British & Irish Botany 7(2): 60-72, 2025

Past lessons and future requirements of reintroduction programmes for *Cypripedium calceolus* (Lady's-slipper Orchid, Orchidaceae)

David Trudgill

Blairgowrie, Scotland

Corresponding author: davetrudgill@googlemail.com

This pdf constitutes the Version of Record published on 14 August 2025.

Abstract
In the past *Cypripedium calceolus* was widespread in a narrow band on limestone soils in north England, but by the 1930’s only one plant was left in the wild. Current efforts to re-introduce it into areas where it previously grew are having limited success. It is suggested that that the programme of re-introduction should be extended to areas further north, that the genetic basis of the introductions should be widened, and that seed should be used as the main means of introduction as it has several advantages over plants. The Cypripedium Committee needs to be more open and the involvement of local communities and organisations increased.

Keywords: Cypripedium Committee; guidelines; ecology; climate change; introduction as seed; assisted migration

Introduction

Although *Cypripedium calceolus* (Lady’s-slipper Orchid) is widely distributed in Europe, in Britain its historical distribution was restricted to a narrow strip across northern England (Fig. 1). However, by the 1930s the wild population had been reduced to just a single plant, largely due to a combination of over-collecting and habitat destruction. Redshaw (2024) describes the discovery and subsequent protection of this last remaining wild plant and its use as one of the parents in a programme of reintroduction into the areas where it previously grew. This reintroduction programme is based on the production of plants, from seed, by micropropagation (pioneered by Svante Malmgren).

