



FORUM

The decline of moths in Great Britain: a review of possible causes

RICHARD FOX Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset, UK

Abstract. 1. Population declines among insects are inadequately quantified, yet of vital importance to national and global biodiversity assessments and have significant implications for ecosystem services.

2. Substantial declines in abundance and distribution have been reported recently within a species-rich insect taxon, macro-moths, in Great Britain and other European countries. These declines are of concern because moths are important primary consumers and prey items for a wide range of other taxa, as well as contributing to ecosystem services such as pollination.

3. I summarise these declines and review potential drivers of change. Direct evidence for causes of moth declines is extremely limited, but correlative studies and extrapolation from closely related taxa suggest that habitat degradation (particularly because of agricultural intensification and changing silviculture) and climate change are likely to be major drivers. There is currently little evidence of negative population-level effects on moths caused by chemical or light pollution, non-native species or direct exploitation.

4. I make suggestions for future research with a focus on quantifying impacts of land management practices, light pollution and climate change on moth population dynamics and developing evidence-based measures that can be incorporated into agri-environment schemes and other policy initiatives to help reverse the widespread decline of moths in Great Britain and beyond.

Key words. Biodiversity conservation, climate change, habitat degradation, light pollution, macro-moths, population trends.

Introduction

The Earth is undergoing a period of substantial decreases in biodiversity and mass extinction of species (Pimm *et al.*, 1995; Dirzo & Raven, 2003; Butchart *et al.*, 2010; May, 2010; Mooney, 2010), which threaten ecosystem services and the welfare of the human race (Balmford & Bond, 2005; Millennium Ecosystem Assessment, 2005; Schröter *et al.*, 2005; Biesmeijer *et al.*, 2006; Rockström *et al.*, 2009; UK National Ecosystem Assessment, 2011). However, the decline and extinction rates of insects, which comprise the majority of terrestrial biodiversity, are inadequately quantified and poorly understood (McKinney, 1999; Dunn, 2005; Thomas, 2005). A contributory factor to this knowledge gap is the highly variable population dynamics of many insect species (Wilson & Roy, 2009). Long time series of data are required to identify significant directional trends amid

the statistical ‘noise’ of population cycles and short-term responses to stochastic environmental events (Conrad *et al.*, 2004).

Until recently, large spatial-scale assessments of long-term insect trends were restricted to a few charismatic, well-studied, but species-poor, taxa such as butterflies and bumblebees, in some developed nations, particularly in western Europe (Maes & Van Dyck, 2001; Warren *et al.*, 2001; Fox *et al.*, 2006a; Fitzpatrick *et al.*, 2007; Kosior *et al.*, 2007; Goulson *et al.*, 2008; van Swaay *et al.*, 2008; Van Dyck *et al.*, 2009; Cameron *et al.*, 2011). Thomas *et al.* (2004b) showed that butterfly declines exceeded comparable changes among birds and vascular plants in Great Britain. These examples provide insight into insect diversity trends, but concerns remain over how representative they are across insect taxa (e.g. Hambler & Speight, 2004; but see Thomas & Clarke, 2004).

Recently, studies of moths have generated the first evidence of national-scale declines in a species-rich insect taxon (Conrad *et al.*, 2006; Mattila *et al.*, 2006, 2008; Groenendijk & Ellis, 2011). Such studies are important as they corroborate the use of taxa such as butterflies as indicators of wider insect biodiversity

Correspondence: Richard Fox, Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP, UK.
E-mail: rfox@butterfly-conservation.org

trends, but also because the greater diversity of moths may facilitate an improved understanding of the drivers of change and the impacts that insect declines will have on other organisms, communities and ecosystem functioning.

This article reviews current knowledge about moth declines and the potential drivers of change in Great Britain (and elsewhere in western Europe). The five main causes of biodiversity loss and changes in ecosystem services in the UK (UK National Ecosystem Assessment, 2011) are examined in relation to moths, as well as an additional potential driver, light pollution. This review is topical at a time of resurgent interest in ecological research on moths, stimulated, in part, by the discovery of the widespread and substantial declines in this taxon (Sutherland *et al.*, 2006).

Moth declines in Britain and beyond

Although national-level extinctions (Parsons, 2003) and decreased distribution and abundance of selected diurnal macro-moths had already been documented (Groenendijk & van der Meulen, 2004), the analyses of the Rothamsted Insect Survey (RIS) monitoring data yielded the first quantitative understanding of the severity of population decline among moths.

The RIS, a nationwide network monitoring UK moth populations, has been operated by Rothamsted Research since 1968 and provides one of the longest-running and most spatially extensive data sets of a species-rich insect taxon anywhere in the world (Conrad *et al.*, 2007; Woiwod & Gould, 2008). Monitoring at one RIS site (Rothamsted, UK) commenced in 1933 and has demonstrated a substantial decrease in abundance and diversity of moths during the 1950s (Woiwod & Gould, 2008). Furthermore, detailed national studies of an individual species, *Arctia caja* garden tiger, also demonstrated severe population and site occupancy declines for this once-common species and paved the way for a more comprehensive assessment (Conrad *et al.*, 2002). Analysis of a 35-year data set (1968–2002) for 337 macro-moth species (those for which adequate data were available) revealed significant decreases (Conrad *et al.*, 2004). The total abundance of individual macro-moths caught by the RIS network decreased in the whole of Great Britain (31% decrease over 35 years) and in southern Britain (44% decrease) (Conrad *et al.*, 2006). The total abundance of moths did not decrease in northern Britain, a finding corroborated by a smaller study of RIS data from a single site by Salama *et al.* (2007) and also by butterfly trends (Bretton *et al.*, 2011).

