Title: **Interactions between plant genome size, nutrients and herbivory by rabbits, molluscs and insects on a temperate grassland**

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ABSTRACT

Angiosperm genome sizes (GS) vary c. 2,400-fold. Recent research has shown that GS influences plant abundance, and plant competition. There are also tantalising reports that herbivores may select plants as food dependent on their GS. To test the hypothesis that GS plays a role in shaping plant communities under herbivore pressure, we exploit a grassland experiment that has experimentally excluded herbivores and applied nutrient over 8 years. Using phylogenetically-informed statistical models and path analyses, we show that under rabbit-grazing, plant species with small GS generated the most biomass. In contrast, on mollusc and insect-grazed plots, it was the plant species with larger GS that increased in biomass. GS was also shown to influence plant community properties (e.g. competitive strategy, total biomass) although the impact varied between different herbivore guilds (i.e. rabbits versus invertebrates) and nutrient inputs. Overall, we demonstrate that GS plays a role in influencing plant-herbivore interactions, and suggest potential reasons for this response, which include the impact of GS on a plant's response to different herbivore guilds, and on a plant's nutrient quality. The inclusion of GS in ecological models has the potential to expand our understanding of plant productivity and community ecology under nutrient and herbivore stress.

Key words: Genome size, herbivory, plant community ecology, competition, nitrogen, grassland experiment.

1

1. INTRODUCTION

Terrestrial ecological communities are shaped by interactions between plants and herbivores, in which the availability of resources play a central role [e.g. 1]. These interactions and their components are driven by a number of biotic and abiotic, top-down and bottom-up factors [2], one of which is nutrient availability, where a near-universal pattern following nutrient enrichment is an increase in plant biomass and a decrease in plant species diversity [3, 4]. Nutrient availability also mediates the impact of herbivores on plant biomass and on community structure. For example, plants with access to nutrient resources are better able to tolerate herbivory [5]. In addition, grazing pressure on fertilized plant communities is associated with increased plant functional diversity [6]. Herbivores can counteract a decrease in plant species loss following nutrient enrichment by keeping fast-growing plants in check and promoting the growth of less competitive, but better defended taxa [7, 8]. Conversely, higher nutrient concentrations promote investment in plant growth rather than plant defences, increasing leaf palatability [9]. The production of enzymes and other proteins in growing plant tissues can also increase nitrogen (N) and phosphorus (P) concentrations, and such nutritious tissues are often favoured by herbivores, especially during the growing season [e.g. 10].

Numerous studies have shown that certain plant functional traits can influence and mediate plant responses to stress caused by herbivory [e.g. 11, 12], and since plants form the basis of terrestrial food chains, any factor that can influence plant abundance and productivity has implications for all trophic levels. One factor that has been little explored in considering plant herbivore interactions is plant genome size (GS; i.e. the amount of DNA in the unreplicated haploid nucleus – 1C-value), which ranges c. 2,400-between plant species [13]. Genome size can impact a wide diversity of plant traits, influencing how and where plants grow and interact across different ecosystems [14]. It may also impact how plant communities respond to grazing pressure, and plant-herbivore interactions. Certainly, there are tantalising reports which suggest that GS can play a role in herbivore choice, although the responses are variable, e.g. some herbivorous insects favour polyploid over diploid cytotypes of the same species [15-18] or vice versa [19]; and cows may graze preferentially on a tetraploid versus diploid grass cytotype [20]. There are several reasons as to why plant GS might play

29 such a role in plant herbivore interactions. For example, plant species with very large genomes (e.g.
30 1C–values ≥ 25 pg (1 pg=978 Mbp) are slow growing, obligate perennials, perhaps due to longer DNA
31 replication times [21]. Such plants are likely to recover poorly following herbivory compared with
32 faster growing, more competitive species with smaller GSs. In addition, GS can influence leaf
33 stoichiometry, as GS is positively correlated with leaf N concentrations [22], which could influence
34 herbivore preference.

35 This paper explores the hypothesis that there are interactions between plant GS and herbivory that
36 influence plant community composition and dynamics. We predict that plant communities under
37 grazing pressure are primarily composed of species with smaller GS in contrast to communities
38 where herbivores have been experimentally excluded, because tissue recovery from herbivore
39 damage may be slower and costlier to produce in taxa with larger genomes and/or plants with larger
40 genomes are nutritionally favoured by herbivores. We take advantage of an ongoing long-term
41 ecological experiment which includes experimental manipulations of herbivory and nutrients (N and
42 P). The experiment was established in 1992 at Nash's Field, Silwood Park, UK, on an acid
43 mesotrophic grassland with intense herbivory by rabbits (*Oryctolagus cuniculus*) which are a
44 keystone species. Our results reveal that GS clearly plays a key role in influencing interactions
45 between herbivores, nutrients, and plant biomass production. However, we also show that the
46 direction of these interactions is dependent on the type of herbivore guild, with analyses at the
47 plant community level revealing contrasting interactions and dynamics imposed by rabbit versus
48 invertebrate (mollusc and insect) herbivory.

2. METHODS

(a) Study site

The experimental study was started in 1992 on Nash's Field in Silwood Park, UK (National Grid reference 41/944691). Rabbits have been present at this site since their recovery from myxomatosis in the 1950s, and their grazing has prevented the establishment of woody species (e.g. *Quercus* species) and the succession from grassland to woodland. The experiment is set up in a split-plot, factorial design, comprising a total of eight herbivore exclusion treatments (± insect x ± mollusc x ± rabbits) (Fig. SI.1). Each herbivore exclusion block ($22m^2$) is further divided in half with pH-controlled (limed at pH = 7, and unlimed at pH = 4.1) plots. In the first three years of the experiment, the limed plots also received one of three herbicide treatments: – grasses, – forbs, and control. At the smallest plot level ($4m^2$) are the nutrient treatments, which comprise 12 combinations of: ± nitrogen (N) as ammonium nitrate (100 kg ha^{-1}), ± phosphate (P) (35 kg ha^{-1}), ± potassium (K), and ± magnesium (Mg), all of which are added once a year. Insects are controlled by a permethrin synthetic pyrethroid and dimethoate-40; molluscs (snails and slugs) by metaldehyde pellets; and rabbits by wire mesh fencing [23]. Insecticide and molluscicide are applied three times a year. Small mammals such as field voles (*Microtus agrestis*) and large mammals such as roe deer (*Capreolus capreolus*) are not excluded by rabbit fencing. In the first three years, herbicide was also applied within each herbivore plot for plant type control (± grasses ± forbs). The natural plant community is an intensely rabbit-grazed sward dominated by perennial C3 grasses, primarily *Festuca rubra,* but other common species include *Agrostis capillaris*, *Holcus lanatus*, *Arrhenatherum elatius* (Poaceae), and *Jacobaea vulgaris* (Asteraceae). We based our investigations on data from 190 limed, herbicide-free plots in the species-level analyses, and 556 limed plots in the plant community analyses.

We focus on limed plots rather than the acidic (pH 4.1) unlimed plots to avoid the confounding effects that would result from interactions between fertilization, in particular N, soil acidity, and aluminium toxicity [24]. In addition, the analysis of limed plots enables comparisons with the only

74 other analyses published on interactions between fertilizers and genome size in the generation of
75 biomass [40, 47], which are both also from temperate grassland field sites.

76 **(b) Data collection**

77 For analyses, we used biomass data collected in 1997 and 2000 from the 556 limed 4m^2 subplots; we
78 excluded 20 plots containing *Pteridium aquilinum* (an invasive fern) to focus on angiosperm plant
79 communities. Where possible, species were sampled in 2015 to estimate their GS (1C-value) using
80 standard flow cytometry methods [25, see Table SI.1 for details]. GS were estimated from one to
81 eight individuals of 36 species collected from Nash's Field, with species with known cytotypes
82 (different ploidy levels) being more extensively sampled. We used our own GS estimates when the
83 coefficients of variations were <5 % in the flow cytometry analysis, and obtained the remaining 1C-
84 values from the prime values given in the Plant DNA C-values database [26] (Table SI.2). No infra-
85 specific differences in ploidy level were found.
86
87 **(c) Phylogenetic data**

88 We pruned the DaPhnE phylogenetic tree [27], to include the 56 species present in the data with the
89 R package *ape* [28]. We tested whether assumptions of a Brownian motion model were met (e.g.
90 branch length is proportional to amount of variation) with the *caper* package [29]. The most
91 appropriate tree was one in which the branch lengths were transformed using the cladogram option
92 in FigTree (http://tree.bio.ed.ac.uk/software/figtree/, version 1.4.3). We used this tree to account
93 for non-independent evolutionary relationships among species in the statistical analyses (Fig. SI.2).
94 Phylogenetic signal in log-transformed 1C-values was significant (Pagel's lambda= 0.761, p <0.0001,
95 Blomberg's K= 0.502, p= 0.001; estimated with *phytools* [30]).
96
97 **(d) Data analysis**

98 We first tested the effect of GS and experimental treatment on plant above-ground biomass at the
99 species level. We then tested the effects of herbivory and macronutrient input on mean GS at the

community (plot) level. Finally, we carried out path analyses to explore dynamics between plant community properties (*sensu* [31]): community-weighted mean (CWM) GS, CWM C-strategy (see below), total biomass, and phylogenetic diversity, under the experimental treatments. Statistical analyses were carried out in R version 3.3.3 [32].

We refer to the C-strategy of a species as the competitor strategy in Grime's C - S (stress tolerant) - R (ruderal) plant strategies [33]. Each species is attributed to one, or more often, to a combination of these strategies (following [34]), based on how a species persists in its natural habitat, and where the sum of these values is equal to one (Table SI.2).

(i) Species level analyses

We analysed the effect of GS, herbivore exclusion, and nutrient treatment on plant biomass at the species level using phylogenetic generalised linear mixed models (PGLMM) with Bayesian estimation, by fitting Markov chain Monte Carlo generalised linear mixed models from the R package *MCMCglmm* [35]. Ideally, we would have analysed all the species in the model here, but this was not possible because many species were very rare, and in an experiment containing 556 plots, this gave a dataset with many absences (zeros). Statistically, comparisons of treatment effects on species biomass cannot be made on species with such few occurrences, preventing us from testing whether the treatment is having an effect versus whether species occurrence is random. Consequently, and after excluding plots where herbicides had been applied, (i) we limited the analysis to those species that occur on two or more herbivore treatments. This criterion still left the data too zero inflated for analysis because so many species were so uncommon that rounding to the nearest tenth of a percent equaled 0 (see Table SI.12). Therefore: (ii) we limited the analysis to the most common species that had at least 1% of biomass on two or more plots. Together these two criteria did enable the model to converge, leaving for analysis a total of n = 12 species analysed over 190 plots. The results, whilst being restricted to the common species, generated data that support, and are fully

125 congruent with, the community level analyses in the forthcoming sections, where all species, their
126 genome sizes and biomass data are considered together in the same models.

127 We analysed species biomass in two-parts, similar to a hurdle model. Species presence/absence
128 were first fitted in a logistic model, testing the probability of a species occurring on a plot, given the
129 experimental treatments. The second part uses biomass data and fits only the non-zero biomass of
130 the 12 species. The biomass data were log-transformed and analysed using MCMCglmm, assuming a
131 Gaussian distribution. The exclusion of insects, molluscs, rabbits, and the application of N, P, and K
132 fertilizer were scored as binary factors, with untreated plots coded as the reference levels. Genome
133 size was centred on the median GS of the 12 species. Evolutionary non-independence was controlled
134 for by specifying a correlation matrix estimated from the phylogeny. Random effects were specified
135 as: block + block x fencing + species + phylogeny.

136 We first tested four-way interactions between GS, N, P, and herbivore exclusion. Phosphorus
137 showed no significant interactions with herbivore exclusion, consequently, models were re-fitted
138 without P in these interactions. Similarly, Mg had no effect on species occurrence and biomass and
139 was removed to simplify the model. Fixed effects were thus specified as: (GS x insecticide x N) + (GS
140 x molluscicide x N) + (GS x fencing x N) + (GS x N x P) + (molluscicide x insecticide x fencing) + K. We
141 used priors where nu=0.002 and variance=1 [35] and ran the model with 2.5 million generations
142 including a burn-in of 30,000 and a thinning interval of 500. We ran three chains for each model and
143 assessed multiple chain convergence and trace and autocorrelation plots [36].

144

145 **(ii) Community level analyses**

146 We investigated the effects of GS, herbivore exclusion, and nutrient treatment at the community
147 level. Each plot is representative of a plant community growing under various combinations of
148 nutrient availability and herbivore guilds. For each plot (n = 556), CWM GS was estimated using the
149 phylogenetic generalized least squares method (PGLS). We fitted regressions with a Brownian
150 motion correlation structure derived from the phylogeny [37], and maintained the same

phylogenetic correlation structure across all plots. Species GS was log-10 transformed, and species percent biomass was used for weighting: gls ($\log_{10}$ GS ~ 1, cor= corBrownian (phylogeny), weights= varFixed(~1/species biomass)). We then back-transformed this mean, for use in the subsequent analyses and figures, to facilitate interpretation. To assess whether CWM GS is a function of herbivory and nutrient application, we fitted linear mixed effect (LME) models with the *lme4* package [38] where each herbivore type (insect, mollusc, rabbit) and each nutrient (N, P, K, Mg), were scored as binary factors, and with random effects reflecting the split-plot design (plot/fencing/herbicide). Herbicide treatment was also included as a fixed effect, to account for its application in the early years of the experiment. Interactions between herbivore and nutrient treatments and the significance of each factor were tested using maximum likelihood (ML) stepwise model reduction methods, and the final most reduced model refitted with restricted ML (REML). Estimations of parameter significance (p-values) were obtained with the lmerTest package [39].

(iii) Confirmatory Path Analysis

To determine how herbivore guilds, nutrient availability, and GS impact plant communities, we examined the effects of N, P, K and: 1) rabbit exclusion, and 2) mollusc and insect exclusion on plant community structure using confirmatory path analysis. Specifically, we tested (i) whether GS influenced the abundance of plants with a C-strategy (*sensu* Grime [33]) at the community level [e.g. 40]; (ii) how the abundance of plants with a C-strategy impacts total biomass and phylogenetic diversity; and (iii) the role of herbivory and nutrients on these community properties. Data were partitioned into two datasets: 1) unfenced plots and fenced plots (rabbit exclosures) to test the effect of rabbit exclusion (n=144 plots without insecticide or molluscicide treatment), and 2) ± insect and ± mollusc treatment (within rabbit exclosures only) (n= 281).

We examined four plant community properties: (i) CWM GS; (ii) CWM C-strategy; (iii) total above-ground community biomass (estimated from total dry sample weight); and (iv) phylogenetic diversity. CWM C-strategy of each plot was calculated from each taxon's C-strategy (estimated with

177 PGLS, as described above). Phylogenetic diversity (PD) corresponds to Faith's PD [41] and is the sum
178 of the phylogenetic branch lengths of each community, estimated with the *picante* package [42].

179 We used directional separation (*d-sep*) path analysis methods [43] to assess fourteen hypotheses
180 about the effects of experimental treatment (herbivore exclusion, N and P plus K fertilizer) on the
181 plant community properties (Fig. SI.3, see also Table SI.3 for a more complete description of *d-sep*
182 methods). The conditional independencies were fitted with LME models [48,49]. Random effects
183 were specified as plot/fencing/herbicide in the rabbit exclusion analyses, and as plot/herbicide in
184 the insect-mollusc exclusion analyses. Herbicide treatment was also accounted for as a fixed effect.
185 The experiment was fitted as herbivore treatment x N x P + K + herbicide; where herbivore
186 treatment = ± rabbits, or ± insects x ± molluscs. Continuous independent variables were
187 standardized by two standard deviations [44] with the 'rescale' function from the *arm* package [45].
188 Because p-values are the main determinant in assessing acyclic diagrams, each equation was also
189 systematically fitted with ten unequal variance structures using the 'varIdent' function from the
190 *nlme* package [37] to account for heteroscedasticity in the residuals (Table SI. 3). We retained the p-
191 value from the regression resulting in the lowest second-order AIC (AIC*c*), which corrects for small
192 sample sizes, implemented in *MuMIn* [46], but only if an analysis of variance showed that a
193 regression fitted with the variance structure was significantly better ($p<0.05$) than without.
194 Interactions among community properties, and between the experiment and community properties,
195 were not allowed. We present one directed acyclic diagram for each dataset, based on the CIC-
196 statistic and a preference for a more parsimonious diagram (Table SI.4), but this does not exclude
197 alternative hypotheses that passed the goodness of fit tests. The conditional R^2 values for LME
198 equations were estimated with *MuMIn*, and are measures of how much variance is explained by
199 both fixed and random effects [46].

200

3. RESULTS

Of the 56 species collected during the field sampling, 12 species generated at least 1% mean biomass in at least two herbivore treatments. Seven were grasses (Poaceae): *Agrostis capillaris*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca rubra*, *Holcus lanatus*, *Holcus mollis*, and *Phleum pratense* subsp. *bertolonii.* The remaining five were *Cirsium arvense*, *Jacobaea vulgaris* (Asteraceae), *Plantago lanceolata*, *Veronica chamaedrys*, (Plantaginaceae), and *Rumex acetosa* (Polygonaceae). Overall, for the 56 species, GS ranged from 0.28 pg/1C in *Juncus effusus* to 11.06 pg/1C in *Ranunculus repens* (Table SI.2).

(a) Species occurrence and species biomass are a function of interactions between GS, herbivory, and nutrients

We investigated the impact of herbivores, nutrient treatment, and species GS on the occurrence and biomass of the 12 species listed above. Herbivore exclusion and GS significantly impacted species occurrence. With insect exclusion, the probability of a species occurrence (inv.logit(B)) was 0.813 (95% credible intervals (CI) = 0.397, 0.974, pMCMC=0.0425) increased by 0.472, or 47.2% in comparison to control plots with all herbivores present (Table SI.5A). Two significant interactions between GS and herbivores were apparent: (i) GS and rabbit exclusion - species with larger GS were more likely to be present on plots without rabbits. Each pg increase in GS was associated with an 8.0% increased likelihood of a species occurrence (inv.logit(B)=0.573, CI=0.530, 0.613, pMCMC<0.0002), in comparison to control plots (inv.logit(B)=0.49, Table SI.5A); (ii) GS and mollusc exclusion - removing molluscs increased the probability of a species with a smaller GS being present. Each pg decrease in GS was associated with a 6.6% increase in species occurrence (inv.logit(B)=0.427, CI=0.387, 0.465, pMCMC=0.0020, Table SI. 5A).

