Hodgson, J. G., Tallowin, J. R. B., Dennis, R. L. H., Thompson, K., Poschlod, P., Dhanoa, M. S., Charles, M., Jones, G., Wilson, P., Band, S. R., Bogaard, A., Palmer, C., Carter, G. and Hynd, A. 2014. Changing leaf nitrogen and canopy height quantify processes leading to plant and butterfly diversity loss in agricultural landscapes. *Functional Ecology.* 28 (5), pp. 1284-1291.

Functional Ecology

Functional Ecology 2014, **28**, 1284–1291 doi: 10.1111/1365-2435.12253

Changing leaf nitrogen and canopy height quantify processes leading to plant and butterfly diversity loss in agricultural landscapes

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Summary

1. We describe a novel method for quantifying ecosystem drivers that potentially compromise the effectiveness of agri-environment schemes. We use three sources of data that for many countries are already in the public domain: governmental agricultural statistics, which provide a quantitative assessment of farming intensity in the 'working landscape', data on threat status and species distribution for plants and butterflies from conservation agencies and similar bodies and functional traits of plant species abstracted from published data bases.

2. Changes in land use alter ecosystem processes which in turn modify both biodiversity and representation of functional types at the landscape scale. We interpret functional shifts to quantify important ecological drivers of floristic and faunal change and their causal land use origins.

3. We illustrate the power of this approach by means of a worked example. We demonstrate that despite conservation policies to counteract them, eutrophication, identified by leaf nitrogen content, and abandonment, correlated with plant canopy height, are still causing biodiversity loss to native higher plants and butterflies in the English countryside.

4. We use our analyses to suggest how conservation policies can be made more effective and discuss how similar approaches could be applied elsewhere.

Key-words: agri-environment schemes, butterflies, conservation, ecosystem processes, flowering plants, functional types

Introduction

Despite their many other roles (Kleijn *et al.* 2006), European agri-environment schemes are regarded by the EU as the most important instrument of policy for conserving biodiversity in agricultural landscapes (EEA 2004), a view shared within England (DEFRA 2002). However, although large sums of money have been spent, overall diversity loss in productive agricultural landscapes has not been arrested (Kleijn & Sutherland 2003; Kleijn *et al.* 2006, 2011; Whitfield 2006). Arguably, part of the problem stems from the fact that policies tend to target end points, for example numbers of species and amount of habitat, rather than the ecosystem processes that gave rise to them. Failure to meet targets can identify that there is a problem but not necessarily its exact mechanistic origin. Why not, instead, look directly at the ecosystem processes themselves? An extensive literature demonstrates that studies of ecosystem processes and associated species traits can generate useful insights into reasons for vegetational change under a wide range of scenarios (e.g. Grime 2001; Wright *et al.* 2004; Kremen 2005; Ackerly & Cornwell 2007;

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Garnier *et al.* 2007; Kleyer *et al.* 2008; de Bello *et al.* 2010; Kattge *et al.* 2011). Moreover, animals are directly or indirectly nutritionally dependent upon plants and share their habitats, so there should be parallel responses in both flora and fauna. Identifying and quantifying the causes of decline is the first step towards suggesting remedial protocols relevant to both.

Encouragingly, for many countries, the raw materials for analysis are already in the public domain. In addition to data on species distribution and biodiversity (distribution atlases and similar sources), governmental agricultural statistics allow us to estimate the intensity of farming, and there are now ecological data bases (e.g. Kattge *et al.* 2011) that provide the traits necessary to identify ecological specialization, at least for plants. Here, we assess the potential advantages of the novel approach of integrating agricultural statistics, biodiversity data and functional traits relating to ecosystem processes into analyses of the effectiveness of conservation initiatives. We further illustrate the power of this methodology by means of a worked example. We quantify important ecosystem drivers that are causing biodiversity loss to native higher plants and butterflies in the English countryside and establish that conservation has failed effectively to counteract them. Finally, we use our analyses to suggest how conservation policies can be made more effective and to discuss how the same approach could be applied elsewhere.

Materials and methods

Prior to analyses, three independent elements relating to the status of plants and butterflies in the English countryside are defined, and their use justified. Firstly, we consider agricultural drivers of floristic and faunal change. In a preliminary analysis, we identify the most appropriate quantitative predictor of intensity of agricultural land use. Secondly, we define protocols for species selection and identify appropriate sources of data on species status and distribution. Thirdly, we characterize the flora ecologically in relation to plant traits likely to affect abundance following changes in agricultural land use and point out modifications in methodology necessary to include butterflies. Finally, we describe how quantitative agricultural, conservation and ecological assessments can be integrated to provide an overview of the effectiveness of recent conservation in the English countryside and elsewhere.

