survival and abundance of each genotype at the end of the 5-year experimental period.

4. The DNA marker data were used to create, for the first time, a genotype abundance hierarchy describing the structure of a community at the level of genotypes. This abundance hierarchy revealed wide variation in the abundance of genotypes within species, and large overlaps in the performance of the genotypes of different species.

5. Each genotype achieved a consistent level of abundance within genetically diverse communities, which differed from that attained by other genotypes of the same species. The abundance hierarchy of genotypes within species also showed consistency across communities differing in their initial level of genetic diversity, such that species abundance in genetically impoverished communities could be predicted, in part, by genotypic identity.

6. Three species (including two canopy-dominants) experienced shifts in their community-level genotype abundance hierarchies that were consistent with an increased influence of genotype–environment interactions in genetically impoverished communities.

7. Our results indicate that under relatively constant environmental conditions the species abundance structure of plant communities can in part be predicted from the genotypic composition of their component populations. Genotype–environment interactions also appear to shape the structure of communities under such conditions, although further experiments are needed to clarify the magnitude and mechanism of these effects.

Key-words: community ecology, community genetics, competition and coexistence, genetic diversity, genotype–environment interactions, grasslands, species diversity

Journal of Ecology (2007) **95**, 895–907
doi: 10.1111/j.1365-2745.2007.01275.x

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Introduction

It has long been held (Antonovics 1976) that the organization and structure of ecological communities is in part determined by the genetic diversity of their constituent populations. Genetic components to community structure are becoming evident in a variety of community processes such as succession (Proffitt *et al*. 2005), species coexistence (Booth & Grime 2003), and in the resistance and resilience of communities to environmental challenges (Hughes & Stachowicz 2004; Reusch *et al*. 2005). The possible role of intraspecific diversity in maintaining species diversity, although still poorly understood, has been the longest studied aspect of the genetics of plant communities (Antonovics 1976; Turkington & Harper 1979; Aarssen & Turkington 1985). In this sphere, genetic diversity potentially offers an attractive solution to the apparent paradox (Gause 1934) that mixtures of ecologically similar species are often observed in the natural world. Competitive hierarchies amongst coexisting species, often observed to be transitive at the species level (Goldberg & Landa 1991; Grace *et al*. 1993; Shipley 1993), may in fact be intransitive at the level of individual genotypes (Aarssen 1989; Taylor & Aarssen 1990), such that species identity is not always a reliable predictor of success through competition. Moreover, species that seem to overlap substantially in niche (Mahdi *et al*. 1989) may individually show adaptive differences at the scale of resolution of the genotype (Ennos 1985). Such adaptive diversity might allow a greater degree of species coexistence than is apparent from consideration of species-level niches alone (Vellend 2006). Adaptive genetic diversity is also thought to be critical in enabling species to persist when the prevailing environmental conditions change (Bradshaw 1952; Gregory & Bradshaw 1965; Kettlewell 1973; Snaydon & Davies 1982). Models of species coexistence that rely on intransitive competitive hierarchies amongst genotypes or on intraspecific adaptive diversity involve the interaction between individual genotypes and their environment, such that fitness is determined by a product of genotype and environment (a genotype by environment interaction, Haldane 1946). In the community context this leads to the expectation that no genotype of any species is maximally fit in all the environments contained within the community (e.g. Aarssen 1983, 1989).

To date, experimental investigations of the significance of genetic diversity to plant communities have relied largely on extrapolation from much simpler experimental units, such as pairwise competition experiments between genotypes, to infer the community-level consequences of genetic diversity (e.g. Taylor & Aarssen 1990). Field-based studies that explore this area (Prentice *et al*. 1995, 2006; Odat *et al*. 2004) have encountered particular challenges because environmental and demographic complexities may affect both the species and the genetic structures within natural communities. An alternative strategy is to conduct replicated experiments using simplified model communities in which the genetic diversity of multiple component species is manipulated while other variables are held constant. In such an experiment, Booth & Grime (2003) demonstrated that genetically impoverished communities, each consisting of a unique set of genotypes, became more divergent in their species composition, and lost species diversity faster, than more genetically diverse communities of initially identical species composition. The divergence in composition observed between replicate communities was most conspicuous in the experimental treatment in which each species was represented by a single genotype.

The effects of genetic impoverishment reported by Booth & Grime (2003) could have been caused by two mechanisms at the level of the genotype. These mechanisms are not mutually exclusive:

1. Under the *deterministic model* the fitness or abundance of each genetic individual in a community depends upon genetic characteristics that vary among individuals and that control the expression of traits, such as morphology or growth rate. The abundance of a species is determined additively by the total performance of all the genotypes that represent it within a population (i.e. by the genotypic composition and functional attributes of each genotype). In the experimental design applied by Booth & Grime (2003) reduction of genetic diversity acted to sample genotypes and their traits randomly from the total pool of genotypes. At low diversity, the abundance of species could change because the abundance characteristics of the genotypes representing them changed. Under such conditions a greater variance in species abundance is expected among genetically impoverished communities than among communities possessing genetic diversity. This is because particular traits are expressed consistently (fixed) in those populations comprising genetically impoverished communities.

2. The second proposed mechanism, the *contingent model*, implies an impact of genetic diversity on the community-level outcome of interactions between plants, or between plants and components of their biotic or abiotic environments (genotype by environment interactions). A key feature of this model is that genotypic fitness in genetically impoverished communities is contingent on elements of the environment (e.g. the identity of coexisting genotypes) that are heterogeneous within communities or whose prevalence varies with genetic impoverishment. As such, neither genotype abundance nor species abundance in these communities is expected to be predictable from the performance of each genotype in genetically diverse communities. All genotypes of a given species within impoverished communities may either 'win' or 'lose', resulting in the greatest variance in species abundance amongst these communities. Conversely, in more genetically diverse communities the expression of dominance by some species and the rate of exclusion of others may be moderated by intransitivity in the competitive relationships amongst genotypes (Aarssen 1983, 1989).

