

Changes in nectar supply: A possible cause of widespread butterfly decline

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Abstract Recent studies have documented declining trends of various groups of flower-visiting insects, even common butterfly species. Causes of these declines are still unclear but the loss of habitat quality across the wider countryside is thought to be a major factor. Nectar supply constitutes one of the main resources determining habitat quality. Yet, data on changes in nectar abundance are lacking. In this study, we provide the first analysis of changes in floral nectar abundance on a national scale and link these data to trends in butterfly species richness and abundance. We used transect data from the Dutch Butterfly Monitoring Scheme to compare two time periods: 1994–1995 and 2007–2008. The results show that butterfly decline can indeed be linked to a substantial decline in overall flower abundance and specific nectar plants, such as thistles. The decline is as severe in reported flower generalists as in flower specialists. We suggest that eutrophication is a main cause of the decline of nectar sources [*Current Zoology* 58 (3): 384–391, 2012].

Keywords Butterflies, Eutrophication, Habitat quality, Land use, Nectar resources, Pollinators

Flower-visiting insects play an important role in maintaining biodiversity and ecosystem services such as pollination, which corresponds to a great economic value (Losey and Vaughan, 2006; Potts et al., 2010). Declines of domestic bees and wild pollinators thus could have significant implications for society (Kremen et al., 2002). The emerging threat of a global ‘pollinator crisis’ was expressed over a decade ago (Kearns et al., 1998). Since then, declines of pollinator and other flower-visiting insects have been confirmed in North America and Europe: honeybees and wild bees in the USA (van Engelsdorp, 2010; Kremen et al., 2002), honeybees and butterflies in Europe (Potts et al., 2010; Van Swaay et al., 2010), wild bees and hoverflies in the UK and the Netherlands (Biesmeijer et al., 2006) and bumblebees in the UK and Belgium (Goulson et al., 2008; Williams and Osborne, 2009). Recently, even common generalist butterflies have been found to decline in abundance, in addition to previously known declines of habitat specialists (Van Dyck et al., 2009; Forister et al., 2010).

The main driver of decline in flower-visiting insects is generally thought to be the loss of suitable habitat through land-use changes (Potts et al., 2010). Among the various determinants of habitat quality, the loss of

floral nectar resources has been most frequently proposed as a major factor contributing to flower-visiting insect declines (Potts et al., 2010). Indeed, many studies have shown that insect abundances are highly correlated with the abundance of floral nectar sources. Thus, butterfly and bumblebee abundance and species richness are higher in grassland patches with greater flower abundance (Öckinger and Smith, 2006; Kuussaari et al., 2007). Flower-rich field margins in agri-environment schemes also harbour more butterflies (Dover et al., 1990; De Snoo et al., 1998; Aviron et al., 2010; Pywell et al., 2011) or other pollinators (Kleijn et al., 2001; Westphal et al., 2003) and, conversely, less butterflies are found in sprayed field margins around genetically modified, herbicide resistant crops where flowers are suppressed (Roy et al., 2003). Still, solid evidence of actual declines in floral nectar abundance at the landscape scale is lacking. The only data analyzed thus far consist of distribution data, reflecting changes in the frequency of species but not in their abundance, let alone the abundance of floral resources. Moreover, the data analyzed have only been linked indirectly to changes in pollinator occurrence (e.g. Biesmeijer et al., 2006; Carvell et al., 2006; Kleijn and Raemakers, 2008). Indeed, Potts et al., (2010) conclude that ‘the current

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challenge is to better quantify the relative importance of a range of drivers' to explain the decline of flower-visiting insects.

In this study, we used simultaneously collected data on floral and butterfly abundance on a national scale to link changes in flower abundance over a 13-year period with changes in the abundance of butterflies. Butterflies are taken as representatives of flower-visiting insects. Although their role in pollination is reportedly of minor importance (Jennersten, 1984) or limited to specialized plants (Jennersten, 1984; Bloch et al., 2006; Lind et al., 2008), butterflies may enhance pollination by other pollinators (Carvlaheiro et al., 2011) and they can be regarded as suitable bioindicators for flower-visiting insects (Pe'er and Settele, 2008; Pywell et al., 2011). We determine the extent of the changes in flower resources and butterflies and test the association of the population density of individual species with changes in flower abundance. We use butterfly species with different associations with flower abundance to assess long-term annual trends of flower-associated and flower-indifferent butterflies. Finally, we discuss possible causes of the observed changes.

1 Material and Methods

1.1 Data collection

Butterfly and flower abundances were obtained from the Dutch Butterfly Monitoring Scheme for two time periods: 1994–1995 and 2007–2008. Butterfly numbers represent weekly counts for all species between April 1st and September 30th along permanent transects under suitable weather conditions (details on methods in Pollard and Yates, 1993). Each transect consists of a series of usually 20 sections of 50 m length and 5 m width. The transects are distributed over the whole country; imbalances in geographical distribution are accounted for in trend analysis by a weighting procedure according to landscape type (Van Swaay et al., 2002).