ESTIMATING THE PUTATIVE DRIVER OF FLORISTIC AND FAUNISTIC CHANGE: INTENSITY OF AGRICULTURAL LAND USE

Governmental statistics (DEFRA 2006) have not previously been used directly to assess agricultural impacts on biodiversity and species composition in the English countryside. We tested two candidates: area of wheat as a percentage of arable land and the number of dairy cattle relative to beef cattle and sheep (with values corrected for differences in body size and metabolic rate by converting numbers of animals to livestock units in accordance with guidelines (MAFF 1969; RDS 2006)). The price of wheat has historically been a crucial economic driver of agricultural change and an index of agri-economic prosperity (Thirsk 1997), and, even now, a positive relationship can be detected within Europe between national wheat yields and vulnerability of arable weeds (Storkey *et al.* 2012). Also, in the 1960s and 1970s, milk production was highly profitable (RDS 2006). Area of wheat as a percentage of arable land predicts both the percentage of the farming landscape in each English county under arable cultivation (positive relationship, $R^2 = 0{\cdot}61$; $P < 0{\cdot}001$) and that under permanent grassland (negative relationship, $R^2 = 0{\cdot}44$; $P < 0{\cdot}001$). Moreover, it also identifies the percentage area of two habitats particularly associated with 'less farmable' landscapes: rough grazing ($R^2 = 0{\cdot}67$; $P < 0{\cdot}001$) and farm woodland ($R^2 = 0{\cdot}11$; $P = 0{\cdot}03$). By contrast, percentage dairy cattle predicts only one of the above variables and does so more weakly (rough grazing: negative relationship, $R^2 = 0{\cdot}17$; $P < 0{\cdot}01$). Percentage wheat was, therefore, our preferred quantitative assessment of agricultural intensity.

Our values relate to 1970. This is towards the end of a period, starting in 1939, of more or less unidirectional economic pressure to increase agricultural output and profitability throughout England, but before the major policy shift of using agri-environment initiatives as a mechanism of nature conservation (Thirsk 1997; Marren 2002). Our historical measure of agricultural intensity allows us to quantify enduring effects on biodiversity and species composition of this less 'conservation-friendly' period of land management (and any subsequent deleterious impacts). We argue that the effectiveness, at a national scale, of agri-environment schemes and other parallel conservation initiatives will be inversely related to the strength of any 'enduring effects' identified.

ESTIMATING THE IMPACTS OF CHANGING LAND USE ON THE FLORA IN THE ENGLISH COUNTRYSIDE

Choice of species

Recent accounts (Preston, Pearman & Dines 2002a) subdivide the British and Irish flora into three groupings: native, archaeophyte (naturalized before 1500 AD) and neophyte (introduced after 1500 AD). The first group is the most consistently associated with the countryside rather than with urban and industrial habitats (Preston, Pearman & Dines 2002a) and is of greatest conservation concern. It is, therefore, the subject of this investigation. This choice was important since different historical subsets exploit different parts of the English landscape. For example, in a preliminary analysis, we found that the biodiversity of neophytes correlates (positively) with population density rather than with agricultural statistics. This is perhaps because many neophytes are horticultural escapees.

To narrow further the ecological focus of this investigation, species of shaded terrestrial habitats, which are perhaps more affected by forestry than agriculture, and aquatic species were also excluded. Minor taxa (microspecies, subspecies and hybrids) were also omitted.

Conservation status

Plant species were classified into five groupings of descending conservation concern: '*threatened*' – species 'threatened' or 'near threatened' in Great Britain (Cheffings & Farrell 2005), '*rare*' – designated as nationally rare or nationally scarce in Great Britain (Cheffings 2004), '*uncommon*' – other species restricted to <25% of English 10 km grid squares, '*decreasing*' – widespread species, in >25% of English grid squares and recorded in Preston, Pearman & Dines (2002a) with a negative change index, '*increasing*' as with '*decreasing*' but change index positive.

