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An evaluation of the UK distribution of *Eleocharis palustris* subspecies *palustris* (Cyperaceae) using herbarium material

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Abstract

Eleocharis palustris (Common Spike-rush) occurs at two ploidy levels, represented in Britain by subsp. *palustris* (2n = 16) and subsp. *waltersii* (2n ≈ 38). Although the species is widespread and considered of low conservation concern, the distribution of the lower-ploidy subsp. *palustris* has remained poorly understood because material has rarely been identified or verified at subspecies level. As a result, its status, habitat associations, and potential vulnerability in the UK have been unclear. Herbarium vouchers from major UK collections were examined using a non-destructive method that allowed stomatal size to be measured directly from dried specimens. Stomatal size differs consistently between the two ploidy-defined subspecies, being smaller in subsp. *palustris* and larger in subsp. *waltersii*, allowing subspecies assignment from herbarium material. Based on verified material, a revised UK distribution for *Eleocharis palustris* subsp. *palustris* is presented. The subspecies shows a predominantly southern and eastern distribution, most frequently associated with coastal grazing marshes, tidal portions of rivers, and river floodplains, with fewer inland occurrences in fenland and floodplain habitats. In contrast, subsp. *waltersii* is more widely distributed across Britain and occurs across a broader range of wetland habitats.

Differences in ploidy level are proposed as a factor influencing the contrasting distributions of the two subspecies, with smaller stomatal size in subsp. *palustris* potentially linked to differences in plant water relations and competitive interactions. Towards the edge of its range, subsp. *palustris* occurs at relatively few and often isolated sites, where interactions with subsp. *waltersii*, including asymmetric hybridisation, may increase vulnerability to loss. By clarifying the historical distribution and habitat associations of subsp. *palustris*, this study provides a baseline for assessing its current status and for guiding future field surveys and conservation assessments in the UK.

Keywords: Common Spike-rush; subspecies delimitation; herbarium vouchers; ploidy level

Introduction

Eleocharis R.Br. (Cyperaceae) is a genus of flowering plants known as spike-rushes. These perennials have a worldwide distribution (Global Biodiversity Information Facility, GBIF) and, as the Greek derivation of the name (*helos*, marsh, and *charis*, grace/beauty) suggests, are mainly marsh-dwellers growing in aquatic or mesic habitats. *Eleocharis palustris* (L.) Roem. & Schult. has a northern circumboreal distribution (GBIF). Like many *Eleocharis* species, it is clonal and can form extensive stands through networks of long rhizomes. In some locations, populations may persist as long-lived genets, and the combination of clonal growth and broad geographic range is associated with an unusually wide breadth of chromosome numbers and sizes within the genus (Strandhede & Dahlgren, 1968).

Defining the two subspecies of *Eleocharis palustris*, subsp. *palustris* and subsp*. waltersii*

Håkansson (1928) first described two different chromosome numbers in *E. palustris* ($2n = 16$ and $2n = 38$) and noted associated differences in achene size (Håkansson, 1929). Walters (1949) divided the *E. palustris* cytotypes into two subspecies based on differences in chromosome number and morphology, naming them *E. palustris* subsp. *microcarpa* Walters and subsp. *vulgaris* Walters. These names were later treated as synonyms of subsp. *palustris* and subsp. *waltersii*, respectively. Strandhede's exhaustive revision of *Eleocharis* subser. *Eleocharis* (1966, 1968), based on chromosome counts from approximately 3500 plants across 1100 localities mainly in northern Europe, further refined subspecies delimitation (Table 1). The *New Flora of the British Isles* (Stace, 2019) provides the current definition used in the UK, broadly following Strandhede's work. It should be noted that plants of both subspecies exhibit considerable phenotypic variation in height and vigour.

