Research

Fine-scale community and genetic structure are tightly linked in species-rich grasslands

Raj Whitlock^{1,*}, Mark C. Bilton², J. Phil Grime¹ and Terry Burke¹

¹*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

²*Department of Plant Ecology, University of Tübingen, 72076 Tübingen, Germany*

Recent evidence indicates that grassland community structure and species diversity are influenced by genetic variation within species. We review what is known regarding the impact of intraspecific diversity on grassland community structure, using an ancient limestone pasture as a focal example. Two genotype-dependent effects appear to modify community structure in this system. First, the abundance of individual constituent species can depend upon the combined influence of direct genetic effects stemming from individuals within the population. Second, the outcome of localized inter-specific interactions occurring within the community can depend on the genotypes of participating individuals (indicating indirect genetic effects). Only genotypic interactions are thought to be capable of allowing the long-term coexistence of both genotypes and species. We discuss the implications of these effects for the maintenance of diversity in grasslands. Next, we present new observations indicating that losses of genotypic diversity from each of two species can be predicted by the abundance of other coexisting species within experimental grassland communities. These results suggest genotype-specific responses to abundance in other coexisting species. We conclude that both direct and indirect genetic effects are likely to shape community structure and species coexistence in grasslands, implying tight linkage between fine-scale genetic and community structure.

Keywords: community genetics; community ecology; genetic diversity; species diversity; grassland; direct genetic effect

1. INTRODUCTION

There is increasing interest in the role played by intra-specific genetic diversity in mediating the structure and dynamics of communities and ecosystems, which has given rise to a field of enquiry called *community genetics* [1,2]. Initially, most researchers in this field focused on systems in which genetic diversity in one focal species (usually a dominant plant species) influences the structure of a community of other dependent species. Members of this dependent community can exploit the focal species for food, growth or as habitat, either directly or indirectly, and each may constitute a small quantity of community biomass relative to the focal species (e.g. [3–5]). Grasslands are another well-studied model system for community genetics, providing a slightly different perspective [6–11]. In these systems, the community under study is typically made up of coexisting plant species, each of which may be genetically diverse. In many older, species-rich grassland communities, a more equitable distribution of total community biomass is often observed between the most abundant species. Thus, genetic diversity across many component species may be driving or responding to community structure.

In 1997, Booth & Grime [10] created a unique experimental system that provided opportunities to investigate the community genetics of a species-rich grassland community. Using this resource, they showed that genetic diversity within the component populations of this community was able to modify plant community structure and species diversity. Our purposes in this paper are twofold. First, we synthesize and review recent progress in our understanding of the relationship between genotypic diversity and community structure in species-rich grasslands. Second, we present new data on the relationship between retention of genotypic diversity within populations and the abundance of other coexisting species within the community. Table 1 contains a guide to terminology and a summary of experiments, to which we refer in both sections of this paper.

2. COMMUNITY GENETICS OF SPECIES-RICH GRASSLANDS

(a) *Ecological context*

The majority of the species diversity present in the most species-rich grasslands can be observed at scales less than 1 m². In some of these systems, up to 32 species can be found in areas of 0.25 m² [18]. At still finer scales, it is common to find in excess of 10 species present, and often rooted within an area 10 × 10 cm (100 cm²; [19,20]). Part of the explanation for this diversity is likely to involve the cycles of periodic grazing that these grasslands experience.

* Author for correspondence (r.whitlock@sheffield.ac.uk).

One contribution of 13 to a Theme Issue ‘Community genetics: at the crossroads of ecology and evolutionary genetics’.

Table 1. Glossary of terminology and summary of key experiments referred to in the text.

term	explanation
(a) <i>glossary</i>	
direct genetic effect	phenotypic properties of an individual that stem from expression of that individual's own genes, specifically the additive genetic component [12,13]. In this study, we deal with clonal genotypes; thus we assume that a proportion of the phenotypic variation among genotypes has an additive genetic basis
$g \times e$ interaction	interactions in which different genotypes vary in their phenotypic responses to environmental variation
$g \times g$ interaction	interactions in which different genotypes vary in their phenotypic responses to the genotypic identity of other interacting individuals
genetic diversity	any of several measures of allelic diversity, richness or evenness
genotype	a genetically unique individual including all living material derived from this by vegetative or clonal reproduction or propagation
genotypic diversity	richness or evenness of distinct genotypes within a population
indirect genetic effect	phenotypic effect driven by the (additive) genetic component to phenotype in a second interacting individual. Although originally restricted in its usage to conspecific individuals, here we use the term <i>sensu lato</i> to include situations in which the interacting individuals can be from different species [12,13]
interaction neighbourhood	a spatial zone where neighbouring individuals interact with each other to influence each other's acquisition of resources, e.g. containing plants whose canopies overlap, shade or contact the canopy of a neighbouring individual
(b) <i>summary of key experiments</i>	
Booth and Grime communities/ experiment	experimental limestone grassland communities contained in 0.6 m lysimeter boxes in which genotypic diversity was varied (up to 16 genotypes per community) at constant initial species diversity (11 species; [10])
Fridley and Grime communities/ experiment	experimental limestone grassland communities in which both species (up to eight species) and genotypic diversity (up to eight genotypes) were manipulated in containers that contained heterogeneity in soil depth and type [14]
Fridley <i>et al.</i> pot experiment	simplified competition experiment in pots involving different genotypes of <i>C. caryophylla</i> and <i>K. macrantha</i> and a single genotype of <i>C. rotundifolia</i> . Pots were subjected to different nutrient regimes and defoliation treatments [15]
genotype archive	living library of plants originally collected from a 10 × 10 m plot of species-rich grassland at Cressbrookdale. The archive is propagated clonally, and forms the raw material for setting up experiments [10]
trait-screening experiments	any of three separate experiments in which genotypes of <i>C. caryophylla</i> , <i>F. ovina</i> and <i>K. macrantha</i> were grown individually under monoculture on nutrient-rich compost. Trait measurements were collected from clonal replicates of each genotype [16,17]

These limit competitive exclusion via shading and litter accumulation, and prevent the succession to woodland, which would otherwise occur under dereliction [21–24]. In addition, the low concentrations of major mineral nutrients (e.g. N, P, K) maintain diversity by reducing the vigour of potentially robust species capable of exerting competitive dominance over other species in the community [23–26]. The diversity of species of arbuscular mycorrhizal fungi (AMF) present within the rhizosphere can also contribute to plant species coexistence in grasslands [27,28]. Furthermore, different grassland plant species can support distinct communities of AMF [29]. This indicates that AMF might form part of the (biotic) niche of grassland species. It has been suggested that insufficient abiotic niche differentiation exists among limestone grassland species to support the diversity present in these communities [30]. However, a growing body of evidence points to the importance of soil depth, pH and soil hydrology as variables that allow some degree of niche separation and species coexistence within grasslands more generally [30–32].

