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Benefits of agri-environment schemes for butterflies are mediated by botanical diversity and floral resource availability

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ABSTRACT

Agri-environment schemes (AES) are a substantial conservation policy lever, and could be critical to meeting current biodiversity targets, if AES facilitate population increases in farmland species such as butterflies. Although butterflies are commonly studied in relation to AES, most studies do not demonstrate whether the observed benefits of AES are due to the provision of suitable breeding habitat (which could drive population recovery) or by providing only floral / nectar resources for adults. These floral resources may attract adults from a wider area, without necessarily supporting population recovery. Piecewise structural equation models were used to analyse biodiversity survey data, to separate direct effects of AES on butterflies at two spatial scales (area around the transect on which butterflies were observed and AES in the surrounding landscape), and to disentangle the relative impact of floral resources for adult butterflies versus species richness of the whole plant community, a proxy for larval host plants. The response of butterflies with graminoid-feeding larvae were analysed, to further separate the effects of AES on adult and larval life-cycle stages. Indirect benefits of AES on butterfly abundance and species richness were positively mediated by both floral resources and botanical richness, and both variables had impacts similar in scale. Butterflies with graminoid-feeding larvae were positively related to graminoid cover, providing further support for an AES effect on butterflies that is mediated by the provision of larval hosts. This provides valuable evidence of the effectiveness of AES for butterflies and highlights the importance of AES options that increase richness of potential larval host plants alongside those providing floral resources.

1. Introduction

Land use change is the primary driver of biodiversity loss across the globe (Jaureguiberry et al., 2022; Outhwaite et al., 2022). Over the last 70–80 years, agricultural intensification together with a reduction in areas of semi-natural habitat have been the primary drivers of farmland biodiversity loss across Western Europe (Löffler et al., 2023). To combat the ongoing loss of biodiversity, agri-environment schemes (AES) have been developed in over 200 countries globally (Wuepper et al., 2024), including many countries in Europe (Batáry et al., 2015; Cullen et al., 2021). AES involve government-funded payments to farmers to implement management designed to achieve environmental policy objectives, including supporting biodiversity. AES covered an area of 5571 thousand hectares and cost £1226 million within England in 2024 (Defra et al., 2025). AES vary in scope, and include options to create and manage specific habitats such as species-rich grasslands, hedgerows and flower-rich margins, in order to support wildlife such as birds, small mammals and invertebrates. AES are part of a suite of interventions which may contribute to achieving the UK Government's legally-binding targets to halt species decline in England by 2030 and to improve species abundance by at least 10% by 2042 (Bane et al., 2023). Given the expenditure on these schemes and their potential role in

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achieving legal targets, it is vital that we understand whether AES can be effective in reversing biodiversity decline.

Studies investigating the impact of AES on biodiversity have found conflicting results. Some studies show that AES management has increased the abundance and/or richness of birds (Walker et al., 2018) and some insect taxa (Marja et al., 2022). However, other studies have reported mixed results (Kleijn et al., 2006; Kleijn and Sutherland, 2003) calling into question the effectiveness of AES in reversing population declines. Furthermore, the research evidence for some taxonomic groups, including many invertebrate orders, is limited. Butterflies are often a target taxon of AES due to their substantial declines in recent years (Fox et al., 2023), with intensive agricultural practices a key driver (Habel et al., 2019; Warren et al., 2021). Evidence for the effectiveness of AES on butterflies is generally positive, finding that butterfly abundance was higher on AES treatments with grassy margins (Field et al., 2007; Field and Mason, 2005) and margins with grass and wildflowers (Kolkman et al., 2022; Meek et al., 2002) and more broadly across a suite of AES options (Jarvis et al., 2025). These abundance increases may contribute to positive population trends in landscapes with relatively high levels of AES implementation, compared to those with little or no AES (Redhead et al., 2022), though such population responses to AES have thus far only been shown for a few butterfly species.

Providing both nectar resources and larval host plants in intensively managed farmland has been shown to be important for observed butterfly abundance and richness (Pywell et al., 2004; Rundlöf et al., 2008). However, it remains unclear whether the increases in butterflies on AES options reported in some studies are due to local population growth or merely the temporary spatial aggregation of the mobile adult insects. In butterflies, population growth is most strongly related to larval resources (the quantity and quality of larval hostplants) rather than adult resources, such as nectar (Thomas et al., 2011). Blumgart et al. (2023) found that moth diversity and abundance was higher in AES field margins which were sown with a variety of wildflowers, and that this was driven by the availability of larval hostplants, but there is no equivalent study for butterflies. Therefore, in order to understand whether AES are contributing to increased butterfly populations, it is crucial to disentangle whether the observed benefits are simply due to a 'honeypot' effect attracting adult butterflies from the wider landscape (e.g. to feed on nectar), or whether they are providing valuable breeding habitat (larval hostplants) to enable local population growth.