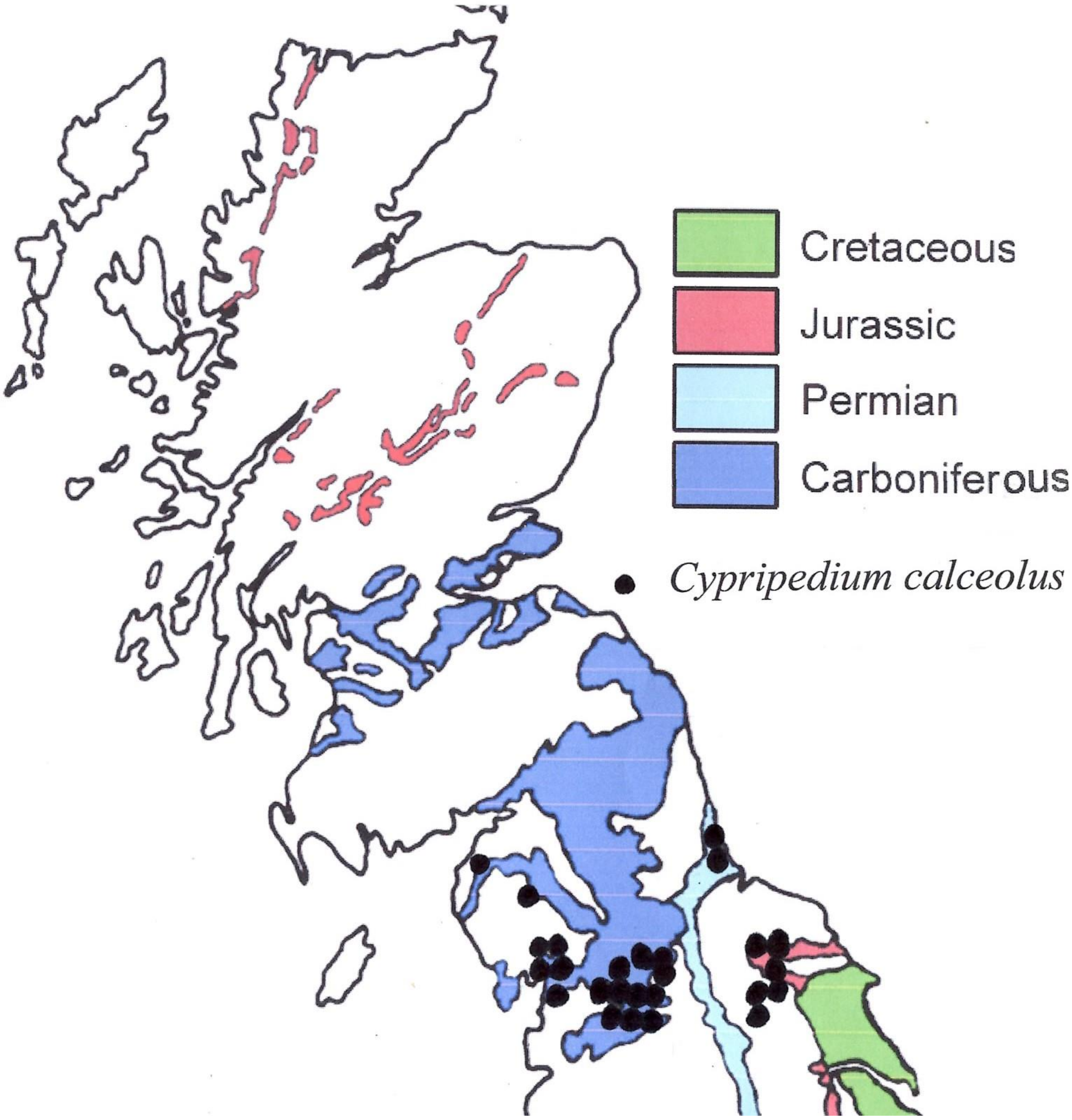

Figure 1. Generalised map showing some of the areas with extensive limestone rocks in northern Britain (www.showcaves.com), and past and present known distribution of *Cypripedium calceolus* (taken from BSBI maps). Some areas with small bands of limestone rocks are not shown (e.g. in Islay, Kintyre, Skye and Shetland). Records for Derbyshire have not been included as all are judged probable introductions (Redshaw, 2024).

Immature seed is used because the mature seeds were found to be dormant, and the seed is grown axenically on a nutrient medium because the fungi that promote seed germination and growth in nature have not been identified. The resulting seedlings are grown-on in pots prior to their reintroduction.

The project started in the late 1980's and by 2002 more than 1500 plants of *C. calceolus* had been planted-out at sixteen sites in northern England (Ramsey, 2003). Since then, many more have been introduced across a total of 22 sites. This programme of reintroduction is managed by the Cypripedium Committee, a 'group led by Natural England that oversees the recovery of *C. calceolus*'. However, the survival of the plants reintroduced into the wild appears to have been poor. It is important for many reasons that this reintroduction programme is a success. This article considers the future options and prospects for producing self-sustaining populations of *C. calceolus* in Britain based on the currently available information.

Distribution and abiotic requirements

Kull (1999) reviewed the distribution of *C. calceolus* and the associated abiotic conditions in which it grows. She described it as mainly a boreal species that is rare in regions with an Atlantic climate because it needs cold, frosty winters and cannot tolerate exposure to summer heat. Its west/east distribution ranges from Britain in the west, across northern and central Eurasia to Rebun Island in Japan. Its north/south distribution is from northern Scandinavia to north-east Spain and northern Italy, where the remaining populations are isolated relics confined to cooler, upland areas. It favours shady, deciduous and mixed woodland, and stone-strewn slopes. In Britain it was confined to a narrow, *c.*90 km wide band stretching *c.*150 km east–west across northern England on soils overlying calcium- and magnesium limestones (Fig. 1). Redshaw (2024) discounted the records for Derbyshire, arguing that they were all recent introductions. In the UK, all the sites where it was recorded in the past appear to have been scrubby woods with oak (*Quercus* sp.), Ash (*Fraxinus excelsior*) and Hazel (*Corylus avellana*) on steep rocky limestone slopes (JNCC, n.d.).

Kull (1999) reported that in Estonia *C. calceolus* thrived best in woodland where the amounts of light reaching the herb layer are decreased by between 60% and 80%. However, seedlings and young plants were most abundant in areas with less shading. She also commented that it did not withstand competition from taller plants and that *C. calceolus* was favoured by fires that destroyed the lower layers of vegetation. Richard Bateman (2025, *pers. comm.*) has seen it growing in a range of habitats including amongst dense herbaceous vegetation on a sandy island surrounded by a massive calcareous fen in E. Poland, rocky limestone hillsides in S. France, Sweden and Switzerland, and even on the roadside with no shade near Vercors in S. France (altitude *c.*2000 m). Svante Malmgren (2025, *pers. comm.*) states that in S. Sweden it is confined to dense deciduous forests on calcareous soils but further north, where it is much cooler, it is often found on high-level slopes in open woodland. He was very surprised to learn that the only remaining wild plant in England grows on a grassy slope with a few small shrubs in upper Wharfedale. Malmgren commented that *C. calceolus* has broad, thin leaves adapted for growing in the shade and cannot withstand heat or strong sunshine.

Rusconi *et al*. (2023) analysed 34 *C. calceolus* sites in Switzerland and concluded that the most favourable shared several characteristics. Frequently present were *Juniperus communis* (Common Juniper), *Equisetum telmateia* (Great Horsetail), and/or *Gymnadenia conopsea* (Chalk Fragrant-orchid). The soils were all alkaline, contained >15% organic matter and had a high cation exchange capacity (= a high ability to retain plant nutrients). It is thought to prefer moderately moist, base-rich, nutrient-poor soils that do not suffer from drought. An analysis of 11 soils where *C. calceolus* grew in Estonia and Germany found the Ca content ranged from 3.0 g/kg to 30.5 g/kg (Kull 1999). However, an analysis of soils at several sites in Estonia and Latvia revealed large variations in pH, Ca, K, N, Mg, P and organic matter (Kull, 1999; Klavina & Ostvalde, 2017).

