Experimental sward islets: the effect of dung and fertilisation on Hemiptera and Araneae

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Abstract. 1. Cattle avoid grazing around their dung. This pattern persists after the decomposition of the initial dung patch leading to the formation of taller grass patches, termed islets. It is known that islets hold a disproportionate amount of the arthropods in grazed grasslands.

2. An experimental manipulation was set up to investigate the relative effects of vegetation structure and nutrient input on arthropod distributions. Herbivorous bugs (Hemiptera) and predatory spiders (Araneae) were sampled in artificially generated islets treated with dung, fertiliser, a cutting regime to mimic grazing and a fallow control.

3. The densities of both Hemiptera and Araneae were affected by the presence of increased nutrient input through dung and fertiliser. The densities of different herbivore taxonomic families were influenced by food plant quality and the predators by the subsequent increase in prey density.

4. Delphacidae (Hemiptera) showed a preference for taller more nutrient rich swards treated with fertiliser, whereas Cicadellidae (Hemiptera) were more abundant in those swards treated with dung. Lycosidae (Araneae) were more common in dung-treated swards, whereas Linypiidae (Araneae) were more common in the taller fertiliser-treated swards.

5. Higher Hemiptera species richness was found in the fertiliser- and dung-treated swards. It is believed that this effect was because of nutrient availability.

6. It is likely that the presence of cattle dung islets in grazed grassland plays an important role in the maintenance of biodiversity, through increasing structural heterogeneity.

Key words. Agriculture, Auchenorrhyncha, Cicadellidae, Delphacidae, grassland, grazing, Hemiptera, heterogeneity, Linyphiidae, Lycosidae.

Introduction

Grazing herbivores can have an indirect effect on the diversity and abundance of many arthropod groups, as grazing modifies the structure and quality of grassland habitats (Dennis *et al.*, 1998, 2001; Morris, 2000; Kruess & Tscharntke, 2002; Dennis, 2003). In general due to regular and major defoliation events, intensively grazed pastures are usually considered of lower biodiversity value compared with the taller vegetation in field margins

Correspondence: Alex Dittrich, Animal and Environmental Research Group, Department of Life Sciences, Anglia Ruskin University, East Road, Cambridge, CB1 1PT, UK. E-mail: alex.dittrich@anglia.ac.uk and other such habitats (Bayram & Luff, 1993; Morris, 2000; Bell *et al.*, 2002). However, herbivores do not graze pastures evenly, resulting in a degree of patchiness in the ecological impact of intensive grazing. In particular, cattle have been known for some time to avoid feeding around the dung of conspecifics (Weeda, 1967; Macdiarmid & Watkin, 1972b; Bac *et al.*, 1998; Bosker *et al.*, 2003) which leads to the formation of taller sward around the dung (Macdiarmid & Watkin, 1972b; Bac *et al.*, 1998). This avoidance is thought to primarily be owing to an initial aversion caused by smell of the dung (Marten & Donker, 1964, 1966; Macdiarmid & Watkin, 1972b; Dohi *et al.*, 1991; Bac *et al.*, 1998). However, this avoidance persists after the decay of the dung patch, because of factors, such as nutrient imbalance in the sward (Plice, 1952).

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Desender (1982) and Maelfait and De Keer (1990) used the name islets for these structures, because of their likeness to islands of tall grass vegetation dispersed amongst short sward. Cattle dung sward islets can cover a relatively large proportion of the grazed pasture. Marten and Donker (1964) reported 38-47% of pasture was untouched by cattle at the end of a grazing season and rejection may persist for up to 18 months (Norman & Green, 1958). Agronomically, islets are generally considered wasted pasture (Macdiarmid & Watkin, 1972b), and work has been directed into how they can be reduced. Novel suggestions such as sweetening agents to increase the palatability of islet sward (Marten & Donker, 1964) and long-standing management practices, such as topping and the redistribution of dung by chain harrowing (Weeda, 1967; Lacefield et al., 1996), have all been implemented to reduce the dominance of unused sward in grazed pasture.

Little is known about the ecological role of cattle dung sward islets, but studies have looked at structurally similar grassland microhabitats. Some grasses naturally form tussocks and these can be modified by the presence of livestock (Cherrett, 1964; Dennis et al., 1998, 2001; Dennis, 2003). Tussocks, like dung islets, are often interspersed throughout heavily grazed pastures (Cherrett, 1964). It is likely that cattle dung sward islets and tussocks share many characteristics; such as sheltered microclimate, limited trampling by livestock and a greater structural height, which are all important in determining arthropod richness (Dennis et al., 1998, 2001). Cherrett (1964) found an abundance of web-building spiders (Araneae) in Nardus stricta L. tussocks in contrast to the heavily grazed sward. In other studies beetles (Coleoptera) were abundant in Dactylis glomerata L. and Deschampsia caespitosa (L.) tussocks (Luff, 1966), and planthoppers (Hemiptera: Auchenorrhyncha) in those of Nardus stricta (Dennis, 2003).