Flowers were grouped in 14 categories of important nectar plants on the basis of known flower visiting preferences (Bos et al., 2006) (Table 1). Flowers were counted at monthly intervals between early May and early August. Counts were recorded as the number of inflorescences using a simple scale: 1–10, 11–50, >50 for each 50 m section.

Data on vegetation management (grazing, mowing, sod-cutting, scrub removal, tree felling) were available for most transects. Changes in botanical composition between time periods were examined in a subsample of 116 quadrats from 27 transects on semi-natural grass-

lands.

2.2 Data analysis

Combined butterfly and flower counts were available from 215 transects in 1994–1995 and 216 transects in 2007–2008. We assigned each transect to one of 7 main landscape types: coastal dunes, Pleistocene sandy soils (divided into farmland, semi-natural grassland, heathland and forest), lowland peat grasslands and urban areas. Three other landscape types (riverine, marine clay and calcareous regions) were represented by few transects only and excluded from the analysis. All yearly butterfly abundances per transect were transformed as $\log(n+1)$. Flower abundances per transect were expressed as the average log-transformed value per 50 m section for each flower group as well as for total flower abundance, including zero values in case of absence. Outliers were discarded from the analysis.

We first determined differences of flower abundance on transects between time periods using GLM in JMP 5.0.1 (Sall et al., 2005) with landscape type as an additional factor. Interactions between time period and landscape type were checked to assess differences in trends between landscape types. To account for variation in volunteer recording effort, a second Yes-No factor was added, indicating whether a given transect was counted in both periods or in just a single period. If the interaction of this factor with period was significant, only transects counted in both periods were considered.

Secondly, we assessed correlative responses of butterfly abundance and species richness to flower abundance of separate flower groups and all groups combined at the transect level. Analyses at the species level were restricted to 23 sufficiently abundant species (Table 1), including the national Red-List species *Plebejus argus* and *Ochlodes sylvanus*. For individual species, only transects where the species was sighted were included and only flower abundances recorded during the flight period of the butterflies were taken into consideration. The analysis was carried out using GLM with time period as an additional factor. Interactions effects between flower abundance and time period were included to check for inconsistencies in effects of flower abundance between periods.

Thirdly, we calculated annual trends of groups of butterfly species whose abundance was closely associated with the abundance of different flower groups. In this analysis, we used all transects from the Dutch Butterfly Monitoring Scheme for the period 1992–2009, including those where flower abundance was not recorded. When the associations between butterfly and

Table 1 Significant relations between flower abundance (total and individual flower groups) and butterfly species richness and abundance (total and individual species)

	Total Flowers	<i>Cirsium</i> <i>/Carduus</i>	<i>Centaurea</i>	Yellow Asteraceae	Other Asteraceae	<i>Buddleja</i>	<i>Calluna</i>	<i>Erica</i>	<i>Eupatorium</i>	<i>Lythrum</i>	<i>Rubus</i>	Apiaceae	Brassicaceae	Papilionaceae	Other nectar plants
No. species	++++	++++	++					+++	++++				+		
No. butterflies	+++	++++	+++										++		
<i>Aglais io</i>	+++	+++			+	++++			++++						+
<i>Aglais urticae</i>						+++	+		++						
<i>Anthocharis cardamines</i>															
<i>Aphantopus hyperantus</i>		+									+				
<i>Araschnia levana</i>		+						+	++			+++			
<i>Celastrina argiolus</i>								++++							
<i>Coenonympha pamphilus</i>				+											
<i>Gonepteryx rhamni</i>						++		+	++	+					
<i>Lasiommata megera</i>			+++				+		+						
<i>Lycaena phlaeas</i>			+	++++											
<i>Maniola jurtina</i>		+++	++												
<i>Ochlodes sylvanus</i>								+++							
<i>Pararge aegeria</i>											++				
<i>Pieris brassicae</i>			++			++++		+							
<i>Pieris napi</i>	++++	+++						++	++++	+++	+	+++	++++	+	
<i>Pieris rapae</i>	++++	+	+	++		++			+++	++		++++	++++	++	
<i>Plebejus argus</i>								++++							
<i>Polygonia c-album</i>		+				++++			+						
<i>Polyommatus icarus</i>	++++		++	++++	++									++++	
<i>Pyronia tithonus</i>	++				++										
<i>Thymelicus lineola</i>		++++	+		++++									+	
<i>Vanessa atalanta</i>	++					++++			++++						
<i>Vanessa cardui</i>			++			+++			+						

+ $P < 0.05$, ++ $P < 0.01$, +++ $P < 0.001$, ++++ $P < 0.0001$. Species nomenclature follows Settele et al. (2008).

flower abundances are consistent, such trends should be expected to be an indicator for the trend of the associated flower group. Trends were calculated for all individual species using time series analysis with missing data, based on log-linear regression analysis (Van Swaay et al., 2002). Yearly values were then averaged over the different species to generate the overall trend for a certain butterfly group.

