A revised Red List of British butterflies

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Abstract

1. Regular reassessment of extinction risk is critical to prioritise conservation action during the current period of rapid, anthropogenic biodiversity change.
2. Butterflies are a flagship group for insect monitoring and conservation, as they are highly visible, well studied and exhibit rapid responses to environmental change. Here, we use systematic population monitoring data from the UK Butterfly Monitoring Scheme and citizen-science derived occurrence records to provide an updated assessment of extinction risk in Great Britain (GB) by applying current International Union for Conservation of Nature (IUCN) criteria to 62 butterfly species.
3. The resulting regional Red List categorises four species as Regionally Extinct, 24 (41% of the remaining, extant species) as threatened (8 Endangered and 16 Vulnerable), 5 (9%) as Near Threatened and 29 (50%) as Least Concern. Recent reduction in population size (Criterion A) based on smoothed, long-term time series of abundance and occurrence data, was responsible for most of the threatened or Near Threatened categorisations.
4. While the status of some species improved, likely due to conservation efforts, the revised Red List demonstrates an ongoing deterioration in the status of GB butterflies, with a 26% increase in threatened species since the previous assessment.
5. A greater proportion of butterflies was classed as threatened than for most other GB taxa. While this may stem from greater data availability for butterflies than most other groups (thus allowing tests of extinction risk against more criteria), it highlights the need to reinvigorate conservation efforts for these charismatic insects.

Keywords
abundance trend, extinction risk, IUCN, Lepidoptera, occupancy, threatened species

INTRODUCTION

The extinction (or regional extirpation) risk of many insect populations is changing rapidly, as is our ability to measure it. There is now substantial evidence for the rapid decline of insects, at least in anthropogenic landscapes in western Europe and North America (Dirzo et al., 2014; Pilotto et al., 2020; Wagner, 2020; Warren et al., 2021; Wepprich et al., 2019). The suspected drivers of decline, such as industrial agriculture, climate change, urbanisation and pollution (Forister et al., 2021; Nessel et al., 2021; Piano et al., 2020; Raven & Wagner, 2021), are increasing in extent, intensity and impact (Díaz et al., 2019). In marked contrast are local increases driven by environmental restoration (e.g. aquatic insects; Outhwaite et al., 2020) and biodiversity conservation measures (e.g. Schultz & Crone, 2015), and range expansion in response to climate change (e.g. Poniatowski et al., 2020).

In parallel with these population changes, the recent development of statistical approaches that enable the analysis of opportunistic sightings (Altwegg & Nichols, 2019; Bird et al., 2014; Dennis et al., 2017; Isaac et al., 2014; Pardo et al., 2013) has allowed the production of temporal trends in occupancy for many insect taxa for the first time (Jönsson et al., 2021; Outhwaite et al., 2019; Powney et al., 2019; Soroye et al., 2020; Termaat et al., 2019). Taken together
with existing long-term, standardised, insect monitoring schemes (Bell et al., 2020; Hällfors et al., 2021; Thomaat et al., 2015; Warren et al., 2021), which are also increasing in taxonomic scope and geographical extent, there have never been better data available to assess extinction risk.

In this rapidly changing world, the International Union for Conservation of Nature (IUCN) Red List process provides an objective, quantitative and consistent means to assess the extinction risk of species (Mace et al., 2008). In order to remain current and relevant, IUCN recommend that species are reassessed at least every 10 years, and preferably every 5 years, resources permitting (IUCN, 2016). The last Red List assessment of butterflies in Great Britain (GB) was undertaken in 2006/2007, although it was not published for several years thereafter (Fox et al., 2011). A revision of this Red List is thus long overdue.

Thanks to a long tradition of citizen science (Pocock et al., 2015), GB biodiversity is probably the most thoroughly monitored in the world (Burns et al., 2018), with information on both the abundance and distribution of butterflies spanning many decades. Standardised monitoring of butterfly abundance has been carried out since 1976 under the UK Butterfly Monitoring Scheme (UKBMS), using a combination of fixed-route transects (sampled weekly from April to September) and various reduced-effort methodologies focussed on individual species or randomly selected 1 km × 1 km grid squares. Counts can be combined across weeks and sites to produce annual indices of relative abundance for each butterfly species. In 2019, butterfly numbers were monitored at just over 3000 sites, sufficient coverage to generate long-term abundance trends for all but one of the species that breed regularly in the United Kingdom (Brereton et al., 2020). Concurrently, the Butterflies for the New Millennium (BNM) distribution recording scheme collates butterfly occurrence records across the United Kingdom. Records are opportunistic and sampling is neither standardised nor systematic, but spatial and temporal coverage are high and occupancy models can be used to estimate species’ distribution change over time while accounting for recording effort bias (Fox et al., 2015).

