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Recent trends in UK insects that inhabit early successional stages of ecosystems

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Improved recording of less popular groups, combined with new statistical approaches that compensate for datasets that were hitherto too patchy for quantitative analysis, now make it possible to compare recent trends in the status of UK invertebrates other than butterflies. Using BRC datasets, we analysed changes in status between 1992 and 2012 for those invertebrates whose young stages exploit early seral stages within woodland, lowland heath and semi-natural grassland ecosystems, a habitat type that had declined during the 3 decades previous to 1990 alongside a disproportionally high number of Red Data Book species that were dependent on it. Two clear patterns emerged from a meta-analysis involving 299 classifiable species belonging to ten invertebrate taxa: (i) during the past 2 decades, most early seral species that are living near their northern climatic limits in the UK have increased relative to the more widespread members of these guilds whose distributions were not governed by a need for a warm micro-climate; and (ii) independent of climatic constraints, species that are restricted to the early stages of woodland regeneration have fared considerably less well than those breeding in the early seral stages of grasslands or, especially, heathland. The first trend is consistent with predicted benefits for northern edge-of-range species as a result of climate warming in recent decades. The second is consistent with our new assessment of the availability of early successional stages in these three ecosystems since *c*. 1990. Whereas the proportion and continuity of early seral patches has greatly increased within most semi-natural grasslands and lowland heaths, thanks respectively to agri-environmental schemes and conservation management, the representation of fresh clearings has continued to dwindle within UK woodlands, whose floors are increasingly shaded and ill-suited for this important guild of invertebrates. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **115**, 636–646.

ADDITIONAL KEYWORDS: grassland – heathland – insect conservation – land management – vegetation structure – woodland.

INTRODUCTION

The datasets assembled since the 1960s by the UK Biological Records Centre (BRC), and for birds by the British Trust for Ornithology (BTO), form the most complete, longest running, and most accurate record of species' changing distributions and abundance for any nation. Among many applications, they have enabled conservationists not only to identify which species are changing in status in the UK but increasingly also to detect similar or contrasting patterns in the changes experienced by groups of species that possess similar or contrasting attributes or sensitivities (e.g. Parmesan *et al*., 1999; Warren *et al*., 2001; Thomas *et al*., 2004; Smart *et al*., 2005; Ellis *et al*., 2007). These patterns, in turn, may suggest one or multiple environmental drivers as being responsible for observed changes which, when confirmed experimentally, has informed conservationists, policy makers and other stakeholders of measures that may mitigate or reverse the biodiversity loss in question.

For all their depth and breadth, it has long been recognised that the BRC (and related) datasets are

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very uneven in coverage between taxa (Prendergast *et al*., 1993; Isaac & Pocock, 2015), to the extent that until recently only butterflies out of 39 invertebrate groups for which recording schemes existed up to 2000 were sufficiently complete for quantitative analyses of change to be valid (Thomas, 2005). A vast majority of the records received (80–90% of the total) is for just three groups: vascular plants, birds, and butterflies. The average butterfly species is recorded over 5000 times each year, dwarfing the rate for other invertebrate taxa (Fig. 1): comparable rates are 783 records/species year^{-1} for dragonflies (Odonata), 477 for moths and, 61 for hoverflies (Syrphidae) and just 20 for wasps (Vespoidea).

Before the advent of modern, e.g. Bayesian, modelling techniques (Isaac *et al*., 2014a), the incompleteness of records of invertebrates necessitated indirect or semi-quantitative comparisons between their taxa or ecological groups. For example, Thomas & Clarke (2004) and Thomas (2005) employed accumulation curves of species' discovery dates to show that extinction rates in UK butterflies were similar to those experienced by ten other invertebrate taxa once the relative completeness of recording was taken into account, an approach also used by Carvalheiro *et al*. (2013) to assess changes in species richness in insect pollinators. Prior to these, one useful analysis for conservation by Thomas & Morris (1994) involved a simple classification of the number of species listed as extinct, endangered or vulnerable in the early UK Invertebrate Red Data Books (Shirt, 1987; Bratton, 1990, 1991; Merrett, 1990; Falk, 1991; Wallace, 1991; Hyman & Parsons, 1992; Kirby, 1992; Parsons, 1993) – datasets largely compiled by BRC, and later by JNCC, staff and colleagues in the 1960s–80s – with the successional stage (where attributable) that was exploited within various ecosystems by their constraining young stages (*sensu* Thomas, 1984, 1991). This revealed (Fig. 2 from Thomas & Morris, 1994) that the large majority of threatened and rapidly declining invertebrates in the 1960s to *c.* 1990 depended on one of the two extremes of successional stages that exist within semi-natural UK ecosystems: bare ground and the earliest seral stages of grassland, lowland heathland and woodlands; and the saproxylic habitats generated by ancient rotting trees. In contrast, although the species richness of many taxa was greatest in the four intermediate stages of successions listed in Figure 2 (e.g. Morris, 2000), few of their inhabitants were acutely threat-

