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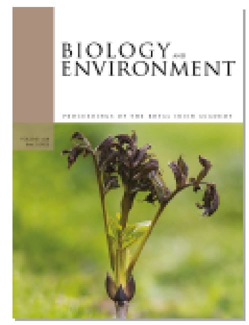

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TWIN PRESSURES OF INTENSIFICATION AND ABANDONMENT NEGATIVELY IMPACT GRASSLAND BIODIVERSITY IN THE BURREN

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ABSTRACT

A major component of Earth's dry surface is human-managed grassland, making the relationships among management actions, grassland biodiversity and ecosystem services of great ecological interest. Common management practices—fertiliser addition and large herbivore grazing—influence grassland diversity and productivity. The Nutrient Network, a distributed research effort, investigates these relationships across grasslands at a global scale. The Burren contains internationally important grasslands with high biodiversity maintained by traditional farming practices. Using six years of data from the Slieve Carran Nutrient Network site, we examine the effects of fertilisation and large mammal herbivory on plant diversity and biomass in a unique Irish context. We find 1) fertiliser addition and herbivore exclusion both decrease diversity and increase biomass, and 2) independent of our experimental treatments, biomass increased throughout the study. Our findings on treatment effects align with results from the wider Nutrient Network experiment. Additionally, the increase in biomass during the study is consistent with an abandonment effect. This research shows twin pressures of agricultural intensification and abandonment of traditional management practises detrimentally impact Burren grassland biodiversity. This is relevant to future management decisions, as biodiversity provides key ecosystem services in the Burren, including supporting tourism that contributes to local economies.

INTRODUCTION

Grasslands are the primary terrestrial land use globally, encompassing over 20% of the world's dry surface (Ramankutty *et al*. 2008). They cover a wide range of habitats and vary greatly in terms of management, productivity, cultural value and conservation status, providing multiple benefits to people (Binder *et al*. 2018; Millennium Ecosystem Assessment 2005). Productive grasslands support livestock and, at the same time, diverse grasslands provide a myriad of regulating, cultural and provisioning ecosystem services (Haughey *et al*. 2018; Allan *et al*. 2015; Balvanera *et al*. 2013). Historically, and through ongoing agricultural changes in the last century, human management affects grassland ecology. Land use changes such as intensification or abandonment, fertilisation and grazing regimes influence the productivity and diversity of grasslands. It is, therefore, important to have both general and site-specific understanding of how management affects the ecological processes that maintain biodiversity, productivity and species composition within grasslands.

DRIVERS OF GRASSLAND PRODUCTIVITY AND DIVERSITY

Two key human influences on grassland ecosystems are nutrient addition and large mammal herbivory. Human activities have greatly increased the availability of nutrients in terrestrial systems (Foley *et al*. 2007), raising primary productivity and reducing species diversity (Crawley *et al*. 2005; Harpole and Tilman 2007). Human alteration of grazing regimes also influences both productivity and biodiversity (Millennium Ecosystem Assessment 2005; Foley *et al*. 2011). Plant species face a trade-off between coping with low nutrient environments and competing for light (Dybzinski and Tilman 2007). When nutrient availability in grassland systems is increased, nutrient-limited species can outcompete their low nutrient-competent neighbours (Hautier *et al*. 2009). At the same time, a trade-off also exists between competing for light and investing in herbivore defences (Lind *et al*. 2013; Grime and Pierce 2012). As a result, even in high nutrient systems, herbivores are expected to 'rescue' (maintain) species diversity by a) creating light availability through disturbance and biomass removal and b) selectively grazing on species with lower herbivory defence (Borer *et al.* 2014). Though there is clear evidence of the relationship between nutrient addition and diversity loss, the underlying mechanism behind this relationship is not always clear (Adler *et al.* 2011; Grace *et al.* 2014). Soil, climate, grazing regime and species identity all influence these relationships (Bakker *et al.* 2006; Dwyer and Laughlin 2017; Faucon *et al.* 2017). While some general ecological patterns have been found in grassland systems, some relationships can be context specific.

THE NUTRIENT NETWORK

The Nutrient Network (NutNet) is a globally distributed collaborative research network established to investigate how nutrient addition and herbivory affect grassland productivity, diversity and composition at the global scale (Borer *et al.* 2014). NutNet uses consistent methodology across environmental gradients with realistic levels of complexity to directly compare the relationship between, and the mechanisms underpinning, productivity and diversity across the globe. When investigating the effects of nutrient addition and herbivory on productivity and diversity, a multi-site study by Borer *et al.* (2014) showed rescue effects of herbivory on grassland diversity in nutrient enhanced systems. In 2015, we established a NutNet site at Slieve Carran to test whether the relationships established in Borer *et al.* (2014) are borne out in the unique context of a highly diverse calcareous Irish grassland. Though the NutNet study sites were designed to be analysed in the context of a globally distributed experiment, it is nonetheless informative to report the striking evidence of how human management alters the grassland ecology in the context of the Burren.

UNIQUE IRISH CONTEXT

The Burren is one of the most unique ecological systems in Europe due to the co-occurrence of artic-alpine and Mediterranean flora which are otherwise geographically and climatically distinct (Webb and Scannell 1983). Covering an area of approximately 350km^2, it is characterised by its landscape of exposed limestone rock and deposited boulder clay, containing low intensity livestock farmland and semi natural grasslands supporting high floral diversity. Some 70% of Ireland's native plant species are found in a land area equating to approximately 1% of the total land area of the island of Ireland (Webb and Scannell 1983).

