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Enhancing pollinator biodiversity in intensive grasslands

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Summary

1. Increased agricultural intensification has led to well-documented declines in the fauna and flora associated with intensive grasslands in the UK. We aimed to quantify the effectiveness of different field margin management strategies for putting bumblebee and butterfly biodiversity back into intensive grasslands.

2. Using four intensive livestock farms in south-west England, we manipulated conventional management practices (addition of inorganic fertilizer, cutting frequency and height, and aftermath grazing) to generate seven grass-based treatments along a gradient of decreasing management intensity. We also tested two more interventionist treatments which introduced sown components into the sward: (i) a cereal, grass and legume mix, and (ii) a diverse conservation mix with kale, mixed cereals, linseed and legumes. These crop mixtures were intended to provide forage and structural resources for pollinators but were not intended to have agronomic value as livestock feed. Using a replicated block design, we monitored bumblebee and butterfly responses in 27 plots (10×50 m) in each farm from 2003 to 2006.

3. Bumblebees were most abundant, species-rich and diverse in the sown treatments and virtually absent from the grass-based treatments. The diverse conservation mix treatment supported larger and more diverse bumblebee assemblages than the cereal, grass and legume mix treatment. The sown treatments, and the most extensively managed grass-based treatments, had the highest abundance, species richness and diversity of adult butterflies, whereas butterfly larvae were only found in the grass-based treatments.

4. Bumblebee and butterfly assemblage structure was driven by floral abundance, floral richness, the availability of nectar resources, and sward structure. Only vegetation cover was correlated with butterfly larval abundance.

5. *Synthesis and applications*. This study has identified management options in the margins of intensive grasslands which can enhance bumblebee and butterfly biodiversity. Extensification of conventional grass management by stopping fertilization, reducing cutting frequency and not grazing, benefits butterflies. However, to enhance bumblebees requires a more interventionist approach in the form of sowing flower-rich habitat. Both approaches are potentially suitable for adoption in agri-environment schemes in the UK and Europe.

Key-words: agri-environment scheme, bumblebees, butterflies, cutting, grazing, intensive grassland, pollinators

Introduction

Pollinators have a key function in the maintenance of terrestrial ecosystem integrity through their role in plant reproduction, the products of which support a wide range of invertebrates, birds and mammals (Wilson *et al*. 1999; Woodcock *et al*. 2007). Pollinators also provide goods and services to society, with many of the world's crops being dependent upon pollinators for their productivity (Klein *et al*. 2007).

A growing body of evidence indicates that pollinators are in decline around the world (e.g. National Research Council 2006) and that losses in some countries and regions are set to

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continue. In the UK, bees have shown marked shifts in their distributions since 1980, with many species showing significant declines (Biesmeijer *et al.* 2006). Similarly many British butterflies have shown drastic changes in their distributions, with some species contracting and some species expanding over the last 60 years (Asher *et al.* 2001; Thomas *et al.* 2004). For bees and butterflies, the intensive management of agro-ecosystems appears to be a driver of the declines (Tscharntke *et al.* 2005). While bumblebees are known to pollinate wildflowers in the UK, butterflies probably play a minor role (Jennersten 1984); however, both groups are referred to as pollinators in this study.

Population declines of higher plants (Blackstock *et al.* 1999), invertebrates (Duffey *et al.* 1974) and birds (Vickery *et al.* 2001) have all been attributed to management intensification in the UK grasslands. High fertilizer application rates with frequent intensive defoliation, whether by grazing or cutting for silage to optimize harvested forage quality, are characteristics of modern livestock farming (Vickery *et al.* 2001). These practices have produced low nature value grasslands with degraded species pools and structurally homogenous swards (Vickery *et al.* 2001; Tallowin *et al.* 2005).

Re-seeding and fertilization decrease plant diversity in grasslands and thus reduce food source availability for invertebrates (Duffey *et al.* 1974; Tilman 1987). Associations between pollinators and floral resources have been demonstrated for nectar and pollen by adult bees (Carvell 2002; Potts *et al.* 2003), for nectar by adult butterflies and for host-plants by butterfly larvae (Smart *et al.* 2000). Grazing and cutting remove existing floral food resources (Duffey *et al.* 1974; Morris 2000; Kruess & Tscharntke 2002) and reduce tussock grass structures which provide shelter for invertebrates (Morris 2000; Woodcock *et al.* 2007) including butterflies (Saarinen *et al.* 2005).

Approximately 40% of agricultural land in England and Wales is classified as permanent or temporary grassland (Defra 2006). There are some options to improve grasslands for biodiversity through existing agri-environment schemes, such as the Entry Level Stewardship (Defra 2005). 'Permanent grassland with very low inputs' (Option EK3) is an example; however, because of the low uptake and geographic coverage, the environmental value appears limited. In contrast, the use of field margins managed specifically for biodiversity enhancement has been an effective Entry Level Stewardship option in arable systems (Meek *et al.* 2002; Carvell *et al.* 2004; Pywell *et al.* 2004).

Therefore, there is a major opportunity to develop novel practices to improve existing intensive grasslands for pollinators. Management techniques which increase the spatial and temporal availability of key resources for pollinators have the potential to deliver widespread benefits if incorporated into existing agri-environment schemes. Manipulation of fertilization, cutting and grazing regimes is one possibility for identifying pollinator-friendly practices, and introducing novel habitat types (e.g. flower-rich margins) is another.

This study aims to quantify the response of pollinators to management treatments aimed at reducing the intensity of land use in existing improved grasslands. By understanding the underlying mechanistic basis for the response of pollinators to grassland management, it will be possible to identify practical management options to enhance pollinator biodiversity in intensive grasslands. To do this, we tested the hypotheses that: increasing the diversity of forage resources will enhance the diversity of pollinators, specifically (i) grasses and forbs as host plants for butterfly larvae, and (ii) forbs providing nectar (and pollen) resources for adult bumblebees and butterflies; and, increasing the architectural complexity of swards will benefit adult butterflies by providing increased shelter and more favourable microclimatic conditions.

Materials and methods

STUDY SITES

Experiments were performed on four lowland farms in the UK, two in Devon and two in Somerset: North Wyke (N50°46′14″, W3°55′46″), Heywoods (N50°48′38″, W3°55′40″), Bickenhall (N50°58′47″, W2°59′29″) and South Hill (N50°57′40″, W3°02′53″). Farms were typical for the region, located on clay loam soils, separated by at least 8 km within each county and classified as species-poor *Lolium perenne* leys.