Species above-ground biomass was influenced by interactions between GS, herbivory and N (Table SI.5B). In control plots, the estimated effect of GS was a c. 62% increase in species biomass per pg increase in GS (exp(B)=1.618, CI=1.19, 2.36, pMCMC=0.0057). The above-ground biomass of the 12 species was further impacted by three interactions between GS and experimental treatments. On

plots with all herbivores present, the addition of N increased species biomass by more than two-fold (exp(B)=2.33, CI=1.186, 2.358, pMCMC=0.0105). However, this was dependent on GS, with most of the biomass increase coming from species with small GS - on +N plots, biomass decreased by c. 23% per pg increase in GS (exp(B)=0.765, CI=0.608, 0.974, pMCMC=0.0243, Table SI.5B). The second interaction was an increase in biomass of species with larger GS on plots without rabbits - species biomass increased by 21% per pg increase in GS in comparison to control plots (exp(B)=1.2099, CI=1.047, 1.396, pMCMC=0.0117)). This contrasted with the third interaction observed as the amount of biomass produced by species with larger GS on plots decreased with mollusc exclusion - a biomass decrease of c. 14% per pg increase in GS was observed when molluscs were excluded compared to control plots (exp(B)=0.8604, CI=0.736, 0.987, pMCMC=0.0466)). Insect removal did not significantly affect growth of the 12 species.

(b) Herbivory and nitrogen influence community-weighted mean (CWM) GS

For community level analyses, CWM GS were estimated for all 556 plots using biomass values for the 56 species; these ranged from 1.36 pg/1C (on a plot with +N and -rabbits and -molluscs (i.e. insects only) to 8.61 pg/1C (on a plot with +N and -rabbits). For control plots (all herbivores present, no nutrient input) the CWM GS was estimated at 5.76 pg/1C (95% confidence interval (CI) 5.02, 6.50) (Table SI.7).

The most parsimonious linear mixed effects (LME) model (obtained with stepwise reduction, Table SI.6) revealed that: (i) on unfertilized plots, the biomass from plants with larger GS increased without rabbits - CWM GS of plots increased by 1.10 pg/1C when rabbits were excluded compared to control plots (Fig. 1, CI=0.26, 1.95, p=0.0538, Table SI.7). This effect became significant with the addition of N, with CWM GS of plots increasing by 0.33 pg/1C with rabbit exclusion, compared to control plots (CI=0.46, 1.73, p=0.0008)). (ii) In contrast, the biomass from plants with smaller GS increased on plots with both mollusc and insect exclusion and N input. The CWM GS of plots decreased by 2.73 pg/1C on +N plots with rabbit grazing only (B=1.433, CI=0.52, 2.35, p=0.0024). (iii) Nitrogen

fertilizer decreased CWM GS of plots with all herbivores present by 1.87 pg/1C (CI=-2.42, -1.32, p<0.0001), and (iv) P fertilizer decreased CWM GS by 0.31 pg/1C (CI=-0.54, -0.08, p=0.0078). (v) CWM GS of plots with only insect grazing (rabbit and mollusc exclusion) and N fertilization decreased by 1.54 pg/1C compared to control plots (Fig. 1, CI=-2.10, -0.28, p=0.0114, Tables SI.7).

We also estimated CWM GS (i) without including a phylogenetic correlation structure; (ii) with GS untransformed; (iii) with the lambda parameter optimised; and showed that these were similar to CWM GS used above and that the key results presented here remain unchanged (Fig. SI.4 and Table SI.9).

(c) Contrasting and similar effects of rabbit and invertebrate herbivory on plant community properties

Using confirmatory path analysis, we investigated how the following four plant community properties were influenced by each other and by herbivory and nutrient treatments: (i) CWM GS, (ii) CWM C-strategy (i.e. species competiveness), (iii) total above-ground community biomass, and (iv) phylogenetic diversity (Fig. 2a and b, Fig. SI.5 and Tables SI.10 (rabbit exclusion) and SI.11 (insect and mollusc exclusion) for complete regression tables of Fig. 2a and b respectively).

In testing the impact of rabbits, the four community properties were influenced by various factors. The interaction between N input and rabbit exclusion increased CWM GS by 0.99 pg (CI=0.44, 2.24, p=0.0047) (Fig. 2a, Table SI.10). CWM C-strategy increased with N input (B=0.089, CI=0.04, 0.15, p=0.0016), and with CWM GS (B=0.025, CI=0.02, 0.04, p<0.0001), particularly on plots without rabbits (Fig. SI.6a, b). Total biomass increased with rabbit exclusion and N input (B=19.97, CI=10.85, 29.08, p=0.0001). The single largest standardized effect is the reduction in phylogenetic diversity with rabbit exclusion (B=-15.48, CI=-22.16, -9.54, p=0.0003).

In contrast, removal of molluscs and insects did not reduce phylogenetic diversity. Instead, N input, and to a lesser extent, K input, were the main drivers of this (B=-12.11, CI=-18.54, - 5.68, p=0.0004; and B=-3.58, CI=-6.02, -1.15, p=0.0052 respectively) (Fig. 2b, Table SI.11).

The main driver influencing occurrence of species with a competitive life strategy (i.e. CWM C-strategy) was a four-way interaction between insect and mollusc exclusion and +N and +P input, increasing CWM C-strategy by 0.23 units (CI=-0.46, -0.11, p=0.002). Similar to ± rabbit plots, CWM C-strategy also increased with CWM GS (B=0.025, CI=0.02, 0.03, p<0.0002, Fig. SI.6c-f). Total biomass increased significantly with both +N and mollusc (but not insect) removal by a mean of 28.05 g (in dry weight) (p=0.0073). In addition, increased biomass was associated with increased CWM C-strategy (B=65.65, CI=43.63, 85.97, p<0.0001). Finally, in contrast to rabbit exclusion, a four-way interaction between +N, +P, insect and mollusc exclusion led to a decrease of 2.39 pg in CWM GS (p=0.0464). Total biomass and phylogenetic diversity were not significantly associated with each other in both path analyses.

(d) Changes in species composition with herbivore exclusion and N fertilizer

Species that increased with rabbit exclusion, include the larger genomed *Arrhenatherum. elatius* (8.61 pg/1C), and to a lesser extent *H. mollis* (4.1 pg/1C), and *D. glomerata* (4.4 pg/1C). The response of *F. rubra* (7.31 pg/1C) was dependent on N, decreasing on -N plots, and increasing on +N plots. The removal of molluscs led to an increase in the smaller genomed *H. lanatus* (1.7 pg/1C), followed by *P. pratense* subsp. *bertolonii* (1.99 pg/1C) and *H. mollis* (4.1 pg/1C), at the expense of the larger genomed *F. rubra* and *A. elatius*. In contrast, species that increased most with just insect removal had a range of GS and included *A. elatius* (on –N plots), *H. mollis* (on +N plots), *J. vulgaris* (2.25 pg/1C), *C. arvense* (1.42 pg/1C), and *H. lanatus*; whilst *A. capillaris* (3.6 pg/1C) and *F. rubra* decreased.

Within fenced plots, species that increased with removal of molluscs and insects include *H. mollis*, *H. lanatus*, *D. glomerata*, *Achillea millefolium* (7.98 pg/1C)), *P. pratense* subsp. *bertolonii*, and *V. chamaedrys* (2.16 pg/1C). *Holcus mollis* increased consistently on +N plots, whereas *F. rubra*, *A. capillaris*, *C. arvense* (1.42 pg/1C), decreased on -N plots (see also Fig. SI.7 for biplots representing species abundances for the experimental treatments, and Table SI.12 for percentage change in species biomass).

4. DISCUSSION

The experiment at Nash's Field involves the input of nutrients and the exclusion of grazing by molluscs, insects and rabbits, allowing us to detect significant interactions between GS, herbivory and N fertilization. We show that these interactions impact plant community structure, plant biomass production and species diversity. Previous work showed that plant community structure was influenced by interactions between plant GS and nutrients directly, and that species with larger GS only contributed significant biomass to plant communities when nutrients were not limiting [40, 47]. We did not observe this effect here, perhaps because: (i) The experiment is still young (data were collected only 6 to 8 years after the start of the experiment), compared with the Park Grass (>150 years) and Rengen Grassland (>70 years) Experiments, and thus plant communities may still be adapting to the experimental treatments and are in a transient state [48]; (ii) Since the 1950s intensive rabbit grazing is known to have been prevalent in the area used to establish Nash's Field Experiment in 1992 and this would have influenced the species that colonised the plots towards those that are grazing-tolerant and/or grazing-resistant [49, 50].

(a) Impact of rabbit herbivory

We observed that the plant species which generated most biomass on rabbit-grazed plots had smaller GS than those on ungrazed plots, especially when N fertilizer was added. There could be because:

(i) Rabbits preferentially eat plant taxa with large GS. Plant species which increase in biomass when herbivores are excluded are generally species that are preferentially grazed by herbivores [51]. Rabbits are known to favour high-nutrient plants [52]. N input qualitatively alters plant nutrient content [53] and plants growing under higher N may be more attractive to consumers and increase herbivore numbers [10, 54]. Potentially rabbits may prefer species with larger GS because at the cellular level, they have higher N and P content (both DNA and RNA are rich in these macronutrients) compared to species with smaller GS [53, 55]. In addition, plants with

larger cells may be more palatable as cell size tends to increase with GS, and larger and fewer cells per leaf would decrease the amount of cell wall, potentially rendering the plant more succulent.

(ii) Plant taxa with smaller GS are better able to recover from the rabbit grazing pressure. Rapid growth might be best achieved in plants with small GS which have faster cell cycle times, shorter durations of DNA synthesis, and hence shorter minimum generation times [reviewed in 14], and may be less constrained by nutrient availability for growth and repair [56]. Indeed, tolerance to grazing may be a key survival trait on fertilized plots, where rabbit abundance can be four times greater than on unfertilized plots [57]. Rabbits generate sustained stresses that impact grassland composition and dynamics, such as the selection of plants with rapid growth rates [58]. Rapid growth rate is fundamental to tolerance of herbivory, allowing for regrowth of damaged tissue. Such regrowth is achieved via rapid resource allocation, increased photosynthetic rates, and increased nutrient uptake [59]. Trade-offs may therefore exist between the biochemical costs associated with building and maintaining a large genome and tolerance to herbivore damage.

(iii) Plant taxa with smaller GS may be less constrained to allocate resources to the production of secondary metabolites for defence. Investment in defence has been shown to lead to decreased rates of photosynthesis, and the diversion of elemental resources such as C and N towards the production of defence compounds at the expense of growth [60]. Defence is also costly in both water and nutrient resources [61], leads to the remobilization of elements to roots [62], and would compete with the N and P costs of building and maintaining a large genome, especially in nutrient deficient environments.

In addition to the direct effects of preferential grazing, rabbits increase habitat and resource heterogeneity by trampling, burrowing, decreasing ground cover, and deposition of droppings. These effects may enable functionally more diverse species to colonize the community [7]. We observed that the presence of rabbits leads to a significant increase in phylogenetic diversity, which is also associated with a decrease in plant species with a competitive life strategy and a decrease in

356 total biomass (Fig. 2a). Rabbit grazing on the fast-growing, dominant plants keeps these in check,
357 allowing the establishment of subordinate species. This effect has also been reported across various
358 types of grasslands with mammalian herbivores, but depends on plant productivity, generally being
359 positive in grasslands with high productivity, but decreasing plant diversity when productivity is low
360 [63, 64]. Experiments are now needed determine whether plants with larger GSs, are indeed of
361 higher nutrient quality, altered N and P contents and different recovery periods following damage by
362 herbivory.

363 **(b) Impact of invertebrate herbivory**

364 In contrast to rabbit grazing, mollusc and insect grazing leads to communities composed of plants
365 with larger GS. In the absence of fertilizer, mollusc and insect herbivory appear to mitigate the
366 effects of rabbit grazing, as plant communities on plots with no herbivores have similar CWM GS as
367 the control plots where all herbivores are present (Fig. 1). Numerous studies have shown that
368 molluscs have species-specific food preferences, which relate to different food qualities and a plant's
369 palatability, the latter being influenced by, for example, the presence of plant anti-herbivory
370 chemicals, silica content, and a plant's pubescence which can deter feeding [65]. Molluscs are also
371 reported to have a preference for seedlings, however in a temperate grassland seedling recruitment
372 is low, where plant regeneration is mostly via vegetative regrowth [23]. Potentially the invertebrates
373 at Nash's Field are specialists on plants or plant organs that are not favoured by rabbits. Nutrient
374 acquisition strategies vary between and within these herbivore guilds, and the scale and impact of
375 different insect herbivores (predominantly grasshoppers) on grassland plant community biomass has
376 been shown to be linked closely with, for example, mandibular trait diversity [66]. It is possible that
377 insects as a guild feed on a larger range of species and tissues than molluscs as a guild, making the
378 effects of insects on community plant GS more difficult to detect.

379 Whilst insect and mollusc herbivory decreased total community biomass, the effects of insects and
380 molluscs on community composition were negligible when fertilizers were added, perhaps because
381 fertilizers can obscure the effects of nutrient recycling by grazers, although interactions are complex

[1]. The application of N and K led to a reduction in phylogenetic diversity, for which the presence of insects and molluscs did not compensate. This is opposite to the significant effect of rabbits; their larger size and activities (as noted above) may result in more pronounced effects on plant diversity [63]. Previous findings on the unlimed plots at Nash's Field, included a decrease in species diversity with insect removal, and, to some extent, mollusc removal [23]. The effects of insects and molluscs may take longer to occur on limed plots, as these do not have the additional stress of low pH conditions.

(c) Genome size and ecological models

Investigations of plant traits have uncovered global trends that help to predict plant responses to abiotic and biotic factors [67-69]. Here we propose that GS should also be considered as an important plant functional trait which influences plant community structure through bottom-up (nutrients) [70] and top-down (herbivory) interactions with GS. We show here that larger CWM GS is linked with higher CWM C-strategy, which is, in turn, linked with increased community biomass. Higher species competitiveness is also associated with decreased species diversity in the absence of rabbit grazing. Through plant consumption, herbivores also influence plant community composition, including the abundance of plants with a competitive life strategy, which can impact nutrient cycling by altering litter quality [1]. The effect of GS on plant tolerance to herbivory, and possible influence on herbivore preference may also have wider ecological impact, influencing processes such as N cycling, and hence add a new dimension to improve the performance of ecological models.

Data accessibility

All data will be made available in Dryad if the manuscript is accepted.

Competing interests

We have no competing interests.

Authors' contributions

MSG and DK carried out field-work and GS estimation. MSG carried out the data analyses. MJC established the experimental plots, assisted with species identification and provided biomass data. RAN provided statistical advice. MSG, IJL, and ARL devised the fieldwork, analyses, and wrote the manuscript. All authors read, revised, and approved the final manuscript.