A recent study by Helden et al. (2010) illustrated that sward islets contained a disproportionately greater number of arthropods in a field (approximately 50%) relative to the proportion of pasture that the islets cover (25%). Furthermore, the proportion of arthropods in the islets was inversely related to an increase in sward height. This illustrates their importance as refugia, when the surrounding sward height is reduced by grazing. Other studies have looked at cattle dung sward islets, but the general breadth of knowledge is sparse. Desender (1982) looked at their potential as possible habitats for hibernating carabid beetles. The cattle dung islets proved beneficial as they were not trampled by cattle, and the deeper sod layer provided a more suitable microhabitat. Furthermore, although less carabids were found in the islets than edge sites, such as field margins, they covered a greater area of pasture so therefore are potentially very ecologically important. De Keer et al. (1986) and Maelfait and De Keer (1990) reported that the taller areas of vegetation around cattle dung islets were beneficial for overwintering spiders, in particular those of the families Lycosidae and Linyphiidae.

Until recently other arthropod groups abundant in agricultural grassland, such as sap-sucking Hemiptera (Haddad *et al.*, 2000; Kruess & Tscharntke, 2002; Helden *et al.*, 2008), have not been explored in the context of cattle dung sward islets. Helden *et al.* (2010) looked at abundance and density of the major arthropod orders, Araneae, Coleoptera, Diptera Hemiptera and Hymenoptera, within islets in pastures. It is likely that many groups benefit from the increased height and structure of the sward within an islet, which may provide ameliorated microhabitat. It is also possible that nutrient input from dung (Norman & Green, 1958; Macdiarmid & Watkin, 1972a; Jørgensen & Jensen, 1997) could potentially lead to more favourable feeding conditions for herbivorous taxa, as nutrient input increases plant quality and nutrient subsidy (Sedlacek et al., 1988). Furthermore, although the islets have taller vegetation, the botanical compositions are largely unchanged from that of the grazed sward (Macdiarmid & Watkin, 1972a,b; Helden et al., 2010). It is therefore likely that the patterns in arthropod distributions in islets are largely unaffected by botanical composition. Hemiptera in particular are known to respond favourably to increases in food plant quality (Prestidge, 1982). The higher densities of these phytophagous guilds would then act to attract polyphagous predators such as Linyphiidae and Lycosidae (Araneae) (Lang, 2003).

Modern farming practices have resulted in the loss of many structures beneficial for wildlife, such as hedgerows (Gillings & Fuller, 1998). Lack of heterogeneity is blamed for the loss of farmland biodiversity at many different levels, from arthropods to small mammals and birds (Vickery et al., 2001; Benton et al., 2003). Furthermore, in land that has been severely fragmented by agricultural practices, inter-patch connectivity between these habitat islands is important to ensure persistence of populations (Baudry et al., 2003). It is possible that the behaviour of cattle and the production of cattle dung sward islets provide a buffer to the deleterious effects of intensive farming. By increasing the structural heterogeneity, sward islets may help to maintain in-field arthropod communities and may also contribute to a habitat backbone (Snep & Ottburg, 2008) connecting other habitats, enabling the persistence of populations. Enhanced arthropod diversity positively impacts upon other groups such as insectivorous mammals (Huusela-Veistola & Vasarainen, 2000), birds (Murray & Clements, 1994; Gillings & Fuller, 1998; Vickery et al., 2001) and amphibians (Gibbs, 1998; Joly et al., 2003). Moreover, the maintenance of a heterogeneous sward may help to counter the risk of pest outbreaks in simplified grassland habitats (Van Emden & Williams, 1974; Purvis & Curry, 1981).

In this study, two groups of ecologically important and abundant arthropods were investigated in relation to islets: the Araneae (a predatory group) and Hemiptera (a predominantly herbivorous group). Araneae were studied because of their important ecological role as generalist predators, and the relationships they have with other guilds as part of the polyphagous predator complex (e.g. Sunderland *et al.*, 1985, 1986, 1999). Hemiptera were studied because of the effect that both nutrient input and structural heterogeneity has on their group composition (e.g. Prestidge, 1982; Morris & Plant, 1983; Dennis *et al.*, 1998; Hollier *et al.*, 2005) and because of known predator–prey interactions between Araneae and Hemiptera (Heong *et al.*, 1992; Lang, 2003).

Helden *et al.* (2010) found that islets contain more arthropods than could be explained by vegetation height alone. To investigate the reasons for this pattern an experiment was set up with artificial islets. There were three ungrazed islet treatments; dung, fallow, and fertilised and a cut sward treatment (also acting as a

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lower comparison of the linear relationship between vegetation height and arthropod abundance). It was hypothesised that both nutrient input and vegetation height would influence density and distribution of arthropods. Specifically, it was predicted that dung islets would contain more arthropods than fallow because of the input of nutrients from the dung, and that there would be no difference in abundance between dung and fertilised islets.

Methods

Site location and treatments

The experimental site was located 7.2 km south of Cambridge in Stapleford (OS Grid Reference: TL 4859 5299). The plot was extensively managed wild lowland calcareous grassland, ungrazed by large herbivores, with shallow topsoil on a chalk base. The experiment was set up on the 6 June 2009.

