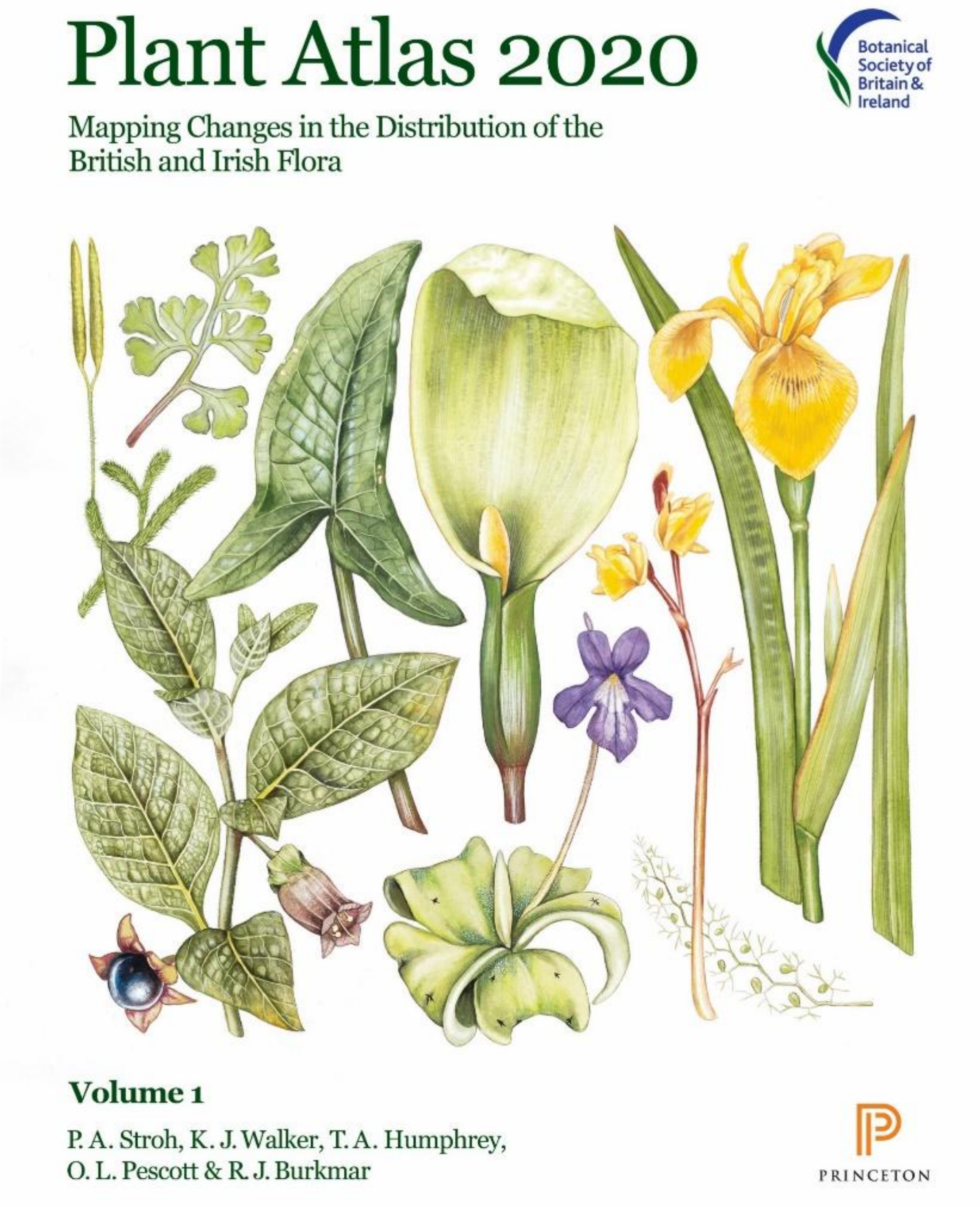
Scotland's changing flora

A summary of key findings from *Plant Atlas 2020*



A report to NatureScot, February 2025

Kevin Walker, Tom Humphrey, Pete Stroh, Matt Harding (Botanical Society of Britain and Ireland) & Oli Pescott (UK Centre for Ecology and Hydrology)

Acknowledgements

We would like to express our gratitude to the BSBI volunteer recorders in Scotland without whose efforts *Plant Atlas 2020* would not have been possible. We would also like to thank Sarah Smyth for her comments and advice on the contents of this report and to NatureScot who funded its production.

Recommended citation:

Walker, K.J., Humphrey, T.A., Stroh, P.A., Harding, M. & Pescott, O.L. 2025. *Scotland's changing flora. A summary of key findings from* Plant Atlas 2020. A report by the Botanical Society of Britain and Ireland (BSBI) for NatureScot.

Summary

Plant Atlas 2020 is the Botanical Society of Britain and Ireland's (BSBI) third distribution atlas of the British and Irish flora and follows atlases published in 1962 and 2002. The current survey involved 1,000s of amateur botanists who recorded vascular plants and charophytes growing in wild locations in c. 3,900 10 × 10 km squares (hectads) that make up Britain and Ireland between 2000 and 2019. These data were collated centrally and used to produce 'dot-distribution' maps for 3,495 taxa at the 10 × 10 km (hectad) scale. The maps were published as a book and on a website (plantatlas2020.org) alongside information on a taxon's origin, history, habitats, ecology, trends, conservation, phenology, and altitudinal range 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 for Britain, Ireland, England, Wales, Scotland, Northern Ireland, and the Republic of Ireland.

Here we focus on the trends for Scotland. Of the 2,870 taxa mapped for Scotland, long-term trends (LTT) were calculated for 1,428 taxa (50%) and short-term trends (STT) for 2,047 taxa (71%). The most likely driver of these trends was attributed to the 200 taxa that had increased or decreased the most (based on their model-based certainty), over both the long- and short-term, giving 800 assessments in total. These assessments were based on expert knowledge and included an assessment of recording bias (i.e. the extent to which trends were influenced by systematic differences in the ways species or groups of species had been recorded between survey periods).

The results of *Plant Atlas 2020* showed that 48% of natives and 66% of archaeophytes were estimated to have declined in range at the hectad scale in Scotland since the 1950s, whereas 56% of neophytes were estimated to have increased. The short-term trends were very similar for natives with 51% of species estimated to have declined, whereas a lower proportion of archaeophytes were estimated to have declined (51%) and a greater proportion of neophytes were estimated to have increased (68%).

In Scotland plants that were estimated to have increased the most over both the long- and short-term were mainly non-natives that had either escaped from gardens (LTT 33%, STT 50%) or had been increasingly utilised by humans (LTT 24%, STT 24%). The latter included many trees and shrubs that had been deliberately planted, most notably the conifer Sitka Spruce *Picea sitchensis*, which displayed the greatest increase of any plant in Scotland over both the long- and short-term. The third largest group were species where increases related to recording bias (LTT 22%, STT 14%), mainly because of targeted surveys of specific habitats in one survey period (e.g. waterbodies, arable). The fourth largest group were mainly native species that had benefitted from increasing eutrophication caused by human activities (LTT 15%, STT 9%). Other drivers were less important but included increases in the range of some species in response to warmer winters with fewer frosts (e.g. Mossy Stonecrop *Crassula tillaea*, Bee Orchid *Ophrys apifera*).

The 10 plant species that increased the most in Scotland (in order of model-based certainty).

Long-term (1930-2019)	**Short-term (1987-2019)**
Sitka Spruce *Picea sitchensis*	Garden Lady's-mantle *Alchemilla mollis*
American Willowherb *Epilobium ciliatum*	Deergrass *Trichophorum germanicum*
Lodgepole Pine *Pinus contorta*	Early Pampas-grass *Cortaderia richardii*
Sea Mayweed *Tripleurospermum maritimum*	Japanese Rose *Rosa rugosa*
Hybrid Bluebell *Hyacinthoides* x *massartiana*	Daffodil cultivars *Narcissus* agg.
Norway Spruce *Picea abies*	Spanish Bluebell *Hyacinthoides hispanica*
Montbretia *Crocosmia* x *crocosmiiflora*	Hybrid Larch *Larix* x *marschlinsii*
Sheep's-fescue *Festuca ovina*	Butterfly-bush *Buddleja davidii*
Common Hemp-nettle *Galeopsis tetrahit*	Montbretia *Crocosmia* x *crocosmiiflora*
Douglas Fir *Pseudotsuga menziesii*	Lodgepole Pine *Pinus contorta*

In Scotland the groups of plants that were estimated to have declined the most over the long-term were arable species due to abandonment of small-scale cropping and intensification of arable management (31%) and specialists of infertile soils that had declined to more intensive management and eutrophication of grasslands and heathlands (30%). The other main groups were plants formerly utilised by humans (13%) and wetland (9%) and woodland plants (5%) that had declined because of habitat changes. The long-term declines of some upland plants were attributed to overgrazing (6%) whereas recording bias accounted for a further 6% of species.

The 10 species that decreased the most in Scotland (in order of model-based certainty)

Long-term (1930-2019)	**Short-term (1987-2019)**
Wild Radish *Raphanus r.* ssp. *raphanistrum*	Quillwort *Isoetes lacustris*
Corn Marigold *Glebionis segetum*	Awlwort *Subularia aquatica*
Corn Spurrey *Spergula arvensis*	Oblong-leaved Sundew *Drosera intermedia*
Charlock *Sinapis arvensi*	Blunt-leaved Pondweed *Potamogeton obtusifolius*
Wild Pansy *Viola tricolor*	Small Pondweed *Potamogeton berchtoldii*
Italian Rye-grass *Lolium multiflorum*	Pedunculate Water-starwort *Callitriche brutia*
Black-bindweed *Fallopia convolvulus*	Perfoliate Pondweed *Potamogeton perfoliatus*
Corn Mint *Mentha arvensis*	Autumnal Water-starwort *Callitriche hermaphroditica*
Arctic Eyebright *Euphrasia arctica*	Alsike Clover *Trifolium hybridum*
Red Dead-nettle *Lamium purpureum*	Shoreweed *Littorella uniflora*

The groups that had declined the most over the short-term were broadly similar although the order was different. Most notably, recording bias accounted for most declines (34%) largely because targeted surveys of waterbodies in the 1980s/90s exaggerated declines as many populations have not been visited since then. Other groups included specialists of infertile soils that declined due to eutrophication (19%), wetland (16%) and arable (14%) species due to habitat change, and upland species due to overgrazing (7%). Notably, there was a small number of species that had declined because of climate change (2%) including loss of snow-beds and more intensive winter storms.

Plant Atlas 2020 has revealed how the Scottish flora has changed over the last century, particularly the spread of non-native species and negative impacts of land management, pollution, and climate. These findings provide a powerful evidence-base for nature recovery, conservation and research, and highlight the changes needed to protect, restore and enhance the Scottish flora in the decades ahead. 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 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 of Britain and Ireland following previous 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 species accounts, maps, photographs and information on trends, conservation designations, phenology, apparency, and altitudinal range (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, however, 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 Scotland, including a novel assessment of drivers for the 200 species that increased or decreased the most over the long- and short-term, giving 800 assessments in total. When attributing drivers, we included an assessment of recording bias as this is often vital 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 (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 Scotland. Note that there are sampling biases inherent in all unstructured survey, 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 Scotland summarised here.

