

England's changing flora

A summary of the results of *Plant Atlas 2020*

Plant Atlas 2020

Mapping Changes in the Distribution of the
British and Irish Flora



Volume 1

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Summary

Plant Atlas 2020 is the Botanical Society of Britain and Ireland's (BSBI) third distribution atlas of the British and Irish flora and involved surveys of ferns, flowering plants and charophytes growing in the c. 3,900 10 × 10 km squares (hectads) that make up Britain and Ireland. These surveys were undertaken by 1000s of amateur botanists between 2000 and 2019 and the records collected were used to produce 'dot-distribution' maps for 3,495 taxa at the 10 × 10 km (hectad) scale. Maps for individual species were published in a book (Stroh *et al.*, 2023) and on a website (plantatlas2020.org) alongside information on their origin, history, habitats, ecology, trends, conservation, phenology, and altitudes in Britain and Ireland.

A modelling approach with a correction for recording effort (Frescalo) was used to generate trend estimates for changes in hectad occupancy across four time periods (1930-1969, 1987-1999, 2000-2009, 2010-2019). Both long- (1930-2019) and short-term (1987-2019) trends were produced for most taxa at the scale of Britain, Ireland, England, Wales, Scotland, Northern Ireland, and the Republic of Ireland.

Of the 3,362 taxa mapped for England, long-term trends were calculated for 1,513 taxa (45%) and short-term trends for 2,214 taxa (66%). The most likely driver was attributed to the 300 species that increased or decreased the most over both the long- and short-term (based on their model-based certainty). These attributions were based on expert judgement and included an assessment of recording bias (i.e. the extent to which trends were driven by recording behaviour).

The results showed that 65% of natives and 64% of archaeophytes were estimated to have declined in range at the hectad scale in England since the 1950s, whereas 62% of neophytes were estimated to have increased. The short-term trends were similar with 69% of natives and 63% of archaeophytes estimated to have declined whereas 69% of neophytes were estimated to have increased.

The 10 plant species that increased the most in range in England (in order of their model-based certainty)

Long-term (1930-2019)	Short-term (1987-2019)
Garden Privet <i>Ligustrum ovalifolium</i>	Argentinian Vervain <i>Verbena bonariensis</i>
Lawson's Cypress <i>Cupressus lawsoniana</i>	Water Bent <i>Polypogon viridis</i>
Variegated Yellow Archangel <i>Lamium galeobdolon</i> subsp. <i>argentatum</i>	Garden Lady's-mantle <i>Alchemilla mollis</i>
Hybrid Bluebell <i>Hyacinthoides x massartiana</i>	Mexican Fleabane <i>Erigeron karvinskianus</i>
Bread Wheat <i>Triticum aestivum</i>	Bilbao Fleabane <i>Erigeron floribundus</i>
New Zealand Pigmyweed <i>Crassula helmsii</i>	Druce's Crane's-bill <i>Geranium x oxonianum</i>
Danish Scurvygrass <i>Cochlearia danica</i>	Rye Brome <i>Bromus secalinus</i>
Two-rowed Barley <i>Hordeum distichon</i> s.l.	Phacelia <i>Phacelia tanacetifolia</i>
Grey Alder <i>Alnus incana</i>	Guernsey Fleabane <i>Erigeron sumatrensis</i>
Cherry Laurel <i>Prunus laurocerasus</i>	Narrow-leaved Ragwort <i>Senecio inaequidens</i>

In England plants that had increased the most over both the long- and short-term were ornamental escapes from gardens (33% and 47% respectively) or species deliberately planted for forestry, landscaping and amenity (25% and 28% respectively). Other groups that had increased include more southerly distributed species that have benefited from

climate change (11% and 7%) or species adapted to increased disturbance and eutrophication caused by human activities (10% and 1%) including coastal halophytes that have spread inland along roadsides (2% and 1%). Recording bias accounted for 11% and 8% of increasing trends over the long and short term respectively, largely because of changes in taxonomy and recording behaviour not accounted for by the Frescalo model.

The 10 plant species that decreased the most in range in England (in order of their model-based certainty)

Long-term (1930-2019)	Short-term (1987-2019)
Corn Buttercup <i>Ranunculus arvensis</i>	Canadian Waterweed <i>Elodea canadensis</i>
Good-King-Henry <i>Blitum bonus-henricus</i>	Wild Pansy <i>Viola tricolor</i>
Shepherd's-needle <i>Scandix pecten-veneris</i>	Stinking Chamomile <i>Anthemis cotula</i>
Annual Knawel <i>Scleranthus annuus</i>	Good-King-Henry <i>Blitum bonus-henricus</i>
Stinking Chamomile <i>Anthemis cotula</i>	Tall Rocket <i>Sisymbrium altissimum</i>
Corn Spurrey <i>Spergula arvensis</i>	Heath Groundsel <i>Senecio sylvaticus</i>
Wild Radish <i>Raphanus raphanistrum</i> subsp. <i>raphanistrum</i>	Horned Pondweed <i>Zannichellia palustris</i>
Prickly Poppy <i>Roemeria argemone</i>	Pond Water-crowfoot <i>Ranunculus peltatus</i>
Silver Hair-grass <i>Aira caryophyllea</i>	Pepper-saxifrage <i>Silaum silaus</i>
Wild Pansy <i>Viola tricolor</i>	Slender Soft-brome <i>Bromus lepidus</i>

In England plants that had declined the most over the long- and short-term were poor competitors of infertile grasslands and heathlands that have suffered from widespread loss or modification due to intensive land management (32% and 26% respectively). Similar declines were observed for wetland plants due to increased eutrophication, pollution and habitat change associated with human activities (28% and 28% respectively) and arable plants due to the intensification of agricultural management since the 1950s (19% and 13% respectively). Other major drivers of change include a decline in the management of woodlands (e.g. coppicing) over the long-term (8% and 3% respectively) and a decline in human use for agricultural, culinary or medicinal uses (5% and 6% respectively). Recording bias accounted for 4% and 15% of decreasing trends over the long and short term respectively, largely because of changes in taxonomy and recording behaviour.

Plant Atlas 2020 has revealed how much the English flora has changed over the last century, particularly the spread of non-native species and negative impacts of changes in land management, increased eutrophication and pollution of land and water and the increasing impacts of climate change; these findings provide a powerful evidence-base for nature recovery, conservation, and research and highlights the changes needed to protect, restore and enhance our native flora in the decades to come. These measures include better protection for plants, the restoration of the ecological conditions that they need, managing land more sustainably, putting plants at the centre of conservation schemes, strengthening research, monitoring and surveillance, and raising awareness of the threats plants face and the vital role they play in our daily lives.

Introduction

Plant Atlas 2020 is the Botanical Society of Britain and Ireland's (BSBI) third distribution atlas for the vascular plants and follows atlases published in 1962 (Perring & Walters, 1962) and 2002 (Preston *et al.*, 2002). It was launched in March 2023 and the main outputs included a two-volume book (Stroh *et al.*, 2023), summary reports for Britain (Walker *et al.*, 2023) and Ireland (Faulkner, 2023) and a website presenting the maps, alongside species accounts written by experts, photographs, and information on trends, conservation designations, phenology, apparency, and altitudinal ranges (see plantatlas2020.org). The book included long- and short-trends for most species at the scale of Britain and Ireland, whereas the website also included trends for England, Scotland, Wales, Northern Ireland, and the Republic of Ireland. Except for a few paragraphs in the summary reports, this country-level information has not been assessed in detail.

In this report, we provide a summary of the main findings of *Plant Atlas 2020* for England, including a novel assessment of drivers for the 300 species that increased or decreased the most over the long- and short-term. When attributing drivers, we included an assessment of residual recording bias (i.e. that not accounted for by the model used) as this is important when interpreting trends, especially for species that have been the subject of taxonomic changes or targeted surveys in one survey period. Whilst we did not undertake a formal 'risk-of-bias' assessment as recommended by Boyd *et al.* (2022), the approach taken here still provides an indication of where care is needed when interpreting trends for conservation and land management decision-making. Nomenclature for vascular plants follows Stace (2019).

Methods

A detailed description of the survey methods and analyses are given in the introductory chapters of Stroh *et al.* (2023) which is free to download at <http://plantatlas2020.org>; here we provide a summary of the approach taken and issues pertinent to England. Note that there are biases in any unstructured or semi-structured sampling, and *Plant Atlas 2020* is no exception; readers are encouraged to read Chapter 6 of Stroh *et al.* (2023), which covers these biases in more detail and describes the modelling approach used to provide the species and grouped trends for England summarised here.

Field survey

Fieldwork for *Plant Atlas 2020* was carried out mainly by amateur, expert botanists between 2000 and 2019 and was built on equivalent surveys undertaken in the 1950s and between 1987 and 1999; in these periods, botanists recorded all ferns, flowering plants and charophytes¹ they found growing in wild locations within the c. 3,900 10 × 10 km grid squares (hectads) that make up Britain and Ireland including the Isle of Man and the Channel Islands. In the most recent survey undertaken between 2000 and 2019, records were submitted electronically to the BSBI and collated centrally (from 2010 onwards) within the BSBI records database (BSBI Distribution Database). This allowed efficient targeting of

¹ Charophytes are plant-like multicellular algae that have traditionally been recorded by botanists and so were included in *Plant Atlas 2020*.

fieldwork to areas where coverage was poor as well as the checking and validating of records and maps online.

The coverage achieved during the 2000-2019 survey was very good, with 178,000 recording days² completed and over 26 million records submitted by the end of the project. However, recording effort was variable, being greatest close to major population centres in lowland Britain and lowest in uplands regions with low population density, such as the Scottish Highlands and much of rural Ireland (Fig. 1).