The potential effects cattle dung islets have on arthropod abundance and diversity were tested using a series of artificial pasture islets. Four treatments were used. Dung was applied to replicate the production of a natural dung islet. Artificial fertiliser was applied in the form of ammonium sulphate, to improve the nutrient content of the grass and stimulate growth without the addition of dung. A fallow treatment in which the grass was left untouched acted as a control, and a cut sward was established to mimic grazing activity.

Prior to the application of treatments, the grass was cut to a length of 3 cm after which the islets were delimited using cylindrical wire cages. These were constructed from chicken wire [24 mm galvanised wire netting (L) 1.0 m × (W) 0.6 m] to cover the islets and prevent any grazing activity from herbivorous mammals present at the site. The wire cages were constructed to form 1 m circumference cylinders 0.6 m in height. Each cage was affixed to the ground using 177×3 mm stainless steel pegs. These cages were set up in advance of treatment application to enable accurate plot placement.

After the construction and positioning of the wire cages, the sample treatments were added, with six replicates of each (Fig. S1). The position of each treatment was determined within a six by four randomised block design using the randomisation function in Microsoft Excel (version 2007). The islets were each placed one metre apart, measured from the centre of the neighbouring islet.

The cut plots were manually trimmed to 3 cm with shears every 10 ± 2 days depending on weather. No cutting occurred for 10 days prior to the sampling date. The fertilised grass plots were maintained given a single application of ammonium sulphate ([(NH₄)₂SO₄ - % NPK 21-0-0) at a rate of 53 g m⁻², evenly distributed over sward within the cage. For the dung plots, 1.4 kg of freshly evacuated dung was collected from a local beef herd the same morning that the experiment was set up. This was positioned so that it was uniformly round with a diameter of 15 cm, in the centre of each dung plot. The fallow plots were left untouched, from the initial cutting prior to cage placement.

The area in between the islets did not have to be cut at any point because the grazing activity of wild rabbits (*Oryctolagus* *cuniculus* L.) maintained the grass length below 5 cm. The decision therefore was made not to disturb the experimental plots further by cutting the matrix between the islets.

Arthropod collection and habitat characterisation

The arthropod collection occurred on 2 August 2009 and was carried out using a Vortis Insect Suction Sampler (Burkard Manufacturing Co Ltd, Rickmansworth, Herts, UK) (Arnold, 1994). The islet cages were removed for 1 h prior to sampling, to reduce disturbance. Although, only one sampling event was carried out it was considered this was appropriate given the fact that suction sampling is an effective method of removing all arthropods in relatively small areas (Brook et al., 2008), and so any subsequent sampling in these areas would therefore have been strongly biased. Sampling was randomised using the randomisation function in Microsoft Excel using an individual identifier assigned to each plot. Each plot was sampled for a total of 1 min (four separate 15 s sampling efforts to ensure the whole islet was sampled); a modification of the method used by Brook et al. (2008). Grass height measurements were taken following the suction sampling using the Filips folding plate pasture metre (http://www.jenquip.co.nz/pasturem.htm) and all plant species were recorded on each plot following suction sampling. Monocots and dicots were identified using Sinker (1975) and Gibbons and Brough (2008), respectively.

The samples collected for each islet were preserved in a solution of 70% ethanol in the field. The arthropods were then sorted into orders. Subsequently, Araneae were sorted into family, and all juveniles that could not be identified, counted. Hemiptera were sorted into nymphs of different families, and adults were identified to species, with the exception of Aphidoidea which were counted. Family level identification of Hemiptera was carried out using Unwin (2001) and Araneae using Roberts (1995). Species level identification of Hemiptera was carried out using Le Quesne (1960, 1965, 1969) and Le Quesne and Payne (1981). The family level identification of Hemiptera nymphs was with Zenner *et al.* (2005).

Statistical methods

To determine the level of significance between each treatment and arthropod abundance generalised linear models (GLMs) were used in all instances. All statistical modelling was performed using R version 2.9.2 (R: Development-Core-Team, 2009). Standard error (\pm) is given in parenthesis after all stated mean values.

Arthropod abundance was firstly corrected for vegetation height (arthropod abundance/vegetation height); thereafter referred to as arthropod density. In the arthropod density and treatment models, arthropod density was modelled as the response variable, and treatment and plant species richness (number of plant species per plot) as explanatory variables. In all cases, Poisson or quasipoisson error structures were defined using the family directive, because the response variable data was based on counts. Quasipoisson was used in cases where the

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deviance in the model was much greater or lower than the degrees of freedom and Poisson when there was less differentiation. The biodiversity R package (Kindt & Coe, 2005) was used to calculate overall treatment effects for the model used, the Fstatistic stated in parenthesis with degrees of freedom. The different treatments (dung, fallow, fertiliser and cut) were treated as parameter estimates, so that the significant differences between each treatment could be confirmed with Z- or t-statistics - a component of the glm output. To determine how vegetation height affected the abundance of arthropods GLMs were also used, with quasipoisson error structures defined using the family directive. Arthropod abundance in this case was modelled as the response and vegetation height as the explanatory variable. The R package BiodiversityR (Kindt & Coe, 2005) was used to determine the deviance and to get a better interpretation of the conformity of the GLMs; this function calculates the percentage of deviance explained (DE) by a GLM. In all cases, this is sighted as DE after the significance of the GLM is stated in parenthesis. GLMs were used instead of linear regression in this case because the data set was not normally distributed; the significant difference from normality was confirmed with the Shapiro-Wilk test. Vegetation height was modelled as the response variable, and treatment as the explanatory variable in the GLMs comparing vegetation height between treatments. Gaussian error structures were used following confirmation of normal distribution with the Shapiro-Wilk test. Gaussian error structures follow an identity link between the linear predictor and the mean whereas Poisson error structures use a log link function between the linear predictor and the mean of the distribution.