If genetic diversity has an impact on grassland community structure and diversity, it must do so within the

specific context of the environmental filters defined by the factors listed above. These filters select for sets of species with particular sets of adaptations to the local environment, which determine the type and species composition of grassland community that develops [33,34]. Within each local environmental context, genetic diversity may then be important in defining increments in species diversity [35], or in dictating dynamics and responses to perturbation [36]. Specifically, genetic diversity may play a role in providing a range of phenotypes that could exploit distinct portions of niche space, or by providing a large-enough sample of phenotypes from which one or a few genotypes manage to establish and prosper in the event of ecosystem-scale environmental change. In other words, there may be effects of genetic variation *per se*, and of the presence of particular genetic variants within a sample of genotypes.

(b) *Effects of genetic diversity on community structure*

Booth & Grime [10] used natural species-rich limestone grassland occurring within Cressbrookdale National Nature Reserve, in Derbyshire, UK, as a model to study the effects of genetic diversity on

plant community structure. They carried out a long-term experiment in which the genotypic diversity of component populations of plant communities was manipulated against an initially constant background of species diversity (hereafter the Booth and Grime communities [10]). This, and other experiments described below, relied on a *genotype archive* consisting of 16 putative *genotypes* (genetically unique individuals) of each of 11 plant species collected as established individuals, using spatially random sampling from within a 10 × 10 m field plot in Cressbrookdale. The majority of individuals within the genotype archive were found to be genetically unique through subsequent DNA marker genotyping [37]. Genotypic diversity was manipulated by assembling model plant communities via random selections of clonally propagated genotypes of each of the 11 species from the genotype archive: either 16, 4 or 1 genotypes per species. All assembled communities contained the same 11 species. Weeding, and the prevention of seed production, ensured that the same set of planted genotypes was forced to interact over the course of the experiment (i.e. there was no sex to generate new recombinant genotypes). A key result of this experiment was that the rate of decline in species diversity over time (Shannon index) was least pronounced in the most genetically diverse communities. After 5 years of growth, the genetically diverse communities retained the greatest species diversity. This novel effect has since been verified in an independent experiment (the Fridley and Grime communities [14]). These experiments have raised considerable conceptual challenges regarding the mechanism through which the effects of genetic variation scale to the community level. This is because it is possible for the phenotype (traits) of individuals to be mediated by the expression of their own genes (via *direct genetic effects*; see glossary of terms in table 1), and by local interactions between individuals (involving *indirect genetic effects*). However, the community-level effects of genetic diversity are a product of the combined influence of both of these effects across all component individuals and *interaction neighbourhoods*. Thus, there exist differences in scale between the source of the genetic effects (individuals and interaction neighbourhoods) and their outcomes, which may be both at the individual or neighbourhood level, and the community level.

(c) *Direct genetic effects: genotypic composition, traits and species abundance*

The most parsimonious explanation for the results observed in the Booth and Grime communities is the action of a 'variance reduction effect' [38]. This effect operates via the random sampling of genotypes from a fixed pool of genotypes, such that replicates of the more diverse treatments are expected to be more similar in genotypic composition than the relatively more impoverished treatments. More specifically, the abundance of populations that are genetically impoverished is dictated disproportionately by direct genetic effects stemming from the particular genotypes that dominate those populations [37]. Depending on the genotypes involved, this mechanism

will lead to greater or lesser population abundance in genetically impoverished communities, relative to genetically diverse communities, with a concomitant change in species evenness (diversity). In order to determine whether this mechanism underpinned the greater levels of species diversity observed in genetically diverse communities, Whitlock *et al.* [37] tracked the performance of individual genotypes of six species in these communities directly, using molecular markers. This work revealed that mean genotype abundance in all but one of these species was correlated across communities, regardless of the differing levels of genetic diversity within these communities. This suggests that direct genetic effects were the most important for determining the effects of genetic diversity on community-level (cf. individual-level) structure observed in the Booth and Grime communities. *Genotype-by-environment* ($g \times e$) or *genotype-by-genotype* ($g \times g$) interactions (involving indirect genetic effects) appeared to play a lesser role in determining the effects of genetic diversity at the community scale [37]. It was suggested [15] that the relative weakness of $g \times e$ was due to the comparatively constant environment of the Booth and Grime communities, but subsequently a similar effect was observed in experimental communities that contained considerable environmental heterogeneity (the Fridley and Grime communities). For each of four species in which biomass could be measured at the individual level in these communities, there was a strong main effect of genotype on plant biomass [14]. For two of these species (*Koeleria macrantha* and *Succisa pratensis*), the hierarchy in genotype biomass was consistent between communities varying in levels of experimentally manipulated species diversity and genotypic diversity. Conversely, the genotype biomass of *Festuca ovina* and *Helictotrichon pratense* individuals showed strong interactions with these variables.

The role of direct genetic effects in mediating community structure in the Booth and Grime communities has been investigated using traits measured under genotypic monoculture, for three of the study species used in this experiment [16,17]. The sedge *Carex caryophyllea* showed a simple relationship between traits measured on individual genotypes grown in monoculture and their performance in genetically and species-diverse communities, with the exception of one outlier genotype (figure 1a; [17]). A multivariate trait summary (interpreted as a measure of plant size) predicted the performance of the genotypes of this species after 5 years growth in the model communities synthesized by Booth & Grime [10] (figure 1a). Genotypes that were large in size (negative trait score) under genotypic monoculture tended to achieve higher abundance in the Booth and Grime communities.

Furthermore, plant size observed in monoculture allowed prediction of the species abundance of *C. caryophyllea* populations with known initial genotypic composition in the Booth and Grime [10] communities (figure 1d). Monoculture trait screening has also been carried out on the populations of two other species (*F. ovina* and *K. macrantha*), using living material propagated from the genotype archive [16]. The situation for *K. macrantha* reflects that in

Figure 1. Traits measured in genotype monoculture predict genotype performance and species abundance in communities that possess both genetic and species diversity. Trait score relates to the score of a genotype on the 'size' principal component from principal components analysis of monoculture trait data [17]. More negative trait scores indicate greater plant size. Plots (a)–(c) show the correspondence between the trait score of each genotype and its performance in the Booth and Grime communities (16-genotype treatment). Each point in plots (d)–(f) refers to a community with unique genotypic composition in the Booth and Grime experiment [10]. A single randomly selected community replicate represented the 16-genotype communities as these possessed identical initial genotypic composition. Population trait score is the sum of trait scores of all genotypes composing a species' population that were included initially in that community. Species abundance is the pin-quadrat abundance observed in year 5 of the Booth and Grime communities. Regression lines are shown where the regression is significant at $p < 0.05$. The dashed regression line and the R^2 value in (a) omit the outlier visible at the top of this plot [17]. Plus symbols, 16-genotype; open triangles, 4-genotype; filled circles, 1-genotype.

C. caryophylla; monoculture size scores for individual *K. macrantha* genotypes predict both genotype performance and species abundance in the Booth and Grime communities (figure 1c,f). In contrast, genotype does not predict the performance of *F. ovina* individuals in the Booth and Grime communities (figure 1b), and there is no obvious relationship between traits and species abundance (figure 1e). This outcome mirrors observations from the Fridley and Grime communities, which suggest that the phenotypes of *F. ovina* individuals are sensitive to $g \times e$ and $g \times g$ interactions. Together, these observations indicate that the abundance of some species in grassland communities is dominated by direct genetic effects with more limited $g \times e$, while the abundance of other species is more strongly influenced by $g \times e$ and $g \times g$. A key challenge is to understand why species may vary in the importance of indirect genetic effects and whether we can predict which species they will be.