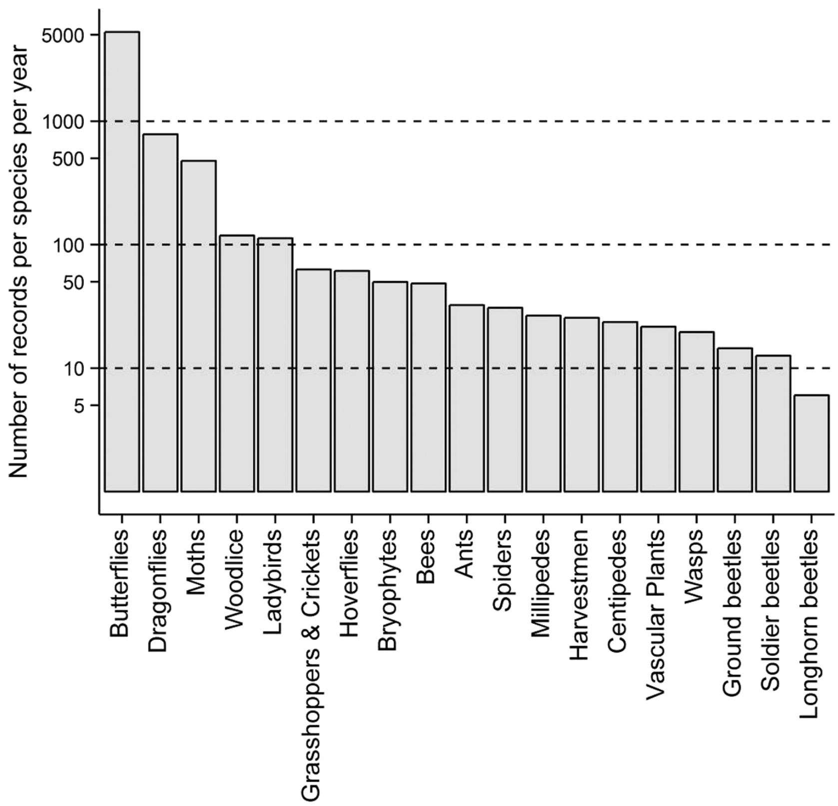

Figure 1. Recording intensity for selected BRC datasets, 1992–2012, measured as the number of records per species per year.