The foregoing clearly illustrates the difficulties of identifying sites suitable for the reintroduction of *C. calceolus.* And this is all before other factors such as the availability of pollinators and the threats posed by herbivores, such as deer, slugs and voles, have been considered. It is even more difficult to identify the best planting locations within sites. A study of *C. calceolus* in SW Poland (Formnik *et al*., 2021) showed that trees played an important role in structuring its spatial distribution. The most significant predictor was the distance to the nearest *Abies alba* (Silver Fir).

Ecology and population dynamics

Cypripedium calceolus is a perennial, long-lived herb with a horizontal, branching rhizome. Each autumn two buds develop at the tip of each rhizome and the larger one produces the above-ground shoot in the following year. The smaller bud may produce an additional shoot in subsequent years so that, over time, compact clumps can develop that produce many shoots. The roots are unbranched, up to 50 cm in length, and live for several years (Kull, 1999). Mycorrhizal fungi belonging to the family Tulasnellaceae have been isolated from the roots of mature *C. calceolus* (Shefferson *et al*., 2005). These fungi have a role in the uptake of mineral nutrients as the leaves of *C. calceolus* were shown to be significantly enriched with fungal-derived ^{15}N. However, plants of *C. calceolus* were not enriched with fungal-derived ^{13}C (Gerbauer & Schiebold, 2017) and, consequently, it appeared to be a fully autotrophic species. In contrast, other woodland orchids with green leaves, such as *Cephalanthera* and *Epipactis* are mixotrophic species. They are enriched with ^{13}C, indicating that they have acquired a significant proportion of their carbon from their associated mycorrhizal fungi (Schiebold *et al*., 2017).

Gerbauer & Schiebold (2017) observed that *C. calceolus* was slightly enriched with fungal derived ^{2}H and concluded that it might still acquire some carbohydrates from its symbiotic fungi. However, Yeh *et al*. (2017) observed movement of carbohydrate compounds in both directions between autotrophic orchid species and their associated mycorrhizal fungi, the fungi being the main beneficiaries. They concluded the plants supplied the fungi with carbohydrate compounds in exchange for minerals and possibly water. It appears, therefore, that *C. calceolus* is effectively an autotroph species dependent on photosynthesis to provide all its carbon requirements. If so, it may not be well-adapted to growing in the partial shade under trees, but it is often restricted to growing there because of its relative inability to withstand the stresses and competition found in better illuminated areas.

Cypripedium calceolus grows in clumps up to 70 cm across that may include several different clones. This is because new plants growing from seed tend to appear close to older plants, but it is unclear whether this pattern is due to the older plants having colonised the most favourable patches, or because they have increased the suitability of the area surrounding them (Kull, 1999). Sexual reproduction is infrequent in many populations of *C. calceolus* and, perhaps to compensate for this limitation, the plants increase mainly vegetatively and can be very long-lived.

The flowers produce a faint scent but no nectar and are designed to ensure cross pollination by mainly small, solitary species of burrowing bees. Pollinating bees enter the opening in front of the labellum but are prevented from leaving through the same opening by the downward projecting rim. They escape by crawling through the narrow base of the labellum where any pollen they are carrying is deposited on the stigma. The bees then exit the flower through openings on either side of the column; this requires them to squeeze beneath one of the two anthers, thereby collecting fresh packages of pollen. Many species of bees have been identified as pollinators and there are regional differences (Antonelli *et al.*, 2009); Claessens & Kleynen (2011) listed as pollinators 20 species of Hymenoptera and three of Diptera. *Cypripedium calceolus* produces relatively few seeds, firstly because there are only one or two flowers per stem and, secondly because rates of pollination are usually low. Overall, only 10.5% of flowers produced mature capsules when eight Estonian populations were monitored over 11 years (Kull, 1999). Estimates of seed numbers per capsule also vary. Nicole *et al.* (2005) estimated a mean of 13,000 seeds per capsule, whereas Malmgren (*pers. comm.*), who has opened many capsules, found a maximum of *c.*3000 seeds per capsule. Kull (1999) reported the numbers of seeds in five capsules ranged from 5,940 to 16,700, but *c.*50% lacked viable embryos. Neiland & Wilson (1999) observed that contamination of orchid stigma with foreign pollen decreased the proportion of viable embryos, nectarless species being most affected. However, this is unlikely to be the major reason for non-viable embryos in *C. calceolus* because the stigma is shielded by the labellum.