(d) Reconciling neighbourhood-scale $g \times g$ and community-level direct genetic effects

In the sections above, we have set out evidence for the existence of direct genetic effects that influence

community-level structure. Now, we move on to consider a body of evidence from a broader set of study systems, which has shown that the outcome of more localized competitive interactions between neighbouring plant individuals of different species can depend upon the genotypes of those individuals ($g \times g$ interactions; [7,8,11,39,40]). Evidence for fine-scale $g \times g$ competitive interactions and reversals in genotypic hierarchy also exists for species-rich grassland communities [14,15,37]. However, in some species, the strength of these local $g \times g$ effects appears to be relatively smaller than the direct genetic effects that are capable of influencing community-level structure even in the presence of environmental heterogeneity. For example, if $g \times g$ were sufficiently strong, then direct genetic effects on genotype performance or species abundance at the community level should not have been visible (or at least so prominent) in the Booth and Grime communities, or for *K. macrantha* and *S. pratensis*, in the Fridley and Grime communities.

The observation that the outcome of competition in interaction neighbourhoods can be genotype-specific led Aarssen [41,42] to propose the 'competitive

combining ability' hypothesis. This hypothesis states that interspecific interactions between different sets of genotypes at a local scale can lead to alternative outcomes of interspecific competition, with species *A* out-competing species *B* in one local collection of genotypes, but *B* out-competing *A* in another (i.e. an intransitive competitive hierarchy among genotypes). In other words, there is a genotype-by-genotype interaction for competitive ability and no single genotype performs best in all competitive interaction neighbourhoods. The relative weakness of $g \times g$ for some species in our experimental grassland communities seems to suggest the existence of generalist genotypes that are equally fit in all interaction neighbourhoods in the community, a situation that is at odds with the competitive combining ability hypothesis, and the maintenance of diversity. Why do natural populations of these species in the field not become dominated by similar generalist genotypes with a concomitant cost to species richness, as observed within our experimental communities? Below, we consider some possible explanations for this apparent paradox of diversity maintenance:

(1) Recurrent sex and recruitment in the field are sufficient to sustain genotypic diversity. A key difference between our experiments and the situation in the field is that in the former, seed production and subsequent recruitment were prevented. Simulation and modelling approaches have indicated that even low levels of recruitment are capable of sustaining a diversity of clones in populations that otherwise reproduce clonally [43,44]. In addition, many species in species-rich calcareous grasslands are long-lived, out-breeding and iteroparous, with overlapping generations. These characteristics are expected to lead to relatively higher effective population sizes [45], which in turn can retard the loss of genetic variation by drift. While attractive in its simplicity, this explanation finds fault in the fact that the genetic variation in our grassland populations is visible to selection (i.e. it is not neutral). For example, some genotypes in these populations have growth characteristics that predispose them to success under particular experimental conditions [10,15–17,37]. Under these conditions, it is not clear that genotypic diversity would be maintained, and genetic variation in the phenotype of persisting clones should be eroded to an optimum value.

(2) The existence of community-level direct genetic effects on species abundance does not preclude a role for selection in maintaining intraspecific diversity, via the localized occurrence of $g \times g$ or $g \times e$ interactions for fitness within interaction neighbourhoods. Under this explanation, the combined influence of direct genetic effects stemming from all individuals in the population contributes to the regulation of species abundance at the community level. Simultaneously, local indirect genetic effects and interactions ($g \times g$) or environmental interactions ($g \times e$) mediate the success of the less competitive genotypes in at least a proportion of the interaction neighbourhoods in the community. The maintenance of genetic diversity across heterogeneous environments is a subject that has received a great deal of attention in the literature

[46]. Both diversifying selection in space and across time are thought capable under certain conditions of maintaining stable genetic polymorphisms [47–50], although it is less clear whether this mode of selection can maintain quantitative genetic variation above the levels expected under mutation-selection balance [51–54]. If, as seems likely in grasslands, direct genetic effects involving genotype size or competitive ability do act to influence species abundance, we must ask what forces maintain other less competitive genotypes in those interaction neighbourhoods where they achieve fitness. It is possible that these latter trade off a lesser competitive ability through vegetative or clonal growth with a greater ability to reproduce sexually [16,17,55–59]. Spatial heterogeneity of soil depth, moisture, pH or nutrient status, or unpredictable (inter-annual) climatic perturbations such as drought are likely candidate forces of selection that could provide opportunities allowing this reproductive strategy to be successful [30–32,60]. A key problem with this general explanation is that we do not know to what extent direct genetic effects on species abundance and the maintenance of genetic variation through diversifying selection might be able to co-occur either within or distributed among species. What would the expected consequences of any such co-occurrence be for equilibrium levels of genetic variation, or community structure?

(3) Presumed direct genetic effects on species abundance are in fact phenotypic effects driven predominantly by non-additive components to the phenotype (including maternal and epigenetic effects), which mask underlying genetic responses to environmental heterogeneity. Under this argument, our putative direct genetic effects influencing species abundance in reality constitute a phenotypic correlation across interaction neighbourhoods arising predominantly from environmental or non-additive genetic contributions to the phenotype. One possibility is that this phenotypic correlation is a product of experimental clonal propagation of the shared natal history of each genotype, i.e. a persistent maternal effect [61–63] or an epigenetic effect. Natural populations of clonal plants often contain high proportions of unique genotypes [37,64]. Conversely, in our experiments, genets occurred as multiple disconnected ramets both within and among communities. The importance of this is that experimental designs based around extensive clonal propagation could produce phenotypic correlations that do not reflect the true underlying genetic response to environmental heterogeneity across interaction neighbourhoods [65–67]. These phenotypic correlations could mask the underlying genetic architecture (including negative genetic correlations) that result when a set of alleles with high fitness in one interaction neighbourhood are detrimental in another (e.g. [67]).

In order to understand the mechanisms through which genetic diversity influences community structure and species coexistence, future work will need to address several large gaps in our knowledge. First, we need to understand the relative importance of sexual and asexual reproduction in systems where

both these modes of reproduction are possible. This will allow us to understand the role of sex in maintaining diversity, and to appreciate to what extent community structure and dynamics are products of heritable components of phenotype. This may require a long-term research strategy for grassland systems, given that the species that inhabit species-rich grasslands are frequently slow growing and long-lived [23]. Second, we need to understand the spatial scales over which genotypes of different species are distributed and interact in the field, i.e. what is the scope for $g \times e$, $g \times g$ and $g \times g \times e$ for fitness? This information is relevant to the scales at which genetic and species diversity are maintained in the field, but will also tell us about the potential for individual genotypes to become locally dominant and drive changes in species abundance. In the next section of this paper, we extend our perspective on grassland community genetics to consider the degree to which individual populations of six species lose their genetic diversity over time as a function of the abundance of other coexisting species in the community.