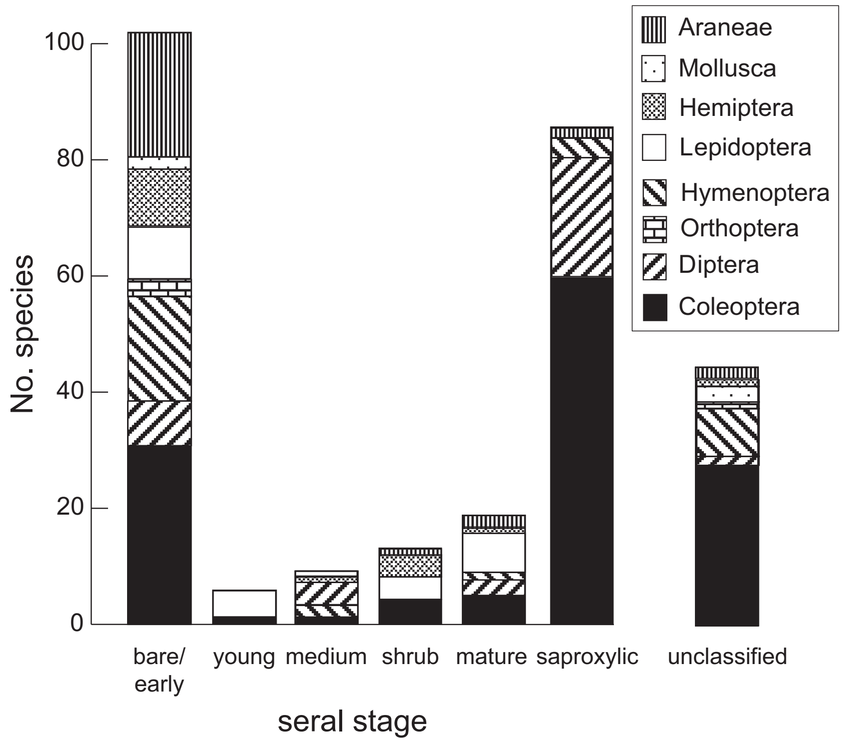

Figure 2. The distribution of threatened Red Data Book UK invertebrates in different successional stages of UK woodlands, grasslands, heaths and dunes in the 1960s to1990, redrawn from Thomas & Morris 1994. Note that species richness for most taxa is greatest in intermediate seral stages.

ened. For woodland ecosystems, this confirmed two earlier analyses of threatened species (Fuller & Warren, 1991; Warren & Key, 1991), and was consistent with the fact that although the area of woodland ecosystem in the UK had increased significantly during the same period (and had roughly doubled since its nadir after the Napoleonic wars), modern woods had become increasingly homogenous and shady (e.g. Keith *et al*., 2009), and had almost lost the sequential sunny open clearings once commonly generated by coppicing, wood pasture and other obsolete practices. In parallel was the near disappearance of antique trees experiencing 'the second half of their natural lives' (Rackham, 1980, 2001, 2006), again due to changing forestry products and management, and health-and-safety concerns. Similarly, the decline of guilds of species that required early seral vegetation in lowland heathlands and unimproved semi-natural grasslands coincided with the progressive abandonment for agriculture of the large majority of both ecosystems during the first 8 decades of the 20th century, exacerbated in the 1950s to 1980s by the disappearance due to myxomatosis of rabbits as an effective grazing force (Smith, 1980; Webb, 1986; Rose *et al*., 2000; English Nature, 2002).

Complementary autecological studies revealed two non-exclusive mechanisms that restricted certain species to early seral stages in woodland, heath and grassland. First, ectothermic species for which the UK is the northern limit of their distributions tend to be restricted to the warmest micro-climates. Soil surface temperatures in early successional habitats are often 5–8 °C warmer than the micro-climates that surround the same resources growing in more shaded vegetation (Thomas, 1983, 1991, 1993; Curtis & Isaac, 2015). For example, under current climates the optimum habitat of the thermophilous ant *Myrmica sabuleti* in the UK is a grassland or heathland sward with a mean height in spring and autumn of 1.5–2.5 cm tall, whereas its preferred niche shifts to 5–8 cm tall turf under the warmer climates of south-east Sweden, and to 30–45 cm tall vegetation in central southern France where the local climate is 2–3 °C hotter still (Thomas *et al*., 1998). Second, some of the above species, and many others, exploit a resource that is itself restricted to early seral stages or bare ground for reasons other than micro-climate (Thomas & Morris, 1994).

The knowledge of these patterns, and supporting results from autecological studies describing the constraining processes (e.g. Thomas, 1983, 1984, 1991; Cherrill & Brown, 1990; Thomas *et al*., 1986; Thomas, Simcox & Clarke, 2009; Erhardt & Thomas, 1991), led to the restoration of increased grazing, especially in spring and autumn, in many undergrazed or abandoned semi-natural grasslands, at first mainly on nature reserves and increasingly later on through agri-environmental stewardship agreements (e.g. Brereton *et al*., 2005), arguably saving two declining butterflies, *Lysandra bellargus* and *Hesperia comma* from UK extinction (Thomas, Simcox & Hovestadt, 2011; O'Connor, Hails & Thomas, 2014) and enabling *Maculinea arion* to be successfully reintroduced to carefully prepared sites (Thomas *et al*., 2009). Similar restorations of the near-absent pioneer stages of lowland heathland were made for conservation reasons from the 1990s onwards, again following decades of abandonment in most regions. In comparison, the creation of early successions in UK woodland has apparently remained piecemeal and minimal (Anon, 2003b; Harmer, 2004).