Conrad *et al.* (2006) also found that 66% of the 337 species studied had negative population trends and that 21% of the species had decline rates $> 30\% 10 \text{ year}^{-1}$ (equivalent to the IUCN threshold levels for Red List threat categories). That these 337 species are considered widespread and generally common in Britain (Skinner, 2009; Waring *et al.*, 2009) underscored the significance of Conrad *et al.*'s findings for biodiversity conservation (Fox *et al.*, 2006b). A similar proportion of species had undergone substantial population decreases in northern Britain and southern Britain, but many more species had increased in

the north and this appears to account for the lack of a significant trend in overall moth abundance there compared to the south (Fox *et al.*, 2006b).

Parallel decreases in the abundance or distribution of macro-moths have now been reported from other European countries. Groenendijk and Ellis (2011) found a pattern of change among 733 macro-moth species in the Netherlands, which was strikingly similar to the British findings: 71% of Dutch species decreased in abundance and the total abundance of moths decreased by one-third (1980–2009). Both studies also highlighted a minority of species that had markedly increased in abundance.

Utilising long-term distribution records, Mattila *et al.* (2006, 2008) showed significant overall decreases in the distribution of macro-moths in the families Geometridae and Noctuidae (590 species in total) in Finland and a study of Lepidoptera at a nature reserve in southern Sweden revealed high rates of local extinction over a 50-year period (27% of 597 study species were deemed to have become extinct vs. 4% that had colonised the area) (Franzén & Johannesson, 2007). Preliminary analysis of the new National Moth Recording Scheme data set in the UK also indicated severe distribution declines among some macro-moth species (Fox *et al.*, 2011b).

Several of these studies examined ecological traits and life history attributes in relation to rates of distribution or population change, but the results varied considerably. For example, in Great Britain and the Netherlands, species overwintering in the adult life-cycle stage had positive population trends over time (Conrad *et al.*, 2004; Groenendijk & Ellis, 2011), whereas Mattila *et al.* (2006) found adult overwintering to be a significant predictor of increased extinction risk and Franzén and Johannesson (2007) found no effects of overwintering strategy on species persistence. However, range size and larval specificity correlated consistently with rates of decline or extinction risk, mirroring studies on butterflies (Warren *et al.*, 2001; Koh *et al.*, 2004; Nilsson *et al.*, 2008). Rarer species were associated with greater losses or increased likelihood of extinction (Franzén & Johannesson, 2007; Groenendijk & Ellis, 2011) and monophagous species were more likely to have declined or become extinct than less-specialised species (Franzén & Johannesson, 2007; Mattila *et al.*, 2008).

Taken together, these studies provide overwhelming evidence of moth declines on a large geographical scale and mirror previous studies of less species-rich taxonomic groups such as butterflies. Such losses are likely to have substantial impacts at higher and lower trophic levels, because of the importance of moths as herbivores, pollinators and prey items (e.g. Proctor *et al.*, 1996; Vaughan, 1997; Wilson *et al.*, 1999; Wickramasinghe *et al.*, 2004; Devoto *et al.*, 2011) and may affect the delivery of some ecosystem services. Yet, the causes of pervasive moth declines are poorly understood.

Drivers of change in moth populations

Habitat loss, degradation and fragmentation

The destruction and modification of habitats by human activity is regarded as the foremost cause of global biodiver-

sity loss (Diamond *et al.*, 1989; Brooks *et al.*, 2002; Dirzo & Raven, 2003; Fahrig, 2003). Habitat loss (including deterioration in quality and the isolation effects of fragmentation) has also been identified as the principle driver of butterfly declines in Europe (e.g. Asher *et al.*, 2001; Maes & Van Dyck, 2001; Warren *et al.*, 2001; Wenzel *et al.*, 2006; Bulman *et al.*, 2007; Hanski & Pöyry, 2007; Van Dyck *et al.*, 2009; Öckinger *et al.*, 2010). Consequently, it seems probable that habitat loss will have influenced moth abundance and distributions in Britain (Fox *et al.*, 2006b), although habitat degradation patterns vary geographically and, therefore, impacts on species are expected to differ between areas. It is possible that the better performance, on average, of moth populations in northern Britain stems from lower levels of habitat degradation relative to the southern half of Britain, although a climatic explanation, or a combination of both, is also plausible (see section Climate change).

There is little direct evidence for habitat loss, degradation or fragmentation effects on moth populations in Britain (or elsewhere). However, as for butterflies, there is considerable circumstantial evidence that the widespread destruction of semi-natural habitats has had a severe impact on specialist moths, and it has been implicated in the extinction of species, including *Laelia coenosa* reed tussock and *Lymantria dispar* gypsy moth because of wetland drainage, and *Emmelia trabealis* spotted sulphur as a result of afforestation and agricultural intensification (Majerus, 2002). Habitat changes may also have played a role in the declines of species such as *Pyrausta sanguinalis* in sand dunes, *Aspitates gilvaria* straw belle and *Siona lineata* black-veined moth on unimproved grassland, *Heliothis maritima* shoulder-striped clover and *Coscinia cribraria* speckled footman on lowland heath and *Pareulype berberata* barberry carpet in hedgerows (Fox *et al.*, 2010).

Fragmentation effects have been detected in few empirical studies of moths (Öckinger *et al.*, 2010), but generally biodiversity impacts from fragmentation *per se* tend to be relatively small compared to the effects of habitat loss and habitat quality (Thomas *et al.*, 2001; Fahrig, 2003; Hodgson *et al.*, 2009). In addition, theory predicts that mobile species are less likely to experience negative effects of isolation. Mobility is poorly understood in most moth species (apart from long-distance migrants, e.g. Chapman *et al.*, 2011), but recent evidence suggests that many species are relatively mobile (Franzén & Nilsson, 2007; Merckx *et al.*, 2009a, 2010a,b; Betzholtz & Franzén, 2011; E.M. Slade, T. Merckx, T. Riutta, D. Redhead, D. Bebbler, P. Rioridan & D.W. Macdonald, unpubl. data; but see Nieminen, 1996; Nieminen *et al.*, 1999). Thus, while fragmentation might be expected to be important for some specialised species with low to intermediate mobility (Thomas, 2000), it is unlikely to be a principle driver of the declines of many widespread moths in Britain and elsewhere.

