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

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ABSTRACT

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 three 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 two 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; (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.

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 very uneven in coverage between taxa (Prendergast *et al*., 1993; Isaac & Pocock, this volume), 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) are for just three groups: vascular plants, birds and butterflies. The average butterfly species is recorded over 5,000 times each year, dwarfing the rate for other invertebrate taxa (Fig. 1): comparable rates are 783 records/species/year 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 10 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-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 threatened. 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 eight decades of the 20th century, exacerbated in the 1950s-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 microclimates. Soil surface temperatures in early successional habitats are often 5-8^{o}C warmer than the micro-climates that surround the same resources growing in more shaded vegetation (Thomas, 1983, 1991, 1993; Curtis & Isaac, 2014). 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 5-8cm 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^{o}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; 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 *et al.,* 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, 2003; Harmer, 2004).

Here, we reprise Thomas & Morris' (1994) study of trends in invertebrate status of the 1960s-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; (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 <5cm tall as measured by Stewart *et al*.'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 three 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 to 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-early '80s 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, 2003; Harmer, 2004).

ANALYSING CHANGE IN TERRESTRIAL INVEREBRATES

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-stage's habitat that determines site carrying capacities and population trends (e.g. Morris, 1981, 2000; Morris & Lakhani, 1979; Morris & Rispin, 1982; Cherrill & Brown, 1990; Thomas, 1991; Elmes *et al*., 1998; Thomas *et al*., 2001; Thomas, Simcox & Hovestadt, 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 <5cm 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, twenty two 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 three 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, 50000 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.

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; RSPB, 2002; 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 five decades - and indeed since 1870 (Anon, 2003b) and even from the 1830s (Warren & Key, 1991; Fuller & Warren, 1991, 1993), 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; 2003; 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 s.e.m) 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 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.

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; (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; Suggitt *et al*., 2012; Lawson *et al*., 2012; Curtis & Isaac 2014). For example, Thomas (1991, 1999) showed that a ~2^{o}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 7-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 three 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 two 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-1980s. Certainly, mechanistic studies of the remarkable recoveries of three early seral grassland butterflies (*Maculinea arion*, *Lysandra bellargus, 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; Fuller & Warren, 1993; Thomas, 1991; 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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FIGURE LEGENDS

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 1960s-1990, redrawn from Thomas & Morris 1994. Note that species-richness for most taxa is greatest in intermediate seral stages

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}, $n = 109$, $P < 0.001$

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

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

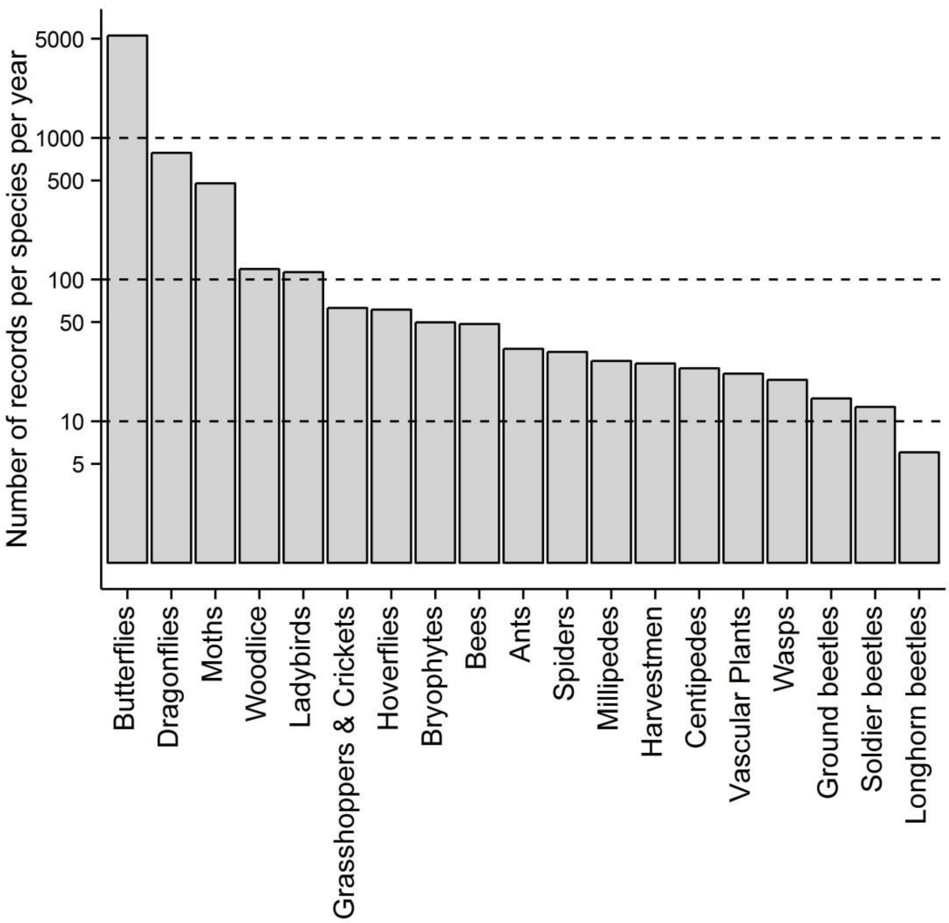
Taxon name	Total	Heathland	Grassland	Woodland
Ants	13	3	2	10
Bees	59	16	5	40
Butterflies	13	3	7	5
Grasshoppers, Crickets	7	0	3	5
Ground beetles	7	6	1	0
Hoverflies	62	2	5	57
Longhorn beetles	16	0	0	16
Soldier beetles	9	0	0	9
Spiders	20	18	13	0
Wasps	93	24	3	68
TOTAL	299	72	39	210