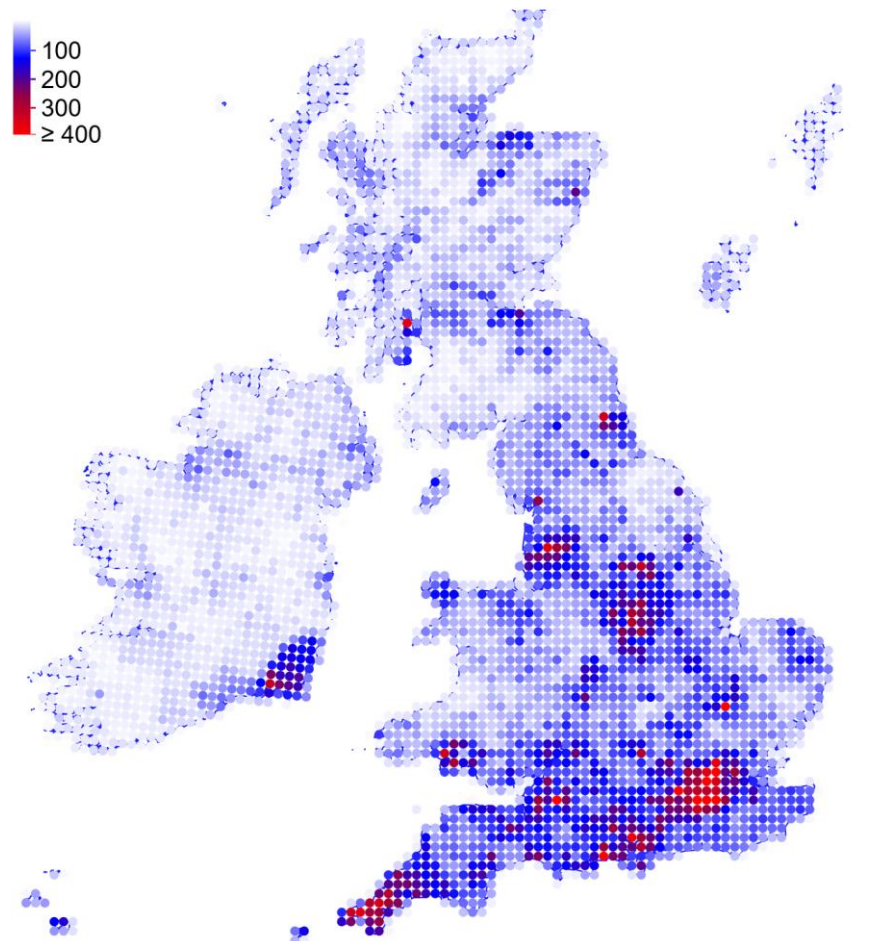


Figure 1. The number of recording days undertaken within each 10 × 10 km square (hectad) in Britain and Ireland during fieldwork for *Plant Atlas 2020* (2000-2019).

As Figure 1 shows, many parts of lowland England had the greatest coverage, especially urban conurbations and their hinterlands in southeast England, the Midlands and northern England, as well as vice-counties that were very well surveyed during the 2000-2019 period, notably Cambridge, Cornwall, Derbyshire, Hampshire, Northumberland, Nottinghamshire, and Somerset, which in some cases reflected the publication of county Floras (Fig. 2; Table

² A recording day is a standard measure of recording activity and is defined as a recording event when 40 or more species were recorded in a 2 × 2 km square (tetrad) on a single visit.

1). Once fieldwork was completed at the end of 2019, BSBI staff spent considerable time checking the maps and assigning status³ to new hectad occurrences for species, often with the help of BSBI vice-county recorders.

Figure 2. English counties floras published since 2000 (see Table 1 for details).

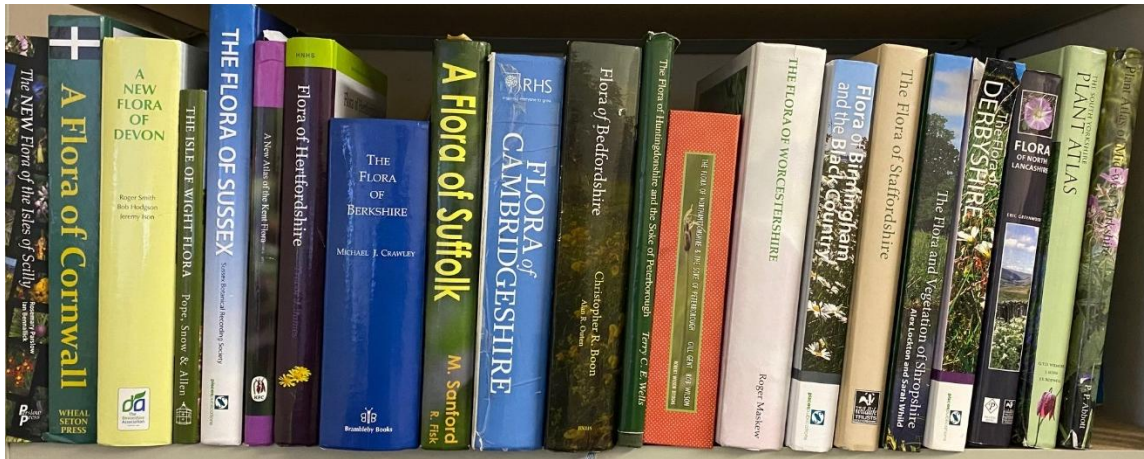


Table 1. English county floras published since 2000.

County (vice-county)	Record unit	Recording period	Author(s)
Isles of Scilly (1)	0.1 km	2000-2016	Parslow & Bennallick (2017)
Cornwall (1, 2)	1 km	2000-2019	French (2020)
Devon (3, 4)	2 km	2000-2014	Smith et al. (2016)
Wight (10)	1 km	1987-2002	Pope et al. (2003)
Sussex (13, 14)	2 km	2000-2015	Abraham et al. (2018)
Kent (16, 17)	2 km	1991-2010	Philp (2010)
Hertfordshire (20)	2 km	1987-2005	James (2009)
Berkshire (22)	Various	Various	Crawley (2005)
Suffolk (25, 26)	2 km	2000-2010	Sanford & Fisk (2010)
Cambridgeshire (29)	Various	Various	Leslie (2019)
Bedfordshire (30)	2 km	1987-2006	Boon & Outen (2011)
Huntingdonshire (31)	2 km	1967-2000	Wells (2003)
Northamptonshire (32)	2 km	2005-2012	Gent & Wilson (2012)
Worcestershire (37)	2 km	1987-2008	Maskew (2014)
Black Country (37, 38, 39)	1 km	1997-2012	Trueman et al. (2012)
Staffordshire (39)	2 km	1995-2008	Hawksford & Hopkins (2011)
Shropshire (40)	1 km	1985-2015	Lockton & Whild (2015)
Derbyshire (57)	2 km	1994-2014	Willmot & Moyes (2015)
North Lancashire (60, 64)	2 km	1964-2012	Greenwood (2012)
South Yorkshire (63)	1 km	2001-2010	Wilmore et al. (2011)
Mid-west Yorkshire (64)	2 km	1980-2004	Abbott (2005)

Assessing changes in distribution

To assess changes in distribution, the hectad occurrences of each species were compared across the recording periods for the three plant distribution atlases published by the BSBI (Perring & Walters, 1962; Preston *et al.*, 2002; Stroh *et al.*, 2023; Fig. 3). To do this a local

³ For all species native to Britain or Ireland, each hectad occurrence was mapped as either native or alien to differentiate between the native and introduced range.

frequency scaling model (Frescalo) was used that estimated an adjustment for variable recording effort over time and space based on the observed frequencies of locally common ‘benchmark’ species (see Hill, 2012). The resulting relative frequency estimates are those of a taxon relative to these benchmark species within the occupied areas. Readers should consult Pescott *et al.* (2019) for more detail on the method and for a justification for its specific application at 10km/broad date-class distribution used here.



Figure 3. The three national plant distribution atlases published by the Botanical Society of Britain and Ireland in 1962 (left), 2002 (middle) and 2023 (right).

The relevant date-classes used for our analyses matched the recording campaigns for the three BSBI atlases namely 1930-69, 1987-1999, 2000-2009, and 2010-2019 for ‘long-term’ trends, whereas ‘short-term’ refers to trends across the 1987-1999, 2000-2009, and 2010-2019 classes only. Note that the date-class 1970-1986 was not used for any trend calculations as the relative attention paid to taxa within this period was too much at variance with species’ true relative frequencies for the recording effort adjustment model used to be valid.

When interpreting the trends presented in *Plant Atlas 2020* it is important to be aware of the following methodological issues that affect the published trend calculations:

- Trend calculations used all mapped data available for a taxon, regardless of assigned native and alien status at the hectad scale. This means that for many nationally native and archaeophyte taxa, trends incorporate modern (neophyte) introductions (e.g. Italian Lords-and-Ladies *Arum italicum*, Pendulous Sedge *Carex pendula*, Cornflower *Centaurea cyanus*, Stinking Iris *Iris foetidissima*, Welsh Poppy *Papaver cambricum*, Wood Forget-me-not *Myosotis sylvatica*).
- The long-term trend was only calculated for a subset of taxa and aggregates that were mapped in the 1962 *Atlas*, although some unmapped taxa were included as aggregates (see ‘Modelled trend summaries’ on page 31 of Stroh *et al.* 2023 for further details).

- Some taxa that have been recorded inconsistently in the past due to taxonomic changes or identification difficulty were either excluded or treated as aggregates (e.g. *Agrostis canina* agg. including Velvet Bent *A. canina* s.s. and Brown Bent *A. vinealis*). These exclusions also included many hybrids and subspecies, and all microspecies of the large apomictic genera of hawkweeds *Hieracium*, brambles *Rubus*, and dandelions *Taraxacum*.
- Although analysed, results for native taxa present in 15 or fewer hectads in Britain within the relevant time periods covered by the trend are not presented as there was typically very high uncertainty in the modelled outputs due to their very low frequency. Likewise, neophytes occurring in 30 or fewer hectads between 1987 and 2019 across the whole of Britain and Ireland were excluded from the analyses of short-term trends.
- Whilst the Frescalo method addresses variable recording effort over time and space, like any generalised approach used across hundreds of taxa, it has limited ability to account for specific systematic biases in data, such as changes in recording behaviour or surveys targeting species or species groups independently of the overall expenditure of effort. In this report we have used expert opinion to highlight where we feel that these recording biases are relevant to the interpretation of both long- and short-term trends. Whilst this is not a full 'risk-of-bias' assessment, it should guide readers in their understanding of the underlying cause(s) of change in the distribution of plants in England over the last century.

Trend metrics

The Frescalo model outputs a relative frequency estimate for a species in each time-period, along with a measure of uncertainty (its standard deviation). To take account of this uncertainty, a random sample of 100 compatible linear trends were fitted to these frequency estimates per time-period (Fig. 4a) and the slopes and standard deviation were then used to calculate the mean slope and its model-based certainty. It is important to note that resulting species trend estimates can be ordered in terms of their mean absolute slope (ignoring their certainty) or model-based certainty. In most cases, the latter has been used here as these are the species with the most 'certain' trends (see 'Metrics of change on page 18 of Stroh *et al.* (2023) for further details).

The distribution of these 100 slope estimates (Fig. 4b) was also used to visualise the overall trends within five trend categories (Fig. 4c & 4d); strong decline, moderate decline, stable, moderate increase, and strong increase. The reader is referred to Pescott *et al.* (2022) for a justification of this approach. For ease of interpretation, these five categories have been combined into three trend categories (decrease, stable, increase) to summarise trends for all species in relation to national status (Fig. 6).