Assessing extinction

Records from Preston, Pearman & Dines (2002a) were subdivided into older and modern records. The presence or absence of old and of modern records for a species is determined not just by the past or present existence of the species within a study area. Other important considerations include intensity of sampling, the experience of the recorder and the amount of taxonomic support available to help with identification and to boost awareness of the possible occurrence of currently unrecorded species (Preston, Pearman & Dines 2002a). Nevertheless, we have tentatively subdivided the three groupings as follows: extant (present 1987–1999), recently extinct (extinct 1970–1986) and older extinctions (extinct before 1970). The justification for this is twofold. Firstly, the most recent survey of the flora is much more complete than previous ones (Preston, Pearman & Dines 2002a). Thus, most cases where old records have not been refound are likely to represent genuine extinctions or at least to indicate reduced abundance. Secondly, we are looking at plant characters that vary greatly within major taxa. Such characters are unlikely to be strongly affected by any taxonomic inconsistencies between episodes of recording.

Estimating biodiversity

English administrative districts (counties) differ in size, and, therefore, larger counties tend to have more species simply because they are large. To correct for such differences, area was regressed against number of native species for each county. The relationship between floristic biodiversity (number of native species within each English county within the recording period 1987–99) and area (hectares) was as follows:

$$Biodiversity = 397.7 area^{0.207} (n = 43,\ p < 0.001,\ R^2 = 0.41).$$

To make our values independent of area, biodiversity is expressed as the uncorrected residuals from this regression equation with high values for residuals identifying regions of high biodiversity and low values for areas of species impoverishment.

USING PLANT FUNCTIONAL TRAITS TO QUANTIFY THE KEY ECOSYSTEM DRIVERS OF FLORISTIC CHANGE

Soil fertility

Intensive agricultural land use is characterized by the heavy usage of fertilizers. Importantly, in this context, the concentration of available soil nutrients is a key driver of ecosystem processes. It regulates species attributes of fundamental importance to nutrient use and cycling within ecosystems (e.g. maximum relative growth rate, litter decomposition rate and palatability to unspecialized herbivores, all high on fertile soils – see Díaz *et al.* (2004); Wright *et al.* (2004); Hodgson *et al.* (2005b)). Thus, through increased soil fertility, fertilizer addition impacts fundamentally on ecosystem processes, and it is this ecological aspect in which we are primarily interested. Accordingly, leaf nitrogen content is used to assess soil fertility. It further correlates positively with concentrations of other inorganic plant macronutrients (Garten 1976; Thompson *et al.* 1997) and with the plant attributes listed above.

We estimated leaf nitrogen content from a general predictor equation in Hodgson *et al.* (2005a) based on specific leaf area, dry matter content and size, and mean values were calculated for the native species within each English county within the recording period 1987–99, weighted according to abundance (number of hectads) within the county.

Canopy height

Since few English native plant species exploit arable land, much floristic diversity is probably restricted, at least within arable regions, to little utilized or unmanaged habitats. Abandonment results in increased sward height and the decline of short species. Accordingly, we use maximum canopy height to assess the impact of abandonment. Maximum canopy height class values of each native species (1 ≤50 mm; 2 = 50–99 mm; 3 = 100–299 mm; 4 = 300–599 mm; 5 = 600–999 mm; 6 = 1·0–3·0 m) were abstracted from Grime, Hodgson & Hunt (2007) or assessed in an identical manner.

Butterflies

Protocols are essentially those adopted for plants. Species of shaded terrestrial habitats, which are perhaps more affected by forestry than agriculture, and of tall wetland habitats are excluded. Fox *et al.* (2007) is used to divide species between high/medium and low threat status. Records from Asher *et al.* (2001) are subdivided into three classes comparable to those utilized for plants: extant (present 1987–1999), recently extinct (extinct 1970–1986) and older extinctions (extinct before 1970). Again, it is assumed that a majority of older records that have not been refound represent extinctions. The most recent butterfly survey is much more complete than previous ones (Asher *et al.* 2001), and most old records are likely to represent genuine extinctions or at least to indicate that the species is now more difficult to find (i.e. has reduced abundance).