Finally, changes in botanical composition in the quadrats on semi-natural grasslands were analyzed using plant species-specific Ellenberg indicator values for nitrogen as an indicator for productivity (on a scale of 1 to 9 for oligotrophic to eutrophic conditions, respec-

tively; Oostermeijer and Van Swaay, 1998). A productivity estimate was calculated for each quadrat as the average Ellenberg indicator value of all contributing species.

2 Results

2.1 Changes between 1994–1995 and 2007–2008

Both butterfly abundance and species richness declined significantly from 1994–1995 to 2007–2008 (Fig. 1; Supplementary Material Table SOM1). From the total of 53 observed species, 50 were observed during the first period and 45 during the second period. Species richness per transect declined by 2 species on average

and butterfly numbers decreased by 28%.

Total flower abundance decreased significantly by 34% (Fig. 1; Supplementary Material Table SOM1), without significant variation in change between landscape types ($P=0.16$). Total flower abundance correlated most strongly with the abundance of Papilionaceae ($r=0.74$; $P<0.0001$) and Yellow Asteraceae ($r=0.63$; $P<0.0001$). Changes between periods were consistent in that the flower abundance varied more between periods than between the two years within each period (average number of flowers per 1-km transect for the four different years: 1994: 1589, 1995: 1702, 2007: 1205, 2008: 893).

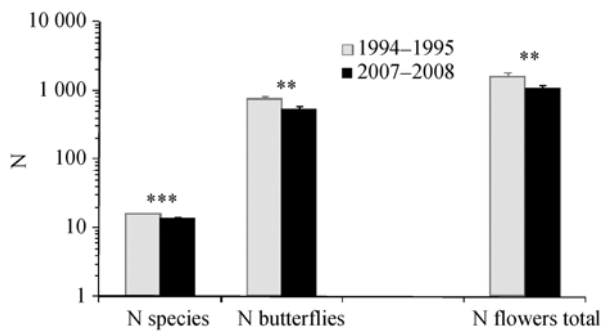


Fig. 1 Changes in butterfly species richness and abundance and in flower abundance (+SE) along transects of the Dutch Butterfly Monitoring Scheme between 1994–1995 (grey) and 2007–2008 (black)

** $P<0.01$; *** $P<0.001$.

The abundance of individual flower groups on butterfly transects was only weakly correlated ($r=0.10$ on average, with a maximum of 0.53 for Papilionaceae and Yellow Asteraceae). Decreases for individual flower groups (Fig. 2; Supplementary Material Table SOM1) were significant for thistles *Cirsium/Carduus* (–34%), *Centaurea* (–11%) and other nectar plants (–52%), again without significant differences in trend between landscape types and with a greater difference between periods than between years within each period. Not all flower groups showed a decline. Increasing flower abundance was found for bramble (*Rubus*) (+38%), heather *Calluna vulgaris* (+16%) and Apiaceae (+40%). Heather changes varied between landscape types ($P=0.034$) with a particularly strong increase on heathland (+74%) but no declines in other landscape types. Changes in the abundance of Apiaceae also differed between landscape types ($P=0.038$), with declines in the dunes (–54%), semi-natural grassland on lowland peat (–32%) and urban areas (–26%) in contrast to increases on sandy soils in farmland (+145%) and semi-natural

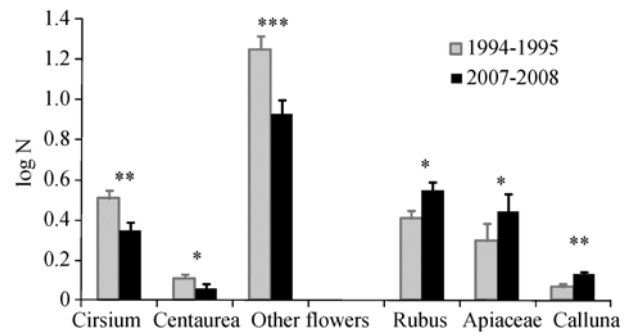


Fig. 2 Changes in flower abundance (+SE) of different taxonomic groups along transects of the Dutch Butterfly Monitoring Scheme between 1994–1995 (grey) and 2007–2008 (black)

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

grassland (+48%). Yellow Asteraceae showed no overall change, but variation in change between landscape types ($P=0.016$), with declines in urban areas and farmland on sandy soils (both –55%) and increases in forest on sandy soils (+48%) and on heathland (+307%).

2.2 Butterfly associations with flower abundance

Butterfly overall abundance and species richness were positively correlated ($r=0.69$, $P<0.0001$) and significantly increased with greater overall flower abundance and with the abundance of thistles and *Centaurea* (Table 1; Supplementary Material Table SOM2). High *Eupatorium* and *Erica* flower abundances were especially associated with high butterfly species richness, whereas high Brassicaceae flower abundance rather correlated with high butterfly abundance, especially *Pieris* species.