EXPERIMENTAL DESIGN

Nine experimental treatments were applied using a randomized block design (Table 1). Treatments were established in April 2002 and monitored annually from 2003 to 2006. Experimental plots were established in field margins on permanent pastures (> 5 years old) and were 50 × 10 m with the long axis running parallel to and adjacent to the hedgerow which formed the boundary surrounding all fields.

Table 1. Management practices applied to experimental plots

Code	Treatment	N fertilizer	May cut height	July cut height	Grazed
T1	Conventional silage management	Yes	5 cm	5 cm	Yes
T2	Unfertilized	No	5 cm	5 cm	Yes
T3	Raised mowing height	Yes	10 cm	10 cm	Yes
T4	No aftermath grazing	Yes	5 cm	5 cm	No
T5	Single early cut	No	10 cm	No cut	No
T6	Single late cut	No	No cut	Cut in July	No
T7	No summer disturbance	No	No cut	No cut	No
T8	Under-sown spring cereal	Yes	No cut	Cut in July (second year)	No
T9	Sown complex mix	Yes	No cut	No cut	No

Three replicates of each treatment were established in each of the four farms, giving 12 replicate blocks, and treatments were randomly assigned within blocks.

Treatments 1 to 4 were grass-based treatments that used modifications of conventional improved grassland management practices to manipulate the existing sward and provided a factorial design enabling any interaction between fertilizer input, silage stubble height and/or aftermath grazing intensity on pollinator biodiversity to be examined. Treatments 5 to 7 looked at the effects of temporal variation in cutting dates on unfertilized grassland margins. These grass-based treatments represent variations on established management practices found in intensive lowland grasslands. In contrast, Treatments 8 and 9 were intended to replace species-poor agricultural grassland with a mix of plant species to provide structure, seed, nectar and pollen resources over 1–2 growing seasons. Herbage harvested from these treatments (i.e. in years 2 or 3 following their establishment) would have little or no agronomic value as a livestock feed.

Treatment 1 was the control and was under conventional silage management (Table 1) with NPK fertilization, two cuts to 5 cm (May and July) and aftermath grazing. Treatments 1, 3 and 4 received inorganic fertilizer at rates equivalent to 225 kg nitrogen, 22 kg phosphorus and 55 kg potassium ha^{-1}. Grass swards were cut at either 5 or 10 cm height in May and/or July (T1–T4). Cattle-grazed treatments 1 to 3 in September until the sward height was 5–7 cm. Treatments 5–7 were extensively managed with no grazing or fertilization with a single sward cut each year. Treatment 7 was left undisturbed throughout the summer months and was topped once during early spring each year. Treatments 8 and 9 involved the complete replacement of the existing grass sward by sowing a mixture of species into a prepared seed bed. Treatment 8 plots were sown in April with spring barley and under-sown with a grass and legume mix. The grass mix included *Dactylis glomerata*, *Agrostis capillaris*, *Phleum pratense*, *Festuca rubra* ssp. *litoralis*, *Cynosurus cristatus*, *Anthoxanthum odoratum* and *Lolium perenne*. The legume mix included *Trifolium pratense*, *T. repens*, *Lotus corniculatus*, *Vicia sativa* and *Medicago lupulina*. Each plot was cut in July in the year following sowing. Treatment 9 was sown in April with kale, quinoa, mixed cereals (barley, triticale and oats), linseed and legumes (*T. pratense*, *T. repens*, *L. corniculatus* and *V. sativa*). For successful establishment, kale seedlings require reduced competition, and therefore, treatment 9 plots were split with the 5 × 50 m section closest to the boundary hedge sown with kale and quinoa and the outer 5 × 50 m section sown with the rest of the mixture. Because of the high fertility of intensive grassland soils, sown areas develop high plant cover, which allows little regeneration from shed seed by many of the sown species. For annual, biennial or short-lived perennial plant species, which comprised many of the sown species, re-sowing is essential in order to consistently obtain the food resources that they provide for different invertebrate guilds. Treatments 8 and 9 were re-sown annually each year in new plots to accommodate between year variability in establishment and the first temporal replicate of treatment 8 was retained for the duration of the experiment, and following cutting, it was subsequently managed as treatment 6.

BOTANICAL COMPOSITION, NECTAR RESOURCES AND VEGETATION STRUCTURE

For the duration of the experiment, the percentage cover of all vascular plant species was recorded in August of each year; this period was chosen to allow sufficient time for recovery after the second cut and was prior to grazing. Five fixed 1 × 1 m quadrats were placed at equal distances along a diagonal transect in each experimental plot. Estimates of nectar resources were made in June and September of each year using 10 randomly placed 30 cm diameter quadrats in each experimental plot. In each quadrat, the number of flowers per seed heads for each species, which were rooted in the quadrat, were recorded. The number of heads was used as a surrogate measure for nectar availability as direct measurement of nectar parameters in the field is impractical (Potts *et al.* 2003). Nectar sources were partitioned into those sources that were legumes, and those which were other forbs (not including legumes). While flower per seed heads are only an indirect measure of nectar availability (and possibly pollen availability), we use the term nectar throughout the remainder of the manuscript.

The continuous environmental variables measuring plant and nectar resource availability within the experimental plots were selected as known drivers of pollinator communities: abundance of nectar flowers and total nectar abundance for adult bumblebees; abundance of nectar flowers, total nectar abundance and sward structure for adult butterflies; and abundance of host plants and sward structure for butterfly larvae. From the full botanical data set collected for the experiment, a forage plant for each pollinator group was only included in models if it was: (i) a known resource for pollinators; (ii) present in more than one experimental plot for all sites and years; (iii) covering at least 50 cm^2 for all plots summed for all years. Using these criteria, abundance data for 14 forb taxa were used in the bumblebee model (Supporting Information, Appendix S5a), 14 forb taxa were used in the butterfly model (Supporting Information, Appendix S5b) and 15 forb/grass taxa in the larva model (Supporting Information Appendix S5c). For butterflies, larval host-plants and adult nectar flowers were identified using the 'British butterfly host-plant and nectar source' database (www.geocities.com/pgll@btopenworld.com/resources/resources.htm, last accessed 29 February 2008). Bumblebee flowers were identified using Prŷs-Jones & Corbet (1991). Predictors in the models were floral cover ($Cover_{floral}$), floral species richness (SR_{floral}), nectar resources from legumes ($Nectar_{legume}$), nectar sources from forbs not including legumes ($Nectar_{forb}$) and sward structure (Sward).