Here, we reprise Thomas & Morris' (1994) study of trends in invertebrate status of the 1960s to *c.* 1990 by applying modern statistical techniques to the increasingly rigorous BRC datasets for 1992–2012. We also assess recent changes in the structure of three UK ecosystems (woodland, semi-natural grassland, lowland heathland). We restricted our analysis to the early seral stages of UK woodlands, lowland heathlands and semi-natural grasslands to test the following predictions: (i) due to recent climate warming, southern-restricted species, i.e. those that reach their northern climatic limits in southern UK, will have increased in status in comparison with more widespread species that exploit early seral stages; and (ii) species that breed on the woodland floor will have declined relative to those that exploit early stages within grasslands and lowland heaths owing to the widespread restoration of this habitat type in the two latter ecosystems.

MATERIAL AND METHODS

Defining early seral stages in woodland, lowland heathland and semi-natural grasslands

We used the criteria employed by Thomas & Morris (1994). For woodland, this encompassed regenerating coppice and coppice-with-standards in the first 5 years after a clearance, together with recently felled and wind-blow areas of woodland, wood pasture, and other forms of management that resulted in unshaded herb-rich woodland floors; permanently open (typically taller, denser) grassland plagioclimaxes within woods such as rides and glades were excluded, although it is recognised that certain 'early successional' species breed along the edges of ditches and on unshaded boundary banks. For heathland, we used 'pioneer heath' following a fire, swiping or grazing, as defined by Webb (1986), Thomas *et al*. (1999) and Rose *et al*. (2000). For grassland we included land with > 30% bare ground, or with > 5% bare ground and a sward of < 5 cm tall as measured by Stewart, Bourn & Thomas 's (2001) direct method (Morris *et al*., 1994; Thomas *et al*., 1999; Morris, 2000).

Structural changes in UK ecosystems, 1990–2010

We first assessed the perceived wisdom that, as a result of conservation management and agri-environmental schemes, UK lowland heathlands and semi-natural grasslands contained a substantially higher proportion of early successional stages in 1990–2010 than in the previous 3 decades, whereas the majority of woodlands are generally considered to possess increasingly closed canopies and shadier, hence cooler, understories and floors. Unfortunately, large-scale monitoring of vegetation structure in all three ecosystems was substantially reduced and largely confined to internal reports in 1990–2010 compared with earlier decades. For lowland heathlands, we searched the literature and web for descriptions of recent management at national and county scales. Data for the more extensive semi-natural grassland areas were less accessible: instead we present our own combined measurements of grassland sward structure made on 109 sites in the 1970s to early 1980s and repeated on the same sites in 1999–2010 (Thomas *et al*., 2001, 2009; O'Connor *et al*., 2014; JA Thomas & DJ Simcox unpublished). Sites were located across Hampshire, Isle of Wight, Dorset, Somerset, Gloucestershire, Devon and Cornwall in southern England, and ranged from acid and neutral grasslands to chalk and limestone downland. In both periods, the large majority of sites were managed for agriculture rather than as nature reserves, although most were in Higher or Entry-level Stewardship in the more recent period. For woodland, we accepted the Forestry Commission's various National Inventories of Woodland and Trees, and the analyses of Forestry Commission scientists (e.g. Anon, 2003b; Harmer, 2004).