Flower groups with the most numerous associations with individual butterfly species were *Eupatorium*, *Buddleja*, *Cirsium*, *Centaurea* and *Erica*; the significant associations with *Erica* were also obtained when considering only transects on heathlands and semi-natural grasslands. None of the butterflies strongly responded to *Calluna* (even within heathlands) or to the remaining group of other nectar plants.

Most butterfly species responded to more than one flower resource. Various species (*A. io*, *P. napi*, *P. rapae* and *P. icarus*) showed a strong association with total flower abundance. More species-specific associations were found for *L. megera* on *Centaurea*, *P. aegeria* on *Rubus* and *L. phlaeas* on Yellow Asteraceae. The abundance of the two Red-List species *P. argus* and *O. sylvanus* only responded positively to *Erica* abundance. Three species showed only weak relations to flower abundance: *C. pamphilus*, *A. hyperantus* and *A. cardamines*.

2.3 Trends of flower-associated butterfly groups

The three species least associated with flower abundance (as shown in Table 1) showed a non-significant increase over the years ($R^2=0.14$, slope= -0.0050 ± 0.0030 , $P=0.12$ for *C. pamphilus*, *A. hyperantus* and *A. cardamines*). Compared to this reference group, the relative trend of the five species showing the strongest correlative response to total flower abundance (*A. io*, *P. napi*, *P. rapae*, *P. icarus* and *P. tithonus*) showed a significant decline over time ($R^2=0.45$, slope= -0.0155 ± 0.0043 , $P=0.0024$), with a 37% lower abundance in 2009 than in 1992 (Fig. 3). Even stronger declines relative to the reference group were found for species associated with thistles ($R^2=0.69$, slope= -0.0247 ± 0.0041 , $P<0.0001$; *T. lineola*, *M. jurtina*, *P. napi* and *A.io*) and *Centaurea* ($R^2=0.60$, slope= -0.0241 ± 0.0050 , $P=0.0002$; *L. megera*, *P. brassicae*, *M. jurtina* and *P. icarus*; excluding *V. cardui* as a migrant).

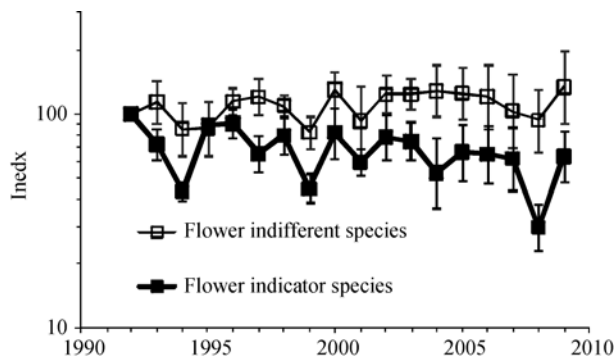


Fig. 3 Trends in the abundance ($\pm SE$) of five flower-associated butterfly species and three flower-indifferent butterfly species

The index has a value 100 in the initial year 1992.

The comparatively small number of species especially associated with increasing flower groups did not decline in abundance, showing either no significant trend over time ($R^2=0.02$, slope -0.0047 ± 0.0075 , $P=0.54$ for *A. levana*, associated with *Apiaceae*) or a significant increase ($R^2=0.63$, slope $+0.0413\pm 0.0079$, $P<0.0001$ for *P. aegaeria*, associated with *Rubus*).

2.4 Changes in weather, management and vegetation

The weather in both time periods showed comparable temperatures during spring and summer, ranging from 16.4 to 17.0 C between years. Precipitation from early April to late September was higher in 2007 than in 1995 (429 vs. 232 mm; despite an extremely dry April in 2007), but differed little between 2008 and 1994 (312 vs. 291 mm).

Overall management did not vary between time pe-

riods ($P=0.68$; Likelihood ratio test). Transect locations were mostly managed by standard cutting (36%), rotational cutting (33%) or grazing (9%). A minor fraction of the locations (19%) did not show signs of being managed at all.

The Ellenberg productivity value of semi-natural grasslands remained unchanged overall (mean difference -0.07 ± 0.08 ; $P=0.40$ paired *t*-test). However, the slope of the regression line differed significantly from unity (0.68 ± 0.05 ; $P<0.0001$), with a decrease in productivity value above the overall average of 4.5 and an increase below average (Fig. 4).

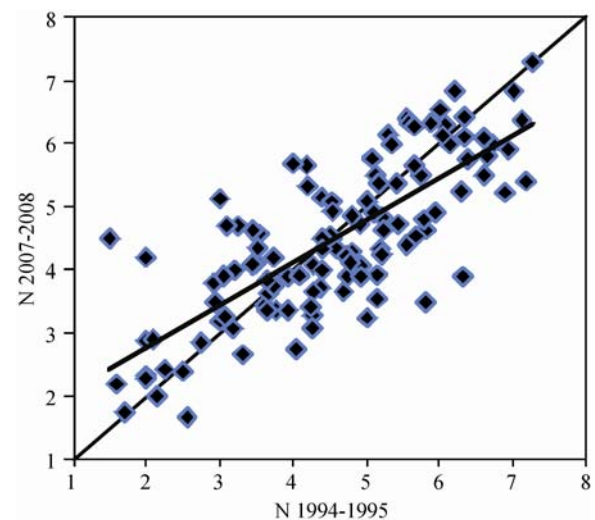


Fig. 4 Comparison of Ellenberg productivity values along butterfly transects in semi-natural grasslands between 1994-1995 and 2007-2008

The trend line (thick line) deviates significantly from the line of equality (thin line).