Coarse-grain vegetation was measured as sward structure (leaf and stem density within the sward) and estimated using the 'drop disk' method (Stewart, Bourn & Thomas 2001). In April, June, July and September of each year, 25 measurements were made at regular intervals along a diagonal transect in each plot.

POLLINATOR SAMPLING

Standardized transect walks were used to measure the abundance and species richness of bumblebees and butterflies on each treatment plot following the methods described by Teräs, (1983) and Pollard & Yates (1993). Adult bumblebees and butterflies were recorded using a 50-m permanent transect route running along the centre line of each experimental plot. Each transect was surveyed once in June, July, August and September and walked at a rate of *c.* 15 m min^{-1} to count bumblebees and butterflies within 2·5 m of the recorder. Walks were carried out between 10·00 and 17·00 h, when weather conformed to Butterfly Monitoring Scheme standards (Pollard & Yates, 1993). The six most common British bumblebees were recorded: *Bombus terrestris*, *B. lucorum*, *B. hortorum*, *B. lapidarius*, *B. pratorum* and *B. pascuorum.* As workers of *B. terrestris* and *B. lucorum* cannot be reliably distinguished in the field, these species were treated as an aggregate species (Prŷs-Jones & Corbet 1991). Adult butterflies were identified to species. Lepidoptera larvae were collected in April, June, July and September of each year on two 10-m transects using 20 sweeps of a net on each, and counted but not identified to species.

ANALYSIS

Adult bumblebees, adult butterflies and butterfly larvae were analysed separately using the summed abundance of each species in a given year. Repeated-measures analysis using mixed models (SAS 9·01) was used to analyse the response of pollinators to the treatment effects and continuous environmental variables. Response variables were the abundance ($\log_e N + 1$), species richness ($\log_e N + 1$) and diversity (Shannon–Wiener) of butterflies and bumblebees and the abundance of ($\log_e N + 1$) of butterfly larvae. All models used an autoregressive covariance structure to account for increased similarity between repeated measures in adjoining years. The random effects of the model were site, field nested within site, and replicate block nested within field (Woodcock *et al.* 2007). Since management practices associated with the treatment will affect the continuous environmental variables recorded in each plot, it is not possible to test their effects on pollinators within a single model. Three models were therefore used for each pollinator group: Model 1 tested for responses to the explanatory variables of year, treatment and the treatment × year interaction; Model 2 tested the effect of year, the continuous environmental variables and their interaction with year; Model 3 tested whether the addition of the significant environmental variables defined in Model 2 to those of Model 1 explained additional variance to the treatment effects. All models were simplified by deletion of least significant factors (except as part of a significant interaction) and degrees of freedom were calculated by the iterative Satterthwaite method (Schabenberger & Pierce 2002). Whether Model 3 explained additional variance in the species data to that of the treatment-only model (Model 1) was assessed using Akaike's Information Criterion (AIC). AIC allows models with different numbers of parameters to be directly compared with each other, where the lowest AIC value indicates a better fit to the data (Bozdogan 1987). Between-treatment differences in response variables were tested for significance using a *post hoc* pairwise comparison.

Results

Over the four experimental years, 896 bumblebees were observed and assigned to one of five species groups; numbers varied markedly between years 2003 (78), 2004 (614), 2005 (46) and 2006 (158). *Bombus terrestris/lucorum* was the most common taxon with 356 individuals, followed by *B. pascuorum* (242), *B. lapidarius* (231), *B. hortorum* (58), and *B. pratorum* (9) (see Supporting Information, Appendix S1a). A total of 1217 adult butterflies were observed (273 in 2003, 390 in 2004, 412 in 2005 and 142 in 2006) and identified to one of 22 species (Supporting Information, Appendix S1b). The three most abundant species were *Maniola jurtina* (meadow brown, 694 individuals), *Pieris rapae* (small white, 122 individuals) and *Aglais urticae* (small tortoiseshell, 98 individuals); all other species comprised less than 69 individuals. The total number of butterfly larvae collected was 1152 with 245 in 2003, 229 in 2004, 521 in 2005 and 157 in 2006.

RESPONSE OF POLLINATORS TO MANAGEMENT TREATMENT

Effects of year and the significant treatment × year interaction were caused by high between-year variation, however, with the highest values of the response variables (abundance, species richness and diversity) for treatment. Thus, the sown treatments 8 and 9 supported the highest abundance, species richness and diversity. Although effects of the sown treatments were not consistent between years, the magnitude of the superiority of the sown treatments relative to the grass manipulation (T1–T7) was on the whole consistent within a given year. Hence, the significant treatment effects (independently of the treatment × site interaction) provide a useful indication of the overall response of bumblebee abundance, species richness and diversity to the nine treatments over the 4-year period (Schabenberger & Pierce 2002). Both sown treatments, T8 and T9, had significantly higher bumblebees numbers than any grass-based treatment, T1–T7, in 2003 ($P \leq 0{\cdot}0105$ in all cases) and 2004 ($P < 0{\cdot}0001$ in all cases), while T9 had the highest abundance of bumblebees in all years (Fig. 1a; Supporting Information, Appendix S2a). Bumblebee species richness exhibited an identical pattern to abundance (Fig. 1b; Supporting Information, Appendix S2b), and was characterized by highest richness in the sown plots in all years, with T9 also supporting more species than T8 in 2005 ($P = 0{\cdot}0071$) and 2006 ($P < 0{\cdot}0001$). T9 was significantly more diverse than the grass treatments ($P \leq 0{\cdot}0033$ in all cases) and T8 ($P \leq 0{\cdot}0022$ in all cases) in all years, except in 2004 where both sown treatments had similar diversity values and were more diverse than T1–T7 ($P < 0{\cdot}0001$ in all cases; Fig. 1c; Supporting Information, Appendix S2c). Abundance and species richness for all treatments (except 3, 4 and 7) increased significantly between 2003 and 2004 ($P \leq 0{\cdot}0493$ in all cases) and then dropped in 2005 ($P \leq 0{\cdot}0493$ in all cases; Fig. 1; Supporting Information, Appendix S2d). Treatment 9 showed an increase in all bumblebee parameters between establishment years, 2003 and 2005, and the second year of growth, 2004 and 2006 ($P \leq 0{\cdot}0058$ in all cases).