The ecological characters of butterflies depend strongly on habitat (Dennis & Shreeve 1991; Dennis, Shreeve & Van Dyck 2003; Dennis 2010). Nevertheless, these characters remain less clearly defined than those of the plants whose habitats they share (Dennis, Shreeve & Van Dyck 2003; Dennis 2010). We are, therefore, largely dependent upon plant data to link flora and fauna. The simplest approach would be to treat butterfly food plants as direct predictors of rarity, but we have instead used them to assess habitat fertility and canopy height within butterfly habitats. Our reasons for this approach are as follows. Firstly, if the presence or absence of suitable food plants directly controls butterfly distribution, we would expect rare butterflies to utilize rare food plants and common butterflies to utilize common food plants. However, the food plants of many rare and endangered butterflies are common. Moreover, butterfly food plants are generally much more abundant and geographically extensive than the butterflies they support (see Dennis & Shreeve 1991 Asher *et al.* 2001; Preston, Pearman & Dines 2002a; Preston *et al.* 2002b; Dennis 2010). Secondly, the range of life history attributes of butterflies and their food plants show parallel trends (Dennis *et al.* 2004). For example, larval life span, which correlates with speed of development of butterflies, is negatively correlated with leaf nitrogen content of larval food plants (Dennis *et al.* 2012). Moreover, in Sweden, a recent expansion in geographical range is a particular feature of species with a nitrogen-rich larval diet (Betzholtz *et al.* 2013).

Methodology broadly follows that for plants above with details of butterfly food plants abstracted from Dennis (2010). Trait values for all food plants have been averaged to categorize ecologically each butterfly species. Since the plants eaten by the larva are often different from those utilized for nectar by the adult butterfly, we have calculated two sets of values, one for the larval and one for the nectar food plants.

Analyses

Firstly, the relationship between farming intensity and biodiversity was assessed using the Pearson correlation coefficient.

Subsequently, average functional trait values for counties were correlated with both farming intensity and biodiversity, and plant functional traits in plant and butterfly groupings of different conservation status were compared using one-way ANOVAS with statistical differences between groupings identified by Tukey's test using the IBM SPSS 20 statistics package.

Results

EUTROPHICATION: A DIRECT EFFECT OF INTENSIVE AGRICULTURAL LAND USE ON THE ENGLISH FLORA

After correcting for the effect of area on biodiversity, richness of native plant species within English regions (counties) is negatively correlated with the intensity of agricultural land use (Fig. 1a), quantifying the well-documented impact of productive agriculture on the biodiversity of the English countryside (see Preston *et al.* 2002b).

When mean leaf nitrogen concentration for the native floras of English counties was regressed against floristic biodiversity, high biodiversity was strongly linked with an increased abundance of nutrient-poor, slower-growing native plants (Fig. 1b; see also Marren 2002; Preston *et al.* 2002b; Braithwaite, Ellis & Preston 2006). In particular, slow-growing species appear to suffer higher rates of extinction than fast-growing ones in more intensively farmed English counties. Mean leaf nitrogen of extinct species is negatively, and that of extant species positively, correlated with agricultural intensity (Fig. 1c). Thus, data on leaf nitrogen content of species, a good predictor of both plant growth rate and underlying soil fertility (Garten 1976; Thompson *et al.* 1997; Díaz *et al.* 2004), provide quantitative evidence that on agriculturally managed land 'active' management processes designed to boost crop yields (e.g. fertilizer additions, herbicide application and cultivation practices) tend to have favoured faster-growing species of fertile and disturbed habitats. Consistent with this, we found that the lower biodiversity in the most intensively farmed parts of England results from the exclusion of slow-growing species of infertile soils (intolerant of both eutrophication and severe disturbance) from these regions.

MARGINALIZATION: AN INDIRECT EFFECT OF INTENSIVE AGRICULTURAL LAND USE ON THE ENGLISH FLORA

Since perhaps less than 5% of English native plant species exploit arable land, much floristic diversity probably now resides (at least within arable regions) in unmanaged (or infrequently managed) habitats outside the 'working agricultural landscape'. An impact of abandonment is expected to result in increased sward height, leading to the decline and ultimately extinction of short species. Consistent with this, and the work of others (Preston *et al.* 2002b; Braithwaite, Ellis & Preston 2006), we find that quantitative changes in canopy height are a major determinant of the changing distribution and abundance of native perennial plant species. Intensive farming appears to have encouraged tall species at the expense of shorter ones (Fig. 2a). Moreover, the shortest species were apparently the first to go extinct; mean canopy height can be ordered as follows: pre-1970 extinctions <1970–1986 extinctions < extant flora (Fig. 2b). Unsurprizingly, therefore, conservation status is also very much a function of canopy height. Threatened species have on average the shortest and common increasing species the tallest canopies (Fig. 2c). Thus, superimposed upon direct agricultural impacts such as ploughing and fertilizer additions (Fig. 1b–c), 'passive' processes related to abandonment, mediated via their impact on sward height, further impede the conservation of biodiversity in more intensively farmed landscapes. These changes, increased eutrophication and the relaxation or abandonment of meadows and pastures, are similar to those recorded from farmland elsewhere in Europe (e.g. Marini *et al.* 2009; Gustavsson *et al.* 2011; Vassilev *et al.* 2011; Poschlod 2014).