Analysing change in terrestrial invertebrates

Selection of species

Our analyses are based on ten invertebrate groups for which adequate data exist (Table 1). Where known, we classified invertebrate species by the successional stage and ecosystem that is exploited by the larval or nymph stage (equating to both the nest site and adjoining adult forage area for social insects), since in the large majority of autecological studies it is the availability and abundance of the immature feeding-

Table 1. The number of early successional species analysed by taxonomic group in each UK ecosystem

Taxon name	Total	Heathland	Grassland	Woodland
Ants	13	3	2	10
Bees	59	16	5	40
Butterflies	13	3	7	5
Grasshoppers, Crickets	7	0	3	5
Ground beetles	7	6	1	0
Hoverflies	62	2	5	57
Longhorn beetles	16	0	0	16
Soldier beetles	9	0	0	9
Spiders	20	18	13	0
Wasps	93	24	3	68
TOTAL	299	72	39	210

stage's habitat that determines site carrying capacities and population trends (e.g. Morris & Lakhani, 1979; Morris, 1981, 2000; Morris & Rispin, 1982; Cherrill & Brown, 1990; Thomas, 1991; Elmes *et al.*, 1998; Thomas *et al.*, 2001, 2011).

Where available we used the criteria employed by Thomas & Morris (1994) described above. For other species we defined their dependency on early successional habitat for each ecosystem, as by the following characteristics. For woodland, the key features of early successional habitat were the availability of light and increased warmth at ground level, which provide a variety of resources for early seral invertebrates, including foodplants that are 'shaded out' in closed canopy woodland (e.g. violets). Another example is fallen wood in direct sunlight, which provides warm nesting resources for certain species of aculeate Hymenoptera. For both grassland and heathland, we defined early successional species as those known to have direct associations with areas of bare, re-vegetating ground in the sun, or plagioclimaxes of < 5 cm tall.

All species in these ten taxonomic groups were then assessed against these criteria by JAT (butterflies) and ME (all other taxa), using a combination of published material and natural history experience. This resulted in 299 invertebrate species which could be confidently classified as being dependent on early successional habitats, and for which adequate records existed from which to calculate recent trends. By this classification, 22 species appear in multiple categories. The full set of species and their habitat associations are listed in the Table S1.

For each of these 299 species, we calculated the latitude of the northern range margin from the biological records spanning 1992–2012. We fitted a gamma distribution to the latitude of each unique grid cell and the range margin was calculated as the 95th quantile of this distribution: this method has been shown to minimise the bias in estimated range margin when recorder effort is uneven (Hassall & Thompson, 2010). Based on this metric, the range margins of species in our dataset fall between 50.7° (the south coast of England) and 60.8° (Shetland), with a mean of 53.7° (Leeds).

Estimating trends in species status

For each species in our dataset, we estimated the linear trend in status between 1992 and 2012. For butterflies, we used published trend estimates from the UK Butterfly Monitoring Scheme (Botham *et al.*, 2013). For other taxonomic groups, standardised monitoring data are unavailable, so we estimated the change in distribution from the biological records. We employed the 'well-sampled sites' method (Isaac *et al.*, 2014b), which aims to remove the noise and bases the statistical inference on a 'well-sampled' subset of the data. For each taxonomic group, we arranged the records into unique combinations of date and 1 km^2 grid cell. We used the median number of species recorded across visits as the threshold number of species required for a visit to be included in the analysis (including species not classified as early successional), since visits with fewer species recorded probably represent incomplete sampling (Van Strien *et al.*, 2010). We then selected sites with at least 3 years of data, ensuring we retained only the 'well sampled' examples (Roy *et al.*, 2012). Linear trends in status were estimated from species-specific binomial generalised linear mixed effects models. The quantity being modelled is the annual change in log-odds that the species in question is recorded on an average visit (Isaac *et al.*, 2014a).

Hypothesis testing

We modelled interspecific variation in species trends in relation to our hypotheses using a Bayesian meta-analysis (Hartung, Knapp & Sinha, 2008) that incorporates uncertainty in the trend estimates for each species. The model contains the trend estimate for each species, the associated standard error, the northern range margin and a logical variable for each of the three habitat types under consideration. The range margin data were centred on the latitude of Birmingham (52.5°); thus parameter estimates for the three habitat types can be interpreted as the mean trend for species whose range margin falls in central England.

We implemented the model in JAGS (Plummer, 2003) with vague priors, 50 000 iterations for each of three chains, a thinning rate of two and a burn-in of 2000 iterations. From the model, we extracted the posterior distribution of the effect sizes for each parameter of interest (range margin, heathland, woodland and grassland) as well as derived parameters for the post-hoc contrasts of heathland-woodland species, grassland-woodland and grassland-heathland species.