Much AES research has focused on the impact of individual AES options on biodiversity (Field et al., 2007; Rundlöf et al., 2008), but mobile species such as butterflies are likely to encounter multiple AES option types. To address this, approaches have been developed to aggregate AES impacts over a range of options targeting biodiversity outcomes (Staley et al., 2022; Redhead et al., 2022), in order to assess overall impacts of AES in the surrounding area on taxa including butterflies (Jarvis et al., 2025). An advantage of this aggregation approach is that AES across option types can be assessed at multiple spatial scales, accounting for the fact that AES beyond the field or farm scale may be influencing mobile species such as butterflies which can forage over distances of more than a kilometre. Previous work has shown that butterfly richness and abundance show positive responses to the amount of AES across landscapes of 3 × 3 km, suggesting that butterfly populations are benefitting from food or other resources provided across relatively large areas (Jarvis et al., 2025).

Here, we investigated the effects of AES on butterflies in terms of both a smaller scale at which the butterflies were recorded (transect), and the landscape-scale, and determine whether and how these effects are mediated by different components of the botanical community. We use data from a landscape-scale species monitoring survey of AES (LandSpAES, Staley et al., 2022) to look at AES effects at the small-scale around the immediate sampling location (the transect section along which butterflies were recorded) and the landscape scale (3 × 3 km) on butterflies. AES intensity was quantified using gradients, which included uptake of AES options that target butterflies specifically, as well as those which benefit other mobile taxa (Jarvis et al., 2025; Staley et al., 2022).

To determine whether the effect of transect-scale AES on adult butterflies is due to the 'honeypot' effect or due to butterflies utilising the habitat for breeding, we use structural equation models to look at how transect-level floral resources and botanical richness mediate the relationship between small-scale AES and butterflies, and quantify direct effects of AES which are not mediated by vegetation. To further understand whether AES are providing habitat for breeding butterflies, we also look at the relationship between AES and graminoid-feeding butterflies and how this is mediated by the botanical community. Graminoid-feeding butterflies only use grasses as larval hostplants, and grasses do not provide any food resources for adult butterflies. Therefore, if AES has a positive effect on graminoid feeding butterflies that is mediated by graminoid cover, we can infer that it is likely because AES are benefitting immature life stages rather than adult butterflies. As it has previously been shown that butterflies, which can forage over distances of more than a kilometre, also respond to the AES in the surrounding landscape (Jarvis et al., 2025) we include landscape scale (3×3 km) AES to account for this effect and expect to see the same relationship here.

Through these analyses we tested the following hypotheses:

H1) Positive effects of AES in the immediate vicinity on all butterflies can be attributed to increases in both floral resource availability and the richness of potential host plant species (measured as higher plant species richness) in the area where butterflies are monitored.

H2) Effects of AES in the immediate vicinity on graminoid-feeding butterflies will be more clearly linked to provision of host plants (using graminoid cover as a proxy) than is the case for all butterflies, because graminoid plants offer only larval resources for this subset of butterflies and no floral resources.

H3) Due to their mobile nature, AES in the surrounding landscape (3 × 3 km) also has a positive effect on both all butterflies and graminoid-feeding butterflies, in addition to the positive effects of AES in the immediate vicinity.

2. Methods

We use data from Staley et al. (2022) which assessed the impacts of AES management at the local (1 km^2) and landscape (3 km^2) scale on six taxonomic groups including butterflies. The survey was conducted annually across four regions or National Character Areas (NCAs https://nationalcharacterareas.co.uk/) between 2017 and 2021 (except for 2020 due to the impacts of the Covid-19 pandemic) resulting in four years of repeated survey data. Within each region, nine 1 km survey squares were sampled for mobile taxa and vegetation, and local and landscape AES gradients were calculated. Here, we used butterfly and plant data from four lowland regions: Dunsmore and Feldon, High Weald, the Fens, and South Suffolk and North Essex Clayland. Upland regions were also surveyed as part of the larger survey but were not included here due to differences in the extent and scale of the upland AES options present. Comprehensive detail on the methods can be found in Staley et al. (2021), (2022).