In contrast, it seems highly plausible that the widespread destruction of semi-natural habitats that took place across Britain during the twentieth century had substantial impacts on moths. These were rarely documented through site-based population monitoring at the time (although see Woiwod & Gould, 2008), and land-use change effects cannot easily be assessed retrospectively. However, recent research has started to shed

light on the impacts of land use on moth populations, by contrasting different levels of management intensity.

Agricultural management. Agriculture is a dominant and socioeconomically important land use in Britain and much of Europe and is also of great importance for biodiversity (Bignal & McCracken, 1996; Halada *et al.*, 2011). However, agricultural intensification generally reduces habitat area, quality and heterogeneity through the interlinked impacts of increased agrochemical use, changes in tillage/grazing practices and larger cropped areas and is widely recognised as a major driver of biodiversity decline (Donald *et al.*, 2001; Benton *et al.*, 2002, 2003; Robinson & Sutherland, 2002; Kleijn *et al.*, 2009). The substantial drop in moth abundance and diversity recorded on farmland at Rothamsted between the 1940s and 1960s was concomitant with agricultural intensification of the surrounding land (Woiwod & Gould, 2008). Specific changes included a move from grassland to arable cultivation, removal of hedgerows and uncultivated areas to increase field size and built development. A number of other recent studies have also implicated aspects of intensification with reduced moth populations (see below).

Taylor and Morecroft (2009) reported significant increases in moth abundance and species richness on a farm in southern England, following organic conversion and simultaneous entry into an agri-environment scheme (AES) and the adoption of less-intensive farming techniques. Wickramasinghe *et al.* (2004) found significantly higher species richness and diversity of moths on organic farms than on conventional ones in a study of 24 pairs of (livestock and mixed) farms in Britain. The authors ascribed this difference to the reduced use of agrochemicals, but many other factors could also be responsible. Pocock and Jennings (2008) conducted a similar study, but were able to separate out several different elements of intensification. They found the greatest effects on moth abundance related to the presence or absence of field boundaries (moths benefited from boundaries), both in arable and in pasture fields, with relatively little impact from either agrochemical inputs or the switch from hay to silage cropping regimes. This corroborates findings that the area of hedges and bushes in the local environment around RIS traps on the Rothamsted Estate was an important predictor of moth abundance and diversity (Woiwod & Gould, 2008).

Work by Merckx *et al.* (2009a,b, 2010a,b) also highlighted the importance of field boundaries for moths in agricultural settings. The presence of hedgerow trees and 6-m-wide grassy field margins were both significantly correlated with increased moth abundance and diversity (Merckx *et al.*, 2009b). Such field margins, but not hedgerow trees, were management options for which 'entry level' AES payments were available at the time of the studies. Hedgerow trees had the greater effect, but only when targeted management advice resulted in elevated levels of AES uptake in the surrounding landscape (Merckx *et al.*, 2009b). Hedgerow trees had a positive impact on a wide range of moths, not just those species that utilise them as larval hostplants, possibly because they provide sheltered micro-climates in relatively exposed landscapes (Merckx *et al.*, 2010a).

Another study (Fuentes-Montemayor *et al.*, 2011) found benefits for moths from AES management at farms in Scotland.

Conversion of conventional arable or improved pasture fields to more species-rich grassland under AES resulted in increased abundance and species richness of moths. Other AES options, including the creation of extensively managed margins, also led to increased moth numbers and abundance, but no effects were found for AES hedgerow management.

Agricultural use of chemicals, both fertilisers and pesticides, increased enormously as an integral part of agricultural intensification during the latter half of the twentieth century. With direct and indirect (e.g. via impacts on larval hostplants, nectar sources, vegetation structure and composition) effects on many taxa both within cropped areas and on field margins (Freemark & Boutin, 1995; McLaughlin & Mineau, 1995; Longley & Sotherton, 1997), these agrochemicals may have played a prominent role in the decline of moths in Britain. However, disentangling the relative contributions of fertilisers or pesticides from other elements of agricultural intensification at a landscape or national scale is problematic (Benton *et al.*, 2003; although see Gibbs *et al.*, 2009).

Ongoing agricultural development will alter the patterns of agrochemical use and the nature of the substances deployed. Such changes may increase or decrease potential impacts on biodiversity and should be evaluated prior to introduction. For example, genetically modified herbicide-tolerant crops alter pesticide regimes and aim to improve the efficacy of weed control, with potential impacts on plants and associated invertebrates both within the crop and on field margins (Roy *et al.*, 2003). Novel crops (e.g. biofuel and biomass), increasing resistance to pesticides and changing food security conditions may drive increased intensification and additional exposure to existing and future agrochemicals (Sutherland *et al.*, 2008).