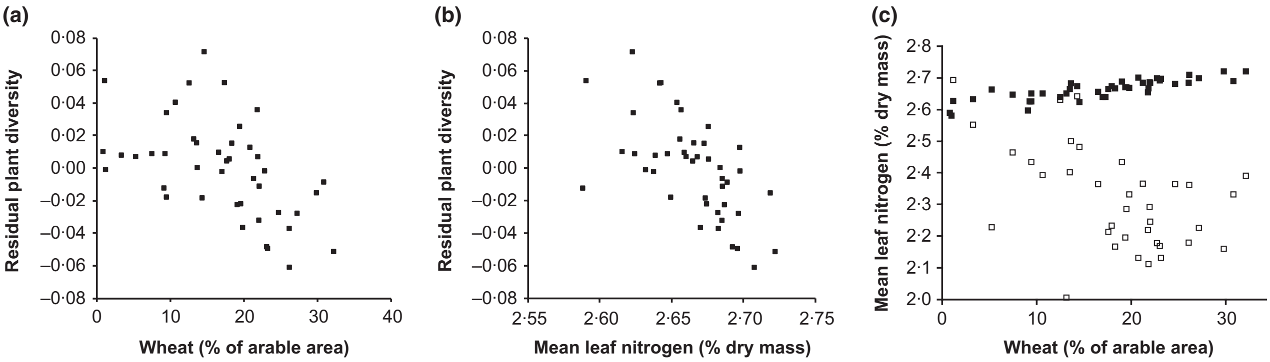

Fig. 1. Intensity of farming defines biodiversity and leaf nitrogen content in the native English flora. Biodiversity is negatively correlated with both (a) intensity of agricultural land use ($r = -0{\cdot}52$, $P < 0{\cdot}001$) and (b) mean leaf nitrogen concentration ($r = -0{\cdot}63$, $P < 0{\cdot}001$). (c) Mean leaf nitrogen concentration is correlated with intensity of agricultural land use. This relationship is positive for 'extant' species, recorded 1987–1999, (■, $r = 0{\cdot}84$, $P < 0{\cdot}001$) and negative for 'extinct', pre-1987, species (□, $r = 0{\cdot}61$, $P < 0{\cdot}001$). In all graphs, each data point represents an English county.

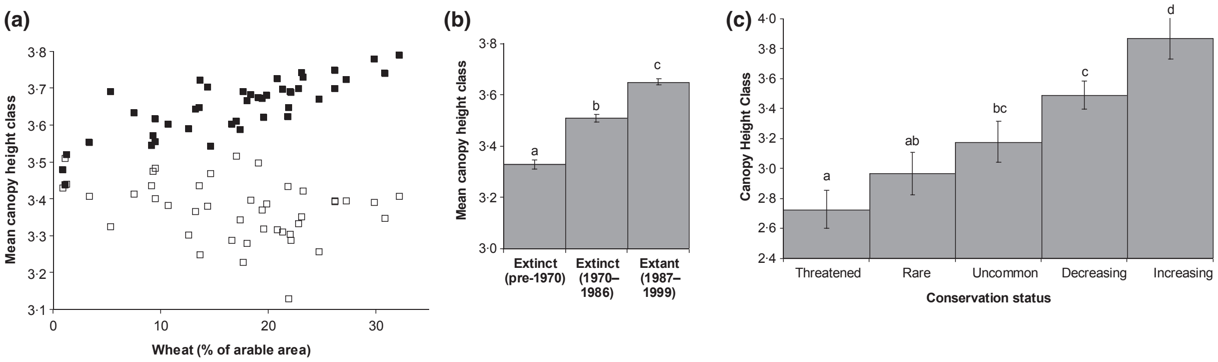

Fig. 2. Intensity of farming, canopy height and conservation status. (a) Intensity of farming defines canopy height (extant flora (■, $r = 0{\cdot}81$, $P < 0{\cdot}001$) and extinct flora (□, $r = 0{\cdot}32$, $P < 0{\cdot}05$). Canopy height predicts (b) vulnerability to extinction and (c) conservation threat in the English flora. In (a), each data point represents a county and in (b) and (c), species groupings are separated with bars identifying standard errors, and groupings with the same letters are not statistically significantly different at $P < 0{\cdot}05$.