The Burren's unique hydrology (Drew 1990; Osborne *et al.* 2003), geology (Jeffrey 2003) and cultivation history (Dunford and Feehan 2001) history all contribute to its highly diverse flora. Historically, the Burren comprised a rich soil supporting extensive pine woodlands, which were cleared for cultivation by early farmers, resulting in soil erosion (Feeser and O'Connell 2010, 2009). By the seventeenth century, most of the remaining hazel woodlands were cleared, converting the landscape into a mostly open farmed landscape (Feeser and O'Connell 2009). Permeable limestone rock and shallow soil lead to low water availability during summer months (Drew 1990). Combined with warming characteristics of the exposed rock, relativity high soil temperature is maintained well into the winter months, extending the growing season. These features lead to the locally adapted practice of transhumance or 'winterage', where livestock forage in the lowlands in summer before being moved to the uplands in winter (Dunford and Feehan 2001). Winter grazing prevents dominant plants from monopolising resources, reducing competition for nutrients, light and space (Borer *et al.* 2014; Parr *et al.* 2009). The absence of summer grazers allows flowering plants to thrive, flower and reproduce while physical disturbance and biomass removal through grazing during winter foraging allows for an increase in potential seedling establishment (Jutila and Grace 2002).

In light of agricultural intensification and reduction in traditional land management across Europe (Quintas-Soriano *et al.* 2016; Zabel *et al.* 2019), a mechanistic and context-specific understanding of the drivers of grassland diversity is relevant to navigating environmental and agricultural sustainability issues. Here, we describe the effects of globally important agricultural managements—nutrient addition and large herbivore grazing—on biodiversity and productivity in a species diverse grassland in the Burren.

OTHER BURREN STUDIES

Large herbivore exclosures have been used previously to investigate the relationship between traditional management (grazing) and diversity and productivity in the Burren. Moles *et al.* (2005) found a steep decline in overall plant diversity in a fenced exclosure, with grass species increasing in abundance, concluding that the disturbance provided by grazing animals is integral to the conservation of Burren grassland biodiversity. Deenihan *et al.* (2009), in a follow-up study at the same exclosure, found increased heather and scrub cover and decreased grassland and pavement cover during the fifteen-year exclosure experiment, also concluding that there was a loss of diversity as a result. Notably, a similar (though smaller in scale) shift towards heather and scrub was observed in unfenced plots, suggesting that the traditional management regime within the National Park may not be effective in prevent scrub encroachment. Additionally, over a three-year exclosure experiment, Long (2011) found significant decreases in both plant species richness and Simpson's Diversity Index across four grassland exclosure sites. Long (2011) noted the complete loss of certain species such as *Euphrasia* agg*, Linum catharticum, Odontites vernus* and *Rhinanthus minor* from some or all fenced plots, as well as decreases in *Prunella vulgaris* and both *Trifolium pratense* and *T. repens*. In contrast, a minority of species were found to increase in cover in response to the fencing, including *Potentilla erecta* and *Pteridium aquilinum*, though the most consistent increases were in grass species cover (all species combined). Long (2011) also found significant increases in litter in fenced and, to a lesser extent, unfenced (control) plots.

AIMS

Here, we examine the effects of nutrient addition and exclusion of large herbivores on the productivity and biodiversity in traditionally managed high nature value grassland in the Burren National Park, Co. Clare. We quantified changes in grassland productivity (biomass) and diversity (species richness, Shannon diversity, inverse Simpsons index and species evenness) across treatments over six years to assess the individual and combined effects of fertilisation and grazing. We aim to provide quantitative evidence for the interacting effects of these management actions, and to assess whether general relationships between biodiversity and management actions found in other grassland systems are borne out in the floristically unique grasslands of the Burren.

METHODS

STUDY SITE

The experiment was conducted on calcareous grassland at Slieve Carran (N53.07202, W-8.992624) in the Burren National Park, Co. Clare. The site has been traditionally managed with annual winter cattle grazing, which has been reduced in recent years. The site at the top of a small hillock at an elevation of 112m above sea level, with a mean annual temperature of 9.8 degrees Celsius and 1,320mm of mean annual precipitation. We found 85 vascular plant species during the experiment (Table S4), putting Slieve Carran in the 81st percentile for species richness out of 128 NutNet sites globally. There are two forms of human activity at the study site. 'Management' refers to the National Parks and Wildlife Service (NPWS) traditional winter grazing, and 'treatment' refers to the experimental manipulations (i.e. fencing and nutrient addition) carried out within the context of this grassland study. In addition to the intended experimental treatments, there were unanticipated changes in the management at the site with a reduction in grazing over the course of the experiment.

EXPERIMENTAL TREATMENTS

The experiment was arranged in three blocks, each containing ten 5 x 5m plots. Within each block there is one unfenced control plot, and seven plots each receiving annual addition of a fully factorial fertiliser treatment of Nitrogen (N), Phosphorus (P) and Potassium (K) in single, double and three-way combinations. Each block also has a herbivore exclosure (fenced plot) with NPK addition, and a fenced plot with no added nutrients. Fenced plots were constructed with aviary wire mesh extending 2m in height. Fertiliser was added annually in April as described in Table S1. Permanent plots were established during year one when initial measurements and soil cores (Table S2) were taken prior to treatments being established. Field data were collected in late July and early August and dry weight of biomass obtained. For full details of treatment and data collection, see https://nutnet.org/exp_protocol and https://nutnet.org/nutrients.

DATA COLLECTION AND ANALYSES

Data were collected for one pre-treatment year (2015), and for five subsequent years of experimental manipulation (2016–20). Every year in each plot, we conducted relevés, determining species identity and percent cover in 1 x 1m permanent quadrats, and collected 10cm x 2m biomass strips from successive positions from which we obtained dry weight. We used General Linear Mixed Models (GLMMs) (Bates *et al*. 2015) to determine whether four key treatments—control (i.e. unfenced plots with no nutrient addition), fencing, NPK and NKP + fencing—were associated with changes in biomass, species richness, Shannon diversity, inverse Simpsons index and species evenness over the course of the experiment. We addressed non-independence in the data arising from repeated sampling by including the experimental blocks as random effects in our models and assessing models with multiple optimisers to account for the low number of replicates (three) of the blocks. We also used the 'vegan' community ecology package *(Oksanen et al*. 2020) to apply Permutational Multivariate Analysis of Variance to a Jaccard dissimilarity matrix (Jaccard 1912) to assess whether the treatments and management actions at the site were driving changes in species identity among plots. We concentrate our formal analysis here on the NPK and fence treatments and do not analyse the one-way and two-way nutrient addition treatments here due to lack of power in the site-level experimental design to detect relatively small changes in biomass and diversity. Analyses were done in R Studio version 3.6.3 (R Core Team 2020). All code used in this study is available at DOI: 10.5281/zenodo.6967631.