Often, subtle aspects of habitat quality are vital for population persistence. Change in the grazing intensity of agricultural land is known to alter habitat quality critically for many taxa, including butterflies, vascular plants and some specialist moth species. For example, increased intensity of livestock grazing almost led to the extinction of *Zygaena viciae* New Forest burnet from Britain (Young & Barbour, 2004). Experimental reduction in the high intensity of livestock grazing typical of commercial upland agriculture led to significant increases in moth abundance and species richness (Littlewood, 2008). While less-intensive grazing may benefit grassland insects, the permanent abandonment of traditional pastoral agriculture, leading to rapid ecological succession, can be detrimental (Balmer & Erhardt, 2000; Bourn & Thomas, 2002; Öckinger *et al.*, 2006; van Swaay *et al.*, 2006; Settele *et al.*, 2009; Stefanescu *et al.*, 2009). Such abandonment is thought to have contributed to declines of moth species in Britain such as *Adscita statices* forester and *Hemaris tityus* narrow-bordered bee hawk-moth (M. Parsons, pers. comm.).

Woodland management. Native broad-leaved and coniferous woodlands are important habitats for a wide range of taxa in Britain, including a high proportion of the macro-moth species. Although woodlands of high biodiversity value have been destroyed, the net amount of broad-leaved woodland has increased in Britain over recent decades, in stark contrast to the amount of other semi-natural habitats. And yet, the changing status of key monitored taxa, such as birds, butterflies and

plants, clearly indicates a decrease in woodland biodiversity (Fuller *et al.*, 2005; van Swaay *et al.*, 2006; Carey *et al.*, 2008; Fox *et al.*, 2011a). A range of factors are responsible for these declines but, for butterflies, the main causes appear to be altered structural diversity, botanical communities and micro-climatic conditions associated with a shift towards high-forest management (including the cessation of traditional practices such as coppicing), leading to increasing shade and fewer open, early-successional habitats (Warren & Key, 1991; Sparks *et al.*, 1996; Asher *et al.*, 2001; van Swaay *et al.*, 2006; Clarke *et al.*, 2011). Conrad *et al.* (2004) found that moth species utilising deciduous trees as larval hostplants tended to have negative population trends in Britain, while the few species (such as *Thera britannica* spruce carpet and *Panolis flammea* pine beauty) that exploit coniferous trees generally increased. The latter is hardly surprising, given the massive expansion of conifer plantations (a 20-fold increase, 1800–1980) in Britain.

Moth species assemblages vary between woodland types and along geographical gradients, but also within woods (e.g. species associated with mature trees, others with edge habitats or open, grassland conditions in rides and glades) and even between age-classes of managed areas such as coppice coupes (Broome *et al.*, 2011).

T. Merckx, R. E. Feber, D. Hoare, M. S. Parsons, C. Kelly, N. A. D. Bourn & D. W. Macdonald (unpubl. data) assessed the macro-moth response to standard woodland conservation management practices in a landscape-scale study in southern England. They found that moth abundance increased with the amount of shelter: open, recently coppiced areas had the lowest abundance and standard (narrow) forest rides and blocks of mature woodland had the highest. However, common management techniques to open up woodland for the benefit of taxa such as butterflies, including coppicing and ride widening, did benefit the overall species richness of moths in the woodland landscape. Wide rides, although containing relatively low abundance levels of moths, were as rich in species as the standard rides and mature woodland. Moreover, the introduction of increased structural and micro-climatic heterogeneity increased overall species richness by providing niches for moths that were not found elsewhere in the woods. The authors caution, however, against opening up the sheltered late-successional cores of woodlands as these support high abundance and species richness of many specialist and conservation priority moths that are not found in more open habitats.

Most woodland specialist moths may have benefited from the switch to high-forest management in broad-leaved woodland habitats over recent decades, although they will have been impacted detrimentally by conversion to coniferous forestry. However, it is equally clear that many moths, mostly generalist species of more open habitats (but also some specialists such as *Anania funebris* and *Minoa murinata* drab looper) will have undergone substantial decreases in abundance and distribution as a result of changing woodland management.

Urbanisation. The impacts of urbanisation on biodiversity are complex. Increasing urban land cover typically replaces and fragments semi-natural habitat, leading to decreases in biodiversity, particularly among specialist species (Bergerot *et al.*, 2010;

Gaston & Evans, 2010; UK National Ecosystem Assessment, 2011). However, urbanisation can also cause increases in biodiversity among particular taxa (McKinney, 2008). In addition to habitat loss, urbanisation also generates other environmental changes that might alter biodiversity including local climatic effects, chemical, light and sound pollution and the introduction of non-native species. Thus, urbanisation impacts on moths need also to be considered in the context of the effects of climate, pollution and non-native species (see below).

Although reduced levels of moth abundance and diversity have long been associated with urbanisation (Taylor *et al.*, 1978), there do not appear to have been any published studies of the specific impacts of urbanisation on the moth fauna of Britain, nor of the relative value for moths of habitat fragments in urban surroundings compared with other degraded land uses such as intensive agriculture. In California, Rickman and Connor (2003) found no consistent differences between leaf-mining moth communities of remnant habitats in urban vs. agricultural settings.

Urban greenspace, including private gardens, supports diverse moth communities. As with agriculture, intensive management of gardens and parks (including pesticide use) is expected to reduce moth numbers, although quantitative studies are lacking. Recent trends for reduction in garden size, both in new-build developments and through in-fill (building new housing in existing gardens), and loss of vegetated area to hard surfaces (e.g. driveways, parking, patios, decking) and garden buildings (e.g. sheds, greenhouses) (Loram *et al.*, 2008; Smith, 2010; UK National Ecosystem Assessment, 2011) will have reduced resources available to moths, but no population-level studies have been conducted.

In contrast, increased public awareness of biodiversity and interest in 'wildlife gardening' may have improved habitat quality in some gardens and parks, and the cultivation of non-native plants has provided opportunities for a few native and newly colonising moth species (see section Non-native species).