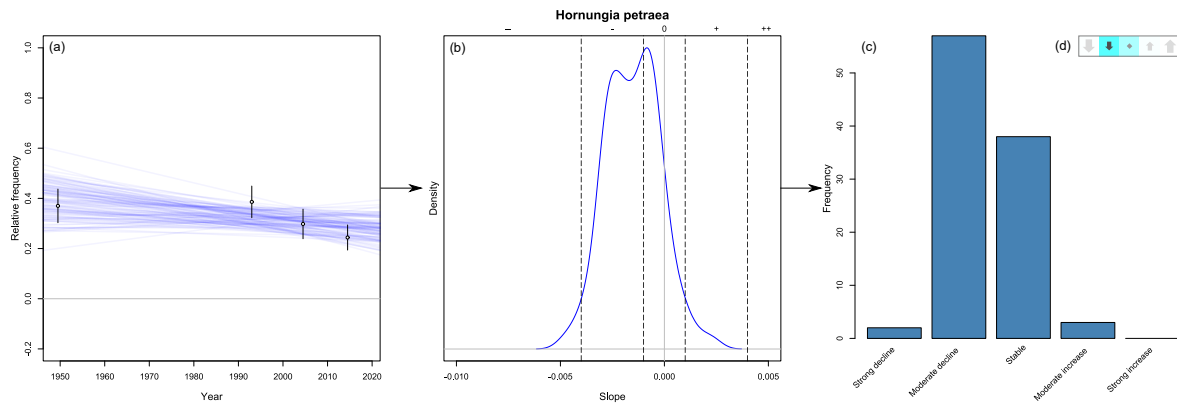


Figure 4. An example of the flow of information and uncertainty through the analyses used to calculate trends for *Plant Atlas 2020*. The example given is *Hutchinsia Hornungia petraea*. In (a) the circles and bars are the Frescalo means and standard deviations for the four time periods, plotted at the median year of each Atlas date-class (1930-1969; 1987-1999; 2000-2009; 2010-2019); the transparent blue lines represent a random selection of 100 trends that are compatible with these estimates. In (b) the smoothed blue line is the distribution of the 100 slope estimates from (a) with stability (0) indicated by an unbroken grey vertical line. The black vertical broken lines in (b) represent the discretization scheme used in (c) which divides the slopes into five easy-to-interpret trend categories. Inset (d) is just a simplified summary of (c) and is presented alongside each species' caption in the *Plant Atlas 2020* book and on the website for trends at the level of Britain and Ireland.

Assigning drivers of change

We focussed on the 300 species with the most 'certain' trends, which is those with the highest model-based certainty rather than absolute mean slope estimates. We therefore undertook 1,200 assessments in total (300 long-term increasing + 300 short-term increasing + 300 long-term decreasing + 300 short-term decreasing). For each trend we assigned the most likely driver of change based on the comments on trends in the second paragraph of the species accounts in Stroh *et al.* (2023) as well as the knowledge of the first author. A brief description of each of these drivers is given in Table 2. It is important to note that 'recording bias' was used to distinguish trends that most likely reflected systematic differences in the way a species had been recorded in successive atlas surveys, for example because of changes in taxonomic or ecological understanding and/or targeted surveys that strongly influenced the rate of reporting. Whilst this was not a full 'risk-of-bias' assessment (*sensu* Boyd *et al.*, 2022) it provides an indication of where care is needed when interpreting trends. Finally, it is also important to note that we only attributed a single driver based on expert knowledge, but many trends are likely to combine responses to multiple drivers.

Grouped trends

As well as trends for individual species, average changes over the long-term are presented for groups of species with the same national status (native, archaeophyte, neophyte) and with similar habitat associations (broad habitats), ecological attributes (Ellenberg indicator values), and biogeographic affinities (major biomes). For national status, we used the slope estimates (without uncertainty) and for ease of interpretation we converted the five change categories (strong decrease, decrease, stable, increase, strong increase) to three (decrease, stable, increase).

In comparison, the slope estimates for the ecological groupings were estimated in a similar way to individual species linear trends but using generalised additive models (GAMs) to capture potential non-linearity; however, a different approach was taken to propagate the uncertainty from the 100 compatible trends to grouped multi-species lines and the reader is referred to Chapter 6 of Stroh et al. (2023) for further details. All grouping variables were taken from Hill *et al.* (2004) with a small number of expert amendments and additions; apart from status, all grouped trends were limited to the long-term analysis since numerous taxa (mainly neophytes) included in the short-term analysis lack values for numerous of the grouping variables used. In these graphs the solid trend lines in these plots represent the median trend across the taxa averaged, and the ribbon or band represents the 90% uncertainty interval for this. Aggregating over taxa within groups should help to reduce bias on average, although it should be borne in mind that such averaging will not eliminate bias where there is a correlation between group membership and the probability of a trend being biased in a particular direction. See Chapter 6 of Stroh et al. (2023) for a fuller discussion of the likely biases in the *Plant Atlas 2020* dataset.

Table 2. The main drivers attributed to species trends in this report.

Driver	Description
Air quality	Changes in air quality due to an increase/decrease of pollutants such as ozone, nitrogen oxides, sulphur dioxide, carbon monoxide, particles, hydrocarbons and metallic pollutants that impact plants and their habitats.
Arable change	Loss or modification of arable habitats due to the abandonment of small-scale cropping and increased intensity of management including the increased use of herbicides and fertilisers and improved screening and/or cleaning of contaminants from seed.
Assisted spread	The assisted spread of plants through the movement of humans, vehicles, and their livestock.
Climate change	Habitat modification caused by the effects of climate warming including the loss of cooler microclimates (e.g. snow patches), increased frequency/severity of droughts, fewer and less severe frosts, increased frequency/severity of storms leading to increased disturbance due to flooding, etc.
Contaminant	The introduction of plants as contaminants in raw materials such as seed, soil, sand gravel, and waste materials such as wool shoddy, etc.
Eradication	The control of plants viewed as pests in agriculture and forestry as well as non-native species impacting native species and habitats.
Eutrophication	Destruction or modification of low fertility habitats due to land use change, increased intensity of management, and increased nutrient inputs from agriculture, pollution, transport, etc.
Garden escape	The spread of ornamental plants away from gardens because of natural dispersal or human movement of propagules in soil, water, garden waste, etc.
Gentrification	The destruction of ruderal/waste habitats through herbicide-spraying, the 'tidying-up' up rural and urban areas, redevelopment of derelict land, etc.
Halophyte inland	The spread inland of coastal halophytes along salt-treated roads.
Herbicide resistance	Plants that have increased in abundance in arable habitats due to their ability to tolerate artificial herbicides such as glyphosate.
Human use	Changing frequency due to human use (e.g. cultivation, planting).
Overgrazing	Changes in distribution due to increased levels of grazing by sheep, rabbits and deer.
Pests & pathogens	Direct loss of species due to spread of novel pests and pathogens and indirect effects due to changes in habitat composition and structure.

Recording bias	Systematic differences in the way a species had been recorded in successive atlas periods due to changes in taxonomy, targeted surveys or recording behaviour.
Wetland change	Destruction or modification of wetland habitats through land use change, changing hydrology (e.g. drainage, engineering, dam construction), management change or through changes in water quality/chemistry.
Woodland change	Destruction or modification of woodland habitats through land use change, afforestation, or changes in management practices.

Results

Species coverage

Table 3 gives a breakdown of the taxa mapped for England in *Plant Atlas 2020* as well as those with estimated trends in relation to national status. Of the 3,495 taxa covered by the *Plant Atlas 2020* project, 3,362 were mapped for England including 1,588 natives, 160 archaeophytes, and 1,614 neophytes. Of those, 1,513 (45%) and 2,214 (66%) had associated long- and short-term trends respectively including 1,133 (71%) and 1,180 (74%) of natives and 144 (90%) and 150 (94%) of archaeophytes respectively. In comparison, only 236 (15%) neophytes had long-term trends as most introductions were not mapped in the 1962 *Atlas*. This figure was much higher for short-term trends (55%) as many more non-natives were mapped in the *New Atlas* (Preston *et al.*, 2002) and therefore the change in distribution could be calculated across the three date-classes used to analyse short-term trends (1987-1999; 2000-2009; 2010-2019).

Table 3. The number of English vascular plant taxa included in *Plant Atlas 2020* that were mapped and for which long- and short-term trend estimates were available.

National status ¹	Mapped in <i>Plant Atlas 2020</i>	Long-term trend		Short-term trend	
		Taxa	%	Taxa	%
Native ²	1588	1133	71	1180	74
Archaeophyte	160	144	90	150	94
Neophyte	1614	236	15	884	55
Total	3362	1513	45	2214	66

1 – National status for England and not Britain as a whole. 2 – Includes species categorised as ‘native or alien’.

Table 4 gives a breakdown of the 1,849 and 1,148 mapped taxa that lacked long- and short-term trends respectively. Over both the long- and short-term most taxa lacking trends were either rare neophytes or natives, hybrids, subspecies, species with complex taxonomy and charophytes all of which had too few data to estimate trends effectively.

Table 4. The number of English vascular plant species that were mapped in *Plant Atlas 2020* but lacked trends for England for the reasons given in the table below.

Reason for lack of trend	Long-term trend	Short-term trend
Rare neophyte (<30 hectads in GB & Ireland)	1262	654
Hybrid taxon	235	188
Rare native (<15 hectads in GB)	103	102
Complex taxonomy	94	62
Subspecies	79	67
Charophyte	31	31

Newly described or discovered	29	28
Regionally extinct in England	16	16
Total	1849	1148

In addition, a small number of species were excluded because they have only been discovered or newly described for England in the last two decades or they are thought to be regionally extinct (Table 5).

Table 5. Plants discovered, newly described or regionally extinct in England.

Discovered or newly described for England since 2000	
Dune Helleborine <i>Epipactis dunensis</i>	Evans' Whitebeam <i>Sorbus evansii</i> Green's
Inland Club-rush <i>Bolboschoenus laticarpus</i>	Whitebeam <i>Sorbus greenii</i>
Scarce Tufted-sedge <i>Carex cespitosa</i>	Herefordshire Whitebeam <i>Sorbus herefordensis</i>
Intermediate Centaury <i>Centaureum intermedium</i>	Leigh Woods Whitebeam <i>Sorbus leighensis</i>
Diaphanous Bladder-fern <i>Cystopteris diaphana</i>	Margaret's Whitebeam <i>Sorbus margaretae</i>
Cypress Clubmoss <i>Diphasiastrum tristachyum</i>	Ship Rock Whitebeam <i>Sorbus parviloba</i>
Upright Forget-me-not <i>Myosotis stricta</i>	Rich's Whitebeam <i>Sorbus richii</i>
Grassington Cinquefoil <i>Potentilla cryeri</i>	Gough's Rock Whitebeam <i>Sorbus rupicoloides</i>
York Ragwort <i>Senecio eboracensis</i>	Symonds Yat Whitebeam <i>Sorbus saxicola</i>
Tongue-orchid <i>Serapias lingua</i>	Observatory Whitebeam <i>Sorbus spectans</i>
Watersmeet Whitebeam <i>Sorbus admonitor</i>	White's Whitebeam <i>Sorbus whiteana</i>
Cheddar Whitebeam <i>Sorbus cheddarensis</i>	New Forest Bladderwort <i>Utricularia breinii</i>
Llangollen Whitebeam <i>Sorbus cuneifolia</i>	Nordic Bladderwort <i>Utricularia stygia</i>
Doward Whitebeam <i>Sorbus eminentiformis</i>	Thin-leaved Horned-pondweed <i>Zannichellia obtusifolia</i>
Twin Cliffs Whitebeam <i>Sorbus eminentoides</i>	
Regionally extinct in England	
Smooth Rock-spleenwort <i>Asplenium fontanum</i>	Downy Hemp-nettle <i>Galeopsis segetum</i>
Interrupted Brome <i>Bromus interruptus</i>	Esthwaite Waterweed <i>Hydrilla verticillata</i>
Davall's Sedge <i>Carex davalliana</i>	Narrow-leaved Cudweed <i>Logfia gallica</i>
Three-nerved Sedge <i>Carex trinervis</i>	Whorled Solomon's-seal <i>Polygonatum verticillatum</i>
Small Bur-parsley <i>Caucalis platycarpus</i>	Violet Horned-poppy <i>Roemeria hybrida</i>
Pigmyweed <i>Crassula aquatica</i>	Rannoch-rush <i>Scheuchzeria palustris</i>
Alpine Bladder-fern <i>Cystopteris alpina</i>	Summer Lady's-tresses <i>Spiranthes aestivalis</i>
Purple Spurge <i>Euphorbia peplis</i>	Marsh Fleawort <i>Tephrosia palustris</i>

The overall diversity of native species, archaeophytes and neophytes recorded at the hectad scale for *Plant Atlas 2020* is shown in Figure 5. Much of lowland England has much higher alpha diversity (i.e. 10 km square richness) relative to the rest of Britain, especially when compared to upland regions in Wales and Scotland. This was most marked for archaeophytes and neophytes which are largely concentrated in southern, southeastern and eastern England.