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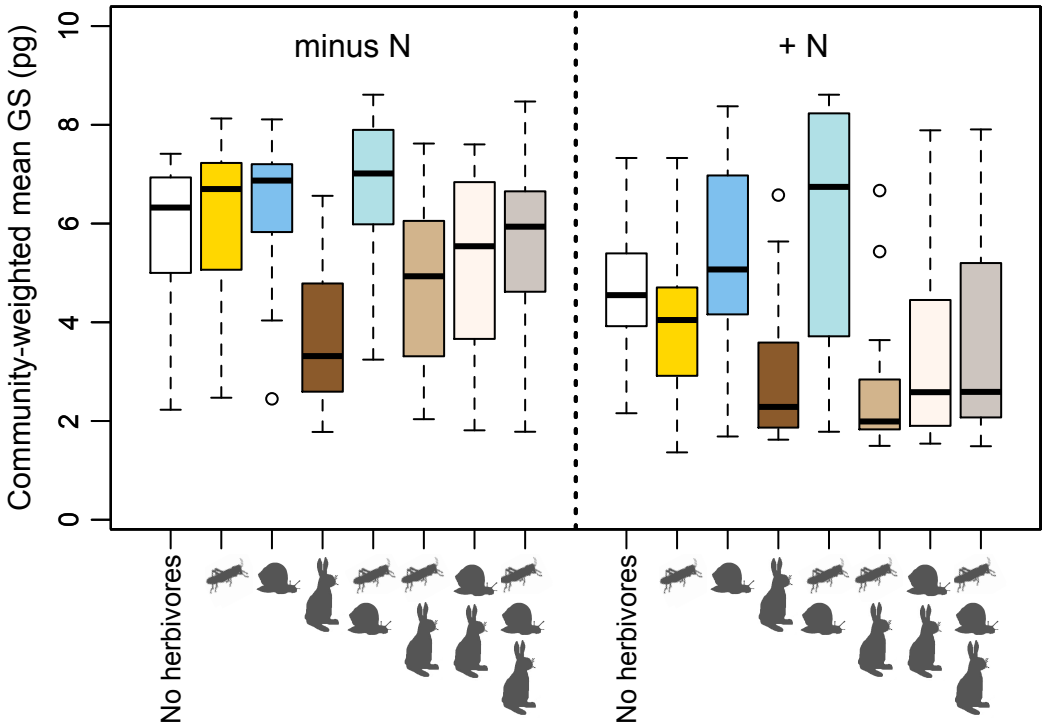
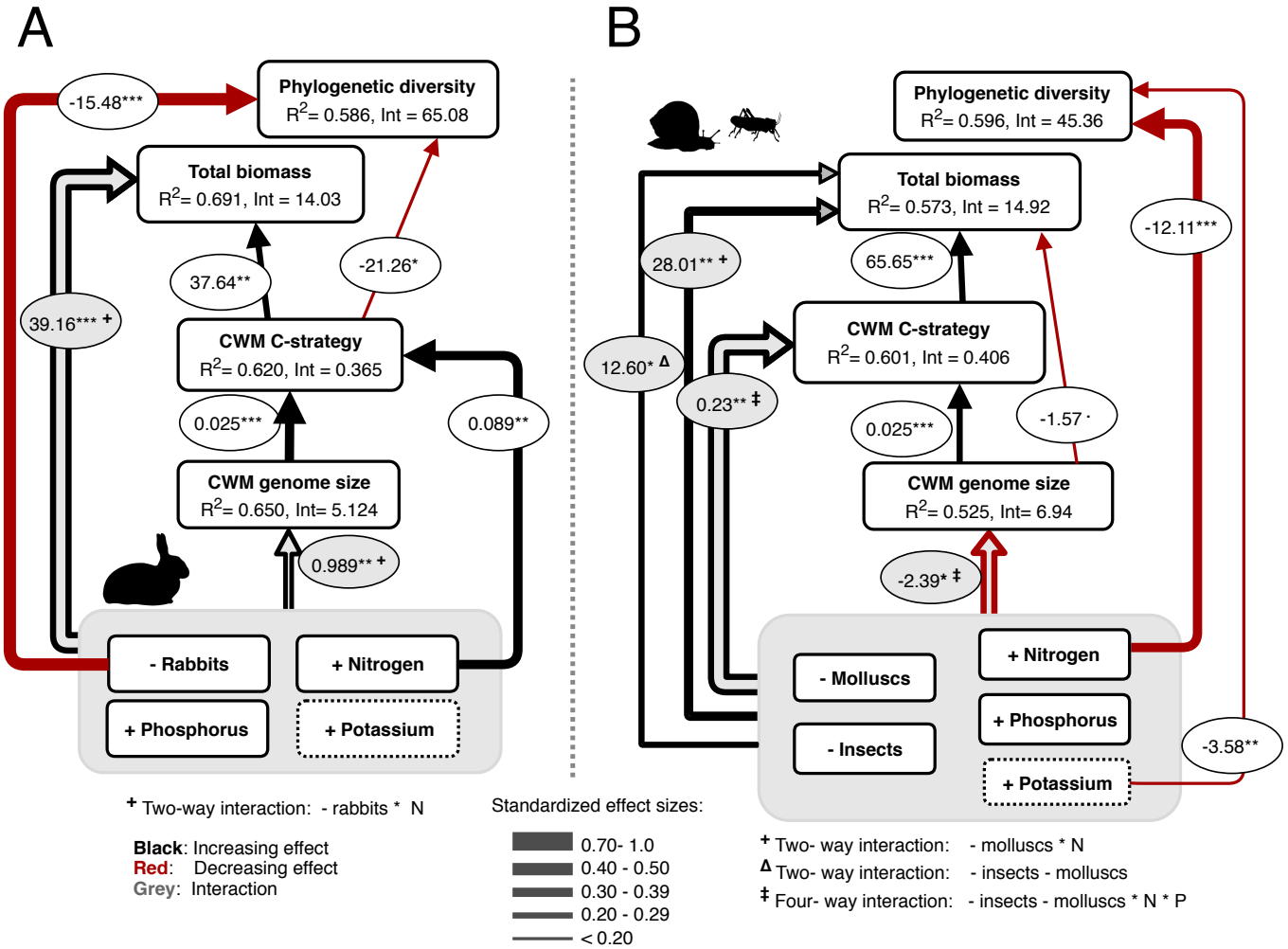
579 **FIGURE LEGENDS**

580 **Fig. 1:** Community-weighted mean genome size (GS; 1C-value, pg) of each plot (n = 556) under eight
581 herbivore exclusion treatments and ± nitrogen (N) input. Herbivore treatments, in order as shown
582 below are: 1) control (all herbivores present); 2) – insects; 3) – molluscs; 4) – rabbits; 5) rabbits only
583 (– insects, – molluscs); 6) molluscs only (– insects, – rabbits); 7) insects only (– molluscs, – rabbits); 8)
584 no herbivores. Boxes show median of community-weighted mean GS, first and third quartiles, and
585 minimum and maximum values (summary statistics in Table SI.8).

586 **Fig. 2:** Path analysis examining effects of (A) rabbit exclusion and (B) mollusc and insect exclusion
587 together with nutrient input (N, P, K) on four plant community properties: (i) community-weighted
588 mean (CWM) genome size (GS), (ii) CWM competitive (C)-strategy, (iii) total biomass, and (iv)
589 phylogenetic diversity. Values in ovals show the effect size of one variable, or interaction, on the
590 other. The conditional R^2 and the intercept are given for each community property. Arrow widths
591 are proportional to standardised coefficients. P-values: ***<0.0001, **<0.001, *<0.05 (see Tables
592 SI.10 and SI.11 for details in A and B respectively). (A) For rabbits, a three-way interaction (± rabbits
593 x N x P) did not contribute significantly towards any community property, thus only two-way
594 interactions were included between ± rabbits, N and P. (B) For molluscs and insects, CWM GS could
595 not be unlinked from total biomass in a conditional independency test, however its partial
596 regression coefficient is below the alpha level (0.050 at p=0.0709).


Community-weighted mean GS (pg)
0
2
4
6
8
10
minus N
+ N
No herbivores
No herbivores


A
-15.48***
Phylogenetic diversity
R2= 0.586, Int = 65.08
Total biomass
R2= 0.691, Int = 14.03
37.64**
-21.26*
39.16*** +
CWM C-strategy
R2= 0.620, Int = 0.365
0.025***
0.089**
CWM genome size
R2= 0.650, Int= 5.124
0.989** +
- Rabbits
+ Nitrogen
+ Phosphorus
+ Potassium
B
Phylogenetic diversity
R2= 0.596, Int = 45.36
Total biomass
R2= 0.573, Int = 14.92
-12.11***
28.01** +
65.65***
CWM C-strategy
R2= 0.601, Int = 0.406
12.60* Δ
0.23** ‡
0.025***
-1.57 ·
CWM genome size
R2= 0.525, Int= 6.94
-2.39* ‡
+ Nitrogen
- Molluscs
+ Phosphorus
- Insects
+ Potassium
-3.58**
+ Two-way interaction: - rabbits * N
Black: Increasing effect
Red: Decreasing effect
Grey: Interaction
Standardized effect sizes:
0.70- 1.0
0.40 - 0.50
0.30 - 0.39
0.20 - 0.29
< 0.20
+ Two- way interaction: - molluscs * N
Δ Two- way interaction: - insects - molluscs
‡ Four- way interaction: - insects - molluscs * N * P

SUPPLEMENTARY INFORMATION

Supplementary Text:

Phylogenetic tree data

Supporting figures SI.1 to SI.7

Supporting tables SI.1 to SI.12

SUPPLEMENTARY TEXT

Phylogenetic data (.tre format)

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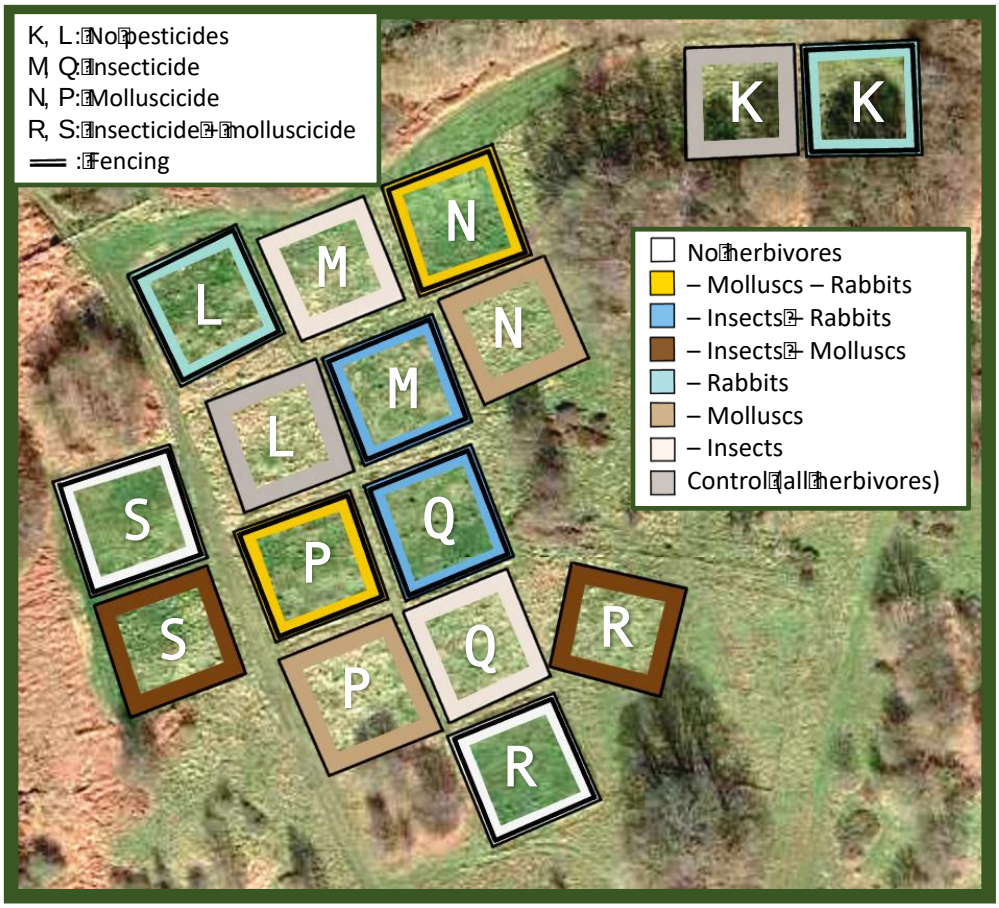


Fig. SI.1 Layout of experimental plots in Nash's Field, established in 1991 at Silwood Park (Imperial College, London). Further details are available at http://www.imperial.ac.uk/silwood-park/research/silwood-lte/nashk-s/.

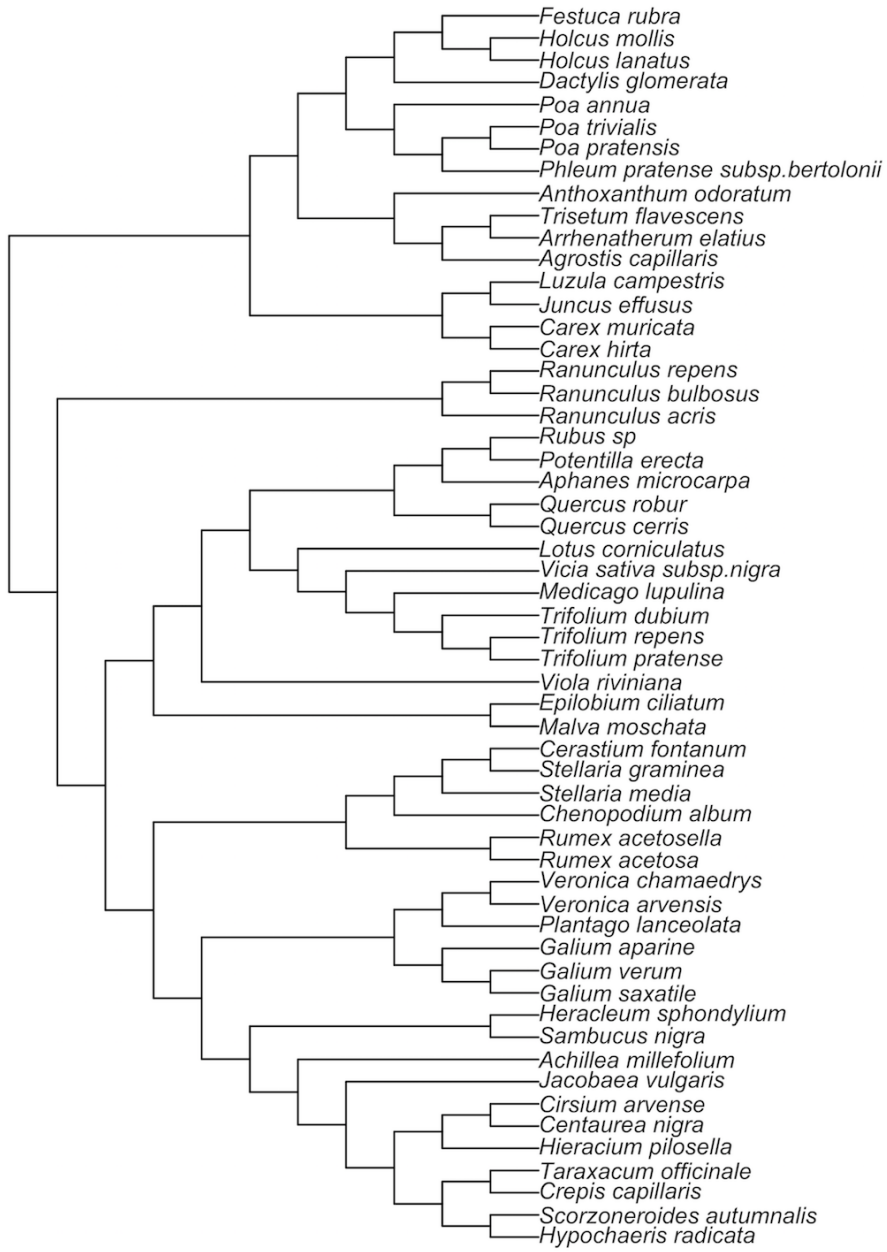


Fig. SI.2 Phylogenetic tree of the 56 species occurring on the 556 limed plots of Nash's Field, Silwood Park, UK.

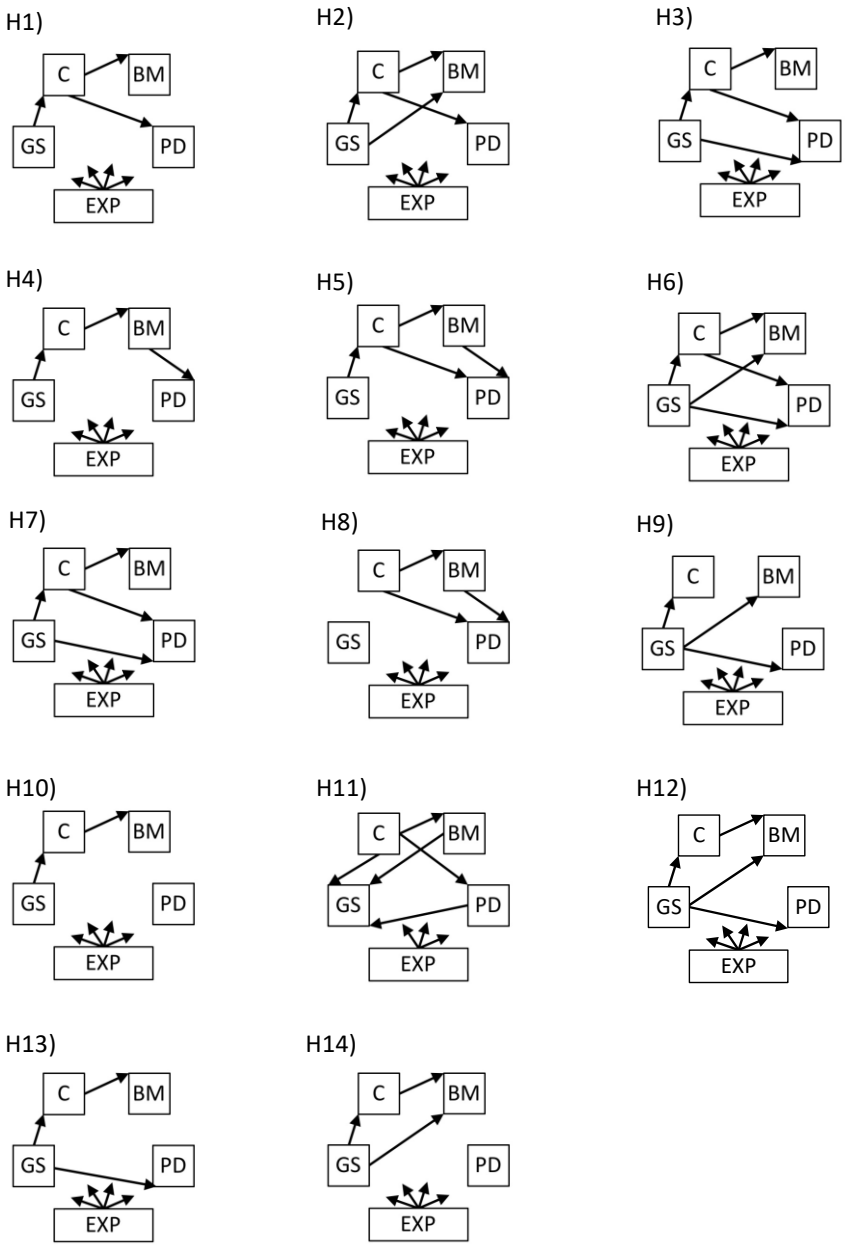


Fig. SI.3 Directed acyclic graphs representing path models investigating the effects exerted by the experiment on the four plant community parameters comprising (i) community-weighted mean genome size (GS), (ii) community-weighted mean competitive (C)-strategy (C), (iii) total community biomass (BM), and (iv) phylogenetic diversity (PD), and how these four properties are associated with each other. These hypotheses are built upon previous studies investigating the influence of GS on plant communities and from examining correlations present in the data. The small arrows pointing towards each variable represent the effect of experimental treatment (EXP: interactions between herbivore exclusion, N and P, plus K). An arrow originates from the experiment to each of the four community properties in all model hypotheses (diagrams H1-H14), except H11, where conditional independence was tested between the experiment and genome size (see also Table SI.3 for a more complete description of *d-sep* methods).