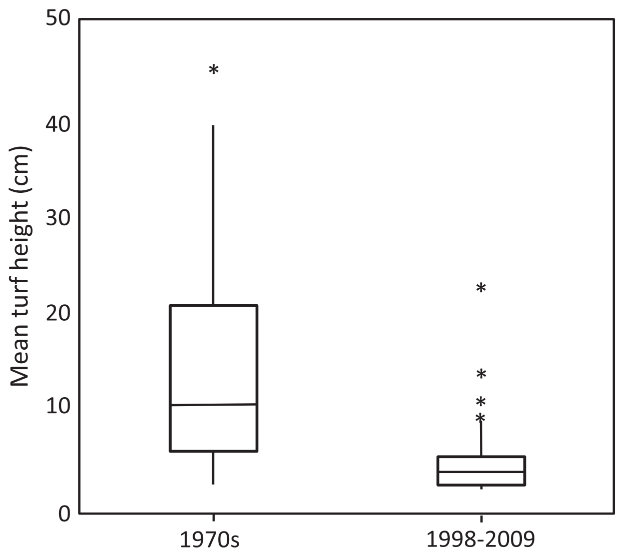

Figure 3. Changes in sward structure in UK semi-natural grasslands between the 1970s and 1998–2009. Boxplots show median value (horizontal), 25–75% quartiles (box), upper and lower values (vertical) and outliers (asterisk); T = 9.43, DF_{122}, n = 109, $P < 0.001$.

RESULTS

Structural changes in UK ecosystems, 1990–2010

Lowland heathland

With one exception of predicted abandonment in future years (Waterhouse, 2006), all references found to the management of UK heathland for the period 1990–2010 indicate a widespread restoration of management, including of early seral stages, to the UK's previously (largely) abandoned heaths. Reports cite restored management for the UK as a whole (e.g. English Nature, 2002; Newton, Diaz & Stewart, 2006; Symes, 2006; Anon, 2014a, b) or for the individual counties in which the UK's major fragments of lowland heath survive, such as Pembrokeshire (Tuddenham, 2006), Staffordshire (Anon, 2012), Cornwall (Anon, 2008), Devon pebblebeds (Anon, 2014c), Dorset (Rose *et al*., 2000; RSPB, 2014), Hampshire (Anon, 2014d), Surrey (Anon, 2014e), Berkshire (Anon, 2014f), and Suffolk and Norfolk (Marrs, Hicks & Fuller, 1986; Dolman & Sutherland, 1992; Anon, 2003a, 2013).

Woodland

Surveys of UK woodland are less piecemeal than those of heathland, but exact quantification of structural changes into successional types is not straightforward. Nevertheless, it is clear from the Forestry Commission's various National Inventories of Woodland and Trees (e.g. Anon, 2003b) that whilst the area of UK under trees has steadily increased in the past 5 decades – and indeed since 1870 (Anon, 2003b) and even from the 1830s (Fuller & Warren, 1991, 1993; Warren & Key, 1991), the net area of woodland that contains early successional stages has fallen progressively and substantially over the past 20 years, and for many decades before (Anon, 2003b, 2013; Harmer, 2004; Keith *et al*., 2009). For example, by 2003 only 0.9% UK woodland was actively managed under coppice or coppice-with-standards, a figure that rises to 2.9% when recently felled and wind-blow areas are included (Anon, 2003b). In Hampshire, where direct comparisons are more robust, Harmer (2004) cites the National Inventory of Woodland and Trees to show that coppiced woodland had declined by 93% between 1947 and 1994–2003.

Semi-natural grassland

Our measurements of sward structure in southern semi-natural grasslands showed a near universal reduction in mean turf height from 14.2 (± 1.1 SEM) cm in the 1970s to 3.7 (± 0.3) cm in 1999–2009 (Fig. 3) in recent years. Interviews with land owners and our own measurements indicate that this shift was largely due to the strictures of agri-environment schemes and, on many sites, to the recovery of rabbits.