There are many possible alternative environmental agents through which the contingent model may operate, in addition to the example given above involving competitive interactions with other genotypes. Specific examples are the reduced probability of pathogen epidemics developing in genetically diverse plant populations (Burdon 1993), the differential palatability of genotypes to herbivory (Graham *et al*. 2001), and the possibility that mutualist bacteria (Chanway *et al*. 1989; Turkington 1996) or mycorrhizal connections (Streitwolf-Engel *et al*. 2001) between specific genotypes can moderate plant growth and the outcome of competition between these genotypes.

The two models represent extremes in a continuum where both mechanisms could contribute to community structure. Both models predict the same patterns of variance in abundance for species across communities with reduced genetic diversity. However, under the deterministic model, the abundance of genotypes is expected to be correlated between genetically diverse and impoverished communities. This pattern is not expected for differences in species abundance generated purely through the contingent model.

Here, we use the model framework described above to explore and help interpret the genetic basis of experimentally generated differences in the species composition and structure of plant communities. Specifically, we used DNA markers to measure the survival and performance of genotypes of six plant species after they had grown for 5 years in experimental communities differing initially in their degree of genetic diversity. We describe, for the first time, the structure of a mature grassland community in terms of the success or fitness of genotypes composing its component species. We find that genetic determinism has a role to play in driving the species abundance structure of communities, but that such determinism cannot on its own account for the composition of genetically impoverished communities. This is the first study of the molecular ecology of multi-species, multi-genotype plant communities. We show that genetic markers can be used to help understand the role of genetic diversity in determining the composition and dynamics of an ecological community.

Methods

STUDY SYSTEM

The long-term experiment exploited in this investigation is described in full elsewhere (Booth & Grime 2003). Here, we summarize particular aspects of the experimental design. In 1998, Booth & Grime (2003) assembled 36 model communities (0.6 m × 0.6 m in size) from experimental populations of 11 plant species, each population drawing upon a pool of 16 'biotypes'. We define a biotype as an individual plant and any of its clonally produced offspring that is presumed to be (but not necessarily) genetically distinct from other biotypes of the same species (i.e. a putative 'genotype'). We use the term genotype *sensu stricto* to denote an individual with demonstrable genetic differences from other genotypes. The experimental biotypes were originally derived from established plants sampled at random from within the same 10 m × 10 m area of limestone pasture at Cressbrookdale in Derbyshire, UK, and were assumed to represent unique genotypes. Some of the biotypes exhibited substantial differences in aspects of their morphology (e.g. Fig. 1), supporting the hypothesis that they were genetically differentiated. The plants were maintained in pots as an archive of clonal biotypes (hereafter designated the clonal archive) and vegetative propagation of this material was used to generate sufficient numbers of individuals to synthesize the communities.

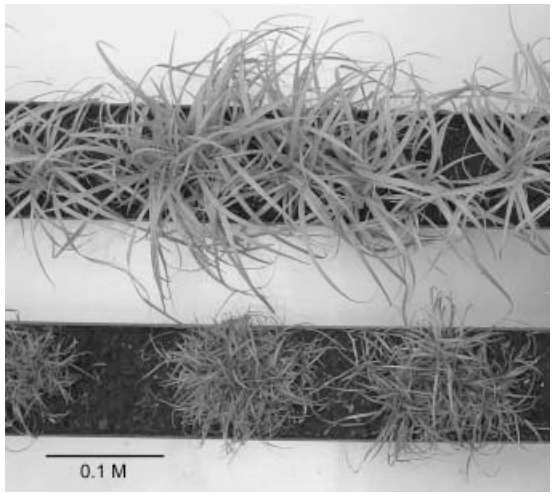

Fig. 1. Morphological differences between two genotypes of the sedge *Carex caryophyllea* that originated from the same 10 × 10 m area of calcareous grassland. The genotype shown in the upper section of the figure was sampled five times from randomly selected locations in the same 10 × 10 m field site.

Each experimental community was initially identical in species composition because the total number of individuals of each species planted in any community was held constant at 16. However, the number of biotypes representing each species in each experimental community was manipulated. This design resulted in the creation of three community types with contrasting levels of genetic diversity: 16, 4 and 1 biotypes per species per community, replicated 10, 10 and 16 times, respectively. Each replicate of the 4- and 1-biotype communities was created by making a random draw from the total pool of 16 biotypes of each species, with the constraint that every biotype was represented in at least one replicate of each genetic diversity treatment. In order to maintain the integrity of the genetic diversity treatments the communities were managed by cutting to simulate grazing and by removing all flowers by hand to prevent plants from dispersing seeds back into their communities (Booth & Grime 2003). This feature of the experimental design also permitted the re-identification of known individuals within genetically diverse communities using DNA markers (see below). We selected

six plant species for study from those included in the experimental communities of Booth & Grime (2003): *Festuca ovina* L., *Koeleria macrantha* (Ledeb.) Schult., *Carex caryophyllea* Latourr., *Succisa pratensis* Moench, *Leontodon hispidus* L. and *Campanula rotundifolia* L. These species included the five most abundant species in the experimental communities, as well as the most subordinate species, *C. rotundifolia.*

INDIVIDUAL IDENTIFICATION USING MOLECULAR MARKERS

The biotypes used to set up the experimental communities were originally sampled at random from a natural grassland community. It was not initially known whether each of the sampled biotypes represented a unique genotype, and therefore our first objective was to test this assumption. For this purpose, we extracted DNA from all the plants in the clonal archive with which to develop molecular markers and test the genetic identity of biotypes.