The seeds of *C. calceolus* have a firm brown fusiform testa, the outer surface of which is not easily wettable (Kull, 1999). The mature seeds appear to be initially dormant and will not germinate *in vitro*. However, it was discovered that immature seeds could be germinated *in vitro* and these have been used to produce the plants for reintroduction through micropropagation. Barsberg *et al.* (2013) reported that lignin was deposited in the testa as the seeds matured and inferred that this induced dormancy. However, they found that seeds of *Dactylorhiza incarnata* (Early Marsh-orchid), which germinated readily, had a very similar lignin content to those of *C. calceolus.* Malmgren (2025, *pers. comm.*) believes that germination is delayed because it takes time for the inner coat around the embryo to break down. When seeds of *C. calceolus* were buried in mesh packets adjacent to 'natural' plants in Denmark germination was not observed until five years after being buried. Ungerminated seeds apparently remained viable after seven years, when most of the lignin had degraded. There had been a marked build-up of $CaCO_3$ deposits on the wall of the testa (Barsberg *et al.*, 2013). These observations indicate that seed of *C. calceolus* is initially dormant and that some seeds can remain viable in the soil for many years.

In nature, seeds of *C. calceolus* germinate and develop into protocorms only when they are colonized by specific mycorrhizal fungi. These fungi have not been identified. The developing protocorms are mycoheterotrophs *i.e.* they derive all their carbon and mineral nutrients from their associated fungi. Development is slow – it takes approximately three years before the first leaves appear above ground and a further six years before they first flower (Curtis, 1943). Although seedlings and young plants are rare in most populations of *C. calceolus*, in Estonia a few sites were found with a high proportion of seedlings and young plants. These sites were distinguished by the presence of 'Pine' trees, by having a relatively greater moss cover and less vascular plant cover, and by being damper and better illuminated (Kull, 2024, *pers. comm.*)

Why seedlings and young plants are infrequent in most populations of *C. calceolus* is unclear, but it may be that when these sites were first colonized there was much less shade, and that the degree of shading has subsequently progressively increased. An alternative explanation is provided by experiments where packets of seed of several Helleborine species were buried at different locations. These have shown that the seed consistently germinated at locations that did not support mature plants, perhaps because their fungal associations change when the orchid seedlings first produce green leaves, and this transition fails at some sites (Bidartondo & Read, 2008; Tesitelova *et al*., 2012).

History of *C. calceolus* reintroductions in Britain

By the early 1900s, *C. calceolus* was thought to be extinct in the wild in Britain, until a single plant was discovered in upper Wharfedale. The location of this plant was kept secret and it was guarded for more than 50 years. In the late 1980s a programme of reintroduction was started, based on plants produced by micropropagation from seed, with the Wharfedale plant as one of the parents (Redshaw, 2024). The reintroduction into northern England of the these micropropagated plants has been funded, at least in part, by the Sainsbury Foundation and it has long been managed and overseen by the Cypripedium Committee and Natural England. Despite the Natural England guidelines requiring 'openness' the Cypripedium Committee has been exceptionally secretive regarding almost all aspects of the programme of reintroduction. Redshaw (2024) states that prior to 2009 the Wharfedale plant and at least two others, one of which came from a garden in Kendal, had been used as parents to produce the seed used for micropropagation. However, a comparison of the plastid DNA of the Wharfedale plant with five other plants growing (mostly in gardens) in England revealed that only one of these five plants had the same DNA polymorphisms as the Wharfedale plant (Fay *et al*., 2009). This plant, from a garden near Hornby, together with the Wharfedale plant, were both deemed to be of English provenance (for details see Redshaw, 2024). The plastid DNA polymorphisms of the four other plants all differed from that of the Wharfedale plant. Two of these, the Kendal plant, and one other were deemed to be recent introductions into Britain, based on comparisons with samples from European plants (Fay *et al*., 2009). The designations of the remaining two plants were not discussed, but they were not classified as native.

According to Redshaw (2024), following this analysis of their plastid DNA only the Wharfedale and Hornby plants were subsequently used as parents. However, subsequently Fay & Taylor (2015, page 28) make the surprising claim that 'based on the plastid DNA analysis by Fay *et al.* (2009) several plants of known English wild source also still exist in cultivation' and that these were also used as parents. Despite making extensive enquiries I have been unable to establish which plants these are, and to determine which plants have been, and are currently being used as parents for seed production.

Knowing the parentage of the reintroduced plants is highly relevant because it was subsequently decided (by the Cypripedium Committee, or English Nature?) that all the plants reintroduced into the wild must be of pure English provenance. As a result, all the reintroduced plants derived from crosses involving a non-native parent (i.e. regarded as at least 50% alien) that still survived were dug up and removed. The total numbers of plants removed, and the 'alien' parents involved, has not been disclosed but they included all the progeny of the plant from the garden in Kendal (Swainson, 2022, *pers. comm.*). The last site from where such plants were removed was the Gait Barrows NNR where a total of '30 or so' plants were dug up and put in pots, the stated aim being to avoid 'outbreeding depression' (Swainson, 2022, *pers. comm.*). However, there seems to have been little prospect of any 'outbreeding' as all the *C. calceolus* at Gait Barrows had the Kendal plant as the alien parent. One unnamed source commented that 'the sacrifice of such plants on the altar of political correctness was completely crazy'. The plants that were removed are presumably still available to pollinating insects, as are the many plants growing in gardens that have recently been imported into Britain from continental Europe.