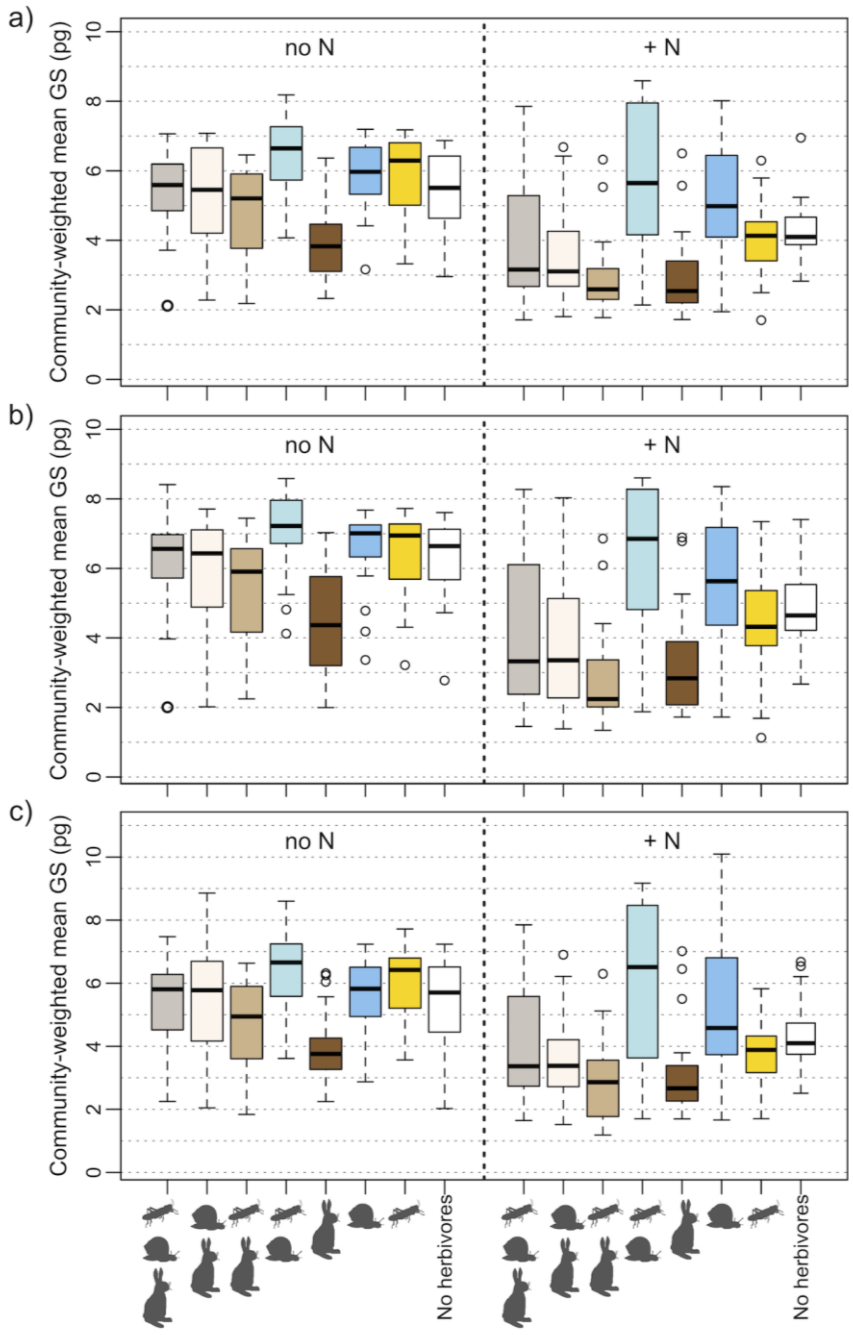


Fig. SI.4 Three alternative estimations of community-weighted mean GS (1C-value in picograms): **a**) simple weighted mean GS, without accounting for phylogenetic non-independence. As in the main text, species GS were log10-transformed, and the weighted mean back-transformed; **b**) estimated with PGLS assuming a Brownian motion of evolution structure (as described in the main text); however GS was *not* transformed; **c**) estimated with PGLS with lambda optimisation, thus relaxing the assumptions of Brownian motion of evolution. As in the main text, species GS were log10-transformed, and the community-weighted mean back-transformed. See also Table SI.9 for significance of experimental treatments (N fertilizer and herbivore exclusions) on community-weighted mean GS.

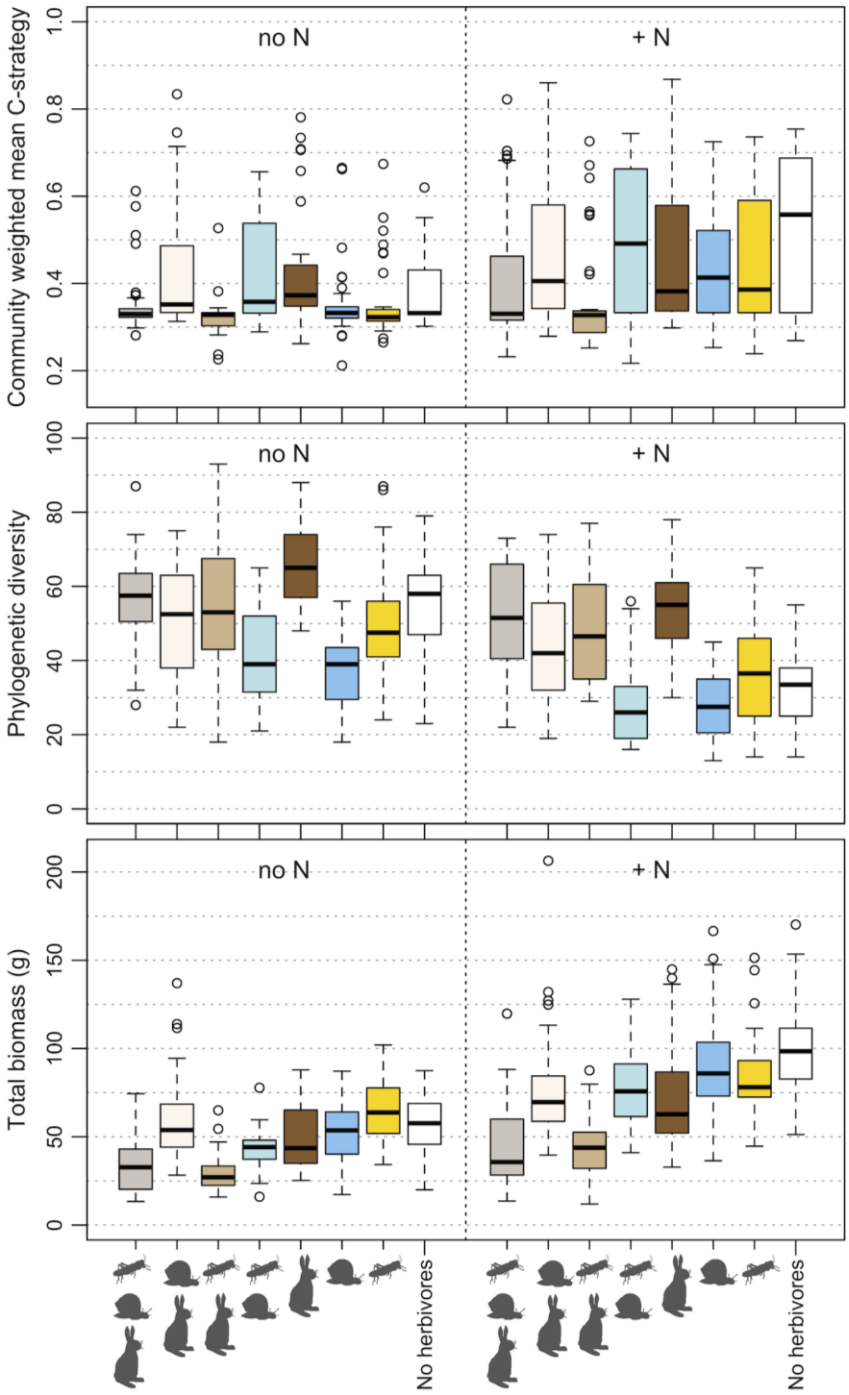


Fig. SI.5 Community-weighted mean competitive (C)-strategy; phylogenetic diversity (Faith's PD [1]), and total community biomass (dry weight g/m^2) (n = 556), shown according to herbivore treatment. Herbivore treatments, in order as shown above are: 1) control (all herbivores present); 2) – insects; 3) – molluscs; 4) – rabbits; 5) rabbits only (– insects, – molluscs); 6) molluscs only (– insects, – rabbits); 7) insects only (– molluscs, – rabbits); 8) no herbivores. See also Table SI.8.

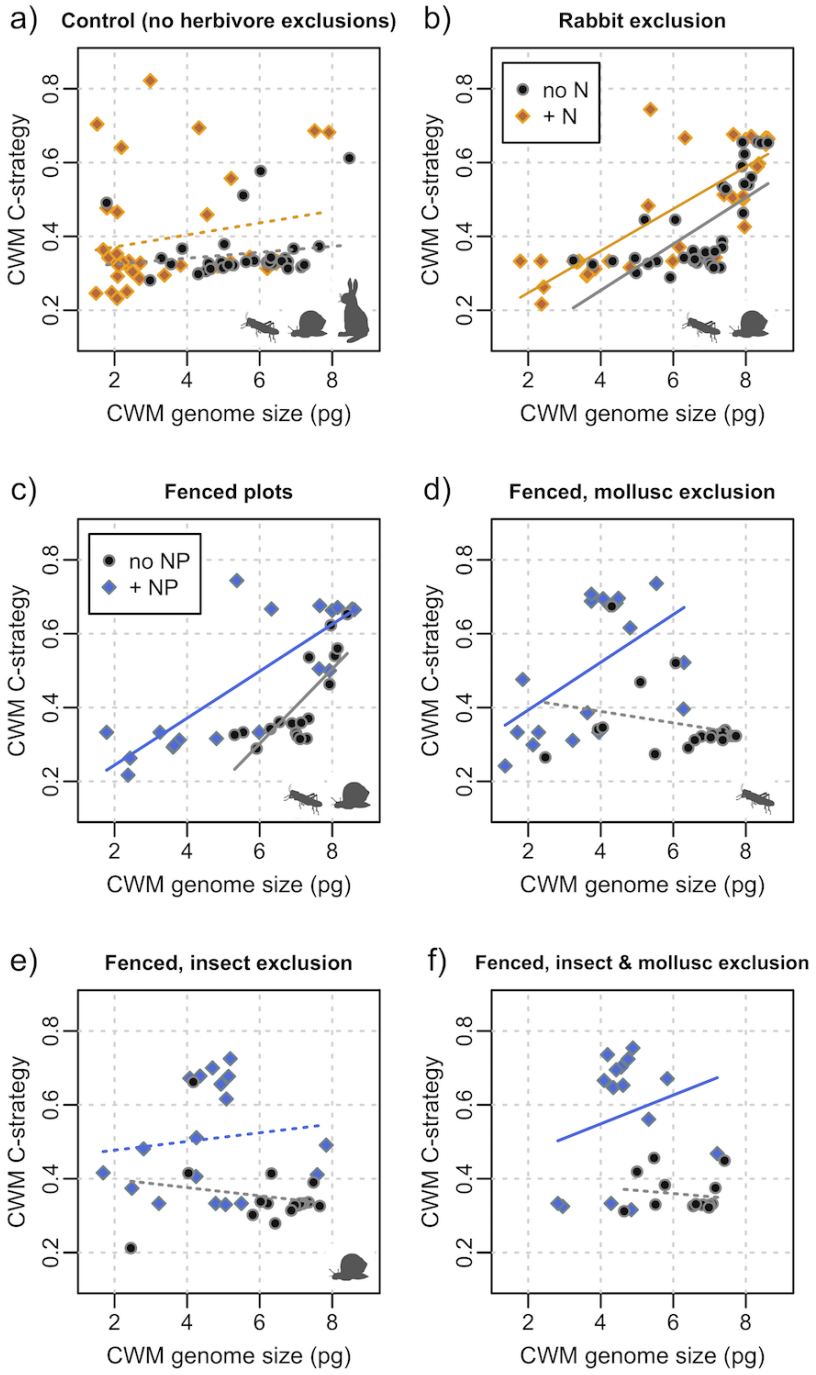


Fig. SI.6 Associations between community-weighted mean (CWM) C-strategy (CWM C-strategy) and CWM GS under different herbivore exclusion treatments and ± N input. Herbivore exclusion treatments correspond to those of the path analyses: effects of rabbit herbivory (**a, b**); and effects of molluscs and insects on fenced plots (**c-f**). The rabbit herbivory path analysis showed that N input (but not P) had a significant influence on CWM GS and CWM C-strategy. In the path analysis on mollusc and insect herbivory, the 4-way interaction [–insects –molluscs N P] was significant, thus shown in **c-f** are plots without N and P input, and with both N and P input. Both community properties were estimated with PGLS, taking phylogeny into account. Trend lines were estimated with a simple bivariate linear model. A solid line shows a significant association ($p < 0.05$), a dashed line shows non-significance.

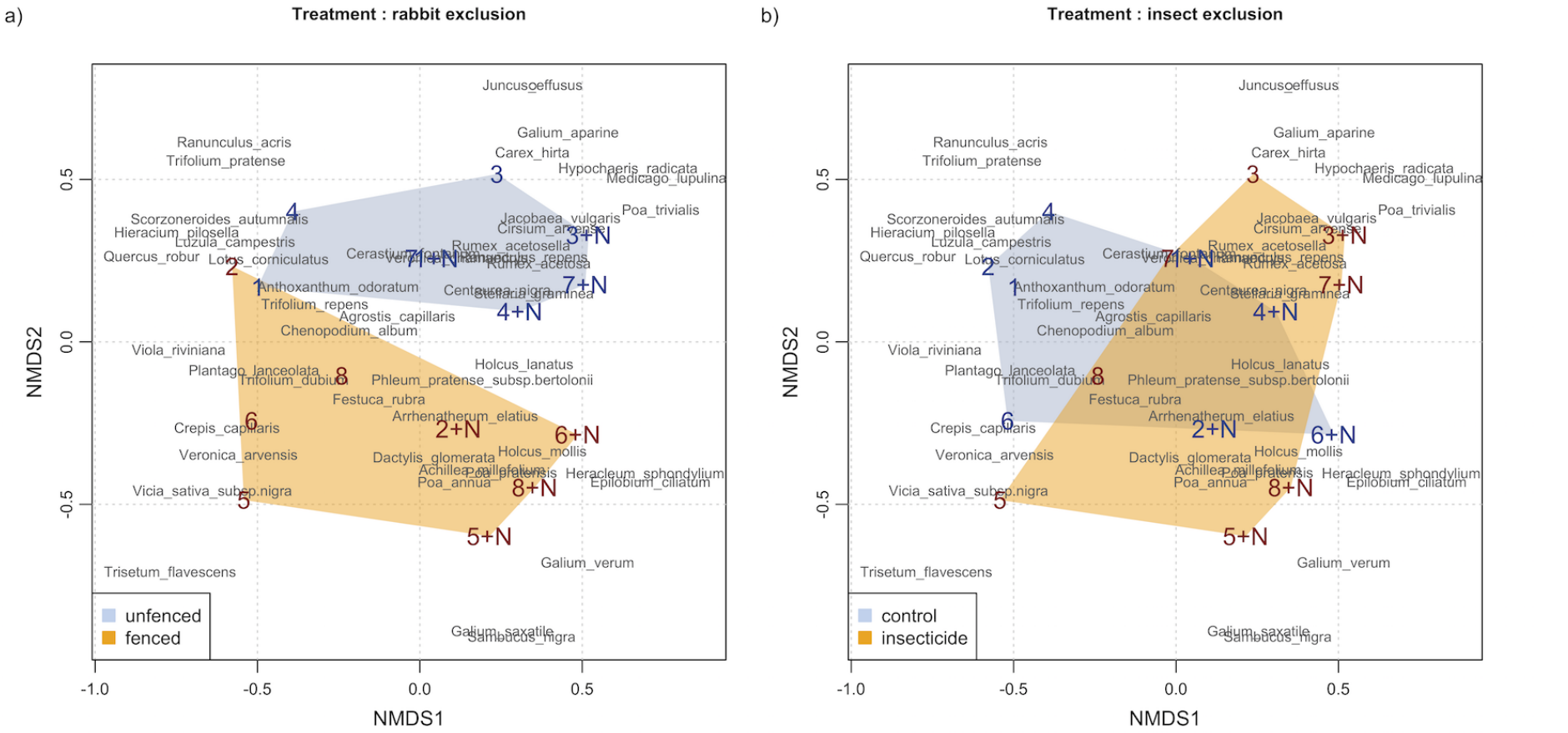
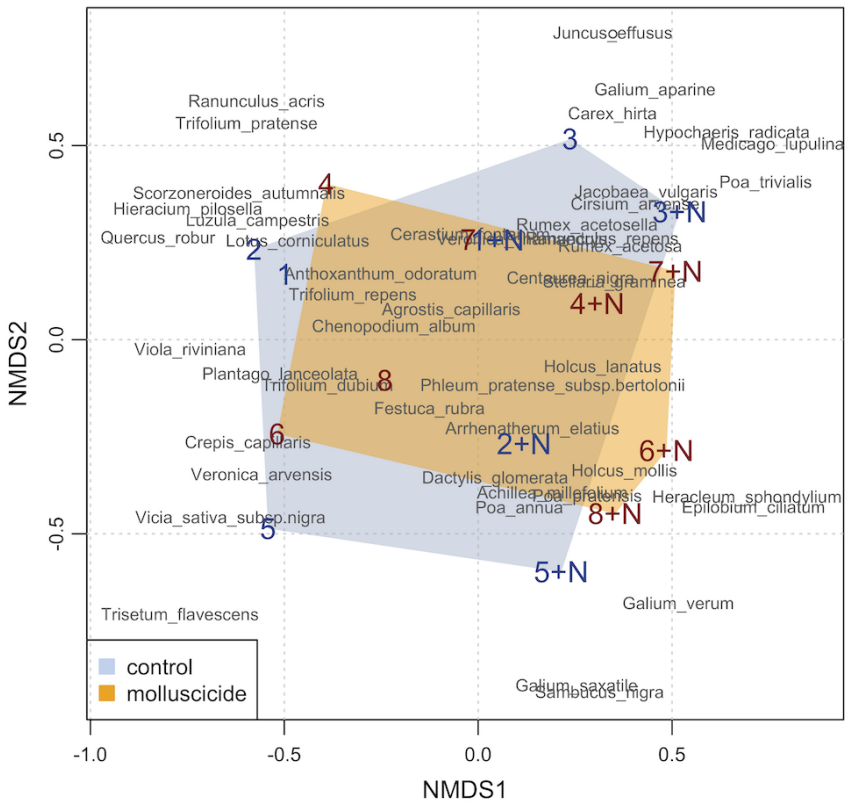