Analyses of these data have revealed rapid status changes over the past 5 decades (Asher et al., 2011; Brereton et al., 2011; Mason et al., 2015; Warren et al., 2001). The most recent published assessment showed that 59% of UK butterfly species had a significant change in abundance and 96% a significant change in distribution over the period 1976–2014 (Fox et al., 2015). In general, habitat specialist butterflies have decreased in abundance and distribution, largely as a result of land-use change, while many generalist species have increased, mainly in response to climate change (Warren et al., 2001).

Reflecting the deteriorating status of many GB butterfly populations, the previous Red List assessment classified 19 species (33% of extant species) as threatened (Critically Endangered, Endangered or Vulnerable) and 11 (19%) as Near Threatened, with an additional four as Regionally Extinct (Fox et al., 2011). Only 28 species (48% extant species) were categorised as Least Concern. On this basis, GB ranks seventh worst out of 33 European countries in terms of mean Red List value for butterflies, a measure of the average level of threat faced by the butterfly fauna of each nation (Maes et al., 2019).

Given ongoing pressure on GB butterflies from anthropogenic environmental drivers (Warren et al., 2021), as well as population stabilisation and recovery due to conservation efforts (Ellis et al., 2011; Lawson et al., 2014; Thomas et al., 2009), the extinction risk of each species is likely to have changed substantially since the last Red List assessment. While Red List classifications differ explicitly from conservation priorities (Cullen et al., 2016; Mace et al., 2008), the quantification of species’ extinction risk through the IUCN criteria provides vital information for conservation practitioners and often catalyses focussed action on threatened taxa (Azam et al., 2016; Betts et al., 2020; Rodrigues et al., 2006). As an up-to-date Red List is an important component of the toolkit available to individuals, organisations and governmental bodies trying to conserve butterflies; here, we present a revised Red List of GB Butterflies prepared using IUCN criteria (IUCN, 2012a) and guidelines (IUCN, 2012b; IUCN Standards and Petitions Subcommittee, 2019).

METHODS

Species selection

We assessed the extinction risk of all native butterfly species with confirmed, long-term and regularly breeding wild populations in GB during all or part of the period 1800–2019. This included common migrant species that breed in GB every year (e.g. Clouded Yellow Colias croceus, Painted Lady Vanessa cardui) and resident species that have become extinct in GB since 1800 (e.g. Black-veined White Aporia crataegi, Mazarine Blue Cyaniris semiargus). The faunistic inventory of GB butterflies was completed in the 1800s (Lobo et al., 2012a) and the first well-documented extinction (of Large Copper Lycaena dispar) also took place that century, so 1800 was deemed an appropriate starting point. At the time the assessment was made, geographically complete species distribution data were available to the end of 2019, therefore that year formed the end point.

Species were excluded from our assessment if evidence for their historical native resident status was lacking or equivocal (e.g. Apollo Parnassius apollo, Arran Brown Erebia ligea). In accordance with IUCN guidance for regional Red Lists (IUCN, 2012b), species that occur in GB only sporadically were classed as vagrants and excluded from the assessment (e.g. Monarch Danaus plexippus, Camberwell Beauty Nymphalis antiopa), even if they are known to have bred occasionally under favourable conditions without establishing lasting populations (e.g. Queen of Spain Issoria lathonia, Long-tailed Blue LamproLES boeticus). Long-tailed Blue is an interesting case, as the frequency of its occurrence and breeding in GB appear to be increasing rapidly following major influxes in 2013 and 2015 (Blencowe & Hulme, 2017; Fox, 2014), perhaps as part of a broader increase in migratory Lepidoptera in response to climate change (Sparks et al., 2005). While it does not currently meet the bar for Red List assessment, it may do when subsequent reviews are undertaken. Large Tortoiseshell Nymphalis polychloros was included in the assessment as it had been resident in GB during much of the period 1800–2019, prior to extinction, but the recent observations of immature stages of this species at Portland, Dorset in 2020 and 2021 (Eeles, 2021) were not considered.
as these data fell outside the selected date range. In total, 62 species were eligible for assessment.