RESULTS

We found that both productivity and diversity changed at our experimental grassland site over the course of the experiment, with biomass generally increasing and measures of diversity generally decreasing over time (Figure 1). On control plots with no added nutrients, plant biomass increased, species richness showed no significant change, and Shannon diversity and the inverse Simpsons index decreased (Figure 2). In unfenced NPK+ and fenced NPK+, species richness and Shannon diversity decreased significantly over the course of the experiment (Figure 2). For the fenced control with no added nutrients, species richness decreased significantly, while neither biomass, Shannon diversity nor inverse Simpsons index showed significant change (Figure 2). Permutational MANOVA (Figure 3) indicates that fencing and nutrient addition treatments (Pseudo-$F = 6.3036$, $R^2 = 0.218$, $p < 0.001$), year (Pseudo-$F = 7.4012$, $R^2 = 0.096$, $p < 0.001$), and the interaction between them (treatment*-year: Pseudo-$F = 2.5599$, $R^2 = 0.074$, $p < 0.001$) account for over 36% of the variance in species identity among plots (see Figure 4 for snapshot of changes in species identity).

DISCUSSION

There was a clear effect of fertiliser addition and herbivore exclusion on both productivity and biodiversity at Slieve Carran, with the effects of the treatments increasing over time. Metrics of productivity and diversity responded differently to the treatments, but the combination of fencing and nutrient addition was consistently important, decreasing diversity and increasing biomass production. As evidenced by significant increases in unfenced control plot biomass, changes in the site management regime appear to have been affecting the plant community since the beginning of the experiment, highlighting the importance of continued management in maintaining this unique and diverse ecosystem.

Theory predicts that, in grassland ecosystems, nutrient addition will increase productivity by shifting the balance to favour species that have invested in light competition over nutrient capture, leading to decreased diversity (Hautier *et al.* 2009). Theory also predicts that large herbivores will maintain diversity by increasing light availability (Borer *et al.* 2014). Both these predictions are borne out at Slieve Carran, as highlighted by the differences in response to the treatments. The combined fertiliser and fencing treatment had the most immediate, the largest and the most consistent influence across diversity and productivity metrics. In the final year of experimental manipulation (Year 6), unfenced plots with no added nutrients had a median of 30 species, while fenced NPK+ plots had a median of just 5 species. The fenced and fertilised treatment prevents herbivory, and the consequent build-up of biomass reduces light availability under the canopy, while simultaneously increasing soil nutrient availability. These results are consistent with findings from grasslands around the globe (Borer *et al.* 2014) but are particularly notable because of the high biodiversity previously maintained at this site by the traditional winter grazing. The findings are also consistent with other exclosure studies from the Burren (e.g. Long 2011; Deenihan *et al.* 2009; Moles *et al.* 2005), which, though limited to grazing exclusion (i.e. the study did not examine the effects of nutrient addition), demonstrated both significant decreases in plant richness and diversity and shifts in species composition. It is yet unclear whether these effects plateau, or whether continued treatment would continue to increase biomass and decrease diversity. Recent work suggests, however, that low intensity herbivory is unlikely to be able keep pace with increasing biomass arising from sustained nutrient addition, particularly in low nutrient systems (Borer *et al.* 2020).

BIOMASS

Though biomass increased across all treatments, with the largest increases in fenced NPK+ treatments, this increase was not significantly different to the increase across unfenced plots with no added nutrients. The increase in biomass across control plots indicates an abandonment effect, consistent with, albeit not as extreme as, the complete experimental exclusion of large herbivores. Traditional winter grazing has been responsible for maintaining high diversity by increasing light availability through physical disturbance and removal of biomass (i.e. Figure 4). Anecdotal evidence of reduction in this management is consistent with the significant increase in biomass across all plots, including unfenced control plots, throughout the experiment. This experiment has not been running sufficiently long to show succession from grassland to woodland in the non-grazed plots. However, hazel saplings and brambles are emerging across the site, suggesting the potential for the transition to hazel woodland with the long-term decrease in traditional management. As the conservation objective for this site includes restoring ‘favourable conservation condition of semi-natural dry grasslands’ (NPWS 2022), increased intensity of conservation grazing may be needed. If monitoring of the site is maintained as conservation grazing is intensified, it may be possible to investigate whether grazing can provide ‘rescue’ from the effects of fertilisation on diversity.