As for the bumblebees, there were significant effects of management treatment, year and treatment × year interaction for the abundance, species richness and diversity of adult butterflies and counts of butterfly larvae (Table 3). This finding reflects again high between-year variability, but treatment supported again the highest value of response variables for adult butterflies. Typically, one or both of the sown treatments 8 and 9 supported the highest abundance, species richness or diversity of butterflies within a particular year. An interaction effect between year and treatment was most apparent for treatment 8, when in years 3 and 4, species richness and diversity dropped dramatically, particularly in relation to the grass manipulations (T1–T7). Considering only the significant treatment response, the sown treatments and extensive grass treatments, T6 and T7, generally supported higher numbers and more species of butterflies than the intensive treatments (T1–T5), although not always significantly so (Fig. 2a,b). Butterfly abundance was significantly greater in T6–T9 than T1–T4 in 2003 and 2004 ($P \leq 0{\cdot}0359$ in all cases, except of T6 vs. T2 in 2003; Supporting Information, Appendix S3a). In 2003 and 2004, butterfly species richness was significantly higher in the sown treatments than the most intensively managed grass-based treatments, T1–T5, ($P \leq 0{\cdot}0135$ and $P < 0{\cdot}0001$

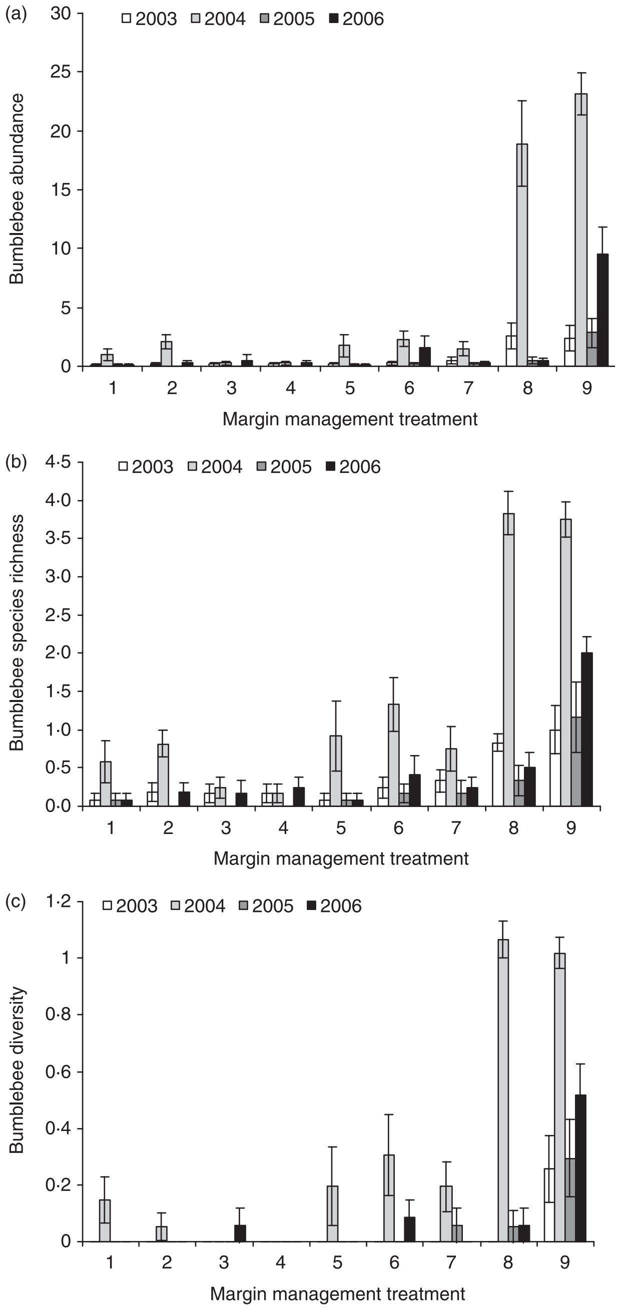

Fig. 1. Response of bumblebees to management treatments: (a) abundance (mean numbers per transect ± SE); (b) species richness (mean number of species per transect ± SE); (c) diversity (mean Shannon-Wiener ± SE). Full description of the management treatments 1–9 is given in the text.

in all cases, respectively), and by 2006, T9 had more species than any other treatment ($P \leq 0{\cdot}0109$ in all cases; Supporting Information, Appendix S3b). The sown treatments were significantly more diverse than grass treatments in 2003 and 2004 ($P \leq 0{\cdot}0253$ in all cases), and T9 was significantly more diverse than all other treatments in 2005 and 2006 ($P \leq 0{\cdot}0148$ in all cases, except T2, 5 and 7 in 2005; Fig. 2c; Supporting Information, Appendix S3c). Both butterfly abundance and species richness tended to increase with year from 2003–2005 within the grass-based treatments (Fig. 2a,b; Supporting Information, Appendix S3d). All butterfly measures significantly increased in T8 from 2003 to 2004 ($P \leq 0{\cdot}0412$ in all cases), and then were lower than the 2004 values thereafter (Supporting Information, Appendix S3d). There was a significant increase in abundance in T9 between 2003 and 2004 ($P \leq 0{\cdot}0134$; Supporting Information, Appendix S3d). For larval abundance, the treatment × year interaction was again caused by variation between years, particularly in the treatment which supported the highest abundances. However, general patterns across all years indicated that within a particular year the more extensively managed grass-based treatments (T5–T7) supported the highest abundances of butterfly larvae. This is in contrast to the pattern seen for adult butterfly preferences for the sown treatments 8 and 9. Grass-based treatments had more butterfly larvae than the sown treatments in 2003 ($P \leq 0{\cdot}0127$ in all cases except T2; Supporting Information, Appendix S4a), all treatments had more larvae than T9 in 2005 ($P \leq 0{\cdot}0020$ in all cases), and the extensive grass treatments, T6–T7, had higher larval abundances than T2 in all years except 2004 ($P \leq 0{\cdot}0296$ in all cases).