2.1. AES gradient scores

In order to quantify the amount of AES intervention, we calculated AES scores at both the transect level and the landscape scale, using the method detailed in Staley et al. (2021), (2022). The AES scores represent broad gradients of AES intervention, calculated from a combination of the AES option uptake area, benefit to mobile taxa from an evidence review, and the payment amount to landowners (Staley et al., 2021). This approach combines multiple types of options in different agricultural habitats, reflecting the scale at which mobile species are likely to be using landscapes across a range of option types (Staley et al., 2021).

Relatively few AES options in England are targeted specifically towards improving the environment for pollinators such as butterflies. For

example, Countryside Stewardship options AB1 and AB8 promote the planting and long-term maintenance of nectar flower mixes and flower-rich margins respectively with the aim to provide food sources and habitat for pollinators (Natural England, 2018). There are other options which may not be targeted towards butterflies specifically or even biodiversity more widely, but have been shown to provide significant benefits to non-target taxa (Staley et al., 2016, 2025). AES can include options with another primary environmental objective that may nonetheless support some biodiversity taxa, for example options to create grassy margins with a main objective of resource protection. Therefore, when attempting to understand the effects of AES on butterflies it is important to consider more than just the butterfly-specific options. The gradient scores included uptake of a range of options relevant to biodiversity, which were identified through an evidence review as part of the method to calculate AES gradient scores.

AES gradient scores were calculated using the following steps:

1) An evidence review was conducted, in order to identify AES management options likely to benefit butterflies, pollinating insects and birds. These were the target mobile taxa monitored under the wider LandSpAES baseline survey, which had sufficient evidence available to include in the review. Further details of the evidence review scope and data extraction are detailed in Staley et al. (2021).
2) AES management options identified through the evidence review were scored according to the type of evidence and the impact on target taxa. A single evidence score was allocated per AES option group for each taxon/functional group with sufficient evidence, based on a combination of the evidence type and impact scores (Table S1 Supplementary materials and see Staley et al., 2021 for further details of scoring). Individual AES options were rarely identified in the literature, thus options were grouped by type of management and habitat for scoring (e. g. grass buffer strip options). Scored option types are in Table S2 (Supplementary material).
3) AES option uptake data consisted of field mapped option data within a 25 m buffer around each transect section, and AES spatial option uptake data provided by Natural England (Staley et al., 2022) for the landscape unit (3 × 3 km). The landscape unit scores were calculated as average AES score for the eight 1 km squares surrounding around the focal 1 km survey square where field surveys took place (Staley et al., 2021).
4) AES gradient scores were calculated per AES management option type by multiplying the evidence scores (1.–2. above), the spatial uptake data of AES options in the area (3.), and the payment rate to farmers collated from AES handbooks (Natural England 2013a, 2013b, 2015). The scores were summed across all the option types present, to provide a single AES gradient score per transect section buffer or landscape unit (Staley et al., 2021, 2022).

2.2. Butterfly and floral resources data

In each of the 36 1 km survey squares, butterflies and floral resources were recorded at 9–11 transect sections, four times a year between May and August, with the exception of a few squares that had three visits in 2017 due to a late survey start (see Table S3 for summary of transect sections and visit numbers). Butterflies were recorded to species level along fixed transect routes using the Pollard walk method (Pollard and Yates, 1993), whereby a surveyor records all butterflies within a 5 m hypothetical box whilst walking along the transect (Fig. 1). Each transect section began and ended at a habitat transition if there was one present, or for a minority of sections ended at a maximum length of 300 m where habitats extended beyond this, therefore each section length was not constant. The total transect length per square was approximately 2000 m long, ±200 m.

We calculated the total abundance and species richness of butterflies for each transect section monitored in each survey year. The total abundance was calculated by summing the abundance of all species sampled across all survey rounds in each year at each unique transect section. Butterfly richness was calculated by summing the number of all unique species sampled across all survey rounds in a given year for each single transect section.

To understand whether the benefits of AES are due to the provision of larval breeding habitat, we also analysed abundance and richness of graminoid feeders, i.e. butterflies which feed on grasses during the larval stage. The larval hostplants of each butterfly species were obtained and used to classify each species as a graminoid or non-graminoid feeder (sources for trait information as described in Staley et al., 2022). Using this subset of the Lepidoptera species (see Table S4 for the list of graminoid vs. non-graminoid feeders), we calculated response variables of total abundance and richness of butterfly species whose larva feed on graminoid plants.