All taxa were assessed at species level. However, a distinction was made between the resident GB populations of Swallowtail Papilio machaon britannicus and vagrant P. machaon gorganus individuals originating from continental Europe. Records (including of rare breeding events) of these vagrants were excluded from the assessment. Taxonomy follows Agassiz (continental Europe). Records (including of rare breeding events) of these vagrants were excluded from the assessment. Taxonomy follows Agassiz et al. (2013) as amended (Agassiz et al., 2019, 2020).

Species data and trend estimation

All analyses were undertaken using R (R Core Team, 2021). Count data gathered by the UKBMS were used to estimate abundance trends for GB butterflies. The UKBMS combines counts from various standardised methods at many sites into annual collated indices for each species using the generalised abundance index method (Dennis et al., 2016) with an additional weighting towards sites where a greater proportion of the species’ flight period has been monitored in that year (Brereton et al., 2018). We calculated UKBMS annual collated indices (on the log10 scale) for GB for each species. Time series of GB collated indices were available for 57 species. The start years of these series varied, with the majority (63%) commencing in 1976, the first year of the UKBMS, and the most recent starting in 2003 (Chequered Skipper Carborocephalus palaemon). Generalised additive models (GAM; Fewster et al., 2000, using the mgcv package, Wood, 2011) were used to fit a smooth spline to the time series for each species, with the level of smoothing equivalent to one knot for each 5 years of the series. This level of smoothing seemed appropriate given the high inter-annual variability of butterfly abundance indices, while still discriminating major features of population change over time. Finally, abundance trends for each species were calculated by fitting a linear regression to the smoothed annual values produced by the spline over the required time period for IUCN criteria. Note that these trends differ in two ways from those published annually by the UKBMS: first, our trends are for GB only and exclude data from Northern Ireland, the Isle of Man and the Channel Islands, which are included in the UKBMS trends; and second, our trends are estimated from smoothed annual collated indices and UKBMS trends are not.

Occurrence records of butterflies in GB were extracted from the BNM database for the period 1970–2019 and used to calculate values of extent of occurrence (EOO), area of occupancy (AOO) and distribution trends over time for each species. This extract comprised 15.4 million species occurrence records. The current EOO of each species was derived by fitting a minimum convex polygon (using the mcp function in the adehabitatHR package; Calenge, 2006) to the 2010–2019 records of that species and then calculating the GB land area (km²) enclosed by the polygon (i.e. excluding areas of sea that cannot possibly provide breeding habitat for butterflies). Species’ AOO was calculated by assigning GB occurrence records for 2010–2019 to unique 2 km × 2 km grid cells (as recommended by IUCN), determining the number of unique cells with records of each species and converting this to area in km². For Glanville Fritillary (Melitaea cinxia), EOO and AOO (as well as distribution trends) were calculated only from records of native resident populations on the Isle of Wight and adjacent mainland (Hampshire) coast, thus excluding clandestine releases of this rare species that have occurred in other parts of southern GB.

Butterfly distribution trends for 57 species were estimated from the BNM data using an occupancy modelling approach (Dennis et al., 2017) to account for detection biases inherent in non-standardised biological recording (Isaac & Pocock, 2015). For each species in each year (1970–2019), occupancy probability was estimated for each 1 km × 1 km grid square and these probabilities were averaged to create an annual occupancy index for the species (following the approach of Dennis et al., 2019). A smoothing spline was then fitted to the annual occupancy indices using the same technique and same level of smoothing as for species’ abundance trends, although the GAMs were applied to the logits of the occupancy indices, before applying a back-transformation to retain the (0,1) probability scale for the smoothed indices. Finally, distribution trends were estimated using logistic regression (to account for the probability scale) through the annual values generated by the smoothing model for the required period.

Application of IUCN criteria

The regional Red List assessment of GB butterflies used IUCN criteria (IUCN, 2012a) and followed IUCN guidelines (IUCN, 2012b; IUCN Standards and Petitions Subcommittee, 2019). Where data permitted, each species was assessed against each of the five IUCN criteria. Criterion C could not be applied to any species as estimates of actual population size do not exist for any GB butterflies – the UKBMS counts and abundance trends that are generated from them are measures of relative not absolute abundance. In addition, we could not apply Criterion E to any species in the assessment, as we were unable to locate any recent quantitative evaluations (e.g. using population viability analysis) of extinction probability for any GB butterfly species. However, the data derived from the UKBMS and BNM schemes enabled the application of IUCN criteria A, B and D, with the highest risk category achieved by each species being taken forward into the next step.