3 Discussion

3.1 Large-scale declines in flowers and butterflies

Our data provide a first confirmation of an associated decline of flower resources and butterflies on a national scale. Flower and butterfly abundance both decreased dramatically (34% and 28%, respectively) in a period of only 13 years. The trends of flower-associated butterfly species showed a 37% decline between 1992 and 2009 in contrast to a stable abundance or a tendency for increase in species whose abundance was not related to flower abundance. These results support the suggestions of an aggravating pollinator crisis (Potts et al., 2010) and offer a possible explanation for recently reported declines of even common species (Van Dyck et al., 2009). Indeed, the declines were strikingly similar for reported flower specialists and flower generalists (see

Jennersten, 1984; Tudor et al., 2004; annual trend slope \pm SE -0.0165 ± 0.0049 for flower generalist species *C. pamphilus*, *L. megera*, *L. phlaeas*, *M. jurtina*, *P. icarus*, *P. napi*, *T. lineola*, *T. sylvestris* and -0.0173 ± 0.0051 for flower specialist species *A. hyperantus*, *B. selene*, *E. tages*, *G. rhamni*, *P. tithonus*).

Most of the butterfly-flower associations found in this study, although constituting correlative evidence, confirm reported flower preferences (e.g. Jennersten, 1984; Corbet, 2000; Tudor et al., 2004; Bos et al., 2006). Only the association between *C. argiolus* and *Erica* rather appears an indirect effect of its higher abundance in wet heathlands; other correlations with *Erica* abundance confirmed expectations and were maintained when restricting the analyses to heathland and semi-natural grasslands.

It is not surprising that butterfly numbers are closely correlated with flower abundance because of its attraction as a foraging resource. Hence, it could be argued that our observations cannot distinguish between the trends in flowers and those of butterflies. However, it is unlikely that our results present a sampling artifact, because of two reasons. First, the trends we observe are derived from transects that are sufficiently long (mostly 1 km) to adequately represent habitat conditions at a landscape scale. Second, the extensive, nationwide population sampling involving >200 sites ensures a sufficient sample size to avoid recording merely local changes. Moreover, De Snoo *et al.*, (1998) investigated this problem in a study on the effects of spraying on field margins and concluded that butterflies were not only more abundant on the flowers in unsprayed field margins, but also more abundant in adjacent control strips where flowers were not promoted. Thus, the observed population trend was a true increase of the butterfly population and not merely the result of increasing butterfly counts on a greater number of flowers. This is also likely to be valid for the results of the present study that was carried out at a larger spatial scale and a much greater sampling effort.

The decline in flower abundance showed surprisingly little variation across landscape types. The sustained decline of flower-associated butterflies over nearly two decades and the observation that this decline is as severe in reported flower generalists as in specialists, provides further support for a causal link in the disappearance of flower resources and the decline of butterflies across the landscape.

3.2 Eutrophication as a possible cause

We examined changes in weather, management and

vegetation along the transects to discover possible drivers of the observed large-scale declines of flower abundance and associated butterflies. Weather and management did not differ clearly between time periods. It is possible that management did change in ways that were not recorded. Thus, cutting frequency appears to have decreased in many areas to reduce costs and cutting by rotary mowers and cutting bars is increasingly replaced by flail cutting, resulting in a higher mortality of larvae in the vegetation (Humbert et al., 2009). Both reduced cutting frequency and the increased use of flail cutters contribute to eutrophication, because nutrients are removed to a lesser extent or not at all (Parr and Way, 1988), and an increase of competitive grasses at the expense of flower resources (Pywell et al., 2011).

Eutrophication also emerged as a possible driver of change from our analysis of botanical changes in semi-natural grasslands; these changes are confirmed by independent data from the national botanical monitoring scheme (L. van Duuren, unpubl. data). Although productivity values along our transects did not change on average, they increased in locations with below average productivity and decreased only in locations above the average. Thus, cutting may have been effective in decreasing productivity on more productive sites, but the less productive sites appear to have suffered from eutrophication. This is all the more severe, since less productive sites are richer in nectar sources from a variety of dicots and are more vulnerable to the encroachment of competitive grasses and tall herbs through eutrophication (Bobbink *et al.*, 1998; Stevens *et al.*, 2004). The trend towards eutrophication is given further support by the observed increases in brambles and Apiaceae (especially on farmland); only few butterfly species showed higher numbers with a greater availability of these two flower groups (Table 1). Increases in Apiaceae probably reflect mainly the spreading of *Anthriscus sylvestris*, which thrives on eutrophic soils. An exception to this trend are the developments on heathlands, where sod-cutting has been successful in reducing nutrient load and ensuing grass encroachment (Bakker and Berendse, 1999), which may explain the observed increase in flower abundance of heather and Yellow Asteraceae.