Fay & Taylor (2015) concluded that the *C. calceolus* native to England had passed through an 'extreme genetic bottleneck'. Luck may not have been the only reason that the Wharfdale plant survived the depredations of the orchid collectors - it could have been missed because it rarely flowered. It did flower in 1930, the year it was discovered, but between 1931 and 1956 it produced only three further flowers (Redshaw, 2024). Thereafter, with improved care involving watering during periods of drought, occasional additions of bonemeal, and protection from herbivores and encroaching vegetation, it has increased vegetatively and flowered more regularly. In 1996 the plant was recorded as having 65 shoots and producing 23 flowers (Fay & Taylor, 2015). The micropropagated progeny of the Wharfedale plant were also slow to flower, the first reintroduced plant taking at least 14 years from when the seed was germinated (Ramsey, 2003).

Because the Wharfedale plant was the only one remaining in the wild in Britain, we cannot know whether there were other, genetically different founder events from which plants such as that from Kendal derived. *Cypripedium calceolus* is classified as a 'native' species (*i.e.* it arrived here without human assistance). Webb (1985) listed eight criteria for determining whether a species is native, or an archaeophyte (*i.e.* introduced with human assistance before 1492 AD). Using his criteria I was uncertain whether *C. calceolus* could, with confidence, be classified as either a native or as an archaeophyte. However, I suggest that for *C. calceolus* the distinction is academic and irrelevant, except for how it might relate to when it first colonized Britain. If it persisted in refugia, or arrived naturally before rising sea levels covered the land-bridge linking Britain to Continental Europe, it is unclear why the many other areas in Britain with base-rich soils were not colonized, particularly those further north (see Fig. 1). If *C. calceolus* arrived later, after the land bridge was inundated (*i.e.* <8,000 years ago), the seed would have had to travel at least 400 km across the North Sea to establish a foothold in northern England. Although the probability of this happening is small (Trudgill, 2025), it is not impossible as seven species of orchids have reached Iceland. One, *Platanthera hyperborea*, came from Greenland *c.*600 km away (Bateman & Rudall, 2015), and the others probably from Scotland or Norway, distances of 800 km and 1000 km respectively. However, several other potential orchid colonists have been unsuccessful in making this journey.

There are at least three possible options as to why the distribution of *C. calceolus* was restricted to a narrow band of land across northern England. (1) There was no other suitable habitat in Britain, (2) there was suitable habitat elsewhere in Britain (Fig. 1), but there had been insufficient time for adequate numbers of seeds to spread to these more distant areas, or (3) it was previously present in these areas, but was not recorded. We know it must have arrived well before the early 1600s because Miss Thomsine Turnstall was recorded as collecting it in 1629 (presumably for payment; Redshaw, 2024). We will never know for certain how, or when *C. calceolus* arrived in Britain, but its historic pattern of distribution is consistent with (2) above, *i.e.* it is a relatively recent arrival. The Anglo-Saxons bringing it here as plants c.1000 years before Miss Turnstall started digging them up is just one of several options.

The original intention of the Cypripedium Committee was to ensure that the reintroduced plants were genetically diverse (Ramsey, 2003), presumably to minimise the likelihood of inbreeding depression. The history of the Wharfedale, Hornby and Kendal plants, all of which were initially used as parents, is unclear. The Kendal plant was believed to have been originally collected from the wild, and Redshaw (2024) postulated that it might have derived from a different founder event to that of the Wharfedale and Hornby plants. Given that the progeny of crosses made between the Kendal and the Hornby plants proved particularly vigorous (Corkhill, quoted in Redshaw, 2024), the decision to subsequently remove any such surviving plants seems particularly unwise, especially as the fewer the numbers of plants remaining the greater the impact if any are dug up and stolen.