Trends in status of UK invertebrates, 1992–2012

Proximity to range margins

Our Bayesian meta-analysis reveals that species trends are negatively correlated with the position of

Table 2. Results from the Bayesian meta-analysis comparing the trends in species status across habitat types and by range margin. Numbers describe the posterior distribution of effect sizes for each parameter. Parameter estimates for each habitat type can be interpreted as the mean trend of species whose range margin falls in central England. The estimate for range margin is the difference in trend associated with each extra degree of latitude. Trends for individual species are listed in Table S1

Parameter	Mean	Standard deviation	95% credible intervals
Range margin (all ecosystems)	−0.00307	0.00076	−0.00457, −0.00158
Heathland	−0.00001	0.00274	−0.00541, 0.00532
Woodland	−0.00439	0.00177	−0.00787, −0.00093
Grassland	−0.00264	0.00263	−0.00778, 0.00252

their northern range margins (Table 2). This indicates that species restricted to southern distributions have done well compared with more widespread species, which is consistent with the hypothesis that thermophilous species with climatically restricted distributions have benefitted from recent climate warming. The parameter estimate (e.g. −0.00308 for all species) is the change in trend per degree northerliness.

Relative changes of early successional invertebrates in different ecosystems

There are consistent differences in the mean trends of early successional species inhabiting each of the three ecosystems. Controlling for the latitudinal range margin, species in woodland have declined relative to the other two groups, heathland species have increased and grassland species are intermediate (Fig. 4). The Bayesian meta-analysis indicates that we can be 73% confident that woodland species have declined relative to grassland species, 73% confident that grassland species have declined relative to heathland species, and 94% confident that woodland species have declined relative to heathland species.

We can interpret our results in absolute, as opposed to relative, terms by estimating the latitude of the range margin at which the average species has zero net trend. For Heathland this lies at 52.5° (Birmingham), for Grassland at 51.6° (Wallingford) and for Woodland at 51.1° (Dover). Species with range margin south of this point have increased on average, more northerly species have declined. Put another way, it is the latitude north of which the benefits of recent climate are outweighed by habitat degradation and shading.

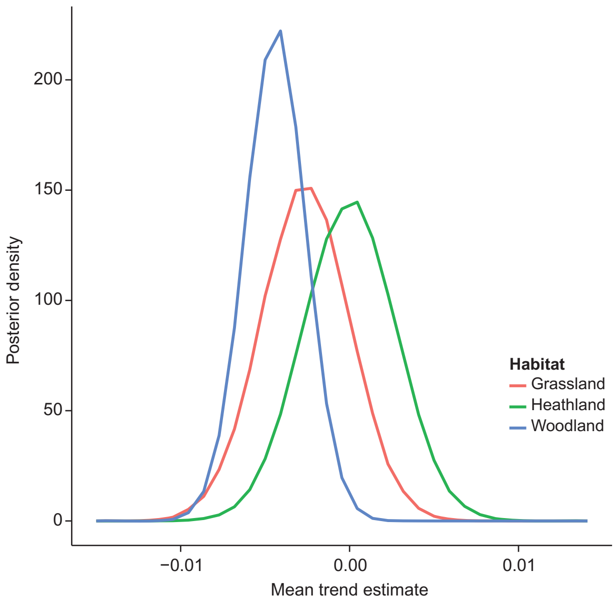

Figure 4. Posterior distribution of effect sizes for the mean trend of species in each ecosystem, from our Bayesian meta-analysis.

DISCUSSION

The improved coverage of UK invertebrate recording, combined with modern statistical approaches that compensate for datasets that were previously too patchy for quantitative analysis, have enabled us to make the first direct comparison of recent trends in status of UK invertebrates other than butterflies under different types of land management; in this case the previously threatened (Thomas & Morris, 1994) inhabitants of early successional stages in woodland, semi-natural grassland and lowland heathland ecosystems. Two clear patterns emerge: (i) most early seral species that are living near their northern climatic limits in the UK have increased relative to more widespread members of these guilds whose distributions were not governed by a need for a warm micro-climate; and (ii) independent of climatic constraints, species that are restricted to the earliest stages of woodland regeneration have fared considerably worse than those breeding in the early seral stages of grasslands or, especially, heathland.