Habitat loss summary. Direct evidence of the impact of historical habitat loss, decreasing quality or fragmentation on moth abundance or diversity is largely lacking. However, the weight of contemporary evidence suggests that reducing the intensity of agricultural management (including at field boundaries) and reinstigating traditional management to recently neglected broadleaved woodlands increase moth abundance and diversity at the landscape scale. The implication is that the predominant trends in land-use management in twentieth-century Britain and concomitant loss of breeding habitat must have resulted in considerable declines for many moth species.

Chemical pollution

Eutrophication (increased soil and water fertility caused by unintended nutrient inputs from fossil fuel combustion and agriculture) is altering the plant composition and vegetation structure of many habitats, often in conjunction with other drivers such as management intensity and climate change (Bobbink *et al.*, 1998; Van der Wal *et al.*, 2003; Hartley & Mitchell, 2005).

Biodiversity of plant and insect populations (e.g. butterflies) correlates negatively with nitrogen input (Pollard *et al.*, 1998; Stevens *et al.*, 2004; Öckinger *et al.*, 2006; WallisDeVries & van Swaay, 2006), so there may be substantial, unquantified impacts on moth populations resulting from such chemical pollution.

Links between other forms of chemical pollution and moth populations appear completely unstudied in Britain. It has been suggested that the population increases seen among moths that utilise lichens and algae as larval hostplants (e.g. the footman moths in sub-family Lithosiinae) might be linked to the recovery of some of these organisms following amelioration of sulphur dioxide pollution (Fox *et al.*, 2006b). However, there is no direct evidence for such causality. Similarly, while there has been much research into the impacts of pollution by heavy metals and other chemicals on humans, other vertebrates and plants (e.g. Sharma & Agrawal, 2005), there have been few studies involving moths. Negative fitness impacts of chemical pollution on moth larvae have been shown in Europe (Mitterböck & Fuhrer, 1988; van Ooik *et al.*, 2007; van Ooik & Rantala, 2010), but population effects have not been established.

In summary, there is no evidence currently available to suggest that chemical pollution in its many, complex and interacting forms is a driver of change in moth populations in Britain. However, as a key constituent of agricultural intensification and through negative effects on the insects themselves, larval hostplants and other essential resources, it is probable that chemical inputs in the form of herbicides, insecticides and fertilisers have contributed to the decline of Britain's moth populations.

Light pollution

Many moth species are attracted to artificial light, although the mechanistic basis for this behaviour is not entirely clear (Young, 1997). Artificial light elicits a wide range of responses in many animal and plant species, but there is insufficient knowledge about impacts in the wild, especially among invertebrates (Longcore & Rich, 2004; Rich & Longcore, 2006; Sutherland *et al.*, 2006; Poot *et al.*, 2008; Royal Commission on Environmental Pollution, 2009; Stone *et al.*, 2009; Bruce-White & Shardlow, 2011).

Outdoor lighting can cause direct mortality, increase exposure to predators and have disruptive effects on various elements of moth behaviour and life cycles (Frank, 2006; Bruce-White & Shardlow, 2011). However, such effects vary between species, populations and even individuals, as well as with the spectral composition of the light sources. Furthermore, direct impacts of light pollution must be quantified separately from the other effects of urbanisation and habitat loss that usually accompany an increase in lighting levels.

Unfortunately, despite a massive increase in background light levels in Britain and many other parts of the globe, there have been few studies on the impact of outdoor lighting on moths (e.g. Eisenbeis, 2006; van Langevelde *et al.*, 2011) and none that have assessed population-level or community-level effects.

Conrad *et al.* (2006) undertook a comparison of moth population trends from the RJS network using satellite data on the change in background illumination levels in Britain. There was

no significant difference between total moth abundance in areas exposed to increased background light levels and those unaffected. However, illumination data were available for only a short period (1992–2000), and therefore this finding does not preclude light pollution as a driver of long-term moth declines in Britain.

In summary, although the attraction of moths to artificial light has been known for centuries and disruptive and fitness-reducing impacts of such attraction have been demonstrated, light pollution remains uninvestigated as a possible cause of population-level changes in moths.

Climate change

Climate change has already caused considerable modification of geographical range, abundance and phenology for many species globally (Parmesan & Yohe, 2003; Gregory *et al.*, 2009; Thackeray *et al.*, 2010; Chen *et al.*, 2011) and is perceived to be a major threat to biodiversity (Thomas *et al.*, 2004a, 2006; Pounds *et al.*, 2006; Ohlemüller *et al.*, 2008; Bálint *et al.*, 2011; Maclean & Wilson, 2011).

In Britain (and elsewhere in north-west Europe), moderate levels of climate warming may bring opportunities for thermally constrained species such as insects and there is strong evidence, for example, that some butterflies have already expanded their ranges and flight periods in response to climate change (Roy & Sparks, 2000; Warren *et al.*, 2001; Hill *et al.*, 2002; Davies *et al.*, 2006; Menéndez *et al.*, 2007). At the same time, climate change may threaten other species through the loss of thermally suitable habitat space (Franco *et al.*, 2006; Wilson *et al.*, 2007; Maes *et al.*, 2010), altered phenological synchrony with hostplants (Singer & Parmesan, 2010) and even hybridisation (Mallet *et al.*, 2011).

Established links between climate change and the decline of moths in Britain are limited at present. Population trends of a small group of northerly distributed species (i.e. those with a southern range margin within Britain) decreased compared with southerly distributed moths (Conrad *et al.*, 2004), and Morecroft *et al.* (2009) found significant decreasing population trends for moth species with more northerly European distributions at northern, upland sites in the UK Environmental Change Network.