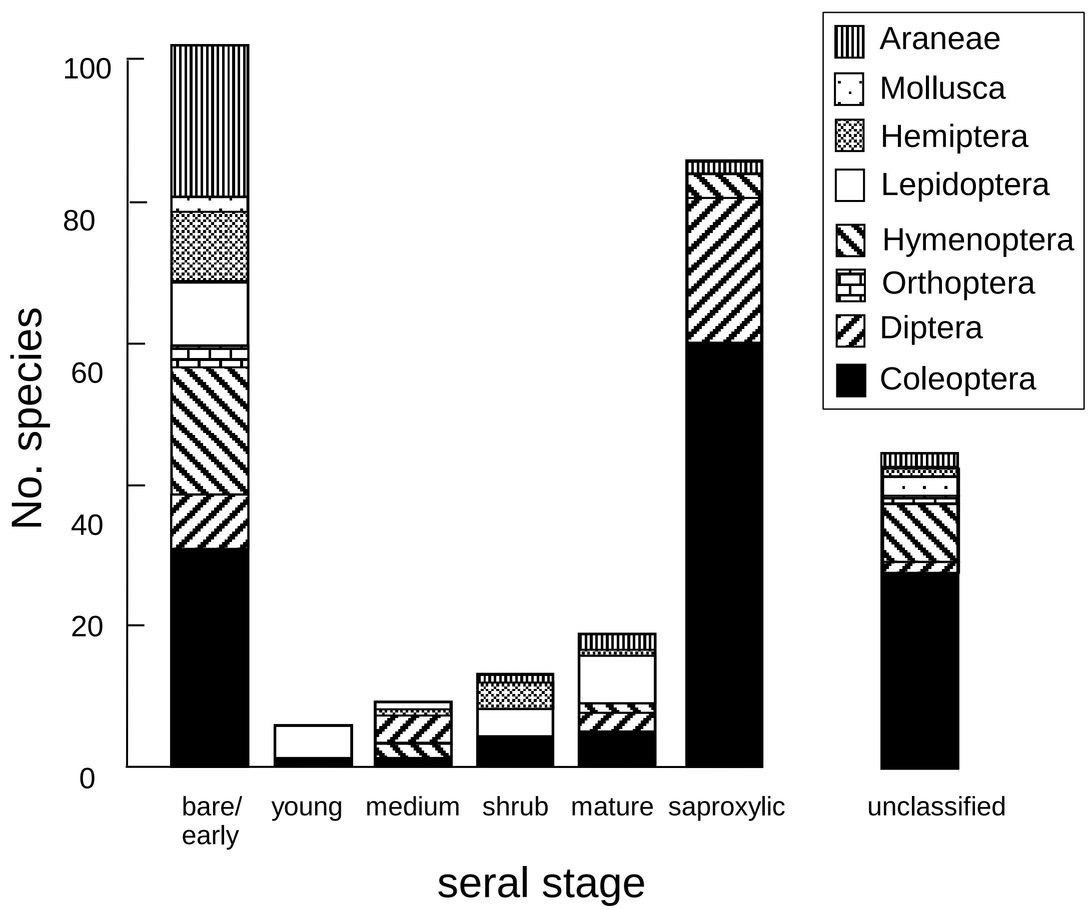
Table 2. Results from the Bayesian meta-analysis comparing the trends in species status across habitat types and by range margin. Numbers describe the posterior distribution of effect sizes for each parameter. Parameter estimates for each habitat type can be interpreted as the mean trend of species whose 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.

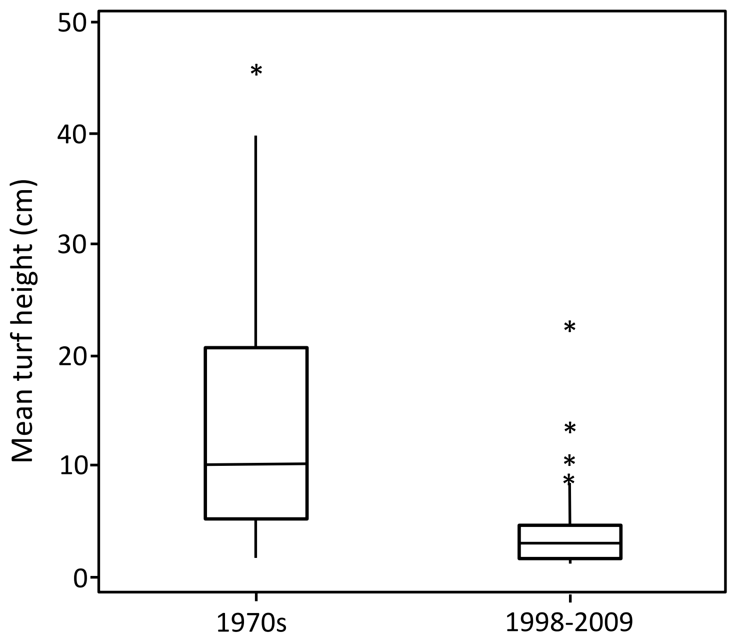
Parameter	Mean	Standard deviation	95% credible intervals
Range margin (all ecosystems)	-0.00307	0.00076	-0.00457, -0.00158
Heathland	-0.00001	0.00274	-0.00541, 0.00532
Woodland	-0.00439	0.00177	-0.00787, -0.00093
Grassland	-0.00264	0.00263	-0.00778, 0.00252

