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Changing environment and orchid distributions close to their northern and southern limits in Britain

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Abstract
The total numbers of tetrad records in the BSBI database collected for 20 species of British orchids in the period 1970-86 were compared with those collected in 2010-19. The species chosen had a northern limit to their distributions somewhere in Britain and comparisons were restricted to changes close to their northern and southern distribution limits. In a 100 km band close to their northern limit, recorded tetrad occupancy decreased for 14 species by a mean of 34% between the two date-classes. Despite Britain warming by 0.9 C° over this period, four species had retreated southwards, and only *Ophrys apifera* (Bee Orchid) and *Anacamptis pyramidalis* (Pyramidal Orchid) had significantly extended their distributions northwards. Changes in tetrad occupancy were also explored in a similar band immediately to the north of the southern tip of the Isle of Wight. Here, tetrad occupancy decreased for 10 of the 20 species by a mean of 33%. In both the northern and southern bands, where a species was recorded in 1970-86, on average in 2010-19 it was re-recorded in only *c.*40% of tetrads. There were large differences between species in apparent rates of colonization of new tetrads. This accounted for most of the differences between species that increased their tetrad occupancy between the two date-classes and those that declined. No account was taken of the increase in the intensity of recording between 1970-86 and 2010-19 but these results provide further strong evidence of the decline of many orchid species, especially in England.

Keywords: tetrad occupancy; range expansion; range reduction; environmental change

Introduction
Britain has warmed by *c.*0.9 C° between 1970 and 2019 and this has enabled many poikilothermic species to extend their distribution northwards. During this period, 41% of native dragonfly species have extended their distributions northwards, and several new species have colonized Britain (Taylor *et al.*, 2021). Similarly, many species of butterflies and moths have extended their distributions northwards (Fox, 2020), but "only species with stable or increasing abundance at core sites have been able to do so" (Muir, 2014). This expansion of distributions is dependent on the availability of suitable habitat and, whilst some native species of butterflies, moths

and dragonflies have increased, others have declined, probably mainly due to loss of suitable habitat.

Compared with butterflies and dragonflies there is relatively little information on the impact of climate change on the distribution of plants in Britain. This article focuses on orchids and uses the maps and database of the Botanical Society of Britain and Ireland (BSBI) (https://database.bsbi.org/) to explore changes between the date classes 1970-86 and 2010-19 in the distributions of 20 species of orchids with a northern limit to their distributions somewhere in Britain. The environmental changes likely to affect orchid distributions are briefly summarised and this is followed by an examination of changes in orchid distributions close to their northern limits. Changes in the southern part of their range are also explored. The implications for future orchid conservation and management are then considered.

Environmental changes

Braithwaite (2010) identified a range of factors implicated in the decline of rare plants in Berwickshire, including quarrying, changes in land use and management, competition from invasive species, flush degradation and muirburn. Species that grow in grassland have been particularly adversely affected by changes in traditional grazing and mowing practices and by 'improvements' such as the application of fertilizers (Stroh *et al*., 2019). By 2011, only 2% of the UK grassland could be classified as high diversity, semi-natural grassland (Bullock *et al*., 2011). Also, grassland has been lost due to the planting of woodlands that has increased from 9% of the land area in 1980 to 13% in 2011 (Quine *et al*., 2011). Other, more subtle changes have occurred, including greater soil compaction resulting from the use of increasingly heavy farm machinery.

Nitrogen (N) precipitation is another concern. Multiple sources are involved, including vehicles and industrial emissions, agriculture (see Plantlife article –'We need to talk about nitrogen', https://www.plantlife.org.uk/uk/our-work/campaigning-change/nitrogen), and natural sources such as volcanoes and lightning. Rates of N deposition range from 10 kg/ha/year in north-west Scotland to over 30 kg in central parts of England. Besides promoting plant growth, N depositions (and SO_2 coming from many of the same sources) acidify soils and there is strong evidence that together these two effects have been involved in driving the loss of sensitive species from substantial areas of the UK (Row *et al.*, 2014). In long-term trials at Rothamsted Experimental Station, species diversity was increased when chalk was applied to experimental plots growing a hayfield flora, whether fertilized or not (http://www.era.rothamsted.ac.uk/Park).