Field survey

Fieldwork for *Plant Atlas 2020* was carried out mainly by amateur botanists between 2000 and 2019 and was built on equivalent surveys undertaken in 1930-1969 and 1987-1999; in these periods, volunteers recorded all species they found growing in wild locations within the c. 3,900 10 × 10 km grid squares (hectads) that make up Britain and Ireland. In the most recent survey (2000-2019), records were submitted to BSBI and collated centrally (from 2010 onwards) within its records database (BSBI Distribution Database). This allowed efficient targeting of 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 days completed and over 26 million records submitted by the end of the project. However, the recording effort was highly variable, being highest 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 Ireland (Fig. 1). Exceptions included vice-counties that were very well surveyed during the 2000-2019 period, notably Cornwall, East Norfolk, Anglesey, Moray and Wexford.

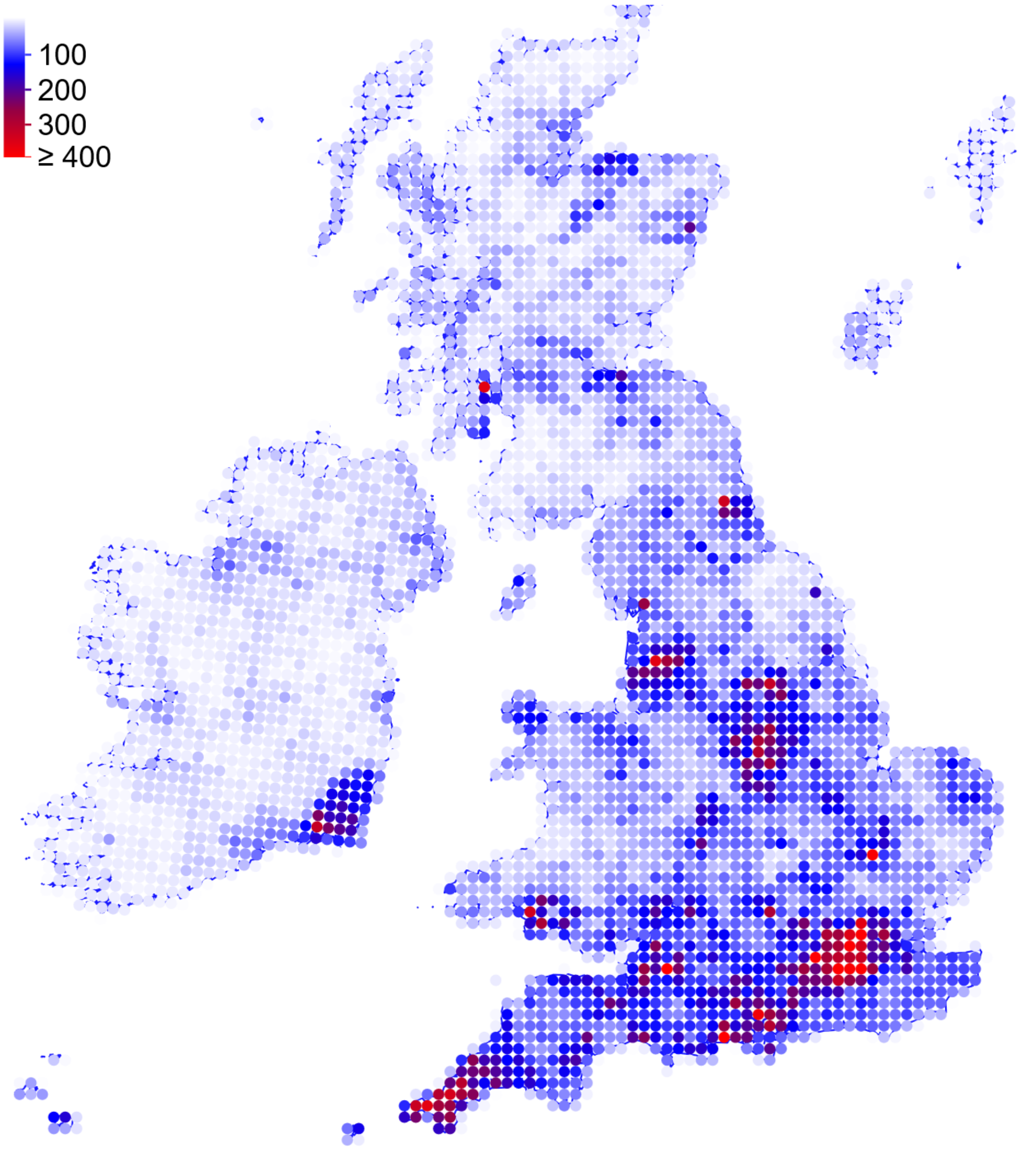


Figure 1. The number of recording days undertaken within each 10 × 10 km square (hectad) in Britain and Ireland during fieldwork for *Plant Atlas 2020* (2000-2019). A recording day is a standard measure of recording and is defined as a single visit to a 2 × 2 km square (tetrad) when 40 or more species were recorded

In Scotland, targeted fieldwork was undertaken to increase coverage in remoter regions and this was improved by surveys of specific species during Scottish Natural Heritage's (SNH) monitoring of the condition of plant features on Sites of Special Scientific Interest (SSSIs) (Sydes, 2008), species monitoring on National Trust for Scotland land (e.g. Watts *et al.*, 2022), the BSBI's *Threatened Plants Project* between 2008-2013 (Walker *et al*., 2017), and more localised surveys of montane species on Ben Nevis (The Nevis Partnership, 2019) and in the Cairngorms National Park (Amphlett, 2013). All these projects provided much needed distribution records for many of Scotland's more localised montane species. During 2000-2019, flora surveys were also undertaken in many Scottish vice-counties, some of which were published as county or island floras including Berwickshire (Braithwaite, 2014), Bute (Hannah, 2019), Lanarkshire (Macpherson, 2016), Renfrewshire (Watson, 2013), and the island of Rum (Pearman *et al*., 2008). Once fieldwork was completed at the end of 2019, BSBI staff and volunteers spent considerable time checking the maps and assigning occurrence status to hectads where a species was mapped for the first time, often with advice from BSBI vice-county recorders.

Assessing changes in distribution

To assess changes in distribution, hectad occurrences 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. 2). To do this a local 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 its occupied areas. Readers should consult Pescott *et al*. (2019) for more detail on the method and for a justification for its specific application at the 10 km/broad date-class distribution used here.

Figure 2. The 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 limitations 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.
- 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 for example due to taxonomic changes 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. However, it should be noted that trends for these taxa in Scotland have been assessed as part of the NatureScot funding to BSBI during 2023-2024 using population monitoring data from a variety of sources and are being used to help determine the revised GB threat statuses (Stroh *et al*., in prep.).
- 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 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 Scotland 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. 3a) 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 linear slope estimates (Fig. 3b) was also used to visualise their variation across five trend categories (Fig. 3c & 3d): 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 (decline, stable, increase) to summarise trends for all species in relation to national status (Fig. 5).

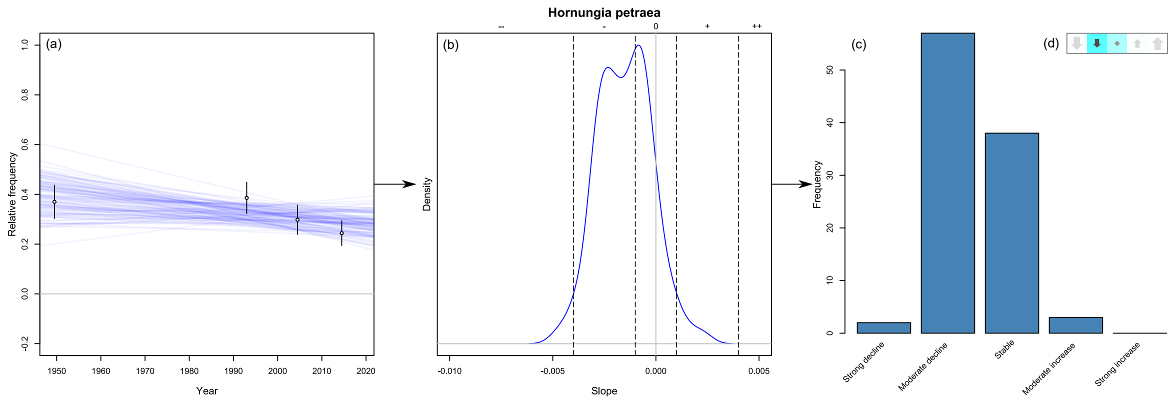


Figure 3. An example of the flow of information and uncertainty through the analyses used to calculate long- and short-term trends for *Plant Atlas 2020*. The example given is Hutchinsia *Hornungia petraea*. In (a) the circles and bars are the Frescalo means and standard deviations for the four time-periods, 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 200 species with the most 'certain' trends, that is those with the highest model-based certainty rather than absolute mean slope estimates. Therefore, we undertook 800 assessments in total: 400 each for increasing and decreasing species (200 long- and 200 short-term). For each trend we assigned the most likely driver of change in distribution 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 (Table 1). 'Recording bias' was attributed to trends that reflected systematic differences in the way a species had been recorded in successive atlas surveys due to improvements in taxonomic or ecological understanding or targeted surveys of certain species or habitats. Whilst this was not a full 'risk-of-bias' assessment (Boyd *et al*., 2022) it provides an indication of where care is needed when interpreting trends. It should also be noted that whilst we have attempted to attribute a single driver, many trends are likely to combine responses to multiple drivers as well as an element of recording bias.

Table 1. Drivers of change used in this report grouped under the relevant IPBES driver (see https://www.ipbes.net/models-drivers-biodiversity-ecosystem-change).

Driver	Description
IPBES driver - Changing use of sea and land	
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.
Afforestation	The introduction of plants associated with commercial forestry (excluding the trees themselves which are included in 'Human use'). This includes species likely to have been introduced in soils attached to tree roots (e.g. Slender Rush *Juncus tenuis*) and species spreading along forestry tracks (e.g. Sand Spurrey *Spergularia rubra*).
Human use	Changing frequency due to increased/decreased human use (e.g. cultivation, planting).
Overgrazing	Changes in distribution due to increased levels of grazing by livestock, rabbits and deer.
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.
IPBES drivers - Changing use of sea and land & Pollution	
Eutrophication	Eutrophication and other change to low fertility habitats due to land use change, increased intensity of management, and increased nutrient inputs from agriculture, pollution, transport, etc.
Halophyte inland	The spread inland of coastal halophytes along salt-treated roads.
IPBES drivers - Changing use of sea and land & Direct exploitation of organisms	
Marine change	The destruction or modification of Eelgrass *Zostera* beds due to pollution, disturbance, etc.
IPBES driver - Climate change	
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 and erosion, etc.
IPBES driver - Invasive non-native species	
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.
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.
IPBES driver – Other	
Herbicide resistance	Plants that have increased in abundance in arable habitats due to their ability to tolerate artificial herbicides such as glyphosate.
Recording bias	Systematic differences in the way a species have been recorded in successive atlas periods due to changes in taxonomy, targeted surveys or recording behaviour.