SUPPORTING INFORMATION

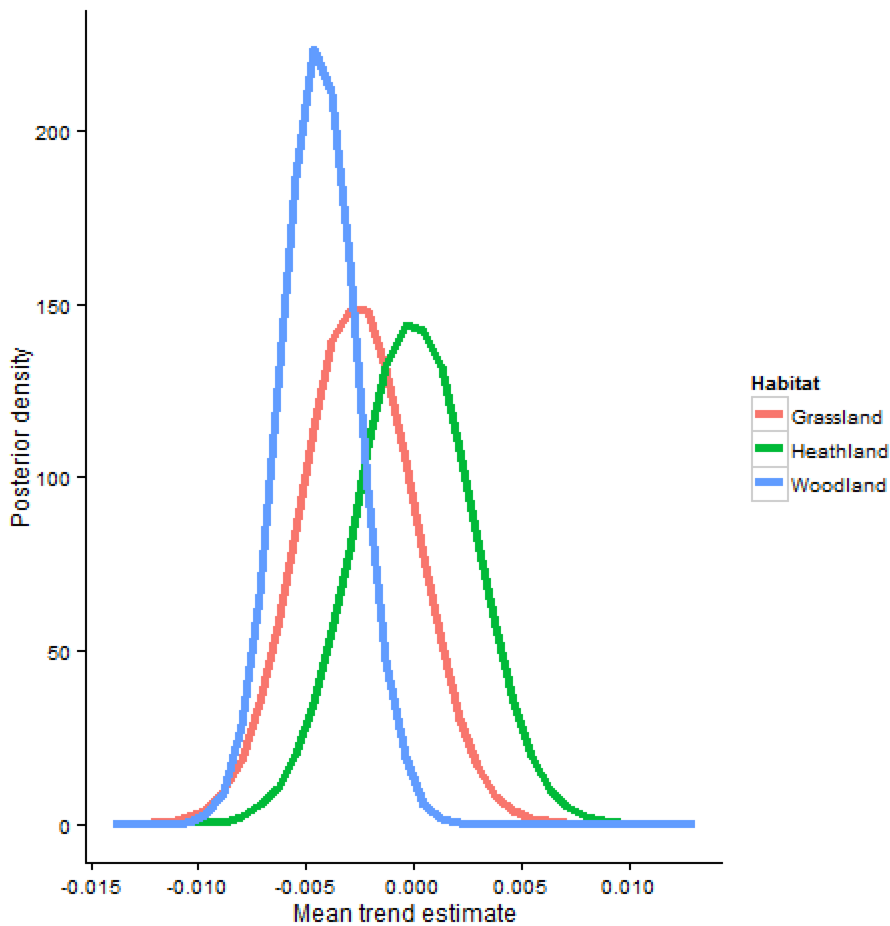
Table S1. The early-successional species used in the analysis, their classification by ecosystem, and their range margins and trends in 1992-2012


Number of records per species per year
5000
1000
500
100
50
10
5
Butterflies
Dragonflies
Moths
Woodlice
Ladybirds
Grasshoppers & Crickets
Hoverflies
Bryophytes
Bees
Ants
Spiders
Millipedes
Harvestmen
Centipedes
Vascular Plants
Wasps
Ground beetles
Soldier beetles
Longhorn beetles


Araneae
Mollusca
Hemiptera
Lepidoptera
Hymenoptera
Orthoptera
Diptera
Coleoptera
No. species
0
20
40
60
80
100
bare/ early
young
medium
shrub
mature
saproxylic
unclassified
seral stage



Mean turf height (cm)
50
40
30
20
10
0
1970s
1998-2009



Posterior density
200
150
100
50
0
-0.015
-0.010
-0.005
0.000
0.005
0.010
Mean trend estimate
Habitat
Grassland
Heathland
Woodland