Criterion A thresholds relate to the rate of reduction in population size of a species over the last 10 years or three generations, whichever is longer. As all GB butterflies have a life cycle duration ≤2 years, trends over the 10-year time period (2010–2019) were used for all species. The thresholds for Criterion A2 were considered most appropriate as the precise causes of population decline are not fully understood for GB butterfly species and the drivers considered to be important have not ceased. Trends in abundance and distribution (occupancy) were calculated for the last 10 years using the annual estimates for 2010–2019 produced from a smoothed model of the whole time series for each species. Almost all species had 10-year trend estimates for both measures and all extant species had a trend for one or the other. As recommended in IUCN guidance, a decline threshold of ≥20% over the 2010–2019 period was used to identify
Near Threatened species. As an additional precaution, the 10-year smoothed abundance and distribution values for each species were examined to check for any recent severe deterioration that might have the potential to cause a rapid change in extinction risk. In such cases, we projected the decline trend forward in time as permitted under Criterion A4. This was done by plotting a linear regression through the smoothed collated index values of recent years (determined by the timing of the deterioration in past index values) and extrapolating it to generate a new 10-year trend that incorporates both past and future years.

Criterion B uses EOO and AOO measures plus other risk factors to categorise species’ extinction risk. Both these measures were calculated for all extant GB butterflies so both were applied. For any species that met the area thresholds for B1 (EOO) or B2 (AOO), the three subcriteria were considered: severely fragmented, continuing decline and extreme fluctuations. The IUCN guidance in defining each of these subcriteria was followed closely. Evidence of continuing decline was provided by the 10-year abundance and distribution trends used in assessment of Criterion A and we categorised a species as prone to extreme fluctuations if its unsmoothed UKBMS collated index varied by at least one order of magnitude during the full time series. Species that only met one subcriterion were classified as Near Threatened. Maps of the EOO and AOO of each species that qualified as threatened are provided in the Supporting Information S1.

Criterion D2 is relevant only for categorising taxa as Vulnerable (because information to test higher levels of threat requires information on absolute population size which is not available for GB butterflies) and applies to species that occur in a very small number of locations (five or fewer) and/or have a very small AOO and where there is a credible threat that could cause rapid extinction. This was applied to all extant GB butterflies.

**Rescue effect**

The third step in a regional Red List assessment involves the consideration of the potential ameliorating effect on regional extinction risk of immigration from populations outwith the study area – the ‘rescue effect’ (IUCN, 2012b). Where species met thresholds for threatened or Near Threatened status on application of the IUCN criteria (as described in the previous section), we assessed the likelihood of a rescue effect from continental Europe and the island of Ireland. Several factors were considered including species’ dispersal ability and proclivity (using references such as Asher et al., 2001 and Chowdhury et al., 2021), the existence of potential source populations within plausible immigration distance (e.g. from GBIF www.gbif.org, the LepiDiv project https://www.ufz.de/european-butterflies/index.php?en=42605 and LepiNet France http://www.lepinet.fr/lep/), the status and trend of the species in potential source areas (e.g. from van Swaay et al., 2011), and the occurrence of suitable breeding habitat in GB within likely reach of immigrants. Where a rescue effect was predicted, the provisional threat status of the species was downgraded by one category.

**Transfer between categories**

As GB butterflies have previously been assessed against the current IUCN criteria (Fox et al., 2011), specific IUCN rules apply to the transfer of species from existing to new threat categories. Accordingly, species that had increased in threat level were transferred immediately but, in cases where the extinction risk had declined, species were only assigned to a lower threat category when they had failed to meet any thresholds for the previous higher category for at least 5 years. In both cases, the reason for the transfer between categories was specified as ‘genuine’ (e.g. increased rate of decline) or ‘non-genuine’ (e.g. new information altering the status such as the discovery of new populations).

Where our assessment found that species no longer met the previous higher threat category, we calculated the necessary EOO, AOO and 10-year abundance and distribution trend estimates for the period 2005–2014 to assess the status of the species 5 years ago. If a species still qualified for its former, higher Red List category on the basis of these 2005–2014 values, then the previous status (from Fox et al., 2011) was retained in the new assessment irrespective of how

| Red List threat category | Number of species qualifying in revised GB Red List | Number of species qualifying in previous GB Red List (Fox et al., 2011) |
|--------------------------|-----------------------------------------------|-------------------------------------------------|
| Regionally Extinct       | 4                                             | 4                                               |
| Critically Endangered    | 0                                             | 2                                               |
| Endangered               | 8                                             | 8                                               |
| Vulnerable               | 16                                            | 9                                               |
| Near Threatened          | 5                                             | 11                                              |
| Least Concern            | 29                                            | 28                                              |
| Total                    | 62                                            | 62                                              |

