

Long-term enhancement of agricultural production by restoration of biodiversity

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Summary

1. Experimental manipulations have shown positive impacts of increased species richness on ecosystem productivity, but there remain some questions about this relationship. First, most studies last < 4 years, which raises issues about whether diversity–productivity relationships are maintained in mature communities. Secondly, the conservation relevance of many studies is debatable. We addressed both issues using long-term experimental studies of the agriculturally relevant hay yield of recreated species-rich grasslands.

2. Grasslands were recreated within replicated experiments in ex-arable fields at two sites in southern England by using either species-poor or species-rich seed mixtures. The species-poor mixture comprised seven grasses as recommended for grassland creation in English agri-environment schemes. The species-rich mixture comprised 11 grasses and 28 forbs and was designed to recreate a typical southern English hay meadow.

3. After 8 years the plots sown with species-rich mixtures resembled target diverse community types. The plots sown with species-poor mixtures had been colonized by a number of forbs but had lower numbers of grasses, legumes and other forbs than the species-rich plots. Increased hay yield of the species-rich plots in the first years of the experiments have been described in an earlier paper, and these differences were maintained after 8 years.

4. In the eighth year the species-rich plots had an average 43% higher hay yield than the species-poor plots. Regression analysis showed that the variation in hay yield was related to differences in the number of non-leguminous forbs and showed no relation to grass or legume numbers. This suggests increased hay yield is an effect of the greater range of life forms exhibited by forbs rather than a simple fertilizing effect of legumes.

5. The nitrogen content and phosphorus content of the hay showed complex treatment effects over time. However, the nutritional value of the hay was above the minimum requirements for livestock.

6. *Synthesis and applications.* The aims of conservationists and farmers can often be in conflict. This study has shown that the recreation of diverse grasslands of conservation value can have a positive impact on hay yield, which benefits the farm business, and this is repeated across differing sites. Because the effect is maintained over time, farm income will be increased in the long term.

Key-words: forage quality, grassland restoration, hay yield, long-term experiment, National Vegetation Classification, soil nutrients, species richness

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Introduction

Experimental work over the last decade has conclusively demonstrated positive effects of greater plant species

richness on some ecosystem functions, especially through increasing biomass production (Schmid & Hector 2004; Hooper *et al.* 2005; Srivastava & Vellend 2005). To some extent, increased production with higher diversity can be explained by chance through the ‘sampling effect’, whereby a greater number of species is more likely to include individual species that are highly productive, such as legumes (Huston & McBride

2002; Thompson *et al.* 2005). However, recent experiments have shown that complementary resource use among species and facilitation also play an important role and so suggest that this is a general relationship (HilleRisLambers *et al.* 2004; Hooper *et al.* 2005; van Ruijven & Berendse 2005).

However, there remain some unresolved questions about the diversity–productivity relationship. Considering experimental methods, it has been pointed out that most diversity–productivity experiments have lasted less than 3 years, with many over only one or two seasons (van Ruijven & Berendse 2005). Thompson *et al.* (2005) have argued that conclusions from studies of immature communities are of limited use in determining whether species richness affects ecosystem function and relationships might be lost in mature vegetation. While the very few studies that have extended for more than 4 years have shown a maintained effect of species richness on production (HilleRisLambers *et al.* 2004; Hooper & Dukes 2004), these criticisms illustrate the need for more long-term studies.

A more philosophical question concerns the relevance of these studies to applied ecological problems. The rationale for most studies is to investigate the consequences of species' extinctions on ecosystem functioning. Therefore, the usual methodology is to construct communities with a reduced number of species that is a random subsample of the total normally present at a site. It has been suggested that this rationale provides little information of practical use to conservation managers (Schwartz *et al.* 2000; Srivastava & Vellend 2005). Particular concerns are that extinction risk is not random among species (Petchey & Gaston 2002; Schl pfer, Pfisterer & Schmid 2005), increased production is probably not important or desirable in (semi)natural ecosystems (Schwartz *et al.* 2000; Srivastava & Vellend 2005) and the drivers of species' extinctions in the real world, such as climate change, pollution and invasive species, will probably have a greater direct effect on ecosystem functioning than the indirect effects of changes in the biota (Srivastava & Vellend 2005).