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

Species name	Taxon	Heathland	Woodland	Grassland	Range margin	Trend estimate	SE[Trend]
Agenioideus cinctellus	Vespoidea	0	1	0	52.291	-0.00404	0.02521
Alopecosa barbipes	Araneae	1	0	1	54.777	0.25464	0.17724
Alopecosa cuneata	Araneae	0	0	1	52.316	0.12250	0.15408
Alopecosa pulverulenta	Araneae	1	0	1	56.617	0.10309	0.03301
Alosterna tabacicolor	Cerambycidae	0	1	0	53.768	0.75284	0.69799
Ammophila pubescens	Vespoidea	1	0	0	51.850	0.01951	0.01777
Anaglyptus mysticus	Cerambycidae	0	1	0	52.908	0.02220	0.09101
Andrena angustior	Apidae	0	1	0	52.879	-0.10291	0.02975
Andrena apicata	Apidae	0	1	0	53.913	-0.02364	0.03017
Andrena argentata	Apidae	1	0	0	51.629	0.00253	0.02290
Andrena bucephala	Apidae	0	1	0	51.933	-0.03225	0.02916
Andrena chrysosceles	Apidae	0	1	0	53.599	-0.06562	0.01130
Andrena clarkella	Apidae	0	1	0	54.403	0.00343	0.01561
Andrena denticulata	Apidae	0	0	1	54.918	-0.04914	0.02477
Andrena falsifica	Apidae	1	0	1	51.747	0.05516	0.13073
Andrena ferox	Apidae	0	1	0	51.099	0.13553	0.07075
Andrena fucata	Apidae	0	1	0	54.637	-0.02727	0.02720
Andrena fuscipes	Apidae	1	0	0	53.211	0.02096	0.01529
Andrena helvola	Apidae	0	1	0	53.946	-0.11546	0.03122
Andrena labiata	Apidae	1	0	1	52.221	0.03722	0.02572
Andrena lapponica	Apidae	0	1	0	56.967	-0.07560	0.03964
Andrena marginata	Apidae	0	0	1	54.940	0.03340	0.03862
Andrena praecox	Apidae	0	1	0	52.869	0.01925	0.02237
Andrena ruficrus	Apidae	0	1	0	58.806	0.41338	0.18915
Andrena subopaca	Apidae	0	1	0	54.100	-0.04411	0.01210
Andrena synadelpha	Apidae	0	1	0	53.427	0.01635	0.02737
Andrena thoracica	Apidae	1	0	0	52.151	-0.02207	0.02545
Anoplius infuscatus	Vespoidea	1	0	0	53.170	-0.00989	0.02555
Anoplius viaticus	Vespoidea	1	0	0	52.762	-0.00356	0.02110
Anthophora furcata	Apidae	0	1	0	54.572	-0.00594	0.01874
Aporus unicolor	Vespoidea	1	0	0	51.750	0.03868	0.05907
Arachnospila minutula	Vespoidea	1	0	0	52.885	0.04352	0.03407
Arachnospila wesmaeli	Vespoidea	1	0	0	53.588	-0.07885	0.07284
Arctophila superbiens	Syrphidae	0	1	0	56.159	-0.05086	0.03057
Argogorytes mystaceus	Vespoidea	0	1	0	54.450	0.04564	0.03169
Argynnis adippe	Papilionidea	0	1	0	55.614	-0.05390	0.00769
Aricia agestis	Papilionidea	0	0	1	52.876	-0.00877	0.00866
Auplopus carbonarius	Vespoidea	0	1	0	51.872	0.17634	0.03869
Baccha elongata	Syrphidae	0	1	0	54.558	-0.02514	0.00799
Blera fallax	Syrphidae	0	1	0	57.338	-0.92724	0.64728
Boloria euphrosyne	Papilionidea	0	1	0	56.354	-0.01260	0.00645
Brachyopa bicolor	Syrphidae	0	1	0	52.761	0.06018	0.06269
Brachyopa insensilis	Syrphidae	0	1	0	57.178	-0.15357	0.05280
Brachyopa pilosa	Syrphidae	0	1	0	53.996	-0.00813	0.04598
Brachyopa scutellaris	Syrphidae	0	1	0	54.237	-0.02250	0.02050
Brachypalpoides lentus	Syrphidae	0	1	0	54.334	0.00825	0.02117
Brachypalpus laphriformis	Syrphidae	0	1	0	53.891	0.01100	0.03180
Caliadurgus fasciatellus	Vespoidea	0	1	0	52.149	0.02425	0.02957