DNA was extracted using the CTAB protocol of Rogers & Bendich (1994), with some minor species-specific modifications as described by Whitlock (2004). Inter-simple sequence repeat (ISSR) DNA markers (Zietkiewicz *et al*. 1994) were developed for each plant species. The PCR primers used for ISSR analysis are shown in Table 1. PCR was carried out in a total volume of 10 L containing PCR reaction buffer IV (ABgene), 1.5–2.5 mM $MgCl_2$ (ABgene), 0.2 mM dNTPs, 0.5 M of each of two different ISSR primers, 0.25 units of Thermoprime plus DNA polymerase (ABgene) and 10 ng template DNA. Thermocycling conditions for PCR consisted of a 4-min denaturation stage at 94 C; 35 cycles of 94 C for 30 s, 52 C for 1 min and 72 C for 1 min; and a final extension of 10 min at 72 C. Diluted PCR products were separated and sized by polyacrylamide gel electrophoresis on an ABI 377 sequencer using a ROX-labelled size standard.

Table 1. Sequences of ISSR primers used for the identification of genotypes within genetically diverse plant communities

Primer	Sequence 5′–3′	Reference
RF01	AGAGAGAGAGAGAGAGT	Huang & Sun (2000)
RF04	CTCTCTCTCTCTCTCTG	Whitlock (2004)
RF05	GAGAGAGAGAGAGAGAT	Whitlock (2004)
RF06	VDHTCTCTCTCTCTCTC	Whitlock (2004)
RF09	RRRTTCTTCTTCTTCTTCT	Whitlock (2004)
RF10	RRGATCATCATCATCATCA	Whitlock (2004)
RF11	YYCTAGTAGTAGTAGTAGT	Whitlock (2004)

ISSR fingerprints obtained from samples of the biotypes in the clonal archive were examined in order to determine whether each represented a unique genotype. A fingerprint was considered genetically unique when it exhibited at least one band that distinguished it from fingerprints of other individuals and when this result was consistent over independent genotyping trials. The apparent genetic identity of different individuals can result either from clonal propagation or insufficient resolution of the genetic markers. Therefore, the power of the ISSR fingerprints to distinguish unique genotypes was tested by computing an overall probability of genetic identity (P_{ID}) for the primer combinations used to identify genotypes in each species. This value was calculated for each ISSR band as $P_{ID} = (p_l^2)^2 + (2p_lq_l)^2 + (q_l^2)^2$ (modified after Waits *et al.* 2001; L. P. Waits, pers. comm.) where p and q are the frequencies of the two alleles at the locus underlying an ISSR band. The total P_{ID} for a primer combination was calculated by chain multiplication of the individual P_{ID}s for each locus within the primer combination. Different bands within and among primer combinations were assumed to represent independently inherited genetic loci. Table 2 gives the P_{ID} values calculated using ISSR genotypes from unique individuals in each experimental population. The probability of identical genotypes matching purely by chance was less than 10^{-6}.

GENETIC SURVEY OF COMMUNITY COMPOSITION

The survival and relative abundance of each of the 16 genotypes of the six study species was determined within every 4- and 16-genotype experimental community by sampling leaf tissue and then identifying the genotype of the resulting samples using the ISSR molecular markers. This survey was conducted once after 5 years' growth of the experimental communities. All results presented in this paper refer to the survival and abundance of genotypes and species at this stage of the experiment. We used a 100-position (10×10 square) point-quadrat frame (described in Booth 2001) to determine locations for leaf-tissue sampling within each community. This quadrat frame had an area equal

Table 2. Summary of ISSR analysis for each study species. ISSR primer combinations used to identify genotypes are shown along with the power of these ISSR markers to discriminate individuals (P_{ID})

Species	ISSR primer combinations	Total number of ISSR bands	Total P_{ID}
Festuca ovina	RF04-09	43	3.20×10^{-7}
Koeleria macrantha	RF04-10	58	6.81×10^{-9}
Carex caryophyllea	RF04-06, RF05-01	68	2.53×10^{-11}
Succisa pratensis	RF04-06, RF04-11	75	6.19×10^{-13}
Leontodon hispidus	RF04-06	95	2.39×10^{-15}
Campanula rotundifolia	RF04-06	78	4.58×10^{-13}

Table 3. Sampling strategy for a survey of the survival and relative abundance of plant genotypes within 20 communities initially possessing either 4 or 16 genotypes of each component species. The numbers of samples of leaf tissue recovered within each replicate community using point quadrat sampling are indicated for each study species. ALL indicates that every visible living shoot was sampled within each community surveyed. The mean species abundance (measured as point-quadrat pin contacts) across all experimental communities in the year 2002 (R. E. Booth, unpubl. data) is given as an indication of the ease with which samples can be recovered by point quadrat sampling

Species	16-genotype	4-genotype	Total	Mean species abundance
Festuca ovina	50	30	800	52.7
Koeleria macrantha	50	30	800	66.5
Carex caryophyllea	50	30	800	64.7
Succisa pratensis	50	30	800	34.0
Leontodon hispidus	30	30	600	31.6
Campanula rotundifolia	ALL	ALL	471	11.1

to that of the plant communities being sampled (0.6 m × 0.6 m). A random sequence of numbers was used to determine a sequence of positions within the point-quadrat frame through which a metal pin was dropped vertically into the leaf canopy of each community. Leaf material was removed from a single individual of each target species that contacted this pin. This process was repeated until the full target sample size within a community had been collected for a given species.

As the aim of sampling was to estimate the relative abundance of genotypes within communities, we used a lower target sampling intensity (~30) to survey 4-genotype communities than that employed for surveying 16-genotype communities (~50; Table 3). It was necessary to reduce the sampling intensity for 16-genotype communities of *Leontodon hispidus* because of the lower abundance of this species in experimental communities. Every living shoot of *Campanula rotundifolia* was sampled, as this species achieved such a low abundance in experimental communities that point-quadrat sampling would have been inefficient (Table 3). Leaf-tissue sampling was carried out during autumn 2002, after the last species-level point quadrat analysis for that year. Samples of *C. rotundifolia* were collected in May 2003 as senescence of the shoots of *C. rotundifolia* prevented collection during autumn 2002. The relative abundance of a genotype in any 1-genotype community was considered to be 100%.