Grouped trends

The trends are also presented as average changes over the long-term for groups of species with the same national status (native, archaeophyte, neophyte) and with similar ecological attributes, biogeographic affinities and habitat associations. For national status, we used the slope estimates (without uncertainty) and for ease of interpretation we reduced the five change categories (strong decline, decline, stable, increase, strong increase) to three (decline, 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 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 strong correlation between group membership and the probability of a trend being biased in a particular direction (for example, as discussed above, many aquatic plant trends are biased, and therefore aggregate trends based on variables that group these taxa together are also probably biased). See Chapter 6 of Stroh *et al.* (2023) for a fuller discussion of the likely biases in the *Plant Atlas 2020* dataset.

Results

Species coverage

Of the 3,495 taxa covered by the *Plant Atlas 2020* project, 2,870 were mapped for Scotland including 1,285 natives, 158 archaeophytes, and 1,433 neophytes (Table 2). Of these mapped taxa, 50% and 71% had long- and short-term trends respectively, including 73% and 76% of natives and 93% and 89% of archaeophytes respectively. In comparison, only 24% of neophytes had long-term trends as most non-natives were not mapped in the 1962 atlas. This figure was much higher for short-term trends as many more non-natives were recorded for 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 2. The number of Scottish vascular plant taxa included in *Plant Atlas 2020* that were mapped and for which long- and short-term trends were available.

National status[1]	Mapped in *Plant Atlas 2020*	Long-term trend		Short-term trend	
		Taxa	%	Taxa	%
Native[2]	1,285	941	73	975	76
Archaeophyte	152	141	93	136	89
Neophyte	1,433	346	24	936	65
Total	2,870	1,428	50	2,047	71

[1] – Note that status is for Scotland and not Britain as a whole. For example, the British native *Acer campestre* was treated as a neophyte in Scotland. [2] – Incudes species categorised as 'native or alien'.

Most species lacking long- and short-term trends were taxa where the data were too sparse to assess trends effectively including neophytes, hybrids, subspecies, rare natives, or species with complex taxonomic histories (Table 3). A small number of species were excluded because they are extinct in Scotland (Smooth Rock-spleenwort *Asplenium fontanum*, Crested Buckler-fern *Dryopteris cristata*, Hutchinsia *Hornungia petraea*, Fine-leaved Water-dropwort *Oenanthe aquatica*, Alpine Butterwort *Pinguicula alpina*, Arctic Bramble *Rubus arcticus*, Perennial Glasswort *Sarcocornia perennis*, Greater Water-parsnip *Sium latifolium*, Cotton Deergrass *Trichophorum alpinum,* Welsh Groundsel *Senecio cambrensis*) or have only been discovered in Scotland in the last two decades (Garden Angelica *Angelica archangelica* subsp. *littoralis*, Nordic Moonwort *Botrychium nordicum*, Narrow-fruited Water-starwort *Callitriche palustris*, Saltmarsh Sedge *Carex salina*, New Monkeyflower *Erythranthe peregrina*, Dune Helleborine *Epipactis dunensis*, Hare's-foot Clubmoss *Lycopodium lagopus*, Common Cord-grass *Spartina anglica*, Spotted Rock-rose *Tuberaria guttata*). Charophytes are plant-like multicellular algae that have been traditionally recorded by botanists but were not assessed as there were too few historic data on which to estimate trends.

The native taxa that lacked trends were mainly montane species confined to just a handful of sites in Scotland (e.g. Alpine Rock-cress *Arabis alpina,* Norwegian Mugwort *Artemisia norvegica,* Iceland Purslane *Koenigia islandica,* Snow Pearlwort *Sagina nivalis*) or for which Scotland supports most British and Irish populations (e.g. Norwegian Sandwort *Arenaria norvegica,* Alpine For-get-me-not *Myosotis alpestris,* Tufted Saxifrage *Saxifraga cespitosa*). There are also a minority of species that are commoner further south in Britain but just make it into Scotland (e.g. Small Restharrow *Ononis reclinata*) some of which may be extinct or have uncertain status in Scotland (e.g. Divided Sedge *Carex divisa*, Rigid Buckler-fern *Dryopteris submontana*, Bird's-eye Primrose *Primula farinosa*). Note that trends at finer scales for all these rarities have been assessed by experts for the new Great Britain Vascular Plant Red List, due to be completed in 2025, and those present in Scotland as part of NatureScot's funding to BSBI in 2023/24.

Table 3. Scottish vascular plant and charophyte taxa mapped in *Plant Atlas 2020* but for which trends were not produced.

Reason for lack of trend	**Number of taxa lacking a long-term trend**	**Number of taxa lacking a short-term trend**
Charophytes	24	24
Complex taxonomy	64	43
Extinct in Scotland	4	9
Hybrids	108	106
New taxa	10	7
Rare natives (<15 hectads GB)	63	61
Rare neophytes (<30 hectads GB)	1096	514
Subspecies	66	59
Total	1,435	823

The overall diversity of native species, archaeophytes and neophytes at the hectad scale is shown in Figure 4. Much of Scotland has much lower alpha diversity (i.e. 10 km square species richness) relative to the rest of Britain, especially in highland regions and the far north. This was most marked for archaeophytes and neophytes, which are largely concentrated around urban areas in the central belt and coastal regions in eastern Scotland.

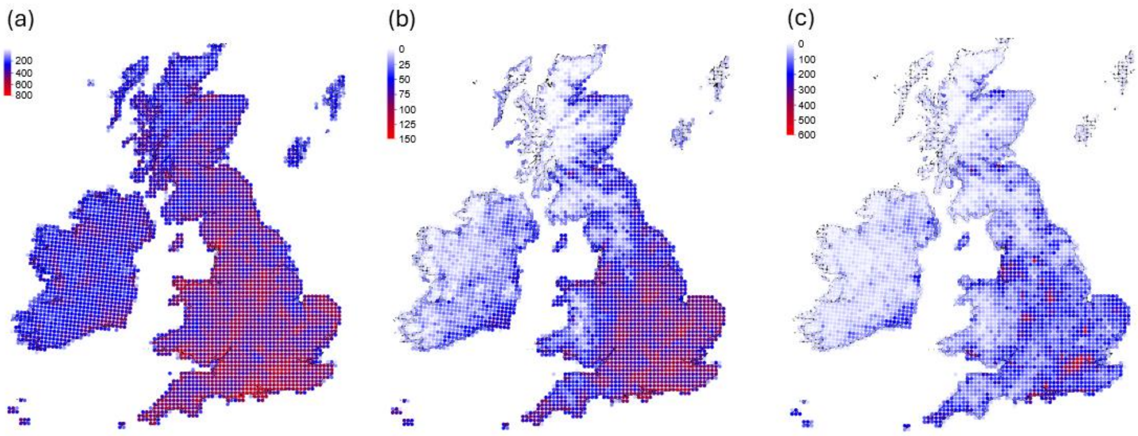


Figure 4. Number of vascular plant species recorded per hectad in Britain and Ireland during 2000-2019 for *Plant Atlas 2020*: (a) native species; (b) archaeophytes; and (c) neophytes. Note the different ranges for species diversity in the keys.

Trends in relation to status

Of the species analysed for Scotland, 48% of natives and 66% of archaeophytes are estimated to have declined in Scotland since the 1950s (the decade when most atlas recording took place during the 1930-69 date class used to calculate long-term trends), whereas 56% of neophytes are estimated to have increased (Fig. 5a). The analyses of the short-term trends showed a similar pattern although a lower proportion of archaeophytes had declined (51%) whereas a greater proportion of neophytes had increased (68%; Fig. 5b).[1]

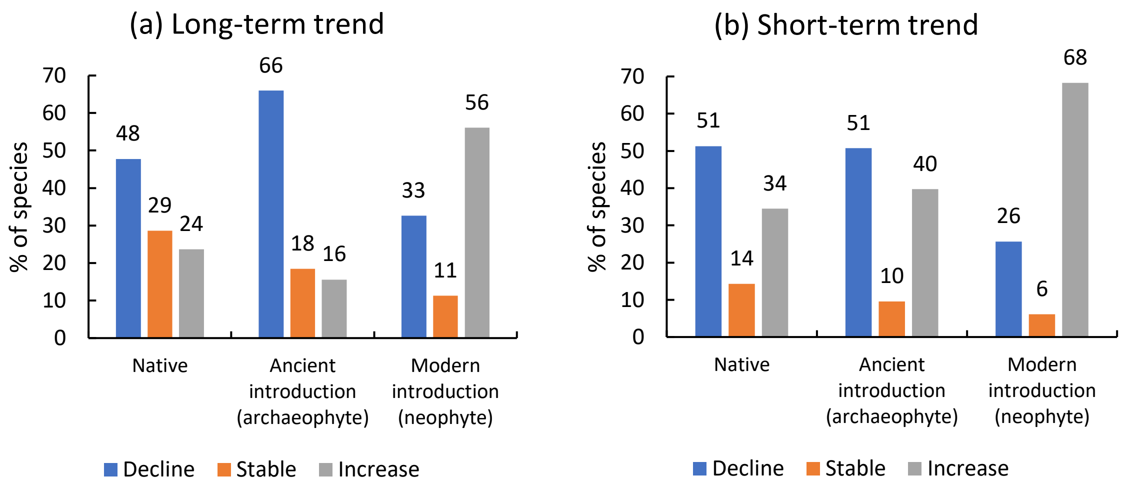


Figure 5. The proportion of plants displaying decreasing, increasing or stable trends at the 10 km square scale in Scotland over the (a) long- (1930-2019) and (b) short-term (1987-2019). Trends are shown in relation to whether species were native to Scotland or introduced by humans.

[1] Note that these figures differ slightly from those quoted for Scotland in the summary report for Britain (Walker *et al*., 2023). This is due to a more accurate classification of the status (native, archaeophyte, neophyte) of species in Scotland that was carried out as part of this project.

These changes were also visualised as grouped non-linear trends (Fig. 6). As a group, natives displayed a consistent decline in relative frequency since the 1950s whereas archaeophytes declined more steeply and at a faster rate until around the turn of the twenty-first century, when the fortunes of some species improved due to the introduction of conservation measures to benefit wildlife on arable land (Pywell *et al*., 2012), as well as the widespread sowing of 'cornfield annuals' such as Corncockle *Agrostemma githago*, Cornflower *Centaurea cyanus* and Corn Marigold *Glebionis segetum* (although it should be noted that these technically represent neophyte rather than archaeophyte populations). In comparison, neophytes showed a steady increase throughout this period reflecting genuine increases in occupancy as well as increased interest in and recording of non-natives by botanists.

The equivalent trends were less certain over the short-term, especially for archaeophytes and neophytes (Fig. 6b). Natives displayed a gradual decline with some recovery in the last decade, possibly reflecting less intensive recording between 2000 and 2009 when *Plant Atlas 2020* had not been formally adopted as a recording scheme by the BSBI. The recovery of archaeophytes already mentioned above is clear from this graph, although with a wide margin of uncertainty. In comparison, neophytes displayed an increase which has become even more marked since 2000, reflecting the increased interest and effort in recording non-natives, a growing concern surrounding their impacts, improved coverage in standard floras and a genuine increase in the distribution of many species.