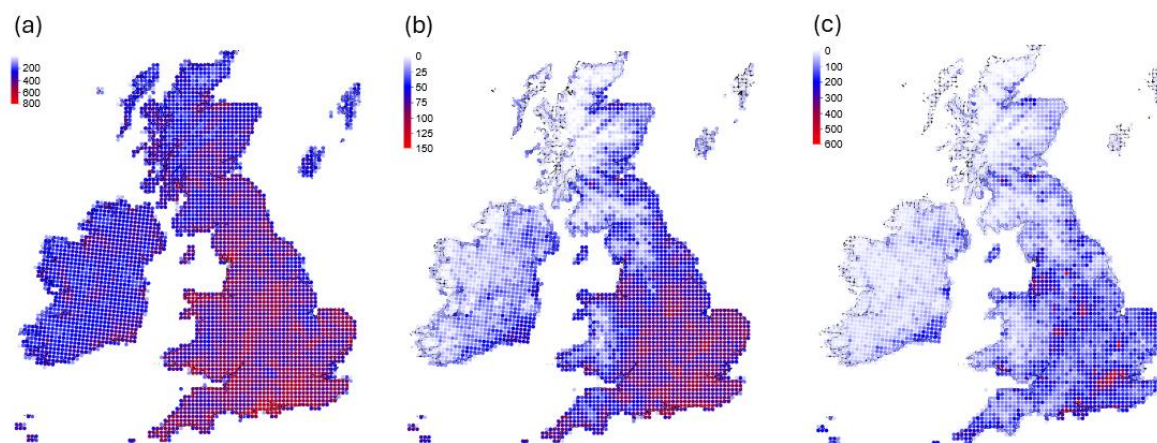


Figure 5. Number of vascular plant species recorded per hectad in Britain and Ireland for *Plant Atlas 2020* between 2000 and 2019: (a) native species; (b) archaeophytes; and (c) neophytes. Note the different ranges for species diversity in the keys.

Trends in relation to status

Of the species analysed for England, 65% of natives and 64% of archaeophytes had decreasing trends in England since the 1950s, whereas 62% of neophytes had increasing trends over the same period (Fig. 6a). The analyses of the short-term trends showed a similar pattern with 69% of natives and 63% of archaeophytes having declined in range and 69% of neophytes having increased (Fig. 6b).

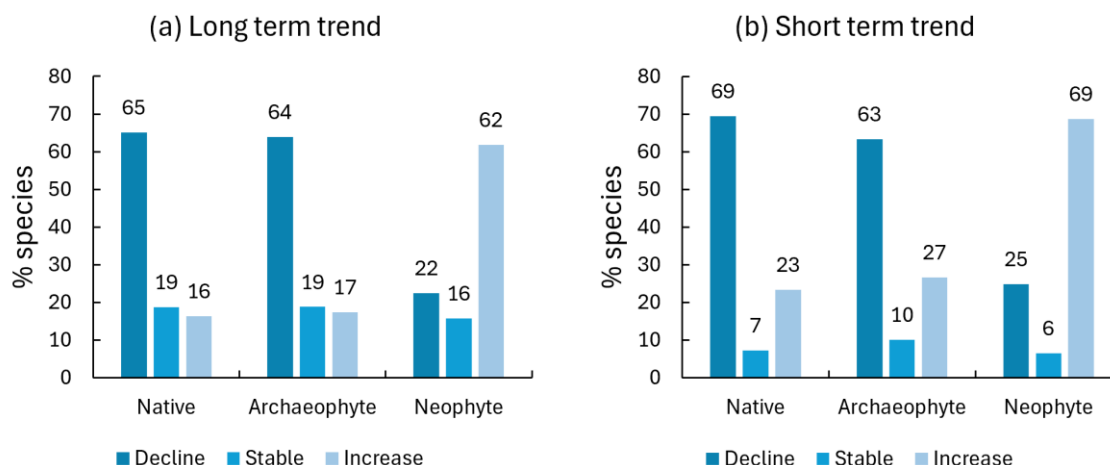


Figure 6. The proportion of vascular plants displaying mean decreasing, increasing or stable trends at the 10 km square scale in England over the (a) long- (1930-2019) and (b) short-term (1987-2019). Trends are shown in relation to whether species are native to England or were introduced by humans before or after 1500 (archaeophytes and neophytes respectively).

The grouped long-term trends show a very similar pattern (Fig. 7a) with natives and archaeophytes having undergone consistent declines in relative frequency since the 1950s whereas neophytes consistently increased as a group over the same period; this reflects genuine increases in occupancy of non-native plants in England although this is also likely to have been strongly influenced by an increase in the recording of non-natives in the wild in

recent decades, especially since their greater coverage in standard field guides since the early 1990s onwards (Stace & Crawley, 2015).

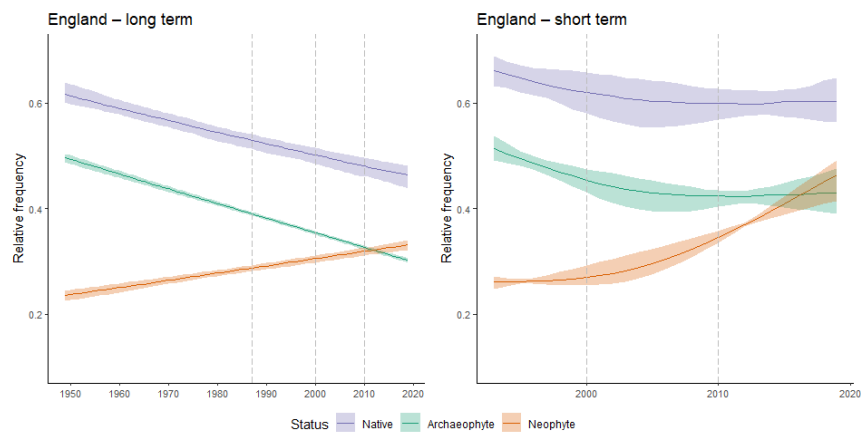


Figure 7. Smoothed status trends for England showing medians (dashed lines) with 90% uncertainty intervals: (a) long-term trend, and (b) short-term trend.

The equivalent short-term trends were similar (Fig. 7b) but in general the declines of natives and archaeophytes were less steep, possibly reflecting a relative reduction in drivers/pressures in recent decades although with a wide margin of uncertainty. In comparison, the increase in the frequency of neophytes had become more marked possibly reflecting a genuine increase in the distribution of many species as well as increased effort in recording their presence in the wild.

Increasing species

Table 5 provides a summary of the top 300 species with the most ‘certain’ increases in England, as opposed to those with the largest absolute mean slopes, summarised in relation to the main driver assigned in *Plant Atlas 2020* or by the first author. As stated above, we have attributed the most likely driver to each species, but most trends are likely to combine responses to multiple drivers and recording bias to some extent, although the large-scale effort component of this should have been minimised by the Frescalo modelling approach described above.

What is most striking about both lists of increasing species is the dominance of neophytes, which accounted for 46% and 80% of species over the long- and short-term respectively. While these positive trends reflect an increasing encounter rate of neophytes in wild locations due to planting and escapes from gardens, it is also partly explained by more systematic recording of non-native plants in recent decades, especially with the increasing number of non-natives included in standard floras from the 1990s onwards (Stace & Crawley, 2015).

Overall, the main group of plants that increased the most in England, accounting for 33% of long- and 47% of short-term trends respectively, were ornamental plants that had escaped from gardens and are now well established in wild locations. Notable examples that are widespread in England include Butterfly-bush *Buddleja davidii*, Montbretia *Crocasmia x crocosmiiflora*, Mexican Fleabane *Erigeron karvinskianus*, Hybrid Bluebell *Hyacinthoides x massartiana*, variegated Yellow Archangel *Lamium galeobdolon* subsp. *argenteum*,

Himalayan Honeysuckle *Leycesteria formosa*, Purple Toadflax *Linaria purpurea*, Fox-and-cubs *Pilosella aurantiaca*, Fringecups *Tellima grandiflora* and Argentinian Vervain *Verbena bonariensis*, as well as neophytes that have negatively impacted native species and assemblages, such as Garden Lady's-mantle *Alchemilla mollis*, Few-flowered Garlic *Allium paradoxum*, cotoneasters *Cotoneaster* spp., New Zealand Pigmyweed *Crassula helmsii*, Giant Hogweed *Heracleum mantegazzianum*, Himalayan Balsam *Impatiens glandulifera*, American Skunk-cabbage *Lysichiton americanus*, Giant-rhubarbs *Gunnera* spp., Green Alkanet *Pentaglottis sempervirens*, Rhododendron *Rhododendron ponticum*, Japanese Rose *Rosa rugosa* and Giant Blackberry *Rubus armeniacus*.

Table 5. The top 300 increasing plants in England over the long- and short-term in relation to main driver and status (Nat = native; Arc = archaeophyte; Neo = neophyte).