**FIGURE 1** The proportion of butterfly species in each IUCN category on the revised GB Red List
much lower the new estimate of extinction risk was. Thus a species classified as Endangered in Fox et al. (2011) that was reassessed as Least Concern in the new 2010–2019 process but which still met any thresholds for Endangered on the basis of 2005–2014 data was retained as Endangered. If a species did not meet the thresholds for the former status when examined for 2005–2014, but did, at that point, qualify for a lower level of threat, then it was afforded that level in the new assessment. For example, a formerly Endangered species reassessed as Least Concern, but which met the criteria for Vulnerable based on 2005–2014 data, was listed as Vulnerable in the new Red List.

**RESULTS**

Four species were listed as Regionally Extinct, all having been absent from GB as resident species for many decades. Of the remaining 58 extant species, 24 species (41%) were classified as threatened (8 as Endangered and 16 as Vulnerable), 5 (9%) as Near Threatened and 29 (50%) as Least Concern (Table 1, Figure 1). Species classified as Regionally Extinct, threatened and Near Threatened are listed in Table 2 and the full Red List assessment is documented in Table S1 (Supporting Information). In total, 23 species were listed as threatened or Near Threatened on the basis of Criterion A2 alone, five under

| Species                  | GB Red List category | European Red List category | EU Red List category |
|--------------------------|----------------------|----------------------------|---------------------|
| Black-veined White       | Regionally Extinct   | Least Concern              | Least Concern       |
| Large Tortoiseshell      | Regionally Extinct   | Least Concern              | Vulnerable          |
| Large Copper             | Regionally Extinct   | Least Concern              | Least Concern       |
| Mazarine Blue            | Regionally Extinct   | Least Concern              | Least Concern       |
| Wood White               | Endangered           | Least Concern              | Least Concern       |
| Wall                     | Endangered           | Least Concern              | Least Concern       |
| Large Heath              | Endangered           | Vulnerable                 | Near Threatened     |
| Grayling                 | Endangered           | Least Concern              | Least Concern       |
| High Brown Fritillary    | Endangered           | Least Concern              | Least Concern       |
| Glanville Fritillary     | Endangered           | Least Concern              | Least Concern       |
| Heath Fritillary         | Endangered           | Least Concern              | Least Concern       |
| Black Hairstreak         | Endangered           | Least Concern              | Least Concern       |
| Swallowtail              | Vulnerable           | Least Concern              | Least Concern       |
| Grizzled Skipper         | Vulnerable           | Least Concern              | Least Concern       |
| Silver-spotted Skipper   | Vulnerable           | Least Concern              | Least Concern       |
| Small Heath              | Vulnerable           | Least Concern              | Least Concern       |
| Scotch Argus             | Vulnerable           | Least Concern              | Least Concern       |
| Pearl-bordered Fritillary| Vulnerable           | Least Concern              | Least Concern       |
| Small Pearl-bordered Fritillary | Vulnerable | Least Concern              | Least Concern       |
| White Admiral            | Vulnerable           | Least Concern              | Least Concern       |
| Marsh Fritillary         | Vulnerable           | Least Concern              | Least Concern       |
| Duke of Burgundy         | Vulnerable           | Least Concern              | Least Concern       |
| Brown Hairstreak         | Vulnerable           | Least Concern              | Least Concern       |
| White-letter Hairstreak  | Vulnerable           | Least Concern              | Least Concern       |
| Silver-studded Blue      | Vulnerable           | Least Concern              | Least Concern       |
| Northern Brown Argus     | Vulnerable           | Least Concern              | Least Concern       |
| Adonis Blue              | Vulnerable           | Least Concern              | Least Concern       |
| Chalk Hill Blue          | Vulnerable           | Least Concern              | Least Concern       |
| Lulworth Skipper         | Near Threatened      | Near Threatened            | Near Threatened     |
| Mountain Ringlet         | Near Threatened      | Least Concern              | Least Concern       |
| Dark Green Fritillary    | Near Threatened      | Least Concern              | Least Concern       |
| Small Blue               | Near Threatened      | Least Concern              | Least Concern       |
| Large Blue               | Near Threatened      | Endangered                 | Endangered          |
Criterion B1 and/or B2 alone, and one (High Brown Fritillary Fabriciana adippe) under both A2 and B2. Criterion D2 did not contribute to the final listing for any species – indeed, no GB butterfly species met the threat threshold under this criterion. In only one case was the provisional grading adjusted because of a realistic rescue effect – Small Tortoiseshell (Aglais urticae) was downlisted from Near Threatened to Least Concern.