These concerns suggest that the only area for which the diversity–productivity relationship does have clear applied relevance is habitat restoration (Srivastava & Vellend 2005). Restoration involves the creation of new communities of conservation value on bare or degraded sites. On farmed land in Europe, agri-environment schemes encourage farmers to create species-rich grasslands on arable land (Pywell *et al.* 2002) or agriculturally improved pasture (Pywell *et al.* 2004). However, farmers need to produce food for livestock, and in an earlier study we showed that seven grasslands recreated with a species-rich seed mixture produced a greater hay yield than those sown with a species-poor mixture (Bullock *et al.* 2001b). Furthermore, the species-rich mixtures at each of the seven sites were designed with particular species combinations to produce grasslands of high biodiversity, in that they resembled traditional hay meadows. This 'win–win'

outcome of increased biodiversity producing greater yield for the farmer addresses the concerns about non-random species combinations, the relevance of increased productivity and the main drivers of species change. Therefore, we returned to two of the sites of the earlier study after 8 years to address the following questions. (i) Are the species-rich communities maintained over 8 years? (ii) Does the diversity–productivity relationship persist after 8 years? (iii) Is the diversity–productivity relationship explained simply by the presence of legumes?

Materials and methods

EXPERIMENTAL DESIGN

The original experiment was set up at seven sites that represented a range of soil types across southern England (Bullock *et al.* 2001b). We continued the study at two sites. The Upper Thames site, in central England (51°53'N, 1°03'W), was on an alluvial gley, which had a neutral pH (6.5) and moderate fertility ($P = 13 \text{ mg L}^{-1}$, $K = 241 \text{ mg L}^{-1}$). The Norfolk Broads site, in eastern England (52°44'N, 1°37'E), was on a humic alluvial gley, which also had a neutral pH (7.1), but had a higher fertility ($P = 28 \text{ mg L}^{-1}$, $K = 202 \text{ mg L}^{-1}$) (Pywell *et al.* 2002). Both sites had been under cereal crops up to the season prior to the experiments, which were initiated in autumn 1994. The original experimental design comprised a number of treatments described in detail by Pywell *et al.* (2002). For this study we concentrated on two of these treatments. Experimental plots were cultivated by plough to a depth of 30–40 cm (the deep cultivation treatment; Pywell *et al.* 2002). The species-rich treatments were sown with seed mixtures designed to create grasslands that resembled species-rich hay meadows typical of the soil type and geographical location. These target communities were derived from the phytosociological classification of British plant communities called the National Vegetation Classification (NVC; Rodwell 1992). For both sites, the appropriate type was MG5a *Cynosurus cristatus*–*Centaurea nigra* grassland: *Lathyrus pratensis* subcommunity. The seed mixture comprised 11 grasses and 28 forbs, including the legumes *Lathyrus pratensis* L., *Lotus corniculatus* L. and *Trifolium dubium* Sibth. (Pywell *et al.* 2002). The species-poor treatment was sown with a seed mixture of seven grasses that was recommended at the time by the UK government for establishing moderately diverse grassland under the guidelines for environmentally sensitive areas (Pywell *et al.* 2002).

Each plot was 6 × 4 m and was separated from others by 1-m guard rows. Treatments were replicated among four blocks at each site. Typical southern English hay meadow management was done at both sites after the first year and involved cutting the vegetation in July, leaving the cut herbage to dry and return seeds for several days before removal, and grazing with 25–40 sheep ha^{−1} for 6–8 weeks between October and December (Pywell *et al.* 2002).