Main driver	Long-term increase					Short-term increase				
	Nat	Arc	Neo	Tot	%	Nat	Arc	Neo	Tot	%
Air quality	1	0	0	1	0	0	0	0	0	0
Assisted spread	0	0	2	2	1	0	0	8	8	3
Climate change	23	6	3	32	11	13	4	4	21	7
Contaminant	1	0	13	14	5	1	0	10	11	4
Eutrophication	21	4	5	30	10	3	0	1	4	1
Garden escape	24	4	71	99	33	9	2	130	141	47
Halophyte inland	7	0	0	7	2	4	0	0	4	1
Herbicide resistance	1	2	1	4	1	0	1	1	2	1
Human use	30	4	42	76	25	8	3	74	85	28
Recording bias	29	2	1	32	11	12	0	12	24	8
Wetland change	2	0	0	2	1	0	0	0	0	0
Woodland change	1	0	0	1	0	0	0	0	0	0
Total species	140	22	138	300		50	10	240	300	
% of total	47	7	46			17	3	80		

The next largest group of plants that have increased were those that have been increasingly utilised by humans since the 1950s, accounting for 25% and 28% of increasing species over the long- and short-term respectively. These include several groups, notably:

- Trees and shrubs that have been widely planted for ornamental or landscaping purposes (e.g. Norway Maple *Acer platanoides*, Grey Alder *Alnus incana*, Red-osier Dogwood *Cornus sericea*, Lawson's Cypress *Cupressus lawsoniana*, Leyland Cypress *C. x leylandii*, Garden Privet *Ligustrum ovalifolium*, Cherry Plum *Prunus cerasifera*, Cherry Laurel *P. laurocerasus*, Swedish Whitebeam *Sorbus intermedia*, Wayfaring-tree *Viburnum lantana*).
- Conifers planted for commercial timber production, including several species that have self-seeded and regenerated within and outside plantations on adjacent moorlands and peatlands (e.g. Sitka Spruce *Picea sitchensis*, Lodgepole Pine *Pinus contorta*, Western Hemlock-spruce *Tsuga heterophylla*).
- Some root and cereal crops that have occurred increasingly as crop relics after planting or where seed has been spilt (e.g. Root Beet *Beta vulgaris* subsp. *vulgaris*, Rape *Brassica napus*, Turnip *B. rapa*, Two-rowed Barley *Hordeum distichon*, Flax

Linum usitatissimum, Bread Wheat *Triticum aestivum*, Rye *Secale secale*, Broad Bean *Vicia faba*, Maize *Zea mays*).

- Crop relics from the sowing of green manure, game cover or 'wildlife seed-mixtures' on farmland or in urban greenspaces (e.g. Borage *Borago officinalis*, Cornflower *Centaurea cyanus*, Quinoa *Chenopodium quinoa*, Chicory *Cichorium intybus*, Purple Viper's-bugloss *Echium plantagineum*, Sunflower *Helianthus annuus*, Phacelia *Phacelia tanacetifolia*, Crimson Clover *Trifolium incarnatum*).
- Ornamentals that have increased due to deliberate planting in wild locations from where they sometimes have spread (e.g. crocuses *Crocus* spp., Snake's-head Fritillary *Fritillaria meleagris*, snowdrops *Galanthus* spp., daffodils *Narcissus* spp., White Water-lily *Nymphaea alba*, Fringed Water-lily *Nymphoides peltata*, Water-soldier *Stratiotes aloides*).

The third main group of increasing species over both the long- and short-term were species that have responded positively to climate change (11% and 7% respectively) or whose trends have been influenced by recording bias (11% and 8% respectively). *Plant Atlas 2020* revealed that around 30 native plants appear to have increased their range in England due to climate change, presumably because milder winters and less severe frosts in recent decades have allowed them to survive further north and west. Some of the most remarkable expansions in range include the southerly distributed orchids Pyramidal Orchid *Anacamptis pyramidalis*, Southern Marsh-orchid *Dactylorhiza praetermissa* and Bee Orchid *Ophrys apifera* and the ferns Hart's-tongue *Asplenium scolopendrium* and Soft Shield-fern *Polystichum setiferum* which have increased their range in the northern half of England. Others notable range expansions include Mediterranean species that were formerly restricted to coastal regions in southern England with mild climates but in recent decades have expanded their ranges northwards and inland, where they have often colonised ruderal habitats subject to drought stress (e.g. Mossy Stonecrop *Crassula tillaea*, Wall Bedstraw *Galium parisiense*, Bulbous Meadow-grass *Poa bulbosa*, Early Meadow-grass *P. infirma*, Four-leaved Allseed *Polycarpon tetraphyllum*). Similar shifts have been noted for several archaeophytes (Wild Leek *Allium ampeloprasum*, Musk Stork's-bill *Erodium moschatum*, Bristly Oxtongue *Helminthotheca echioides*, Keeled-fruited Cornsalad *Valerianella carinata*) and neophytes (Giant Viper's-bugloss *Echium pininana*, Walnut *Juglans regia*, Jersey Cudweed *Laphangium luteoalbum*, Balm-leaved Figwort *Scrophularia scorodonia*).

Recording bias accounted for 11% and 7% of increasing species over the long- and short-term. Many of these species have not been recorded consistently in the past making assessments of change unreliable. There appear to be several reasons for these apparent increases:

- Taxonomic changes leading to greater recognition of a taxon in later recording periods (e.g. Prickly Sedge *Carex muricata*, Spiked Sedge *C. spicata*, scaly-male ferns *Dryopteris affinis* agg., eyebrights *Euphrasia* spp., Sheep's Fescue *Festuca ovina*, Bifid Hemp-nettle *Galeopsis bifida*, Common Hemp-nettle *G. tetrahit*, Yellow-juiced Poppy *Papaver lecoqii*, Intermediate Polypody *Polypodium interjectum*, watercresses

Nasturtium officinale s.s., roses *Rosa* spp., Sea Mayweed *Tripleurospermum maritimum*, Deergrass *Trichophorum germanicum*).

- Improved understanding of the ecology/distribution of a taxon in England that was over-looked in earlier recording periods (e.g. Common Rampion *Fumaria muralis*, French Oat-grass *Gaudinia fragilis*, Spreading Meadow-grass *Poa humilis*, Grey Club-rush *Schoenoplectus tabernaemontani*, Lesser Chickweed *Stellaria pallida*) in some cases because of more intensive surveys of upland regions (e.g. Sheathed Sedge *Carex vaginata*, Northern Marsh-orchid *Dactylorhiza purpurella*, Northern Buckler-fern *Dryopteris expansa*, Bog Pondweed *Potamogeton polygonifolius*, Bog Bilberry *Vaccinium uliginosum*).
- Identification errors that appear to have made a taxon appear more widespread in later recording periods (e.g. Tutsan *Hypericum androsaemum*, Atlantic Ivy *Hedera hibernica*).
- Improved recording of hybrids and non-natives in later recording periods (e.g. *Carex hostiana* × *viridula* s.l., Hybrid Oak *Quercus* × *rosacea*, Spanish-dagger *Yucca gloriosa*).

In England, another major driver of floristic change has been increased eutrophication and disturbance brought about by human activities, in particular agriculture and the development of road and urban infrastructure (10% of long-term trends). These have benefited plants associated with higher nutrient-levels in both soils and water (e.g. Creeping Bent *Agrostis stolonifera*, Sticky Mouse-ear *Cerastium glomeratum*, Great Willowherb *Epilobium hirsutum*, dead-nettles *Lamium* spp., Rough Meadow-grass *Poa trivialis*, Common Chickweed *Stellaria media*, Bulrush *Typha latifolia*) and increased disturbance (e.g. bitter-cresses *Cardamine* spp., Beaked Hawk's-beard *Crepis vesicaria*, Wild Teasel *Dipsacus fullonum*, Prickly Lettuce *Lactuca serriola*, Lesser Swine-cress *Lepidium didymum*, Pineappleweed *Matricaria discoidea*, sow-thistles *Sonchus* spp.).

All other drivers were more minor, the most significant of which were:

- Contaminants, mainly non-native grasses, which had been introduced in seed or raw materials used for agriculture (e.g. Cockspur *Echinochloa crus-galli*, Common Millet *Panicum miliaceum*, American bromes *Ceratochloa* spp., bristle-grasses *Setaria* spp.) but more recently in wild bird seed (e.g. Niger *Guizotia abyssinica*) and in soil via the horticultural trade (e.g. New Zealand Bitter-cress *Cardamine corymbosa*).
- Coastal halophytes that have spread inland along roads treated with rock salt since the 1970s (e.g. Grass-leaved Orache *Atriplex littoralis*, Sea Fern-grass *Catapodium marinum*, Danish Scurvy-grass *Cochlearia danica*, Buck's-horn Plantain *Plantago coronopus*, Reflexed Saltmarsh-grass *Puccinellia distans*, Sea Pearlwort *Sagina maritima*, Lesser Sea-spurrey *Spergularia marina*).
- Arable species that have increased amongst crops due to herbicide resistance (e.g. Great Brome *Anisantha diandra*, Wild Oat *Avena fatua*, Smooth Brome *Bromus racemosus*, Rye Brome *B. secalinus*).

Declining species

Long-term trends

Table 6 provides a summary of the top three hundred species with the most ‘certain’ declines in England (as opposed to those with the largest absolute mean slopes) in relation to the main driver. In contrast to increasing species (Table 5), both lists are dominated by native species which account for 77% and 72% of species respectively whereas archaeophytes account for 18% and 15% and neophytes for 5% and 13% respectively.

Table 6. The top 300 declining plants in England in relation to main driver and status (Nat = native; Arc = archaeophyte; Neo = neophyte).

Main driver	Long-term increase					Short-term increase				
	Nat	Arc	Neo	Tot	%	Nat	Arc	Neo	Tot	%
Arable change	13	42	1	56	19	8	29	2	39	13
Contaminant	0	0	4	4	1	0	0	8	8	3
Eradication	1	0	0	1	0	1	0	2	3	1
Eutrophication	97	0	0	97	32	76	2	0	78	26
Gentrification	0	2	3	5	2	0	1	2	3	1
Human use	2	8	5	15	5	2	10	7	19	6
Overgrazing	1	0	0	1	0	1	0	0	1	0
Pests & pathogens	0	0	2	2	1	0	0	2	2	1
Recording bias	9	1	1	11	4	33	2	11	46	15
Unknown	0	0	0	0	0	1	1	5	7	2
Wetland change	85	0	0	85	28	84	0	0	84	28
Woodland change	23	0	0	23	8	10	0	0	10	3
Total species	231	53	16	300		216	45	39	300	
% of total	77	18	5			72	15	13		

The largest group of long-term decliners in England, accounting for 32% of the species assessed, were plants associated with species-rich grasslands and heathlands found on nutrient-poor soils that have been lost or modified due to increased disturbance and eutrophication associated with human activities (Table 7). Many of these plants are small herbs and grasses that are reliant on grazing and nutrient-poor substrates to reduce competition from more vigorous species; they therefore disappear quickly following agricultural improvement, abandonment, or increasing levels of nutrients from atmospheric sources. Examples that are still relatively widespread in calcareous and neutral grasslands in England include Betony *Betonica officinalis*, Harebell *Campanula rotundifolia*, Lady’s-bedstraw *Galium verum*, Common Rock-rose *Helianthemum nummularium*, Fairy Flax *Linum catharticum*, Common Milkwort *Polygala vulgaris*, Devil’s-bit Scabious *Succisa pratensis* and Wild Thyme *Thymus drucei*; equivalent species of acidic soils include Heather *Calluna vulgaris*, Field Mouse-ear *Cerastium arvense*, Bell Heather *Erica cinerea*, Heath Bedstraw *Galium saxatile*, Trailing St John’s-wort *Hypericum pulchrum*, Bitter-vetch *Lathyrus linifolius*, Tormentil *Potentilla erecta*, and Sheep’s Sorrel *Rumex acetosella*.