3. INTERSPECIFIC INTERACTIONS BETWEEN SPECIES ABUNDANCE AND LOSS OF GENOTYPIC DIVERSITY

(a) *Material and methods*

(i) *Study system*

In 2002, the Booth and Grime communities were surveyed using molecular markers, to determine the survival and abundance of the remaining genotypes in each population of six species during the fifth year of the experiment [37]. The six study species were *F. ovina* L., *K. macrantha* (Ledeb.) Schult., *C. caryophylla* Latourr., *Leontodon hispidus* L., *S. pratensis* Moench and *Campanula rotundifolia* L. (nomenclature follows [68]). The sampling procedure involved recovery of tissue samples that were identified to individual genotypes via profiles of inter-simple sequence repeat (ISSR) PCR assays, from which genotype abundance could be determined [37]. This work resulted in the counts of each genotype still present in each 4- and 16-genotype community, for each of the six study species, 5 years after the communities were created. The sampling design and mean genotype survivorship data for each species are given in Whitlock [37]. The single-genotype communities lacked any intraspecific diversity, and are not considered further in this analysis.

(ii) *Data analyses*

Except where stated, all analyses were carried out using the R software for statistical computing [69]. We measured the level of genotypic diversity of each population of each study species within each 4- or 16-genotype community, using count observations of genetic individuals (genotypes) derived from the ISSR markers in the fifth year of the Booth and Grime experimental communities. We applied a measure of genotypic compositional evenness to each population in each community, defined as [70]:

$$\hat{H} = \frac{n}{n-1} \left[1 - \sum p_i^2 \right],$$

where n is the number of genetic individuals (genotypes) in a sample (experimental community), and p_i is the frequency of genotype i . The summation sign operates over all the genotypes in one population in one community. The measure of genotypic compositional evenness, $\hat{H}$, was expressed as a proportion of its known initial values at the onset of the experiment. Thus, the transformed values represent the proportion of initial diversity remaining 5 years after the communities were assembled.

We used a model-averaging approach [71] to investigate whether the loss of genotypic compositional evenness within individual populations was a function of the abundance of other coexisting species within the 4- and 16-genotype communities 5 years after they were originally assembled. When a number of different statistical models fit a dataset similarly well (or poorly), model averaging allows inference to be based on the group of models, avoiding over-reliance on a single best model. This is advantageous, since traditional step-wise regression approaches that identify a single best model can lead to biases in parameter estimation, inconsistent specification of the best model (depending on the model selection method used) and a proliferation of hypothesis testing that can increase the probability of type I errors [72]. The model used for this series of analyses was a generalized linear model (GLM) with quasi-binomial link function. There were six datasets we wished to investigate; the dependent variable in each was loss of genotypic evenness for one of the six species, a proportion between 0 and 1. Thus, we fit six sets of models, one for each of our study species. Treatment (4- or 16-genotype community) and pin-contact species abundance of our six study species were fitted as fixed effects, with the constraint that a single species could not contribute the dependent variable and one of the covariates within a single model. All models considered under the model-averaging procedure contained the treatment effect, in order to control for possible variation in loss of compositional evenness between treatments caused by the experimental design and sampling regime. No interactions between covariates were considered. Prior to applying the model-averaging procedure, we assessed the extent of collinearity among the species abundance covariates, using correlation analyses. Only one pair of species abundance variables among 15 pair-wise comparisons was significantly correlated (Spearman's $\rho = 0.64$; $p < 0.01$). We used functions within the package MuMIn in R to fit all possible models for each response variable and carry out the subsequent model-averaging analyses. The model sets for each of these analyses were ranked by quasi-AIC (QAIC), and Akaike weights for each model were calculated on the basis of QAIC. A 95% confidence set of models was determined for each analysis. Such a set has a 95 per cent probability of containing the best-approximating model to the true model [71]. Finally, the Akaike weights were used to carry out model averaging for each model parameter, and to determine the relative importance of each of the covariates (the probability that a given covariate, among all those considered, is in the best-approximating model to the true model).

Unconditional 95% confidence intervals were computed around the averaged model coefficients. We compared covariates within each of the six analyses based on their relative importance, and whether or not the confidence intervals about the respective model-averaged coefficients overlapped with zero. We took those covariates with high relative importance, and whose confidence interval did not bracket zero, to provide evidence in support of an association between the covariate (species abundance) and the dependent variable (loss of genotypic evenness).

One of the model-averaging analyses indicated that intraspecific diversity retention within *C. rotundifolia* populations was associated with the species abundance of coexisting *C. caryophylla* populations. In order to follow up and confirm this result, we re-analysed data from the Fridley *et al.* pot experiment [15] in which clonal replicates of a single genotype of *C. rotundifolia* had been grown in pots, each with one of three genotypes of *C. caryophylla* and one of three genotypes of *K. macrantha* from the genotype archive. The abundance of *C. caryophylla* populations within communities has been shown to be controlled by the physical size traits possessed by component genotypes within populations [17,37]. Our model-averaging GLM analysis on the Booth and Grime communities led us to expect that in the pot experiment, individuals of *C. rotundifolia* should have performed better when growing with *C. caryophylla* genotypes that were large in size. To ascertain whether this was the case, we compared the survival and biomass of *C. rotundifolia* individuals growing in the pot experiment with different individual genotypes of *C. caryophylla* whose traits and size had been determined previously [17].

(b) Results

We used GLMs and a model-averaging approach to compare the proportion of genotypic diversity retained in populations of each of six study species with the abundance of different coexisting canopy-dominant species. Genotypic diversity treatment was used as a fixed effect to control for systematic variation in diversity loss attributable to this variable. Averaged models for two of the six study species (*K. macrantha* and *C. rotundifolia*) indicated that, in each case, loss of intraspecific genotypic diversity was associated with the abundance of one other coexisting canopy-dominant species (table 2). For both species, the association between retained genotypic diversity and the abundance of the other coexisting species was positive, such that the greater abundance of a given coexisting species was associated with reduced loss (greater retention) of genotypes. Model-averaging analyses indicated that there was little support for associations between genotypic diversity loss and abundance of coexisting species for the other four study species. The 95% confidence intervals for coefficients of all species abundance covariates overlapped with zero for these four species (results not shown).

Genotypic diversity retention within populations of *C. rotundifolia* was associated with the abundance of *C. caryophylla* in the same community (table 2). In a separate experiment (the Fridley *et al.* pot

experiment), *C. rotundifolia* was grown in pots with each of three different genotypes of *C. caryophylla* and three genotypes of *K. macrantha* [15]. The performance of *C. rotundifolia* was determined by interactions between genotypic identity of the two other species and soil fertility level ($p < 0.05$) [15]. The genotypes of *C. caryophylla* used in this experiment varied in overall size (in the order $Cc04 < Cc13 < Cc09$; [17]). We found that the *C. rotundifolia* plants were more likely to survive when growing with *C. caryophylla* genotype Cc09, the largest genotype of *C. caryophylla*, and least likely to survive when growing with Cc04, the smallest *C. caryophylla* genotype used in this experiment (figure 2a). On average, surviving individuals of *C. rotundifolia* reached highest biomass when growing in pots with the large sedge genotype Cc09. (figure 2b). When all planted individuals of *C. rotundifolia* were taken into account, differences in *C. rotundifolia* biomass occurring between sedge competitor genotypes approached statistical significance ($p < 0.1$). These outcomes were in the direction expected from our previous analyses of losses of genotypic diversity from populations of *C. rotundifolia* in the Booth and Grime communities (table 2).