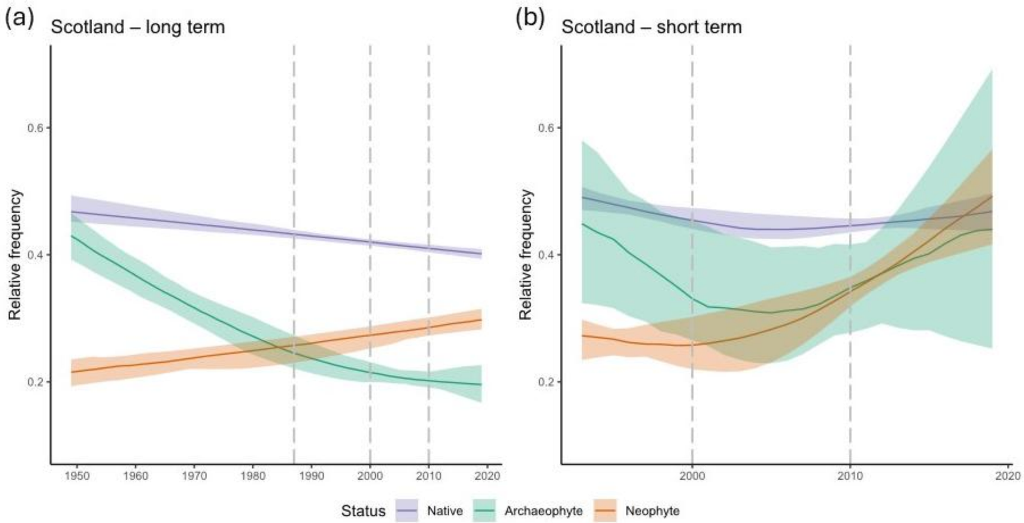


Figure 6. Smoothed trends for Scottish plant species in relation to national status (native, archaeophyte, neophyte) showing medians (solid lines) with 90% uncertainty intervals (colour bands) and displayed over (a) the long- and (b) short-term. The dashed vertical lines mark the beginning/end of each recording period.

Increasing species

Table 4 provides a summary of the drivers for the 200 species with the most 'certain' increases in Scotland over the long- and short-term, as opposed to those with the largest absolute mean slopes (see the electronic appendix for a full list of species and the assigned driver). 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 53% and 70% 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 largest group of plants that had increased the most in Scotland were mainly neophytes that had escaped from public and private gardens and had become established in wild locations, accounting for 33% and 50% of species on the long- and short-term lists respectively (65 and 100 species respectively; Table 4). Notable examples that are widespread in Scotland are Garden Lady's-mantle *Alchemilla mollis,* Montbretia *Crocosmia* x *crocosmiiflora*, Hybrid Bluebell *Hyacinthoides* x *massartiana*, Himalayan Balsam *Impatiens glandulifera*, variegated Yellow Archangel *Lamiastrum galeobdolon* susbp. *argentatum* and Rhododendron *Rhododendron ponticum* as well as other neophytes that have negatively impacted native species and assemblages such as, Few-flowered Garlic *Allium paradoxum,* Cotoneasters *Cotoneaster* spp., New Zealand Pigmyweed *Crassula helmsii*, American Skunk-cabbage *Lysichiton americanus*, and Giant-rhubarbs *Gunnera* spp.

Table 4. The main drivers of the 200 plant species with the most marked increases in distribution over the long- and short-term in Scotland shown in relation to national status (Nat = native; Arc = archaeophyte; Neo = neophyte; Tot = Total). See Table 1 for an explanation of each driver.

	Long-term increase					**Short-term increase**				
Main driver	**Nat**	**Arc**	**Neo**	**Tot**	**%**	**Nat**	**Arc**	**Neo**	**Tot**	**%**
IPBES driver - Changing use of sea and land										
Afforestation	2	0	1	3	2	0	0	1	1	1
Human use	6	3	38	47	24	5	1	42	48	24
Overgrazing in uplands	1	0	0	1	1	0	0	0	0	0
IPBES drivers - Changing use of sea and land & Pollution										
Eutrophication	23	1	6	30	15	14	0	3	17	9
Halophyte inland	3	0	0	3	2	3	0	0	3	2
IPBES driver - Climate change										
Climate change	6	1	0	7	4	3	0	0	3	2
IPBES driver - Invasive non-native species										
Garden escape	5	3	57	65	33	6	3	91	100	50
IPBES driver - Other										
Herbicide resistance	0	0	1	1	1	0	0	1	1	1
Recording bias	41	0	2	43	22	24	1	2	27	14
Total species	87	8	105	200		55	5	140	200	
% of total	44	4	53			28	3	70		

The next largest group of plants that have increased the most were those that have been increasingly utilised by humans since the 1950s, accounting for 24% of species over both the long- and short-term (47 and 48 species respectively). These include several different groups, most notably:

- Trees and shrubs that have been widely planted for ornamental or landscaping purposes, such as Field Maple *Acer campestre*, Lawson's Cypress *Cupressus lawsoniana*, Leyland Cypress *C.* x *leylandii*, Garden Privet *Ligustrum ovalifolium*, Cherry Plum *Prunus cerasifera*, and Cherry Laurel *P. laurocerasus*.
- Conifers planted for commercial timber production, some of which have self-seeded and naturally 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*).
- Ornamentals that have been mass planted along roadsides and in other public spaces, sometimes having spread along watercourses and in discarded soil and garden waste (e.g. Snowdrop *Galanthus nivalis*, Daffodil cultivars *Narcissus* spp.).
- Species sown in seed mixtures for conservation, amenity and landscaping purposes. This includes one of the few archaeophytes to have increased since 2000, Corncockle *Centaurea cyanus*, although this increase was almost entirely the result of neophyte occurrences because of the sowing of 'cornfield' seed mixtures.
- Species increasingly grown as crops or for green manure or game cover in recent decades which are increasingly occurring as relics and volunteers (e.g. Sunflower *Helianthus annuus*, Phacelia *Phacelia tanacetifolia*, Bread Wheat *Triticum aestivum*, Crimson Clover *Trifolium incarnatum*, Broad Bean *Vicia faba*).

Species whose changes were influenced by recording bias were the third largest group and accounted for 22% and 14% of species over the long- and short-term respectively (43 and 27 species respectively). These were mainly species that were very poorly recorded in the past due to taxonomic uncertainties but have been better recorded in recent decades and hence appear to have increased in range. Many were either not or only very rarely recorded during earlier recording periods as most botanists were not familiar with them (e.g. Brown Bent *Agrostis vinealis*, Frog Rush *Juncus ranarius*, Least Duckweed *Lemna minuta*, Deergrass *Trichophorum germanicum*, Sea Mayweed *Tripleurospermum maritimum*) or they were largely ignored due to taxonomic uncertainties or because they were difficult to identify (e.g. sedges *Carex* spp., Common Scurvygrasses *Cochlearia officinalis* agg., Eyebrights *Euphrasia* spp., Male- and Buckler-ferns *Dryopteris* spp., hybrids, Water-cresses *Nasturtium officinale s.s.*, Roses *Rosa* spp.). This group also includes several 'species' which have subsequently been split in two or more species which have only been recorded consistently in recent decades (e.g. Common Hamp-nettle *Galeopsis tetrahit s.s.*, Toad Rush *Juncus bufonius s.s.*, Water-cress *Nasturtium officinale s.s.*, Common Glasswort *Salicornia europaea s.s.*, Northern Deergrass *Trichophorum cespitosum s.s.*). There has also been an increasing tendency to record distinctive subspecies of more common species in recent decades leading to an apparent increase in their range (e.g. Sea Beet *Beta vulgaris* subsp. *maritima*, Sea Radish *Raphanus raphanistrum* subsp. *maritimus*, coastal Curled Dock *Rumex crispus* subsp. *littoreus*).

There was also a distinct group where more systematic surveys had given the false impression that they had increased over time. The most notable are several aquatic species that were poorly recorded historically but were very well recorded in the 1980s/90s due to targeted surveys of waterbodies during the *NCC/SNH Scottish Loch Survey* resulting in apparent long-term increases (e.g. Alternate Water-milfoil *Myriophyllum alterniflorum*, Bog Pondweed *Potamogeton polygonifolius*, Broad-leaved Pondweed *P. natans,* Floating Bur-reed *Sparganium angustifolium*). Similarly, some species of arable habitats have benefited from targeted surveys of arable land in eastern Scotland in recent decades (e.g. Common Ramping-fumitory *Fumaria muralis*, Purple Ramping-fumitory *F. purpurea*). The distribution of some species also appears to have increased presumably because of more systematic or targeted surveys of likely habitats. In Scotland this might account for notable increases in the range of some scarce species such as Coralroot Orchid *Corallorhiza trifida*, Northern Buckler-fern *Dryopteris expansa*, Thread Rush *Juncus filiformis*, and Wood Club-rush *Scirpus sylvaticus*.

The fourth largest group of increasers were species that benefited from eutrophication caused by human activities, accounting for 15% and 9% of long- and short-term trends respectively (30 and 17 species respectively). In terrestrial habitats in Scotland this has included the increase in abundance of mainly native 'weeds' that can tolerate high nutrient levels, such as Creeping Bent *Agrostis stolonifera*, Pendulous Sedge *Carex pendula*, Rosebay Willowherb *Chamaenerion angustifolium*, Wild Teasel *Dipsacus fullonum*, willowherbs *Epilobium* spp., Northern Dock *Rumex longifolia*, and sow-thistles *Sonchus* spp.; whereas in wetland habitats they include Reed Sweet-grass *Glyceria maxima*, Common Duckweed *Lemna minor*, Water Figwort *Scrophularia auriculata* and Bulrush *Typha latifolia*.

All other drivers were relatively minor accounting for 10% and 6% of increasing trends when combined. These include:

- Coastal halophytes that have spread inland along roads treated with rock salt in the winter months (Danish Scurvygrass *Cochlearia danica*, Reflexed Saltmarsh-grass *Puccinellia distans*, Lesser Sea-spurrey *Spergularia marina*).
- Several plants that appear to have increased in range in Scotland due to climate change, most notably milder winters and less severe frosts. Possibly the most notable is Mossy Stonecrop *Crassula tillaea* which has spread rapidly since 2000, possibly with the assistance of humans, in sandy habitats in north-east Scotland. Other southern species that have spread include Bee Orchid *Ophrys apifera*, which was recorded for the first time in Scotland in 2003, Hart's-tongue *Asplenium scolopendrium*, Shining Crane's-bill *Geranium lucidum*, Soft Shield-fern *Polystichum setiferum*, Slender Trefoil *Trifolium micranthum* and Keeled-fruited Cornsalad *Valerianella carinata*.
- Heath Rush *Juncus squarrosus* appears to be one of the few native plants that has benefited from the overgrazing of upland habitats in Scotland, although the extent to which this has been caused and/or exacerbated by other factors such as nitrogen deposition is largely unknown.

- The neophyte Great Brome *Anisantha diandra* appears to one of the few species that has increased in Scotland because of increasing resistance to herbicides, as has been shown for Black-grass *Alopecurus myosuroides* in England (Hicks *et al*., 2021).
- A few species have spread dramatically in habitats associated with afforestation (e.g. Climbing Coydalis *Ceratocapnos claviculata*, Slender Rush *Juncus tenuis*, Sand Spurrey *Spergularia rubra*).

Declining species

Table 5 provides a summary of the drivers for the 200 species with the most 'certain' estimated declines in Scotland over the long- and short-term, as opposed to those with the largest absolute mean slopes (see the electronic appendix for a full list of species and the assigned driver). 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.