The second main group of long-term decliners in England, accounting for 28% of the species assessed, were wetland species that have experienced marked reductions in their range due to a range of factors:

- Fully aquatic and emergent plants of rivers and standing waters that have declined due to increased pollution and disturbance (e.g. Water-plantain *Alisma plantago-aquatica*, Lesser Water-parsnip *Berula erecta*, bur-marigolds *Bidens* spp., Common Spike-rush *Eleocharis palustris*, Water Horsetail *Equisetum fluviatile*, sweet-grasses *Glyceria* spp., water-cresses *Helosciadium* spp., Opposite-leaved Pondweed *Groenlandia densa*, Ivy-leaved Duckweed *Lemna trisulca*, Fine-leaved Water-dropwort *Oenanthe aquatica*, pondweeds *Potamogeton* spp., Fan-leaved Water-crowfoot *Ranunculus circinatus*, Greater Water-parsnip *Sium latifolium*, Water Chickweed *Stellaria aquatica*, Horned-pondweed *Zannichellia palustris*).
- Wetland plants of mires, flushes, fens, marshes and swamps that have declined due to habitat loss and modification due to land use change, drainage and eutrophication (e.g. Sneezewort *Achillea ptarmica*, Lesser Water-plantain *Baldellia ranunculoides*, Flat-sedge *Blysmus compressus*, sedges *Carex* spp., Whorl-grass *Catabrosa aquatica*, Marsh Cinquefoil *Comarum palustre*, marsh-orchids *Dactylorhiza* spp., Round-leaved Sundew *Drosera rotundifolia*, Marsh Horsetail *Equisetum palustre*, Common Cottongrass *Eriophorum angustifolium*, water-dropworts *Oenanthe* spp., Grass-of-Parnassus *Parnassia palustris*, louseworts *Pedicularis* spp., Common Butterwort *Pinguicula vulgaris*, Marsh Stitchwort *Stellaria palustris*, Common Meadow-rue *Thalictrum flavum*, Marsh Arrowgrass *Triglochin palustris*, valerians *Valeriana* spp., Marsh Speedwell *Veronica scutellata*, Marsh Violet *Viola palustris*).

The third main group of long-term decliners in England, accounting for 19% of species assessed, were species associated with arable land that have decreased in range due to the increased intensity of management, most notably increased usage of artificial pesticides, herbicides and fertilisers which has reduced the 'weediness' of crops since the 1950s (Storkey *et al.*, 2012). Such management has led to declines in very widespread species such as Fool's Parsley *Aethusa cynapium*, Sun Spurge *Euphorbia helioscopia*, Black-bindweed *Fallopia convolvulus*, Common Fumitory *Fumaria officinalis*, dead-nettles *Lamium* spp., Scarlet Pimpernel *Lysimachia arvensis*, Common Poppy *Papaver rhoeas*, Corn Spurrey *Spergula arvensis* but also many more localised species that are now rare in arable habitats such as Pheasant's-eye *Adonis annua*, chamomiles *Anthemis* spp., Field Gromwell *Buglossoides arvensis*, Basil Thyme *Clinopodium acinos*, Red Hemp-nettle *Galeopsis angustifolia*, Large-flowered Hemp-nettle *G. speciosa*, Corn Marigold *Glebionis segetum*, Venus's-looking-glass *Legousia hybrida*, Weasal's-snout *Misopates orontium*, Corn Buttercup *Ranunculus arvensis*, Prickly Poppy *Roemeria argemone*, Shepherd's-needle *Scandix pecten-veneris*, Annual Knawel *Scleranthus annuus*, Small-flowered Catchfly *Silene gallica*, Night-flowered Catchfly *Silene noctiflora*, Spreading Hedge-parsley *Torilis arvensis* and cornsalads *Valerianella* spp. The list also includes three species are now functionally extinct in arable habitats in the wild in England (e.g. Thorow-wax *Bupleurum rotundifolium*, Corn Cleavers *Galium tricornutum*, Darnel *Lolium temulentum*). It should be noted that 42 of the 56

species on the list are long established introductions (archaeophytes) adapted to low intensity cropping regimes.

The fourth main group of long-term decliners in England, accounting for 8% of species assessed, were species associated with changes in woodland management, most notably the abandonment of traditional practices such as coppicing since the 1950s. This, combined with increased deer populations, has led to canopy closure in many woods leading to the widespread decline of typical woodland herbs such as Moschatel *Adoxa moschatellina*, Bugle *Ajuga reptans*, Wood Anemone *Anemone nemorosa*, Enchanter's-nightshade *Circaea lutetiana*, Woodruff *Galium odoratum*, Dog's Mercury *Mercurialis perennis*, Early-purple Orchid *Orchis mascula*, Wood Sorrel *Oxalis acetosella*, Sanicle *Sanicula europaea* and Wood Sage *Teucrium scorodonia*.

Table 7. A selection of grassland and heathland species of nutrient-poor soils that have declined in England since the 1950s due to habitat modification and eutrophication.

Calcareous, neutral & damp grassland	Acid grassland & heathland
<i>Agrimony Agrimonia eupatoria</i>	Silver Hair-grass <i>Aira caryophyllea</i>
<i>Green-winged Orchid Anacamptis morio</i>	Early Hair-grass <i>Aira praecox</i>
<i>Betony Betonica officinalis</i>	Wavy Hair-grass <i>Avenella flexuosa</i>
<i>Quaking-grass Briza media</i>	Heather <i>Calluna vulgaris</i>
<i>Clustered Bellflower Campanula glomerata</i>	Field Mouse-ear <i>Cerastium arvense</i>
<i>Harebell Campanula rotundifolia</i>	Pignut <i>Conopodium majus</i>
<i>Spring Sedge Carex caryophyllea</i>	Dodder <i>Cuscuta epithymum</i>
<i>Greater Knapweed Centaurea scabiosa</i>	Broom <i>Cytisus scoparius</i>
<i>Dwarf Thistle Cirsium acaule</i>	Bell Heather <i>Erica cinerea</i>
<i>Meadow Thistle Cirsium dissectum</i>	Heath Bedstraw <i>Galium saxatile</i>
<i>Crosswort Cruciata laevipes</i>	Petty Whin <i>Genista anglica</i>
<i>Lady's-bedstraw Galium verum</i>	Trailing St John's-wort <i>Hypericum humifusum</i>
<i>Autumn Gentian Gentianella amarella</i>	Slender St John's-wort <i>Hypericum pulchrum</i>
<i>Frog Orchid Dactylorhiza viridis</i>	Sheep's-bit <i>Jasione montana</i>
<i>Dyer's Greenweed Genista tinctoria</i>	Bitter-vetch <i>Lathyrus linifolius</i>
<i>Common Rock-rose Helianthemum nummularium</i>	Allseed <i>Linum radiola</i>
<i>Rough Hawkbit Leontodon hispidus</i>	Chaffweed <i>Lysimachia minima</i>
<i>Fairy Flax Linum catharticum</i>	Mat-grass <i>Nardus stricta</i>
<i>Wild Parsnip Pastinaca sativa</i>	Heath Cudweed <i>Omalotheca sylvatica</i>
<i>Burnet-saxifrage Pimpinella saxifraga</i>	Bird's-foot <i>Ornithopus perpusillus</i>
<i>Hawkweed Oxtongue Picris hieracioides</i>	Heath Milkwort <i>Polygala serpyllifolia</i>
<i>Hoary Plantain Plantago media</i>	Trailing Tormenitil <i>Potentilla anglica</i>
<i>Greater Butterfly-orchid Platanthera chlorantha</i>	Tormenitil <i>Potentilla erecta</i>
<i>Common Milkwort Polygala vulgaris</i>	Sheep's Sorrel <i>Rumex acetosella</i>
<i>Salad-burnet Poterium sanguisorba</i>	Biting Stonecrop <i>Sedum acre</i>
<i>Meadow Saxifrage Saxifraga granulata</i>	Heath Groundsel <i>Senecio sylvaticus</i>
<i>Small Scabious Scabiosa columbaria</i>	Golden-rod <i>Solidago virgaurea</i>
<i>Saw-wort Serratula tinctoria</i>	Shepherd's Cress <i>Teesdalia nudicaulis</i>
<i>Devil's-bit Scabious Succisa pratensis</i>	Hare's-foot Clover <i>Trifolium arvense</i>
<i>Autumn lady's-tresses Spiranthes spiralis</i>	Bilberry <i>Vaccinium myrtillus</i>
<i>Wild Thyme Thymus drucei</i>	Heath Speedwell <i>Veronica officinalis</i>
<i>Large Thyme Thymus pulegioides</i>	Heath Dog-violet <i>Viola canina</i>
<i>Zigzag Clover Trifolium medium</i>	

Another important driver of floristic change in England has been a decline in human use leading to the retraction in range of 5% of the species assessed; these include crop and fodder plants (Horse-radish *Armoracia rusticana*, Turnip *Brassica rapa*, Italian Rye-grass *Lolium multiflorum*, Lucerne *Medicago sativa* subsp. *sativa*, Meadow Fescue *Schedonorus pratensis*, Alsike Clover *Trifolium hybridum*) and medicinal and culinary herbs that are less frequently planted or grown than they were in the past (e.g. Wormwood *Artemisia absinthium*, Good-King-Henry *Blitum bonus-henricus*, Creeping Bellflower *Campanula rapunculoides*, Greater Celandine *Chelidonium majus*, Chicory *Cichorium intybus*, Hops *Humulus lupulus*).

Recording bias accounted for 4% of long-term declines assessed. These were mainly species that are difficult to identify and so their trends are likely to be unreliable due to taxonomic uncertainty (e.g. Thyme-leaved Sandwort *Arenaria serpyllifolia* s.s., water-starworts *Callitriche* spp., eyebrights *Euphrasia* spp., tea-plants *Lycium* spp., Narrow-fruited Water-cress *Nasturtium microphyllum*, meadow-grasses *Poa* spp.).

Other drivers were very minor and included former seed contaminants that now very rare (e.g. Thorn-apple *Datura stramonium*, Small Melilot *Melilotus indicus*, rockets *Sisymbrium* spp.) and the increasing scarcity of some formerly widespread non-natives possibly resulting from the impacts of pests and pathogens (e.g. Canadian Waterweed *Elodea canadensis*, Oxford Ragwort *Senecio squalidus*).

Short-term declines

Overall, the main drivers of the short-term trends were broadly similar (Table 6) although the order was different and there was a higher proportion of species attributed to recording biases (15% versus 4%). As for the long-term trends, the key drivers were changes to wetlands and the impacts of eutrophication on semi-natural grasslands and heathlands (28% and 26% of species assessed respectively).