4. DISCUSSION

In the second part of this paper, we investigated the relationship between the retention of genotypic diversity in populations over time and the abundance of other coexisting species within model plant communities. Specifically, we used molecular profiles (ISSRs) to identify and count genotypes of six plant species, 5 years after they had been planted into experimental communities varying in initial genetic diversity (four or 16 genotypes per species).

Our results indicated that the level of genotypic diversity retained by populations of two species (*K. macrantha* and *C. rotundifolia*) was associated with the abundance of different canopy-dominant species coexisting in the Booth and Grime model communities. No such relationships were observed for the remaining four study species, and therefore, these effects are by no means universally present across the species within the Booth and Grime communities. Nevertheless, they provide some of the first evidence implicating genotype-specific interspecific interactions in driving the structure of plant communities that possess a realistic level of species richness and genetic diversity. We suggest that where these interactions occur, species abundance in the first ('interacting') species drives genotypic evenness in the second ('target') species. The interactions take the form of $g \times e$ effects if the abundance of the interacting canopy species is not influenced by its own genetic composition (genotype persistence in the target species varies with biotic environment). However, if species abundance in the interacting species has a genetic component (e.g. figure 1d,f), then $g \times g$ effects are implicated in driving these associations. It is important to recall that direct genetic effects explained species abundance imperfectly in all three of the species where this relationship has so far been

Table 2. Relationship between loss of genotypic diversity from experimental plant populations and the species abundance of other coexisting species in the community, using a model-averaging approach. Results for two analyses are shown (a) with diversity loss from populations of *K. macrantha* as the response variable and (b) with diversity loss from populations of *C. rotundifolia* as the response variable. The models listed in each analysis are a 95% confidence set identified on the basis of quasi-AIC (QAIC), and each includes a fixed effect for treatment (not shown). The models are ranked on the basis of QAIC. The structure of each model (single line of the table) can be identified via the presence of '1' where a particular species abundance covariate was included in that model. The species (contributing abundance covariates) are *C. caryophylla* (*C. car*), *C. rotundifolia* (*C. rot*), *F. ovina* (*F. ovi*), *L. hispidus* (*L. his*), *K. macrantha* (*K. mac*) and *S. pratensis* (*S. pra*). Δ_i and W_i are, respectively, the difference in QAIC between the QAIC best model and the model under consideration, and the Akaike weight (or model selection probability). Relative importance denotes the probability that a given variable, among all those considered, is in the model best approximating to the true model. The coefficient given for each variable is the model-averaged coefficient, and the confidence intervals are confidence intervals about these coefficients that are conditional not on any single model, but on the total confidence set of models that were considered.

variable	<i>L. his</i>	<i>C. car</i>	<i>C. rot</i>	<i>F. ovi</i>	<i>S. pra</i>	QAIC	Δ_i	W_i
(a) response = proportion loss of genetic diversity from <i>K. macrantha</i> populations								
QAIC best model	1					21.97	0	0.251
	1	1				23.42	1.46	0.121
	1		1			23.91	1.95	0.095
	1			1		23.96	1.99	0.093
	1				1	23.96	2.00	0.093
	1	1	1			25.33	3.36	0.047
	1	1		1		25.40	3.43	0.045
	1	1			1	25.41	3.44	0.045
	1		1		1	25.91	3.94	0.035
	1		1	1		25.91	3.94	0.035
	1				1	25.96	3.99	0.034
						26.90	4.94	0.021
	1	1	1	1		27.31	5.34	0.017
	1	1	1		1	27.31	5.34	0.017
	1	1		1	1	27.40	5.43	0.017
	1		1	1	1	27.91	5.94	0.013
			1			28.36	6.40	0.010
		1				28.41	6.44	0.010
relative importance	0.96	0.32	0.27	0.25	0.25			
coefficient	0.0337	-0.0022	-0.0016	0.0002	0.0003			
lower CI	0.0042	-0.0116	-0.0188	-0.0034	-0.0102			
upper CI	0.0632	0.0072	0.0156	0.0037	0.0108			
variable	<i>C. car</i>	<i>L. his</i>	<i>K. mac</i>	<i>F. ovi</i>	<i>S. pra</i>	QAIC	Δ_i	W_i
(b) response = proportion loss of genetic diversity from <i>C. rotundifolia</i> populations								
QAIC best model	1					24.51	0	0.194
	1		1			25.44	0.93	0.122
	1	1				25.66	1.16	0.109
	1			1		26.09	1.59	0.088
	1				1	26.50	1.99	0.072
	1	1		1		26.71	2.21	0.064
	1	1	1			26.88	2.37	0.059
	1		1	1		27.27	2.76	0.049
	1		1		1	27.37	2.86	0.046
	1	1			1	27.65	3.14	0.040
	1			1	1	27.85	3.35	0.036
	1	1		1	1	28.11	3.61	0.032
	1	1	1	1		28.32	3.81	0.029
	1		1	1	1	28.80	4.29	0.023
	1	1			1	28.84	4.33	0.022
	1	1	1	1	1	29.53	5.02	0.016
relative importance	1.00	0.37	0.37	0.34	0.29			
coefficient	0.0213	0.0046	-0.0025	-0.0016	0.0019			
lower CI	0.0051	-0.0124	-0.0118	-0.0082	-0.0140			
upper CI	0.0374	0.0216	0.0069	0.0051	0.0177			

investigated (*C. caryophylla*, *F. ovina* and *K. macrantha*; figure 1). In addition, direct genetic effects appeared to be weakened against a background of extreme genetic impoverishment (communities with one genotype per component species; [37]). Thus, we

suggest that both direct genetic effects and genotypic interactions involving the environment and other coexisting genotypes (indirect genetic effects) occur together in natural grassland communities (§2d, explanation (2)). For example, the grass *K. macrantha*

Figure 2. Performance of individuals of *C. rotundifolia* when grown in competition with three different genotypes of the sedge *C. caryophyllea*. (a) Percentage survival of individuals of *C. rotundifolia* on a log-odds scale (logit of 0 = 50% on the probability scale) and (b) biomass of surviving individuals of *C. rotundifolia*. Data are from the clipped, unfertilized treatment of the pot experiment conducted by Fridley *et al.* [15]. Error bars are standard errors of the mean.

showed evidence of both direct genetic effects influencing its own species abundance (figure 1) and a genotypic response to the abundance of a different species in the community, *L. hispidus* (table 2).

The direction of the interspecific associations that we observed between intraspecific diversity loss and species abundance was surprising. For both of the pairs of species, there was a positive relationship between retention of intraspecific diversity and abundance of the coexisting species. This maintenance of variation need not be a sign of any form of mutualistic interaction; rather it may arise because the interacting species, when abundant, is able to restrict the growth of more competitively dominant genotypes of the target species that would otherwise reduce the evenness (genetic diversity) of their own population.