What is most striking when compared to the list of increasing species is that native species accounted for 70% and 83% of the long- and short-term declines respectively, whereas archaeophytes only accounted for 22% and 11% and neophytes for 8% and 7% respectively.

<u>Long-term decliners</u>

The largest group of long-term decliners in Scotland, accounting for 31% of trends (61 species), were species associated with arable land. Many of these species have become much rarer in Scotland since the 1950s due to the abandonment of small-scale cultivation around crofts in the west and intensification of cropping in the south and east, particularly the increased use of herbicides and inorganic fertilisers (McClean *et al*., 2011). As in other parts of Europe, this intensification of management has reduced the 'weediness' of crops since the 1950s leading to dramatic declines in the range of many species (Storkey *et al*., 2012), particularly long-established weeds adapted to low intensity cropping regimes. In Scotland, declining arable species include many that are now rare or scarce such as chamomiles *Anthemis* spp., Common Cudweed *Filago germanica*, Large-flowered Hemp-nettle *Galeopsis speciosa*, Corn Marigold *Glebionis segetum*, Darnel *Lolium temulentum*, Scarlet Pimpernel *Lysimachia arvensis*, Prickly Poppy *Roemeria argemone*, Shepherd's-needle *Scandix pecten-veneris*, Annual Knawel *Scleranthus annuus* and Night-flowered Catchfly *Silene noctiflora* as well as arable weeds that are still relatively widespread such as Fat-hen *Chenopodium album* agg., Common Fumitory *Fumaria officinalis*, dead-nettles *Lamium* spp., Knotgrass *Polygonum aviculare* agg., Groundsel *Senecio vulgaris*, Corn Spurrey *Spergula arvensis*, Wall Speedwell *Veronica arvensis*, and Field Pansy *Viola arvensis*.

The second largest group of long-term decliners, accounting for 30% of trends (59 species), were native plants associated with infertile grasslands and heathlands that have been lost or modified due to increased anthropogenic disturbance and eutrophication. This driver includes outright destruction due to land use change (e.g. agriculture, mining, housing, transport, quarrying) as well as modification of surviving habitat due to increased intensity of land use, increased nutrient inputs from farming, transport and other human activities or conversely through abandonment and succession to scrub or woodland. Consequently, the list is dominated by poor competitors restricted to infertile soils that disappear quickly where soils are modified through more intensive management, abandonment, or external inputs such as atmospheric pollution. Examples that are still relatively widespread include Harebell *Campanula rotundifolia*, Frog Orchid *Dactylorhiza viridis*, Lady's-bedstraw *Galium verum*, Field Gentian *Gentianella campestris*, Fragrant Orchid *Gymnadenia conopsea s.l.*, Fairy Flax *Linum catharticum*, butterfly orchids *Platanthera* spp., Common Milkwort *Polygala vulgaris*, Bulbous Buttercup *Ranunculus bulbosus*, Yellow-rattle *Rhinanthus minor*, Sheep's-sorrel *Rumex acetosella*, and Wild Thyme *Thymus drucei*; equivalent species of more acidic soils include Mountain Everlasting *Antennaria dioica*, Bell Heather *Erica cinerea*, Cross-leaved Heath *E. tetralix*, Petty Whin *Genista anglica*, Trailing St John's-wort *Hypericum pulchrum*, Sheep's-bit *Jasione montana*, Bitter-vetch *Lathyrus linifolius*, Common Cow-wheat *Melampyrum pratense*, Heath Cudweed *Omalotheca sylvatica*, Lousewort *Pedicularis sylvatica*, Goldenrod *Solidago virgaurea*, Wood Sage *Teucrium scorodonia*, and Heath Dog-violet *Viola canina.*

Table 5. The main drivers of the 200 plant species with the most marked declines in distribution over the long- and short-term in Scotland shown in relation to national status (Nat = native; Arc = archaeophyte; Neo = neophyte; Tot = Total). See Table 1 for an explanation of each driver.

	Long-term decline					**Short-term decline**				
Main driver	**Nat**	**Arc**	**Neo**	**Tot**	**%**	**Nat**	**Arc**	**Neo**	**Tot**	**%**
IPBES driver - Changing use of sea and land										
Arable change	25	33	3	61	31	8	20	0	28	14
Human use	7	10	8	25	13	2	0	3	5	3
Overgrazing	12	0	0	12	6	14	0	0	14	7
Wetland change	17	0	0	17	9	31	0	0	31	16
Woodland change	9	1	0	10	5	5	1	0	6	3
IPBES drivers - Changing use of sea and land & Pollution										
Eutrophication	59	0	0	59	30	36	0	1	37	19
Halophyte inland	0	0	0	0	0	1	0	0	1	1
IPBES drivers - Changing use of sea and land & Direct exploitation of organisms										
Marine change	0	0	0	0	0	1	0	0	1	1
IPBES driver - Climate change										
Climate change	0	0	0	0	0	3	0	0	3	2
IPBES driver Invasive non-native species										
Garden escape	1	0	2	3	2	0	0	4	4	2
Pests & pathogens	1	0	1	2	1	0	0	1	1	1
IPBES driver - Other										
Recording bias	9	0	2	11	6	64	0	3	67	34
Unknown	0	0	0	0	0	0	0	2	2	1
Total species	140	44	16	200	100	165	21	14	200	100
% species	70	22	8	100		83	11	7	100	

The third largest group of long-term decliners, accounting for 13% of trends (25 species), were species that have seen a decline in human use since the 1950s. These include plants formerly grown for animal feed such as such as Bristle Oat *Avena strigosa*, rye-grasses *Lolium* spp., Lucerne *Medicago sativa* subsp. *sativa*, Meadow Fescue *Schedonorus pratensis*, and Alsike Clover *Trifolium hybridum*, as well as medicinal and culinary herbs that used to be grown close to crofts and homesteads such as Good-King-Henry *Blitum bonus-henricus*, Creeping Bellflower *Campanula rapunculoides*, Rampion Bellflower *C. rapunculus*, Caraway *Carum carvi*, Greater Celandine *Chelidonium majus*, Chicory *Cichorium intybus*, Orpine *Hylotelephium telephium*, Sweet Cicely *Myrrhis odorata*, elders *Sambucus* spp. and tansies *Tanacetum* spp. The decline in use of some of these plants and their associated declines in distribution in Scotland are discussed in more detail by Braithwaite (2021).

The fourth largest group of decliners, accounting for 9% of trends (17 species), were associated with the loss or modification of wetlands, in particular acidic mires, which have declined in many areas due to drainage and afforestation (e.g. Great Sundew *Drosera anglica,* Oblong-leaved Sundew *D. intermedia*, Bog-myrtle *Myrica gale*, Marsh Lousewort *Pedicularis palustris*, butterworts *Pinguicula* spp., Small-white Orchid *Pseudorchis albida*).

Both overgrazing and recording bias accounted for 6% of trends (12 and 11 species respectively). The former appears to have been a major driver in upland habitats leading to declines in species sensitive to grazing by sheep and deer such as Brittle Bladder-fern *Cystopteris fragilis*, Hoary Whitlowgrass *Draba incana*, Chickweed Willowherb *Epilobium alsinifolium*, Starry Saxifrage *Micranthes stellaris*, Mountain Sorrel *Oxyria digyna*, Holly Fern *Polystichum lonchitis*, Roseroot *Rhodiola rosea*, Stone Bramble *Rubus saxatilis*, and Mossy Saxifrage *Saxifraga hypnoides*. However, other factors may have played their part including eutrophication and climate change. Recording bias was largely restricted to species where there has been taxonomic uncertainty, especially eyebrights *Euphrasia* spp., as well as past errors in identification that have likely decreased due to improved taxonomic understanding (e.g. Silver Birch *Betula pendula* for Downy Birch *B. pubescens*; Blood-drop-emlets *Erythranthe lutea* for the hybrid with Monkeyflower *E. guttata*; Water Forget-me-not *Myosotis scorpioides* for Creeping Forget-me-not *M. secunda*).

Changes in woodland management and afforestation appears to have caused declines in 5% of the species assessed (10 species), either through direct loss or habitat modification because of replanting with conifers, or overexploitation and overgrazing by livestock and deer over many centuries. These may account for declines of species such as Woodruff *Galium odoratum*, Wilson's Filmy-fern *Hymenophyllum wilsonii*, Dog's Mercury *Mercurialis perennis*, Early-purple Orchid *Orchis mascula* and Sanicle *Sanicula europaea*, especially in western and upland regions where many Atlantic woodlands have deteriorated in quality due to a variety of factors (Ball, 1983).

Other drivers causing the declines of just a few species included the spread of pests and pathogens (e.g. elms *Ulmus* spp.) and declining incidence of species that were formerly more common as contaminants of seed and crops (e.g. Small Melilot *Melilotus indicus*, Tall Rocket *Sisymbrium altissimum*).

<u>Short-term decliners</u>

Whilst there was a lot of overlap in species that declined over the long- and short-term in Scotland, the proportions of species attributed to the main drivers differed (Table 5), most notably the much higher proportion of trends related to recording bias, which accounted for 34% of short-term declines (67 species; Table 5). Most of this group comprised aquatic and bog plants (45 species) that were very well recorded during the 1980s/90s due to targeted surveys during the *NCC/SNH Scottish Loch Survey* (1984-1997) (e.g. water-starworts

Callitriche spp., Six-stamened Waterwort *Elatine hexandra*, spike-rushes *Eleocharis* spp., Floating Club-rush *Eleogiton fluitans*, Lesser Marshwort *Helosciadium inundatum*, quillworts *Isoetes* spp., Shoreweed *Littorella uniflora*, Water Lobelia *Lobelia dortmanna*, water-milfoils *Myriophyllum* spp., White Water-lily *Nymphaea alba*, Least Water-lily *Nuphar pumila*, pondweeds *Potamogeton* spp., water-crowfoots *Ranunculus* Subgenus *Batrachium*, bur-reeds *Sparganium* spp., fine-leaved pondweeds *Stuckenia* spp., Awlwort *Subularia aquatica*, bladderworts *Utricularia* spp., Horned Pondweed *Zanichellia palustris*). Therefore, the smoothed trends for these species are 'humpbacked' with an apparent increase centred on the 1987-1999 recording period and then a sharp decline. The trend graph for Red Pondweed *Potamogeton alpinus* provides an illustrative example (Fig. 7); whilst this species has a relatively stable long-term trend, despite the increase in detection in the 1987-99 period, the short-term trend does show a sharp decline. Although this downward trend may reflect localised losses due to pollution or recreational pressures, this is largely an artefact of targeted surveys in 1987-99 and highlights the extent to which such systematic biases, that are largely independent of general changes in recording between survey periods, can influence analyses of change based on unstructured (opportunistic) records.

Other short-term declines appear to reflect taxonomic uncertainties and therefore variable recording effort (e.g. Slender Lady's-mantle *Alchemilla filicaulis* subsp. *filicaulis*, Slender Sandwort *Arenaria leptoclados*, English Scurvygrass *Cochlearia anglica*, Narrow-fruited Water-cress *Nasturtium microphyllum*, Narrow-leaved Meadow-grass *Poa angustifolia*, Dog roses *Rosa canina s.s.*, Annual Pearlwort *Sagina apetala*, Narrow-leaved Vetch *Vicia sativa* subsp. *nigra*). In a few cases short-term declines may have reflected errors in identification during earlier recording periods: for example, Garden Lupin *Lupinus polyphyllus* recorded in error for Russell Lupin *L.* × *regalis*.