Callicera rufa	Syrphidae	0	1	0	57.629	-0.14564	0.11566
Cantharis decipiens	Cantharidae	0	1	0	54.574	0.09717	0.10988
Cantharis pellucida	Cantharidae	0	1	0	55.162	0.23153	0.13582
Carabus arvensis	Carabidae	1	0	0	57.173	0.07978	0.12257
Cerceris quadricincta	Vespoidea	0	0	1	51.550	0.51466	0.23781
Cerceris quinquefasciata	Vespoidea	0	0	1	52.823	-0.04101	0.02943
Cerceris ruficornis	Vespoidea	1	0	0	52.018	-0.01958	0.02726
Cerceris rybyensis	Vespoidea	1	0	0	52.236	0.02022	0.01011
Cercidia prominens	Araneae	1	0	1	54.923	0.00460	0.16319
Ceropales variegata	Vespoidea	1	0	0	51.255	0.00713	0.06676
Chalcosyrphus nemorum	Syrphidae	0	1	0	54.122	0.02072	0.01509
Cheilosia carbonaria	Syrphidae	0	1	0	51.748	-0.17350	0.04892
Cheilosia impressa	Syrphidae	0	1	0	53.102	0.02994	0.01212
Cheilosia longula	Syrphidae	0	1	0	59.133	-0.06156	0.03911
Cheilosia nigripes	Syrphidae	0	1	0	51.664	0.25157	0.10532
Cheilosia scutellata	Syrphidae	0	1	0	53.730	0.04766	0.02072
Cheilosia semifasciata	Syrphidae	0	1	0	53.738	0.04369	0.27114
Cheilosia soror	Syrphidae	0	1	0	52.347	0.08231	0.02343
Cheilosia variabilis	Syrphidae	0	1	0	54.313	-0.02195	0.00943
Cheiracanthium virescens	Araneae	1	0	0	52.834	0.27955	0.22999
Chelostoma campanularum	Apidae	0	1	0	52.068	0.03492	0.02329
Chelostoma florisomne	Apidae	0	1	0	53.379	0.01324	0.02886
Chorthippus albomarginatus	Orthoptera	0	0	1	52.996	0.01304	0.01479
Chrysis fulgida	Vespoidea	0	1	0	51.507	0.06901	0.08274
Chrysotoxum bicinctum	Syrphidae	1	0	1	54.048	-0.00018	0.00746
Chrysotoxum cautum	Syrphidae	0	1	1	52.670	-0.06476	0.02648
Chrysotoxum festivum	Syrphidae	0	1	0	53.982	0.00787	0.01714
Chrysotoxum verralli	Syrphidae	0	0	1	52.951	0.05075	0.03545
Chrysura radians	Vespoidea	0	1	0	53.078	0.10813	0.09821
Cicindela campestris	Carabidae	1	0	0	57.725	0.03736	0.03645
Cicindela sylvatica	Carabidae	1	0	0	51.329	0.15238	0.41366
Cleptes nitidulus	Vespoidea	0	1	0	54.088	0.00090	0.07687
Cleptes semiauratus	Vespoidea	0	1	0	53.311	-0.02306	0.08420
Clytus arietis	Cerambycidae	0	1	0	53.061	0.04926	0.06593
Coelioxys elongata	Apidae	0	1	0	54.749	-0.00247	0.03177
Coelioxys inermis	Apidae	0	1	0	52.458	-0.09947	0.06066
Coelioxys quadridentata	Apidae	0	1	0	52.379	0.06414	0.30881
Coenonympha pamphilus	Papilionidea	1	0	0	55.347	0.00084	0.00663
Colletes fodiens	Apidae	1	0	0	53.142	-0.09235	0.01990
Colletes succinctus	Apidae	1	0	0	55.965	-0.00482	0.01344
Crabro scutellatus	Vespoidea	1	0	0	51.641	-0.03216	0.03284
Criorhina asilica	Syrphidae	0	1	0	54.042	-0.02848	0.02698
Criorhina berberina	Syrphidae	0	1	0	54.121	-0.00548	0.01432
Criorhina floccosa	Syrphidae	0	1	0	54.378	-0.00747	0.02009
Criorhina ranunculi	Syrphidae	0	1	0	54.308	0.07002	0.02202
Crossocerus annulipes	Vespoidea	0	1	0	53.807	-0.01607	0.01966
Crossocerus binotatus	Vespoidea	0	1	0	53.774	-0.03936	0.05691
Crossocerus capitosus	Vespoidea	0	1	0	53.509	-0.04924	0.05899
Crossocerus cetratus	Vespoidea	0	1	0	53.848	0.02473	0.02551
Crossocerus dimidiatus	Vespoidea	0	1	0	57.307	-0.16640	0.07034
Crossocerus distinguendus	Vespoidea	0	1	0	52.541	0.01393	0.03264
Crossocerus megacephalus	Vespoidea	0	1	0	54.054	0.01419	0.01632
Crossocerus nigritus	Vespoidea	0	1	0	52.973	0.01628	0.04431
Crossocerus podagricus	Vespoidea	0	1	0	53.240	-0.00017	0.01538