Our climate is changing and becoming more variable (Anon., 2018). Since the 1970's measurements of average annual rainfall have increased at most meteorological stations around Britain with increases of more than 20% in some parts of northern England and Scotland. This increase is partly due to more frequent spells of very wet weather (Maraun *et al*., 2008). Short-term extremes, including of drought are also increasing and are probably as important for orchids as are long-term trends. Storm Desmond produced record rainfall across northern England in December 2015, and the summer of 2018 was the hottest since records began (many plants of *Cypripedium calceolus* (Lady's Slipper Orchid) at Gait Barrow in NW Lancashire were killed in 2018 due to the drought). February 2020 was the wettest on record, whilst May 2020 was the driest on record in England, and in March 2021 some sites recorded record high temperatures.

Increasing carbon dioxide (CO_2) concentrations in the atmosphere are of widespread concern because of the associated increase in temperature. Levels of CO_2 have increased from 310 ppm in the 1960's to 410 ppm in 2019, and since the 1970's average temperatures in Britain have increased by *c.*0.9 C°. As a consequence, northern Scotland in the decade to 2020 was as warm as north Yorkshire was in the 1970's (Trudgill, 2020). The numbers of days with an air frost has decreased and orchids are flowering earlier – peak flowering of *Ophrys sphegodes* (Early Spider-orchid) had advanced by an average of *c.*0.5 days per year during the late 1900s-early 2000s (Hutchings, 2010) and first flowering of *Platanthera bifolia* (Lesser Butterfly-orchid) has advanced by *c.*7 days for every degree Centigrade increase in mean temperature during spring and early summer (Trudgill, 2021). Another effect of increasing temperatures is to lengthen the growing season; since the 1900s it has increased by nearly 4 weeks (https://www.climatechangepost.com). Increases in CO_2 also have a small, but direct effect by increasing plant growth and decreasing water use (Taub, 2010). Whilst increasing temperatures might have a negative effect on some northerly distributed species it seems likely that temperature increases should facilitate the northward spread of orchids with southerly distributions. This article examines changes between 1970-86 and 2010-19 in the occurrence and distributions of 20 such species to determine which, if any, have so responded.

Changes in the distribution of orchids close to their northern and southern limits.

Source of data and methods

I used both the BSBI database and the maps to investigate recent changes in the distribution of 20 species of orchids with a northerly limit to their distribution somewhere in Britain. The orchids selected for study (see Table 1) were 18 species whose British distributions in the period 1970-86 were largely restricted to England and Wales. In addition, I included *Anacamptis pyramidalis* and *Epipactis palustris* (Marsh Helleborine) whose distributions extended into northern Scotland. I have, however, omitted the autogamous species *Epipactis dunensis* (Dune Helleborine), *E. leptochila* (Narrow-lipped Helleborine), and *E. phyllanthes* (Green-flowered Helleborine).

Northern limits

The BSBI maps were used to identify the northern limit of each species in 1970-86. Total tetrad (an area 2 km x 2 km) occupancy for the periods 1970-86 and 2010-19 was then determined and compared for each species in a 100 km band immediately to the south of this limit (Table 1). Hectads (area 10 km x 10 km) that did not contain any tetrad records were added to the totals. The northern limits ranged from latitude 51.30 °N in Kent for *Ophrys fuciflora* (Late Spider-orchid) to latitude 57.32 °N for *A. pyramidalis* in South Uist (a latitude difference of one degree is equivalent to *c.*110 km). For *Liparis loeselii* (Fen Orchid) and *Ophrys sphegodes* the 100 km range was increased to include all populations. Three species had one or two outlying, northerly records that were ignored when fixing their northern limit (see Table 1). Species that by 2010-19 had extended their distribution more than 10 km northwards ('Spread north' – Table 1) were identified both from the maps and the database.

Southern limit
Changes in the southern distributions of the same twenty species (Table 2) were explored in a similar, but predetermined band of latitude that extended northwards from the southern tip of the Isle of Wight (lat. 50.57 °N). This band covered the whole of the south coast of England except those parts to the south of Exmouth. Depending on species abundance, tetrad occupancy was then determined in a 50 or a 100 km band to the north of latitude 50.57 °N. For the least abundant species the band was extended to include the whole of the British population ('All' – see Table 2).