To quantify the floral resources available to adult butterflies, abundance of flowers on each herbaceous and woody plant species were recorded on the transects on the same date that butterflies were recorded. Floral resources were recorded multiple times per year at the same time as butterfly data, in order to capture temporal variation, and include both spring-flowering (e.g. hawthorn, *Crataegus monogyna*) and summer-flowering species (e.g. bird's foot trefoil, *Lotus corniculatus*). Floral resources were recorded in two 10 × 5 m quadrats placed one-third and two-

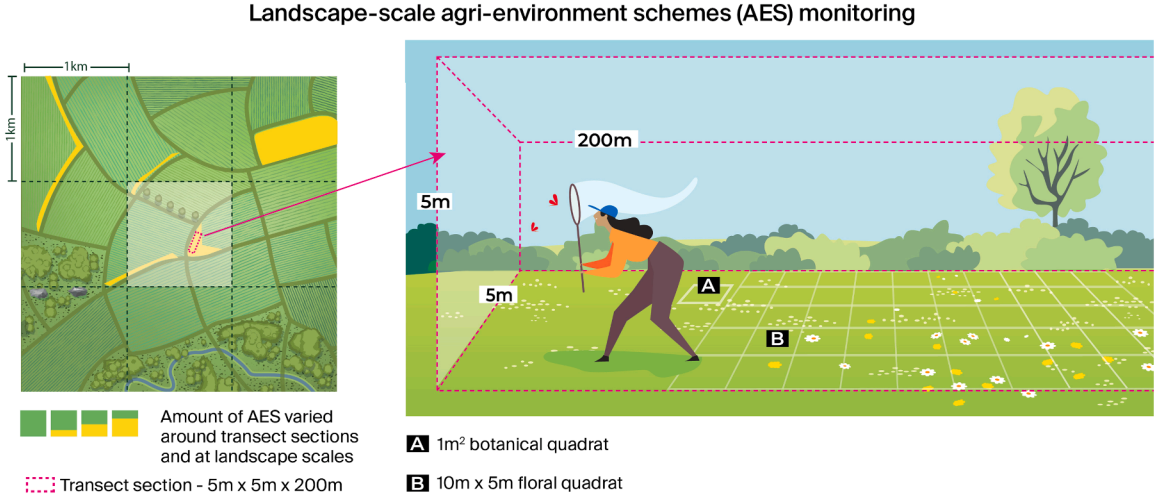


Fig. 1. Representation of the landscape and local transect-section AES gradient score calculation (left) and the collection of butterfly, botanical and floral data along each transect section (right).

thirds of the way along the length of each transect section (Fig. 1). Floral resources were assessed as 'floral units' on each flowering herbaceous species, with floral unit abundance per flowering species, defined following the UK National Pollintor Monitoring Scheme approach (https://ukpoms.org.uk/sites/default/files/pdf/UKPoMS-FIT-Count-Guide-CMYK.pdf). Abundance of flowering units was recorded per species in each quadrat, using an index to categorise the approximate number of floral units in each floral quadrat (Staley et al., 2022; Supplementary Materials Table S5). We calculated a single annual value representing floral resource availability for each butterfly transect section by averaging the index values across the survey year, resulting in a floral resource metric for each unique plot/year combination. Floral richness was calculated as the total richness of flowering plants recorded at that transect section in a particular year within the 10 m × 5 m floral quadrats.

2.3. Vegetation data

Botanical surveys of the full higher plant community were conducted during each May-August survey season in both 2019 and 2021 only, along each transect section on which butterflies were recorded. Five 1×1 m quadrats were placed evenly along the length of a zig zag line running through the butterfly transect section (Fig. 1). Within each quadrat, the cover of each vascular plant species was recorded. In addition, a separate walk-over of each transect section was used to record any extra vascular plant species that were not recorded in the quadrats. Botanical richness was calculated as the total species richness of the plant community at that transect section across the two years of botanical survey (including species counted during the additional walkover). Additionally, we calculated the graminoid cover as the average cover of graminoids across all five 1×1 m botanical quadrats undertaken at each transect section by classifying plants as graminoids or non-graminoids.

2.4. Statistical analysis

To test for direct and indirect effects of transect- and landscape-scale AES as well as floral and botanical variables on butterflies we used piecewise structural equation models (pSEM). pSEMs allow both indirect and direct effects to be modelled which allows us to compare AES effects mediated by floral or botanical variables compared to direct (or unmeasured) effects. Models were run using the psem function from the piecewiseSEM package (Lefcheck, 2016) in R version 4.4.2 (R Core Team, 2024) and were fit as generalised linear mixed-effects models using the lme4 package (Bates et al., 2015). We ran four separate pSEMs, each with a different response variable: butterfly richness, butterfly abundance, graminoid butterfly richness and graminoid butterfly abundance. Butterflies categorised as graminoid feeders are listed in Table S4 (Supplementary material).