In addition, several studies have found links between winter conditions and moth declines, indicative of climatic influence. Population levels of *A. caja* correlate closely, and negatively, with winter precipitation and mean spring temperature, suggesting a link between climate change and the severe decline (89% decrease in population index, 1968–2002) of this moth (Conrad *et al.*, 2002). Furthermore, studies of moth declines in both Britain and the Netherlands found significant relationships between overwintering life-cycle stage and species trend; moths that overwinter in the egg stage had declined (on average) more than others (Conrad *et al.*, 2004; Groenendijk & Ellis, 2011; and a similar result for butterflies in WallisDeVries & van Swaay, 2006). Species overwintering as larvae or pupae had also decreased, while species that are adults during the winter had, on average, increased in both countries.

Another effect of winter and early spring climate has been observed on *Operophtera brumata* winter moth populations in the Netherlands. The synchrony of larval hatching date with the availability of its larval food resource (bud burst of *Quercus robur*) decreased over time, because of larvae hatching in advance of bud burst (Visser & Holleman, 2001). The degree of synchrony was reduced by warmer spring temperatures combined with no change in the incidence of days with frost during the winter. Such asynchrony is predicted to cause a large increase in larval mortality, which is a major driver of population dynamics in this species. Thus, prolonged or high levels of asynchrony might cause population decreases in this moth species, although intense selection pressure to restore synchrony (or adaptive asynchrony) may rapidly redress this problem (van Asch *et al.*, 2007; Both *et al.*, 2009; Singer & Parmesan, 2010).

In contrast, climate change is also expected to benefit elements of Britain's moth fauna. There is already some evidence for range expansion and increased abundance among southerly distributed moth species (i.e. those with a northern range margin in Britain). Morecroft *et al.* (2009) found that species with the most southerly distributions at the European scale showed significant increases in population levels at 10 sites in the UK. The moth species with the greatest population increases in Britain according to Conrad *et al.* (2006) also had increased distribution size, and the northern range margins of a sample of eight macro-moth species had shifted northwards considerably (mean, 79.5 km 10 year⁻¹ northward shift, 1982–2009), rivalling the largest equivalent results for butterflies and Odonata (Hill *et al.*, 2002; Hickling *et al.*, 2005; Fox *et al.*, 2011b). This intimates that southern moths may conform to the general pattern of poleward range expansions recorded among other taxa in Britain and globally (Hickling *et al.*, 2006; Chen *et al.*, 2011). The study by Salama *et al.* (2007) in central Scotland found that increasing moth diversity was positively correlated with mean annual temperature.

The absence of moth abundance decline in northern Britain compared with significant decreases in southern Britain appears to relate to a greater proportion of species with increasing population trends in the north (Conrad *et al.*, 2006; Fox *et al.*, 2006b; Scottish Government, 2007). This pattern is consistent with poleward range expansion and increasing abundance of some moth species through northern Britain in response to climate change. However, other factors, such as different patterns of land use and land-use change in northern Britain, could equally be responsible.

Other generally positive climate change impacts on moths in Britain include increased immigration (Sparks *et al.*, 2005; Morecroft *et al.*, 2009), colonisation (Parsons, 2003, 2010) and phenological change. The latter includes many examples of advancement and increased duration of flight period and additional generations in apparent response to climate warming, both in Britain and elsewhere in Europe (e.g. Fletcher, 2006, 2009; Salama *et al.*, 2007; Altermatt, 2010; Pöyry *et al.*, 2011).

In summary, although the evidence is limited at present, Britain's moths appear to be responding to climate change in qualitatively similar ways to butterflies. There are suggestions of climatic effects leading to the decline of some species, but also clear evidence of apparently positive impacts on species

populations and distributions. Future climate change may, of course, alter this balance if new conditions are unsuitable for moth species in Britain, plus the interaction between climate change and habitat loss, for example through sea-level rises, may damage specialist moth communities of coastal wetland habitats (e.g. *Gortyna borellii* Fisher's estuarine moth; Ringwood *et al.*, 2004).

Non-native species

Globally, non-native species are regarded as a principle driver of biodiversity decline and an ongoing threat to species and habitats (Mack *et al.*, 2000; Manchester & Bullock, 2000; Gurevitch & Padilla, 2004; McGeoch *et al.*, 2010). Many species of non-native plants, vertebrates and invertebrates are established in Britain, and there are numerous negative impacts on native biodiversity (Brown *et al.*, 2008; Lack, 2010; Lever, 2010; Holt *et al.*, 2011).

There have been no quantitative assessments of the impact of non-native species on moth populations in Britain. Nonetheless, negative effects might be expected via the influence of invasive plant species and introduced animals (e.g. deer) on habitat quality and larval hostplant resources. Examples of specific impacts include the invasion of semi-natural habitats of *Zygaena loti* slender scotch burnet, *Z. purpuralis* transparent burnet and *Eudarcia richardsoni* by *Cotoneaster* spp. shrubs (M. Parsons & T. Prescott, pers. comm.). Experiments in the United States found that non-native woody plants supported significantly lower abundance and species richness of moth and butterfly larvae than native trees and shrubs, even if the alien plants were in the same genus as the native hostplants (Burghardt *et al.*, 2010). The impact of new predators is even more poorly understood, with species such as *Harmonia axyridis* harlequin ladybird and the parasitic fly *Sturmia bella* spreading rapidly and having the potential to impact on moth populations as well as other insects (Brown *et al.*, 2011; Gripenberg *et al.*, 2011).

Set against these examples is the success of some colonising and rapidly increasing moths that utilise non-native plants as larval hosts (Parsons, 2003, 2010; Conrad *et al.*, 2006; Fox *et al.*, 2011b). *Lithophane leautieri* Blair's shoulder-knot, for example, utilises Cupressaceae trees and shrubs and, having become established on the south coast of Britain in the mid-twentieth century, spread rapidly northwards (146 km 10 year⁻¹, 1982–2009) and increased substantially in abundance (16.5% year⁻¹, 1968–2002). Other Cupressaceae-feeding moths show similar patterns, including recent colonists (e.g. *Thera cupressata* cypress carpet and *Eupithecia phoeniceata* cypress pug) and native species (e.g. *T. juniperata* juniper carpet and *E. pusillata* juniper pug). The latter moths were formerly restricted to semi-natural habitats where their only native larval hostplant *Juniperus communis* juniper occurs but, in recent decades, both moths have colonised many gardens in which ornamental Cupressaceae species have been planted (Waring *et al.*, 2009).