Table 1. ANOVAS of sowing treatment effects on plant community composition, soil nutrients and components of hay yield, and differences in these effects between sites and years

Variable	Factors and interactions (all d.f. = 1,6)						
	Site	Sowing treatment	Site × treatment	Year	Year × treatment	Year × site	Year × site × treatment
Total species	0.1 ^{nsd}	29**	0.1 ^{nsd}	3.1 ^{nsd}	1.6 ^{nsd}	4.5 ^{nsd}	5.1 ^{nsd}
Grass species	15**	22**	0.1 ^{nsd}	3.8 ^{nsd}	2.6 ^{nsd}	2.6 ^{nsd}	2.1 ^{nsd}
Legume species	8.2*	15**	0.9 ^{nsd}	4.2 ^{nsd}	0.8 ^{nsd}	1.3 ^{nsd}	0.3 ^{nsd}
Forb species	0.9 ^{nsd}	16**	0.1 ^{nsd}	4.7 ^{nsd}	0.1 ^{nsd}	1.2 ^{nsd}	0.7 ^{nsd}
Soil N 0–5 cm	119***	2.9 ^{nsd}	3.2 ^{nsd}	74***	3.6 ^{nsd}	5.2 ^{nsd}	5.6 ^{nsd}
Soil N 6–20 cm	58***	0.1 ^{nsd}	0.1 ^{nsd}	30**	1.2 ^{nsd}	5.0 ^{nsd}	1.3 ^{nsd}
Soil P 0–5 cm	58***	0.1 ^{nsd}	0.2 ^{nsd}	7.3*	0.4 ^{nsd}	1.3 ^{nsd}	0.1 ^{nsd}
Soil P 6–20 cm	108***	0.1 ^{nsd}	0.1 ^{nsd}	25*	0.8 ^{nsd}	2.3 ^{nsd}	0.4 ^{nsd}
Hay yield	0.5 ^{nsd}	6.6*	2.5 ^{nsd}	0.2 ^{nsd}	0.1 ^{nsd}	4.9 ^{nsd}	2.7 ^{nsd}
%N in hay	0.8 ^{nsd}	2.3 ^{nsd}	0.1 ^{nsd}	18**	12*	3.4 ^{nsd}	5.7 ^{nsd}
%P in hay	19*	0.1 ^{nsd}	0.1 ^{nsd}	0.1 ^{nsd}	13*	0.1 ^{nsd}	0.2 ^{nsd}

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; nsd no significant difference.

DATA COLLECTION

From 1995 to 1998 and in 2002, the plant communities were sampled in early June by placing three 0.4 × 0.4-m quadrats at random positions within each plot. All vascular plant species were identified and noted for each quadrat. During the hay cut in each year, a 6 × 1.2-m sample of hay was removed from each plot and weighed fresh. A 500-g subsample was oven-dried at 102 °C for 18 h and the dry weight was used to calculate the dry matter (DM) hay yield. The forage quality of this hay was determined by measuring the percentage nitrogen (%N) of the dried subsamples using the Dumas combustion method, and the percentage phosphorus (%P) using inductively coupled plasma/mass spectrometry (Bullock *et al.* 2001b).

In 1994, 1998 and 2002, 10 soil samples were taken at random positions in each plot using a 6-cm diameter, 20-cm deep auger. The top 5 cm of the cores were separated and then consolidated across the 10 replicates. The remaining 6–20-cm fractions were also mixed. Five-hundred cubic centimetre subsamples of each fraction were analysed for pH, nitrogen and phosphorus using standard methods (Pywell *et al.* 2002).

ANALYSIS

The data up to 1998 are presented by Bullock *et al.* (2001b) and Pywell *et al.* (2002) and, to determine the long-term treatment effects, we concentrated on comparing the 1998 and 2002 data. Treatment effects on vegetation, hay yield and soil nutrient measures and their differences between years and sites were tested using an analysis of variance (ANOVA) model with site, block (nested in site), treatment and site × treatment terms and a repeated-measures structure (using the REPMEAS procedure in SAS 9.1) to contrast 1998 and 2002. Repeated-measures ANOVA was done using univariate procedures, the Huynh–Feldt and the more

conservative Greenhouse–Geisser corrections (Maxwell & Delaney 2003). Both gave identical qualitative results and the P -values for the Greenhouse–Geisser correction are given. Residuals were normally distributed in all analyses. Species occurrence data were combined for all replicates of the same treatment at a site and the TABLEFIT program was used to assess similarity of the restored vegetation to NVC community types (Hill 1996). TABLEFIT calculates the percentage fit between observed occurrence data and that specified for each NVC community.