Species accumulation curves were used to determine the species richness of all Hemiptera that were identified to species within each treatment. Models were computed using *EstimateS* version 8.2.0 (Colwell, 2009). All Simpson's diversity indices were calculated from the Hemiptera identified to species (Fig. 1a), using the standard formula derived from the original work (Simpson, 1949). Using the Simpson's diversity index (*D*), the probabilities of the same species being drawn from a random subset can be calculated. From the Simpson's index, a measure of evenness can be derived ($E_{1/D}$) which is an indicator of equitability of species.

Results

Vegetation type was modelled as a covariate, using the number of different species per replicate in the relevant GLMs. When these covariates were modelled, there were no significant effects on the overall GLM results, therefore, it was decided that the vegetation species richness (i.e. number of other non-grass species) in the context of this study was not a parameter that was significant in determining arthropod density, in any of the treatments. The vegetation type compositions (illustrated in Table S2) were not affected by the addition of the treatments, although the vegetation height was. The distribution of grass heights within the treatments was variable with a range of 2.5-14.5 cm for all treatments. The greatest range was observed within the dung (4.5-12.0 cm) and fallow (6.0-11.5 cm) treatments. The GLM comparing the different vegetation heights between treatments was highly significant ($F_{3,20} = 18.27$, P < 0.001). The fertiliser treatment had the highest mean height 13.8 cm (± 0.7), significantly greater than all other treatments: dung $(t_{23} = 3.58, P = 0.002)$; fallow $(t_{23} = -4.64, P =$ <0.001); cut ($t_{23} = -7.30$, P < 0.001). Dung had the next highest mean vegetation height 9.3 cm (\pm 1.3) significantly greater than the cut treatment ($t_{23} = -3.72$, P = 0.001) but not fallow. Fallow had a mean height of 7.9 cm (± 0.9) this was significantly taller than the cut treatment ($t_{23} = 2.65, P = 0.015$). The cut treatment had the lowest mean height of 4.6 cm (± 0.5).

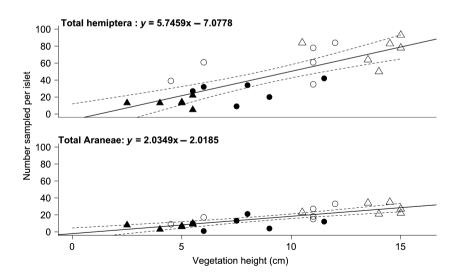


Fig. 1. The relationship between vegetation height and abundance of both the total number of Hemiptera and Araneae. Dashed lines represent 95% confidence intervals. Both Hemiptera ($t_{23} = 3.277$, P < 0.001, DE = 58.97%) and Araneae ($t_{23} = 5.893$, P < 0.001, DE = 59.74%) showed significant relationships between grass height and abundance, using a quasipoisson GLM model. Filled triangles represent the cut treatment, filled circles the fallow treatment, open circles dung and open triangles fertiliser.

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Vegetation height abundance relationship

For the combined sum of all Hemiptera and Araneae, there was a strong positive relationship between vegetation height (explanatory) and abundance (response) (Fig. 1) and this pattern was also apparent with the logical subdivisions of the different groups (e.g. taxonomic family). Cicadellidae showed a strong positive relationship ($y = 3.209x + 3.517, t_{23} = 3.28$, P = 0.003, DE = 33.89%), as did Delphacidae (y = 2.426x $-12.32, t_{23} = 5.98, P < 0.001, DE = 71.08\%$) although delphacids showed the greatest significance. With Araneae, there was no significant relationship between vegetation height (explanatory) and frequency of juveniles ($t_{23} = 1.98$, P =0.060, DE = 13.01%) or Lycosidae (response) ($t_{23} = 1.57$, P = 0.132, DE = 11.59%). However, there was a strong positive relationship between vegetation height and abundance of Linyphiidae (y = 1.3784x - 4.6916, $t_{23} = 6.65$, P < 0.001, DE = 71.25%).

Hemiptera

There were 1054 Hemiptera recorded across all 24 samples, with the majority either Cicadellidae (n = 768) or Delphacidae (Homoptera: Auchenorrhyncha) (n = 221). Other groups that were recorded, Heteroptera (n = 31), Aphids (Homoptera: Aphidoidea) (n = 32) and Aphrophoridae (Homoptera: Auchenorrhyncha) (n = 2), were far less numerous, and were not normally distributed, so excluded from individual analysis, but included in all totals.