It has been estimated that across the EU-25, approximately 47% of (semi-) natural ecosystem areas were subject to nutrient nitrogen deposition leading to eutrophication in 2004 (EEA, 2007). Eutrophication is known to reduce the diversity of flowering plants in grasslands (Bobbink *et al.*, 1998; Stevens *et al.*, 2004). Our study demonstrates a long-suspected link between

the decline in flower abundance and associated butterflies. We suggest that eutrophication may be an important driver of the decline in flower resources. Associated changes towards more cost-effective land use practices may exacerbate these changes. It may be expected that declining floral resources have similar detrimental consequences for other groups of flower-visiting insects. A solution to the diminishing flower abundance across the landscape should be found in a further decrease of nitrogen emissions and effective removal of nutrients by appropriate vegetation management (Pywell et al., 2011).

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Supplementary Online Material

Table SOM1 GLM test results (*P*-values) for changes in butterfly species richness and abundance and changes in flower abundance between time periods (1994–1995 vs. 2007–2008) (NS = not significant, i.e. *P*>0.05; *n*=299 after removing outliers).

	Period	Change	Landscape type	Period x Landscape type	Recording effort	Period x Recording effort	R ²	Comments
<i>Butterflies:</i>								
Species richness	0.0006	Decrease	<0.0001	NS	NS	NS	0.219	Decreases across all landscape types. except for heathland (increase) and semi-natural grassland (stable) on Pleistocene sandy soils
Abundance	0.0033	Decrease	<0.0001	0.0264	NS	NS	0.157	
<i>Flower abundance:</i>								
Total Flowers	0.0063	Decrease	<0.0001	NS	NS	NS	0.174	
<i>Cirsium / Carduus</i>	0.0066	Decrease	<0.0001	NS	NS	NS	0.177	
<i>Centaurea</i>	0.0445	Decrease	0.0119	NS	NS	NS	0.096	
Yellow Asteraceae	NS	NS	<0.0001	0.0158	NS	NS	0.222	Declines in urban areas and farmland on sandy soils and increases in forest on sandy soils and on heathland
Other Asteraceae	NS	NS	<0.0001	NS	0.0119	NS	0.175	
<i>Buddleja</i>	NS	NS	NS	NS	NS	NS	0.069	
<i>Calluna</i>	0.0029	Increase	<0.0001	0.0339	NS	NS	0.390	Strongest increase on Pleistocene sandy soils
<i>Erica</i>	NS	NS	<0.0001	NS	NS	NS	0.229	
<i>Eupatorium</i>	NS	NS	0.0024	NS	0.0042	0.0376	0.138	Period effect NS on transects counted in both periods
<i>Lythrum</i>	NS	NS	0.0002	NS	NS	NS	0.11	
<i>Rubus</i>	0.0171	Increase	<0.0001	NS	NS	NS	0.333	
Apiaceae	NS	Increase (see comment)	<0.0001	0.0138	NS	0.0378	0.239	Period effect significant (<i>P</i> =0.0146; increase) on transects counted in both periods
Brassicaceae	NS	NS	0.0013		NS	0.0349	0.128	Period effect NS on transects counted in both periods
Papilionaceae	NS	NS	<0.0001	NS	NS	NS	0.164	
Other nectar plants	0.0008	Decrease	<0.0001	NS	NS	NS	0.195	

Table SOM2 GLM test results on associations between butterfly abundance and flower abundance; only results with significant effects for Flower groups are shown. Effects of Flower groups are always positive, i.e. more butterflies with more flowers. Significant Period effects are indicated as decreases (–) or increases (+) from 1994–95 to 2007–2008. (NS = not significant, i.e. $P > 0.05$).