Crossocerus styrius	Vespoidea	0	1	0	52.776	-0.26071	0.13003
Crossocerus vagabundus	Vespoidea	0	1	0	51.402	0.01532	0.08614
Crossocerus walkeri	Vespoidea	0	1	0	55.473	0.14261	0.20032
Crossocerus wesmaeli	Vespoidea	1	0	0	53.834	-0.06784	0.01830
Dasysyrphus albostriatus	Syrphidae	0	1	0	54.539	-0.00921	0.01022
Dasysyrphus tricinctus	Syrphidae	0	1	0	55.285	-0.00871	0.01684
Diodontus insidiosus	Vespoidea	1	0	0	52.194	0.02444	0.03837
Dipoena tristis	Araneae	1	0	0	51.620	0.32358	0.29263
Dipogon bifasciatus	Vespoidea	0	1	0	52.145	-0.24031	0.15918
Dipogon subintermedius	Vespoidea	0	1	0	53.768	-0.02850	0.03593
Dipogon variegatus	Vespoidea	0	1	0	54.148	-0.03647	0.03999
Drassyllus praeficus	Araneae	1	0	1	51.681	-0.59076	1.04585
Drassyllus pusillus	Araneae	1	0	1	56.457	0.04690	0.16992
Ectemnius borealis	Vespoidea	0	1	0	51.734	-0.17074	0.07951
Ectemnius cavifrons	Vespoidea	0	1	0	54.733	-0.04827	0.02135
Ectemnius cephalotes	Vespoidea	0	1	0	54.006	-0.01522	0.03348
Ectemnius continuus	Vespoidea	0	1	0	53.148	0.00796	0.01029
Ectemnius dives	Vespoidea	0	1	0	52.713	0.02712	0.04167
Ectemnius lapidarius	Vespoidea	0	1	0	54.670	-0.00055	0.05548
Ectemnius lituratus	Vespoidea	0	1	0	52.019	0.04443	0.01836
Ectemnius ruficornis	Vespoidea	0	1	0	54.104	0.02268	0.03820
Ectemnius sexcinctus	Vespoidea	0	1	0	55.029	0.13194	0.07748
Elampus panzeri	Vespoidea	1	0	0	52.709	0.01157	0.02692
Epeolus cruciger	Apidae	1	0	0	52.848	0.00411	0.01571
Epistrophe diaphana	Syrphidae	0	1	0	52.198	-0.01784	0.03474
Epistrophe eligans	Syrphidae	0	1	0	53.704	-0.00417	0.00621
Epistrophe grossulariae	Syrphidae	0	1	0	55.727	-0.01963	0.00978
Epistrophe nitidicollis	Syrphidae	0	1	0	53.305	-0.07854	0.02660
Episyron rufipes	Vespoidea	1	0	0	53.799	-0.03161	0.01741
Erynnis tages	Papilionidea	0	1	0	54.255	0.00127	0.00379
Eumenes coarctatus	Vespoidea	1	0	0	51.409	-0.06653	0.02646
Eumerus funeralis	Syrphidae	0	1	0	54.612	0.05068	0.02484
Eumerus ornatus	Syrphidae	0	1	0	53.828	-0.01106	0.02445
Eumerus strigatus	Syrphidae	0	1	0	53.697	-0.03304	0.02690
Evagetes dubius	Vespoidea	1	0	0	51.948	-0.01888	0.02843
Ferdinandea cuprea	Syrphidae	0	1	0	54.016	-0.00006	0.00970
Ferdinandea ruficornis	Syrphidae	0	1	0	53.807	0.27480	0.11998
Formica aquilonia	Formicidae	0	1	0	57.996	0.02834	0.14106
Formica cunicularia	Formicidae	1	0	0	52.457	-0.11534	0.05792
Formica fusca	Formicidae	0	1	0	53.040	0.01096	0.01853
Formica lemani	Formicidae	0	1	0	59.393	0.01440	0.06668
Formica lugubris	Formicidae	0	1	0	59.053	0.15407	0.12652
Formica rufa	Formicidae	0	1	0	52.798	-0.01193	0.03354
Formica rufibarbis	Formicidae	1	0	1	51.880	-0.01735	0.07640
Formicoxenus nitidulus	Formicidae	0	1	0	56.522	0.12834	0.09825
Grammoptera ruficornis	Cerambycidae	0	1	0	53.438	0.16457	0.09317
Gymnomerus laevipes	Vespoidea	0	1	0	51.920	0.09550	0.03875
Halictus confusus	Apidae	1	0	0	52.232	-0.01079	0.04704
Hammerschmidtia ferruginea	Syrphidae	0	1	0	57.742	0.09221	0.29046
Heriades truncorum	Apidae	0	1	0	51.618	0.11077	0.02710
Hesperia comma	Papilionidea	0	0	1	51.561	0.00517	0.00762
Hipparchia semele	Papilionidea	1	0	1	55.920	-0.00914	0.00449
Hoplitis claviventris	Apidae	0	1	0	53.233	-0.06654	0.02468
Hylaeus brevicornis	Apidae	0	1	0	53.105	-0.09551	0.01936

Hylaeus confusus	Apidae	0	1	0	52.955	-0.02765	0.02216
Hypsosinga albovittata	Araneae	1	0	1	55.412	-0.69619	0.57786
Lasioglossum fratellum	Apidae	1	0	0	56.510	-0.08430	0.03036
Lasioglossum prasinum	Apidae	1	0	0	51.473	0.04145	0.02327
Lasioglossum semilucens	Apidae	0	1	0	51.528	-0.01399	0.08390
Lasioglossum sexnotatum	Apidae	1	0	0	53.296	-0.01801	0.47088
Lasiommata megera	Papilionidea	0	0	1	55.349	-0.02430	0.00477
Lasius brunneus	Formicidae	0	1	0	51.936	0.09258	0.06889
Lasius fuliginosus	Formicidae	0	1	0	52.746	0.04825	0.04165
Leiopus nebulosus	Cerambycidae	0	1	0	53.690	-0.21114	0.13424
Leptophyes punctatissima	Orthoptera	0	1	0	52.816	-0.02056	0.00924
Leptura quadrifasciata	Cerambycidae	0	1	0	54.647	0.05365	0.49945
Leucozona glaucia	Syrphidae	0	1	0	56.167	-0.01967	0.01192
Leucozona laternaria	Syrphidae	0	1	0	55.234	0.00608	0.01746
Leucozona lucorum	Syrphidae	0	1	0	54.922	-0.03382	0.00688
Mallota cimbiciformis	Syrphidae	0	1	0	54.338	0.03398	0.08399
Malthinus flaveolus	Cantharidae	0	1	0	54.473	-0.30000	0.20066
Malthinus seriepunctatus	Cantharidae	0	1	0	53.082	-0.58303	0.44157
Malthodes fuscus	Cantharidae	0	1	0	56.387	-0.18933	0.32564
Malthodes marginatus	Cantharidae	0	1	0	55.115	-0.71795	0.25950
Malthodes minimus	Cantharidae	0	1	0	53.599	0.37131	0.49238
Meconema thalassinum	Orthoptera	0	1	0	52.798	-0.08442	0.01171
Megachile centuncularis	Apidae	0	1	0	54.434	0.00834	0.01619
Megachile ligniseca	Apidae	0	1	0	52.541	0.03642	0.01802
Megachile maritima	Apidae	1	0	0	53.058	-0.04048	0.01904
Megachile versicolor	Apidae	0	1	0	53.067	-0.03363	0.01222
Megachile willughbiella	Apidae	0	1	0	53.676	-0.01078	0.01088
Meliscaeva auricollis	Syrphidae	0	1	0	55.255	-0.04334	0.00894
Meliscaeva cinctella	Syrphidae	0	1	0	56.461	0.01325	0.01161
Melitaea athalia	Papilionidea	0	1	0	51.744	-0.03460	0.00786
Melitaea cinxia	Papilionidea	0	0	1	51.340	-0.01010	0.01740
Melitta haemorrhoidalis	Apidae	0	1	0	52.907	0.00090	0.03050
Merodon equestris	Syrphidae	0	1	0	54.436	0.01350	0.00917
Micaria silesiaca	Araneae	1	0	0	52.678	-0.04811	1.37994
Micrargus laudatus	Araneae	1	0	1	54.089	-0.48411	0.30389
Microdynerus exilis	Vespoidea	1	0	0	52.097	-0.05485	0.04113
Miscophus concolor	Vespoidea	1	0	0	51.593	-0.12680	0.03681
Molorchus minor	Cerambycidae	0	1	0	52.937	-1.39229	1.24213
Myathropa florea	Syrphidae	0	1	0	54.386	0.01271	0.00514
Myolepta dubia	Syrphidae	0	1	0	52.482	-0.00151	0.07117
Myrmica rubra	Formicidae	0	1	0	53.845	-0.03371	0.04491
Myrmica ruginodis	Formicidae	0	1	0	57.099	-0.01595	0.01865
Nebria salina	Carabidae	1	0	0	57.309	0.01148	0.03025
Nemobius sylvestris	Orthoptera	0	1	0	51.285	-0.00812	0.09114
Nitela borealis	Vespoidea	0	1	0	51.352	-0.25659	0.29494
Nomada flava	Apidae	0	1	0	52.744	-0.03643	0.00916
Nomada fulvicornis	Apidae	1	0	0	52.595	-0.01312	0.02084
Nomada hirtipes	Apidae	0	1	0	52.136	-0.03772	0.05092
Nomada leucophthalma	Apidae	0	1	0	54.148	0.04888	0.02058
Nomada panzeri	Apidae	0	1	0	54.853	-0.03603	0.01833
Nomada rufipes	Apidae	1	0	0	53.046	-0.00317	0.01226
Notiophilus quadripunctatus	Carabidae	1	0	0	52.841	0.27900	0.37374
Nysson spinosus	Vespoidea	0	1	0	54.478	0.11922	0.03757
Nysson trimaculatus	Vespoidea	0	1	0	53.108	0.01008	0.03266