GENETIC IDENTIFICATION OF SURVEY SAMPLES

DNA was extracted from frozen leaf tissue samples of each species and genotyped, as described above. Each sample was identified by comparing its ISSR fingerprint to those generated from individuals of known identity in the clonal archive. Samples that could not be identified unambiguously were discounted from the analysis. A small subset of the genetic fingerprints was identified independently by a colleague, to verify objectivity and consistency of identification. Failure of DNA extraction, and rejection of samples that could not be identified, together accounted for a loss of between 1.4% (*C. caryophyllea*) and 3.2% (*K. macrantha*) of samples.

ANALYSIS OF GENETIC SURVEY DATA

The ISSR survey data yielded counted observations of the number of quadrat pins at which a genotype i of species j was detected in a given community k (C_{ijk}). These raw data were used to calculate the relative abundance (RA_{ijk}) for each of the i genotypes within species j for community k by division with N_{jk}, the number of successfully genotyped leaf specimens of species j in community k. An absolute measure of genotype abundance (A_{ijk}) was defined as $RA_{ijk} \times SA_{jk}$, where SA_{jk} is the species abundance (data from Booth 2001; Booth & Grime 2003) of species j in community k. Units of A_{ijk} are on the same scale as the species abundance data measured by Booth & Grime (2003). In fact, the measure is an estimate of the abundance scores that would have been presented by Booth & Grime (2003) had these experimenters also been able to identify species down to genotype.

The data from the genetic survey of communities were used to assess the survival rate (presence or absence) of genotypes originally planted in 4- and 16-genotype communities at the end of the 5-year experimental period. Species were compared to investigate whether they exhibited any differences in the loss of genotypes from genetically diverse communities across the experimental period.

We explored the genetic structure of the communities with particular reference to the 16-genotype experimental replicates because each of the latter initially contained all 87 of the unique experimental genotypes (see Results) and so comprised a truly replicated set with a presumed close resemblance to natural limestone grassland. We used a chi-squared goodness-of-fit test to test the null hypothesis that the genotypes within species performed equally well over the replicates of the 16-genotype communities. This test compared the total count of each genotype across the 16-genotype communities ($C_{ij16tot}$) with the number expected if each genotype achieved equal abundance. Before the analysis, the observed counts were weighted to take account of situations where some genotypes had been planted more frequently than others in the 16-genotype communities. A higher representation of certain genotypes

had occurred inadvertently because it was discovered (see Results) that some of the biotypes (presumed genotypes) sampled in the Cressbrookdale field site were represented by clones that had been sampled more than once. The weighting procedure involved division of the number of counts achieved by a genotype by the number of times it had originally been planted in the community.

We derived an abundance hierarchy of mean genotype abundance ($\hat{A}_{ij16}$) to describe the overall genetic structure of the 10 true replicates of the 16-genotype communities in their fifth year of growth. This hierarchy included the 87 unique genotypes of the six study species, and enabled the comparison of the hierarchical distribution of genotypes of different species within an ecological community. The hierarchy also allowed an assessment of the extent to which competitive relationships amongst species might have the potential for intransitivity at the genetic level. The mean abundance of each genotype, $\hat{A}_{ij}$, was weighted, as above, to take account of situations where certain genotypes had initially been planted more frequently than others in the 16-genotype communities.

We compared the abundance ($\hat{A}_{ij}$) of each genotype across sets of communities differing initially in genetic diversity, species by species, in order to assess whether the genotype abundance hierarchy in 16-genotype communities predicted genotype abundance in more genetically impoverished communities. The $\hat{A}_{ij}$ values were rescaled within each level of community genetic diversity to account for situations where certain genotypes had been planted more frequently than others due to genetic identity of biotypes. Correlations were used for each species to test whether the mean abundance of genotypes estimated in 16-genotype communities could predict the abundance of genotypes in 4- or 1-genotype communities. The deterministic model of community structure predicts a correlation of genotype abundance across communities differing in genetic diversity because, in communities lacking genetic diversity, species abundance is equal to genotype abundance. Under the contingent model, environmental interactions are expected to influence genotypes to a greater extent in 1-genotype communities, resulting in a breakdown of correlations across communities. Therefore, under the contingent model, any correlation in genotype abundance between the 16- and 1-genotype communities is expected to be weaker than the respective correlation between 16- and 4-genotype communities.

Results

GENETIC UNIQUENESS OF EXPERIMENTAL BIOTYPES

We concluded that biotypes whose genetic profiles matched those of other experimental individuals were clonally identical, given the extremely small probability (Table 2) that such individuals are in reality genetically different. Comparison of ISSR fingerprints revealed that most of the biotypes originally sampled from the field and then included in the experimental communities represented genetically unique individuals (genotypes). However, the experimental populations of *Carex caryophyllea* and *Campanula rotundifolia* contained only 10 and 13 (out of a possible maximum of 16) unique genotypes, respectively. Within the experimental population of the clonal sedge *Carex caryophyllea*, five of the biotypes originally sampled from Cressbrookdale belonged to a single (presumably spatially extensive) genetic clone. This genotype was morphologically large in size and appeared to have a high capacity for clonal growth (Fig. 1, upper genotype). All of the five 1-genotype populations containing this individual occurred in the upper 50% of species-abundance records (Booth & Grime 2003) for *Carex caryophyllea* occurring in 1-genotype communities. The discovery of genetic identity between some biotypes within the experimental population of *C. rotundifolia* was unexpected. However, this result is consistent with our observation that, in the non-reproductive phase, individuals of this species are able to spread clonally by sprawling along the soil (or litter) surface, rooting at the stem nodes (J. P. Grime and R. E. Booth, unpubl. data).