Fig. SI.7 Non-metric multidimensional scaling (NMDS) biplots showing species abundances in two-dimensional space. Stress = 0.173. Experimental treatments are coded as follows: 1 = control (no treatments); 2 = fencing; 3 = insecticide; 4 = molluscicide; 5 = insecticide + fencing; 6 = molluscicide + fencing; 7 = insecticide + molluscicide; 8 = no herbivores (insecticide + molluscicide + fencing). For each treatment, there is also an equivalent with N fertilizer (+ N). Convex hull polygons delineate experimental treatments and the plant species found within them: **a**) ± fencing (rabbit exclusion); **b**) ± insect exclusion; **c**) ± mollusc exclusion; and **d**) ± N fertilizer. See Table SI.12 for species lists with mean percent change in biomass.

c)


Treatment : mollusc exclusion
Juncus_effusus
Galium_aparine
Ranunculus_acris
Carex_hirta
Trifolium_pratense
Hypochaeris_radicata
Medicago_lupulina
Poa_trivialis
Scorzoneroides_autumnalis
Jacobaea_vulgaris
Hieracium_pilosella
Cirsium_arvense
Luzula_campestris
Rumex_acetosella
Quercus_robur
Lotus_corniculatus
Cerastium_fontanum
Ranunculus_repens
Rumex_acetosa
Anthoxanthum_odoratum
Centaurea_nigra
Stellaria_graminea
Trifolium_repens
Agrostis_capillaris
Chenopodium_album
Viola_riviniana
Holcus_lanatus
Plantago_lanceolata
Trifolium_dubium
Phleum_pratense_subsp.bertolonii
Festuca_rubra
Arrhenatherum_elatius
Crepis_capillaris
Veronica_arvensis
Dactylis_glomerata
Holcus_mollis
Achillea_millefolium
Poa_pratensis
Heracleum_sphondylium
Poa_annua
Epilobium_ciliatum
Vicia_sativa_subsp.nigra
Galium_verum
Trisetum_flavescens
Galium_saxatile
Sambucus_nigra
control
molluscicide
NMDS1
NMDS2
-1.0
-0.5
0.0
0.5

d)

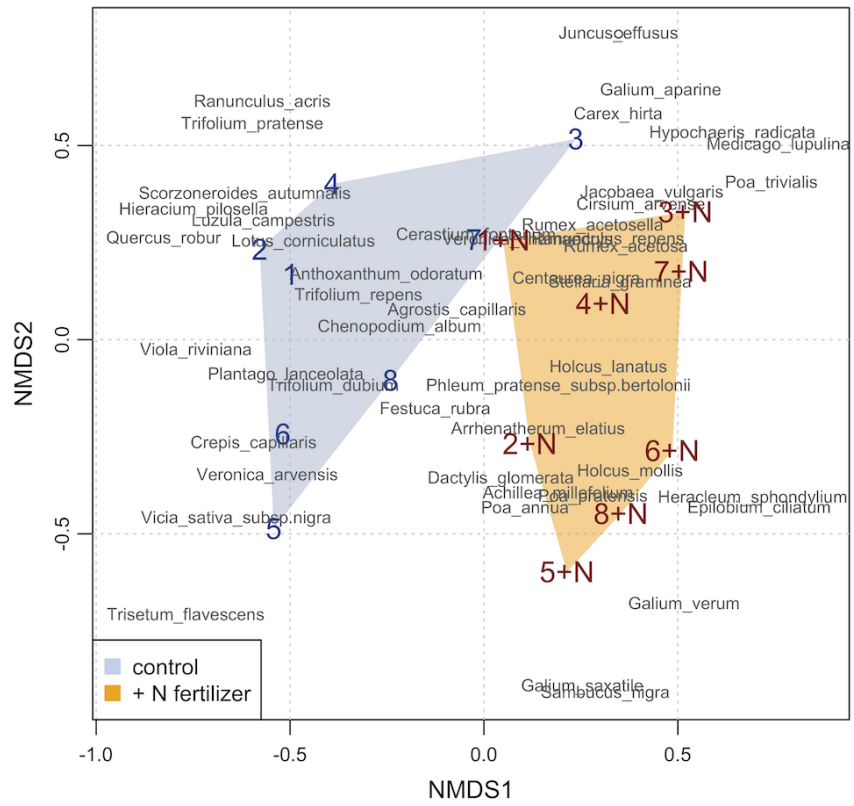

Treatment : N fertilizer
Juncus_effusus
Galium_aparine
Ranunculus_acris
Carex_hirta
Trifolium_pratense
Hypochaeris_radicata
Medicago_lupulina
Poa_trivialis
Scorzoneroides_autumnalis
Jacobaea_vulgaris
Hieracium_pilosella
Cirsium_arvense
Luzula_campestris
Rumex_acetosella
Quercus_robur
Lotus_corniculatus
Cerastium_fontanum
Ranunculus_repens
Rumex_acetosa
Anthoxanthum_odoratum
Centaurea_nigra
Stellaria_graminea
Trifolium_repens
Agrostis_capillaris
Chenopodium_album
Viola_riviniana
Holcus_lanatus
Plantago_lanceolata
Trifolium_dubium
Phleum_pratense_subsp.bertolonii
Festuca_rubra
Arrhenatherum_elatius
Crepis_capillaris
Veronica_arvensis
Dactylis_glomerata
Holcus_mollis
Achillea_millefolium
Poa_pratensis
Heracleum_sphondylium
Poa_annua
Epilobium_ciliatum
Vicia_sativa_subsp.nigra
Galium_verum
Trisetum_flavescens
Galium_saxatile
Sambucus_nigra
control
+ N fertilizer
NMDS1
NMDS2
-1.0
-0.5
0.0
0.5

Table SI.1 (**A**) Flow cytometry results for 36 species collected at Nash's field, Silwood Park, showing the mean estimated 1C-value in picograms (pg) obtained, number of plants measured (n), standard deviation in 1C-value (sdev), and mean target and standard coefficients of variation (CoV). 1C-values were estimated using a Partec CyFlow Space flow cytometer fitted with a Cobalt Samba green (532 nm, 100 mW) laser. Internal standards were either parsley (*Petroselinum crispum* "Champion Moss Curled"; 1C=2.22 pg), pea (*Pisum sativum* "Minerva Maple"; 1C=4.86 pg), tomato (*Solanum lycopersicum*, 1C= 0.98 pg), or rice (*Oryza sativa*; 1C = 0.5 pg) (the 1C-values for the calibration standards were taken from Pellicer and Leitch [2]), and samples were prepared with Galbraith's or LB01 buffers. For some species several flow cytometry runs were made using different calibration standards. These are indicated in the final column below, while the results of all individual flow cytometry runs used to calculate the Mean 1C-values together with the calibration standard used are given in Table SI.1 (B). Note that for species with a high CoV (e.g. > 5 - 8 %), we used the Prime C-value from the Plant DNA C-values database [3]. See Table SI.1 (B) for flow cytometry output of each sample run. The species' C-values used in the statistical analyses are shown in Table SI.2.

Taxon	Mean 1C-value (pg)	n	Sdev	Mean target CoV	Mean standard CoV	Calibration standard(s)
Achillea millefolium	7.98	3	0.03	3.16	3.40	Pea
Agrostis capillaris	3.60	8	0.25	4.43	4.37	Parsley, pea
Anthoxanthum odoratum	7.28	3	0.36	4.05	4.27	Parsley, pea
Arrhenatherum elatius	8.58	3	0.47	3.73	4.71	Parsley, pea
Carex muricata	0.38	7	0.01	6.52	4.61	Parsley, rice, tomato
Centaurea nigra	2.13	2	0.29	7.17	6.23	Pea
Cerastium fontanum	3.23	2	0.20	4.29	3.68	Parsley, pea
Chenopodium album	1.95	1	NA	6.76	6.84	Rice
Cirsium arvense	1.48	1	NA	4.64	3.74	Pea
Crepis capillaris	2.45	2	0.13	8.50	5.81	Pea
Dactylis glomerata	4.44	2	0.21	4.60	5.20	Parsley
Festuca rubra	7.31	2	0.02	5.25	5.46	Pea
Galium aparine	1.11	1	NA	6.88	5.14	Parsley
Galium saxatile	1.72	1	NA	4.21	2.44	Pea
Galium verum	2.25	1	NA	6.99	8.67	Pea
Heracleum sphondylium	2.46	2	0.15	5.09	5.26	Rice, pea
Hieracium pilosella	3.52	2	0.05	6.46	6.95	Parsley
Holcus lanatus	1.70	1	NA	4.14	2.94	Parsley
Holcus mollis	4.03	3	0.04	6.30	7.31	Parsley
Jacobaea vulgaris	2.30	3	0.11	4.21	4.46	Rice, pea
Juncus effusus	0.28	2	0.02	5.37	4.61	Parsley, rice
Lotus corniculatus	1.30	4	0.05	4.75	4.41	Parsley, rice
Luzula campestris	0.40	2	0.01	5.54	4.32	Parsley, tomato
Medicago lupulina	0.55	1	NA	15.07	4.82	Parsley
Phleum pratense subsp. *bertolonii*	1.88	3	0.08	3.13	3.54	Parsley, pea, rice
Plantago lanceolata	1.43	2	0.03	4.99	4.79	Parsley, rice
Poa trivialis	2.01	4	0.02	4.41	3.68	Pea
Ranunculus acris	4.98	2	0.13	3.79	4.24	Parsley
Ranunculus repens	11.06	2	0.14	5.68	5.69	Pea

Table SI.1 (A) continued

Taxa	Mean 1C-value (pg)	n	Sdev	Mean target CoV	Mean standard CoV	Calibration standard(s)
Rubus sp.	0.87	1	NA	19.0	6.72	Parsley
Rumex acetosella	1.07	2	0.01	7.50	6.00	Parsley
Stellaria graminea	1.01	4	0.05	4.22	4.59	Rice, pea
Trifolium repens	1.12	2	0.02	6.41	6.11	Parsley
Veronica chamaedrys	2.16	2	0.02	5.02	3.80	Pea
Vicia sativa subsp. *nigra*	2.21	2	0.02	6.71	5.80	Pea
Viola riviniana	1.48	2	0.15	6.93	4.08	Parsley, pea

Table SI.1 (**B**) Flow cytometry output of individual samples run to estimate the mean 1C-values (pg) of the 36 species given in Table SI.1 (A). It gives the peak values of the target and standard obtained from the flow histograms. The table shows the standard used in each sample and the 1C-value (pg) of the calibration standard used. The target 1C-value is estimated as: (target peak/standard peak) x standard 1C-value. Also shown are the coefficients of variation (CoV) of the target and standard peaks, the estimated genome size (1C-value in pg) of the target.

Taxon	Standard	Standard 1C-value	Target peak	Standard peak	Target 1C-value	Target CoV	Standard Cov
Achillea millefolium	pea	4.86	385.12	235.34	7.95	3.58	3.48
Achillea millefolium	pea	4.86	392.75	239.76	7.96	3.64	3.14
Achillea millefolium	pea	4.86	415.56	251.92	8.02	2.27	3.57
Agrostis capillaris	parsley	2.22	163.54	110.84	3.28	4.58	4.72
Agrostis capillaris	parsley	2.22	287.30	188.10	3.39	3.83	3.60
Agrostis capillaris	parsley	2.22	262.84	166.78	3.50	4.89	5.15
Agrostis capillaris	parsley	2.22	314.98	199.81	3.50	4.51	4.35
Agrostis capillaris	parsley	2.22	198.60	124.31	3.55	4.51	4.51
Agrostis capillaris	parsley	2.22	182.58	111.21	3.64	4.17	4.95
Agrostis capillaris	pea	4.86	201.59	248.93	3.94	4.20	4.23
Agrostis capillaris	pea	4.86	135.91	166.02	3.98	4.77	3.44
Anthoxan. odoratum	parsley	2.22	345.25	110.73	6.92	3.52	4.42
Anthoxan. odoratum	parsley	2.22	346.00	105.60	7.27	4.86	3.56
Anthoxan. odoratum	pea	4.86	289.27	184.06	7.64	3.77	4.82
Arrhenatherum elatius	parsley	2.22	373.76	99.72	8.32	3.50	7.50
Arrhenatherum elatius	parsley	2.22	214.89	55.02	8.67	2.66	3.01
Arrhenatherum elatius	pea	4.86	253.04	140.42	8.76	5.03	3.63
Carex muricata	tomato	0.98	28.60	77.04	0.36	6.37	5.05
Carex muricata	rice	0.50	106.00	140.35	0.38	6.70	4.74
Carex muricata	rice	0.50	108.35	142.57	0.38	6.55	4.44
Carex muricata	parsley	2.22	18.01	104.53	0.38	6.35	4.97
Carex muricata	parsley	2.22	18.21	105.08	0.38	6.79	4.80
Carex muricata	parsley	2.22	18.14	104.03	0.39	6.52	4.91
Carex muricata	rice	0.50	44.81	57.70	0.39	6.36	3.36
Centaurea nigra	pea	4.86	54.17	137.08	1.92	6.41	5.44
Centaurea nigra	pea	4.86	82.71	172.37	2.33	7.93	7.01
Cerastium fontanum	parsley	2.22	96.75	69.51	3.09	5.00	4.52
Cerastium fontanum	pea	4.86	100.63	144.80	3.38	3.57	2.83
Chenopodium album	rice	0.50	143.70	36.78	1.95	6.76	6.84
Cirsium arvense	pea	4.86	58.16	191.51	1.48	4.64	3.74
Crepis capillaris	pea	4.86	100.14	206.88	2.35	10.37	6.06
Crepis capillaris	pea	4.86	78.48	150.03	2.54	6.63	5.55
Dactylis glomerata	parsley	2.22	232.63	120.30	4.29	5.05	5.55
Dactylis glomerata	parsley	2.22	192.52	93.11	4.59	4.15	4.84
Festuca rubra	pea	4.86	267.44	178.24	7.29	5.27	5.34
Festuca rubra	pea	4.86	247.31	164.12	7.32	5.22	5.94

Table SI.1 (B) continued

Taxon	Standard	Standard 1C-value	Target peak	Standard peak	Target 1C-value	Target CoV	Standard Cov
Galium aparine	parsley	2.22	68.14	136.37	1.11	6.88	5.14
Galium saxatile	pea	4.86	172.61	488.13	1.72	4.21	2.44
Galium verum	pea	4.86	67.42	145.49	2.25	6.99	8.67
Heracleum sphondylium	rice	0.50	232.10	49.37	2.35	4.72	5.25
Heracleum sphondylium	pea	4.86	78.63	148.95	2.57	5.46	5.26
Hieracium pilosella	parsley	2.22	221.55	141.21	3.48	6.98	8.36
Hieracium pilosella	parsley	2.22	247.57	154.92	3.55	5.94	5.54
Holcus lanatus	parsley	2.22	147.43	192.18	1.70	4.14	2.94
Holcus mollis	parsley	2.22	245.02	136.48	3.99	6.48	6.43
Holcus mollis	parsley	2.22	121.87	66.82	4.05	5.91	7.51
Holcus mollis	parsley	2.22	244.91	133.96	4.06	6.52	7.99
Jacobaea vulgaris	pea	4.86	72.75	161.09	2.19	4.55	2.60
Jacobaea vulgaris	rice	0.50	113.51	24.88	2.28	4.03	4.93
Jacobaea vulgaris	pea	4.86	97.01	194.88	2.42	4.05	5.86
Juncus effusus	rice	0.50	48.33	88.89	0.27	5.66	5.58
Juncus effusus	parsley	2.22	13.78	103.51	0.30	5.08	3.63
Lotus corniculatus	parsley	2.22	119.58	212.15	1.25	5.34	4.94
Lotus corniculatus	parsley	2.22	140.90	243.72	1.28	4.27	3.17
Lotus corniculatus	rice	0.50	142.91	54.75	1.31	6.17	5.13
Lotus corniculatus	parsley	2.22	153.43	248.56	1.37	3.20	4.40
Luzula campestris	tomato	0.98	24.97	63.08	0.39	5.51	5.16
Luzula campestris	parsley	2.22	21.58	119.88	0.40	5.56	3.48
Medicago lupulina	parsley	2.22	37.89	153.10	0.55	15.07	4.82
Phleum pratense subsp. *bertolonii*	parsley	2.22	111.21	135.99	1.82	4.31	3.54
Phleum pratense subsp. *bertolonii*	rice	0.50	223.27	59.97	1.86	2.32	3.89
Phleum pratense subsp. *bertolonii*	pea	4.86	57.84	142.53	1.97	2.76	3.18
Plantago lanceolata	rice	0.50	112.71	39.86	1.41	4.81	5.84
Plantago lanceolata	parsley	2.22	73.44	112.44	1.45	5.17	3.73
Poa trivialis	pea	4.86	82.92	204.13	1.97	4.37	3.57
Poa trivialis	pea	4.86	82.49	198.88	2.02	4.84	3.74
Poa trivialis	pea	4.86	87.99	212.11	2.02	4.97	4.60
Poa trivialis	pea	4.86	118.46	283.72	2.03	3.47	2.81
Ranunculus acris	parsley	2.22	213.90	97.20	4.89	4.01	3.84
Ranunculus acris	parsley	2.22	186.99	81.93	5.07	3.57	4.63
Ranunculus repens	pea	4.86	251.80	111.63	10.96	6.81	7.18
Ranunculus repens	pea	4.86	545.29	237.58	11.15	4.54	4.19
Rubus sp.	parsley	2.22	14.93	38.12	0.87	19.00	6.72
Rumex acetosella	parsley	2.22	67.70	141.90	1.06	7.03	4.50
Rumex acetosella	parsley	2.22	90.73	186.81	1.08	7.97	7.49
Stellaria grmainea	pea	4.86	53.99	244.42	1.07	3.87	3.44
Stellaria grmainea	rice	0.50	125.98	65.74	0.96	4.91	4.75
Stellaria grmainea	rice	0.50	117.22	58.72	1.00	4.30	5.58
Stellaria grmainea	rice	0.50	105.17	52.09	1.01	3.80	4.57

Table SI.1 (B) continued

Taxon	Standard	Standard 1C-value	Target peak	Standard peak	Target 1C-value	Target CoV	Standard Cov
Trifolium repens	parsley	2.22	71.51	143.44	1.11	6.51	6.53
Trifolium repens	parsley	2.22	75.88	148.80	1.13	6.30	5.68
Veronica chamaedrys	pea	4.86	88.21	199.93	2.14	4.65	3.30
Veronica chamaedrys	pea	4.86	112.32	250.77	2.18	5.39	4.29
Vicia sativa subsp. *nigra*	pea	4.86	86.23	191.09	2.19	7.20	6.15
Vicia sativa subsp. *nigra*	pea	4.86	90.78	198.60	2.22	6.21	5.44
Viola riviniana	parsley	2.22	92.46	150.05	1.37	5.96	3.31
Viola riviniana	pea	4.86	60.17	185.61	1.58	7.90	4.84

Table SI.2 Angiosperm Phylogeny Group IV family [4], genome size (1C-value), C-S-R type and competitive (C)-strategy for each species in the dataset (n=56). In bold are the 12 species with ≥ 1% mean biomass on at least two herbivore exclusion treatment plots, and which comprise the data analysed using PGLMMs. Where applicable, the column "Dif." shows the difference between the C-value that we used to analyse our data, and the C-value that we obtained with flow cytometry. When empty, this indicates we estimated the taxon's C-value by flow cytometry following field sampling at Nash's field, Silwood Park. The remaining 1C-values were obtained from the Plant DNA C-values database [3] (The original reference for the GS data if taken from the C-values database are given in the column labelled 'Ref.'). They were taken from the database when our coefficient of variations were >5-8%, or when we were unable to estimate a C-value with flow cytometry (difference = NA).