RESPONSE OF POLLINATORS TO ENVIRONMENTAL FACTORS

The interaction between the continuous environmental variables measuring nectar and other floral resources with year were almost all found to be significantly correlated with pollinator community parameters entered into the model (Model 2, Tables 2 and 3). Bumblebee abundance, species richness and diversity were associated with floral cover, floral species richness and nectar resources, as well as sward structure. Butterfly abundance was a function of floral abundance, butterfly species richness was a function of floral species richness and butterfly diversity was linked to both floral cover and species richness. Forb nectar sources were associated with all adult butterfly parameters, but legume nectar sources were not. Sward structure was an important predictor for butterfly abundance, species richness and diversity. Only floral cover was linked to butterfly larvae abundance. The significant continuous environmental variables of Model 2 were unable to explain any additional variance above that of the significant treatment and year effects in Model 1 (Model 3, Tables 2 and 3).

The sown treatments had a mean species richness of bumblebee flowers of more than 5, while the grass plots were all less than 3 (Supporting Information, Appendix S5a), and the sown treatments had a mean $\text{Nectar}_{\text{forb}}$ greater than 411 seed heads m^{-2} and mean $\text{Nectar}_{\text{legume}}$ greater than 98 seed heads m^{-2}, while the grass treatments had values less than 34 and 10, respectively (Supporting Information, Appendix S5a).

Discussion

This experiment assessed the effects of manipulating conventional management practices (cutting, inorganic fertilizer application and aftermath grazing) on the butterfly and bumblebee communities in intensively managed grasslands. The

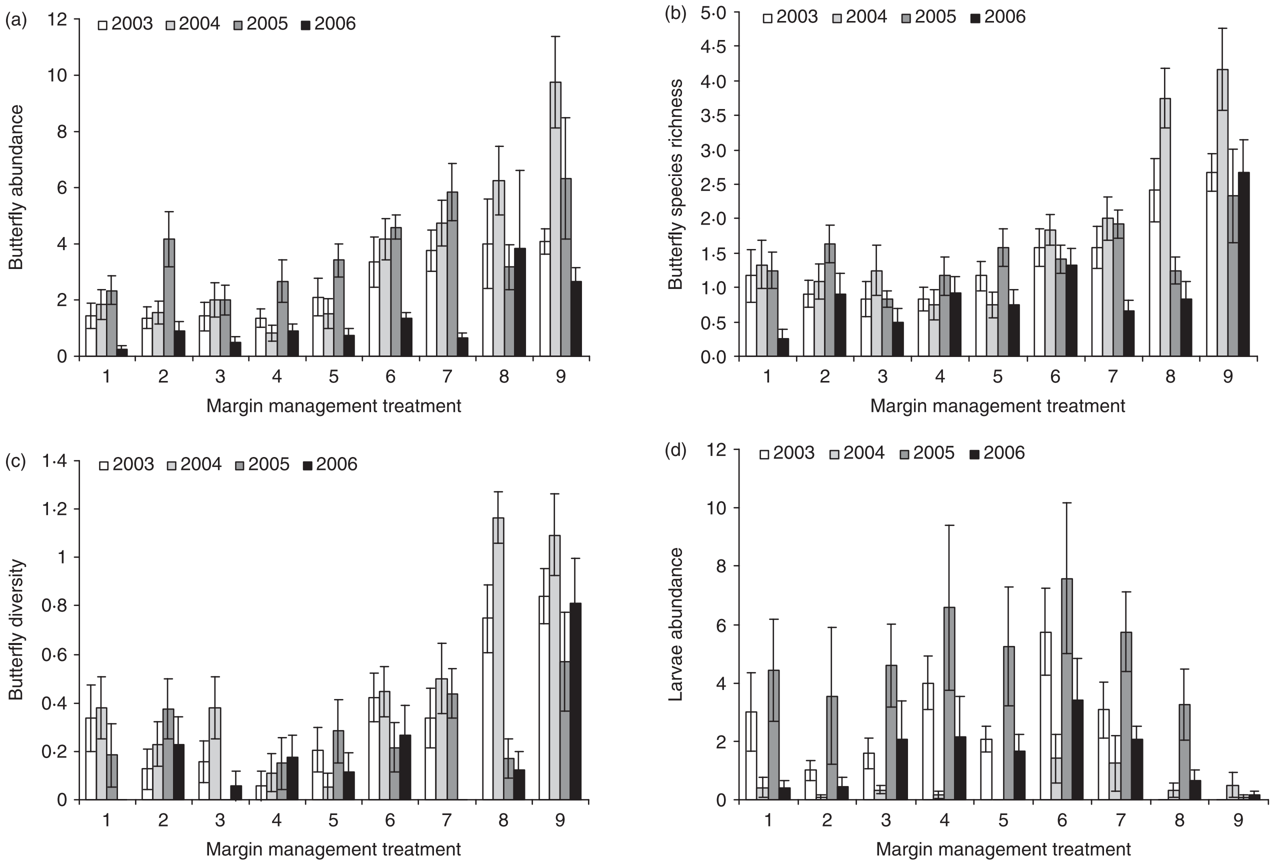

Fig. 2. Response of butterflies to management treatments: (a) abundance (mean number of adult butterflies per transect ± SE); (b) species richness (mean number of species of adult butterfly per transect ± SE); (c) diversity (mean Shannon-Wiener ± SE); (d) larvae abundance (mean number of larvae per transect ± SE). Full description of the management treatments 1–9 is given in the text.

Table 2. Summary of bumblebee model outputs. Model 1 is a repeated-measure analysis with mixed models for the response of bumblebee abundance, species richness and diversity to management treatment and their interaction with year. Model 2 tests the response of bumblebees to continuous environmental variables. Model 3 tests whether any additional variance over Model 1 was explained by the significant environmental variables in Model 2