Since the relationship between retention of genotypic diversity in *C. rotundifolia* and population abundance of *C. caryophyllea* in the Booth and Grime communities was positive, we predicted that individuals of *C. rotundifolia* should perform better when growing with more vigorous or abundant genotypes or populations of *C. caryophyllea*. This prediction was verified in a qualitative sense in a separate simplified pot experiment ([15]; figure 2), supporting the association observed in the more complex Booth and Grime communities. On average, individuals of *C. rotundifolia* showed greatest survival and subsequent biomass production when growing with Cc09, the largest clone of *C. caryophyllea* present in the experimental population of this species. However, it must be stressed that full validation of our suspected species abundance–genotypic diversity associations awaits trials that encompass a greater population of target species genotypes (*C. rotundifolia* in this example). In the meantime, we suggest that one explanation for the results observed in the simplified pot experiment (figure 2) is that certain genotypes

of *C. caryophyllea* exerted a suppressive effect on *K. macrantha* (the third species in the pot experiment) that partially released *C. rotundifolia* from competition with *K. macrantha* (i.e. the biotic environment for *C. rotundifolia* was determined by a $g \times g$ interaction between *C. caryophyllea* and *K. macrantha*). We would not expect this effect to be mediated solely by the influence of the size of *C. caryophyllea* individuals on their competitive ability [73,74], because this does not explain the apparent relative benefit experienced by *C. rotundifolia* when growing alongside Cc09, the largest genotype of *C. caryophyllea* [75]. However, it is also possible that Cc09's guerrilla growth strategy permits a more open canopy structure whose gaps can be exploited by the relatively small and mobile *C. rotundifolia*, but not by the more sessile *K. macrantha* [76]. We have shown (figure 1; [17]) that species abundance in *C. caryophyllea* has a genotypic component. Consequently, if verified, the interspecific relationship between species abundance in *C. caryophyllea* and the retention of genotypic diversity in *C. rotundifolia* is expected to have a basis in the traits possessed by genotypes of *C. caryophyllea* (i.e. a classic $g \times g$ interaction, acting across the interacting species).

Such genetically based interactions between species might have implications for the maintenance of diversity within grassland communities. Fixation of high-fitness genotypes within local subpopulations of particular canopy-dominant species, by competitive, environmental or other means, will drive changes in their abundance via direct genetic effects (figure 1; cf. [8,41,42]). This will result in a local modification of grassland canopy structure that can act as a refugium, facilitating the intraspecific diversity and abundance of certain dependent species (table 2). At broader spatial scales, cycles of species turnover within and among interaction neighbourhoods could then act to enhance the coexistence of both species and genotypes within component populations.

In this paper, we have synthesized existing evidence and provided new data to review and appraise the mechanisms through which genetic diversity regulates the structure of species-rich grassland communities. In our study system, it is becoming clear that interactions including interspecific $g \times g$ play their part in determining local genetic and community structure [14,15,37]. These results are consistent with community genetics results from other systems (e.g. [4,7,8,77–79]). However, our unique experimental manipulations involving genotypic diversity in multiple coexisting species have exposed novel direct genetic effects that influence species abundance, and potential feedbacks between these effects and genotypic composition in other species in the community. These experimental manipulations are not possible in all community genetics study systems. However, we hope that where possible, others will carry them out, in order to understand whether direct genetic effects influencing species abundance or other population attributes are common. Taken together, our evidence establishes a strong basis for concluding that grassland community structure is regulated in part by $g \times g$ interactions between coexisting species, and in part through direct genetic effects occurring within species that can

influence their abundance. In other words, both the genetics of individual species and the genetics of their competitor species act to determine the influence of genetic diversity on community structure. Our results indicate that at fine spatial scales, community structure and genetic structure are bound closely, and that the genetic consequences of interactions within the community may play out over a relatively short time frame: less than 5 years. However, much remains to be discovered regarding the role played by genetic diversity, and the propagation of this diversity through sex, in shaping grassland community structure. A key unknown is why direct genetic effects on species abundance and indirect genetic effects among species appear to be restricted to particular species within the community, and whether we can predict which species will exhibit these effects. It will also be important to understand the quantitative genetic basis of the wide diversity in phenotype that can be found in some grassland populations (e.g. [17]), in order to understand how genetic diversity is maintained in natural communities, and to allow better prediction of the responses of communities to periods of selection imposed by perturbations such as climate change.

This work was supported by the Natural Environment Research Council and the Macaulay Development Trust. We thank J. D. Fridley for allowing us access to his data, and R. F. Preziosi, J. K. Rowntree, D. M. Shuker, D. Johnson and two anonymous referees for their thoughtful comments on earlier versions of this manuscript.