Taxon	Family (n=25)	C-S-R type	C-strategy	1C-value (pg)	Dif. (pg)	Ref.*
Achillea millefolium	Aster.	CSR	0.333	7.98	-	-
Agrostis capillaris	**Poa.**	**CSR**	**0.333**	**3.60**	**-**	-
Anthoxanthum odoratum	Poa.	SR/CSR	0.117	7.28	-	-
Aphanes microcarpa	Rosa.	SR	0	0.58	NA	1
Arrhenatherum elatius	**Poa.**	**C/CSR**	**0.667**	**8.58**	**-**	-
Carex hirta	Cyper.	C/CSR	0.667	0.53	NA	2
Carex muricata	Cyper.	S/CSR	0.167	0.38	-	-
Centaurea nigra	Aster.	CSR	0.333	1.80	0.33	3
Cerastium fontanum	Caryophy.	R/CSR	0.167	3.24	-	-
Chenopodium album	Amaranth.	CR	0.5	1.63	0.32	4
Cirsium arvense	**Aster.**	**C**	**1**	**1.42**	**0.06**	**5**
Crepis capillaris	Aster.	R/SR	0	2.10	0.35	6
Dactylis glomerata	**Poa.**	**C/CSR**	**0.667**	**4.40**	**0.04**	**7, 8**
Epilobium ciliatum	Onagr.	R/CSR	0.167	0.53	NA	9
Festuca rubra	**Poa.**	**CSR**	**0.333**	**7.31**	**-**	-
Galium aparine	Rubia.	CR	0.5	1.03	0.08	10
Galium saxatile	Rubia.	S/CSR	0.167	1.45	0.27	10
Galium verum	Rubia.	SC/CSR	0.417	1.89	0.36	11
Heracleum sphondylium	Apia.	C/CSR	0.667	2.19	0.27	12
Hieracium pilosella	Aster.	S/CSR	0.167	3.45	0.07	13
Holcus lanatus	**Poa.**	**CSR**	**0.333**	**1.70**	**-**	-
Holcus mollis	**Poa.**	**C/CSR**	**0.667**	**4.03**	**-**	-
Hypochaeris radicata	Aster.	CSR	0.333	1.34	NA	14
Jacobaea vulgaris	**Aster.**	**R/CR**	**0.417**	**2.25**	**0.05**	**10**
Juncus effusus	Junca.	C/SC	0.75	0.3	-0.02	15
Lotus corniculatus	Faba.	S/CSR	0.167	1.3	-	-
Luzula campestris	Cyper.	S/CSR	0.167	0.49	-0.1	16
Malva moschata	Malva.	C/CSR	0.667	1.10	NA	28, 29
Medicago lupulina	Faba.	R/CSR	0.167	0.65	-0.1	11
Phleum pratense* subsp. *bertolonii	**Poa.**	**CSR**	**0.167**	**1.88**	**-**	-
Plantago lanceolata	**Planta.**	**CSR**	**0.333**	**1.43**	**-**	-
Poa annua	Poa.	R	0	2.88	NA	-

Table SI.2 continued

Taxon	Family (n=25)	C-S-R type	C-strategy	1C-value (pg)	Dif. (pg)	Ref.
Poa pratensis	Poa.	CSR	0.333	4.24	NA	17
Poa trivialis	Poa.	R/CSR	0.167	2.01	-	-
Potentilla erecta	Rosa.	S/CSR	0.167	0.45	NA	18
Quercus cerris	Faga.	SC	0.5	0.95	NA	19
Quercus robur	Faga.	SC	0.5	0.93	NA	20
Ranunculus acris	Ranun.	CSR	0.333	4.98	-	-
Ranunculus bulbosus	Ranun.	SR	0	5.63	NA	21
Ranunculus repens	Ranun.	CR	0.5	11.2	-0.14	21
Rubus sp.	Rosa.	SC	0.5	0.7	0.17	12, 30
Rumex acetosa	**Polygon.**	**CSR**	**0.333**	**1.65**	**NA**	**22**
Rumex acetosella	Polygon.	SR/CSR	0.117	1.68	-0.61	23
Sambucus nigra	Adoxa.	C	1	15.25	NA	24
Scorzoneroides autumnalis	Aster.	R/CSR	0.167	1.16	NA	12
Stellaria graminea	Caryophy.	CSR	0.333	1.01	-	-
Stellaria media	Caryophy.	R	0	1.05	NA	1
Taraxacum officinale	Aster.	R/CSR	0.167	1.28	NA	23
Trifolium dubium	Faba.	R/SR	0	0.73	NA	25
Trifolium pratense	Faba.	CSR	0.333	0.43	NA	25
Trifolium repens	Faba.	CR/CSR	0.417	1.12	-	25
Trisetum flavescens	Poa.	CSR	0.333	2.55	NA	10
Veronica arvensis	Planta.	SR	0	0.33	NA	26
Veronica chamaedrys	**Planta.**	**CSR**	**0.333**	**2.16**	**-**	**-**
Vicia sativa subsp. *nigra*	Faba.	R/CSR	0.25	2.25	-0.04	27
Viola riviniana	Viola.	S/CSR	0.167	1.35	0.12	3

Notes:

Dactylis glomerata: two references listed in the Plant DNA C-values database, both with the same C-value of 1C = 4.4 pg.

*Malva moschata***:** mean of *M. parviflora* (28) and *M. sylvestris* (29).

Rubus sp.: mean of *R. chamaemorus* (30)*, R. idaeus* (12), and of own measurement.

***Original sources for each C-value:**

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Table SI.3 Conditional independence claims tested in the context of path analyses. Each number refers to a hypothetical directed acyclic path diagram (Fig. SI.3). The d-*sep* path analysis method tests conditional independence between parameters in a path diagram. For example, the conditional independence between community-weighted mean genome size and community-weighted mean C-strategy, given the experimental treatment (i.e. herbivory and nutrient input), can be drawn as genome size ← treatment → competition, and written as: (genome size, competition) | {treatment}[3). Independence between these two community properties is tested while holding experimental treatment constant i.e.: community-weighted mean C-strategy is a function of herbivory, nutrient treatment, and community-weighted mean genome size (competition ~ treatment + genome size). If the p-value for the coefficient of community-weighted mean genome size is below the alpha level ($p \leq 0.05$), this indicates that genome size and C-strategy are not independent of each other for a given experimental treatment.

Each conditional independence claim (set of parameters *not* connected by a path) in a path model is tested in this way to calculate its p-value. A variable may function as a dependent variable (e.g. C-strategy as a function of genome size and the experimental treatments), or as predictor (e.g. C-strategy as a predictor of total biomass). Fisher's C-statistic [5] is calculated from the p-values of the conditional independencies and the Chi-square distributed parameter *k*, which is equal to the number of conditional independencies in the model. The hypothetical path model is rejected when the C-statistic is below the alpha p-value, meaning that useful information is contained in one or more of the missing paths. Another goodness-of-fit statistic is the C-statistic Information Criterion (CICc) [6, 7] which takes into account sample size and the number of parameters in the model.

The experimental treatments were fitted as N x P x herbivore exclusion + K + herbicide (where each is a binary factor, except for herbicide, which is a three-level factor). In terms of the coefficients and p-values returned for each community property, this is equivalent to scoring the experiment as a single factor variable with eight levels in the rabbit exclusion experiment and 16 levels in the ± insects ± molluscs experiment, with additional information on their interactions, while controlling for K and herbicide treatments. We thus have a total of five parameters: the experiment, community-weighted mean genome size, community-weighted mean C-strategy, total biomass, and phylogenetic diversity.

Shown below are the p-values obtained for each conditional independence claim, which were tested with generalised least squares (GLS) with ten different variance structures (varID): 1) plot; 2) N; 3) P; 4) herbivore treatment (HT); 5) N + herbivore treatment; 6) N + P; 7) plot * N; 8) herbivore treatment * N; 9) plot * herbivore treatment * N; 10) herbivore treatment * P * N; and, 11) no variance structure. If the varID column = na, no variance structures were applied. This was assessed by whether it contributed to 1) a lower AICc, and 2) whether the difference in AICc was significant ($p \leq 0.05$) with an ANOVA test. GS= community-weighted mean

genome size of each plot, PD= phylogenetic diversity, BM= total plot biomass, C = mean weighted competitive (C)- strategy of each plot also estimated by PGLS; exp = experimental treatment, i.e.: herbivore * N * P + K. HT = herbivore treatment.

Table SI.3 (A) ± Rabbits:

			± Rabbits			
No.	Conditional independence claim	Claim test	p-value: LME	p-value: LME + varID	varID	ANOVA
1	(GS, PD | exp, C	PD ~ exp + C + GS	0.3594	na	na	na
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
	(BM, PD) | exp, C	PD ~ exp + C + BM	0.5556	na	na	na
2	(GS, PD | exp, C	PD ~ exp + C + GS	0.3594	na	na	na
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.5664	na	na	na
3	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.5664	na	na	na
4	(GS, PD) | exp, BM	PD ~ exp + BM + GS	0.1101	na	na	na
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
	(C, PD) | exp, GS, BM	PD ~ exp + GS + BM + C	0.3084	na	na	na
5	(GS, PD) | exp, C, BM	PD ~ exp + C + BM + GS	0.3799	na	na	na
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
6	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.5664	na	na	na
7	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001

Table SI.3 (A) continued ± Rabbits

8	(GS, PD | exp, C	PD ~ exp + C + GS	0.3594	na	na	na
	(GS, C) | exp	C ~ exp + GS	<0.0001	0.0043	plot*HT*N	<0.0001
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
9	(BM, PD) | exp, C	PD ~ exp + C + BM	0.5556	na	na	na
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.1547	na	na	na
	(C, BM) | exp, GS	BM ~ exp + GS + C	0.0055	0.0088	N+P	<0.0001
10	(GS, PD) | exp	PD ~ exp + GS	0.0485	na	na	na
	(BM, PD) | exp, C	PD ~ exp + C + BM	0.5556	na	na	na
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.1547	na	na	na
11	(BM, PD) | exp, C	PD ~ exp + C + BM	0.5556	na	na	na
	(exp, GS) | PD, C, BM	GS ~ PD + C + BM + exp	<0.0001	<0.0001	plot*HT*N	<0.0001
12	(C, PD) | exp, GS	PD ~ exp + GS + C	0.1547	na	na	na
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.5664	na	na	na
13	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.5664	na	na	na
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.5934	0.7363	N+P	<0.0001
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.1547	na	na	na
14	(GS, PD) | exp	PD ~ exp + GS	0.0485	na	na	na
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.5664	na	na	na
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.1547	na	na	na

Table SI.3 (B) Conditional independence claim tests on plots with ± insects ± molluscs. See Fig. SI.3 for path diagrams being tested below.

± insects ± molluscs

No.	Conditional independence claim	Claim test	p-value: LME	p-value: LME + varID	varID	ANOVA
1	(GS, PD | exp, C	PD ~ exp + C + GS	0.1395	0.0648	HT	0.0163
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
	(BM, PD) | exp, C	PD ~ exp + C + BM	0.2439	0.2556	HT	0.0322
2	(GS, PD | exp, C	PD ~ exp + C + GS	0.1395	0.0648	HT	0.0163
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.1625	0.1778	HT	0.0163
3	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.1625	0.1778	HT	0.0163
4	(GS, PD) | exp, BM	PD ~ exp + BM + GS	0.0587	0.1018	HT	0.0161
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
	(C, PD) | exp, GS, BM	PD ~ exp + GS + BM + C	0.7011	0.7335	HT	0.0163
5	(GS, PD) | exp, C, BM	PD ~ exp + C + BM + GS	0.1025	0.0473	HT	0.0163
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
6	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.1625	0.1778	HT	0.0163
7	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001

Table SI.3 (B) continued ± insects ± molluscs

8	(GS, PD | exp, C	PD ~ exp + C + GS	0.1395	0.0648	HT	0.0163
	(GS, C) | exp	C ~ exp + GS	<0.0001	0	plot*N* P	<0.0001
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
9	(BM, PD) | exp, C	PD ~ exp + C + BM	0.2439	0.2556	HT	0.0322
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.3676	0.8739	HT	0.0163
	(C, BM) | exp, GS	BM ~ exp + GS + C	<0.0001	0	N*P	<0.0001
10	(GS, PD) | exp	PD ~ exp + GS	0.0593	0.0449	HT	0.0116
	(BM, PD) | exp, C	PD ~ exp + C + BM	0.2439	0.2556	HT	0.0322
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.3676	0.8739	HT	0.0163
11	(BM, PD) | exp, C	PD ~ exp + C + BM	0.2439	0.2556	HT	0.0322
	(exp, GS) | PD, C, BM	GS ~ PD + C + BM + exp	<0.0001	<0.0001	plot+N	0.0006
12	(C, PD) | exp, GS	PD ~ exp + GS + C	0.3676	0.8739	HT	0.0163
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.1625	0.1778	HT	0.0163
13	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.1625	0.1778	HT	0.0163
	(GS, BM) | exp, C	BM ~ exp + C + GS	0.0625	0.5167	N*P	<0.0001
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.3676	0.8739	HT	0.0163
14	(GS, PD) | exp	PD ~ exp + GS	0.0593	0.0449	HT	0.0116
	(BM, PD) | exp, GS, C	PD ~ exp + GS + C + BM	0.1625	0.1778	HT	0.0163
	(C, PD) | exp, GS	PD ~ exp + GS + C	0.3676	0.8739	HT	0.0163

Table SI.4 Summary path model goodness-of-fit statistics: Fisher's C-statistic and CICc (C-statistic information criterion) and p-values. P-values above the alpha value (0.05) indicate the conditional independencies are satisfied and the model is a plausible model. The column "V, A" shows the number of vertices and number of arrows for each acyclic path diagram.

± Rabbits					± insect ± molluscs				
No.	V, A	C	p-value	CIC	No.	V, A	C	p-value	CIC
1	5, 7	4.266	0.641	30.648	1	5, 7	12.306	0.055	37.47
2	5, 8	3.184	0.528	31.984	2	5, 8	7.573	0.109	34.937
3	5, 8	2.181	0.703	30.981	3	5, 8	9.178	0.057	36.542
4	5, 7	7.808	0.931	34.19	4	5, 7	11.926	0.064	37.09
5	5, 8	2.979	0.561	31.779	5	5, 8	10.101	0.039	37.464
6	5, 9	1.137	0.566	32.393	6	5, 9	3.634	0.163	33.213
7	5, 9	1.044	0.593	32.3	7	5, 9	5.545	0.163	35.123
8	5, 7	21.511	0.001	47.893	8	5, 7	32.51	<0.0001	57.674
9	5, 7	15.328	0.018	41.71	9	5, 7	27.85	<0.0001	53.014
10	5, 6	12.005	0.151	36.005	10	5, 6	16.019	0.042	39
11	5, 8	19.596	0.001	48.396	11	5, 8	21.243	<0.0001	48.606
12	5, 8	4.869	0.301	32.232	12	5, 8	5.636	0.228	32.999
13	5, 7	5.913	0.433	32.295	13	5, 7	11.18	0.083	36.344
14	5, 7	10.923	0.091	36.087	14	5, 7	11.286	0.08	36.45

Table SI.5 (**A**) Logistic PGLMM: MCMCglmm output where absence/presence (0/1) of the abundant species (n=12) were fitted as a function of genome size (GS), herbivore and nutrient treatment. Insect, rabbit and mollusc exclusion, N, P, and K are scored as ± binary factors. Baseline levels are the untreated plots (i.e. without fencing, without insecticide, without molluscicide and without fertilizer). Random effects (G-structure) account for experimental design, repeated measurements, and phylogenetic correlation. The posterior mean shows the log odds; and means (categorical variables) and slopes (continuous variables) were estimated as the sum of the posterior means for all parameters involved: e.g.: the slope of –rabbits : GS = [GS + (–rabbits:GS)]. These values were transformed with inverse logit [4] to obtain the probability. ":" in the fixed effects denotes an interaction.