In the assessment of population decline under A2, only one species, Meadow Brown (Maniola jurtina), showed a major increase in rate of decline within the last 10 years (2010–2019). The distribution metric derived from smoothed occupancy model estimates showed a substantial drop in the last 3 years of the period, such that the linear regression through the values of all 10 years might risk underestimating the current rate of decline. To ensure the extinction risk of this species was not underestimated, we used a linear regression fitted to just the last 7 years of the smoothed time series (2013–2019), which capture a strong reduction from the last high point (in 2013), and projected forward 3 years to create a new estimated 10-year trend. This showed a projected decrease of 28% (2013–2022), which would see the species qualify as Near Threatened. However, numerous recent and historical sources document long-distance dispersal of Meadow Brown (Chowdhury et al., 2021) and there are many donor populations in continental Europe (where the species is assessed as Least Concern) that are sufficiently close to Britain and so there is clear potential for a rescue effect. As a result, even if the projected distribution trend was used instead of the measured trend, the species would be downlisted and its regional assessment would remain as Least Concern.

## Differences from previous Red List

The same 62 species of GB butterflies were assessed here and in the previous Red List (Fox et al., 2011). The same four species were listed as Regionally Extinct in both assessments, but the number of species assessed as threatened (24) is 26% higher now than in the earlier one (19). Far fewer species are now listed as Near Threatened (5 species compared with 11 previously), leaving the number of species categorised as Least Concern virtually unchanged (Table 1).

In total, 19 species changed categories. Sixteen resulted from ‘genuine’ status change caused by recent increases or decreases in range (AOO) or abundance/distribution trends, while the other three were due to ‘non-genuine’ change caused by improved survey or monitoring data. Five species were retained in a higher Red List category than their provisional assessment indicated because they still met thresholds for higher extinction risk 5 years previously.

Of the 19 species that transferred between categories, the extinction risk of 11 was assessed as higher than previously and that of eight as lower. Most changes were up or down by a single category, but some larger movements occurred. For example, Chequered Skipper moved from Endangered to Least Concern, as a result of targeted survey work led by Butterfly Conservation that has revealed many previously unrecorded colonies of the species, almost doubling its AOO in GB from 424 km² (1995–2004) to 832 km² (2010–2019).

In contrast, Wall (Lasionomata megera) has moved from Near Threatened to Endangered as a result of an increased rate of decline in its distribution. As mentioned in the previous section, several additional butterflies would have been downlisted further in the new assessment but for the requirement for species to have not qualified at higher levels for at least 5 years before being transferred to a lower Red List category.

## DISCUSSION

Our revised regional Red List of GB butterflies categorises four species as Regionally Extinct, 24 species as threatened and five as Near Threatened. This represents a substantial increase in the number of threatened species compared with the previous Red List (19 species listed as threatened) and our results also show that extinction risk is increasing for more species than decreasing. The revised Red List thus clearly demonstrates that the deterioration in the status of GB butterflies continues apace.

Many species previously listed as threatened have retained their places on the revised Red List, with Large Heath (Coenonympha tullia) and Grayling (Hipparchia semele) being uplisted from Vulnerable to Endangered. Seven species have moved from Near Threatened to threatened: Swallowtail, Silver-spotted Skipper (Hesperia comma), Small Heath (Coenonympha pamphilus), Small Pearl-bordered Fritillary (Boloria selene), Adonis Blue (Polyommatus bellargus) and Chalk Hill Blue (P. coridon), which have all been uplisted to Vulnerable, plus Wall, which has moved to Endangered. In addition, one species, Scotch Argus (Erebia aethiops), has moved from Least Concern to Vulnerable, while a second, Dark Green Fritillary (Speyeria aglaja), has been uplisted from Least Concern to Near Threatened.