SURVIVAL AND RELATIVE PERFORMANCE OF GENOTYPES

In the experiment as a whole, the majority of genotypes had survived the 5 years between planting and the genetic census carried out here. None of the genotypes of any of the species selected for study in the communities had been completely lost from any of the three genetic diversity treatments. However, within some replicates of 4- and 16-genotype communities, some genetic individuals were not detected, and were considered to be 'extinct' in these communities. For *C. rotundifolia*, where communities were sampled exhaustively for every living individual, non-detection was a direct indication of the extinction of a genotype within a community. Within the 10 4-genotype communities (in each of which genotypes were initially represented four times), 96.8% of the genotypes originally planted were redetected during the sampling process (Fig. 2). However, in almost all of the 16-genotype communities (where genotypes were initially represented by only one individual), only a proportion of the genotypes originally planted was detected (Fig. 2). The canopy subordinate species *C. rotundifolia* lost the highest proportion of its genotypes from populations within communities, while the more abundant species generally retained a greater proportion of the genotypes that had represented their populations originally. Indeed, all of the genotypes of *S. pratensis* initially planted in 16-genotype communities were almost always re-detected during sampling. Rarefaction analysis using the accumulation curve of Holdridge *et al*. (1971), implemented in the program GIMLET (Valière 2002), confirmed that for

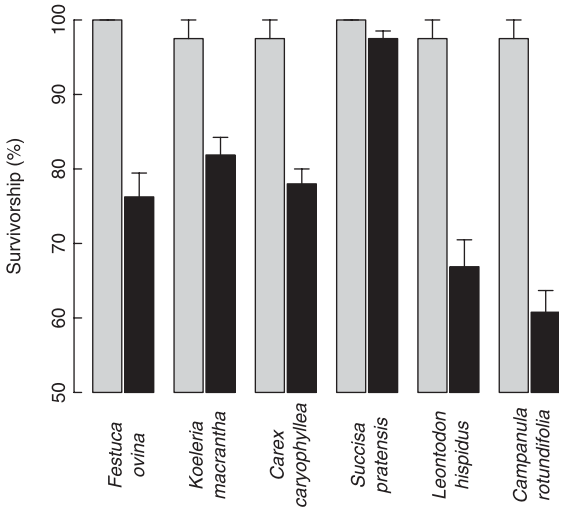

Fig. 2. Mean rate of survivorship of the genotypes of six species within communities initially containing 4 and 16 genotypes of each species. The mean values were calculated across 10 replicate communities for each level of community genetic diversity. Error bars are standard errors. Black bars = 4-genotype communities; grey bars = 16-genotype communities.

Table 4. Chi-square goodness-of-fit test of the null hypothesis that genotype count observations within genetically diverse plant communities are a product of equal growth and size of genotypes. Counts for each genotype were pooled across 10 replicate communities, each initially containing genetically diverse populations of each species

Species	Chi-squared	d.f.	*P*-value
Festuca ovina	138.4	15	< 0.001
Koeleria macrantha	102.2	15	< 0.001
Carex caryophyllea	117.6	9	< 0.001
Succisa pratensis	50.5	15	< 0.001
Leontodon hispidus	75.0	15	< 0.001
Campanula rotundifolia	123.2	12	< 0.001

F. ovina, *K. macrantha* and *Carex caryophyllea*, the non-detection of genotypes was due to the extinction of genotypes, rather than a result of insufficient sampling (data not shown). Rarefaction also indicated that the true number of genotypes of *L. hispidus* surviving in 16-genotype communities may have been higher than the estimates made via direct enumeration.

The total abundance of genotypes across the replicates of the genetically diverse 16-genotype communities (C_{ij}) deviated significantly from that expected assuming no differences in their final number, growth or size (Table 4). This result was consistent across all six species studied, and confirmed that genotypes maintained consistent differences in their performance across the replicates of genetically diverse communities.

GENETIC STRUCTURE OF THE MODEL COMMUNITIES

The hierarchy of mean abundance of genotypes across the replicates of the 16-genotype communities provided insight into the overall genetic structure of a mature pasture community (Fig. 3). It is noteworthy that the three most abundant genotypes in this hierarchy belonged to three different species (*F. ovina*, *K. macrantha* and *Carex caryophyllea*), each of which had a dominant status in the community. Genotypes of these species showed a very wide range in abundance, with the smallest achieving (on average) approximately 10% of the abundance of the largest. There was substantial overlap among the size hierarchies of the three canopy dominants and between these and the hierarchies of the remaining species (Fig. 3b), including some genotypes of subordinate members of the community (e.g. *C. rotundifolia*) that on average out-performed other genotypes of canopy dominants. The small standard errors reflect the consistency with which individual genotypes performed across the 10 replicates of the 16-genotype communities (Table 4).

GENOTYPE ABUNDANCE ACROSS DIVERSITY TREATMENTS

The deterministic model predicts that the fitness of each genotype should be correlated across communities differing in genetic diversity. The mean genotype abundance in 16-genotype communities ($\hat{A}_{ij}$) was correlated significantly and positively with genotype abundance in the other two genetic diversity treatments for all species and treatment comparisons except for *Carex rotundifolia* (both comparisons) and *K. macrantha* [16- vs. 1-genotype comparison (Fig. 4)]. An expectation of the contingent model is that any such correlations in genotype abundance should break down for genetically impoverished communities, as it is in these communities that the impact of genotype–environment interactions is expected to be greatest. The variation in genotype abundance in 1-genotype communities that could not be explained by genotype identity ranged from 51% to 97%. For three species (*K. macrantha*, *Carex caryophyllea* and *S. pratensis*), genotype abundance measured in 16-genotype communities explained a substantially greater proportion of variation in genotype abundance in 4-genotype communities than in 1-genotype communities (Fig. 4). This pattern was particularly pronounced in the clonal sedge *Carex caryophyllea*. For the remaining three species (*F. ovina*, *L. hispidus* and *C. rotundifolia*) the explanatory power of the two correlations was similar (Fig. 4).

Discussion

It has previously been shown that changes in the genetic composition of plant communities are sufficient to modify their species composition (Booth & Grime 2003). Here, we have started to explore the basis for these observations by using molecular markers to investigate the role of genetic variation in shaping patterns of species abundance and community composition in model grassland communities 5 years after they were synthesized.