The GLM comparing the density of total Hemiptera between treatments was highly significant ($F_{3,20} = 3.91$, P = 0.008). The density of total Hemiptera (abundance/vegetation height) was greatest in the dung treated swards (Fig. 2). Between the treatment pairs, there was a significantly greater density of Hemiptera in the dung treatment, compared with the fallow and

cut treatments but not fertiliser treatments. There was also a significantly greater density of Hemiptera in the fertiliser-treated sward compared with the cut swards. The densities of Cicadellidae showed a higher range and lower kurtosis than the other treatments. The median value was closer to the 75th percentile indicating skewed data, towards higher observed frequencies (Fig. 2). The GLM comparing Cicadellidae between treatments was significant ($F_{3,20} = 3.27$, P = 0.020). Dung had the greatest mean density of Cicadellidae, followed by fertiliser, fallow and cut treatments (Fig. 2). Between the individual treatment pairs, there was a significantly greater density of cicadellids in the dung compared with the cut and fallow swards but not fertiliser treated swards (Table 1). The GLM comparing the density of Delphacidae between treatments was also significant $(F_{3,20} = 3.46, P = 0.016)$. The densities of Delphacidae were greatest in the fertiliser treatment. Between the treatment pairs, there was only a significant difference between fertiliser treated and cut swards (Table 1).

The age distributions of Cicadellidae and Delphacidae were very different. Overall 5.7% of the total Cicadellidae population was adult, whereas 92.7% of delphacids was adults. Delphacidae were predominately one species, Javesella pellucida (Fabricius) (n = 221) and 54% of their total population was found in fertiliser treated swards. Javesella dubia (Kirschbaum) (n = 21)although present, were far less numerous. Cicadellidae showed more diversity and there was no apparent dominant genus or species. There were five subfamilies represented in the fertiliser treated swards, three in dung, two in fallow and two in fertiliser. Sample-based rarefaction (species accumulation curves) shows species richness as a function of the number of samples. This is illustrated by the mean rarefied Mao Tau estimate of observed species for each treatment. The species richness of fertiliser and dung was higher than that recorded for cut and fallow. However, there was no significant difference between the pairs fertiliser-dung, and cut-fallow owing to the overlap between the upper and lower 95% confidence intervals (CI). There was

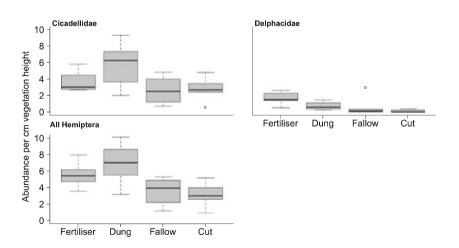


Fig. 2. The densities (abundance per cm vegetation height) of Hemiptera in the different treatments, collected by suction sampling. Boxplots show the median values as the dark horizontal lines; 25th and 75th percentiles as the top and bottom of the boxes. The dashed lines show either 1.5 times the interquartile range together with outliers as small circles, or if there are no outliers, the maximum and minimum values.

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Hemiptera														
		All Hemiptera				Ci	Cicadellidae				Delphacidae			
Intercept	Exp.	Dif	íf.	Ζ	Р	D	iff.	Ζ	Р	Diff.			Р	
Dung	Fertiliser	-1.369		-0.9	0.344	-2	2.184	-1.7	0.084	0.9	23	1.4	0.151	
	Fallow	-3.347		-2.5	0.013*	-3	3.186	-2.6	0.009*	-0.1	16 -	-0.3	0.803	
	Cut	-3.815		-2.9	0.004*	-3	3.046	-2.5	0.013*	-0.6	12 -	-1.4	0.154	
Fertiliser	Fallow	-1.978		-1.6	0.112	-]	.002	-1.0	0.328	-1.0	39 -	-1.6	0.102	
	Cut	-2.446		-2.0	0.045*	-().862	-0.8	0.405	-1.5	35 -	-2.0	0.037*	
Cut	Fallow	0.468		0.4	0.659	(0.140	-0.1	0.882	0.4	96 -	-1.3	0.200	
Araneae														
		All Aran	ieae		Linyphii	dae		Lycosida	ae		Juvenile	s		
Intercept	Exp.	All Aran Diff.	neae t	Р	Linyphiid Diff.	dae t	Р	Lycosida Diff.	ae t	P	Juvenile Diff.	s t	Р	
Intercept Dung	Exp. Fertiliser			P 0.697	• •		P 0.016*	-		P 0.022*			P 0.226	
	<u>^</u>	Diff.	t		Diff.	t		Diff.	t		Diff.	t		
	Fertiliser	Diff.	t -0.4	0.697	0.625	<i>t</i> 2.6	0.016*	Diff.	t -2.5	0.022*	Diff.	t -1.2	0.226	
	Fertiliser Fallow	Diff. -0.191 -0.868	t -0.4 -1.9	0.697 0.067	Diff. 0.625 0.011	<i>t</i> 2.6 0.1	0.016* 0.954	Diff. -0.297 -0.311	t -2.5 -2.5	0.022* 0.020*	Diff. -0.503 -0.540	t -1.2 -1.4	0.226 0.192	

Table 1. The statistical significances of the GLM for each of the Hemiptera and Araneae taxa studied.