The 29 species listed as threatened or Near Threatened in the revised Red List are taxonomically and ecologically diverse, occupying a wide range of different biotopes. However, 86% are habitat specialists (as defined by Asher et al., 2001), the exceptions being Wall, Small Heath, Scotch Argus and White-letter Hairstreak (Satyrium w-album). The dominance of the Red List by habitat specialist species is not surprising as previous analyses of UKBMS and BNM data have shown habitat specialists faring worse than generalists (Warren et al., 2001). For example, multi-species population indicators using UKBMS data show that the habitat specialist butterfly index has decreased by 61% (1976–2020), while that for generalist butterflies (‘wider countryside species’) decreased by 22% (Defra, 2021). This pattern of disproportionate decreases among ecologically specialised species has been found widely elsewhere for butterflies (Delpo et al., 2019; Eskildsen et al., 2015; Habel, Trusch, et al., 2019; Melero et al., 2016; Öckinger et al., 2010; van Swaay et al., 2006) and other taxa (Clavel et al., 2011; MacLean & Beissinger, 2017; Platts et al., 2019).

Declines of habitat specialist butterflies are thought to have been driven by land-use change, including both the destruction of semi-natural habitats and major changes in management intensity (Bubová et al., 2015; Schmitt & Rákosy, 2007; Thomas, 2016; Warren et al., 2001). In highly modified landscapes, in GB and other countries,
agricultural changes during the 20th century have been particularly harmful (Habel, Ulrich, et al., 2019; van Swaay et al., 2006; Warren, 1994; Warren et al., 2021), as has the cessation of traditional woodland management (e.g. coppicing) (Fartmann et al., 2013; Thomas et al., 2015). Elsewhere in Europe, the abandonment of traditionally farmed low-productivity grasslands, with subsequent succession to woodland, has impacted severely on specialist butterflies of open habitats (Bonelli et al., 2018; Herrando et al., 2016; Nilsson et al., 2013; Ubach et al., 2020).

The extinction risk of habitat specialist butterflies is further increased, above and beyond that due to reductions in total population size, by greater isolation between remaining colonies, which limits species’ ability to move through the landscape in response to environmental changes (such as climate change). It is notable, in the context of climate change, that all four GB butterfly species with northerly distributions, reflecting adaptation to cooler and or damper climates, are now listed as threatened (Large Heath, Scotch Argus, Northern Brown Argus Areia artaxerxes) or Near Threatened (Mountain Ringlet Erebia epiphron). Three of these have already shown negative responses to climate change (Franco et al., 2006).

The revised Red List of GB butterflies also offers some encouragement. GB butterflies have been the focus of much conservation effort over several decades, but the direct causal effects of such activity on species’ regional extinction risk and population levels have rarely been established. A notable exception is the case of the Large Blue (Phengaris arion), which became extinct in GB in 1979 and has been the subject of an intensive, ongoing and highly successful reintroduction programme (Thomas et al., 2009). Other conservation programmes have certainly benefitted threatened butterfly species at the landscape scale (Ellis et al., 2011) and are likely to have contributed to the improved status and trends of, for example, High Brown Fritillary (Ellis et al., 2019), formerly classed as Critically Endangered and now downlisted to Endangered, Pearl-bordered Fritillary (Boloria euphrosyne) and Duke of Burgundy (Hamearis lucina) (Ellis et al., 2011), both of which have moved from the Endangered category to Vulnerable. Wood White (Leptidea sinapis) is another threatened butterfly for which much targeted conservation has been undertaken in GB. Its 10-year trends no longer meet the threshold for Endangered, but it has been retained at that level on the revised Red List because the threshold was still exceeded 5 years ago. Ongoing conservation management of this and other priority species will hopefully lead to continued reduction in extinction risk and downlisting when the Red List is further revised.

Butterflies have previously been shown to have suffered larger median distribution declines in GB than birds and vascular plants (Thomas et al., 2004). The proportion of extant butterfly species classified as threatened in the revised Red List, 41%, is substantially higher than that for almost all taxonomic groups that have been assessed in GB. Hayhow et al. (2019) showed that of 8431 species assessed across 11 broad taxonomic groups, 15% of extant species were classed as threatened in GB (e.g. 5% of centipedes and millipedes, 10% non-marine molluscs, 16% spiders, 16% bryophytes and 26% terrestrial mammals). Most insect species that occur in GB are yet to be subject to a regional Red List assessment, but 11% of extant species that have been assessed qualified as threatened (Hayhow et al., 2019). The proportion of threatened butterflies is similar to that of GB bird species (46%, Stanbury et al., 2021), one of the few other groups with long-term data on both abundance and distribution, enabling assessment against most of the IUCN criteria. This greater availability of trend information is demonstrated by the pre-eminence of Criterion A in determining the revised Red List for GB butterflies, in stark contrast to other assessments in Britain and Europe (Maes et al., 2015).