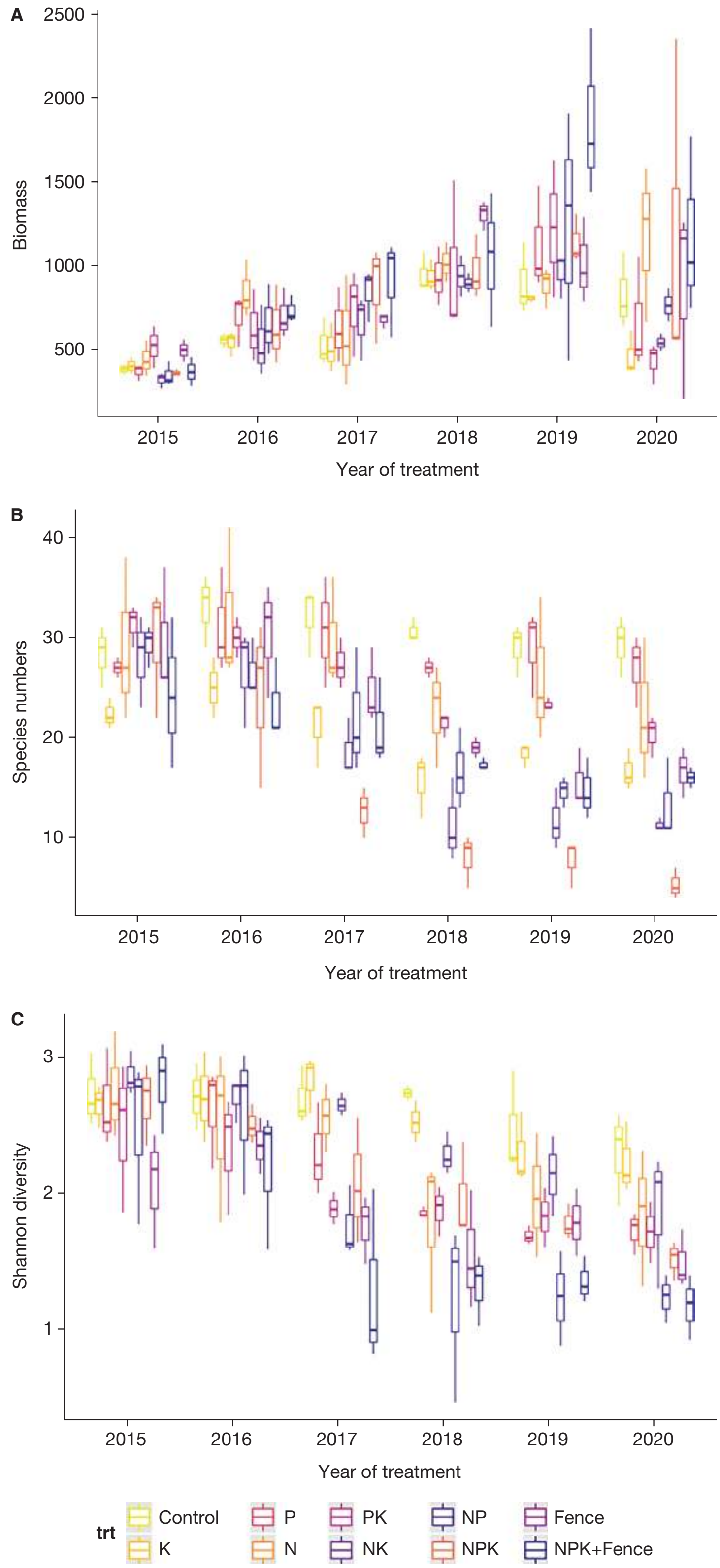


Fig. 1—Grassland biodiversity in experimental plots belonging to the various experimental treatments. Plots based on average values for each treatment over three blocks. Boxes show interquartile range. Central line shows median. Whiskers show 1.5 times the interquartile range. Colours correspond to treatments as described in legend.

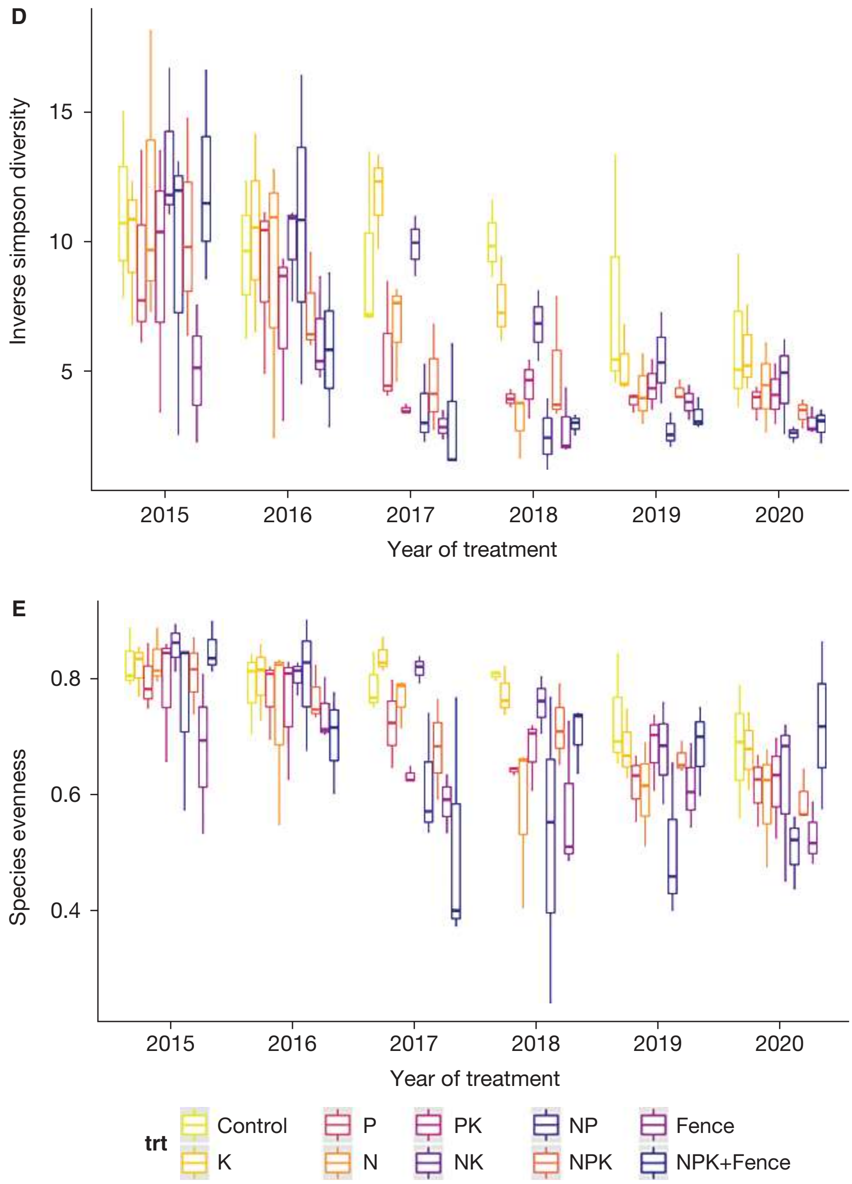
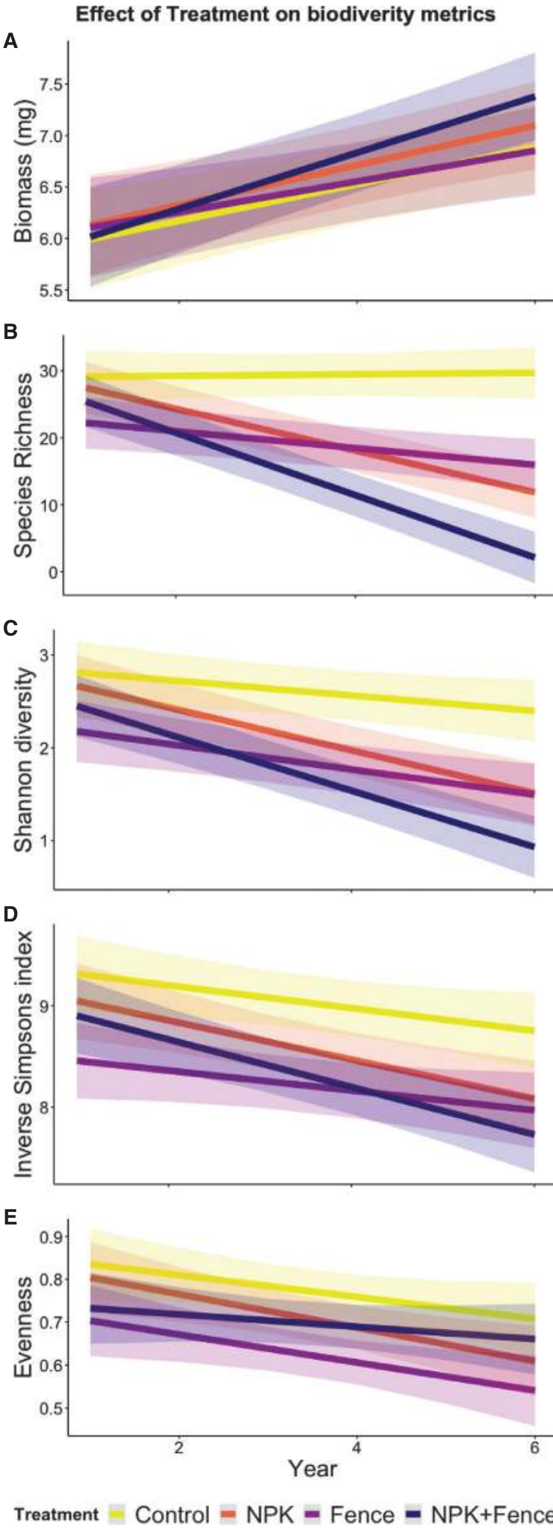