Treatment is modelled as the explanatory and arthropod density as the response, there were 23 degrees of freedom. Diff. – the difference between the experimental treatment (exp.) and the intercept parameter estimate \log_e transformed from the GLM output. For clarification, those results that are significant (P < 0.05) are marked with an *.

0.9

0.376

-0.024

-0.4

0.668

-0.333

-0.9

0.382

considerably greater distance between the 95% CI upper and lower bound, for fertiliser compared with the dung and with fallow compared with cut (Fig. 3). Using the Simpson's diversity index, the greatest likelihood of the same species being drawn from a random subset was within fallow (D = 0.720) and fertiliser treated swards (D = 0.480), whereas the likelihood was much less within cut (D = 0.267) and dung treated swards (D = 0.367). It is clear that the equitability of species is lowest in the fertiliser treated swards ($E_{1/D} = 628.63$) followed by dung ($E_{1/D} = 134.81$), fallow ($E_{1/D} = 25.10$) and cut treated swards ($E_{1/D} = 6.67$). The full species lists for all Hemiptera is reported in Table S1.

-0.362

-0.9

0.388

0.162

Araneae

Cut

Fallow

Araneae were far less numerous than Hemiptera, with 385 individuals recorded. As few Thomisidae (Araneomorphae: Thomisoidea) (n = 5) and Araneidae (Araneomorphae: Araneoidea) (n = 1) were found, they were not separately analysed but were included in the totals. Juveniles (n = 170) and Linyphidae (Araneomorphae: Araneoidea) (n = 181), were the most numerous. Lycosidae (Araneomorphae: Lycosoidea) (n = 28) were far less numerous.

The GLMs comparing the densities of all Araneae and juveniles between treatments were not significant ($F_{3,20} = 1.30$, P = 0.250 and $F_{3,20} = 0.88$, P = 0.469, respectively; Table 1, Fig. 4). The GLM comparing the densities of Lycosidae

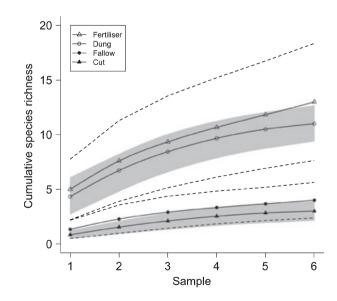


Fig. 3. Species accumulation curves for the adult Hemiptera (excluding Aphidoidea). The mean rarefied species observed (Mau Tao) is plotted against replicate. The upper dashed lines represent the 95% confidence intervals for the fertiliser treatment, the lower dashed lines for the fallow treatment. The upper grey-shaded area represents 95% confidence intervals for the dung treatment, the lower grey-shaded area for the cut treatment.

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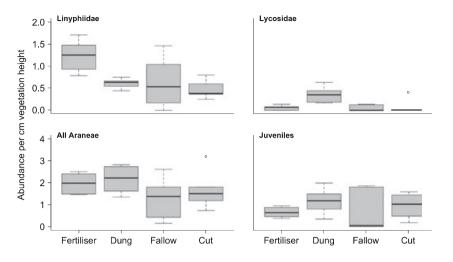


Fig. 4. The densities (abundance per cm vegetation height) of Araneae in the different treatments, collected by suction sampling. Boxplots show the median values as the dark horizontal lines; 25th and 75th percentiles as the top and bottom of the boxes. The dashed lines show either 1.5 times the interquartile range together with outliers as small circles, or if there are no outliers, the maximum and minimum values.

between treatments was highly significant ($F_{3,20} = 5.42$, P = 0.007). The greatest density of Lycosidae was found within the dung treated islets (Table 1), this was significantly greater than all other treatments. The greatest difference was between the dung- and fallow-treated swards. The next highest density recorded was with cut, followed by fertiliser and fallow (Table 1, Fig 4). The GLM comparing Linyphiidae density between treatments was also highly significant ($F_{3,20} = 5.05$, P = 0.009). The densities in fertiliser-treated swards were significantly higher than all other treatments (Table 1). Fallow swards had much lower density, followed by dung and cut. The densities in fertiliser treated swards were significantly higher than all other treatments. The greatest difference was recorded between the fertiliser and cut treatments (Table 1, Fig. 4).

Discussion

The experiment was set up to determine whether it was the input of nutrient into sward or vegetation structure that lead to the greater observed densities of arthropods within islets; a pattern observed by Helden *et al.* (2010). It was clear that although the increase in arthropod abundance and density was influenced by vegetation height, when this was controlled for by correcting for height and modelling arthropods as a density, nutrient input did appear to show independent effects, with the densities of herbivores and predators increasing in those swards with additional nutrient input.