REFERENCES

- Antonovics, J. 1992 Toward community genetics. In *Plant resistance to herbivores and pathogens* (eds R. S. Fritz & E. L. Simms), pp. 426–449. Chicago, IL: University of Chicago Press.
- Whitham, T. G. *et al.* 2003 Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* **84**, 559–573. (doi:10.1890/0012-9658(2003)084[0559:CAEGAC]2.0.CO;2)
- Whitham, T. G. *et al.* 2006 A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* **7**, 510–523. (doi:10.1038/nrg1877)
- Johnson, M. T. J., Lajeunesse, M. J. & Agrawal, A. A. 2006 Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.* **9**, 24–34. (doi:10.1111/j.1461-0248.2005.00833.x)
- Iason, G. R., Lennon, J. J., Pakeman, R. J., Thoss, V., Beaton, J. K., Sim, D. A. & Elston, D. A. 2005 Does chemical composition of individual Scots pine trees determine the biodiversity of their associated ground vegetation? *Ecol. Lett.* **8**, 364–369. (doi:10.1111/j.1461-0248.2005.00732.x)
- Aarssen, L. W. & Turkington, R. 1985 Vegetation dynamics and neighbour associations in pasture community evolution. *J. Ecol.* **73**, 585–603. (doi:10.2307/2260496)
- Turkington, R. & Harper, J. L. 1979 The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. *J. Ecol.* **67**, 245–254. (doi:10.2307/2259348)
- Taylor, D. R. & Aarssen, L. W. 1990 Complex competitive relationships among genotypes of three perennial grasses—implications for species coexistence. *Am. Nat.* **136**, 305–327. (doi:10.1086/285100)
- Odat, N., Jetschke, G. & Hellwig, F. H. 2004 Genetic diversity of *Ranunculus acris* L. (Ranunculaceae) populations inferred in relation to species diversity and habitat type in grassland communities. *Mol. Ecol.* **13**, 1251–1257. (doi:10.1111/j.1365-294X.2004.02115.x)
- Booth, R. E. & Grime, J. P. 2003 Effects of genetic impoverishment on plant community diversity. *J. Ecol.* **91**, 721–730. (doi:10.1046/j.1365-2745.2003.00804.x)
- Kelley, S. E. & Clay, K. 1987 Interspecific competitive interactions and the maintenance of genotypic variation within two perennial grasses. *Evolution* **41**, 92–103. (doi:10.2307/2408975)
- Moore, A. J., Brodie III, E. D. & Wolf, J. D. 1997 Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution* **51**, 1352–1362. (doi:10.2307/2411187)
- Wolf, J. B., Brodie III, E. D., Cheverud, J. M., Moore, A. J. & Wade, M. J. 1998 Evolutionary consequences of indirect genetic effects. *Trends Ecol. Evol.* **13**, 64–69. (doi:10.1016/S0169-5347(97)01233-0)
- Fridley, J. D. & Grime, J. P. 2010 Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology* **91**, 2272–2283. (doi:10.1890/09-1240)
- Fridley, J. D., Grime, J. P. & Bilton, M. 2007 Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *J. Ecol.* **95**, 908–915. (doi:10.1111/j.1365-2745.2007.01256.x)
- Bilton, M. C., Whitlock, R., Grime, J. P., Pakeman, R. & Marion, G. 2010 Intraspecific trait variation in grassland plant species reveals trade-offs and ecological strategy variation that underpins performance in ecological communities. *Botany* **88**, 939–952. (doi:10.1139/B10-065)
- Whitlock, R., Grime, J. P. & Burke, T. 2010 Genetic variation in plant morphology contributes to the species-level structure of grassland communities. *Ecology* **91**, 1344–1354. (doi:10.1890/08-2098.1)
- Al-Mufti, M. M., Sydes, C. L., Furness, S. B., Grime, J. P. & Band, S. R. 1977 A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.* **65**, 759–791. (doi:10.2307/2259378)
- Sykes, M. T., van der Maarel, E., Peet, R. K. & Willems, J. H. 1994 High species mobility in species-rich plant communities: an intercontinental comparison. *Folia Geobot. Phytotaxon.* **29**, 439–448. (doi:10.1007/BF02883142)
- van der Maarel, E. & Sykes, M. T. 1993 Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *J. Veg. Sci.* **4**, 179–188. (doi:10.2307/3236103)
- Watt, A. S. 1957 The effect of excluding rabbits from Grassland B (Mesobrometum) in Breckland. *J. Ecol.* **45**, 861–878. (doi:10.2307/2256961)
- Tansley, A. G. & Adamson, R. S. 1925 Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire–Sussex border. *J. Ecol.* **13**, 177–223. (doi:10.2307/2255283)
- Grime, J. P. 2001 *Plant strategies, vegetation processes and ecosystem properties*, 2nd edn. Chichester, UK: John Wiley & Sons.
- Grime, J. P. 1973 Competitive exclusion in herbaceous vegetation. *Nature* **242**, 344–347. (doi:10.1038/242344a0)
- Willis, A. J. 1963 Branton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *J. Ecol.* **51**, 353–374. (doi:10.2307/2257690)
- Milton, W. E. J. 1940 The effect of manuring, grazing and cutting on the yield, botanical and chemical composition of natural hill pastures. I. Yield and botanical section. *J. Ecol.* **28**, 326–356. (doi:10.2307/2256233)

- 27 van der Heijden, M. G. A., Boller, T., Wiemken, A. & Sanders, I. R. 1998 Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology* **79**, 2082–2091. (doi:10.1890/0012-9658(1998)079[2082:DAMFSA]2.0.CO;2)
- 28 O'Connor, P. J., Smith, S. E. & Smith, F. A. 2002 Arbuscular mycorrhizas influence plant diversity and community structure in a semi-arid herbland. *New Phytol.* **154**, 209–218. (doi:10.1046/j.1469-8137.2002.00364.x)
- 29 Vandenkoornhuyse, P., Ridgway, K. P., Watson, I. J., Fitter, A. H. & Young, J. P. W. 2003 Co-existing grass species have distinctive arbuscular mycorrhizal communities. *Mol. Ecol.* **12**, 3085–3095. (doi:10.1046/j.1365-294X.2003.01967.x)
- 30 Mahdi, A., Law, R. & Willis, A. J. 1989 Large niche overlaps among coexisting plant species in a limestone grassland community. *J. Ecol.* **77**, 386–400. (doi:10.2307/2260757)
- 31 Silvertown, J., Dodd, M. E., Gowing, D. J. G. & Mountford, J. O. 1999 Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* **400**, 61–63. (doi:10.1038/21877)
- 32 Buckland, S. M., Grime, J. P., Hodgson, J. G. & Thompson, K. 1997 A comparison of plant responses to the extreme drought of 1995 in northern England. *J. Ecol.* **85**, 875–882. (doi:10.2307/2960608)
- 33 Wilson, J. B. 1999 Assembly rules in plant communities. In *Ecological assembly rules* (eds E. Weiher & P. A. Keddy), pp. 130–164. Cambridge, UK: Cambridge University Press.
- 34 Keddy, P. A. 1992 Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* **3**, 157–164. (doi:10.2307/3235676)
- 35 Vellend, M. 2006 The consequences of genetic diversity in competitive communities. *Ecology* **87**, 304–311. (doi:10.1890/05-0173)
- 36 Reusch, T. B. H., Ehlers, A., Hammerli, A. & Worm, B. 2005 Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl Acad. Sci. USA* **102**, 2826–2831. (doi:10.1073/pnas.050008102)
- 37 Whitlock, R., Grime, J. P., Booth, R. E. & Burke, T. 2007 The role of genotypic diversity in determining grassland community structure under constant environmental conditions. *J. Ecol.* **95**, 895–907. (doi:10.1111/j.1365-2745.2007.01275.x)
- 38 Huston, M. A. 1997 Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460. (doi:10.1007/s004420050180)
- 39 Lankau, R. A. & Strauss, S. Y. 2007 Mutual feedbacks maintain both genetic and species diversity in a plant community. *Science* **317**, 1561–1563. (doi:10.1126/science.1147455)
- 40 Vavrek, M. C. 1998 Within-population genetic diversity of *Taraxacum officinale* (Asteraceae): differential genotype response and effect on interspecific competition. *Am. J. Bot.* **85**, 947–954. (doi:10.2307/2446361)
- 41 Aarssen, L. W. 1989 Competitive ability and species coexistence: a 'plant's eye' view. *Oikos* **56**, 386–401. (doi:10.2307/3565625)
- 42 Aarssen, L. W. 1983 Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *Am. Nat.* **122**, 707–731. (doi:10.1086/284167)
- 43 Watkinson, A. R. & Powell, J. C. 1993 Seedling recruitment and the maintenance of clonal diversity in plant populations—a computer simulation of *Ranunculus repens*. *J. Ecol.* **81**, 707–717. (doi:10.2307/2261668)
- 44 Bengtsson, B. O. 2003 Genetic variation in organisms with sexual and asexual reproduction. *J. Evol. Biol.* **16**, 189–199. (doi:10.1046/j.1420-9101.2003.00523.x)
- 45 Nunney, L. 1993 The influence of mating system and overlapping generations on effective population size. *Evolution* **47**, 1329–1341. (doi:10.2307/2410151)
- 46 Hedrick, P. W. 2006 Genetic polymorphism in heterogeneous environments: the age of genomics. *Annu. Rev. Ecol. Syst.* **37**, 67–93. (doi:10.1146/annurev.ecolsys.37.091305.110132)
- 47 Christiansen, F. B. 1974 Sufficient conditions for a protected polymorphism in a subdivided population. *Am. Nat.* **108**, 157–166. (doi:10.1086/282896)
- 48 Hedrick, P. W. 1990 Genotype-specific habitat selection: a new model and its application. *Heredity* **65**, 145–149. (doi:10.1038/hdy.1990.81)
- 49 Ellner, S. & Hairston, N. G. 1994 Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *Am. Nat.* **143**, 403–417. (doi:10.1086/285610)
- 50 Hedrick, P. W. 1995 Genetic polymorphism in a temporally varying environment: effects of delayed germination or diapause. *Heredity* **75**, 164–170. (doi:10.1038/hdy.1995.119)
- 51 Gillespie, J. H. & Turelli, M. 1989 Genotype–environment interactions and the maintenance of polygenic variation. *Genetics* **121**, 129–138.
- 52 Byers, D. L. 2005 Evolution in heterogeneous environments and the potential of maintenance of genetic variation in traits of adaptive significance. *Genetica* **123**, 107–124. (doi:10.1007/s10709-003-2721-5)
- 53 Via, S. & Lande, R. 1987 Evolution of genetic variability in a spatially heterogeneous environment: effects of genotype–environment interaction. *Genet. Res.* **49**, 147–156. (doi:10.1017/S001667230002694X)
- 54 Turelli, M. & Barton, N. H. 2004 Polygenic variation maintained by balancing selection: pleiotropy, sex-dependent allelic effects and G × E interactions. *Genetics* **166**, 1053–1079. (doi:10.1534/genetics.166.2.1053)
- 55 Stark, L. R., Brinda, J. C. & McLetchie, D. N. 2009 An experimental demonstration of the cost of sex and a potential resource limitation on reproduction in the moss *Pterygoneurum* (Pottiaceae). *Am. J. Bot.* **96**, 1712–1721. (doi:10.3732/ajb.0900084)
- 56 Piquot, Y., Petit, D., Valero, M., Cuguen, J., De Laguerie, P. & Vernet, P. 1998 Variation in sexual and asexual reproduction among young and old populations of the perennial macrophyte *Sparganium erectum*. *Oikos* **82**, 139–148. (doi:10.2307/3546924)
- 57 Sohn, J. J. & Policansky, D. 1977 The costs of reproduction in the May apple *Podophyllum peltatum* (Berberidaceae). *Ecology* **58**, 1366–1374. (doi:10.2307/1935088)
- 58 Silvertown, J., Franco, M., Pisanty, I. & Mendoza, A. 1993 Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* **81**, 465–476. (doi:10.2307/2261525)
- 59 Sutherland, S. & Vickery, R. K. 1988 Trade-offs between sexual and asexual reproduction in the genus *Mimulus*. *Oecologia* **76**, 330–335. (doi:10.1007/BF00377025)
- 60 Grime, J. P. & Curtis, A. V. 1976 The interaction of drought and mineral nutrient stress in calcareous grassland. *J. Ecol.* **64**, 975–988. (doi:10.2307/2258819)
- 61 Schwaegerle, K. E., McIntyre, H. & Swingle, C. 2000 Quantitative genetics and the persistence of environmental effects in clonally propagated organisms. *Evolution* **54**, 452–461.
- 62 Evans, R. C. & Turkington, R. 1988 Maintenance of morphological variation in a biotically patchy