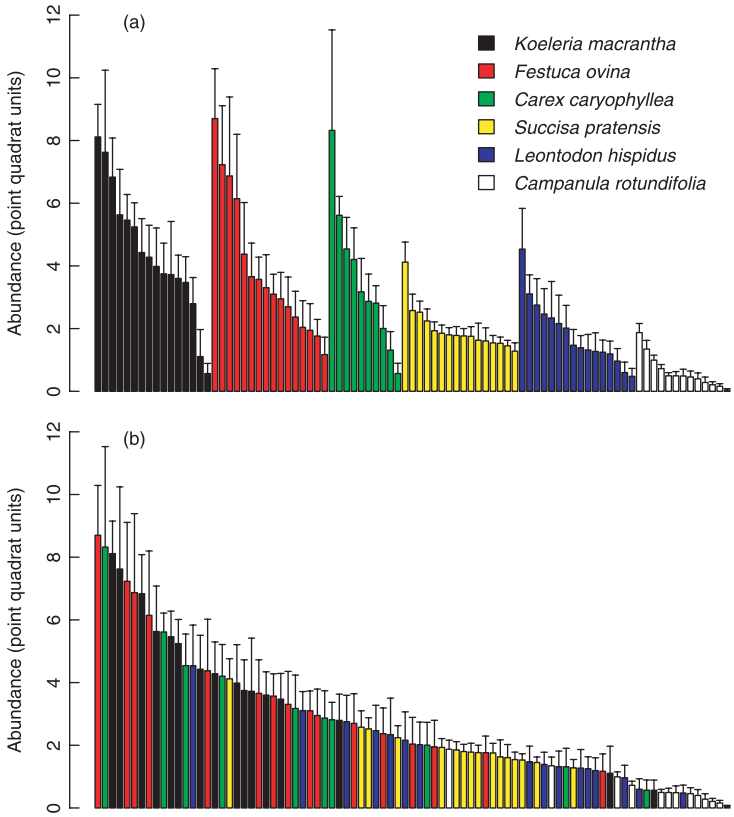

Fig. 3. Mean genotype abundance hierarchy for a genetically diverse plant community (initially containing 87 genotypes representing six coexisting plant species) after 5 years' growth. The mean abundance of each genotype, expressed in units of point quadrat contacts, was derived from a survey of 10 replicate communities, initially identical in species and genotypic composition. Genotype abundance has been weighted where necessary to take account of situations where individual genotypes were represented to a greater extent initially than other genotypes within the same communities. In (a) mean genotype abundance has been ranked within species, whilst in (b) the same data have been arranged by rank across all six species. Error bars are standard errors of the mean.

We found that, under constant community management (environmental) conditions, individual genotypes showed consistency in their performance or fitness, irrespective of the genetic diversity of the communities in which they occurred. The differences in performance between genotypes of the same and different species were, however, substantial. Hierarchies of genotype abundance were found to be correlated between communities differing in levels of genetic diversity for four canopy dominant species, such that the species abundance of populations in genetically impoverished communities could be predicted by their genotypic composition. These findings show that patterns of species abundance in plant communities can be determined, at least in part, by the identity and abundance of specific genotypes within those communities. They provide positive evidence for the involvement of the deterministic model (see Introduction) in structuring grassland communities. However, genotype identity accounted for only part of the variability in species abundance. Three species showed shifts in their genotype abundance hierarchy in genetically impoverished communities that may have been caused by genotype-specific environmental interactions, possibly through competition with the genotypes of other species.

APPLICABILITY OF MODELS PREDICTING COMMUNITY STRUCTURE

We proposed two models (the 'deterministic' and 'contingent' models) as routes by which genetic diversity may influence the species composition and structure of communities. Both models could be used to interpret variation in the structure of natural communities in experiments or in the field, given information on genotypic composition (e.g. from molecular marker studies). However, before this can be attempted more must be known about the genetic structure of natural communities. Do natural communities become genetically impoverished by losing genetic diversity at random, in a process akin to genetic drift, as in our experiment? It may instead be that communities are non-random collections of genotypes, just as they are often non-random assemblages of species (Drake 1990; Grime 1998). Patterns of selection may be all-important in determining the genotypic diversity and composition within communities (e.g. Prentice *et al.* 1995, 2000).

An additional feature of the deterministic model is that the fitness hierarchy of those genotypes that characterize it may depend upon a given set of environmental conditions (e.g. soil nutrient status) common to the