The relationship between vegetation height and arthropod abundance is well known (Purvis & Curry, 1981; Morris & Plant, 1983; Morris & Rispin, 1987; Dennis *et al.*, 1998, 2001; Fenner & Palmer, 1998; Kleijn *et al.*, 2001; Kruess & Tscharntke, 2002). It is likely the patterns observed in this instance are influenced by both microhabitat structure (Kruess & Tscharntke, 2002), and *living space* (Prestidge, 1982; Morris, 2000) as there is simply more space for more arthropods in taller sward. This effect may be influenced by increased shelter and relative humidity within taller swards, when compared with shorter grazed swards (Waterhouse, 1955; Purvis & Curry, 1981). As vegetation height was controlled prior to the addition of treatments it is also likely that vegetation height is proportional to nutrient input in this study, as in other studies (Miles, 1958; Ingestad, 1977). The fertilised replicates were significantly taller than all other treatments, suggesting the highest nitrogen availability. Furthermore, as addition of fertiliser also increases food plant quality in terms of nitrogen content (Prestidge, 1982; Sedlacek *et al.*, 1988), those treatments that have the addition of extra material, in the form of dung or fertiliser, may also have a higher nutrient subsidy (Sedlacek *et al.*, 1988).

Nitrogen availability can increase the abundance of herbivorous guilds within grassland (Prestidge, 1982; Sedlacek et al., 1988; Hartley et al., 2003). Nitrogenous compounds are normally scarce in phloem sap, and are primary limiting factors for sap-sucking consumers (Whitham, 1978; Mattson, 1980). As a result, sap-sucking Hemiptera show positive responses to increasing phloem nitrogen, expressed as increased growth and fecundity (Van Emden & Bashford, 1969; Mattson, 1980; Wang et al., 2006). As in other investigations of grassland arthropods (Waloff & Solomon, 1973; Sedlacek et al., 1988; Haddad et al., 2000; Koricheva et al., 2000; Kruess & Tscharntke, 2002; Helden et al., 2008), Auchenorrhyncha were the most abundant group in this study and the results suggest that nutrient input may have positively influenced their distribution. Conversely, there were a small number of aphids found in this study (n = 32), although abundant in other studies (Haddad *et al.*, 2000). It is possible that the previous low nitrogen input into the experimental plot meant that low numbers had established prior to the experiment, as nitrogen in phloem sap is thought to be the primary limiting factor in aphid growth and development (Whitham, 1978).

Auchenorrhyncha can select host plants on the basis of nitrogen content (Prestidge & McNeill, 1983). The higher densities of

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Delphacids in fertiliser-treated swards may be indicative of the fact that many delphacids are r selected, relying on high quality plant material to suit their nutritional physiologies (Prestidge, 1982). One such delphacid is J. pellucida which undergoes a vertical migration towards lower parts of host plants in summer (Andrzejewska, 1965). Fertiliser-treated swards may provide a more distinct microhabitat gradient that would better facilitate vertical migration, because they are taller, whereas shorter swards might be lacking in such conditions (Waterhouse, 1955; Purvis & Curry, 1981). Ergo, it is possible that a combination of both the nutritional physiology and microhabitat preference helped to determine their distribution patterns; explaining their abundance in fertiliser treated swards. Cicadellids had higher population densities in the dung treated plots. This pattern may be indicative of the feeding preferences of Cicadellidae, as many cicadellids have nutritional physiologies that enable them to survive on lesser quality plant material, compared with delphacids (Prestidge, 1982). This hypothesis, however, assumes dung has a lower nutritional content than fertiliser. It is possible that the hardened dung patch could decrease the rate of vegetation emergence (Weeda, 1967; Macdiarmid & Watkin, 1972b). In this case, vegetation height might not necessarily be directly proportional to nutrient content as height was restricted by the presence of the hardened dung patch. Therefore, the cicadellids could be selecting the highest nitrogen food source relative to shortness of sward. In addition, most cicadellids were nymphs and so it could be possible that because of their smaller size, they require less living space (Prestidge, 1982; Morris, 2000) and were thus able to utilise the microhabitat structure of shorter swards more efficiently than adults. The lower intercept and slope predicted for vegetation height and abundance of Cicadellidae when compared with Delphacidae does seem to suggest that the former group is less limited by vegetation height. Alternatively, as Auchenorrhyncha undergo life stage specific vertical migrations (Andrzejewska, 1965) and nymphs of many species are more common in the litter levels, it is possible that the abundance in the dung plots may reflect a microhabitat more akin to the litter level. Of course, it must be remembered that these results are based on data derived from a single sampling date. They represent an accurate snapshot of the populations in time but it is possible that this picture may be modified because of host dynamics and other phenological changes, and further work could yield other interesting results. For example, cicadellids and delphacids could vary in their spatial distribution relative to islets, because of changes in their requirements at different stages of their life cycle.

Results indicate that there was no significant difference in sward height between the fallow and dung treatments. It is possible that nutrient input resulted in the apparent higher species richness in these treatments – as observed in fertiliser application experiments in natural grasslands (Siemann, 1998; Hartley *et al.*, 2003). However, there was no apparent difference in species richness of Hemiptera between dung- and fertiliser-treated swards. In some cases, the addition of fertiliser can reduce the equitability index of species within a habitat, leading to the disproportional increase in favour of some species over others (Prestidge, 1982; Haddad *et al.*, 2000). The disproportionate representation of *J. pellucida* within the fertiliser-treated swards may have affected

species equitability, as suggested by the Simpson's measure of evenness. Prestidge (1982) observed similar results in a field experiment in which the cicadellid *Zyginidia scutellaris* (Herrich-Schaeffer) was most abundant prior to fertiliser application, and displaced by the delphacids *Dicranotropis hamata* (Boheman) and *J. pellucida* following the application of fertiliser.