Fig. 1 (Continued)—Grassland biodiversity in experimental plots belonging to the various experimental treatments. Plots based on average values for each treatment over three blocks. Boxes show interquartile range. Central line shows median. Whiskers show 1.5 times the interquartile range. Colours correspond to treatments as described in legend.

DIVERSITY

Overall, diversity decreased in response to fertiliser addition and herbivore exclusion. Different diversity metrics—species richness, Shannon diversity, inverse Simpson's index and species evenness—describe diversity in different ways, and so responded differently to the treatments. Inverse Simpsons index decreased through time, possibly in response to the reduction in traditional management, but did not show additional decreases in fertilised plots in comparison to the unfenced controls. While species richness did not decrease in response to the reduction in traditional management (that is, unfenced control plots did not change significantly), richness and Shannon's diversity decreased in response to the fertiliser treatments. These differences reflect the ability of the metrics to describe different dimensions of diversity (Jost 2006). Richness—purely the sum of number of species—most readily detects the loss of species from a plot, Shannon diversity measures proportional change in relative abundance, while inverse Simpsons index gives even more weight to changes in abundance, and so is less affected by the loss of rare species. These differences indicate



Indepentant variable	Biomass (mg) Estimate	Std. Error	t_value
(Intercept)	5.817 *	0.275	21.120
trtNPK	0.122	0.390	0.314
trtFence	0.14	0.390	0.360
trtNPK+Fence	-0.073	0.390	-0.188
year	0.178 *	0.049	3.605
trtNPK:year	0.015	0.070	0.220
trtFence:year	-0.029	0.070	-0.409
trtNPK+Fence:year	0.095	0.070	1.356

Indepentant variable	Species Richness Estimate	Std. Error	t_value
(Intercept)	29.044 *	2.219	13.090
trtNPK	1.556	3.138	0.496
trtFence	-5.533	3.138	-1.763
trtNPK+Fence	1.067	3.138	0.340
year	0.114	0.449	0.255
trtNPK:year	-3.238 *	0.635	-5.100
trtFence:year	-1.371 *	0.635	-2.160
trtNPK+Fence:year	-4.781 *	0.635	-7.529

Indepentant variable	Shannon diversity Estimate	Std. Error	t_value
(Intercept)	2.897 *	0.195	14.880
trtNPK	0.002	0.275	0.007
trtFence	-0.582 *	0.275	-2.113
trtNPK+Fence	-0.142	0.275	-0.516
year	-0.083 *	0.041	-2.010
trtNPK:year	-0.149 *	0.058	-2.545
trtFence:year	-0.054	0.058	-0.923
trtNPK+Fence:year	-0.221 *	0.058	-3.789

Indepentant variable	Inverse Simpsons index Estimate	Std. Error	t_value
(Intercept)	9.426 *	0.227	41.485
trtNPK	-0.186	0.321	-0.578
trtFence	-0.871 *	0.321	-2.711
trtNPK+Fence	-0.291	0.321	-0.904
year	-0.112 *	0.053	-2.127
trtNPK:year	-0.081	0.075	-1.078
trtFence:year	0.014	0.075	0.194
trtNPK+Fence:year	-0.122	0.075	-1.634

Indepentant variable	Evenness Estimate	Std. Error	t_value
(Intercept)	0.861 *	0.053	16.338
trtNPK	-0.018	0.075	-0.240
trtFence	-0.125	0.075	-1.676
trtNPK+Fence	-0.114	0.075	-1.530
year	-0.026	0.013	-1.924
trtNPK:year	-0.013	0.019	-0.713
trtFence:year	-0.007	0.019	-0.374
trtNPK+Fence:year	0.011	0.019	0.593

Fig. 2—Effects of treatments on biomass and diversity. Model estimates of the changes in A. biomass, B. species richness, C. Shannon diversity, D. inverse Simpsons index and E. species evenness in plots with no added nutrients, fenced, NPK and NPK + fenced plots over the course of the experiment. Coloured lines show model estimates for the mean. Coloured bands show 95% confidence intervals. Colours correspond to treatments as described in legend. Adjacent tables show model outputs. Model terms with statistically significant increases are highlighted in blue, and model terms with statistically significant decreases are highlighted in red.