PARALLEL RESPONSES IN ENGLISH BUTTERFLIES TO INTENSITY OF AGRICULTURAL LAND USE

Mean nitrogen content of butterfly food plants, both larval and nectar, can be ordered as follows: pre-1970 extinctions <1970–1982 extinctions < extant flora (Fig. 3a i), and species identified by butterfly conservationists as under serious threat feed on plants of low nitrogen content (Fig. 3a ii). There is also evidence of high extinction rates amongst butterflies with short food plants; mean canopy height of both larval and nectar food plants can be ordered as follows: pre-1970 extinctions <1970–1982 extinctions < extant flora (Fig. 3b i). Furthermore, most butterflies regarded as threatened utilize low-growing food plants (Fig. 3b ii). The parallels with plants are exact. Butterflies associated with low- and slow-growing food plants (i.e. with infertile, managed habitats) have declined.

Discussion

CONSERVATION IN THE ENGLISH COUNTRYSIDE: A TALE OF TWO HALVES

Above, we have provided evidence that twin threats – eutrophication and disturbance in managed habitats and abandonment of marginal habitats – are fundamentally altering the nature of the English countryside. The signature of these threats, clearly detectable in national monitoring data, is an essentially identical pattern of traits for declining species of both plants and butterflies.

Two parallel but essentially separate processes of floristic change appear to be involved in the redistribution of species following altered land use (Hodgson 1986), each presenting a different set of challenges for conservation. On agriculturally managed land, 'active' management processes designed to boost crop yields (e.g. fertilizer additions, cultivation practices and use of herbicides and pesticides to eliminate competition from non-crop species) tend to favour species of fertile and disturbed habitats. These processes result in the early and rapid loss of populations of unfavoured (declining) species and a concomitant recruitment of favoured (increasing) species within farmed landscapes. Here, agri-environment schemes may play an important role in restricting biodiversity loss but are relatively ineffective in restoring lost biodiversity (Walker *et al.* 2004; Kleijn *et al.* 2006; Fagan *et al.* 2008). In the remainder of the non-wooded countryside, that is linear habitats (e.g. roadsides, railway and some river banks) and wasteland (e.g. abandoned commons, disused quarries and gravel pits), direct impacts of agriculture (e.g. fertilizer run-off from adjacent farmland, with possible additional impacts from atmospheric deposition – see Stevens *et al.* 2004), if present at all, are both inadvertent and generally less severe. Here, other 'passive' processes are at work. In particular, vegetation tends to be managed infrequently or not at all, and, without direct conservation management (e.g. mowing or scrub clearance), short-lived and low-growing species are prone to extinction. Many initiatives designed to bring threatened species 'back from the brink' by the restoration of management operate primarily within such marginal habitats (Plantlife 2010). Thus, it is always crucial to know where threatened and other less common species grow. Are they in the managed landscape, where agri-environment schemes may be of benefit, or in unmanaged habitats, where they are largely beyond the reach of such measures? Without an answer to these questions, schemes are unlikely to be successful. Nevertheless, successive national agri-environment schemes have been set up without these questions being answered, and perhaps even without them being asked. The extent to which uncommon species occur within agriculturally managed as opposed to unmanaged parts of the English countryside is not routinely recorded, and to date, there are no plans to rectify this deficiency with a national data base.

LESSONS TO BE LEARNT

The powerful 'environmental filters' of eutrophication (a consequence of fertilizer additions and atmospheric inputs), disturbance (from cultivation) and abandonment