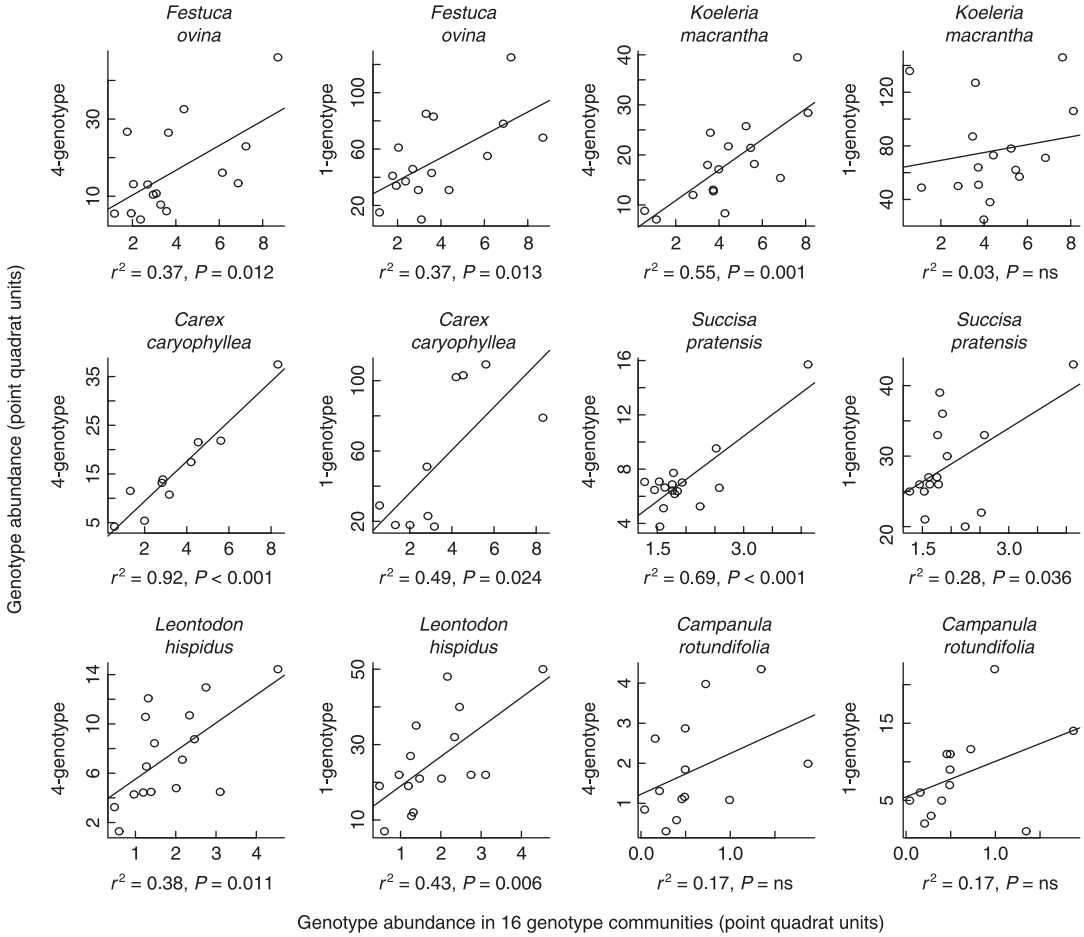

Fig. 4. Comparison of the mean abundance of plant genotypes between communities initially containing 16 and 4 genotypes, and 16 and 1 genotypes of each component species. Abundance is expressed in numbers of pin contacts derived from point-quadrat surveys of the plant communities. Abundance data have been rescaled where necessary to take account of variation in the numbers of each genotype planted in communities within each treatment.

community type under investigation. If these community-wide conditions change, the corresponding hierarchy may also change, although the deterministic mechanism should still be able to influence community composition.

Understanding the effect of genotype–environment interactions on community structure under the contingent model is likely to be particularly challenging given the myriad ways in which genotypes can interact with their environment in natural communities. Experimentation is likely to be key in determining the roles of competition (Aarssen 1989), the pathogenic environment (Thompson & Burdon 1992) or mycorrhizae (Streitwolf-Engel *et al*. 2001) on the structure of plant communities through their constituent plant genotypes.

GENOTYPE SURVIVAL AND ABUNDANCE WITHIN COMMUNITIES

Patterns of genotype survival among species indicated that the canopy subordinate species *C. rotundifolia* lost a greater proportion of its genotypes from genetically diverse communities than did other canopy-dominant species. This species may have suffered a reduction in genetic diversity because competition from more dominant species had impinged on growth and led to the mortality of some individuals representing its populations (McLellan *et al*. 1997). The genotypes of dominant species showed a large range in fitness within communities (Fig. 3), and this diversity may be essential to shield species such as *C. rotundifolia* from competitive exclusion in the longer term. This possibility illustrates the need, for conservation purposes, to consider the range of genotypes sustained in the populations of which grassland communities are composed. Populations possessing a greater variety of genotypes could in addition be more resistant (Hughes & Stachowicz 2004) or resilient (Reusch *et al*. 2005) to environmental challenges, buffering their communities against fluctuation in composition and species loss. It is not yet clear how such population-level resistance or resilience operates at the level of genotypes, although these patterns have been attributed to the effects of facilitative interactions or niche differentiation amongst genotypes (complementarity, Loreau & Hector 2001). However, such examples from species-poor seagrass communities sit uncomfortably with evidence from terrestrial plant communities where resistance and resilience may characterize different community types whose species possess

different suites of life histories and traits (Leps *et al.* 1982; MacGillivray *et al.* 1995; Grime *et al.* 2000). Furthermore, communities of herbaceous plants with ruderal life histories that can show resilience (Grime 2001) might also be typified by populations that have low levels of genetic diversity (Hamrick *et al.* 1992; Nybom 2004).

A further intriguing outcome was our finding that not all of the presumed genotypes initially planted within our communities represented genetically unique entities. For example, within the experimental population of *Carex caryophyllea*, only 10 of the 16 experimental biotypes sampled from Cressbrookdale were genetically unique. One genotype was represented five times in the experimental population of *Carex caryophyllea* (Fig. 1; upper genotype). This genotype possessed a robust phenotype with a high propensity for clonal growth and a large physical size (R. Whitlock, unpubl. data). In communities that contained only this genotype, populations of *Carex caryophyllea* achieved high levels of abundance relative to populations composed of other genotypes. This genotype is therefore implicated in contributing to the wide range in species-level abundance of *Carex caryophyllea* observed among replicates of the 1-genotype communities (Booth & Grime 2003). Given that it was encountered five times in random samples from an area of 10×10 m, it seems likely that this genotype represents a spatially extensive and possibly ancient clone (e.g. Steinger *et al.* 1996). These tentative conclusions are currently under investigation using trait-screening experiments and fieldwork. The discovery of a potentially widespread clone has particular relevance to the structure of unimproved grassland communities, where plant species are often long lived, stress tolerant and clonal (Grime 2001). In such communities, sexual reproduction and recruitment through seed is thought to be a relatively rare event (Putwain *et al.* 1968). Therefore, genotypes with a high capacity for clonal spread have the potential to have a substantial effect on the local structure and species composition of communities.