Non-native species have not been directly linked with moth declines or extinctions in Britain as yet, although there is clear

potential for negative impacts. On the contrary, non-native plants have enabled new moths to colonise Britain and a few native species to extend their distributions.

Exploitation of populations

Collecting of wild specimens of macro-moths was once an integral part of the natural history study of this taxon in Britain. In modern times, despite an increase in popular interest in macro-moths, collecting of specimens is less commonplace. Although over-collecting has often been postulated as a cause of decline or extinction for rare moths and butterflies in Britain, there is little evidence to support the assertion (Young, 1997; Asher *et al.*, 2001), contrary to other taxa (Diamond *et al.*, 1989; Roberts & Hawkins, 1999; Jackson *et al.*, 2001; Rosser & Mainka, 2002; Dirzo & Raven, 2003). Indeed, the large population sizes, phased emergence and short lifespan of many moth species also make it theoretically unlikely that anything but highly organised, exhaustive collecting could impact on any but the rarest localised species. Nevertheless, responsible collecting is strongly urged by relevant UK organisations, and there is a widely accepted code of conduct (Invertebrate Link, 2002).

Young (1997) considered *Z. viciae* to be the only moth species for which there was credible evidence of extinction caused by collecting in Britain. After discovery in 1869, nine sites were found in the New Forest in southern England, attracting large numbers of collectors, and the moth became extinct in 1927. The extinction proved short-lived, however, as another, isolated colony of the moth was later discovered in Scotland. The precise location of this remaining colony has not been publicised to reduce potential damage from collecting.

Synthesis: why have Britain's moths declined?

Substantial decreases have occurred in overall abundance of macro-moths and the populations of many widespread species in Britain and north-western Europe. In some cases, parallel reductions in distribution have been recorded (Conrad *et al.*, 2002; Fox *et al.*, 2011b). However, direct evidence to explain the trends is very limited. Correlative results and extrapolation from better-studied insect taxa (e.g. butterflies) provide the basis for our current understanding of the probable causes of moth declines and can be summarised as follows:

Multiple drivers of change

This review indicates the influence of multiple drivers in the decline of Britain's moths. This is expected as it is improbable that each species in a diverse taxon would be affected by the same environmental and ecological factors. Various elements of habitat degradation, including habitat destruction, reduction in quality, loss of heterogeneity, and increased isolation, resulting from major land-use changes of the twentieth century (agricultural intensification, changing woodland management, urbanisation) are very likely to have had an adverse impact on

moths. For habitat specialist moths, this is a simple truth – the total area of semi-natural habitats such as unimproved calcareous grassland, heathland, fens and lowland raised bogs has decreased substantially. Generalist moths may also have been affected detrimentally by such losses but are, in addition, likely to have declined as changing land management (increased intensity in agricultural landscapes and a switch to high-forest silviculture) reduced available niches.

Research in agricultural and woodland settings show that moth abundance and species richness increase in response to techniques that reverse recent changes in management intensity. There is also correlative evidence that habitats subject to lower levels of management intensity change (e.g. organic farms) have higher abundance and species richness of moths.

Other drivers appear to be important too. There is strong evidence of both positive and negative climate change impacts. Currently, the impacts of chemical and light pollution and non-native species are insufficiently studied and understood to assess accurately. Thus far, most of the recognised impacts of non-native plants are positive, providing novel niches. Of the potential drivers of change considered in this paper, only direct exploitation of moth populations, in the form of collecting, is considered to be negligible in impact across the taxon.

Interactions and synergies

Evidence from other taxa suggests that multiple drivers of population change are likely to interact, often in complex ways, and may produce synergies (Travis, 2003; Brook *et al.*, 2008). Thus, one driver, such as habitat loss, may act to reduce populations to levels where synergistic processes, both intrinsic (e.g. population dynamics, inbreeding depression) and external (e.g. other drivers such as climate change), and stochastic effects form amplifying feedback loops and drive species towards extinction. Such synergies have yet to be identified for moths in Britain, but some have been elucidated for butterflies [e.g. interactions between habitat loss and the negative implications of isolation for populations, and between climate change and nitrogen pollution (WallisDeVries & van Swaay, 2006; Bulman *et al.*, 2007; Hanski & Pöyry, 2007)].

The human activities that shape the environment tend to generate complex mixtures of change. For example, agricultural intensification causes habitat loss, but also changes spatiotemporal structure and heterogeneity, and chemical inputs alter botanical communities. Urbanisation also causes habitat loss, along with changes to the climatic environment, background lighting levels and chemical pollution. Isolating the relative contributions of these drivers to moth declines within the real world of human land use is an enormous challenge that has, as yet, received little attention.

Future perspectives

Much moth research to date has focused on species that are economic pests on agricultural or forestry crops. The conservation biology of moths has been neglected as a research topic,

particularly in comparison with butterflies and, as a result, although widespread declines of moth faunas have been identified recently from Britain and other countries, knowledge of the underlying causes is scant. Fortunately, this has started to change. Ecologists are taking a greater interest in moths, spurred on by the pressing need to understand the causes and implications of biodiversity decline and the opportunities afforded by an ecologically diverse and species-rich taxon supported by large surveillance and monitoring data sets. Sutherland *et al.* (2006) highlighted the need to understand the causes of moth declines as one of 100 ecological questions of high policy relevance, Butterfly Conservation continues to raise awareness of the declines among the public and policy makers alike (e.g. Fox *et al.*, 2006b), and the UK Government added 71 species of widespread but rapidly declining macro-moths to the UK Biodiversity Action Plan as Priority Species with the intention of stimulating research into causal factors and amelioration measures. The maintenance of recording and monitoring schemes gathering spatially extensive, long-term, time-series data on moths is vital to underpin future research and conservation.