Omalus aeneus	Vespoidea	0	1	0	53.052	-0.03772	0.14467
Omalus puncticollis	Vespoidea	0	1	0	52.676	0.16297	0.11620
Omocestus rufipes	Orthoptera	0	1	1	51.906	-0.02174	0.05350
Osmia leaiana	Apidae	0	1	0	53.228	0.05173	0.02022
Osmia parietina	Apidae	0	1	0	54.959	-0.07753	0.10167
Osmia pilicornis	Apidae	0	1	0	51.348	-0.22704	0.07700
Osmia uncinata	Apidae	0	1	0	57.727	-0.14712	0.24414
Oxybelus argentatus	Vespoidea	1	0	0	53.519	-0.00918	0.03338
Oxybelus mandibularis	Vespoidea	1	0	0	52.755	-0.02727	0.03467
Pachytodes cerambyciformis	Cerambycidae	0	1	0	54.639	0.21602	0.23235
Paragus haemorrhous	Syrphidae	0	0	1	53.918	-0.01200	0.01485
Pardosa hortensis	Araneae	1	0	0	52.684	-0.32463	0.35860
Pardosa palustris	Araneae	1	0	1	55.614	0.08267	0.04004
Pardosa saltans/lugubris	Araneae	1	0	1	54.566	0.02241	0.05571
Passaloecus corniger	Vespoidea	0	1	0	53.692	-0.05680	0.02499
Passaloecus eremita	Vespoidea	0	1	0	51.991	0.01243	0.03783
Passaloecus gracilis	Vespoidea	0	1	0	53.748	-0.00646	0.02521
Passaloecus insignis	Vespoidea	0	1	0	52.877	-0.01572	0.06017
Passaloecus monilicornis	Vespoidea	0	1	0	56.908	0.04126	0.22276
Passaloecus singularis	Vespoidea	0	1	0	53.210	0.00026	0.02723
Pelecocera tricincta	Syrphidae	1	0	0	51.077	-0.00920	0.04855
Pemphredon lugubris	Vespoidea	0	1	0	53.944	-0.00310	0.01533
Pemphredon morio	Vespoidea	0	1	0	53.075	-0.09085	0.06327
Philodromus histrio	Araneae	1	0	0	54.902	-0.76922	2.14678
Pholidoptera griseoaptera	Orthoptera	0	1	0	52.760	-0.02271	0.01113
Pirata tenuitarsis	Araneae	1	0	0	54.322	0.24087	0.52673
Plebejus argus	Papilionidea	1	0	1	53.169	-0.01150	0.00715
Podabrus alpinus	Cantharidae	0	1	0	54.801	-0.73700	0.43480
Poecilium alni	Cerambycidae	0	1	0	52.606	-0.35832	0.87635
Pogonocherus hispidus	Cerambycidae	0	1	0	53.285	-0.04778	0.11636
Polyommatus bellargus	Papilionidea	0	0	1	51.399	0.02840	0.01050
Pompilus cinereus	Vespoidea	1	0	0	54.326	-0.03196	0.02003
Portevinia maculata	Syrphidae	0	1	0	54.801	-0.00793	0.01907
Priocnemis agilis	Vespoidea	0	0	1	52.275	0.02905	0.10031
Priocnemis cordivalvata	Vespoidea	0	1	0	53.141	0.07622	0.09891
Priocnemis coriacea	Vespoidea	1	1	0	52.903	0.05216	0.05765
Priocnemis perturbator	Vespoidea	0	1	0	54.382	-0.03117	0.02576
Priocnemis schioedtei	Vespoidea	0	1	0	54.849	-0.03393	0.04255
Priocnemis susterai	Vespoidea	1	1	0	52.962	-0.05347	0.04749
Psenulus concolor	Vespoidea	0	1	0	53.344	-0.07231	0.06861
Psenulus pallipes	Vespoidea	0	1	0	53.131	-0.01310	0.02694
Psenulus schencki	Vespoidea	0	1	0	51.854	-0.08052	0.07623
Pseudepipona herrichii	Vespoidea	1	0	0	50.703	-0.02502	0.06406
Pyrgus malvae	Papilionidea	0	1	0	52.420	-0.00123	0.00551
Rhagium mordax	Cerambycidae	0	1	0	54.861	-0.04967	0.20890
Rhagonycha lignosa	Cantharidae	0	1	0	55.169	0.11089	0.11324
Rhingia rostrata	Syrphidae	0	1	0	52.588	0.18774	0.02910
Rhopalum clavipes	Vespoidea	0	1	0	54.268	-0.06392	0.03430
Rutpela maculata	Cerambycidae	0	1	0	53.314	0.11204	0.06545
Saperda populnea	Cerambycidae	0	1	0	53.918	-0.20391	0.18583
Sapyga quinquepunctata	Vespoidea	0	1	0	53.947	0.01537	0.03136
Scotina gracilipes	Araneae	1	0	0	60.771	-0.43164	0.31692
Sericomyia silentis	Syrphidae	0	1	0	57.442	0.01054	0.00943
Sphecodes miniatus	Apidae	1	0	0	52.321	-0.19837	0.06792