The current position

The reintroduction of *C. calceolus* into areas it formerly occupied in England is clearly proving a challenge, especially when trying to establish self-sustaining populations. By 2002 more than 1500 micropropagated plants had been reintroduced (Ramsey, 2003). Since then, an undisclosed number, certainly many more hundreds of plants, have been introduced into a total of 22 sites in northern England. Presumably these plants were all carefully cared for, but by 2022 *C. calceolus* was recorded at only ten of these sites (Cousins, 2023, *pers. comm*.). The number of surviving plants was not disclosed, but together they had a total of 510 shoots and produced 190 flowers (note that in 1996 the single, native Wharfedale plant produced 65 shoots and 25 flowers). The rate of pollination appears to have been abysmal, capsules being recorded at only one reintroduction site. I understand that only two or three second generation seedlings have ever been recorded, the first of which did not survive. Whilst the results of the 2022 survey might be incomplete because of under-recording due to Covid restrictions, they highlight two problems, both of which probably relate to selection of the planting sites and the precise locations within them: (1) low rates of survival of the introduced plants at most, if not all sites, and (2) very low rates of pollination coupled with lack of establishment of new seedlings.

Orchids tend to have low rates of survival when transplanted back into their natural habitat, one possible reason being that they fail to develop the symbiotic relationships with mycorrhizal fungi that they require to maximise growth and help them compete. However, this was not the case for the native Wharfedale plant and those reintroduced plants that still survived, as all were enriched with ^{15}N, indicating that they had developed an effective relationship with mycorrhizal fungi (Fay *et al*., 2018). There is, however, no corresponding information for the plants that did not survive!

Impact of climate change on choice of introduction sites

The environment where *C. calceolus* used to grow in Britain has greatly changed. Compared with the 1910s, in the decade 2015–2024 the mean annual temperatures recorded by the meteorological stations at Durham and Bradford have increased by 1.59°C and 1.44°C respectively. Rainfall has increased by 3% and 8%, and the mean number of days with an air frost has decreased from 45 to 33 per year for Durham, and from 58 to 39 per year for Bradford. Another significant change has been an increase in the rate of deposition of nitrogen from the atmosphere from *c.*2 kg/ha/year in the 1800s to a peak of *c.*20 kg in 1990s.

The rate of climate change is now accelerating. Kolanowska & Jakubska-Busse (2020) modelled the likely impact of global warming on the future distribution of *C. calceolus* in Europe. In Britain, assuming CO_2 emissions peak around 2040, they classified only northern Scotland as providing a (moderately) suitable habitat. The areas in northern Scotland with a limestone bedrock (of which there are several: Fig. 1) have other potential advantages for the introduction of *C. calceolus* compared with northern England; for example, in the 1990's rates of N deposition were still only 5 kg/ha/year. Considering the longevity of *C. calceolus* it could be argued that attempts to reintroduce it into northern England, especially in the warmer west, are ultimately doomed (Trudgill, 2020), and current efforts should include Scotland, especially the northern half.

Should the orchid reintroduction programme focus on plants or seeds?
The rates of establishment of the micropropagated plants of *C. calceolus* introduced into the many sites across northern England have been very low – just how low is uncertain because this information has not been made openly available. However, a small proportion of plants have established, increased vegetatively, and are flowering, so there has been some modest success. The need now is to look forward and to try to increase rates of establishment. Seed has several advantages over plants as a means of introducing orchids into new sites (Trudgill & Trudgill, 2023). It can be introduced in very much greater numbers than plants, so even the smallest suitable niche within a site is likely to be seeded. Seed is likely to contain more genetic diversity than micropropagated plants, and is much less expensive to produce as it does not need special growth facilities. It can also be produced locally. Consequently, the numbers and types of reintroduction sites can be increased and the whole programme decentralised.

Conclusions
Cypripedium calceolus appears to be 'between a rock and a hard place' when seeking a place to establish and grow. It cannot withstand heat, drought or competition and so, despite probably being autotrophic, it often grows in areas shaded by trees. As a consequence, it is relatively slow growing and tends to be very specific regarding sites where it can successfully be established. This makes choosing sites for its reintroduction, and especially positions within sites, a difficult challenge. It is clear that those involved need to use all the experience and information available if they are to establish populations of *C. calceolus* capable of expanding and colonizing new areas. This could also include an assessment of the abundance of pollinators and herbivores, as well as the many other factors considered above.

I suggest that now is the time to consider how best to move forward as new information has become available and much has changed since the reintroduction programme was started in the early 1990s. There needs to be a reassessment of priorities as the environment has changed over the last 100 years. The genetic diversity and numbers of plants used as parents should be increased to include those that have recently been shown to grow well in Britain (e.g. 'Kendal' × 'Hornby' crosses), irrespective of their supposed provenance. The use of seed as an additional, perhaps the main, means of reintroducing *C. calceolus* should be given serious consideration. In Italy, plants growing in the wild are being hand pollinated to increase their seed production (Simon Pierce, 2025, *pers. comm.*). Simon further comments that where he works the trees are mostly conifers and the seeds of *C. calceolus* fall onto, and germinate in an acidic, rotting, pine-needle mulch. The underlying bed rock is calcareous so he suggests that *C. calceolus* could 'be likened to butterflies where the larval and adult forms have different requirements'.