GENETIC COMPOSITION AND COMMUNITY STRUCTURE

Our measurements of the abundance of genotypes within model plant communities demonstrated that genotypes within (and among) species formed a distinct abundance hierarchy across genetically diverse plant communities that were initially identical in genetic and species composition. A particularly striking feature of this abundance hierarchy was that there was a wide variation in performance of genotypes within species. The genotype–abundance hierarchies of different species overlapped almost completely for the canopy-dominant species, whilst some genotypes of subordinate species were fitter on average than weak genotypes of the dominant species. Residual variation in the success of both more and less abundant genotypes across the replicates of the 16-genotype communities (data not shown) may reflect the modifying impact of competition on the fitness of genotypes in individual local neighbourhoods. This interpretation is congruent with the proposition (Aarssen 1983) that competitive relationships amongst species may be intransitive at the level of the genotype, a mechanism that could allow species coexistence within communities. The seemingly unfit genotypes we observed in our hierarchy could be genotypes that were destined for extinction in the natural grassland community from which they were originally sampled. Alternatively, they may be well adapted to particular microsites in the field that were not represented in our experiment. A further possibility is that these genotypes had an advantage over other individuals in terms of their reproductive output (seed set was prevented in this study), choosing to invest resources in more, or better provisioned, offspring rather than growing through clonal spread (Pannell & Barrett 1998). More detailed examination of the *Carex caryophyllea* genotypes studied here suggests a possible role for flowering in determining the size of clones in communities (unpubl. data).

We found that the abundance of specific genotypes was correlated across communities that differed initially in their genetic diversity. Furthermore, the abundance of species in genetically impoverished communities could in part be predicted by the genotypes that composed them (Fig. 4), suggesting that genotypic composition contributed to community structure, an effect consistent with the deterministic model. The constancy in community-level genotype behaviour observed here implies that, at the scale of our model communities, and in the absence of environmental heterogeneity, species abundance is in part a product of the traits and abundance of genetic individuals comprising each population.

We also observed that genotypic hierarchies were not always consistent across communities with contrasted levels of genetic diversity. For three species, the genotypic hierarchy of 16-genotype communities was a better predictor of the corresponding hierarchy in 4-genotype communities than the hierarchy observed in the 1-genotype communities (Fig. 4). Given, for these species, the lower explanatory power of genotype identity (3–49%) in predicting species abundance in genetically impoverished communities (Fig. 4), it seems possible that the composition of such communities could be mediated in part through the net effects of intraspecific competitive interactions. The shift in abundance hierarchy observed in the clonal sedge *Carex caryophyllea* was particularly pronounced. The successful growth and abundance of this species within communities may be contingent on rhizomatous growth, permitting movement into neighbourhoods containing unfit or compatible genotypes of other species (Turkington & Harper 1979). Other phenomena, such as mycorrhizal connections amongst genotypes (Streitwolf-Engel *et al.* 2001), differential attack by herbivores (Graham *et al.* 2001) or the impact of pathogenic attacks (Burdon & Thompson 1995) could also contribute to the fitness of genotypes and abundance

of species within communities. However, the identities of genotypes initially comprising different model communities were manipulated explicitly in our experimental design. This makes competitive (or facilitative) interactions amongst genotypes prime candidates for driving the shifts in genotypic abundance hierarchies that we observed within genetically impoverished communities.

The direct role of genotypic composition in determining species abundance has been overlooked by other studies that have focused on the outcome of competitive interactions between pairs of genotypes (Turkington & Harper 1979; Kelley & Clay 1987; Taylor & Aarssen 1990; Lüscher *et al*. 1992). However, a more important feature distinguishing our study from these previous studies is our focus on the effect of genetic diversity at the species abundance and community composition scales, rather than on the outcome of competition between pairs of genotypes (e.g. Taylor & Aarssen 1990). Our results indicate that genotypic composition may have a significant direct influence upon species abundance and allows some prediction of species behaviour at the community level. As discussed above, our results do not preclude the existence of strong interactions between pairs of individual plants within and among populations. In fact, a strongly deterministic effect of genotype, operating in the absence of genotype–environment interactions or sexual recruitment, could result in the eventual exclusion of weaker genotypes from populations, possibly threatening both genetic and species diversity. We therefore suggest that the consequences of genetic diversity for plant community structure may be contingent upon the spatial scale under scrutiny. At the neighbourhood scale, interactions between genotypes and a patchy environment may be relatively more important in determining the fitness of individuals (Turkington & Harper 1979; Taylor & Aarssen 1990), allowing genotypes that would on average perform poorly to reproduce in certain favourable neighbourhoods. At the community scale, species abundance and coexistence depends upon the sum performance of all individuals, including their interactions. We therefore predict that genotypic composition will assume an increasing importance as a determinant of species abundance and community composition at increasing spatial scales. Nonetheless, we expect the grassland community from which our genotypes were collected to show a much greater degree of environmental heterogeneity than that present in our relatively simplified model communities. This heterogeneity includes the opportunity for neighbourhood-level competitive interactions in the form of at least 30 other vascular plant species (Furness 1980; Taylor & Aarssen 1990), heterogeneity in nutrient conditions (from dung and urine patches), variability in soil depth and hydrology, and local shading from patches of hazel scrub (R. Whitlock, pers. obs.). Under these conditions, the effects of genotype–environment interactions on species abundance may be larger at both the neighbourhood and the community scale.

The observations recorded here have shown that genotypes within species can achieve widely differing fitness within biologically realistic model communities. Genotypes showed consistency in their performance at the community level, irrespective of the genetic background of the community in which they occurred. Therefore, the genetic composition of communities must, at least in part, make a direct contribution to their structure by determining the traits manifested by individuals within populations. Interactions between genotypes and their environment (possibly competitive interactions with neighbouring genotypes) seem to be partly responsible for the variance of species diversity in genetically impoverished communities. We suggest that, in unimproved calcareous grassland communities maintained under constant management conditions, local differences in community structure may arise as a result of trait diversity within species and the contribution that these traits make to species abundance at the community level. Environmental heterogeneity in the field, the effects of clonal growth and the outcome of competition amongst plants occupying local neighbourhoods all have the potential to modify the species composition of communities via their interactions with community genetic structure.

Acknowledgements

We thank A. S. Jump, K. Tanaka, H. C. Prentice and two anonymous referees for constructive comments on the manuscript. R.W. was supported by a Natural Environment Research Council studentship.

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Received 2 March 2007; accepted 21 May 2007
Handling Editor: Honor C. Prentice