- environment. *New Phytol.* **109**, 369–376. (doi:10.1111/j.1469-8137.1988.tb04207.x)
- 63 Roach, D. A. & Wulff, R. 1987 Maternal effects in plants. *Annu. Rev. Ecol. Syst.* **18**, 209–235. (doi:10.1146/annurev.es.18.110187.001233)
 - 64 Ellstrand, N. C. & Roose, M. L. 1987 Patterns of genotypic diversity in clonal plant populations. *Am. J. Bot.* **74**, 123–131. (doi:10.2307/2444338)
 - 65 Hadfield, J. D., Nutall, A., Osorio, D. & Owens, I. P. F. 2007 Testing the phenotypic gambit: phenotypic, genetic and environmental correlations of colour. *J. Evol. Biol.* **20**, 549–557. (doi:10.1111/j.1420-9101.2006.01262.x)
 - 66 Mitchell, R. J. & Shaw, R. G. 1993 Heritability of floral traits for the wild flower *Penstemon centranthifolius* (Scrophulariaceae): clones and crosses. *Heredity* **71**, 185–192. (doi:10.1038/hdy.1993.123)
 - 67 Shaw, R. G., Platenkamp, G. A. J., Shaw, F. H. & Podolsky, R. H. 1995 Quantitative genetics of response to competitors in *Nemophila menziesii*: a field experiment. *Genetics* **139**, 397–406.
 - 68 Stace, C. 1997 *New flora of the British Isles*, 2nd edn. Cambridge, UK: Cambridge University Press.
 - 69 R Development Core Team. 2008 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
 - 70 Nei, M. 1987 *Molecular evolutionary genetics*. New York, NY: Columbia University Press.
 - 71 Burnham, K. P. & Anderson, D. R. 2002 *Model selection and multimodel inference*. New York, NY: Springer.
 - 72 Whittingham, M. J., Stephens, P. A., Bradbury, R. B. & Freckleton, R. P. 2006 Why do we still use stepwise modelling in ecology and behaviour? *J. Anim. Ecol.* **75**, 1182–1189. (doi:10.1111/j.1365-2656.2006.01141.x)
 - 73 Gaudet, C. L. & Keddy, P. A. 1988 A comparative approach to predicting competitive ability from plant traits. *Nature* **334**, 242–243. (doi:10.1038/334242a0)
 - 74 Goldberg, D. E. 1987 Neighborhood competition in an oldfield plant community. *Ecology* **68**, 1211–1223. (doi:10.2307/1939205)
 - 75 Silvertown, J. & Dale, P. 1991 Competitive hierarchies and the structure of herbaceous plant communities. *Oikos* **61**, 441–444. (doi:10.2307/3545253)
 - 76 Campbell, B. D., Grime, J. P. & Mackey, J. M. L. 1991 A trade-off between scale and precision in resource foraging. *Oecologia* **87**, 532–538. (doi:10.1007/BF00320417)
 - 77 Zytynska, S. E., Fleming, S., Tetard-Jones, C., Kertesz, M. A. & Preziosi, R. F. 2010 Community genetic interactions mediate indirect ecological effects between a parasitoid wasp and rhizobacteria. *Ecology* **91**, 1563–1568. (doi:10.1890/09-2070.1)
 - 78 Tetard-Jones, C. 2007 Genotype-by-genotype interactions modified by a third species in a plant–insect system. *Am. Nat.* **170**, 492–499. (doi:10.1086/520115)
 - 79 Ferrari, J., Via, S. & Godfray, H. C. J. 2008 Population differentiation and genetic variation in performance on eight hosts in the pea aphid complex. *Evolution* **62**, 2508–2524. (doi:10.1111/j.1558-5646.2008.00468.x)