The first pattern is consistent with predicted and observed changes in UK and European butterfly distributions and abundances near their range edges following climate warming in recent decades (Thomas, 1993; Thomas *et al*., 1998, 1999, 2011; Parmesan *et al*., 1999; Warren *et al*., 2001; Lawson *et al*., 2012; Suggitt *et al*., 2012; Curtis & Isaac, 2014). For example, Thomas (1991) and Thomas *et al.* (1999) showed that an ~2 °C increase in mean spring–summer regional climate temperatures would enable the thermophilous butterfly *Plebejus argus*, in its northernmost landscapes, to extend its larval niche from foodplants that were restricted to early successional (pioneer) heathland with south-facing aspects to patches that also contained mid-successional heath growing on any aspect of slope; a relaxation that increased the area and resources available for breeding (and hence carrying capacity: Thomas *et al*., 2011) by seven-fold across a typical heathland landscape whilst simultaneously reducing the mean distance between neighbouring patches of suitable habitat by 55-fold. Although Thomas *et al*., (1999) made similar theoretical estimates, with similar results, for the ant *Myrmica sabuleti* in warming heathlands located near the ant's climatic range limit, Table 2 is the first demonstration of an empirical pattern that suggests that many other early successional terrestrial species across ten invertebrate taxa may have benefitted from the modest climate warming experienced in the UK in 1990–2012.

The pattern emerging from our 1992–2012 meta-analysis of invertebrate trends indicates that species that breed mainly in the early seres of woodland have declined greatly relative to those exploiting the early successions of semi-natural grassland and lowland heath. This diverges from Thomas & Morris' (1994) analysis of invertebrate status during the previous 3 decades, in which the majority of early successional species in all three ecosystems experienced calamitous declines. The first study covered much the same groups sampled in our current analysis, but was crude in comparison being based simply on the categorisation by habitat type of species listed in UK Red Data Books. As such, it was probably biased towards the rarest, most specialised of the early successional species, whereas any bias in the 'well sampled sites' method (Isaac *et al*., 2014b) used here is likely to be towards the commoner species exploiting this habitat type. Nevertheless, with that proviso, we suggest that the observed recent trends in status (Fig. 4) represent a genuine divergence from those in earlier decades. Moreover, these changes are consistent with expectations based on reported changes in the availability of early successional habitats within modern woodland, semi-natural grassland (Fig. 3) and lowland heathland ecosystems. While it is disappointing that large-scale shifts in vegetation structure are today seldom recorded as comprehensively as in the 1960s–1980s, the piecemeal records for lowland heathland – nearly all of which have been managed for nature conservation in the past 2 decades – and our own records for semi-natural grasslands – most of which are now managed under agri-environmental schemes – suggest that early seral stages have recently been restored at a national scale to these two ecosystems, whereas formerly they existed as a bye-product of agriculture targeted exclusively towards food production, a national strategy that resulted in the near abandonment by farmers of less productive, unfertilised semi-natural pastures during the 20th century exacerbated by the loss of rabbits in the 1950s to 1980s. Certainly, mechanistic studies of the remarkable recoveries of three early seral grassland butterflies (*Maculinea arion*, *Lysandra bellargus* and *Hesperia comma*) since the 1990s indicate that the targeted restoration of a 'missing' habitat type was the sole or main factor driving their population changes (Thomas *et al*., 2009, 2011; O'Connor *et al*., 2014).

The structure of UK woodlands, by contrast, continues to shift overall towards high-forest homogeneity (Keith *et al*., 2009), resulting not only in fewer patches of early successional habitats within them but also to decreased spatial continuity in this ephemeral habitat type (Warren, 1987a; Warren & Key, 1991): hence our prediction, prior to this analysis, that the invertebrates whose young stages exploit early seres in woodland would in general have declined more severely compared with other ecosystems. To date, the exact mechanism(s) driving declines in this woodland type have been studied only for phytophagous butterflies (e.g. Warren, 1987a, b, c; Thomas, 1991; Fuller & Warren, 1993; Thomas *et al*., 2011). It is highly desirable that they be extended to a wider range of taxa and life-history traits. Nevertheless, the patterns detectable in BRC datasets send a clear message to conservationists that the restoration, in scale and continuity, of early seral stages in woodlands should be a priority if the diversity of the UK fauna (and by inference flora – Erhardt & Thomas, 1991) is to be sustained.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. The early successional species used in the analysis, their classification by ecosystem, and their range margins and trends in 1992–2012.