Data presentation
The tetrad occupancy records for each species in both northern and southern bands were divided into three groups. The first was for tetrads where a species was recorded in 1970-86 but not in 2010-19 - these records were categorized and counted as having been 'Lost'. The second was for those tetrads where a species was recorded in both 1970-86 and 2010-19 - these were counted as 'Persisted'. The third group was for tetrads where a species was recorded in 2010-19 but not in 1970-86 - these were counted as 'New'. For the southern band these results are given as percentages of the 1970-86 values (Table 2).

A species was classified as having 'Spread north' (final column, Table 1) if there was one or more tetrad records in 2010-19 more than 10 km north of its northern limit in 1970-86.

Problems associated with interpretation of differences in tetrad numbers between 1970-86 and 2010-19
There are several problems and uncertainties associated with the BSBI tetrad occupancy data. Consequently, a degree of judgement is needed when interpreting some of the results. Firstly, the recording period 1970-86 is of a longer duration than that of 2010-19 and, on that basis, it might be expected that the greater numbers of records would have been collected in the period 1970-86. However, there has been a substantial increase in the intensity of recording, as is evident from the increase in total numbers of all records collected for all plant taxa in England. These increased from a total of 4,394,000 records for the period 1970-86 to a total of 12,245,000 records for 2010-19 (A. Amphlett pers. comm.). Trudgill (2022b) showed that, on a national scale, there was a strong correlation between numbers of tetrad records for orchids and the total numbers of records for all plant taxa. Consequently, except for the rare species of orchids whose populations are likely to have all/mostly been discovered by 1970-86, directly comparing orchid tetrad records from 1970-86 with those from 2010-19 (as is done here) is likely to lead to an over-estimate of apparent increases and under-estimate of declines.

A tetrad is an area of 2 x 2 km and discovering a localised orchid population, and re-finding it at a later date, is something of a lottery. Furthermore, the data in the database on internal population in species abundance within tetrads are too imprecise to be usable; there can be major changes in species abundance within a tetrad without any change in its occupancy status, provided at least one plant remains and is recorded. Not all the BSBI records have tetrad resolution, a small proportion are for hectads, a much larger area (10 x 10 km) and, rather than ignore these records, I have added hectad records that contain no tetrad records to the totals in Tables 1 & 2. For the period 2020-19 almost none of the records were for hectads. For 1970-86, in the northern band (Table 1) an overall mean of just 3.7% of records were for hectads.

There will be other errors in the database e.g. when checking a historic record for one orchid I found the map coordinates placed it in the middle of a local loch. A further consideration is that orchids are an iconic group and, especially for rarer species, a greater proportion of populations are likely to have been discovered earlier than for most other plant species.

Results

Changes in orchid tetrad occupancy in their northern 100 km band between 1970-86 and 2010-19

In their 100 km northern band, compared with 1970-86, tetrad occupancy in 2010-19 increased for only six of 20 species (Table 1A). For the remaining 14 species, the total numbers of tetrads where each was recorded had decreased between 1970-86 and 2010-19 by an overall average of 34% (Table 1B). The proportion of tetrads from which a species was 'Lost' between 1970-86 and 2010-19 exceed that in which it 'Persisted' for all except four species (*A. pyramidalis. Ophrys sphegodes, Ophrys fuciflora* and *Orchis purpurea* (Lady Orchid)). The relative success of the six species that increased between 1970-86 and 2010-19 (Table 1A) was due to their greater ability to colonise new tetrads. On average, for this group there was a 2.3:1 ratio of 'New' to 'Lost' tetrads. In contrast, for the second group of fourteen, declining species (Table 1B) the ratio was 0.44:1, emphasising their relative lack of success at colonizing new tetrads. However, it must be remembered that, because the intensity of recording greatly increased between 1970-86 and 2010-19, for all except possibly the rare species, a smaller proportion of occupied tetrads would have been detected and recorded in 1970-86 than in 2010-19. Consequently, it is likely that the observed rates of increase of the six species (1A) are over-estimated, and rates of decline of the fourteen species (1B) are under-estimated.