Results

The species richness of the plant communities at each site and in each treatment did not change between 1998 and 2002, as shown by no significant year effects or interactions of year with site or treatment on the total number of species or the numbers of grasses, legumes or other forbs (Table 1). Despite the fact that none was sown in the species-poor treatments, some forbs colonized, so that frequent species in 2002 included *Lotus corniculatus* and *Trifolium dubium* at the Norfolk Broads site, and *Trifolium dubium* and *Leucanthemum vulgare* Lam. at the Upper Thames site. The best-fit NVC vegetation type for the species-rich treatment (MG5a *Cynosurus cristatus*–*Centaurea nigra* grassland: *Lathyrus pratensis* subcommunity) was the same at both sites and did not change over time: 66% fit in 1998 and 52% in 2002 for the Norfolk Broads, and 75% in 1998 and 64% in 2002 for the Upper Thames. Communities were different in the species-poor treatment, which at the Norfolk Broads was assigned to MG5a (49%) in 1998 and MG5 (*Cynosurus cristatus*–*Centaurea nigra* grassland) in 2002 (43%), and in the Upper Thames to MG6c (*Lolium perenne*–*Cynosurus cristatus* pasture: *Trisetum flavescens* subcommunity) in both 1998 (52%) and 2002 (58%).

The consistency in community composition over time was despite increases in soil nitrogen (N) and

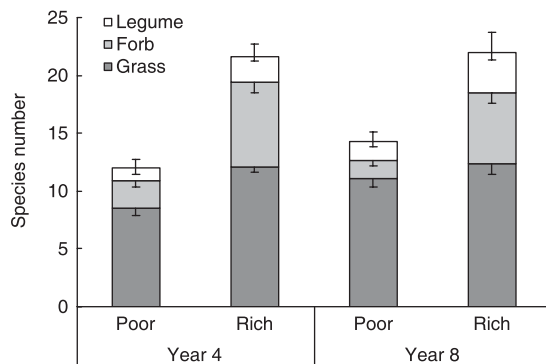


Fig. 1. Differences between sowing treatments and years in the number of species for three taxonomic groups. Downward bars indicate standard errors for each taxonomic group and the upward bars are standard errors for the total species number.

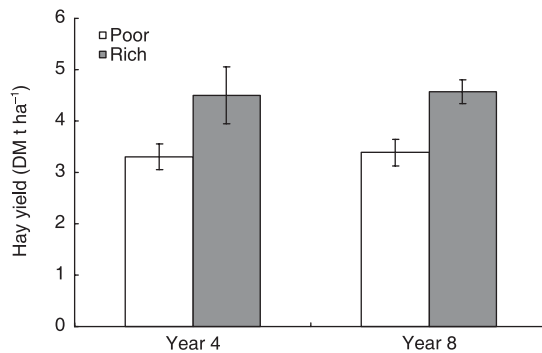


Fig. 2. Hay yield, measured as tonnes of dry matter per hectare, differed between the species-rich and species-poor treatments, but not between years or sites.

phosphorus (P) concentrations over time (Table 1), especially in N which increased between 1998 and 2002 in Norfolk from $0.103 \pm 0.012\%$ to $0.202 \pm 0.008\%$ (soil depth 0–5 cm) and $0.073 \pm 0.003\%$ to $0.123 \pm 0.004\%$ (6–20 cm), and in the Upper Thames from $0.316 \pm 0.044\%$ to $0.489 \pm 0.013\%$ (soil depth 0–5 cm) and from $0.276 \pm 0.038\%$ to $0.418 \pm 0.022\%$ (6–20 cm). The increases in P from 1998 to 2002 were less: in Norfolk from $30.0 \pm 1.96 \text{ mg l}^{-1}$ to $31.5 \pm 2.21 \text{ mg l}^{-1}$ (0–5 cm) and $25.9 \pm 1.53 \text{ mg l}^{-1}$ to $28.5 \pm 1.43 \text{ mg l}^{-1}$ (6–20 cm), and in the Upper Thames from $9.9 \pm 0.83 \text{ mg l}^{-1}$ to $13.6 \pm 0.91 \text{ mg l}^{-1}$ (soil depth 0–5 cm) and from $7.6 \pm 0.89 \text{ mg l}^{-1}$ to $8.5 \pm 0.27 \text{ mg l}^{-1}$ (6–20 cm).