Sphecodes reticulatus	Apidae	0	0	1	52.859	-0.04394	0.02217
Sphegina clunipes	Syrphidae	0	1	0	57.614	-0.03503	0.01856
Sphegina elegans	Syrphidae	0	1	0	55.221	0.02387	0.02632
Sphegina verecunda	Syrphidae	0	1	0	55.837	-0.00030	0.03206
Spilomena beata	Vespoidea	0	1	0	52.928	0.13550	0.06879
Spilomena enslini	Vespoidea	0	1	0	51.772	-0.00142	0.09748
Spilomena troglodytes	Vespoidea	0	1	0	52.760	0.02644	0.05484
Steatoda phalerata	Araneae	1	0	1	58.110	0.09087	0.16420
Stelis breviuscula	Apidae	0	1	0	51.497	0.02220	0.03769
Stelis ornatula	Apidae	0	1	0	52.883	-0.02250	0.07405
Stelis phaeoptera	Apidae	0	1	0	53.037	-0.16186	0.16664
Stenocorus meridianus	Cerambycidae	0	1	0	53.126	0.01609	0.07842
Stenolophus teutonus	Carabidae	1	0	0	52.423	0.10984	0.06991
Stenurella melanura	Cerambycidae	0	1	0	52.885	-0.03620	0.08934
Stigmus pendulus	Vespoidea	0	1	0	52.344	0.01293	0.03571
Stigmus solskyi	Vespoidea	0	1	0	52.604	0.00567	0.03472
Symmorphus connexus	Vespoidea	0	1	0	52.040	0.04591	0.06655
Symmorphus crassicornis	Vespoidea	0	1	0	51.471	0.07755	0.03833
Symmorphus gracilis	Vespoidea	0	1	0	52.912	-0.01203	0.02736
Synuchus vivalis	Carabidae	0	0	1	54.077	0.05568	0.17533
Tetramorium caespitum	Formicidae	1	0	1	52.609	-0.03177	0.04486
Tetrops praeustus	Cerambycidae	0	1	0	53.098	-0.35832	0.87635
Tettigonia viridissima	Orthoptera	0	0	1	52.245	-0.01145	0.03501
Trachyzelotes pedestris	Araneae	0	0	1	52.147	0.20817	0.37991
Trichrysis cyanea	Vespoidea	0	1	0	53.574	-0.02404	0.01377
Trypoxylon attenuatum	Vespoidea	0	1	0	53.309	-0.00579	0.02015
Trypoxylon clavicerum	Vespoidea	0	1	0	53.173	-0.07258	0.02136
Vespa crabro	Vespoidea	0	1	0	52.890	0.15838	0.02138
Volucella inflata	Syrphidae	0	1	0	52.356	0.01568	0.01893
Xanthandrus comtus	Syrphidae	0	1	0	54.005	-0.01545	0.02992
Xanthogramma pedissequum	Syrphidae	0	0	1	52.938	-0.00026	0.01055
Xerolycosa nemoralis	Araneae	1	0	1	51.958	0.66452	0.25383
Xylota segnis	Syrphidae	0	1	0	55.236	-0.01981	0.00578
Xylota sylvarum	Syrphidae	0	1	0	54.580	-0.01981	0.01058
Xylota xanthocnema	Syrphidae	0	1	0	53.440	-0.10713	0.07177