G-structure:	Posterior mean	95% Credible intervals	Eff. sample size
plot	0.614	3.11E-04, 2.10	4940
plot : fencing	0.327	2.77E-04, 1.06	4940
species	5.291	3.57E-04, 13.38	4940
phylogeny	5.781	2.02E-04, 25.07	4940

Fixed effects:	Posterior mean	95% Credible intervals	Eff. sample size	pMCMC	Mean or slope	Probability
Intercept	-0.659	-4, 2.99	4940	0.6332	-0.659	0.341
GS	-0.028	-0.84, 0.72	4940	0.9490	-0.028	0.493
– insects	**2.127**	**0.24, 4.27**	**4940**	**0.0425**	**1.469**	**0.813**
N	-0.401	-1.04, 0.25	4572	0.2304	-1.060	0.257
– molluscs	0.782	-1.2, 2.7	4550	0.3818	0.123	0.531
– rabbits	-1.207	-2.61, 0.06	4940	0.0664	-1.866	0.134
P	0.061	-0.34, 0.48	4940	0.7696	-0.598	0.355
K	-0.241	-0.52, 0.04	4940	0.0850	-0.900	0.289
– insects : GS	-0.032	-0.2, 0.14	5153	0.6988	-0.060	0.485
GS : N	0.140	-0.12, 0.41	5288	0.2988	0.113	0.528
– insects : N	-0.431	-1, 0.19	4940	0.1672	0.636	0.654
– molluscs : GS	**-0.266**	**-0.44, -0.11**	**4940**	**0.0020**	**-0.294**	**0.427**
– molluscs : N	0.357	-0.2, 0.96	4913	0.2308	0.079	0.520
– rabbits : GS	**0.322**	**0.15, 0.49**	**4940**	**< 0.0002**	**0.294**	**0.573**
– rabbits : N	-0.269	-0.8, 0.36	4940	0.3563	-2.537	0.073
GS : P	0.096	-0.08, 0.26	4940	0.2502	0.068	0.517
N : P	-0.247	-0.84, 0.29	4940	0.3968	-1.246	0.223
– insects – molluscs	-1.149	-3.96, 1.52	4687	0.3458	1.102	0.751
– molluscs – rabbits	0.920	-1.21, 2.61	4940	0.2413	-0.164	0.459
– insects – rabbits	-0.784	-2.88, 0.97	4940	0.3057	-0.523	0.372
– insects : N : GS	0.124	-0.11, 0.36	4940	0.3008	0.205	0.551
– molluscs : N : GS	-0.018	-0.26, 0.2	4940	0.8656	-0.172	0.457
– rabbits : GS : N	0.054	-0.18, 0.28	4940	0.6526	0.488	0.620
GS : N : P	-0.121	-0.35, 0.12	4940	0.3219	0.088	0.522
–insects –molluscs –rabbits	0.375	-2.15, 3.17	4940	0.7194	0.405	0.600

Table SI.5 (**B**) Linear PGLMM: MCMCglmm output in which species biomass > 0 was fitted with a Gaussian distribution. Biomass was log-transformed. G-structure shows the variance of the random effects. R-structure = residual variance. GS = genome size. The effects of each category were estimated as the combined effect of all posterior means (coefficients) involved; e.g. change in slope for GS:N:P = GS:N + GS:P + GS:N:P. These effect values were then exponentiated to estimate percent change, where change in percent = 100(exp(effect) – 1).

G-structure:	Posterior mean	95% Credible intervals	Eff. sample size
plot	0.041	1.49E-04, 0.17	4940
plot : fencing	0.145	1.85E-04, 0.42	4940
species	0.391	1.79E-04, 1.75	4940
phylogeny	1.826	3.73E-04, 4.56	4598

R-structure:	Posterior mean	95% Credible intervals	Eff. sample size
units	3.797	3.46, 4.14	5284

Fixed effects:	Posterior mean	95% Credible intervals	Eff. sample size	pMCMC	Effect	exp(Effect)
Intercept	-0.955	-2.8, 0.71	4940	0.2397	-0.955	0.3850
GS	**0.482**	**0.17, 0.86**	**4940**	**0.0057**	**0.482**	**1.6187**
– insects	0.240	-0.74, 1.3	4940	0.6061	0.240	1.2716
N	**0.845**	**0.21, 1.53**	**4940**	**0.0105**	**0.845**	**2.3291**
– molluscs	0.667	-0.31, 1.73	4423	0.1575	0.667	1.9479
– rabbits	-0.740	-1.7, 0.31	5049	0.1458	-0.740	0.4772
P	0.217	-0.19, 0.6	4940	0.2858	0.217	1.2428
K	-0.172	-0.42, 0.07	4940	0.1891	-0.172	0.8423
– insects : GS	-0.108	-0.26, 0.04	4940	0.1640	-0.108	0.8976
GS : N	**-0.268**	**-0.5, -0.03**	**4940**	**0.0243**	**-0.268**	**0.7653**
– insects : N	0.085	-0.53, 0.62	4940	0.7806	1.171	3.2245
– **molluscs : GS**	**-0.150**	**-0.31, -0.01**	**4940**	**0.0466**	**-0.150**	**0.8604**
– molluscs : N	-0.459	-1.04, 0.11	4940	0.1178	1.053	2.8660
– **rabbits : GS**	**0.191**	**0.05, 0.33**	**4940**	**0.0117**	**0.191**	**1.2099**
– rabbits : N	-0.108	-0.68, 0.46	4940	0.7130	-0.002	0.9977
GS : P	-0.053	-0.2, 0.09	4940	0.4830	-0.053	0.9484
N : P	0.238	-0.35, 0.81	5100	0.4198	1.301	3.6735
– insects – molluscs	-0.190	-1.54, 1.11	4940	0.7696	0.717	2.0489
– molluscs – rabbits	0.206	-1.13, 1.53	4940	0.7235	0.133	1.1417
– insects – rabbits	-0.035	-1.43, 1.25	4940	0.9696	-0.535	0.5859
– insects : N : GS	0.012	-0.18, 0.23	4940	0.9154	-0.364	0.6952
– molluscs : N : GS	-0.124	-0.32, 0.09	4940	0.2296	-0.542	0.5815
– rabbits : GS : N	0.156	-0.05, 0.36	4940	0.1304	0.079	1.0827
GS : N : P	-0.183	-0.4, 0.01	4940	0.0781	-0.503	0.6045
– insects – molluscs – rabbits	0.238	-1.57, 2.1	5148	0.7814	0.386	1.4711

Table SI.6 Step-wise model reduction with AIC and p-values of each assessed parameter in testing community-weighted mean genome size. This table shows interactions and variables that have been removed because they do not have a significant influence on the dependent variable. The beginning, most complex model included all four-way interactions between herbivore exclusion treatments and the fertilizers N and P.

Parameter	change in AIC	p-value
K	2	0.8217
Mg	2	0.8801
slope	2.1	0.3934
herbicide	1.1	0.2313
– rabbits – molluscs – insects : N	2	0.9931
– rabbits – molluscs – insects : P	1.9	0.7825
– rabbits – molluscs: N : P	1.3	0.3900
– rabbits – insects : N : P	1.6	0.5406
– molluscs – insects : N : P	1.8	0.6457
– rabbits – molluscs – insects	1.4	0.4503
– rabbits – insects : N	0.9	0.2899
– rabbits – molluscs: P	2	0.9833
– rabbits – insects : P	2	0.9911
– molluscs – insects : P	0.6	0.2342
– rabbits : N : P	1.1	0.3468
– molluscs : N : P	0.1	0.1699
– insects : N : P	1.1	0.3400
– rabbits – insects	2	0.8222
– rabbits : P	-0.5	0.1124
– molluscs : P	-0.7	0.0992
– insects : P	1.9	0.7700
N : P	1.4	0.4489

Table SI.7 Effects of experimental treatment (herbivore exclusion and N and P input) on community-weighted mean genome size (CWM GS). CWM GS (1C-value) on plots with all herbivores and no nutrient input (control plots) = 5.76 pg. The model shows a significant decrease in CWM GS with N fertilizer and rabbit and mollusc exclusion (= +N plots with insect grazing only) to 4.22 pg; and with N fertilizer and mollusc and insect exclusion (= +N plots with rabbit grazing only) to 3.03 pg. CI= 95% confidence intervals. CWM GS estimated using PGLS.

	LME						ANOVA	
	Coef.	CI	Std. error	t-value	p-value	CWM GS (pg)	F value	Pr(>F)
Intercept	5.759	5.02, 6.50	0.453	12.721	< 0.00001	5.76	na	na
– rabbits	1.106	0.26, 1.95	0.485	2.280	0.0538	6.86	27.265	0.0019
– molluscs	-1.013	-2.05, 0.02	0.636	-1.593	0.1465	4.75	6.971	0.0566
– insects	-0.285	-1.15, 0.58	0.534	-0.533	0.6174	5.47	0.474	0.5283
+ N	-1.868	-2.42, -1.32	0.281	-6.636	< 0.00001	3.89	184.67	< 0.00001
+ P	-0.312	-0.54, -0.08	0.117	-2.669	0.0078	5.45	7.125	0.0078
– rabbits – molluscs	0.679	-0.52, 1.88	0.690	0.985	0.3544	6.53	0.017	0.9007
– rabbits : N	1.097	0.46, 1.73	0.325	3.374	0.0008	6.09	4.588	0.0327
– molluscs: N	-0.355	-1.14, 0.43	0.401	-0.885	0.3765	2.52	0.989	0.3206
– molluscs – insects	-0.330	-1.55, 0.90	0.760	-0.434	0.6826	4.13	0.286	0.6207
– insects : N	-0.315	-0.95, 0.32	0.325	-0.969	0.3329	3.29	2.927	0.0877
– rab – mol: N	-1.190	-2.10, -0.28	0.468	-2.540	0.0114	4.22	6.453	0.0114
– mol – ins : N	1.433	0.52, 2.35	0.469	3.054	0.0024	3.03	9.327	0.0024

Table SI.8 Means and standard deviations of community-weighted mean genome size (CWM GS) (1C-value, pg), total biomass, number of species and phylogenetic diversity of plots, shown for each of eight herbivore treatments and ± nitrogen (N) treatment (n = the number of plots included in the analysis of each treatment, out of a total of 556 plots). Control = no treatment (i.e. all herbivores present and no fertilizer input).

Herbivore treatment	N	CWM GS (pg)	Total biomass (g)	Number of species	Phylogenetic diversity	n
Control (all herbivores)	–	5.59 ± 1.43	33.14 ± 15.17	9 ± 2	57.03 ± 12.56	36
– insects	–	5.33 ± 1.68	59.79 ± 23.72	8 ± 3	50.42 ± 14.12	36
– molluscs	–	4.77 ± 1.53	29.79 ± 10.34	9 ± 3	54.03 ± 16.64	36
– rabbits	–	6.72 ± 1.34	43.29 ± 11.23	7 ± 2	41.36 ± 13.05	36
– molluscs – rabbits	–	6.19 ± 1.42	65.79 ± 15.97	8 ± 3	49.5 ± 15.23	36
– insects – molluscs	–	3.78 ± 1.33	48.72 ± 18.59	11 ± 2	65.37 ± 11	30
– insects – rabbits	–	6.42 ± 1.2	52.93 ± 17.3	6 ± 2	37.86 ± 9.75	36
No herbivores	–	5.92 ± 1.26	57.58 ± 15.11	9 ± 2	55.76 ± 12.86	33
All herbivores present	+	3.6 ± 1.96	46.4 ± 24.39	8 ± 3	50.97 ± 15.13	36
– insects	+	3.27 ± 1.7	78.23 ± 31.46	7 ± 3	43.61 ± 14.87	36
– molluscs	+	2.44 ± 1.09	43.61 ± 16.7	8 ± 3	48.72 ± 14.54	36
– rabbits	+	6.07 ± 2.33	76.92 ± 21.44	5 ± 2	28.42 ± 11.19	36
– molluscs – rabbits	+	3.98 ± 1.46	83.85 ± 23.41	6 ± 2	36.25 ± 13.73	36
– insects – molluscs	+	2.82 ± 1.27	74.63 ± 31.13	8 ± 2	54.07 ± 12.08	29
– insects – rabbits	+	5.21 ± 1.81	90.3 ± 30.56	5 ± 1	27.36 ± 8.96	36
no herbivores	+	4.62 ± 1.28	100.83 ± 26.24	6 ± 2	33.47 ± 10.54	32

Table SI.9 Most reduced linear mixed effect model output showing the effects of experimental treatments on three alternative estimations of community-weighted mean genome size (CWM GS). Prior to model reduction, CWM GS was estimated for each plot: **A**) CWM GS was estimated without accounting for phylogenetic non-independence (i.e. it is simply weighted by species biomass). Similar to the community-weighted means estimated in the main text, GS was log10-transformed prior to the estimation, and back-transformed for ease of interpretation and comparison; **B**) CWM GS estimated with PGLS as described in the text, however GS was *not* log-transformed; **C**) CWM GS was log10-transformed and estimated with PGLS, however the lambda parameter was allowed to be estimated (rather than fixed at 1 which assumes a Brownian motion of evolution). The last column contains the estimated CWM GS (1C-value in pg) of plots under each of the treatments on left. This table shows that LME output is very similar between different estimations, the key results remaining unchanged. See also Fig. SI.4.

A)

CWM GS, without phylogeny						
	Coef.	CI	Std. error	t-value	p-value	Mean GS (pg)
Intercept	5.669	5.02, 6.31	0.387	14.644	< 0.0001	5.67
– rabbits	0.962	0.21, 1.71	0.447	2.154	0.0650	6.63
– molluscs	-0.751	-1.65, 0.15	0.541	-1.388	0.1987	4.92
– insects	-1.530	-1.94, -1.12	0.213	-7.196	< 0.0001	4.14
+ N	-0.287	-1.02, 0.45	0.443	-0.648	0.5477	5.38
+ P	-0.197	-0.44, 0.05	0.126	-1.568	0.1175	5.47
– rabbits – molluscs	0.442	-0.60, 1.48	0.622	0.711	0.4997	6.32
– rabbits : N	1.050	0.57, 1.53	0.246	4.277	< 0.0001	7.39
– molluscs: N	-0.470	-1.06, 0.12	0.303	-1.554	0.1208	4.16
– molluscs – insects	-0.429	-1.47, 0.62	0.629	-0.683	0.5266	2.96
– insects : N	-0.365	-0.84, 0.11	0.246	-1.487	0.1376	3.49
– rabbits : P	-0.390	-0.73, -0.05	0.177	-2.208	0.0277	6.04
– rab – mol : N	-1.021	-1.71, -0.33	0.354	-2.885	0.0041	5.59
– mol – ins : N	1.188	0.50, 1.88	0.355	3.352	0.0009	3.02

B)

CWM GS estimated with PGLS, GS untransformed						
	Coef.	CI	Std. error	t-value	p-value	Mean GS (pg)
Intercept	6.419	5.73, 7.11	0.410	15.676	< 0.0001	6.42
– rabbits	0.810	0.03, 1.59	0.469	1.728	0.1087	7.23
– molluscs	-0.996	-1.96, -0.03	0.575	-1.732	0.1078	5.42
– insects	-0.307	-2.55, -1.53	0.469	-0.654	0.5248	6.11
+ N	-2.040	-1.09, 0.48	0.263	-7.76	< 0.0001	4.38
+ P	-0.352	-0.56, -0.14	0.109	-3.217	0.0014	6.07
– rabbits – molluscs	0.643	-0.48, 1.76	0.667	0.964	0.3530	6.88
– rabbits : N	1.297	0.70, 1.89	0.304	4.272	< 0.0001	6.49
– molluscs: N	-0.517	-1.25, 0.21	0.374	-1.381	0.1680	2.87
– molluscs – insects	-0.250	-1.37, 0.87	0.667	-0.375	0.7136	4.87
– insects : N	-0.284	-0.88, 0.31	0.304	-0.935	0.3503	3.79
– rab – mol : N	-0.980	-1.83, -0.13	0.438	-2.241	0.0255	4.64
– mol – ins : N	1.309	0.46, 2.16	0.438	2.988	0.0029	3.33

Table SI.9 continued

c) CWM GS estimated with PGLS, lambda parameter optimised

	Coef.	CI	Std. error	t-value	p-value	Mean GS (pg)
Intercept	5.598	4.86, 6.33	0.445	12.569	< 0.0001	5.60
– rabbits	0.890	0.04, 1.74	0.493	1.806	0.1081	6.49
– molluscs	-0.981	-1.99, 0.03	0.615	-1.593	0.1462	4.62
– insects	-0.405	-1.24, 0.43	0.511	-0.793	0.4658	5.19
+ N	-1.300	-1.85, -0.75	0.282	-4.613	< 0.0001	4.30
+ P	0.041	-0.32, 0.40	0.186	0.222	0.8246	5.64
– rabbits – molluscs	0.806	-0.36, 1.97	0.682	1.182	0.2737	6.31
– rabbits : N	1.086	0.51, 1.66	0.298	3.650	0.0003	6.27
– molluscs: N	-0.252	-0.97, 0.47	0.370	-0.680	0.4965	3.07
– molluscs – insects	-0.223	-1.40, 0.96	0.725	-0.308	0.7713	3.99
– insects : N	-0.193	-0.77, 0.39	0.298	-0.649	0.5168	3.70
– rabbits : P	-0.497	-0.92, -0.08	0.215	-2.315	0.0210	6.03
+ N + P	-0.507	-0.92, -0.09	0.215	-2.355	0.0189	3.83
– rab – molluscs: N	-1.484	-2.32, -0.65	0.430	-3.450	0.0006	4.36
– mol – insects: N	1.065	0.23, 1.91	0.431	2.470	0.0139	5.18

Table SI.10 Linear model output for each for the community properties in the path analysis model in Fig. 2 **(± rabbits**). CW = community-weighted.