Model	Abundance ($\log_e N + 1$)	Species richness ($\log_e N + 1$)	Diversity (Shannon–Wiener)
1	Treatment: $F_{8,176}$ = 54·1*** Treatment × year: $F_{24,273}$ = 11·1*** Year: $F_{3,273}$ = 83·6*** AIC = 667·3	Treatment: $F_{8,147}$ = 34·3*** Treatment × year: $F_{24,280}$ = 5·08*** Year: $F_{3,280}$ = 60·6*** AIC = 337·5	Treatment: $F_{8,174}$ = 39·5*** Treatment × year: $F_{24,294}$ = 10·0*** Year: $F_{3,294}$ = 56·4*** AIC = −71·8
2	Year: $F_{3,365}$ = 4·72** Floral cover and species richness Cover$_{floral}$: $F_{1,300}$ = 44·20*** Cover$_{floral}$*Yr: $F_{3,389}$ = 3·93** SR$_{floral}$: $F_{1,287}$ = 10·15** SR$_{floral}$*Yr: $F_{3,385}$ = 5·20** Nectar resources Nectar$_{forb}$: $F_{1,401}$ = 5·96* Nectar$_{forb}$*Yr: $F_{3,404}$ = 3·66* Nectar$_{legume}$: $F_{1,398}$ = 13·10*** Nectar$_{legume}$*Yr: $F_{3,404}$ = 1·21 ns Sward structure Sward: $F_{1,335}$ = 40·90*** Sward*Yr: $F_{3,388}$ = 8·49*** AIC = 793·1	Year: $F_{3,369}$ = 0·91 ns Floral cover and species richness Cover$_{floral}$: $F_{1,293}$ = 57·92*** Cover$_{floral}$*Yr: $F_{3,390}$ = 2·23, ns SR$_{floral}$: $F_{1,311}$ = 4·71* SR$_{floral}$*Yr: $F_{3,389}$ = 3·81* Nectar resources Nectar$_{forb}$: $F_{1,411}$ = 3·38 ns Nectar$_{forb}$*Yr: $F_{3,410}$ = 2·66* Nectar$_{legume}$: $F_{1,398}$ = 11·47*** Nectar$_{legume}$*Yr: $F_{3,405}$ = 1·40, ns Sward structure Sward: $F_{1,350}$ = 31·96*** Sward*Yr: $F_{3,392}$ = 3·75* AIC = 402·5	Year: $F_{3,376}$ = 11·21*** Floral cover and species richness Cover$_{floral}$: $F_{1,338}$ = 12·01* Cover$_{floral}$*Yr: $F_{3,398}$ = 3·58* SR$_{floral}$: $F_{1,290}$ = 2·32 ns SR$_{floral}$*Yr: $F_{3,396}$ = 3·50* Nectar resources Nectar$_{forb}$: $F_{1,404}$ = 10·70** Nectar$_{forb}$*Yr: $F_{3,401}$ = 5·55** Nectar$_{legume}$: $F_{1,401}$ = 0·00 ns Nectar$_{legume}$*Yr: $F_{3,399}$ = 4·78** Sward structure Sward: $F_{1,347}$ = 30·47*** Sward*Yr: $F_{3,398}$ = 18·23*** AIC = 14·5
3	AIC = 750·4: Model 1 is best	AIC = 415·9: Model 1 is best	AIC = 58·0 Model 1 is best

*P < 0·05; **P < 0·01; ***P < 0·001; ns, P > 0·05. Coding for environmental variable is given in the Methods.

Table 3. Summary of butterfly model outputs. Model 1 is a repeated-measure analysis with mixed models for the response of adult butterfly abundance, species richness diversity and butterfly larvae abundance to management treatment and their interaction with year. Model 2 tests the response of butterflies to continuous environmental variables. Model 3 tests whether any additional variance over Model 1 was explained by the significant environmental variables in Model 2

Model	Abundance ($\log_e N + 1$)	Species richness ($\log_e N + 1$)	Diversity (Shannon–Wiener)	Larvae abundance ($\log_e N + 1$)
1	Treatment: $F_{8,167}$ = 21·9*** Treatment × year: $F_{24,281}$ = 2·04** Year: $F_{3,281}$ = 32·5*** AIC = 801·4	Treatment: $F_{8,155}$ = 22·3*** Treatment × year: $F_{24,275}$ = 2·69*** Year: $F_{3,275}$ = 14·3*** AIC = 515·9	Treatment: $F_{8,143}$ = 24·0*** Treatment × year: $F_{24,282}$ = 3·54*** Year: $F_{3,282}$ = 13·9 ***AIC = 415·2	Treatment: $F_{8,157}$ = 12·3*** Treatment × Year: $F_{24,284}$ = 1·72* Year: $F_{3,284}$ = 33·8 ***AIC = 957·6
2	Year: $F_{3,371}$ = 7·63*** Floral cover and species richness $Cover_{floral}$: $F_{1,316}$ = 13·08*** $Cover_{floral}$*Year: $F_{3,383}$ = 0·35 ns SR_{floral}: $F_{1,361}$ = 2·34 ns SR_{floral}*Year: $F_{3,390}$ = 0·41 ns Nectar resources $Nectar_{forb}$: $F_{1,411}$ = 6·64* $Nectar_{forb}$*Year: $F_{3,401}$ = 3·17* $Nectar_{legume}$: $F_{1,399}$ = 0·55 ns $Nectar_{legume}$*Year: $F_{3,412}$ = 0·79 ns Sward structure Sward: $F_{1,333}$ = 32·64*** Sward*Year: $F_{3,379}$ = 3·48* AIC = 944·6	Year: $F_{3,372}$ = 4·56** Floral cover and species richness $Cover_{floral}$: $F_{1,290}$ = 2·68 ns $Cover_{floral}$*Year: $F_{3,391}$ = 0·78 ns SR_{floral}: $F_{1,337}$ = 14·80*** SR_{floral}*Yr: $F_{3,398}$ = 2·39 ns Nectar resources $Nectar_{forb}$: $F_{1,409}$ = 5·35* $Nectar_{forb}$*Year: $F_{3,412}$ = 3·04* $Nectar_{legume}$: $F_{1,407}$ = 0·39 ns $Nectar_{legume}$ *Year: $F_{3,412}$ = 3·13* Sward structure Sward: $F_{1,343}$ = 20·01*** Sward*Yr: $F_{3,393}$ = 5·38** AIC = 662·8	Year: $F_{3,368}$ = 3·03* Floral cover and species richness $Cover_{floral}$: $F_{1,288}$ = 4·19* $Cover_{floral}$*Year: $F_{3,387}$ = 1·57 ns SR_{floral}: $F_{1,310}$ = 22·26*** SR_{floral}*Yr: $F_{3,395}$ = 2·77* Nectar resources $Nectar_{forb}$: $F_{1,387}$ = 6·60* $Nectar_{forb}$*Year: $F_{3,400}$ = 4·91** $Nectar_{legume}$: $F_{1,4·06}$ = 0·04 ns $Nectar_{legume}$*Yr: $F_{3,405}$ = 4·03** Sward structure Sward: $F_{1,335}$ = 12·42*** Sward*Yr: $F_{3,389}$ = 4·20** AIC = 560·2	Year: $F_{3,380}$ = 0·78 ns Floral cover and species richness $Cover_{floral}$: $F_{1,341}$ = 18·43*** $Cover_{floral}$*Year: $F_{3,386}$ = 3·68* SR_{floral}: $F_{1,338}$ = 2·41 ns SR_{floral}*Yr: $F_{3,372}$ = 0·34 ns Nectar resources N/A Sward structure Sward: $F_{1,392}$ = 2·93 ns Sward*Year: $F_{3,393}$ = 2·35 ns AIC = 1045·8
3	AIC = 880·1: Model 1 is best	AIC = 631·7: Model 1 is best	AIC = 571·4: Model 1 is best	AIC = 992·6: Model I is best