As with the long-term trends, the second main group of short-term decliners were species associated with infertile basic and acid soils that have declined due to increasing eutrophication of habitats, accounting for 19% of trends (37 species). This includes many grassland and heathland species of infertile soils mentioned above but notable additions that appear to have undergone more marked declines in recent decades included Spring Sedge *Carex caryophyllea*, Carnation Sedge *C. panicea*, Flea Sedge *C. pulicaris*, Little Mouse-ear *Cerastium semidecandrum*, Mat-grass *Nardus stricta*, Hare's-foot Clover *Trifolium arvense*, Knotted Clover *T. striatum*, and Spring Vetch *Vicia lathyroides*.

The third largest group of short-term decliners were species associated with the loss or modification of wetlands, accounting for 16% (31 species) of short-term trends. As with long-term changes, species of bogs and mires featured prominently, especially those associated with acid upland habitats in Scotland such as sedges *Carex* spp., Marsh Cinquefoil *Comarum palustre*, Round-leaved Sundew *Drosera rotundifolia*, Many-stalked Spike-rush *Eleocharis multicaulis*, Marsh Pennywort *Hydrocotyle vulgaris*, Bogbean *Menyanthes trifoliata*, Grass-of-Parnassus *Parnassia palustris*, Marsh Lousewort *Pedicularis palustris*, Pillwort *Pilularia globulifera*, Common Butterwort *Pinguicula vulgaris*, Lesser Spearwort *Ranunculus flammula*, Marsh Arrowgrass *Triglochin palustris*, Marsh Speedwell *Veronica scutellata* and Marsh Violet *Viola palustris*.

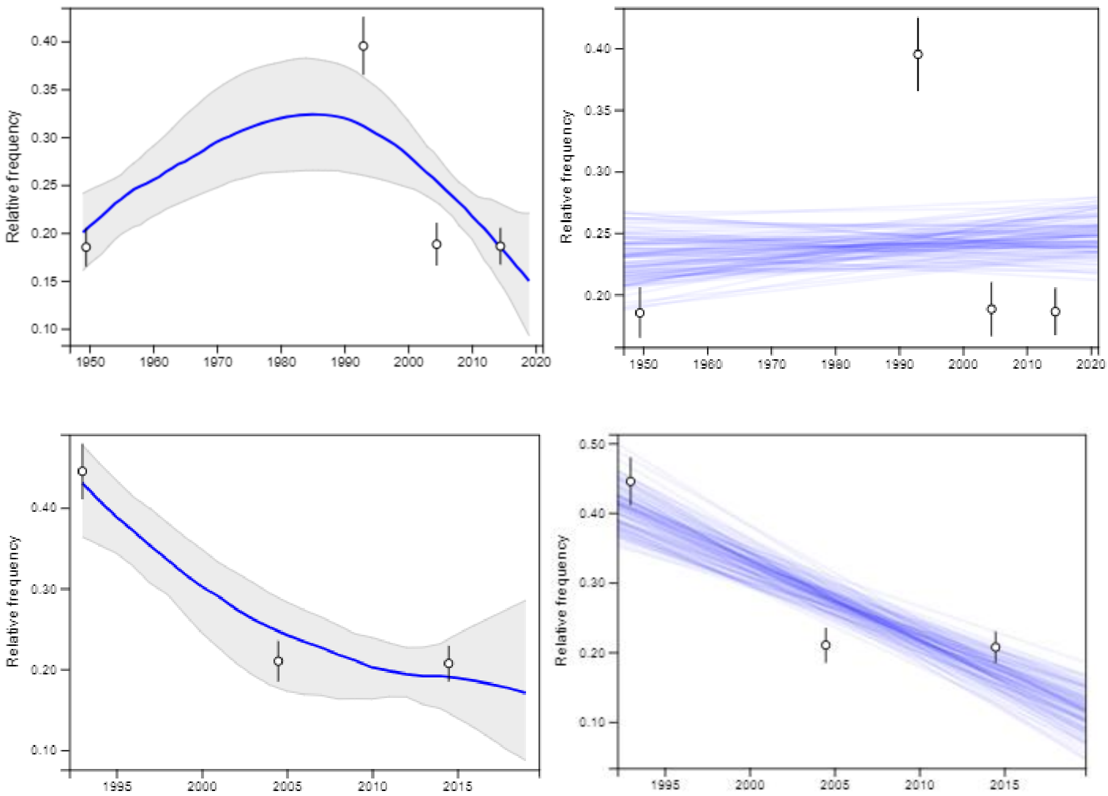


Figure 7. Time-trend graphs for Red Pondweed *Potamogeton alpinus* in Scotland. The long- (top) and short-term (bottom) trends are shown as smoothed (left) and linear (right) trends fitted to the values for each recording period. The long-term plots show how the increased survey effort in the 1987-1999 period (due to the NCC/SNH Loch Survey) has influenced the short-term trends whereas the overall long-term linear trend is less affected and relatively stable.

Species of arable habitats were the fourth largest group of short-term decliners, accounting for 14% (28 species) of trends, emphasising the continued decline of this group due to the intensification of cropping practices and abandonment of small-scale cultivation described under long-term trends. With three exceptions (Black Bent *Agrostis gigantea*, Turnip *Brassica rapa*, Flixweed *Descurainia sophia*) these were all species included under long-term declines.

As with long-term declines, species that have declined because of overgrazing were the fifth largest group, accounting for 7% (14 species) of short-term declines. These included several upland species sensitive to grazing pressure (Green Spleenwort *Asplenium viride*, Parsley Fern *Cryptogramma crispa*, Brittle Bladder-fern *Cystopteris fragilis*, Limestone Bedstraw *Galium sterneri*, Three-leaved Rush *Juncus trifidus*, Mountain Melick *Melica nutans*, Dwarf Willow *Salix herbacea*) including, most notably, Highland Cudweed *Omalotheca norvegica* which is known to have undergone sharp declines at some sites in Scotland due to overgrazing by red deer (Geddes & Payne, 2006).

Changes in woodland management and a decline in human use accounted for 3% of declines (6 and 5 species respectively) with the former including three characteristic ferns of Atlantic woods (Tunbridge Filmy-fern *Hymenophyllum tunbrigense*, Wilson's Filmy-fern *H. wilsonii*, Oak Fern *Gymnocarpium dryopteris*).

Relatively few declines were directly associated with climate change, but there now seems to be growing evidence that some montane species reliant on late-lying snow are declining at their lower altitudinal limits (e.g. Alpine Lady-fern *Athyrium distentifolium*, Moss Campion *Silene acaulis*) (Stroh *et al*., 2023). Although trend data were not available for Snow Pearlwort *Sagina nivalis*, population monitoring on Ben Lawers has shown a steep decline in numbers of this snow-bed specialist (Watts *et al*., 2022) which may be indicative of a wider trend. In comparison, changes in the range of Oysterplant *Mertensia maritima* in Scotland may be due to the increased frequency and severity of winter storms (Stroh *et al*., 2023).

Grouped trends

Broad habitats

The grouped trends for arable and grassland habitats shown in Fig. 8a and 8b below indicate consistent long-term decreases reflecting the increased intensity of agricultural management of these habitats in Scotland since the 1950s, as described above. The slight inflexion in the trend for neutral grasslands is difficult to interpret but may reflect an increase in the distribution of associated species because they are more generalist than those of acidic and calcareous grasslands, and can exploit a wider range of conditions, as well as seed sowing as part of grassland restoration and creation schemes.

The grouped trends for broadleaved woodlands (Fig. 8a) suggest a relatively stable flora since the 1950s, although occurrence datasets such as these can tell us relatively little about the actual condition of the typical wood at small scales, which may have declined due to factors such as pollution and overgrazing. In comparison, species of coniferous woods have shown a slight increase, presumably reflecting the large increase in area of this habitat due to afforestation since the 1950s. As elsewhere in Britain, the grouped trends for linear habitats have experienced a slight decline, presumably due to the intensification of land use and eutrophication of linear habitats such as road verges, hedgerows, riverbanks, etc.

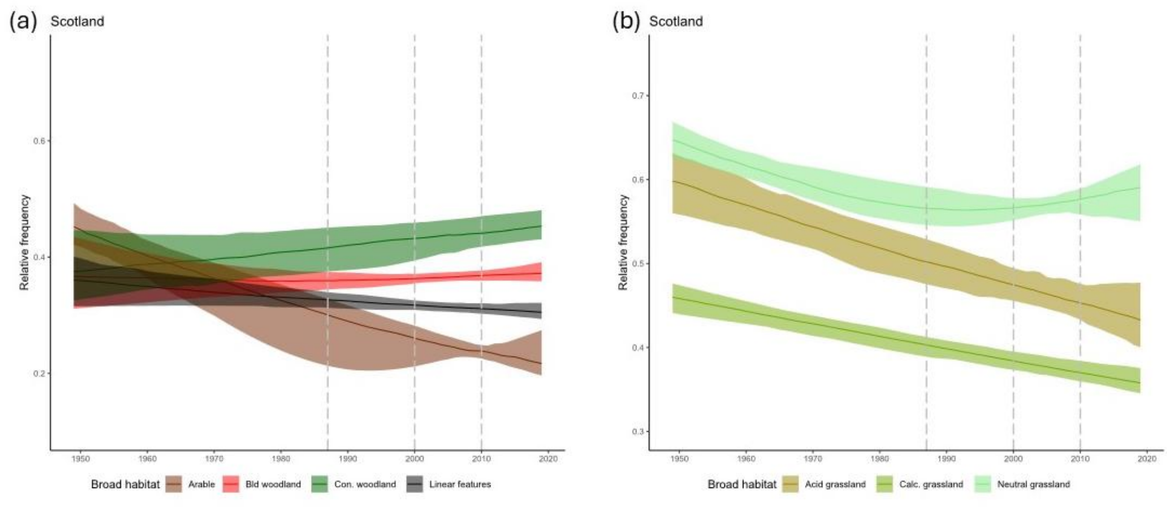


Figure 8. Smoothed group trends for habitats in Scotland showing medians (solid lines) with 90% uncertainty intervals (colour bands): (a) arable, broad-leaved woodland, coniferous woodland, linear habitats, and (b) acid, calcareous and neutral grassland. The dashed vertical lines are the beginning and end years for each recording period.

The grouped trends for bog-associated species (Fig. 9a) probably largely reflect the increased recording effort during the 1980s and 1990s, due to targeted surveys of many bog pool systems as part of the *NCC/SNH Scottish Loch Survey*, and so it is difficult to interpret how these species have fared with respect to factors that are likely to have affected these habitats in Scotland (e.g. drainage, afforestation, atmospheric pollution, changing grazing regimes, etc.). Likewise, there is large uncertainty around the trends for dwarf shrub heath, especially during the baseline period, possibly due to the large contribution of rare species with variable trends. Similarly, montane species appeared to have experienced a slight overall decline, with this becoming more marked in recent decades, possibly because of a combination of factors including climate change, overgrazing and atmospheric pollution as shown in a few recent studies (Britton *et al*., 2009; Ross *et al*., 2012).