Northward spread

Six of the 20 species were recorded in 2010-19 from one or more tetrad that was more than 10 km north of their 1970-86 northern limit. However, four of these six species were recorded from only one such northerly tetrad (Table 1). For these four species it is too early to know whether these single northerly out-posts are part of a longer-term trend as their ability to persist and spread further north is, as yet, unknown. Two species, *Ophrys apifera* and *A. pyramidalis*, had multiple northerly records and were the only species that had convincingly extended their range northwards. *Ophrys apifera* was recorded from seventeen tetrads and *A. pyramidalis* from nine tetrads to the north of their 1970-86 distribution limit (Table 1A). In 1999 the northern limit of *Ophrys apifera* was near Newcastle-upon-Tyne. Twenty years later its distribution had progressively extended northwards as far as Edinburgh and Glasgow. This northward spread is probably continuing - in 2021 we discovered a single flowering plant of *Ophrys apifera* (Fig. 1) in the edge of a gravel drive close to a house near Blairgowrie (lat. 56.59 °N). The seed from which it grew came from a plant of *Ophrys apifera* growing nearby in a pot. In Scotland in the Western Isles by 2010-19 *A. pyramidalis* had extended its distribution 110 km northwards from South Uist in 1970-86 to near Callanish in Lewis. In contrast, in the east of Scotland the range of *A. pyramidalis* had slightly contracted, probably due to loss of suitable habitat.

Table 1. Latitude of northern limit (in 1970-86) and total numbers of tetrad records in the northern 100 km of each species' range in 1970-86 and 2010-19. 'Spread north' records the number of tetrads where a species was recorded in 2010-19 more than 10 km north of the 1970-86 northern limit. The species are arranged in descending order depending on the relative change in tetrad occupancy between 2010-19 and 1970-86.

Species	**North limit latitude**	**Total tetrads**		**Numbers of Tetrads[1]**		
		1970 -86	**2010-19**	**Lost**	**Persisted**	**New**
A. Species that increased						
Dactylorhiza praetermissa	54.98	4	20	4	0	20
Anacamptis pyramidalis	57.32	8	28	3	5	23
Ophrys apifera	54.98	59	173	39	20	153
Himantoglossum hircinum	52.70[2]	6	12	5	1	11
Ophrys sphegodes	51.83[3]	41	43	16	25	18
Cephalanthera damasonium	52.52	116	131	62	54	77
Mean (% of 1970-86)[4]		**39**	**68**	**22 (63)**	**18 (37)**	**50 (223)**
B. Species that decreased						
Epipactis palustris	56.19[2]	7	7	5	2	5
Orchis purpurea	51.46	56	51	24	32	19
Orchis anthropophora	52.99	23	17	12	11	6
Spiranthes spiralis	54.21	22	18	13	9	9
Ophrys fuciflora	51.30	12	9	5	7	2
Orchis simia	51.70	4	3	2	2	1
Epipactis purpurata	52.54	141	74	111	30	44
Ophrys insectifera	54.73	53	35	30	23	12
Orchis militaris	52.40	6	5	4	2	3
Herminium monorchis	51.94	66	31	38	28	3
Neotinea ustulata	54.74	21	8	14	7	1
Anacamptis morio	54.55[2]	53	19	43	10	9
Cephalanthera rubra	51.83	5	3	3	2	1
Liparis loeselii	52.80[3]	17	5	13	4	1
Mean (% of 1970-86)[4]		**29**	**19**	**18 (62)**	**11 (38)**	**8 (26)**

[1] See text for definition of categories
[2] Northern outliers ignored when fixing northern limit.
[3] Northern band was extended to include all populations
[4] Means of percentages of 1970-86 tetrad numbers. These means are directly comparable with those in Table 2.

Figure 1. ***Ophrys apifera*** **in 2021 growing in the edge of a gravel drive at Newmill, near Blairgowrie.**

Southward retreat of northern limit in 2010-19

The northern limit of *Orchis simia* (Monkey Orchid), *Ophrys insectifera* (Fly Orchid), and *Anacamptis morio* (Green-winged Orchid) in England in 2010-19 had retreated more than 10 km south of the limit in 1970-86. However, although *A. morio* had retracted southwards in England by >40 km, in Ayrshire in 2010-19 it had apparently increased as it was recorded from three tetrads compared with two in 1970-86. In 1974, a small population of *Orchis simia* was found at Spurn Point, over 250 km from the nearest known British source of seed. This population persisted until 1983 when the site was washed into the sea (Harrap & Harrap, 2009).