Each model included the following hypothesised continuous explanatory variables: transect-level AES score, landscape-level AES score, botanical richness, floral richness, floral resources, and graminoid cover. Pearson correlations were conducted between vegetation variables to ensure they were not strongly correlated with each other (Table S6, Supplementary material). Additionally, we included the transect section length and temperature in the shade at the time of each butterfly survey as control variables to account for any differences in butterfly activity. Finally, year and region were included as random effect variables. Butterfly richness and graminoid feeding butterfly richness were modelled as Poisson distributed variables, abundance was modelled as negative binomial variables. All the variables used in the structural equation modelling are detailed in Table S3 (Supplementary materials). Explanatory variables were standardized prior to model fitting by subtracting the mean and dividing by the standard deviation. This was done to improve model fit where variables were on vastly different scales. The a priori hypothesised causal structure of the relationships between measured variables are illustrated in Fig. 2.

Overall model fit of the piecewiseSEM was assessed using the Fisher C statistic, whereby $p > 0.05$ indicates a good fit and marginal and conditional R^2 were calculated (Nakagawa et al., 2017). The relative importance of each explanatory variable in the model was assessed using the standardised coefficient and associated P value. Conditional independence assumptions within the structural equation model were tested with d-separation tests which test for potential missing paths (e.g. between landscape level AES and vegetation metrics).

3. Results

Thirty-three butterfly species were recorded across all the sites over the four years, and a total number of 56,564 butterflies recorded. The median butterfly richness per transect section was 7, and the median abundance was 23. Eleven of the 33 species were classed as graminoid-feeders. See Table S3 for a more detailed summary of the butterfly data, for example median, maximum and minimum abundance per year, and Table S4 for a list of butterfly species recorded.

The model fit of all piecewiseSEMs tested were assessed as good according to the Fisher C statistics (Table S7) and no missing paths were identified using the d-separation tests.

3.1. All butterfly species responses to direct and indirect effects of agri-environment schemes

The path diagrams for total butterfly abundance and butterfly richness responses are represented in Fig. 3. Paths represent both the direct and indirect causal relationships that were tested. The indirect paths are mediated by the four vegetation variables. The relative importance of each explanatory variable is shown by the standardised coefficients next to the arrows (Fig. 3).

AES at the transect section level had a significant positive effect on the floral resource availability, floral richness, botanical richness and the percentage cover of graminoids, with the strongest effects on floral richness and resource availability. The botanical richness, floral richness, and floral resource availability in turn each had a significant positive effect on both butterfly abundance and richness (Fig. 3). There was no effect of graminoid cover on either total butterfly abundance or richness. The effects of the AES-mediated botanical richness, floral richness and floral resource availability on butterfly richness were of similar magnitudes. In contrast, both floral richness and floral resource availability were both roughly twice as important than botanical richness as drivers of butterfly abundance.

Direct (i.e. not mediated by plant variables) positive effects of AES at both the transect and landscape levels were observed on both butterfly abundance and richness. The standardised coefficients are comparable between nodes, thus the direct effects of transect and landscape AES on butterfly richness were of a similar magnitude, whereas for butterfly

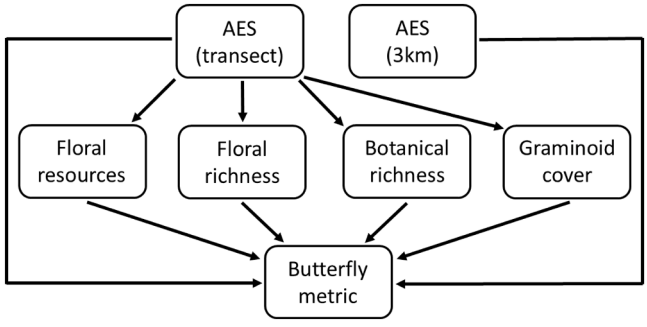


Fig. 2. A priori hypothesised causal structure of the relationships between AES score at the transect-section level (AES(tr)), landscape level (AES(3 km)), transect-scale botanical and floral variables, and the butterfly response variable tested.