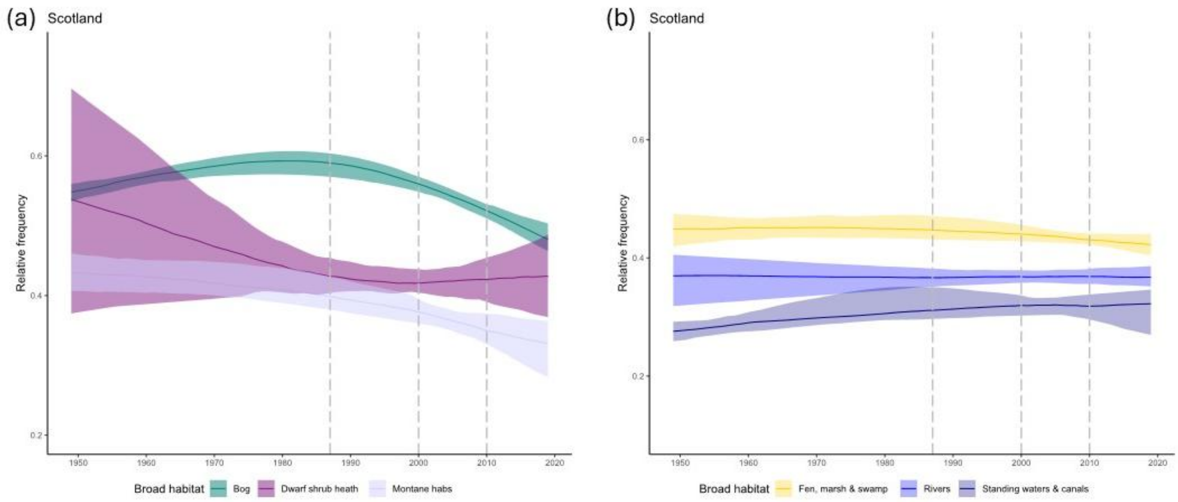


Figure 9. Smoothed group trends for habitats in Scotland showing medians (solid lines) with 90% uncertainty intervals (colour bands): (a) bog, dwarf shrub heath, montane, and (b) fen, marsh & swamp, rivers, standing waters & canals. The dashed vertical lines are the beginning and end years for each recording period.

The grouped trends for wetland habitats (Fig. 9b) appear more stable, although again the slight ‘humps’ in the middle of the curves for fen, marsh and swamp and standing waters and canals may reflect the intensive surveys of wetlands as part of the *NCC/SNH Scottish Loch Survey* as described above. Overall, there appears to have been a very slight increase for standing waters, little change for rivers and streams and an overall slight decline for fen, marsh and swamp.

In comparison to most other habitats, species associated with coastal habitats (sand dunes, shingle, saltmarshes, maritime cliffs, etc.) showed very little change to their overall distribution since the 1950s (Fig. 10).

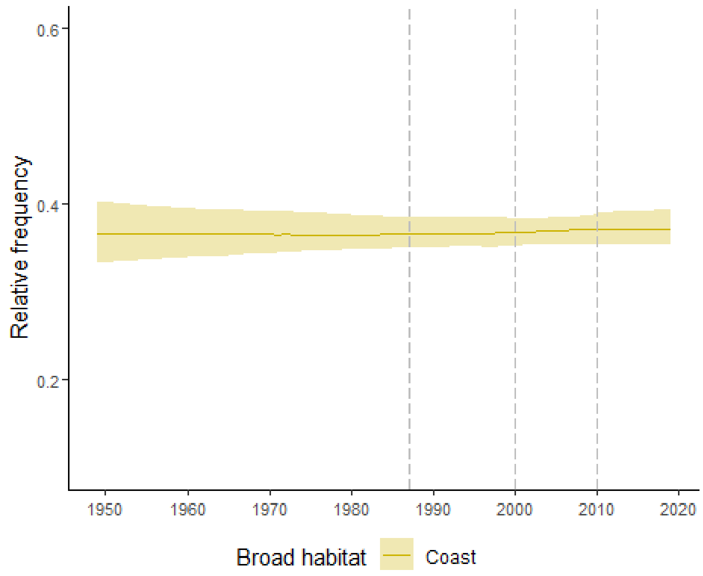


Figure 10. Smoothed group trend for coastal habitats in Scotland showing median (solid line) with 90% uncertainty interval (colour band). The dashed vertical lines are the beginning and end years for each recording period.

Ellenberg indicator values

The grouped trends for Ellenberg moisture values (Hill *et al*., 2004) showed a clear pattern with species associated with dry or moist soils (e.g. grasslands, dwarf-shrub heaths, etc.) exhibiting consistent declines since the 1950s, whereas species of constantly moist sites have been relatively stable as a group (Fig. 11a). The trends for wetland species and aquatics, however, are more complex and, as described for these habitats above, the 'humps' around the mid-point of the curves reflect greater recording intensity during the 1980s and 1990s. The overall trends for these groups are therefore difficult to interpret. In comparison, the grouped trends for Ellenberg light are clear (Fig. 11b): species associated with the most open habitats have declined since the 1950s whereas species associated with semi-shade and shade have shown slight increases, presumably reflecting the widespread loss of open habitats compared to the stability of woodland and scrub species.

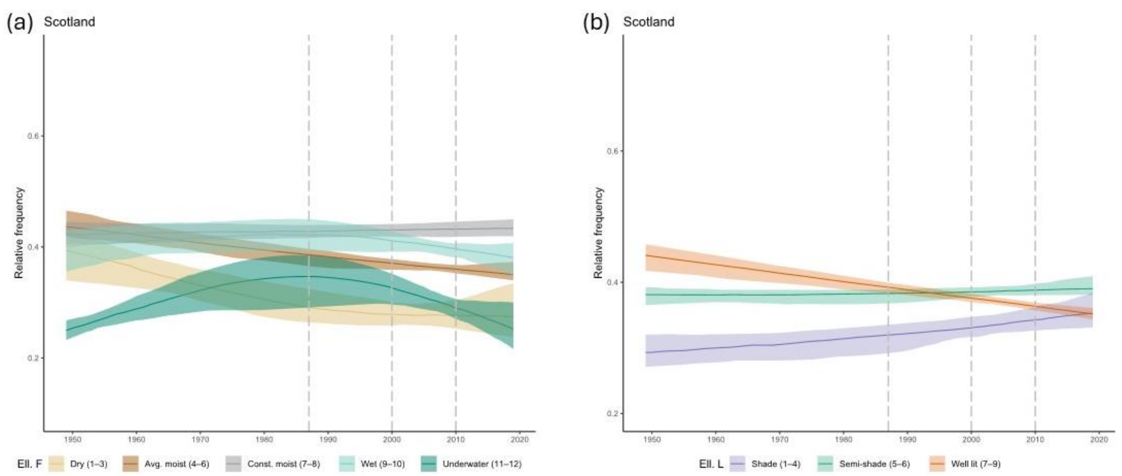


Figure 11. Smoothed group trends for Ellenberg indicator values in Scotland showing medians (dashed lines) with 90% uncertainty intervals (colour bands): (a) Ellenberg (F) moisture, and (b) Ellenberg (L) light. The dashed vertical lines are the beginning and end years for each recording period.

The grouped trends for Ellenberg fertility (Fig. 12a) show that species associated with the least fertile soils have suffered the most consistent decline of fertility groupings since the 1950s; as discussed above, after arable species this is the largest group of declining species, due to increased disturbance and eutrophication caused by human activities. Species associated with very fertile soils displayed a similar trend although with less certainty, especially in the baseline period, and these may reflect the general 'tidying up' of farmland and urban areas leading to the loss of habitats where these specialists used to occur (e.g. manure heaps, farmyards, shoddy fields, docks, waste ground, etc.). In comparison, species associated with soils of intermediate fertility, which encompasses most species, have only shown a very slight decline but with high certainty.

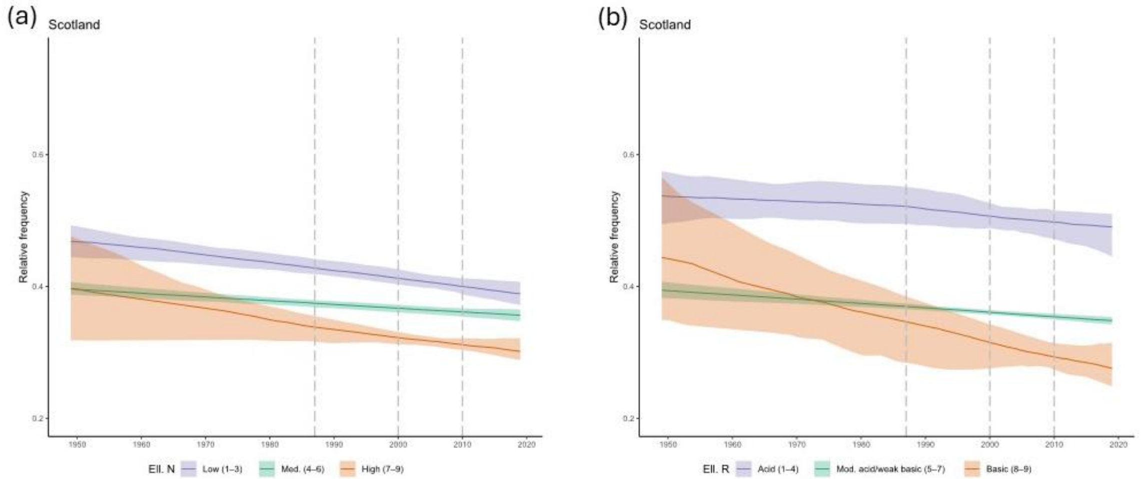


Figure 12. Smoothed group trends for Ellenberg indicator values in Scotland showing medians (dashed lines) with 90% uncertainty intervals (colour bands): (a) Ellenberg (N) fertility, and (b) Ellenberg (R) soil reaction. The dashed vertical lines are the beginning and end years for each recording period.

The grouped trends for soil reaction (Fig. 12b) show that species associated with basic soils in Scotland (e.g. calcareous communities on basic and ultrabasic rocks, shell sands, etc.) have shown a dramatic decline since the 1950s, but with low certainty, presumably reflecting the rarity of these habitats and the species associated with them in Scotland. At the other extreme plants of acidic habitats have been more stable as a group, although with a slight decline in recent decades. Similarly, plants of intermediate reaction have undergone a slight decline as a group but with very high model-based certainty.

<u>Major biomes</u>

The grouped trends for species belonging to the 10 major biomes present in the British and Irish flora (Preston & Hill, 1997) are shown in Fig. 13. The most northerly biomes (the Arctic-montane, Boreo-arctic montane, Boreal-montane, Boreo-temperate), show 'humped' distributions reflecting recent declines possibly due to changes brought about by climate change and/or land use changes, although recording biases in upland regions in more recent decades cannot be ruled out. In comparison, Wide-boreal species showed a slight increase, although this is a very small group of mainly generalist species with wide distributions, many of which are associated with ecosystems disturbed by human activities (e.g. Tufted Hair-grass *Deschampsia cespitosa*, Field Horsetail *Equisetum arvense*, Common Cottongrass *Eriophorum angustifolium*, Red Fescue *Festuca rubra*, Meadow Buttercup *Ranunculus acris*).