Northern outposts - other species
Epipactis phyllanthes is not included in this analysis but it appears to have made a relatively huge jump northwards. It was not recorded from Scotland before 2010, but in 2010-2019 it was reported near Forres on the Moray Firth – *c.*260 km north of its next known location. It appears to be spreading locally as in 2021 it was recorded from three tetrads. Several other orchid species have briefly extended their northward distribution. A population of *Epipactis purpurata* (Violet Helleborine) was recorded in the period 1987-1999 near Leeds, 120 km north of its previous range and one of *Ophrys sphegodes* was recorded 60 km north near Thetford, but neither were recorded after 2000.

Changes in tetrad occupancy in southern Britain.
As a generalization, between 1970-86 and 2010-19 rates of loss and of persistence of the twenty species of orchids were not greatly different between the southern and northern parts of their ranges. However, ten species increased their tetrad occupancy in the south. These were the same six species that had increased in the north plus *A. morio*, *E. purpurata*, *Orchis anthropophora* (Man Orchid) and *Spiranthes spiralis* (Autumn Lady's-tresses). The remaining ten species declined by an average of 33%. This was similar to their mean rate of decline across the whole of England (37%) whether calculated using the totals or the individual percentages for species.

Compared with 1970-86, in 2010-19 the southern distribution limit for six species had moved northwards by >10 km. Four species - *E. purpurata*, *Neotinea ustulata* (Burnt Orchid), *Orchis anthropophora* and *Ophrys insectifera* (Fly Orchid) - were no longer recorded from the Isle of Wight, *L. loeselii* had been lost from its single site in north Devon and *E. palustris* was not re-recorded from its single site near Penzance. It seems more likely that most of these losses were a consequence of local factors rather than climate change. In contrast, *Himantoglossum hircinum* (Lizard Orchid), *O. purpurea* and *S. spiralis* extended their distributions southwards (*H. hircinum* and *S. spiralis* onto Jersey).

Although not detailed here. I did explore changes in tetrad occupancy of five species with a southern distribution limit well to the north of the south coast of England. No changes in their southern limit were observed for *E. atrorubens* (Dark-red Helleborine), *Corallorhiza trifida* (Coralroot Orchid) and, if an outlying record near Southampton is ignored, *D. purpurella* (Northern Marsh-orchid). A small northward shift was observed for *Pseudorchis albida* (Small–white Orchid), and *Neotinea cordata* (Lesser Twayblade).

Discussion
The BSBI database is an exceptional resource and in this, and three other articles (Trudgill 2022a, 2022b, 2022c) I have used it to explore changes between 1970-86 and 2010-19 in orchid occurrence and distributions in the British Isles. It should, however, be noted that during this period there have been changes in the objectives and methods of recording (Trudgill 2022c). There are other problems and biases, as briefly mentioned above. Bell (2015) used the BSBI database to explore recent changes in the distribution of native plants in Britain in relation to climate change. She concluded that many plant species are not advancing northwards because the

'effects of human disturbance are stronger drivers of distribution than climate change'. She also concluded that 'natural dispersal mechanisms are no longer facilitating spread'.

Table 2. As for Table 1 but for tetrad occupancy in a band immediately north of latitude 50.57 °N (Isle of Wight). The numbers of tetrads between 1970-86 and 2010-19 from which a species was 'Lost', where it 'Persisted', and those where it was recorded in 2010-19 but not in 1970-86 ('New') are all expressed as percentages of the values for 1970-86.