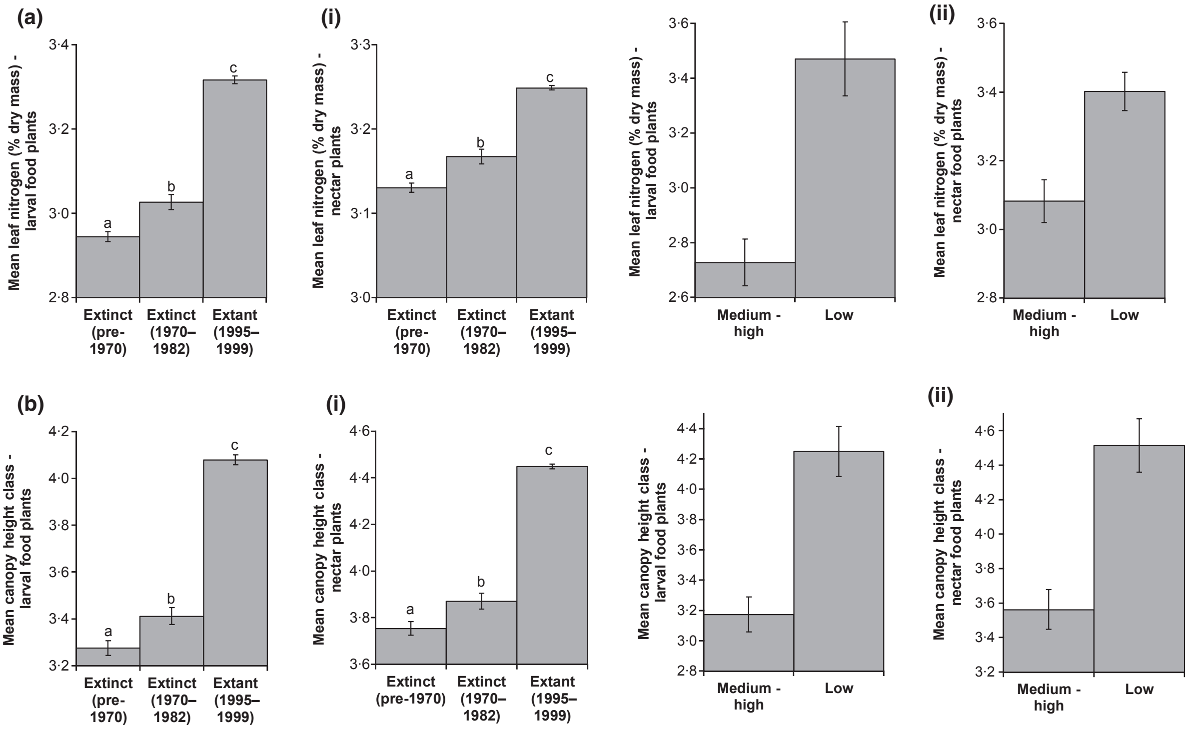

Fig. 3. Vulnerability to extinction (i) and conservation status of English farmland butterflies (ii) patterns with (a) leaf nitrogen and (b) canopy height of their larval and nectar food plants. In (i) conventions as in Fig. 2b–c and in (ii) $P < 0{\cdot}01$.

of marginal land have shaped and are still shaping the composition and distribution of England's native plants and butterflies. The major beneficiaries of these ecological processes have been the relatively few common species of improved grassland and arable land (Preston *et al*. 2002b; Tallowin *et al*. 2005; Braithwaite, Ellis & Preston 2006; Kleijn *et al*. 2011). As a result, the biodiversity of the English countryside is declining, and much of what remains now lies outside the 'economically viable farmed landscape'. Moreover, because many long-lived plant species can persist temporarily in unfavourable habitats, we suspect that a significant proportion of the biodiversity still remaining in the more intensively farmed portions of the English countryside is both transient and unsustainable.

We quantify two main causes of the ineffectiveness of past schemes. Firstly, from the outset, the severity of impacts resulting from the post-1939 shift towards intensive mechanized farming has been underestimated (Marren 2002). How else can the broad-brush, relatively untargeted nature of early agri-environment schemes be explained? Secondly, there is a lack of integration between schemes operating in farmland and those on land under other ownership. Although the recognition of 'multifunctionality' within the countryside (see OECD (2001); Willemen *et al*. (2010)) in terms of land use is important for economic planning, it has less relevance to threatened flora and fauna, which exploit both sides of the divide. A failure to appreciate the increasing restriction of less common species to the 'non-working' landscape and to counteract effectively the fragmentation of dispersal corridors within the general countryside (Römermann *et al*. 2008; Lawton *et al*. 2010) may be a consequence of this 'fractured' conservation policy.

MAKING THE MOST OF THE AVAILABLE DATA

Effective conservation management in changing landscapes will always depend for guidance upon a good understanding of the ecological processes shaping the flora and fauna. An extension of the approach outlined here to include additional conservationally important taxa (e.g. birds) is, therefore, recommended. With interdisciplinary cooperation amongst ecologists, the status of any plant or animal grouping can be similarly analysed. All that is needed are (a) reliable distributional data, (b) the habitat utilized by each species categorized in terms of plant communities (so that, as for butterflies, a list of associated plants can be generated) and, of course, (c) access to relevant trait data. Plant communities can be ecologically categorized in a similar way to that used here for species (see Hodgson *et al*. 2005a,b).