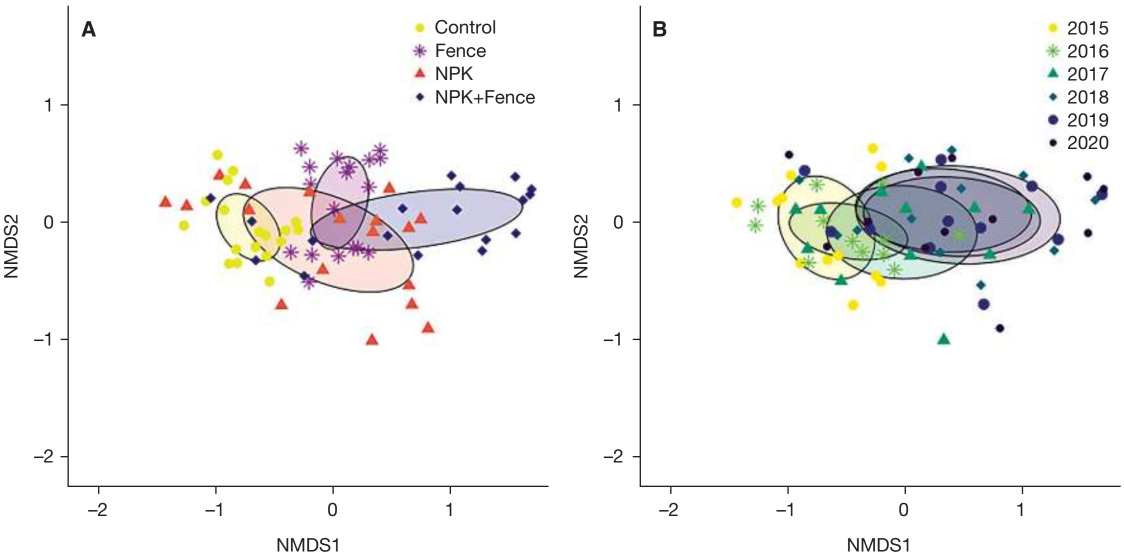


Fig. 3—Nonmetric Multidimensional Scaling of compositional dissimilarity by A) treatment and B) year. Two-dimensional ordination of Jaccard's dissimilarity in species' identity among plots. Each point corresponds to an individual experimental plot in a single year. The shapes and colours of points correspond to unfenced and fenced plots with no added nutrients, unfenced NPK+ and fenced NPK+, and years 2015-2020.

that the reduction in winter grazing caused shifts in relative abundance, while the most immediate effect of nutrient addition was the loss of rare species, followed to a lesser extent by changes in ratios of abundance. This may imply that while nutrient addition and herbivory may appear to counterbalance one another, they work through different mechanisms and so affect aspects of grassland diversity in different ways.

Analysis of Jaccard dissimilarity indicates that treatment, management and their interaction account for over 36% of differences in species identity between plots, implying these actions are contributing to species turnover. Given the link between species identity, function and service (Luck *et al*. 2009; Byrnes *et al*. 2014), particularly in the context of agricultural land managed for its biodiversity and cultural benefits (Binder *et al*. 2018), this provides further evidence for the negative effects of both intensification and abandonment on grasslands in the Burren.

LIMITATIONS

The three-replicate design of the experiment is not ideally suited to answering questions about an individual study site; consequently, our models had relatively low statistical power. While this did not constrain our ability to detect large changes, it could have hampered our ability to detect smaller effects. For example, stochastic differences in initial plot biomass would be expected to average out over high numbers of replicate blocks. Initially low Shannon diversity and inverse Simpsons index values in fenced control plots may have obscured the effects of complete herbivore exclusion without the influence of fertiliser. Visually, Shannon diversity in fenced control plots showed a downward trend, but our models did not have sufficient power to detect statistical significance. We use statistical analysis to provide evidence of a correlation between variables measured in our experiment—response variables (biomass and diversity), and nutrient addition and year. We consider available information about the system (unquantified reduction in winter grazing) to inform our interpretation of these results. However, the reduction in winter grazing was not part of the original experimental design and this leads to limitations. Including experimental Burren sites from more than one location may have shown differences in management, providing a contrast to the effects of relaxation of traditional management at the Slieve Carran site. While nutrient addition appears to have had a larger impact on diversity than fencing, we cannot compare the effects of fencing to a true control due to the reduction in winter grazing. Including other sites at which grazing was not reduced would allow us to explicitly test the effects of grazing reduction in addition to the effects of nutrient addition and grazing exclusion tested at our site. However, despite these limitations, our experiment demonstrates clearly the detrimental combined effects of nutrient addition and herbivore exclusion to this highly biodiverse grassland system.