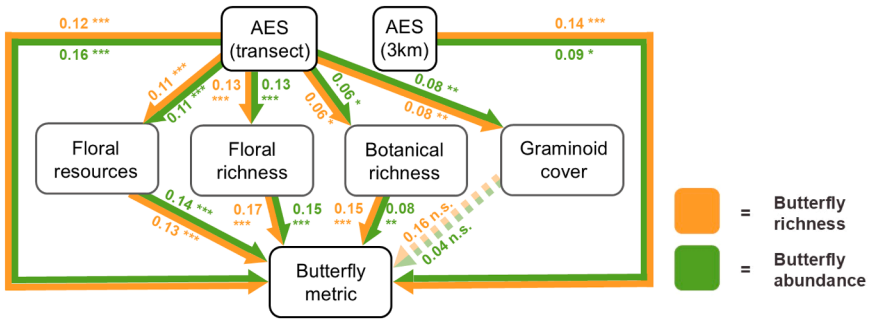


Fig. 3. Visualisation of piecewiseSEM path diagrams showing the drivers of total butterfly abundance (in green) and total butterfly richness (in orange). The standardised coefficients are displayed numerically next to the corresponding arrow. Transparent dashed lines represent non-significant relationships. Note the effects of AES on botanical and floral metrics are the same in analyses of total butterflies and grass-feeding butterflies (Fig. 4 below).

abundance the direct effect of transect AES was much greater than that of landscape AES.

3.2. *Graminoid-feeding butterfly responses to direct and indirect effects of agri-environment schemes*

The path diagrams constructed for the response variables of graminoid-feeding butterfly abundance and richness are represented in Fig. 4. AES at the transect section level had a significant positive effect on the floral resource availability, floral richness, botanical richness, and the percentage cover of graminoids, these relationships were the same as in the analyses of all butterfly species (Fig. 3 above).

The botanical richness and floral richness in turn had significant positive effects on both graminoid-feeding butterfly abundance and richness (Fig. 4). We found a significant positive effect of graminoid cover on graminoid-feeding butterfly abundance, but no effect on species richness. Similarly, there was a weak positive effect of floral resource availability on graminoid-feeding butterfly abundance, but no effect on richness. The positive direct effects of transect and landscape AES on graminoid-feeding butterfly richness were of a similar magnitude. In contrast, we found a significant positive direct effect of transect AES, but no effect of landscape AES, on graminoid-feeding butterfly abundance (Fig. 4).

4. Discussion

Our analysis demonstrates that AES benefits to butterflies are being delivered in multiple ways. Firstly, we found indirect benefits of AES to butterflies delivered via changes in the local vegetation which butterflies use, both as adult and larval food sources. This resulted in an observed increase in adult butterfly abundance and richness along transect sections where there are many and varied floral resources for adults to feed on, and where the richness of potential larval host plants is highest. This provides evidence to support our first hypothesis: small-scale AES effects on all butterflies can be at least partially attributed to increases in both floral resource availability and the richness of potential host plant species (measured as higher plant species richness) in the immediate vicinity where butterflies are monitored. Secondly, we also show direct benefits of AES at the transect and landscape-level, demonstrating that AES provide additional benefits beyond the vegetation metrics assessed. Our novel finding that AES impacts butterflies in multiple ways, including effects mediated through vegetation likely providing larval food resources, in addition to direct effects at the transect-scale and landscape-scale, suggests that the benefit of AES for butterflies extends beyond the provision of a 'honeypot' of floral resources to attract adult butterflies into the surveyed transects.

We found evidence that the increase in butterfly abundance and richness under high levels of AES at the transect scale was mediated by the provision of both resources for adults in the form of nectar from floral resources, and by the provision of resources for immature life stages. Butterflies use plants as hosts for their larval stages, with plants providing both habitat and food source for immature caterpillars (Rundlöf et al., 2008). Many butterfly species have evolved highly specialised associations with host plants, restricting larval diet breadth to a small number of plant species or genera (Dyer et al., 2007; Ehrlich, Raven, 1964). Thus, we used the richness of the botanical community as a proxy for the number of larval host species present, and found that both the richness and the number of butterflies recorded were positively associated with botanical richness. This suggests that a more speciose plant community is providing more host plants for early life stages.