Butterflies	Flower group	Flower abundance	Period	Period x Flower abundance	Landscape type	R ²	Comments on interactions
Abundance	Brassicaceae	0.0003	NS	NS	<0.0001	0.150	
Abundance	<i>Centaurea</i>	0.0084	0.0440 –	NS	<0.0001	0.155	
Abundance	<i>Cirsium/Carduus</i>	<0.0001	NS	NS	<0.0001	0.167	
Abundance	Total flowers	0.0007	0.0407 –	NS	<0.0001	0.155	
Species richness	Brassicaceae	0.0044	0.0041 –	NS	<0.0001	0.228	
Species richness	<i>Centaurea</i>	0.0018	0.0032 –	NS	<0.0001	0.237	
Species richness	<i>Cirsium/Carduus</i>	0.0001	0.0032 –	NS	<0.0001	0.247	
Species richness	<i>Erica</i>	0.0002	0.0003 –	NS	<0.0001	0.246	
Species richness	<i>Eupatorium</i>	0.0001	0.0004 –	NS	<0.0001	0.261	
Species richness	Total flowers	<0.0001	0.0053 –	NS	<0.0001	0.274	
<i>Aglais io</i>	<i>Buddleja</i>	<0.0001	<0.0001 –	0.0098	0.0007	0.263	stronger association in Period 1
<i>Aglais io</i>	<i>Cirsium/Carduus</i>	0.0003	<0.0001 –	0.0305	0.0026	0.259	stronger association in Period 1
<i>Aglais io</i>	<i>Eupatorium</i>	<0.0001	<0.0001 –	0.0002	0.0002	0.284	stronger association in Period 1
<i>Aglais io</i>	Other Asteraceae	0.0275	<0.0001 –	NS	0.0011	0.212	
<i>Aglais io</i>	Other nectar plants	0.0423	<0.0001 –	NS	0.0001	0.210	
<i>Aglais io</i>	Total flowers	0.0002	<0.0001 –	NS	0.0001	0.243	
<i>Aglais urticae</i>	<i>Buddleja</i>	0.0006	<0.0001 –	NS	NS	0.279	
<i>Aglais urticae</i>	<i>Calluna</i>	0.0296	<0.0001 –	NS	<0.0001	0.232	
<i>Aglais urticae</i>	<i>Eupatorium</i>	0.0043	<0.0001 –	NS	NS	0.244	
<i>Aphantopus hyperantus</i>	<i>Cirsium/Carduus</i>	0.0280	NS	NS	<0.0001	0.231	
<i>Aphantopus hyperantus</i>	<i>Rubus</i>	0.0349	NS	NS	<0.0001	0.227	
<i>Araschnia levana</i>	Apiaceae	0.0004	0.0391 –	0.0078	0.0008	0.155	stronger association in Period 2
<i>Araschnia levana</i>	<i>Cirsium/Carduus</i>	0.0117	NS	NS	<0.0001	0.119	

To be continued

Butterflies	Flower group	Flower abundance	Period	Period x Flower abundance	Landscape type	R ²	Comments on interactions
<i>Araschnia levana</i>	<i>Erica</i>	0.0164	0.0322 –	NS	<0.0001	0.139	
<i>Araschnia levana</i>	<i>Eupatorium</i>	0.0048	0.0287 –	NS	0.0019	0.127	
<i>Celastrina argiolus</i>	<i>Erica</i>	<0.0001	<0.0001 +	<0.0001	0.003	0.280	strong association in both periods, but stronger in Period 2
<i>Coenonympha pamphilus</i>	Yellow Asteraceae	0.0192	0.0038 +	NS	<0.0001	0.356	
<i>Gonepteryx rhanni</i>	<i>Buddleja</i>	0.0033	0.0007 –	NS	0.0015	0.159	
<i>Gonepteryx rhanni</i>	<i>Erica</i>	0.0130	0.0004 –	NS	<0.0001	0.152	
<i>Gonepteryx rhanni</i>	<i>Eupatorium</i>	0.0082	0.0003 –	NS	0.0068	0.156	
<i>Gonepteryx rhanni</i>	<i>Lythrum</i>	0.0181	0.0003 –	NS	0.0056	0.144	
<i>Lasionnata megera</i>	<i>Calluna</i>	0.0209	<0.0001 –	NS	<0.0001	0.181	
<i>Lasionnata megera</i>	<i>Centaurea</i>	0.0004	<0.0001 –	0.047	<0.0001	0.214	stronger association in Period 1
<i>Lasionnata megera</i>	<i>Eupatorium</i>	0.0153	<0.0001 –	NS	0.0021	0.178	
<i>Lycæna phlaeas</i>	<i>Centaurea</i>	0.0147	NS	NS	<0.0001	0.228	
<i>Lycæna phlaeas</i>	Yellow Asteraceae	<0.0001	NS	NS	<0.0001	0.270	
<i>Mantola jurtina</i>	<i>Centaurea</i>	0.0038	0.0288 +	NS	<0.0001	0.298	
<i>Mantola jurtina</i>	<i>Cirsium/Carduus</i>	0.0002	0.0023 +	NS	<0.0001	0.304	
<i>Ochlodes sylvanus</i>	<i>Erica</i>	0.0008	NS	NS	<0.0001	0.209	
<i>Pararge aegeria</i>	<i>Rubus</i>	0.0016	<0.0001 +	NS	<0.0001	0.211	
<i>Pieris brassicae</i>	<i>Buddleja</i>	<0.0001	NS	NS	NS	0.124	
<i>Pieris brassicae</i>	<i>Centaurea</i>	0.0053	NS	NS	<0.0001	0.063	
<i>Pieris brassicae</i>	<i>Erica</i>	0.0304	NS	NS	<0.0001	0.069	
<i>Pieris napi</i>	Apiaceae	0.0002	NS	NS	<0.0001	0.137	
<i>Pieris napi</i>	Brassicaceae	<0.0001	NS	NS	0.0001	0.167	
<i>Pieris napi</i>	<i>Cirsium/Carduus</i>	0.0002	NS	NS	<0.0001	0.138	
<i>Pieris napi</i>	<i>Erica</i>	0.0082	NS	NS	<0.0001	0.120	
<i>Pieris napi</i>	<i>Eupatorium</i>	<0.0001	NS	NS	<0.0001	0.172	