It is hoped, therefore, that the next decade will see a continued surge in research interest leading to better comprehension of the changes taking place in Britain's moth fauna. The following issues and questions are proposed to help understand and reverse the decline.

- 1 What is the complete picture of change for Britain's moths? Overall abundance has decreased, but the differing trends between northern and southern halves of Britain provide a natural contrast that might shed light on the causes of change. Are the differences attributed to less-intensive land use and more extensive semi-natural habitats in northern Britain or do they arise from climate change driving increases in range and abundance for southerly distributed moth species? Furthermore, population and/or distribution trends have been calculated for fewer than half of the *c.* 900 macro-moth species and only a tiny proportion of the *c.* 1600 micro-moths. Long-term distribution data have now been gathered by the National Moth Recording Scheme for all macro-moths in the UK (Fox *et al.*, 2011b), and could be used to generate distribution trends and estimates of range margin shift. Revised national population trends from the ongoing RIS would also yield more up-to-date information, and critical statistical analysis might yield further insight into the underlying causes. Trend analyses are currently impossible for all but a small minority of micro-moths (e.g. the Pyralidae), but greater co-ordination of micro-moth recording at the national level could generate suitable data in the medium term.
- 2 As agricultural intensification is considered to be a major driver of moth declines in Britain, improved understanding of the impacts of different elements of agricultural management is required. Identification of the key factors that depress moth abundance and diversity would facilitate efforts to reverse the trends (e.g. through AES). For example, 'What are the rela-

tive impacts of initial loss of habitat to cropped land vs. the subsequent agricultural management?', 'How important is local habitat heterogeneity?' and 'What role do pesticides play in relation to other aspects of crop cultivation?'

- 3 More research is needed into land management techniques that attempt to mitigate against biodiversity loss (Warren & Bourn, 2011). If moth declines are to be reversed and wider biodiversity policy targets met, evidence-based AES prescriptions, woodland management practices and urban landscape designs are needed. Currently, there is little evidence that AES have benefited biodiversity, despite huge budget expenditure, at the national and European scale (Kleijn *et al.*, 2011; but see Brereton *et al.*, 2008). Crucially, the impact of such management techniques on populations is a vital but seldom addressed issue. Most studies, including those on moths, focus on recording changes in the abundance and species richness of adult animals in relation to management treatments and make no assessment of reproduction, immature stages or population dynamics (e.g. Feber *et al.*, 1996; Pywell *et al.*, 2004; Merckx *et al.*, 2009b; Haaland *et al.*, 2011). Management techniques may simply concentrate mobile adults within the landscape (e.g. at nectar resources) without contributing substantially to improved fitness or increased population levels. Worse still, interventions aimed at improving biodiversity might have a negative impact via source-sink effects (Severns, 2011).
- 4 An equally critical question concerns the optimal targeting of AES for maximum benefit and cost-effectiveness. Theoretical and (limited) empirical evidence suggests benefits from clustering AES participation in the landscape (Merckx *et al.*, 2009b; Gabriel *et al.*, 2010), targeting extensively farmed land that retains relatively high levels of biodiversity (Kleijn *et al.*, 2009) and, conversely, focusing on 'simple' landscapes where agriculture already dominates and semi-natural habitats are isolated (Tschardt *et al.*, 2005). An associated debate concerns the relative merits of setting land aside (or taking land out of cultivation) for biodiversity conservation (land sparing) vs. reducing the intensity of agricultural management on farmland to benefit wildlife at the expense of production (land sharing) (Green *et al.*, 2005; Hodgson *et al.*, 2010). Apart from the recent work of Merckx *et al.* (2009b), there is no information on these contrasting strategies that relates directly to moths in Britain.
- 5 The impact of outdoor, artificial lighting and background light pollution on moths and other nocturnal biodiversity is a topic requiring urgent ecological research (Sutherland *et al.*, 2006). It is imperative that such studies aim to elucidate and quantify population-level effects and that research focuses on artificial lighting of types and intensities commonly experienced by wild moth populations. Does artificial light cause negative population-level effects in moth populations

through increased mortality and disruption of life cycles and behaviour? If so, what measures can be taken to reduce these impacts (e.g. through choice of lighting type, power, quantity and orientation, placement of lights and the periods that they are operated)?

- 6 Finally, although many impacts of climate change have been recorded for butterflies and other taxa in Britain, little is known about the responses of moths to weather and climate (with the exception of *A. caja*, Conrad *et al.*, 2002). It would be insightful to assess the range margin shifts of all macro-moth species in Britain, utilising the National Moth Recording Scheme database, and to attempt to relate shifts to climate change, habitat and larval hostplant distribution. In addition, the species richness of the macro-moth fauna in Britain provides a good opportunity to detect poleward or uphill retreats of high-altitude or northerly distributed species, which have proved rather elusive thus far.

The requirement for a research and conservation response elicited by the recently discovered widespread declines of moths in Britain and beyond is substantial and challenging. These declines are one of the clearest signals yet of catastrophic biodiversity loss caused by anthropogenic environmental and land-use changes, which is of great conservation concern and threatens ecosystem services upon which the human race depends. Understanding and taking measures to reverse the declines of diverse insect faunas, such as Britain's macro-moths, are vital steps back from the brink.

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