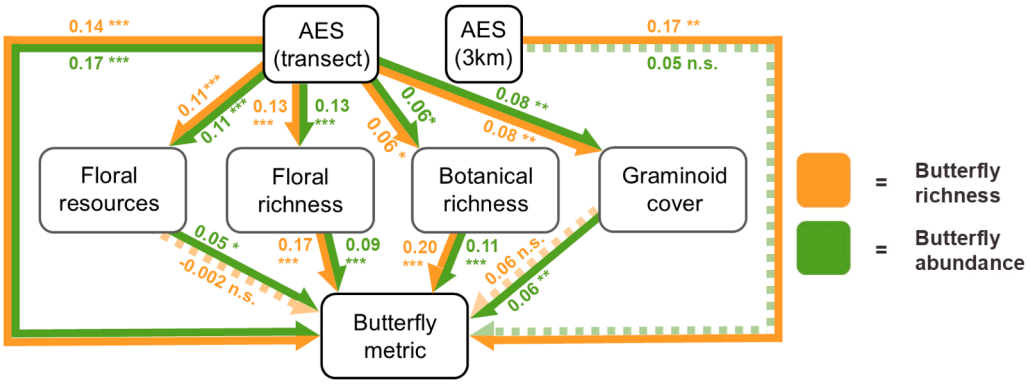


Fig. 4. Visualisation of piecewiseSEM path diagrams showing the drivers of lowland graminoid-feeding butterfly abundance (in green) and total graminoid-feeding butterfly richness (in orange). The standardised coefficients are displayed numerically next to the corresponding arrow. Transparent lines represent non-significant relationships. Note the effects of AES on botanical and floral metrics are the same in this analysis of grass-feeding butterflies and the analyses of total butterflies (Fig. 3 above).

To further explore the potential role of AES in influencing butterfly communities through increasing butterfly larval host plants, we modelled graminoid-feeding butterflies separately. Our results showed that graminoid cover correlated positively with the abundance of graminoid-feeding butterflies, providing strong support for an AES effect on butterflies which is mediated by the provision of larval hosts. We found no evidence to support an overall effect of graminoid cover on the whole butterfly community, suggesting that it would be unlikely for graminoid cover to be positively impacting butterflies through a provision of microclimate, shelter or other physical benefits which would affect all butterflies. This leads us to accept our second hypothesis, which was: AES effects in the immediate vicinity where graminoid-feeding butterflies are monitored can be more clearly attributed to provision of host plants (using graminoid cover as a proxy) than for all butterflies, because graminoid plants offer only larval resources for this subset of butterflies.

Provision of larval hosts has been shown to be important for other Lepidoptera. Blumgart et al. (2023) found higher moth diversity and abundance in grass margins sown with a variety of larval host plants compared to grass only. Similarly, they concluded that larval host plant provision was more important in determining diurnal moth species richness than nectar sources (Blumgart et al., 2023). Additionally, we found that floral resources, floral richness and botanical richness were all also positively linked to graminoid-feeding butterfly abundance, suggesting that in adult stages these species are also responding to the provision of floral resources. The separate impact of botanical richness above the effect of graminoid cover also indicates a potential additional benefit of botanical richness beyond food provision.

In addition to the benefits of AES via vegetation, we found direct benefits of AES provision on butterfly abundance and richness at both the transect and landscape level. The direct benefits found at transect scale suggest that AES may be providing other benefits to butterflies in the form of shelter, structural habitat heterogeneity, protection from in-field management (e.g. pesticides, grazing) or other resources within the immediate area.

Previous research also supports the role of AES in the wider landscape in supporting species richness and abundance of all butterflies (e.g. Jarvis et al., 2025; Larkin and Stanley, 2021) and some macro-moths (e.g. Alison et al., 2016), though here we demonstrated it for the first time for graminoid-feeding butterflies. This supports hypothesis three: AES in the surrounding landscape (3 × 3 km) has a positive effect on both all butterflies and graminoid-feeding butterflies, in addition to the positive effects of AES in the immediate vicinity. Previous studies have addressed adult butterfly responses to management relevant to AES at both landscape and local scales. Rundlöf et al. (2008) looked at organically managed fields vs. conventional fields, in landscapes with high vs. low levels of organic management. They found that local-scale butterfly richness and abundance both responded to local organic management, and that butterfly richness also related to organic management at the landscape-scale. Larkin and Stanley (2021) investigated pollinating insect responses to grassland management, using a local variable of grassland habitat quality derived from presence of indicator species as a proxy for AES management and the cover of semi-natural grassland as a landscape variable. They found that butterfly richness and abundance responded to landscape-scale semi-natural grassland cover, but not to local grassland quality (Larkin and Stanley, 2021).