The effects of the treatments on the plant communities were also clear from the ANOVAs. The species-rich treatment had consistently more grass, legume, other forb and total species than the species-poor treatment (Fig. 1), with no difference between the sites in these effects (i.e. no site \times treatment interactions; Table 1).

The sowing treatments also affected hay yield (Table 1 and Fig. 2), with a mean 43% higher yield in the species-rich plots (based on comparison of plots within blocks), and these effects did not vary between sites or over time (i.e. no interactions of treatment with site or year; Table 1). The relationships between species

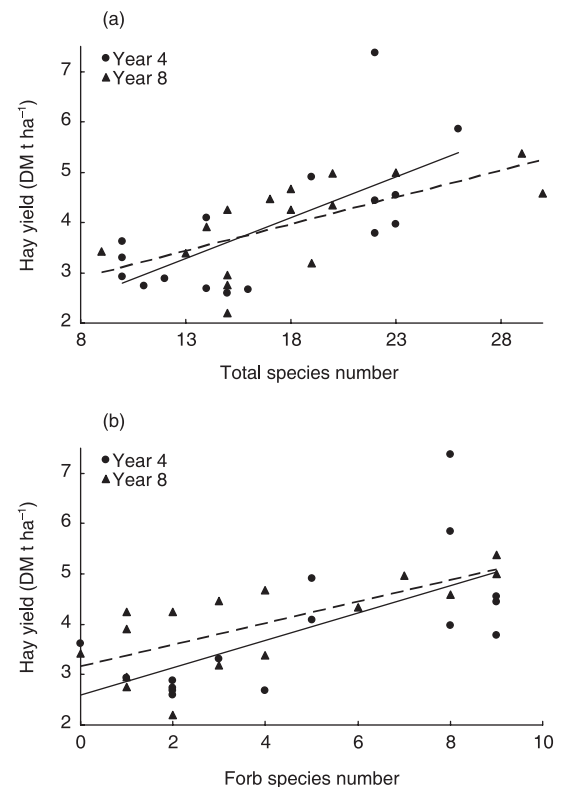


Fig. 3. The relationship of (a) total plant species number and (b) forb species number with the hay yield of each experimental plot in year 4 (1998) and year 8 (2002). Significant regression lines (see text) are shown for the year 4 (complete line) and year 8 (dashed line) data.

number of a plot and its hay yield were explored with analysis of covariance (ANCOVA) and regression. Data from 1998 and 2002 were analysed separately to avoid pseudoreplication through the use of two measures from the same plot. ANCOVA showed no effect of site on the relationship between species number and hay yield (results not shown), so we merged data from both sites and used linear regression. Hay yield increased significantly with higher total species number (Fig. 3a) in 1998 ($r^2 = 0.47$, $n = 16$, $P < 0.01$) and 2002 ($r^2 = 0.42$, $n = 16$, $P < 0.01$). Species were assigned to grasses, legumes or other (i.e. non-leguminous) forbs and the number of species in each group was included as a predictor in a stepwise linear regression with backwards elimination for 1998 and 2002. Species numbers of grasses and legumes were eliminated from both models, and number of other forb species was the only significant predictor (Fig. 3b) both in 1998 ($r^2 = 0.44$, $n = 16$, $P < 0.01$) and in 2002 ($r^2 = 0.52$, $n = 16$, $P < 0.01$).