Community-weighted mean genome size (1C-value, pg)

	Estimate	Std. Error	95% CI	t value	Pr(>|t|)
Intercept	5.124	1.020	3.24, 7.06	5.021	0.0188
– rabbits	1.339	1.277	-1.08, 3.76	1.049	0.4664
N	-1.694	0.404	-2.47, -0.92	-4.195	0.0001
P	-0.100	0.412	-0.9, 0.7	-0.243	0.8088
K	-0.137	0.247	-0.61, 0.34	-0.552	0.5820
– grass (herbicide)	0.741	0.511	-0.24, 1.72	1.45	0.1973
– forbs (herbicide)	1.025	0.511	0.04, 2.01	2.007	0.0916
– rabbits : N	1.344	0.466	0.44, 2.24	2.881	0.0047
– rabbits : P	-0.433	0.466	-1.33, 0.47	-0.928	0.3550
N : P	-0.594	0.466	-1.49, 0.31	-1.274	0.2049

Community-weighted mean C-strategy

	Estimate	Std. Error	95% CI	t value	Pr(>|t|)
Intercept	0.365	0.069	0.21, 0.52	5.311	0.0693
– rabbits	0.042	0.032	-0.02, 0.1	1.308	0.2034
N	0.089	0.028	0.04, 0.15	3.22	0.0016
P	0.011	0.027	-0.04, 0.06	0.43	0.6681
K	0.030	0.016	0, 0.06	1.84	0.0681
– grass (herbicide)	-0.063	0.028	-0.11, -0.01	-2.207	0.0648
– forbs (herbicide)	-0.002	0.029	-0.05, 0.05	-0.057	0.9560
CW mean genome size	0.025	0.005	0.02, 0.04	4.674	< 0.0001
– rabbits : N	-0.023	0.031	-0.09, 0.03	-0.743	0.4590
– rabbits : P	0.001	0.030	-0.06, 0.06	0.025	0.9799
N : P	0.009	0.030	-0.05, 0.07	0.286	0.7756

Total biomass (g/m^2)

	Estimate	Std. Error	95% CI	t value	Pr(>|t|)
Intercept	14.037	10.186	-5.47, 34.86	1.378	0.2688
– rabbits	10.212	8.795	-9.14, 29.35	1.161	0.4068
N	8.978	4.172	0.98, 16.92	2.152	0.0332
P	5.427	4.219	-2.63, 13.48	1.287	0.2005
K	3.614	2.551	-1.28, 8.47	1.417	0.1589
– grass (herbicide)	3.522	2.972	-2.23, 9.34	1.185	0.2381
– forbs (herbicide)	0.293	2.937	-5.45, 6	0.1	0.9207
CW mean C-strategy	37.640	12.292	14.06, 62.69	3.062	0.0027
– rabbits : N	19.974	4.773	10.85, 29.08	4.185	0.0001
– rabbits : P	-5.440	4.773	-14.55, 3.68	-1.14	0.2565
N : P	5.272	4.772	-3.83, 14.39	1.105	0.2713

Table SI.10 continued

Phylogenetic diversity

	Estimate	Std. Error	95% CI	t value	Pr(>|t|)
Intercept	65.081	4.336	56.05, 72	15.009	< 0.0001
– rabbits	-15.477	3.656	-22.16, -9.54	-4.233	0.0003
N	-3.143	3.240	-9.63, 2.88	-0.97	0.3339
P	-0.101	3.284	-6.5, 6.21	-0.031	0.9756
K	-2.653	1.981	-6.61, 1.05	-1.339	0.1830
– grass (herbicide)	7.998	3.042	3.77, 12.66	2.629	0.0398
– forbs (herbicide)	-5.469	3.027	-10, -1.18	-1.807	0.1223
CW mean C-strategy	-21.259	8.239	-30.36, -2.28	-2.58	0.0139
– rabbits : N	-6.666	3.715	-13.9, 0.47	-1.794	0.0752
– rabbits : P	2.620	3.715	-4.52, 9.85	0.705	0.4821
N : P	-3.964	3.714	-11.12, 3.25	-1.067	0.2879

Table SI.11 Linear mixed effect model output for each of the community properties in the path analysis in Fig. 3 **(± insects ± molluscs**). CW= community-weighted, CI = confidence intervals.

Community-weighted mean genome size (1C-value, pg)

	Estimate	Std. Error	95% CI	t-value	p-value
Intercept	6.943	0.777	5.70, 8.18	8.934	0.0001
– insects	-0.771	1.075	-2.48, 0.94	-0.718	0.5035
– molluscs	-0.938	1.075	-2.65, 0.77	-0.873	0.4208
N	-0.483	0.446	-1.34, 0.37	-1.084	0.2796
P	-0.697	0.449	-1.56, 0.16	-1.55	0.1223
K	-0.043	0.169	-0.37, 0.28	-0.253	0.8004
– grass (herbicide)	0.158	0.264	-0.36, 0.67	0.6	0.5583
– forbs (herbicide)	0.274	0.268	-0.24, 0.80	1.021	0.3244
– insects – molluscs	1.073	1.528	-1.37, 3.50	0.702	0.5117
– insects : N	-0.014	0.630	-1.22, 1.19	-0.023	0.9819
– molluscs : N	-1.448	0.630	-2.66, -0.24	-2.298	0.0224
– insects : P	0.938	0.630	-0.27, 2.15	1.489	0.1379
– molluscs : P	0.824	0.630	-0.38, 2.03	1.308	0.1922
N : P	-0.329	0.630	-1.54, 0.88	-0.523	0.6018
– insects – molluscs : N	0.155	0.907	-1.58, 1.90	0.171	0.8646
– insects – molluscs : P	-1.957	0.905	-3.69, -0.22	-2.162	0.0316
– insects : N : P	-1.096	0.891	-2.8, 0.61	-1.229	0.2202
– molluscs : N : P	-0.224	0.891	-1.93, 1.48	-0.252	0.8016
– insects – molluscs : N : P	2.571	1.284	0.10, 5.02	2.002	0.0464

Community-weighted mean C-strategy

	Estimate	Std. Error	95% CI	t-value	p-value
Intercept	0.406	0.057	0.31, 0.50	7.106	0.0006
– insects	-0.041	0.079	-0.17, 0.08	-0.524	0.6223
– molluscs	-0.031	0.079	-0.16, 0.09	-0.395	0.7089
N	0.088	0.031	0.03, 0.15	2.827	0.0051
P	0.040	0.032	-0.02, 0.10	1.252	0.2118
K	0.014	0.012	-0.01, 0.04	1.207	0.2287
CW mean genome size	0.025	0.004	0.02, 0.03	5.77	0.0000
– grass (herbicide)	-0.088	0.017	-0.12, -0.05	-5.082	0.0002
– forbs (herbicide)	0.000	0.018	-0.04, 0.03	-0.022	0.9829
– insects – molluscs	0.048	0.112	-0.13, 0.23	0.427	0.6862
– insects : N	-0.041	0.044	-0.12, 0.04	-0.92	0.3583
– molluscs : N	-0.009	0.045	-0.09, 0.08	-0.213	0.8318
– insects : P	-0.043	0.044	-0.13, 0.04	-0.975	0.3306
– molluscs : P	-0.049	0.044	-0.13, 0.04	-1.1	0.2724
N : P	-0.036	0.044	-0.12, 0.05	-0.814	0.4165
– insects – molluscs : N	0.125	0.063	0, 0.25	1.966	0.0504
– insects – molluscs : P	0.105	0.064	-0.02, 0.23	1.647	0.1008
– insects : N : P	0.187	0.063	0.07, 0.31	2.987	0.0031
– molluscs : N : P	0.171	0.062	0.05, 0.29	2.745	0.0065
– insects – molluscs : N : P	-0.283	0.090	-0.46, -0.11	-3.129	0.0020

Table SI.11 continued **± insects ± molluscs**

Total biomass (g/m²)

	Estimate	Std. Error	95% CI	t-value	p-value
Intercept	14.923	6.949	2.46, 28.01	2.147	0.0339
– insects	9.157	6.737	-3.23, 21.48	1.359	0.1769
– molluscs	26.591	6.744	14.2, 38.93	3.943	0.0001
N	25.264	6.270	13.38, 37.33	4.029	0.0001
P	-2.659	6.265	-14.59, 9.35	-0.424	0.6717
K	3.595	2.348	-0.87, 8.09	1.531	0.1270
CW mean C-strategy	65.655	11.309	43.63, 85.97	5.806	0.0000
CW mean genome size	-1.570	0.866	-3.17, 0.08	-1.814	0.0709
– grass (herbicide)	4.147	3.638	-2.26, 10.49	1.14	0.2678
– forbs (herbicide)	0.023	3.560	-6.20, 6.24	0.006	0.9950
– insects – molluscs	-23.151	9.747	-41.01, -5.25	-2.375	0.0192
– insects : N	1.492	8.741	-15.25, 18.15	0.171	0.8646
– molluscs : N	-23.804	8.804	-40.62, -7.00	-2.704	0.0073
– insects : P	9.271	8.778	-7.54, 25.99	1.056	0.2919
– molluscs : P	-0.815	8.774	-17.63, 15.9	-0.093	0.9261
N : P	7.572	8.741	-9.16, 24.24	0.866	0.3872
– insects – molluscs : N	24.815	12.639	0.82, 49.08	1.963	0.0507
– insects – molluscs : P	-2.824	12.695	-26.92, 21.53	-0.222	0.8241
– insects : N : P	-2.374	12.567	-26.18, 21.82	-0.189	0.8503
– molluscs : N : P	6.648	12.499	-17.05, 30.69	0.532	0.5953
– insects – molluscs : N : P	-2.636	18.211	-37.68, 31.78	-0.145	0.8850

Phylogenetic diversity

	Estimate	Std.Error	95% CI	t-value	p-value
Intercept	45.363	4.942	37.37, 53.36	9.179	0.0000
– insects	-5.111	6.654	-15.79, 5.57	-0.768	0.4711
– molluscs	7.722	6.654	-2.96, 18.40	1.16	0.2893
N	-12.111	3.353	-18.54, -5.68	-3.612	0.0004
P	1.584	3.380	-4.90, 8.06	0.469	0.6397
K	-3.585	1.272	-6.02, -1.15	-2.818	0.0052
– grass (herbicide)	-0.740	2.503	-5.61, 4.13	-0.295	0.7721
– forbs (herbicide)	-8.265	2.535	-13.18, -3.33	-3.261	0.0056
– insects – molluscs	8.768	9.490	-6.53, 23.99	0.924	0.3896
– insects : N	3.389	4.742	-5.70, 12.48	0.715	0.4755
– molluscs : N	3.167	4.742	-5.92, 12.26	0.668	0.5049
– insects : P	3.222	4.742	-5.87, 12.31	0.68	0.4975
– molluscs : P	0.833	4.742	-8.26, 9.92	0.176	0.8606
N : P	-1.667	4.742	-10.76, 7.42	-0.351	0.7255
– insects – molluscs : N	-10.602	6.827	-23.65, 2.52	-1.553	0.1217
– insects – molluscs : P	1.010	6.817	-12.00, 14.13	0.148	0.8823
– insects : N : P	-1.889	6.706	-14.74, 10.97	-0.282	0.7784
– molluscs : N : P	-6.944	6.706	-19.80, 5.91	-1.036	0.3014
– insects – molluscs : N : P	-1.797	9.674	-20.43, 16.65	-0.186	0.8528

Table SI.12 Change in species mean percent of above-ground biomass, measured as dry weight, per herbivore exclusion treatment, relative to the control plots (plots without herbivore exclusion i.e. plots with rabbits, molluscs, and insects), and by N treatment. Mean percentages were rounded, thus plants with very low biomass may equal to 0.

	– rab	– rab	– rab – mol	– rab –mol	– mol	– mol	– ins – rab	– ins – rab	– ins	– ins	– all	– all	– ins – mol	– ins – mol
	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N
Achillea millefolium	0.4	0	-0.3	-0.2	0.1	-0.2	-0.6	-0.6	-0.6	-0.5	1.9	3.9	-0.6	-0.5
Agrostis capillaris	-7.1	-10.6	-8.5	-12.1	0.9	-1.7	-8.1	-11.8	-8.7	-10.6	-5	-11.9	-6.5	-10.3
Anthoxanthum odoratum	-0.4	-0.8	-0.7	-0.8	0.4	-0.3	-0.6	-0.7	-0.7	-0.8	-0.2	-0.8	-0.8	-0.7
Aphanes microcarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arrhenatherum elatius	17.9	26.6	-3.3	-5.9	-3.3	-8.1	-0.5	0.6	6.3	2.1	0.7	-3.7	-1.6	-3
Carex hirta	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0
Carex muricata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Centaurea nigra	0.3	0	0	0	0	1.1	0	0	0	0	0	0	0	0
Cerastium fontanum	0	-0.2	0	-0.2	0	-0.1	0	-0.2	0	-0.2	0	-0.2	0	-0.2
Chenopodium album	-0.3	0	-0.3	0.1	-0.3	0	-0.3	0	-0.3	0	-0.3	0	-0.3	0
Cirsium arvense	-1.1	-4.3	-0.2	-3.5	-1	-2.2	-1.1	-4	3.7	2.6	-0.8	-4	2.8	-0.6
Crepis capillaris	0	-0.1	1.3	-0.1	0.2	0	0.2	-0.1	0	0	0.2	-0.1	0	-0.1
Dactylis glomerata	0.3	0.3	7	7.4	0	0	3	2.7	2.8	0.8	2.3	1.8	0.1	0
Epilobium ciliatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Festuca rubra	-5.4	5.2	8.4	2.5	-6	-13.2	7.6	15	-4.5	-8.3	-7.6	-7.6	-24.3	-21.1
Galium aparine	0	0	0	0	0	0	0	0	0.2	0.1	0	0	0	0
Galium saxatile	0	0	0	0	0	0	0.7	2.3	0	0	0	0	0	0
Galium verum	0	0	0	0	0	0	0	0	0	0	0	0.7	0	0
Heracleum sphondylium	0	0	0	0.6	0	0	0	0	0	0	0	0	0	0
Hieracium pilosella	0	0	-0.1	0	-0.1	0	-0.1	0	-0.1	0	-0.1	0	-0.1	0
Holcus lanatus	-3.8	-13	-3.8	-4.1	6	18.2	-1.9	-15.3	1	3.3	1.1	-11.5	7.1	7.3
Holcus mollis	1.1	1.8	1.9	17.6	1.5	6.4	3	14.4	-0.5	7.4	6.7	34.5	8.1	15.9

Table SI.12 continued

	– rab	– rab	– rab – mol	– rab –mol	– mol	– mol	– ins – rab	– ins – rab	– ins	– ins	– all	– all	– ins – mol	– ins – mol
	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N
Hypochaeris radicata	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0
Jacobaea vulgaris	-1.3	-0.6	-1.3	-0.6	-1	-0.5	-1.3	-0.6	1.5	4	-1.3	-0.6	12.1	13
Juncus effusus	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Lotus corniculatus	0.5	0	-0.1	0	-0.1	0	-0.1	0	-0.1	0	0.1	0	0.4	0
Luzula campestris	-0.7	-0.1	-1.3	-0.1	-0.5	-0.1	-1.3	-0.1	-1.3	-0.1	-1.3	-0.1	-1	-0.1
Malva moschata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phleum pratense subsp. *bertolonii*	0	0	0.1	1.7	3.1	1.3	0	0.5	0.1	0.3	1.2	1.7	0.7	0
Plantago lanceolata	-0.4	-0.2	0.3	-0.1	-0.4	-0.2	0.2	-0.2	-0.4	-0.2	-0.1	-0.2	-0.3	-0.2
Poa annua	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Poa pratensis	0.7	0.1	-0.1	1.4	-0.1	0.4	0	2.1	0	0.9	0.8	1.7	0.6	0.3
Poa trivialis	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0
Potentilla erecta	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus cerris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus robur	0.3	0	0.1	0	0	0	0	0	0	0	0	0	0	0
Ranunculus acris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus bulbosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus repens	-0.3	-0.1	-0.2	0	-0.2	0	-0.3	-0.1	-0.1	0.1	-0.3	-0.1	0.2	0.8
Rubus fruticosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex acetosa	-0.1	-0.3	-0.1	-0.2	0.5	1.1	0	-0.1	0.9	1.3	0.2	-0.3	0.5	0.2
Rumex acetosella	-0.2	-2.2	-0.2	-2.2	-0.2	-1.1	-0.2	-2.2	-0.2	-2	-0.2	-2.2	0.5	-1.5
Sambucus nigra	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scorzoneroides autumnalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stellaria graminea	0.1	-0.2	0	0.1	0.4	0.2	-0.1	-0.3	0	-0.1	0.1	-0.2	0.2	1.1

Table SI.12 continued

	– rab	– rab	– rab – mol	– rab –mol	– mol	– mol	– ins – rab	– ins – rab	– ins	– ins	– all	– all	– ins – mol	– ins – mol
	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N	no N	+ N
Stellaria media	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium dubium	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
Trifolium pratense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium repens	0	0	0	0	0.3	0	0	0	0	0	0.4	0	0.1	0
Trisetum flavescens	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
Veronica arvensis	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
Veronica chamaedrys	-0.9	-1.2	0.3	-1.1	-0.6	-0.9	-0.8	-1.2	0.6	0	-0.3	-0.8	2	-0.1
Vicia sativa subsp.*nigra*	0.3	0.1	1.1	0	0.1	0	2.6	0	0	0	1.7	0	0.2	0
Viola riviniana	0	0	0	0	0	0	0	0	0	0	0	0	0	0

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