Species	**Band width km**	**Total tetrads**		**Percent of numbers in 1970-86**		
		1970-86	**2010-19**	**Lost**	**Persisted**	**New**
A. Species that increased						
Anacamptis pyramidalis	50	74	370	42	58	357
Ophrys apifera	50	66	309	58	42	426
Himantoglossum hircinum	All	28	57	68	21	182
Dactylorhiza praetermissa	50	215	429	71	29	171
Spiranthes spiralis	50	155	264	59	41	130
Cephalanthera damasonium	50	38	51	71	29	105
Epipactis purpurata	100	127	156	73	27	96
Orchis anthropophora	100	93	105	44	56	61
Ophrys sphegodes	All	41	44	39	61	46
Anacamptis morio	50	185	185	77	23	77
Mean		**102**	**197**	**61**	**39**	**165**
B. Species that decreased						
Orchis purpurea	All	53	49	38	63	36
Orchis militaris	All	6	5	50	50	33
Ophrys insectifera	100	120	113	58	43	52
Ophrys fuciflora	All	12	9	42	58	17
Orchis simia	All	4	3	50	50	25
Epipactis palustris	100	59	41	68	32	37
Cephalanthera rubra	All	5	3	60	40	20
Neotinea ustulata	100	80	33	70	30	11
Herminium monorchis	100	68	23	71	29	4
Liparis loeselii	All	17	5	76	24	6
Mean		**42**	**28**	**58**	**42**	**24**

The results reported here fully accord with Bell's (2015) conclusions. There can be little doubt from the results presented here that the majority of orchid species with a northern distribution limit somewhere in Britain have not extended their distributions northwards, and some appear to have retreated southwards. This is despite Britain warming by 0.9 C° since the 1970's and orchid seed being structured to be distributed on currents of air.

For orchids, there is clear evidence that climate is not the factor limiting northward spread. Recently, we have grown in a meadow near Blairgowrie, from seed, two species (*Anacamptis morio* - Fig. 2, and *Dactylorhiza praetermissa* (Southern Marsh-orchid) - Fig. 3), both of which are 100's of kilometres north of their previous northern limit. Similarly, as reported above, species such *E.*

phyllanthes, *E. purpurata* and *Orchis simia* have (naturally?) established northern colonies at great distances from their previous northern limits.

Persistence between 1970-86 and 2010-19 was low for most of the species in both the south and the north of Britain with an overall mean loss of tetrad occupancy of *c.*60%. Total tetrad occupancy decreased for 14 species in the north and ten species in the south. However, tetrad occupancy data provides an incomplete picture of the changes between the two time periods. We know that the total numbers of records for all plant taxa collected in 2010-19 was much greater than in 1970-86 (nearly three-fold more), but no adjustment has been made for this increase. Also, changes within tetrads have not been determined but, because losses within tetrads precede those of tetrads, these will be greater than those for the tetrads, especially when a species is declining (Trudgill, 2022c). Consequently, it is almost certain that all species except *Ophrys apifera,* and probably *A. pyramidalis*, *Cephalanthera damasonium* (White Helleborine) and *D. praetermissa,* declined between 1970-86 and 2010-19 in both the northern and southern parts of their ranges, and that the amounts by which they declined were greater than indicated in Tables 1 and 2.

Figure 2. ***Anacamptis morio* (Green-winged Orchid) flowering in 2021 in a meadow at Newmill, near Blairgowrie, in eastern Scotland.**

Figure 3. ***Dactylorhiza praetermissa*** **(Southern Marsh-orchid) flowering in 2021 in a meadow at Newmill, near Blairgowrie, eastern Scotland.**

Orchid population numbers and distributions are strongly influenced by both their persistence over time (Trudgill, 2016) and by their ability to establish new colonies (Trudgill, 2015). The results reported here show that for many species both were low close to their northern and southern limits in Britain, making it inevitable that they will decline. *Ophrys apifera* appears to be a notable exception due to its greater ability to colonise new sites. The northward spread of *Ophrys apifera* has been remarkable (Bell, 2015, Trudgill, 2017a) and it seems likely that it will continue its northwards invasion. Trudgill (2017a) suggested that northern Scotland might have warmed just sufficiently for *Ophrys apifera* to grow near Blairgowrie (latitude 56.59 °N). In 2021 this suggestion was confirmed (Fig. 1). The increase and expansion of *O. apifera* northwards demonstrates what might be possible for other species of orchids if all the circumstances are favourable. In western Scotland, *A. pyramidalis* is also expanding its distribution (Table 1), spreading northward by more than 100 km in the Western Isles. Since 2016 we have spread seed of *A. pyramidalis* across a meadow near Blairgowrie (Trudgill, 2019) and now have a thriving population of >650 plants (Fig. 4).