Other concerns of those with a remit to conserve the countryside may be similarly studied. For example, there are comparable data sets for alien plants. Importantly, however, alien biodiversity is less affected in England by agricultural land use. Instead, it is centred on regions of high population density (data not shown) – reflecting, perhaps, the fact that the English are 'a nation of gardeners'.

FUTURE PROSPECTS FOR CONSERVATION IN THE ENGLISH COUNTRYSIDE

Encouragingly, the most recent agri-environment schemes are more focussed (Natural England 2009), and the future of English conservation is now under review, with issues relating to ecosystem function, species mobility and population dynamics 'centre stage' (Lawton *et al.* 2010). An integration of policies for conserving biodiversity within and outside farmland would provide many benefits. For example, the countryside could routinely be made more 'butterfly-friendly' by additionally maintaining the quality of food resources in non-farmed parts of the landscape (e.g. stream banks and roadside verges, hedgerows and green lanes; Dennis 2010; Dennis *et al.* 2013). 'Unimproved' pasture, a target habitat for many agri-environment schemes, is a particularly important source of larval food plants. It is generally, however, a less adequate source of the often taller nectar-rich flowers utilized by adult butterflies. Grazing and mowing abandoned land, even at low intensities and only every few years, can greatly reduce biodiversity loss (Rudmann-Maurer *et al.* 2008). Thus, the sympathetic management of nearby marginal habitats to promote the survival and flowering of nectar-producing species has the potential to dramatically increase the population size and the diversity of butterflies present in the English countryside (see Jonason *et al.* 2012).

Our understanding of how ecosystems function remains far from perfect. Nevertheless, we have the information to quantify changes in species composition and to interpret their causes. This ecological knowledge is sufficiently robust to allow us to conserve our flora and fauna far more effectively than at present. We trust that, both in England and elsewhere, future improvements to schemes can be generated not, as in the past, by 'learning from mistakes' but by predicting and anticipating potential problems with reference to ecological and economic theory and through experimentation and data analysis.

Conclusions

No one concerned with the conservation of the English countryside will be surprized by our quantitative assessment that eutrophication and abandonment remain the key drivers of biodiversity loss in agricultural landscapes. Perhaps more surprizing is how clearly both processes are revealed, at the landscape scale and for both plants and butterflies, by a simple desk study using widely available data on agricultural intensity, species distributions and plant traits. Moreover, our results are interpretable simply and unambiguously in terms of cause (land use factors and ecosystem drivers) and effect (changing biodiversity and representation of plant and animal functional types). Our approach can be used to generate an overview of the effectiveness of current policies, to guide improvements with respect to both focus and implementation and to monitor the outcome of those improvements.

While we expect the 'functional approach' described here to be universally applicable in farmed landscapes, we accept that in other countries, some details of the analysis may require modification. In particular, we suspect that percentage wheat may not always be the best agricultural statistic for predicting farming intensity. Equally, although we chose to use a methodology that relates the ecology of plants directly to measurable functional traits (Hodgson *et al.* 2005a), estimates of soil fertility derived from patterns of occurrence in the field, available for Central Europe as Ellenberg nitrogen numbers (Ellenberg *et al.* 1991), are equally effective (see Preston *et al.* (2002b)) and may be available for more species. Once local issues of identifying the most appropriate indices have been resolved, there is the prospect of a simple and robust methodology that can consistently guide conservation policies to a more efficient and cost-effective future.

Acknowledgements

This study is an informal and unfunded extension of the European Science Foundation (ESF) supported CLIMB (Changing Land use and its IMpact on Biodiversity) networking project initiated in 1998. It would not have been possible without access to data holdings of the Botanical Society of the British Isles (Preston, Pearman & Dines 2002a) and the UK Department for Environment, Food and Rural Affairs (DEFRA 2006), both in the public domain. Distributional data on butterflies came from the Butterflies for the New Millennium recording scheme (Asher *et al.* 2001), courtesy of Butterfly Conservation, and were provided in electronic form by Richard Fox (Butterfly Conservation). The only 'private' data, our leaf measurements, are freely available, as they are now incorporated within the TRY data base (Kattge *et al.* 2011). David Roy (Biological Records Centre) helped to ascribe these data to the different English counties. Kevin Gaston and Natural England made valuable comments on an earlier version of the article.

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Received 1 July 2013; accepted 18 December 2013
Handling Editor: Edith Adam