In the wider European context, GB butterflies have evidently fared poorly over recent decades. Only 9% of 434 extant butterfly species assessed at the continental scale were classified as threatened and even fewer (7% of 419 extant species) within the European Union (van Swaay et al., 2010). Birds show a similar pattern, with a much lower proportion (13%) threatened in Europe compared with GB (BirdLife International, 2021), while non-marine molluscs, in contrast, have a much higher level of extinction risk at the European scale (30% of extant species assessed are threatened; Cuttelod et al., 2011). Most of the butterflies identified as threatened in the GB revised list are Least Concern at the European scale (Table 2) and only two (Marsh Fritillary Euphydryas aurinia and Large Blue) are afforded protection under the EU Habitats Directive. Only the Large Blue has a lower extinction risk in GB compared with the continental-scale assessment, a reflection of the success of the ongoing reintroduction project in GB (Thomas et al., 2009). The different timescales of the GB and European assessments make direct comparisons difficult, however. But GB is not alone among European countries in having suffered substantial declines in its butterfly fauna and subsequent relatively high numbers of species categorised as threatened. Indeed, six other countries, running in a broad swathe from GB through the Low Countries and Denmark to central Europe, have even higher mean Red List values for butterflies than GB (Maes et al., 2019). Butterfly declines across these countries are largely attributed to the expansion of intensively managed agricultural and urban land (Eskildsen et al., 2015; Habel, Ulrich, et al., 2019; Maes & Van Dyck, 2001; Van Dyck et al., 2009; van Strien et al., 2019).

Estimating trends for input into Red List assessments is not straightforward (Didham et al., 2020; Fournier et al., 2019), even for taxa such as GB butterflies that have long-running time series data on abundance. Numerous studies have highlighted the unreliability of estimating species abundance trends over short periods (Connors et al., 2014; Cusser et al., 2021; Fox et al., 2019; Keith et al., 2015; Wauchope et al., 2019; White, 2019), especially for taxa with high inter-generational population variability, such as Lepidoptera (Taylor & Taylor, 1977; Williams, 1961). We mitigated for this problem by fitting a flexible, smoothing spline model to the full time series of abundance data available for each species and then estimating the trend over the last 10 years from the modelled values (Akçakaya et al., 2021; IUCN Standards and Petitions Subcommittee, 2019). This approach reduces the influence of boom or bust years on the trend estimate, thus reducing the likelihood of underestimating or exaggerating extinction risk, while still using a current (i.e. last 10 years) assessment of species’ population trajectory.
Among insects, butterflies play iconic and important roles as umbrella species for biodiversity conservation (e.g. New, 1997; Spitzer et al., 2009), flagship species for public engagement (Barua et al., 2012; Lewandowski & Oberhauser, 2017; Preston et al., 2021; Schlegel & Rupf, 2010) and as bioindicators of environmental change (Gerlach et al., 2013; Hill et al., 2021; Parmesan, 2003; Wilson & Fox, 2021). As a consequence, and because of the ongoing impacts of anthropogenic drivers, it is vital to maintain up-to-date assessments of butterfly extinction risk. Such evaluations provide objective and ecologically relevant evidence to support the selection and prioritisation of species for legal protection and conservation action at the national level and to leverage public and political support and funding (Betts et al., 2020; Habel et al., 2020). Many national Red Lists of insect taxa are published in the ‘grey’ literature, making them difficult to locate and compare. Publication in peer-reviewed journals should increase access and wider use, as well as contributing to the ongoing development of best practise in estimating extinction risk and facilitating comparisons between countries (e.g. Maes et al., 2019).

In conclusion, capitalising on the abundant quantitative data on GB butterflies gathered over many decades by citizen scientists, the revised Red List demonstrates the continued increase in extinction risk facing these charismatic insects and the ongoing challenge to conserve them (Warren et al., 2021).

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CONFLICT OF INTEREST
The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT
The processed data that support the findings of this study are openly available in the Supporting Information file and in Zenodo at http://doi.org/10.5281/zenodo.5901336. The UKBMS site index data used to estimate species abundance trends are openly available in the NERC Environmental Information Data Centre at https://doi.org/10.5285/180a1c76-bceb-4264-872b-deddfe67b3de. The raw BNM data used to estimate species occurrence trends are available on request from Butterfly Conservation.

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### Supporting Information

Additional supporting information may be found in the online version of the article at the publisher’s website.

**Figure S1** Supplementary File

**Table S1** Detailed IUCN Red List assessment for GB butterflies

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