If seed is used it will need to be mixed with a carrier material to ensure large areas can be covered uniformly (Trudgill & Trudgill, 2023). One disadvantage of seed is that, because initially it will be dormant, it may take a decade or more to determine whether any plants have been produced. However, we can be much more hopeful that any resulting plants are growing in the 'right' place and likely to prosper in the longer term.

Using seed is practical. If the aim is to deliver ten seeds per m^2 then, depending on their fertility, the product of the smallest capsules might be expected to cover a 20 m x 5 m strip along the edge of a woodland, and the seed from larger capsules would suffice for a strip exceeding 100 m. Using seed will require a change in the approach. Hundreds of flowers may need to be hand pollinated to produce the large numbers of seeds needed to adequately cover several sites. Hand pollination is relatively simple (Malmgren, 2025, *pers. comm*.) but involves removing the anthers with forceps (Pierce, 2025, *pers. comm.*) and requires supervised practice; and currently there is a lack of trained volunteers (Mags Cousins, 2024, *pers. comm*.). The past secretiveness of the Cypripedium Committee is partly responsible for this and more openness and involvement of local communities, and members of societies such as the Hardy Orchid Society and the Botanical Society of Britain and Ireland, is desirable if this limitation is to be overcome. The aim, I suggest, should be for local activists to feel they 'own' the reintroduction sites.

The Cypripedium Committee and those involved at Kew appear to be unnecessarily secretive. Everyone understands and accepts the need to protect information regarding the locations of the sites of reintroduction to minimise the likelihood of plants being dug up and stolen. However, information on the progress of the reintroduction programme, especially the meaningful details, are also mostly being withheld, leading to concerns why this should be so (Jacob, 2023; Redshaw, 2024). Perhaps this is not deliberate but due to other pressures. However, it is contrary to the guidelines produced by Natural England, the body supposedly overseeing the activities of the Committee.

Another concern is that the plants currently available for the general public to buy 'online', or through the horticultural trade, are exclusively of continental origin, and also may be the American species *C. parviflorum* (Pierce, 2025, *pers. comm.*). Whilst *C. parviflorum* is morphologically almost identical to *C. calceolus*, 'it occupies a much broader range of habitats' (Pierce, 2025, *pers. comm.*). The Cypripedium Committee should consider if it is desirable to harmonise the genotypes of the plants available to the general public with those being reintroduced, and how this might be achieved.

Finally, and perhaps most importantly, all of England is likely to become too warm for *C. calceolus* due to climate change over the next 50 years (Kolanowska & Jakubska-Busse, 2020; Trudgill, 2020). As many plant species are likely to be seriously affected, it is essential that those deciding policy around plant reintroductions and assisted migrations should take such projections into account. Consideration should, therefore, be given to extending the reintroduction of *C. calceolus* in Britain to higher altitude sites, especially potentially suitable areas further north in Scotland.

Acknowledgements. I thank Richard Bateman, Ian Denholm, Svante Malmgren and Simon Pierce for many helpful comments and suggestions.

References

Antonelli, A., Dahlberg, J.C., Carlgren, K.H.I. & Appelqvis, T. 2009. Pollination of the Lady's slipper orchid (*Cypripedium calceolus*) in Scandinavia: taxonomic and conservational aspects. *Nordic Journal of Botany* 27:266-273.

Barsberg, S., Rasmussen, H.N. & Kodal, N. 2013. Composition of *Cypripedium calceolus* (Orchidaceae) seeds analyzed by attenuated total reflectance IR spectroscopy: In search of understanding longevity in the ground. *American Journal of Botany* 100**:**2066-2073.

Bateman, R. & Rudall, P. (2015). Earth, wind, fire and ice: orchid hunting in Iceland. *Journal of the Hardy Orchid Society* 12(3):83–91.

Bidartondo, M.I. & Read, D.J. 2008. Fungal specificity bottlenecks during orchid germination and development. *Molecular Ecology* 17:3707–3716.

Claessens, J. & Kleynen, J. 2011. The flower of the European orchid: form and function. Published by the authors, Voerendaal, Netherlands.

Claessens, J. & Kleynen, J. 2013. The pollination of European orchids: part 2: *Cypripedium* and *Cephalanthera*. *Journal of the Hardy Orchid Society* 10(4):114-119.

Curtis, T.J. 1943. Germination and seedling development in five species of *Cypripedium* L. *American Journal of Botany* 30:199-206.

DEFRA & Natural England. 2025. Reintroductions and conservation translocations: code, guidance and forms. [online] [Accessed 11 August 2025]. Available at: <https://www.gov.uk/government/publications/reintroductions-and-conservation-translocations-in-england-code-guidance-and-forms>

Fay, M.F., Bone, R., Cook, P., Kahandawala, I., Greensmith, J., Harris S. & Pederson, H.A.E. 2009. Genetic diversity in *Cypripedium calceolus* (Orchidacreae) with a focus on north-western Europe, as revealed by plastid length polymorphisms. *Annals of Botany* 104(3):517–525.