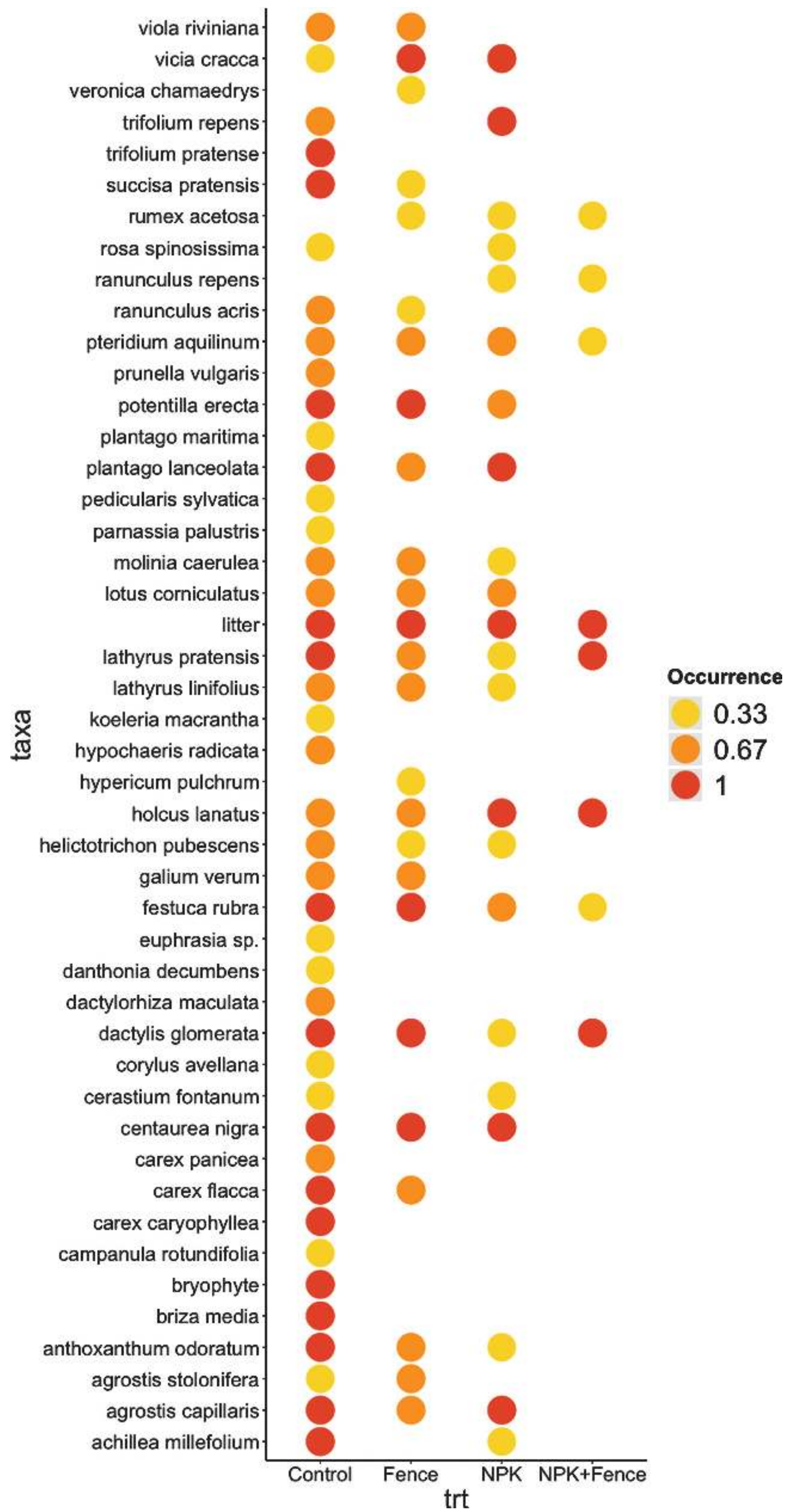


Fig. 4—Species occurrence in final year of treatment (2020). Occurrence of the 44 species recorded in the final year of the experiment across the four main treatments. Dots are coloured by whether a species occurred in 1/3 plots (yellow), 2/3 plots (orange) or 3/3 plots (red). White/ blank spaces represent no occurrence of a species in any plots of a particular treatment in 2020.

CONCLUSION

We provide quantitative evidence that nutrient addition and herbivore exclusion together decreased biodiversity and increased productivity (plant biomass) at Slieve Carran. Loss of rare species is the most immediate response to nutrient addition, while change in relative abundance is the more immediate result of the reduction in grazing. Our results are consistent with findings from a global network of manipulative grassland experiments, as well as a suite of smaller-scale local exclusion studies, showing that nutrient addition and large mammal herbivory can respectively decrease and rescue grassland diversity. Our findings strengthen the case for the maintenance of winter grazing and no nutrient addition as strategies for managers seeking to promote high grassland biodiversity. Additionally, our findings support winter grazing as a management strategy to help reduce the loss of biodiversity in systems under low levels of nutrient addition.

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SUPPLEMENTARY MATERIAL

Table S1—Nutrient application rates. Nutrients were applied at a rate of 10 g m^{-2} y^{-1} by elemental mass. Plots = 25 m^2, 15 plots per nutrient treatment (5 treatments x 3 replicates). *Micronutrients (mixture of Ca, Mg, S, B, Cu, Fe, Mn, Mo, Zn) were only applied in the 1st treatment year.

Fertilizer	*g plot^{-1} year^{-1}*	*kg experiment^{-1} year^{-1}*
Slow-release Urea (43% N)	581	8.7
Triple Super Phosphate	1272	19.1
Potassium Sulphate	558	8.4
Micronutrients*	2500	37.5

Table S2—Soil assay data. Assay of Slieve Carran soil samples collected in the pre-experiment year (2015). C, N, P and K refer to Carbon, Nitrogen, Phosphorus and Potassium respectively.

Block	plot	%C	%N	P (ppm)	K (ppm)	pH
1	1	8.258	0.643	7	185	5.5
	2	9.613	0.786	13	237	5.6
	3	7.715	0.62	8	184	5.5
	4	7.075	0.544	5	215	5.4
	5	6.556	0.525	6	146	5.4
	6	6.192	0.492	9	167	5.3
	7	6.113	0.48	5	162	5.4
	8	7.627	0.582	4	222	6.4
	9	7.354	0.572	4	205	5.5
	10	8.49	0.745	10	262	5.6
2	11	7.718	0.633	7	172	5.4
	12	7.102	0.554	5	163	5.2
	13	8.083	0.66	5	136	5.6
	14	7.517	0.546	4	147	5.3
	15	7.242	0.552	4	137	5.4
	16	9.411	0.711	7	176	5.9
	17	6.916	0.549	5	191	5.3
	18	9.24	0.792	6	238	5.7
	19	6.418	0.493	3	152	5.3
	20	8.439	0.612	4	176	5.3
3	21	8.146	0.577	7	182	5.6
	22	12.307	0.892	9	134	6
	23	7.111	0.502	3	168	5.5
	24	9.111	0.697	6	151	5.4
	25	8.945	0.649	5	155	5.3
	26	5.999	0.482	3	131	5.4
	27	9.011	0.625	4	152	6.3
	28	9.223	0.654	6	164	5.4
	29	7.956	0.612	5	127	5.4
	30	6.915	0.512	5	127	5.1
Site mean		**7.927**	**0.610**	**5.800**	**172.133**	**5.513**

Table S3. Extended soil assay including micronutrients.