Compared to long-term trends, wetland change topped the list, accounting for 28% of the species assessed, suggesting that drivers such as aquatic pollution have become more prominent, relative to other drivers, in recent decades. Once again aquatic and emergent plants featured prominently on the list of species assessed, with many additional species to those already listed under the long-term trends (e.g. Common Water-starwort *Callitriche stagnalis*, Mare's-tail *Hippurus vulgaris*, Alternate Water-milfoil *Myriophyllum alterniflorum*, Yellow Water-lily *Nuphar lutea*, pondweeds *Potamogeton* spp., yellow-cresses *Rorippa* spp., Water Dock *Rumex hydrolapathum*, Arrowhead *Sagittaria sagittifolia*, Common Club-rush *Schoenoplectus lacustris*). There were also several species associated with marginal habitats (e.g. Marsh Foxtail *Alopecurus geniculatus*, Small Sweet-grass *Glyceria declinata*, Tufted Forget-me-not *Myosotis laxa*, Pink Water-speedwell *Veronica catenata*) and fens and flushes (e.g. Common Yellow-sedge *Carex demissa*, Alternate-leaved Golden-saxifrage *Chrysosplenium alterniflorum*, Marsh Hawk's-beard *Crepis paludosa*, Blunt-flowered Rush *Juncus subnodulosus*).

The second main group of short-term decliners in England, accounting for 26% of the species assessed, were species associated with infertile basic and acid soils that have declined due to increased disturbance and eutrophication of their habitats. Many of these

have already been mentioned above but notable additions that appear to have undergone more marked recent declines include Kidney-vetch *Anthyllis vulneraria*, Upright Brome *Bromopsis erecta*, Adder's-tongue *Ophioglossum vulgatum*, Globeflower *Trollius europaeus* and Spring Vetch *Vicia lathyroides*.

The third main group of short-term decliners in England, accounting for 15% of the species assessed, were apparent declines driven by changes in recording behaviour (recording bias). There appear to be three main groups:

- Species where taxonomic uncertainties had led a decline in reporting (e.g. Hairy Lady's-mantle *Alchemilla filicaulis* subsp. *vestita*, Thyme-leaved/Slender Sandwort *Arenaria serpyllifolia/leptoclados*, Narrow-fruited Water-cress *Nasturtium microphyllum*, Narrow-leaved Vetch *Vicia sativa* subsp. *nigra*).
- Species that have been over-recorded in the past, sometimes for other similar taxa (e.g. Leopard's-bane *Doronicum pardalianches*, Garden Lupin *Lupinus polyphyllus*, tea-plants *Lycium* spp., Solomon's-seal *Polygonatum multiflorum*, Dwarf Cherry *Prunus cerasus*, Bridewort *Spiraea salicifolia*, Confused Michaelmas Daisy *Symphyotrichum novi-belgii*, Common Comfrey *Symphytum officinale*).
- Aquatic species that were intensively recorded during the 1990s leading to apparent decline since then due to less systematic reporting (e.g. water-starworts *Callitriche* spp., Rigid Hornwort *Ceratophyllum demersum*, Spiked Water-milfoil *Myriophyllum spicatum*, Fringed Water-lily *Nymphoides peltata*, pondweeds *Potamogeton* spp., water-crowfoots *Ranunculus* subgen. *Batrachium*, Unbranched Bur-reed *Sparganium emersum*, Fennel Pondweed *Stuckenia pectinata*). These changes are reflected in 'humpback' trends over the long-term.

The fourth main group of short-term decliners in England, accounting for 13% of the species assessed, were arable species which continue to decline for the reasons given above, but less dramatically than over the preceding five decades. Species displaying short-term declines included both those that are still widespread (e.g. Black-bindweed *Fallopia convolvulus*, Common Fumitory *Fumaria officinalis*, hemp-nettles *Galeopsis tetrahit* agg., dead-nettles *Lamium* spp., White Champion *Silene latifolia*, Field Pansy *Viola arvensis*) as well as rarities that were formerly more widespread (e.g. Dense Silky-bent *Apera interrupta*, Basil Thyme *Clinopodium acinos*, Cat-mint *Nepeta cataria*, Rough Poppy *Roemeria hispida*, Shepherd's-needle *Scandix pecten-veneris*, Night-flowered Catchfly *Silene noctiflora*).

Other drivers were more minor and included plants that are less widely used by humans (e.g. Caraway *Carum carvi*, Tree Lupin *Lupinus arboreus*, Dwarf Elder *Sambucus ebulus*), former seed contaminants (e.g. Hungarian Brome *Bromopsis inermis*, Hairy Rocket *Erucastrum gallicum*, Foxtail Bristle-grass *Setaria italica*) and woodland plants that have declined due to changes in woodland management and/or deer grazing (e.g. Wood Vetch *Ervilia sylvatica*, Giant Fescue *Schedonorus giganteus*).

Grouped trends

Broad habitats

The grouped trends for arable and grassland habitats (Figs 8a & 8b) show consistent long-term declines reflecting the increased intensity of agricultural management of these habitats in England since the 1950s as described above. Likewise, the grouped trends for bog and heath (Fig. 8c) showed a consistent long-term decline reflecting the impact of the increasing intensity of land management since the 1950s. In England this resulted in the widespread loss and degradation of bogs and heaths due to drainage, afforestation, pollution, over-grazing and conversion of these habitats to farmland in the lowlands. The same downward trend was observed for wetland habitats (Fig. 8d) for many of the reasons mentioned above, but also due to increased pollution and disturbance of standing and running waters.

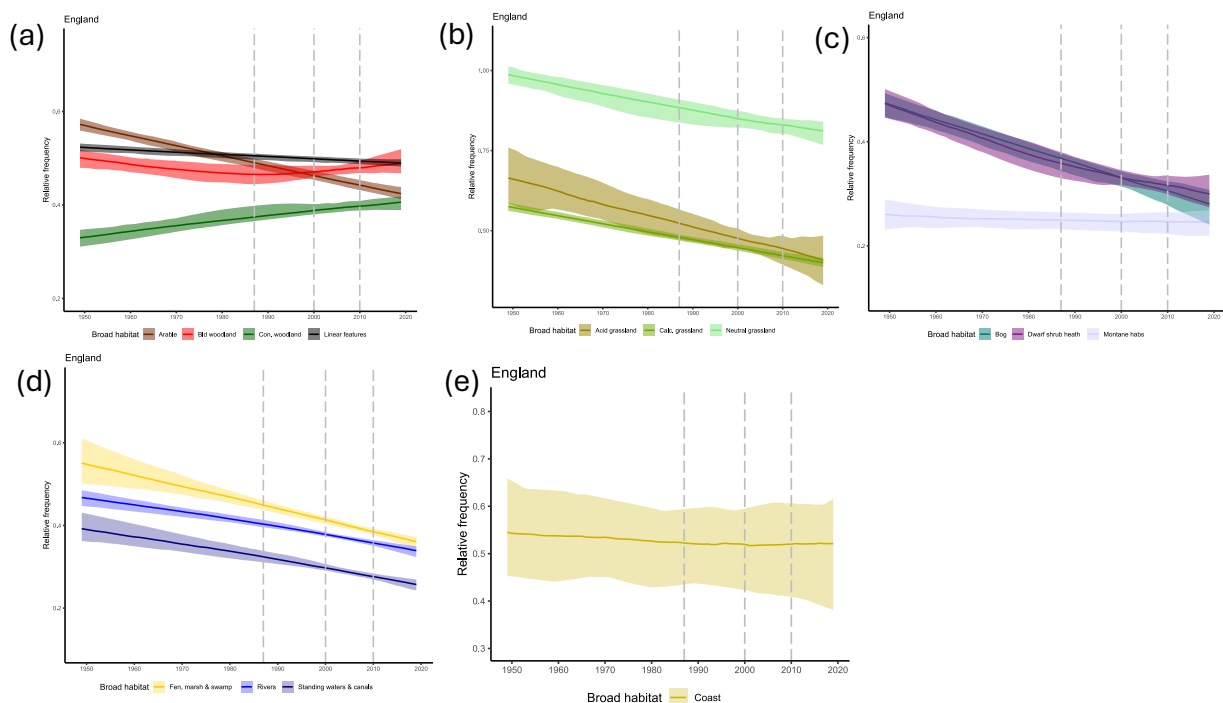


Figure 8. Smoothed group trends for habitats in England showing medians (dashed lines) with 90% uncertainty intervals: (a) arable, broad-leaved woodland, coniferous woodland, linear habitats, (b) acid, calcareous and neutral grassland; (c) bog, dwarf shrub heath, montane, (d) fen, marsh & swamp, rivers, standing waters & canals, and (e) coastal communities.

In comparison, the grouped trends for broadleaved woodlands (Fig. 8a) suggest a relatively stable flora since the 1950s although it should be noted that many woodland species have persisted at the landscape scale in wooded habitats such as hedgerows whilst declining at more local scales within small woods (Kimberley *et al.*, 2014). In comparison, the overall trends for species associated with coniferous woods have shown a consistent increase presumably reflecting the large increase in area of land planted with conifers over the last seven decades. As elsewhere in Britain, the grouped trends for linear habitats have experienced a slight decline in England, presumably due to the intensification of land use and eutrophication of linear habitats such as road verges, hedgerows, riverbanks, etc.

In comparison, the grouped trends for montane habitats and coasts showed little change since the 1950s and reflects the relative stability of these habitats when compared to those intensively used for other land use activities.

Ellenberg indicator values

The grouped trends for Ellenberg moisture show a clear pattern with species associated with the driest or wettest soils and aquatics having suffered the greatest declines as groups since the 1950s whereas species moist soils have suffered much less pronounced declines (Fig. 9a). The grouped trends for Ellenberg light show that species of open habitats have declined the most since the 1950s whereas species associated with semi-shade and shade have suffered slight declines historically but have become more stable in recent decades (Fig. 9b).