*P < 0·05, **P < 0·01, ***P < 0·001, ns P > 0·05, N/A analysis not applicable. Coding for environmental variable is given in the Methods.

study is novel in that it investigated multiple management techniques in combination, looked at the responses of more than one pollinator group, and in parallel, assessed the floral resources driving community structure with the whole experiment comprising a high level of spatial replication carried out over 4 years.

PERFORMANCE OF GRASS AND SOWN TREATMENTS

Overall, the relative performance of the grass-based and sown treatments varied between the pollinator groups studied. Bumblebees were most abundant and diverse in the sown treatments and were virtually absent from the grass plots. Adult butterflies were also most common and speciose in the sown plots; however, the most extensively managed grass treatments were nearly as good at supporting butterflies. In contrast, the sown plots were poor sites for butterfly larvae, probably reflecting the lack of suitable host plants. Treatment × year interactions were found for both the bumblebees and the butterflies; however, the interpretation of these interactions is likely to be subject to several competing explanations that we could not discriminate between in this study. A potentially major factor driving the variability in treatment quality between years was the relatively small size of the field margin plots used in this study (individual plots being 10 × 50 m). At a landscape scale, the contribution that such plots can make to support bumblebee colonies or to provide food plants for butterflies may be limited, as population changes for individual species observed in this study were unlikely to be driven by resources provided by the experimental treatments (e.g. pollen and nectar within flowers). Instead, factors which could not be controlled by the experimental design are likely to have been driving population change of an individual species, e.g. population cycles, loss or change in management of habitats outside of the study plots or responses to weather conditions. As population sizes of individual species change between years, potentially in an asynchronous way, their contribution to total abundance, species richness or diversity within each treatment would also change. Such differences may be driving the high levels of between-year variability in the ability of the nine treatments to support butterfly and bumblebee populations. However, the identification of consistent patterns across years, particularly the superiority of the sown treatments 8 and 9, does provide a basis for recommending these treatments as specific management recommendations, independently of inter-year fluctuations in their value.

Total bumblebee abundance varied markedly across years, with 2004 being a particularly good year for English bumblebees (as the warm dry summer of 2003 may have allowed greater nest provisioning) and 2005 being very poor (as the wet summer of 2004 may have suppressed nest provisioning). High levels of inter-annual fluctuations are characteristic of bee communities (Williams, Minckley & Silveira 2001) and reflect the effects of climate, forage and nesting resource variability. Even with the inter-annual variation, the value of the sown treatments was not fully realized until the second year following establishment, which can be seen for T8, and both sowings of T9. The introduction of sown species enhanced the availability of bumblebee floral resources (especially *Trifolium* spp., *Lotus corniculatus* and *Vicia sativa*) as has been observed in other studies (e.g. Holzschuh *et al.* 2007), and cultivation (i.e. ploughing, preparation of a seed bed and drilling) also encouraged the establishment of other 'magnet' species such as *Cirsium*, *Ranunculus* and *Taraxacum* spp. found in the seed bank (Carvell 2002). The abundance and species richness of bumblebees in T8, however, returned to low levels, similar to the grass plots, in years 3 and 4 post-sowing. Treatment 9 plots were not intended for use after 2 years due to risk of pernicious weed establishment after the biennial kale had set seed, leaving bare patches. The treatments based on the existing sward (T2 and T5–7) were expected to show some succession with the cessation of fertilizer inputs, at least in 2003 and 2004. After 2004, little further successional change was expected, and hence, it is more representative of biodiversity benefits from establishing such treatments over the duration of an Environmental Stewardship agreement. For T1–3 and T4, all of which continued to receive fertilizer, there was little successional change in the plant community; thus, all years can be assessed as representative.

Floral and nectar resource diversity are known drivers of bee community structure (Potts *et al.* 2003). Floral abundance, species richness and the availability of nectar (and pollen) flowers, especially in the form of legumes, were all drivers of bumblebee community composition (Table 2). Overall attempts to increase the floral diversity of the managed grass plots over a 4-year period to provide bumblebee resources had little effect, and this result is reflected in the consistently low number of nectar-providing species found in all grass plots.

The extensively managed grass-based plots (T6 and T7) and the sown treatments had the highest butterfly biodiversity. These plots contained many butterfly nectar plants such as *Cirsium*, *Ranunculus*, *Senecio*, *Veronica* and *Vicia* spp. (Supporting Information, Appendix S5b) and provided good shelter (sward height > 20 cm compared to other grass plots T1–T5, < 15 cm; Supporting Information, Appendix S5b). Abundance of butterflies and butterfly flowers was highly correlated, as were butterfly species richness and flower species richness (Table 3); this is consistent with other studies (Krauss, Steffan-Dewenter & Tscharntke 2003; Pywell *et al.* 2004), suggesting that both aspects of plant communities could be manipulated together to benefit butterflies. The provision of nectar resources from non-legume forbs were important drivers, as reported for arable farm studies (e.g. Pywell *et al.* 2004).

Butterfly abundance and species richness increased with time and this suggests that the value of the grass-based treatments also increased through time. Although there was high inter-annual variation for all butterfly parameters, sown T8 performed well relative to grass treatments in the establishment year, and even better in the second year. In year 1, the plots were mainly barley with some *Vicia sativa*, and in year 2, there was an increase in grasses, *Lotus*, *Medicago Lupulina* and *Cirsium* species. It is only after the second year that the treatment was cut which resulted in the loss of floral resources. The utility of the sown treatment for butterflies may only be short-term, as the plot composition changes with time and floral resources are lost as plots become dominated by grasses and/or are cut. Treatment 9 was more variable in its value for butterflies compared to treatment 8 and the unpredictability may reflect factors such as poor establishment and/or persistence of some sown species between different years.