The nutrient content of the hay varied in a more complicated manner (Table 1 and Fig. 4). The percentage nitrogen content increased over time and, while it was higher in the species-rich treatment in 1998, this effect was lost by 2002, leading to a year \times treatment interaction. The percentage phosphorus content also showed a year \times treatment interaction because, while the hay from the species-rich treatment had a higher

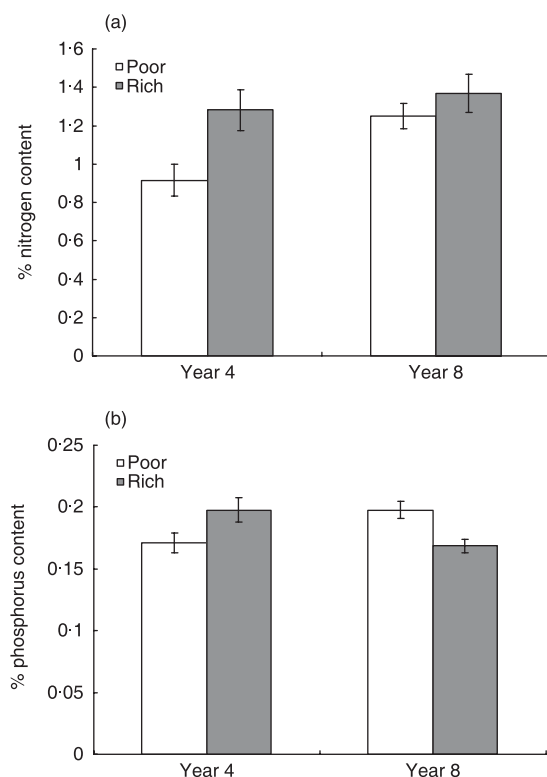


Fig. 4. The nutrient content of hay harvested from species-poor and species-rich treatments in each year, in terms of (a) % nitrogen and (b) % phosphorus content.

phosphorus content in 1998, by 2002 the species-poor treatment had the greater phosphorus concentration. These effects were consistent across the sites despite the greater phosphorus concentration in the hay from Norfolk (0.2%) compared with the Upper Thames (0.17%; Table 1).

Discussion

While the positive effect of plant species richness on productivity is uncontroversial, doubts have been raised about the long-term stability of this relationship and its relevance for applied conservation (Srivastava & Vellend 2005; Thompson *et al.* 2005). With this study we have shown that restoration of species-rich communities of conservation value can increase agriculturally relevant hay production and that this effect is maintained over at least 8 years.

Other studies that have extended beyond 3 years have found a maintained effect of species richness on productivity (HilleRisLambers *et al.* 2004; Hooper & Dukes 2004; Hofmann & Isselstein 2005; Schlöpfer, Pfisterer & Schmid 2005; van Ruijven & Berendse 2005) and some have even shown an increase in this effect over time (Hooper & Dukes 2004; van Ruijven & Berendse 2005). Thompson *et al.* (2005) suggest that over time the species richness of a community will be determined by the soil fertility: so productivity, determined by soil fertility, will affect diversity rather than *vice versa*. This is not an issue if the low diversity treat-

ments are well below the maximum species richness achievable for a site, where such a maximum may be described by the 'hump-back' effect of fertility on species richness (Grime 2001). Indeed, in addressing the consequences of species loss, that is exactly the aim of most diversity–productivity studies (Hooper *et al.* 2005). In applying these ideas to restoration ecology, we are asking whether setting more ambitious aims for the species richness of the restored community has effects on ecosystem functions.

Soil fertility limits the identity and number of plant species that can establish in a restored site (Pywell *et al.* 2003; Walker *et al.* 2004), and methods to diversify agriculturally improved grassland have to ameliorate effects of high nutrients (Bullock & Pywell 2005). However, seed limitation plays an important role in determining the plant community that develops (Hutchings & Booth 1996; Pywell *et al.* 2002). Seed banks of arable land are dominated by annual weeds (Pywell *et al.* 2002) and those of resown species-poor agricultural grassland contain few species not already present in the vegetation (Bullock *et al.* 1994). Colonization by seed dispersal is generally slow and stochastic, particularly in depauperate landscapes under intensive agriculture (Bullock *et al.* 2002). Therefore, as we have shown in this study, the composition of the seed mixture sown in a restoration can have long-term effects on the composition and diversity of the resulting vegetation. The fact that species differences were maintained between small, adjacent plots subject to hay-cutting (which can disperse seeds long distances; Bullock *et al.* 2003) suggests that the vegetation established from the species-poor seed mixtures was resistant to further colonization (Pywell *et al.* 2002).