The two main family groups of spider that were identified in this study (Linyphiidae and Lycosidae) can be grouped into two specific guilds, Linyphiidae (trappers) and Lycosidae (pursuers) (Ehmann, 1994). The more numerous Linyphiidae in this study, can be predominantly classed as sit and wait predators that trap prey in webs (Ford, 1978; Sunderland et al., 1986, 1999; Ehmann, 1994), although some Linyphiidae are not tied to their webs and are more active hunters (Harwood et al., 2003). Linyphiids can be placed in two subfamilies, members of Erigoninae build small webs close to the ground (c. 4 cm^2), whereas the members of Linyphiinae produce much larger (c. 65 cm²) above-ground webs (Sunderland et al., 1986). It is likely that combinations of these two strategies might dictate the distribution patterns of linvphilds within grazed pasture. The action of grazing will reduce the structure of the grass limiting the suitability to those that rely on web building in the upper canopy of taller vegetation (Cherrett, 1964). As the linyphilds that were found in this study were at higher densities in fertiliser treated swards they may be Linyphiinae which select taller swards for building larger aerial webs, where the chances of prey interception are greater (Harwood et al., 2003). Conversely, It is also possible that the increased litter and cover of the fertiliser treatment, may provide an enhanced microhabitat for Collembola; an important food source for linyphilds (Bell et al., 2002; Harwood et al., 2003), and one for which the surface-hunting Erigoninae are known to base their habitat choice upon (Harwood et al., 2003).

Lycosids have been recorded to feed on Auchenorrhyncha (Heong *et al.*, 1992; Lang, 2003). They are active predators that either expend energy searching for prey (Ford, 1978; Ehmann, 1994) or ambushers that wait for prey utilising vibratory stimuli from the substratum (Greenquist & Rovner, 1976) or visual cues (Lizotte & Rovner, 1988). It is likely that whilst the fertiliser-treated swards may be too dense, thus preventing normal hunting behaviour and inhibiting light, the dung-treated swards had both high prey densities and ideal structure. Bayram and Luff (1993) found lycosids to be more abundant in the shorter sward between tussocks than within tussocks. In this study, dung-treated swards were shorter than fertiliser-treated swards and appeared to have a more open structure than the fertiliser treated swards.

It is clear that the action of grazing modifies the structure of grass producing a less humid and sheltered environment, which is potentially less favourable to many grassland arthropods (Waterhouse, 1955; Purvis & Curry, 1981). In addition, it results in the destruction of specific feeding niches, like taller grass shoots and specific plant structures (Andrzejewska, 1965; Purvis & Curry, 1981; Kruess & Tscharntke, 2002). Conversely, the rejuvenation of plant tissue because of re-growth of grazed plant, can increase availability of young and nutrient rich plant tissue, which may be beneficial to herbivores (Kruess & Tscharntke, 2002), and although tall grassland supports more

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species, some groups are characteristic of shorter swards (Morris, 2000). The role of islets in maintaining structural and nutritional heterogeneity may be important in sustaining the biodiversity of arthropods within commercially managed pastures. It is possible that in many agricultural grasslands both islets and grazed swards have a high nutrient subsidy as the level of nutrient input may be enhanced by general fertiliser application. In this context, the densities of arthropods found within islets may be primarily responding to the increased structure and shelter provided by the islets rather than the nutrient subsidy. Spiders, the predatory component studied, appeared to respond to a combination of both the density of prey and the structure of sward. Spiders are possibly most constrained by the structural characteristics of the sward as they require very specific habitat variables for normal behaviour. In contrast, Hemiptera appeared to be influenced strongly by both structure and nutrient status (Prestidge, 1982; Sedlacek et al., 1988; Hartley et al., 2003). These two functionally contrasting groups of arthropods help to indicate some of the varied responses to islet generated heterogeneity. In doing so, they illustrate some of the ways in which cattle dung islet status may play an important role in the maintenance of a diverse arthropod fauna in an otherwise poor habitat.

Acknowledgements

The authors would like to thank Hilary Conlan for the use of land for the pasture experiment and Amy Moir for her assistance with the arthropod collection. The Animal and Environmental Research Group and Dawn Hawkins at Anglia Ruskin University are also to be thanked for the funding to write this article.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/j.1752-4598.2011.00133.x.

Appendix S1. The distribution of different plant species within the experimental plots.

Figure S1. The experimental plot area.

 Table S1. The full species lists of all identified adult Hemiptera.

Table S2. The distributions of respective monocot. and dicot. plant species across each of the treatments.

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Accepted 24 January 2011

First published online 11 October 2011

Editor: Alan Stewart Associate editor: Nick Littlewood