In contrast to adult butterflies, the sown plots performed poorly for butterfly larvae in all years owing to a general absence of commonly utilized host-plants (e.g. *Agrostis*, *Lolium* and *Holcus* spp., Supporting Information, Appendix S5c). By contrast, the more extensive grass-based plots had a higher abundance of host-plants, thereby providing more oviposition opportunities for adult butterflies.

Although bumblebees and adult butterflies responded to our management treatments, this may not necessarily relate to population growth but could reflect attraction of pollinators to new resources. However, the measures of butterfly larvae distributions do relate more directly to reproduction.

POLICY RELEVANCE AND RECOMMENDATIONS

Pollinator biodiversity in improved grasslands can be effectively enhanced by introducing novel flower-rich habitats; however, the benefits are likely to be relatively short-term as sown mixtures become increasingly dominated by pernicious weeds. Longer-term enhancement can be achieved through re-sowing of margins, but this has implications in terms of time and resources needed by farmers. Re-sowing may also be necessary to control pernicious weed problems (e.g. *Cirsium arvense*), which may present a disincentive to adoption and would therefore require suitable farmer incentives, such as agri-environmental scheme payments or similar schemes. While the sowing of crop mixtures can provide forage and structural resources for pollinators, if harvested it would not be of sufficient agronomic value to feed to livestock.

An alternative option, which favours butterflies but not bumblebees, is to reduce management intensity on areas of existing grassland. Stopping fertilization together with the implementation of a single cut and/or low-intensity grazing to produce a more heterogeneous sward structure has the potential to produce good quality habitats for some butterflies (e.g. Erhardt 1985). This approach represents a straightforward option for farmers to implement relative to the sown treatments. Management regimes that reduce disturbance to swards during the growing season will deliver significant benefits to other grassland invertebrates (Woodcock *et al*. 2007). In practical terms, the management of T1–5 can be readily incorporated into conventional silage making systems, as the timing of cutting coincides with conventional cutting times.

What emerges is that there is no single solution to enhancing biodiversity in grasslands across a wide range of taxa as their habitat requirements vary markedly. There are always likely to be trade-offs between different species groups depending on how their life-history traits relate to the modified habitats (Kruess & Tscharntke 2002). In this case, extensive grass-based treatments support butterflies but not bumblebees. In addition, the dense swards of the extensive plots provide bird food, in the form of beetles (Woodcock *et al*. 2007), but remain relatively inaccessible for birds (Cole *et al*. 2007). Even within a taxon, there are contrasting habitat requirements with some butterflies requiring dense swards for shelter (e.g. *Aphantopus hyperantus* and *Pyronia tithonus*) and others requiring more open habitats (e.g. *Polymmatus icarus* and *Lasiommata megera*) (Fry & Lonsdale 1991).

The dual approaches of the Entry Level Stewardship (ELS) and Higher Level Stewardship (HLS) in the UK Environmental Stewardship (Defra 2005) are potential tools which could adopt both modifications to grassland management: sowing and extensification. ELS aims to encourage a large number of farmers across a wide area of farmland to deliver simple yet effective environmental management which have wide biodiversity benefits. The extensification of some existing improved grasslands, by applying the management methods tested in treatments 6 and 7 in this experiment, could have major implications for the conservation of widespread and common butterfly species, although the benefits for threatened species requiring elaborate protection measures, and for bumblebees, would be questionable. HLS aims to deliver significant environmental benefits in high-priority situations and areas, and requires more complex management (than ELS) where land managers need advice and support. The introduction of sown margins has been successful in supporting greater numbers and diversity of bumblebees in arable systems (e.g. Carvell *et al*. 2004), but has yet to be fully tested within improved grassland systems. The adoption of sown margins in the HLS, could have impacts on both butterflies and bumblebees, but the benefits are likely to be localized as HLS is highly geographically targeted. One advantage of careful placement of flower-rich margins in grasslands is that existing habitat patches could be linked together, enabling pollinators to forage and disperse along linear features.

Without widespread intervention in the management of improved grasslands, many pollinator species are likely to continue to decline (Tscharntke *et al*. 2005). Agri-environment schemes are compulsory in EU Member States, and represent a potentially powerful tool to halt and reverse the loss of pollinators in agro-ecosystems. While the effectiveness of some scheme options has been questioned (Kleijn *et al*. 2006), the ability of schemes as a whole to support farmland wildlife is generally accepted (Potts *et al*. 2006). Given the large proportion of agricultural land in Europe used intensively for grazing and silage, there are potentially wide-scale biodiversity benefits if pollinators can be introduced back into these systems. Pollinators not only have a high intrinsic value in themselves, but deliver essential ecosystem services; butterfly larvae also represent a key food group for many farmland birds (Wilson *et al*. 1999), and therefore, they would have additional benefits in supporting food chains.

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Supporting Information

Additional Supporting Information may be found in the online version of this article

Appendix S1a. Species list for bumblebees

Appendix S1b. Species list for adult butterflies and abundance of butterfly larvae

Appendix S2a. Pairwise comparisons for bumblebee abundance response to treatment in 2003 to 2006

Appendix S2b. Pairwise comparisons for bumblebee species richness response to treatment in 2003 to 2006

Appendix S2c. Pairwise comparisons for bumblebee diversity response to treatment in 2003 to 2006

Appendix S2d. Pairwise comparisons for bumblebee response to year within a treatment

Appendix S3a. Pairwise comparisons for adult butterfly abundance response to treatment in 2003 to 2006

Appendix S3b. Pairwise comparisons for adult butterfly species richness response to treatment in 2003 to 2006

Appendix S3c. Pairwise comparisons for adult butterfly diversity response to treatment in 2003 to 2006

Appendix S3d. Pairwise comparisons for adult butterfly response to year within a treatment

Appendix S4a. Pairwise comparisons for butterfly larvae abundance response to treatment in 2003 to 2006

Appendix S4b. Pairwise comparisons for butterfly larvae response to year within a treatment

Appendix S5a. Botanical data summary for bumblebees

Appendix S5b. Botanical data summary for adult butterflies

Appendix S5c. Botanical data summary for butterfly larvae

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