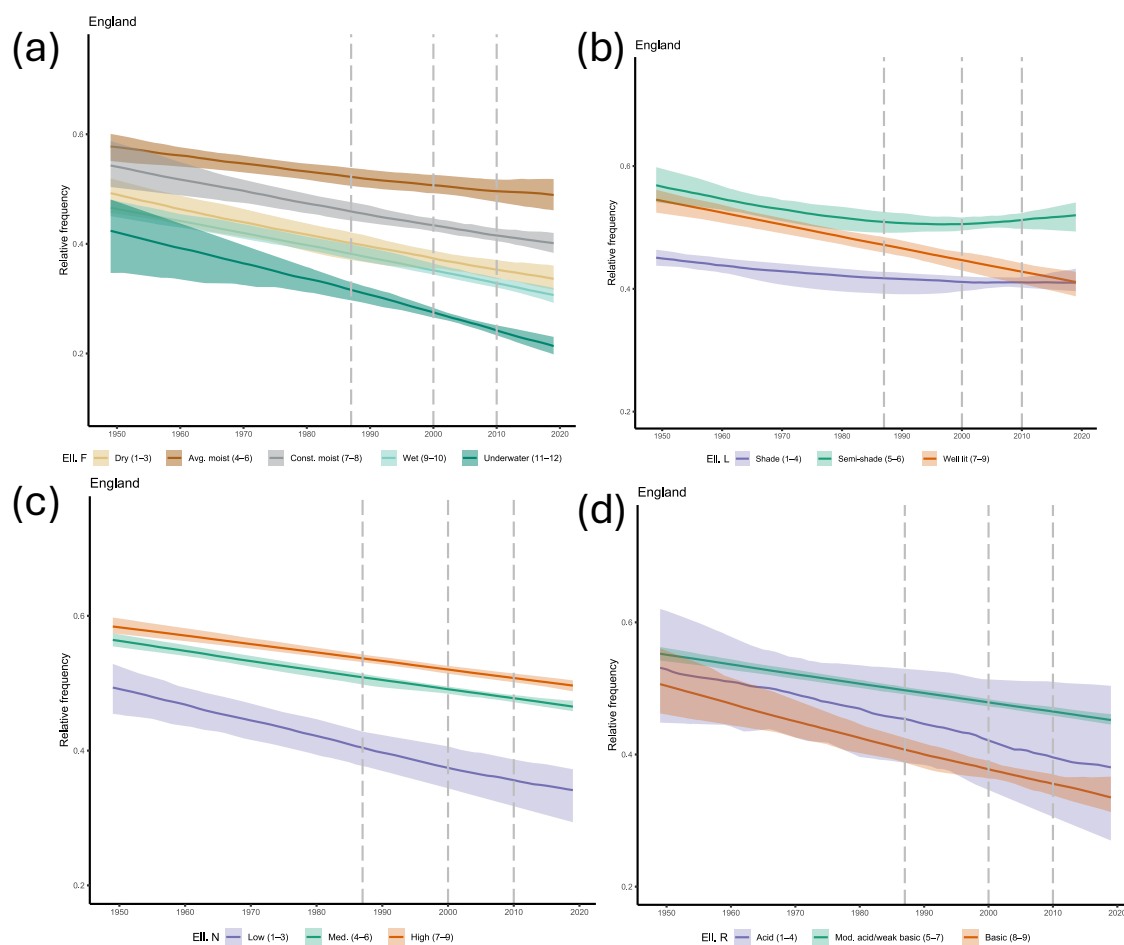


Figure 9. Smoothed group trends for Ellenberg indicator values in England showing medians (dashed lines) with 90% uncertainty intervals: (a) Ellenberg-F moisture, (b) Ellenberg-L light, (c) Ellenberg-N fertility, and (d) Ellenberg-R soil reaction.

The grouped trends for soil fertility (Fig. 9a) show that species associated with nutrient-poor soils have suffered the most consistent declines in England since the 1950s due to increased disturbance and eutrophication caused by human activities whereas declines for species of moderate and high-nutrient soils have been much less marked. The grouped trends for soil reaction (Fig. 9d) show a similar downward trend for species associated with the most acid and basic soils (e.g. chalk and limestone grasslands), albeit with lower certainty for

calcifuges. In comparison, plants of intermediate reaction have undergone less marked declines (Fig. 9d).

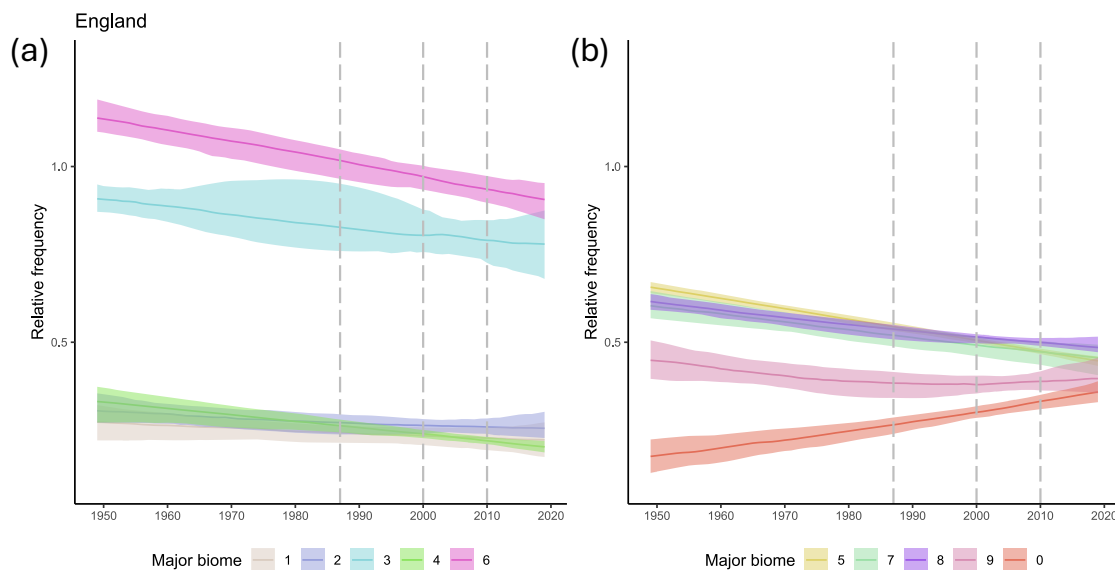


Figure 10. Major biome smoothed trends for England showing medians (dashed lines) with 90% uncertainty intervals: (a) 1 = Arctic-montane; 2 = Boreo-arctic montane; 3 = Wide-boreal; 4 = Boreal-montane; 6 = Wide-temperate; and (b) 5 = Boreo-temperate; 7 = Temperate; 8 = Southern-temperate; 9 = Mediterranean-Atlantic; 0 = Mediterranean).

Major biomes

The grouped trends for species belonging to the ten major biomes present in the British and Irish flora (Preston & Hill, 1997) are shown in Figure 10. The most northerly Arctic-montane, and Boreo-arctic montane biomes, which include the majority of truly montane species in England (e.g. Alpine Lady's-mantle *Alchemilla alpina*, Alpine Bistort *Bistorta vivipara*, Dioecious Sedge *Carex dioica*, Alpine Clubmoss *Diphasiastrum alpinum*, Crowberry *Empetrum nigrum*, Variegated Horsetail *Equisetum variegatum*, Hare's-tail Cottongrass *Eriophorum vaginatum*, Fir Clubmoss *Huperzia selago*, Alpine Cinquefoil *Potentilla crantzii*, Yellow Saxifrage *Saxifraga aizoides*, Purple Saxifrage *Saxifraga oppositifolia*, Hairy Stonecrop *Sedum villosum*, Cowberry *Vaccinium vitis-idaea*) had the most stable trends of all the grouped biomes categories with only a very shallow decline. In comparison, species of the Wide-boreal and Boreal-montane biomes, which comprises a mixture of coastal, lowland and upland species (e.g. Thrift *Armeria maritima*, Melancholy Thistle *Cirsium heterophyllum*, Parsley Fern *Cryptogramma crispa*, Tufted Hair-grass *Deschampsia cespitosa*, Wood Crane's-bill *Geranium sylvaticum*, Sea Plantain *Plantago maritima*, Bird's-eye Primrose *Primula farinosa*, Globeflower *Trollius europaeus*, Mountain Pansy *Viola lutea*), displayed more marked declines. Likewise, all three Temperate biomes (Boreo-temperate, Wide-temperate and Temperate), which make up the bulk of the English flora, showed consistent declines since the 1950s reflecting the greater impacts of land use change and intensity in lowland landscapes over the last 70 years. In comparison, the results for the southerly biomes were markedly different. Overall, species within the Southern-temperate and Mediterranean-Atlantic biomes displayed shallow declines but with an upwards trend in recent decades because of an expansion in range for some species in response to climate change over recent decades (e.g. Pyramidal Orchid *Anacamptis pyramidalis*, Mossy Stonecrop *Crassula*

tillaea, Lizard Orchid *Himantoglossum hircinum*, Spotted Medick *Medicago arabica*, Corky-fruited Water-dropwort *Oenanthe pimpinelloides*, Bee Orchid *Ophrys apifera*, Early Meadow-grass *Poa infirma*, Four-leaved Allseed *Polycarpon tetraphyllum*, Soft Shield-fern *Polystichum setiferum*, Keeled-fruited Cornsalad *Valerianella carinata*). Finally, the small group of Mediterranean species were the only category to have consistently increased in range since the 1950s. This small group is made of non-native species (e.g. Three-cornered Garlic *Allium triquetrum*, Greater Qualing-grass *Briza maxima*, Fennel *Foeniculum vulgare*, Opium Poppy *Papaver somniferum*) and so the overall trends presumably reflect a combination of increasing escape from gardens and improved reporting of non-natives more generally.

Conclusions

Plant Atlas 2020 has revealed the extent to which the English flora has changed over the last century. England now has a more diverse non-native flora than it did in the 1950s, largely because of the large number of non-natives (neophytes) that have either escaped from gardens or been planted in the wild, a minority of which have impacted native assemblages (e.g. Garden Lady's-mantle *Alchemilla mollis*, New Zealand Pigmyweed *Crassula helmsii*, Himalayan Balsam *Impatiens glandulifera*, American Skunk-cabbage *Lysichiton americanus*, Sitka Spruce *Picea sitchensis*, Rhododendron *Rhododendron ponticum*). Over the same period, many native plants have declined due to the loss and degradation of semi-natural habitats because of the increasing intensity of land management for agriculture and forestry, as well as an increase in human infrastructure (e.g. roads, rail, urban, industry, etc.). In England these changes have disproportionately impacted nutrient-poor grasslands, heathlands and wetlands. Many arable plants have also declined due to changes in cropping regimes, increased use of herbicides and improved seed cleaning. Conversely, some native species adapted to fertile soils have increased, as have a small number of southerly distributed species due to climate change (e.g. Mossy Stonecrop *Crassula tillaea*, Early Meadow-grass *Poa infirma*, Soft Shield-fern *Polystichum setiferum*, Bee Orchid *Ophrys apifera*).

The evidence from *Plant Atlas 2020* provides a firm basis for plant conservation in England and points to several actions that will be needed for our flora to recover in the decades ahead:

1. Strengthen protection for plants and other wildlife to ensure that the best sites are safeguarded and managed effectively to benefit the plants they were originally set up to preserve.
2. Extend the area of high-quality habitat available for plants through the introduction of more proactive and targeted measures that benefit biodiversity.
3. Manage land, water, and soil more sustainably by relaxing or removing management activities that are known to have reduced the diversity and resilience of our native flora in the past such as intensive management of pasture, the use of chemical herbicides, over- or under-grazing, drainage of wetlands and peatlands, afforestation of mires and bogs, and the burning of heathlands. In addition, measures are needed to ensure that tree-planting is carefully planned so that important habitats for biodiversity and carbon storage are protected (Walker *et al.*, 2022).

4. Considering the needs of plants, and planning to manage and restore differing vegetation types to benefit them, should be a central ecological tenet of conservation measures and efforts for nature recovery more generally.
5. Develop more robust and effective plant monitoring and surveillance that tracks trends in relation to habitats and key drivers of change (pressures, threats, interventions).
6. Despite their importance to humans, plants are still overlooked and undervalued. To ensure they are adequately protected, and action is taken to address the substantial and ongoing population declines revealed by *Plant Atlas 2020*, we need to increase awareness of the vital roles they play in our everyday lives and the threats they continue to face.

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