To be continued

Butterflies	Flower group	Flower abundance	Period	Period x Flower abundance	Landscape type	R ²	Comments on interactions
<i>Pieris napi</i>	<i>Lythrum</i>	0.0002	NS	NS	<0.0001	0.141	
<i>Pieris napi</i>	Papilionaceae	0.0103	NS	NS	<0.0001	0.118	
<i>Pieris napi</i>	<i>Rubus</i>	0.0297	NS	NS	<0.0001	0.111	
<i>Pieris napi</i>	Total flowers	<0.0001	NS	NS	<0.0001	0.143	
<i>Pieris rapae</i>	Apiaceae	<0.0001	<0.0001 –	NS	<0.0001	0.298	
<i>Pieris rapae</i>	Brassicaceae	<0.0001	<0.0001 –	NS	<0.0001	0.276	
<i>Pieris rapae</i>	<i>Buddleja</i>	0.0057	<0.0001 –	NS	<0.0001	0.259	
<i>Pieris rapae</i>	<i>Centaurea</i>	0.0215	<0.0001 –	NS	<0.0001	0.249	
<i>Pieris rapae</i>	<i>Cirsium/Carduus</i>	0.0460	<0.0001 –	NS	<0.0001	0.234	
<i>Pieris rapae</i>	<i>Eupatorium</i>	0.0008	<0.0001 –	NS	<0.0001	0.253	
<i>Pieris rapae</i>	<i>Lythrum</i>	0.0082	<0.0001 –	NS	<0.0001	0.243	
<i>Pieris rapae</i>	Papilionaceae	0.0055	<0.0001 –	NS	<0.0001	0.246	
<i>Pieris rapae</i>	Total flowers	<0.0001	<0.0001 –	0.0216	<0.0001	0.285	stronger association in Period 2
<i>Pieris rapae</i>	Yellow Asteraceae	0.0013	<0.0001 –	NS	<0.0001	0.267	
<i>Plebejus argus</i>	<i>Erica</i>	<0.0001	NS	0.0001	NS	0.544	strong association in both periods, but stronger in Period 2
<i>Polygonia c-album</i>	<i>Buddleja</i>	<0.0001	NS	NS	NS	0.092	
<i>Polygonia c-album</i>	<i>Cirsium/Carduus</i>	0.0244	NS	NS	NS	0.054	
<i>Polygonia c-album</i>	<i>Eupatorium</i>	0.0154	NS	NS	0.0484	0.054	
<i>Polyommatus icarus</i>	<i>Centaurea</i>	0.0072	0.0285 –	NS	<0.0001	0.214	
<i>Polyommatus icarus</i>	Other Asteraceae	0.0085	0.0268 –	NS	<0.0001	0.215	
<i>Polyommatus icarus</i>	Papilionaceae	<0.0001	0.0312 –	NS	<0.0001	0.341	
<i>Polyommatus icarus</i>	Total flowers	0.0002	NS	NS	<0.0001	0.215	
<i>Polyommatus icarus</i>	Yellow Asteraceae	<0.0001	NS	NS	<0.0001	0.232	
<i>Pyronia tithonus</i>	Other Asteraceae	0.0018	NS	NS	<0.0001	0.282	
<i>Pyronia tithonus</i>	Total flowers	0.0064	NS	NS	<0.0001	0.254	

To be continued

Butterflies	Flower group	Flower abundance	Period	Period x Flower abundance	Landscape type	R ²	Comments on interactions
<i>Thymelicus lineola</i>	<i>Centaurea</i>	0.0217	<0.0001 –	NS	<0.0001	0.172	
<i>Thymelicus lineola</i>	<i>Cirsium/Carduus</i>	<0.0001	<0.0001 –	NS	0.0002	0.193	
<i>Thymelicus lineola</i>	Other Asteraceae	<0.0001	<0.0001 –	NS	<0.0001	0.216	
<i>Thymelicus lineola</i>	Papilionaceae	0.0157	<0.0001 –	NS	0.0006	0.164	
<i>Vanessa atalanta</i>	<i>Buddleja</i>	<0.0001	0.0495 –	<0.0001	0.0036	0.211	strong association in both periods, but stronger in Period 2
<i>Vanessa atalanta</i>	<i>Eupatorium</i>	<0.0001	0.0219 –	NS	0.0255	0.173	
<i>Vanessa atalanta</i>	Total flowers	0.0096	NS	0.0136	0.0423	0.093	stronger association in Period 2
<i>Vanessa cardui</i>	<i>Buddleja</i>	0.0009	NS	NS	NS	0.071	
<i>Vanessa cardui</i>	<i>Centaurea</i>	0.0043	NS	NS	NS	0.054	
<i>Vanessa cardui</i>	<i>Eupatorium</i>	0.0277	NS	NS	NS	0.044	