Block	Plot	pct C	pct N	ppm P	ppm K	ppm Ca	ppm Mg	ppm S	ppm Na	ppm Zn	ppm Mn	ppm Fe	ppm Cu	ppm B	pH
1	1	8.258	0.643	7	185	2104	123	42	59	3.3	190	692	0.3	1.2	5.5
	2	9.613	0.786	13	237	2298	151	39	63	4.3	236	542	0.6	1.3	5.6
	3	7.715	0.62	8	184	1514	121	31	50	4.8	161	560	0.4	1	5.5
	4	7.075	0.544	5	215	1654	115	31	54	8.6	125	528	0.7	1	5.4
	5	6.556	0.525	6	146	1169	110	36	48	4.1	154	650	0.2	1	5.4
	6	6.192	0.492	9	167	1115	115	29	51	3.1	87	514	1.3	0.8	5.3
	7	6.113	0.48	5	162	1052	105	35	47	4	166	714	0.2	0.9	5.4
	8	7.627	0.582	4	222	3480	133	37	47	2.7	144	537	0.9	1	6.4
	9	7.354	0.572	4	205	1613	109	33	57	4.4	107	431	1.2	0.9	5.5
	10	8.49	0.745	10	262	1963	148	41	52	10.7	182	489	2.2	1.2	5.6
2	11	7.718	0.633	7	172	1881	128	43	57	5.8	131	463	1.4	1.1	5.4
	12	7.102	0.554	5	163	1316	106	28	53	3.3	108	359	1.2	0.8	5.2
	13	8.083	0.66	5	136	2171	107	35	53	3.9	220	351	2	1	5.6
	14	7.517	0.546	4	147	1310	91	33	51	4	231	376	1.4	0.8	5.3
	15	7.242	0.552	4	137	1682	106	19	50	4.8	195	345	1.3	0.9	5.4
	16	9.411	0.711	7	176	2657	121	36	58	12.8	257	481	1.3	1.4	5.9
	17	6.916	0.549	5	191	1142	116	32	54	6.2	149	485	1.6	0.9	5.3
	18	9.24	0.792	6	238	3114	136	39	64	4.3	194	295	2.2	1.7	5.7
	19	6.418	0.493	3	152	1042	101	30	52	3.1	229	548	0.6	0.8	5.3
	20	8.439	0.612	4	176	1454	112	31	58	4.2	171	499	1.6	0.9	5.3
3	21	8.146	0.577	7	182	1892	117	33	49	4.5	236	465	1.4	1	5.6
	22	12.307	0.892	9	134	3504	121	50	54	3.7	265	525	0.7	2.1	6
	23	7.111	0.502	3	168	1398	98	35	54	7.1	249	626	0.6	0.9	5.5
	24	9.111	0.697	6	151	2056	136	37	67	11.3	250	431	1.9	1	5.4
	25	8.945	0.649	5	155	1539	125	35	62	3.2	233	509	0.8	0.9	5.3
	26	5.999	0.482	3	131	1124	91	34	52	19	315	495	1.1	0.7	5.4
	27	9.011	0.625	4	152	3492	126	36	60	6	303	319	1.9	1.1	6.3
	28	9.223	0.654	6	164	1861	133	40	55	11.1	227	353	1.4	0.9	5.4
	29	7.956	0.612	5	127	2185	107	37	60	19.3	260	405	1.6	1	5.4
	30	6.915	0.512	5	127	930	104	40	57	5.2	173	429	1.6	0.6	5.1
Site average		**7.927**	**0.610**	**5.800**	**172.133**	**1857.067**	**117.067**	**35.233**	**54.933**	**6.427**	**198.267**	**480.533**	**1.187**	**1.027**	**5.513**

Table S4—Species list

Achillea millefolium
Agrostis capillaris
Agrostis stolonifera
Ajuga reptans
Anemone nemorosa
Anthoxanthum odoratum
Briza media
Bryophyte
Calluna vulgaris
Campanula rotundifolia
Carex caryophyllea
Carex flacca
Carex panicea
Carex pulicaris
Centaurea nigra
Cerastium fontanum
Conopodium majus
Corylus avellana
Cynodon sp.
Cynosurus cristatus
Dactylis glomerata
Dactylorhiza fuchsii
Dactylorhiza maculata
Dactylorhiza sp.
Danthonia decumbens
Euphrasia sp.
Festuca ovina
Festuca rubra
Galium saxatile
Galium verum
Gymnadenia conopsea
Helictotrichon pubescens
Holcus lanatus
Hypericum pulchrum
Hypochaeris radicata
Koeleria macrantha
Lathyrus linifolius
Lathyrus pratensis
Leontodon autumnalis
Leontodon hispidus
Linum catharticum
Lotus corniculatus
Luzula campestris

Table S4 (Continued)—Species list

Luzula campestris
Luzula multiflora
Mentha arvensis
Molinia caerulea
Neottia ovata
Odontites vernus
Orchis mascula
Parnassia palustris
Pedicularis palustris
Pedicularis sylvatica
Pilosella officinarum
Pimpinella saxifraga
Plantago lanceolata
Plantago maritima
Platanthera sp.
Poa pratensis
Poa trivialis
Potentilla erecta
Potentilla sterilis
Prunella vulgaris
Pteridium aquilinum
Ranunculus acris
Ranunculus repens
Rhinanthus minor
Rosa spinosissima
Rosa xanthina
Rubus vestitus
Rumex acetosa
Scorzoneroides autumnalis
Sesleria caerulea
Sonchus asper
Succisa pratensis
Taraxacum campylodes
Thymus polytrichus
Thymus praecox ssp. Polytrichus
Trifolium medium
Trifolium pratense
Trifolium repens
Trisetum flavescens
Unknown orchidaceae sp.
Veronica chamaedrys
Vicia cracca
Viola riviniana