Species of the temperate biomes (Wide-temperate, Temperate, Southern-temperate) comprise most of the British flora and all showed consistent declines over the long-term, reflecting many of the declines described above. In comparison, the most southerly distributed species associated with the Mediterranean-Atlantic and Mediterranean biomes, displayed an increase in recent decades, albeit with lower certainty, due to the increasing ranges of more southerly distributed species that have spread in Scotland due to the warming climate (e.g. Mossy Stonecrop *Crassula tillaea*, Bee Orchid *Ophrys apifera*, etc.).

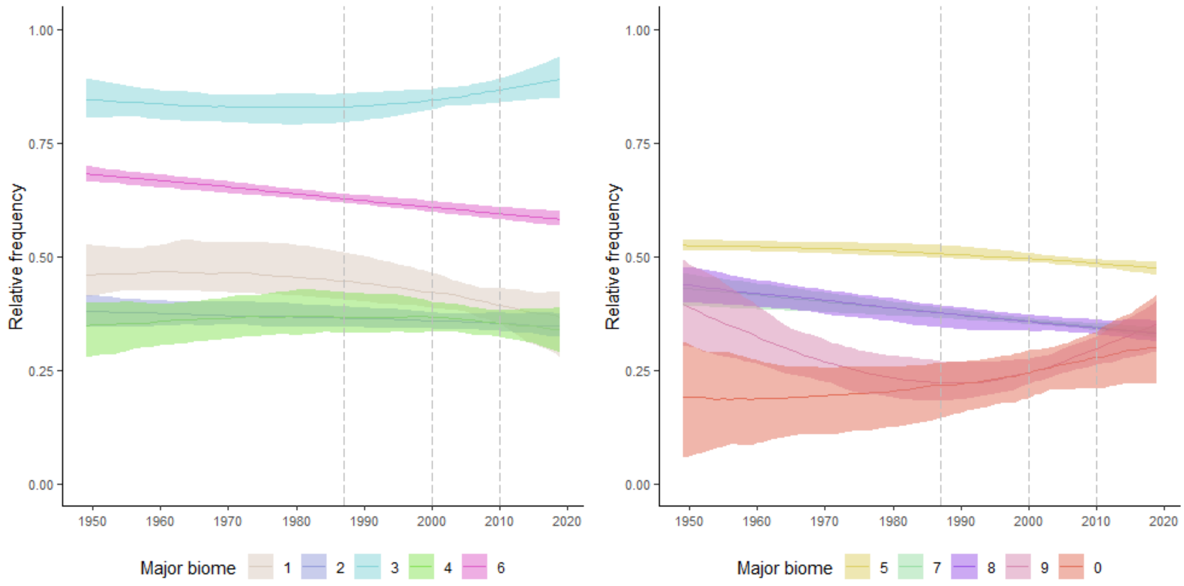


Figure 13. Major biome smoothed trends for Scotland showing medians (dashed lines) with 90% uncertainty intervals (colour bands): (a) 1 = Arctic-montane; 2 = Boreo-arctic montane; 3 = Wide-boreal; 4 = Boreal-montane; 6 = Wide-temperate; (b) 5 = Boreo-temperate; 7 = Temperate; 8 = Southern-temperate; 9 = Mediterranean-Atlantic; 0 = Mediterranean. The dashed vertical lines are the beginning and end years for each recording period.

Conclusions

Plant Atlas 2020 has revealed the extent to which the Scottish flora has been transformed over the last century. Many native specialists of infertile soils have declined due to increased disturbance (habitat loss and degradation) and eutrophication associated with more intensive land management activities. This period has also witnessed a massive loss of arable weeds in Scotland, including many archaeophytes, because of the abandonment of small-scale cropping in the west and intensification of arable cultivation in the east. There are also indications that some Scottish montane species have declined over a long period due to overgrazing, and more recently because of climate change. An assessment of changes to Scotland's aquatic flora has been complicated by systematically uneven recording over time, but there seems to have been a decline of wetland species associated with mires and bogs, presumably caused by widespread afforestation with conifers, drainage, and atmospheric pollution in upland regions.

There has been an increase in the diversity of non-native flora since the 1950s. Some of these aliens are now impacting native assemblages, such as Rhododendron *Rhododendron ponticum* and the conifer Sitka Spruce *Picea sitchensis*, which is now regenerating on peaty soils away from plantations throughout Scotland, even at high altitudes (Watts, 2023; Walker & Harding, 2024).

The evidence from *Plant Atlas 2020* provides a firm basis for plant conservation in Scotland 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.

References

Amphlett, A. 2013. *The Flora of the Cairngorms National Park. A Rare Plant Register*. BSBI, Scottish Natural Heritage and Cairngorms National Park Authority.

Ball, M.E. 1983. Native woodlands in the Inner Hebrides. *Proceedings of the Royal Society of Edinburgh* **83B**: 319-339.

Boyd, R.J., Powney, G.D., Burns, F., Danet, A., Duchenne, F., Grainger, M.J., Jarvis, S.G., Martin, G., Nilsen, E.B., Porcher, E., Stewart, G.B., Wilson, O.J. & Pescott, O.L. 2022. ROBITT: A tool for assessing the risk-of-bias in studies of temporal trends in ecology. *Methods in Ecology & Evolution* **13**: 1497–1507.

Braithwaite, M.E. 2014. *A short Flora of Berwickshire*. Privately published, Hawick.

Braithwaite, M.E. 2021. Scotland's heritage of naturalised medicinal plants. *British & Irish Botany* **3**: 74-89.

Britton, A.J., Beale, C.M., Towers, W. & Hewison, R.L. 2009. Biodiversity gains and losses; Evidence for homogenisation of Scottish alpine vegetation. *Biological Conservation* **142**: 1728-1739.

Faulkner, J. 2023. *Ireland's Changing Flora. A Summary of the Results of Plant Atlas 2020*. Durham: Botanical Society of Britain and Ireland.

Geddes, C. & Payne, A.G. 2006. Loss of *Gnaphalium norvegicum* from Angus Scotland. *BSBI News* **102**: 26–27.
Hannah, A. 2019. *Isle of Bute Flora*. Privately published, Bute.
Hicks, H., Lambert, J., Pywell, R., Hulmes, L., Hulmes, S., Walker, K., Childs, D.Z. & Freckleton, R.P. 2021. Characterizing the environmental drivers of the abundance and distribution of *Alopecurus myosuroides* on a national scale. *Pest Management Science* **77**: 2726–2736.
Hill, M.O. 2012. Local frequency as a key to interpreting species occurrence data when recording effort is not known. *Methods in Ecology and Evolution* **3**: 195–205.
Hill, M.O., Preston, C.D. & Roy, D.B. 2004. *PLANTATT. Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Huntingdon: Centre of Ecology and Hydrology.
Macpherson, P. 2016. *Flora of Lanarkshire*. Pisces Publications, Newbury.
McClean, C.J., van den Berg, L., Ashmore, M.R. & Preston, C.D. 2011. Atmospheric deposition explains patterns of plant species loss. Global Change Biology **17**: 2882–2892.
Pearman, D.A., Preston, C.D., Rothero, G.P. & Walker, K.J. 2008. *The Flora of Rum. An Atlantic Island Reserve*. Privately Published, Truro.
Perring, F.H. & Walters, S.M. (Eds.) 1962. *Atlas of the British Flora*. London: Thomas Nelson & Sons Ltd.
Pescott, O.L., Humphrey, T.A., Stroh, P.A. & Walker, K.J. 2019. Temporal changes in distributions and the species atlas: How can British and Irish plant data shoulder the inferential burden? *British & Irish Botany* **1**: 250–282.
Pescott, O.L., Stroh, P.A., Humphrey, T.A. & Walker, K.J. 2022. Simple methods for improving the communication of uncertainty in species' temporal trends. *Ecological Indicators* **141**: 109117.
Preston, C.D. & Hill, M.O. 1997. The geographical relationships of British and Irish vascular plants. *Botanical Journal of the Linnaean Society* **124**: 219-226.
Preston, C.D., Pearman, D.A. & Dines, T.D. (Comps. & Eds.) 2002. *New Atlas of the British and Irish Flora*. Oxford: Oxford University Press.
Pywell, R.F., Heard, M.S., Bradbury, R.B., Hinsley, S., Nowakowski, M., Walker, K.J. & Bullock, J.M. 2012. Wildlife-friendly farming benefits rare birds, bees and plants. *Biology Letters* **8**: 772–775.
Ross, L.C., Woodin, S.J., Hester, A.J., Thompson, D.B.A. & Birks, H.J.B. 2012. Biotic homogenisation of upland vegetation: patterns and drivers at multiple scales over five decades. *Journal of Vegetation Science* **23**: 755-770.
Shrubsole, G. 2023. *The Lost Rainforests of Britain*. William Collins, London.
Stace, C.A. 2019. *New Flora of the British Isles*. Fourth edition. Suffolk: C&M Floristics.
Stace, C.A. & Crawley, M.J. 2015. *Alien Plants*. William Collins, London.
Storkey, J., Meyer, S., Still, K.S. & Leuschner, C. 2012. The impact of agricultural intensification and land-use change on the European arable flora. *Proceedings of the Royal Society B* **279**: 1421-1429.
Stroh, P.A., Walker, K.J., Humphrey, T.A., Pescott, O.L. & Burkmar, R.J. 2023. *Plant Atlas 2020. Mapping Changes in the Distribution of the British and Irish Flora.* 2 volumes. Durham & Princeton: Botanical Society of Britain and Ireland and Princeton University Press.
Stroh, P.A. *et al*. In prep. *A new vascular plant Red List for Great Britain*.

Sydes, C. 2008. Can we protect threatened Scottish arctic-alpine higher plants? *Plant Ecology & Diversity* **1**: 339–349.
The Nevis Partnership, 2019. *The North Face Survey. Discovering the hidden side of Ben Nevis*. Fort William: The Nevis Partnership
Walker, K.J. & Harding, M. 2024. The spread of Sitka spruce *Picea sitchensis* in Britain and Ireland. Evidence from botanical surveys and implications for biodiversity and forestry. *Scottish Forestry* **78**: 36–41.
Walker, K.J., Stroh, P.A. & Ellis, R.W. 2017. *Threatened plants in Britain and Ireland*. Durham: Botanical Society of Britain and Ireland.
Walker, K.J., Pinches, C.E. & Trippier, B. 2022. Right tree, right place: using botanical heatmaps to inform tree-planting. *BSBI News* **150**: 40–44.
Walker, K.J., Stroh, P.A., Humphrey, T.A., Roy, D.B., Burkmar, R.J. & Pescott, O.L. 2023. *Britain's Changing Flora. A Summary of the Results of Plant Atlas 2020*. Durham: Botanical Society of Britain and Ireland.
Watson, K. 2013. *The Flora of Renfrewshire*. Pisces Publications, Newbury.
Watts, S.H. 2023. High mountain trees: altitudinal records recently broken for eleven different tree species in Britain. *British & Irish Botany* **5**: 167–179.
Watts, S.H., Mardon, D.K., Mercer, C., Watson, D., Cole, H., Shaw, R.F. & Jump, A.S. 2022. Riding the elevator to extinction: Disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand. *Biological Conservation* **272**: 109620.