This is not to say that seed mixtures can be designed to create highly diverse communities on any site. However, in the moderately fertile conditions of our study sites, as long as there is no further fertilizer addition, it is possible to establish moderately rich communities if appropriate species are added (Pywell *et al.* 2003) and extensive management by cutting and grazing reduces the dominance of competitive species (Bullock *et al.* 2001a; Pywell *et al.* 2004). The large increases in soil nitrogen and small increases in phosphorus over time probably reflected build up in organic matter in this ex-arable soil (Marrs 1993) but seemed to have had little effect on the plant community.

We can conclude little here about the exact mechanisms by which increased species richness led to higher productivity. Other studies designed to disentangle the mechanisms tend to show that both the chance inclusion of highly productive species such as legumes (the sampling effect) and complementary resource use among functionally different plants in more species-rich communities are important (HilleRisLambers *et al.* 2004; Hooper & Dukes 2004; van Ruijven & Berendse 2005). However, it is sometimes suggested that the presence of legume species may largely explain the diversity–productivity relationship (Thompson *et al.* 2005). Indeed,

our species-poor seed mixtures contained only grasses, which might support such a conclusion. However, these plots were rapidly colonized by legumes and other forb species and our earlier analysis (Bullock *et al.* 2001b) showed that, while total species number was a good predictor of productivity differences, the number of legume species was not. In this study, legume species number was again a poor predictor of hay yield but the number of other forb species was a good predictor. Hofmann & Isselstein (2005) showed increased production in grasslands diversified by over-sowing with forbs and pointed out that forb species show a wide range of temporal and spatial growth patterns and so would be expected to show complementary resource use.

Farmers must bear some cost and income foregone when embarking on restoration of species-rich grasslands on former arable land or intensive grassland. Although they gain compensation through agri-environment payments, some of this loss could be recouped by increasing yield from the restored land. In our earlier paper (Bullock *et al.* 2001b) we showed some limited recompense of the extra cost of the species-rich seed from the increased hay yield but pointed out that, because seed is a one-off cost, and if the hay yield differential is maintained, profit will be achieved over time. Using current prices from seed catalogues, the species-rich seed mixture would cost £660 more per hectare than the species-poor mixture, but farmers get a payment of £280 ha⁻¹ under the Defra Higher Level Stewardship Scheme (www.defra.gov.uk/erdp/schemes/es) for sowing seed mixes containing a range of forbs. This reduces the cost to £380 ha⁻¹. Using the yearly differences in yield from the first to fourth years (Bullock *et al.* 2001b) and assuming the differences from the fifth year onwards are as measured in the eighth year, it would take 4–6 years after sowing to recoup costs in the Norfolk Boards and 10–14 years in the Upper Thames. Hay prices vary among years and so we used the January prices for 'baled meadow hay' in England for each year 2002–06 to calculate these range of recoup times. Obviously these rough calculations ignore interest and inflation.

However, the quality of the hay should also be taken into account, and this showed changes over time. In the fourth year both nitrogen and phosphorus concentrations of the hay were slightly higher in the species-rich treatment, which concurs with the findings of Hofmann & Isselstein (2005) for nitrogen content. In 1998 and 2002 the species-rich hay had a nitrogen content near the 1.3% level, below which performance of farmed cattle is decreased (Tallowin & Jefferson 1999). The species-poor hay was well below this concentration in 1998 but was similar to the species-rich hay in 2002 (Fig. 4). The lower limit for phosphorus in hay to maintain weight gain in cattle is about 0.15% (Tallowin & Jefferson 1999). This was exceeded in both treatments in both years, although the phosphorous content of the species-poor hay overtook that of the species-rich hay in 2002. It is not clear what drove these changes in treat-

ment effects on forage quality over time and, although the species-rich hay was on average better quality (through the effects on nitrogen content), these patterns merit further investigation. Furthermore, the nutritional quality of feed can affect meat quality, for example by changing muscle characteristics (Geay *et al.* 2001; Hoch *et al.* 2005), but little is known about the links between biodiversity, animal performance and the quality of farm products such as meat and milk.

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