Fay, M. & Taylor, I. 2015. 801. *Cypripedium calceolus* Orchidaceae. *Curtis's Botanical Magazine* 32(1):24–32.

Fay, M.F., Feustel, M., Newlands, C. & Gebauer, G. 2018. Inferring the mycorrhizal status of introduced plants of *Cypripedium calceolus* (Orchidaceae) in northern England using stable isotope analysis. *Botanical Journal of the Linnean Society* 186(4):587–590.

Foremnik, K., Krawczyk, W., Surmacz, B. & Malicki, M. 2021. Effects of forest stand structure on population of endangered orchid species *Cypripedium calceolus* L. *Journal for Nature Conservation* 64:1-9.

Gerbauer, G. & Schiebold, J.M.I. 2017. *Stable isotope abundance analysis as a tool for understanding orchid mycorrhizal nutrition*; 27-34. In: Swarts, N.D. & Kingsley, W.D., eds. Conservation methods for terrestrial orchids. J. Ross Publishing.

Jacob, B. 2023. *The orchid outlaw*. London: John Murray.

JNCC. n.d. 1902 Lady's-slipper orchid *Cypripedium calceolus* [online]. [Accessed 13 August 2025]. Available at: <https://sac.jncc.gov.uk/species/S1902/>

Kirillova, I. & Kirillova, D. 2021. Population dynamics, reproductive success, and seasonal development of *Cypripedium calceolus* under different growing conditions as a response to weather factors. *Contemporary Problems of Ecology* 14(5):472-482.

Klavina, D. & Ostvalde, A. 2017. Comparative chemical characterisation of soils at *Cypripedium calceolus* sites in Latvia. *Proceedings of the Latvian Academy of Science* 71:43-51.

Kolanowska, M. & Jakubska-Busse, A. 2020. Is the lady's-slipper orchid (*Cypripedium calceolus*) likely to shortly become extinct in Europe? - Insights based on ecological niche modelling. *Plos One* 15(1):e0228420.

Kull, T. 1998. Fruit-set and recruitment in populations of *Cypripedium calceolus* L. in Estonia *Botanical Journal of the Linnean Society* 126:27–38

Kull, T. 1999. *Cypripedium calceolus. Journal of Ecology* 87:913-924.

Neiland, M.R.M., Wilcock, C.C. 1999. The presence of heterospecific pollen on stigmas of nectariferous and nectarless orchids and its consequences for their reproductive success. *Protoplasma* 208:65–75.

Ramsey, M. 2003. Re-establishment of the Lady's-slipper Orchid in the UK. *Re-introduction News* 22:26-28.

Redshaw, P. 2024. Dales Slipper: Past - Present. *Naturally Red Publications, Silsden, Yorkshire.*

Rusconi, O., Steiner, T., Bayon, C. Le, & Rasmann, S. 2023. Soil properties and plant species can predict population size and potential introduction sites of the endangered orchid *Cypripedium calceolus. Plant Soil* 487:467–483.

Schiebold, J. M. I., Bidartondo, M. I., Karasch, P., Gravendeel, B. & Gebauer, G. (2017). You are what you get from your fungi: nitrogen stable isotope patterns in *Epipactis* species. *Annals of Botany* 119:1085-1095

Shefferson, R.P. Weiss, M., Kull, T. & Taylor, D.L. 2005. High specificity generally characterizes mycorrhizal association in rare lady's slipper orchids, genus *Cypripedium*. *Molecular Ecology* 14:613–626.

Tesitelova, T., Tešitel, J., Jersáková, J., Ríhová, G. & Selesse, M.A. 2012. Symbiotic germination capability of four *Epipactis* species is broader than expected from adult ecology. *American Journal of Botany* 99(6):1020-1032.

Trudgill, D. 2020. Temperature and orchids 1) Winter chilling, global warming and hardy orchids (especially *Cypripedium calceolus*). *Journal of the Hardy Orchid Society* 17(3):80-85.

Trudgill, D. & Trudgill, J. 2023. Creating an orchid meadow using seed. *Journal of the Hardy Orchid Society* 20(4):114-127.

Trudgill, D. 2025. Orchid Seed – 1) Numbers, weight and dispersal. *Journal of the Hardy Orchid Society* 22(3):(in press).

Yeh, C.-M., Chung, C.M., Liang, C.K. & Tsai, W.C. 2019. New insights into the symbiotic relationship between orchids and fungi. *Applied Science* 9(3):585-594.

ISSN: 2632-4970

https://doi.org/10.33928/bib.2025.07.060