It was possible to partition the transect-scale effects of AES on butterflies between effects mediated by the plant community and direct effects, as discussed above. We were not able to partition the landscape-scale effects of AES on butterflies, as we did not have plant data available at landscape-scale. Many butterfly species are highly mobile and can forage across the landscape-scale distances used in this study. It is possible that the adult butterflies recorded along transects were also foraging across plant communities in the larger landscape units that were affected by AES provision at the landscape-scale, and thus similar mechanisms were operating at both spatial scales, though this cannot be tested here at landscape-scale. Other mechanisms could also explain the positive effects of landscape scale AES seen in this study and others. For example, AES uptake could be associated with better landscape connectivity, opening up more resources, or reduced predation risk. Unpicking responses at broad spatial scales will require more research but it is clear that AES impacts on butterflies are operating at both very local and landscape level scales.

The results of this study highlight the multiple ways in which widespread AES options may be delivering benefits to butterflies. Importantly, this is despite few AES options directly targeting butterflies. Where widespread AES options are targeted at pollinating insects, they are often designed to deliver resources for adults (i.e. nectar) rather than immature life stages (larval host plants). The exception to this are a few instances of bespoke AES management which target support for a particular conservation priority butterfly species (e.g. grazing management under AES for *Polyommatus coridon* Chalk Hill Blue focused on increasing the abundance of its larval host plant, Brereton et al., 2008), but these options tend to be restricted to specific regions and habitat specialisms. The LandSpAES project approach allows us to integrate across a range of widespread AES options which may provide benefits to butterflies in multiple life stages and in multiple ways (via food and other resources). Our study only observed adult butterflies; it would be informative to also monitor other life stages to better understand where AES may be having highest benefits for butterfly populations e.g. in improving survival or reproduction. Some butterfly species have multiple generations per year which makes such an analysis complicated but important, particularly as other drivers such as climate change are also impacting butterfly life cycles (Warren et al., 2021). In addition, a resurvey of the LandSpAES sites currently underway will allow population change to be assessed, in relation to AES at multiple spatial scales.

The strengths of this study are the use of a large, spatially resolved dataset to investigate how positive effects of AES on butterflies are mediated by the plant community. The multi-scale approach to testing AES effects both at landscape-scale and at the transect-scale, quantified in the same way as AES gradient scores at each scale, is another major strength of this study. The main limitation is that data were only available for adult butterflies, and so the links between AES provision of larval host plants and butterfly metrics are inferred rather than demonstrated directly. We were unable to have complete temporal matching between vegetation and butterfly surveys, with the botanical richness and graminoid cover variables only measured in 2019 and 2020. We were therefore unable to capture any year to year fluctuations in these variables due to e.g. drought. Building on the results found in this study, further work sampling larval abundance and species richness or monitoring butterfly oviposition in AES options would provide clearer evidence still of the relative contribution of larval host plants versus floral resources in butterfly resources to AES. In addition, we have not considered other elements of landscape complexity which may contribute to butterfly communities such as the connectivity of AES within the landscape e.g. in providing foraging corridors. Finally, the remaining 'direct' effects of AES on butterflies could be investigated in further work, for example by investigating the effects of other habitat features such as hedgerow trees which have previously been shown to be important for some moth species (Merckx et al., 2009, 2010).

If AES are to contribute to legal targets in order to halt species decline in England by 2030 and to improve species abundance by at least 10% by 2042 (Bane et al., 2023), AES management will need to support population growth of butterfly and moth species, along with other key species groups. The provision of larval host plants as breeding habitat will likely enable butterfly populations to increase and thus contribute towards meeting the targets. Our analyses suggest that current, widespread AES options can play a role in providing host plants for butterfly larvae. Increasing the uptake of widespread, biodiversity-relevant AES options, along with the development and implementation of specific AES options to create breeding habitat, would likely maximise the role of AES in supporting butterfly population growth.

CRediT authorship contribution statement

Hannah A. Risser: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Susan G. Jarvis:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Lisbeth Hordley:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Richard Fox:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Marc S. Botham:** Writing – review & editing, Methodology, Conceptualization. **Emily Upcott:** Writing – review & editing, Resources, Methodology, Investigation, Data curation. **John W. Redhead:** Writing – review & editing, Data curation, Conceptualization. **Morag E. McCracken:** Writing – review & editing, Resources, Project administration, Data curation. **Gavin M. Sirwardena:** Writing – review & editing, Funding acquisition, Conceptualization. **Joanna T. Staley:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110771.

Data availability

The full spatially-referenced data cannot be published in full, as LandSpAES is an ongoing project and data publication is restricted by privacy commitments made to landowners. Summary data can be made available on request.

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