Figure 4. *Anacamptis pyramidalis* (Pyramidal Orchid) flowering in our meadow at Newmill, near Blairgowrie.

So far, I have attributed all the recent changes in orchid distributions to direct effects on the orchids themselves, but it may not be that simple. Orchids tend to occupy specific niches and to have specific insect pollinators. Also, to initiate germination they all require their seed to be colonised by a mycorrhizal fungus and, for most species, colonisation of their roots by mycorrhizal fungal is probably important for their subsequent growth. The effect of the environmental changes over the last 50 years on the distributions, abundance and effectiveness of both pollinators and of the specific mycorrhizal fungi is largely unknown. However, Kolanowska *et al.* (2021) suggested that global warming in Australia is likely to affect the distribution of the orchid *Leporella fimbriata* (Fringed Hare Orchid) less than that of its specific ant pollinator. Consequently, it is not possible with certainty to separate any effects the recent environmental changes may have had on mycorrhizal fungi and insect pollinators from those directly on the plants.

Conservation, especially of rare plant species, has mainly focussed on prevent further population losses. The project to reintroduce and increase the number of populations of *Cypripedium calceolus* (Lady's Slipper Orchid) is a notable exception (Ramsey & Stewart, 1998). As the environment is certain to further change and warm, the ultimate objective of conservation must be to increase both population numbers and the distribution range of rare and vulnerable species of orchids (and of other rare/endangered plant species). By this measure, little progress has been made.

The future

Further environmental changes are inevitable over the next 50 years as CO_2 concentrations in the atmosphere are certain to continue to increase. Modelling by the Met Office (Anon., 2018) predicts that by 2070 Britain will have further warmed by a minimum of 0.8 C° and by a potential maximum of 4.8 C°. The median value is an increase of 2.8 C° in mean annual temperature over the next 50 years (Anon., 2019). Such an increase will result in northern Scotland becoming as warm in 2070 as southern England is in 2020. Although climate change will be a threat to some species it will be an opportunity for others. Two species of *Serapias* spp. already have a toe-hold in England and other Continental species could follow and thrive – provided their pollinators are already here or come with them. However, as discussed above, it will be an additional challenge for others. Orchids that require a period of winter chilling such as *C. calceolus* are likely to suffer (Trudgill, 2020). Kolanowska & Jakubska-Busse (2020) explored various climate change options and concluded that by 2070 *C. calceolus* will be lost from 30% to 60% of its current European habitat. A warming climate probably will be accompanied by an increase in the number and magnitude of extreme weather events and these will impact on farming, on other components of the orchid's environment, and on orchid pollinators, and possibly mycorrhizal fungi.

Doxford & Freckleton (2012) modelled the dynamics of changes in the records of 1781 species of plants during the 20th Century. They concluded that species that were locally abundant were more likely to spread and were less likely to go locally extinct than those that were rare. The local availability and distribution of suitable habitat was a key driving factor. They found that 'long-distance colonisation was very rare'. Consequently, as species become rarer they can be caught in a circle of decline. They produce less seed and the numbers of sources of that seed also diminish as their populations become fewer, smaller and more isolated. As result, the probability of them spreading locally, and especially to more distant sites is also diminished. It is further diminished if potentially suitable, unoccupied sites are also rare, small, distant, or unfavourably managed. To reverse this trend requires an increase in the effectiveness with which any seeds that are produced are able to colonise new, suitable sites. The steps required to achieve this are obvious, but not without controversy. Foremost, on which everyone agrees, is a need to increase the numbers of locally available, potentially suitable sites. When only small amounts of seed are produced, and local spread is not happening, it also makes practical sense to translocate some of that seed to, and spread it across potentially suitable sites (De hert *et al*., 2013). The need for this approach increases with increasing distance as the probability of new sites being naturally colonised progressively decreases with the distance from the source of the seed (Trudgill, 2015, 2017b). Hence, for very distant sites, introducing seeds or plants are the only realistic options. However, establishing populations at new sites is only the first step. To provide an opportunity for further local, natural spread it is also necessary to ensure the persistence of any orchids that do colonize new sites (Trudgill, 2016), and this is dependent on appropriate, long-term management.

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