Table 1. Cytological and morphological definitions of *Eleocharis palustris* subsp. *palustris* and subsp. *waltersii*

Feature	Source	E. palustris subsp. palustris	E. palustris subsp. waltersii
Chromosome number	Walters (1949)	2*n* = 16	2*n* = (37)38(39)
Stomata size	Walters (1949)	50–65 μm	65–85 μm
	Strandhede & Dahlgren (1968)	39–49 μm	54–70 μm
	Stace (2019)	(35) 39–49 (56) μm	(50) 54–70 (77) μm
Achene length	Walters (1949)	(1.1) 1.2–1.4 (1.5) mm	(1.3) 1.45–1.8 (2.0) mm
	Strandhede (1966); Strandhede & Dahlgren (1968)	(1.1–) 1.2–1.5 (–1.6) mm	(1.3–) 1.4–1.8 (–1.9) mm

Feature	Source	E. palustris subsp. palustris	E. palustris subsp. waltersii
	Stace (2019)	1.2–1.4 (1.5) mm	(1.3) 1.5–2 mm
Middle spike glume length	Walters (1949)	2.75–3.5 mm	3.5–4.5 mm
Flower number in a spike	Walters (1949)	40–70	20–40
Glume description	Walters (1949)	Rather pale, often light brown or straw-coloured, usually more easily detached from ripe spike than in subsp. *waltersii*.	Variable in colour, but usually brownish.

Distribution
Strandhede (1961) regarded subsp. *palustris* as cosmopolitan, with a widespread distribution, but replaced by subsp. *waltersii* in Western Europe. Subsp. *waltersii* was described as widespread in north, west and central Europe, extending north as far as mid-Scandinavia. He described it as rarer or absent from southern Europe, including around the Mediterranean. The lack of ease of identification has made it difficult to confirm distributions in many countries. The Mediterranean area has since been shown to have populations of subsp. *waltersii* (Jiménez-Mejías & Luceño, 2007; Tison et al., 2014; Lastrucci et al., 2020). In the Czech Republic, it is reported to be more frequent in the western part of the country (Kaplan et al., 2015). Walters (1949) described subsp. *palustris* as the rarer of the two subspecies in the UK.

Ecology
As the separation of the subspecies has been inconsistent, the data are more limited. Strandhede (1966) documented a certain geographic and ecological isolation between subsp. *palustris* and subsp. *waltersii*, yet it was also clear that there was evidence of sympatric occurrence, as indicated by shared habitat requirements and distributions (Walters, 1949; Jiménez-Mejías & Luceño, 2007). In a distribution study of the two subspecies in the Czech Republic, Kaplan et al. (2015) showed that subsp. *palustris* had a slightly higher tolerance to saline and drier conditions but a lower competitive tolerance. Both subspecies grew well at lower altitudes, but there was an increased ability for subsp. *waltersii* to prevail at middle altitudes. Similarly, in France, Julve (2019) reported very few differences in habitat but observed that subsp. *palustris* appeared to be slightly more tolerant with respect to soil salinity, less demanding in soil moisture but more demanding in atmospheric humidity, and showed an increased preference for finer substrates, such as sandy soil. Lastrucci et al. (2020) showed little evidence for geographic and ecological separation in the distribution pattern of the two taxa in Italy.

A need to evaluate material using non-destructive methods
Eleocharis palustris is categorised as Least Concern on the IUCN Red List of vascular plants (Lansdown, 2013) and is also considered to be of least concern in Britain. The

conservation status of its subspecies is, however, more difficult to assess, as they are infrequently recorded at subspecific rank (Stroh et al., 2023). In northwest Europe, subsp. *palustris* may nevertheless be more vulnerable, given its apparent rarity and limited recording at subspecific level.

Records downloaded from the BSBI Database (accessed December 2025) indicate that *E. palustris* sensu lato is widespread nationally (Fig. 1). The apparent distribution of *E. palustris* subsp. *waltersii* was more patchy and appears to be influenced by variation in recording intensity and taxonomic resolution, with records often clustered in areas where individual recorders have worked at the subspecific level.

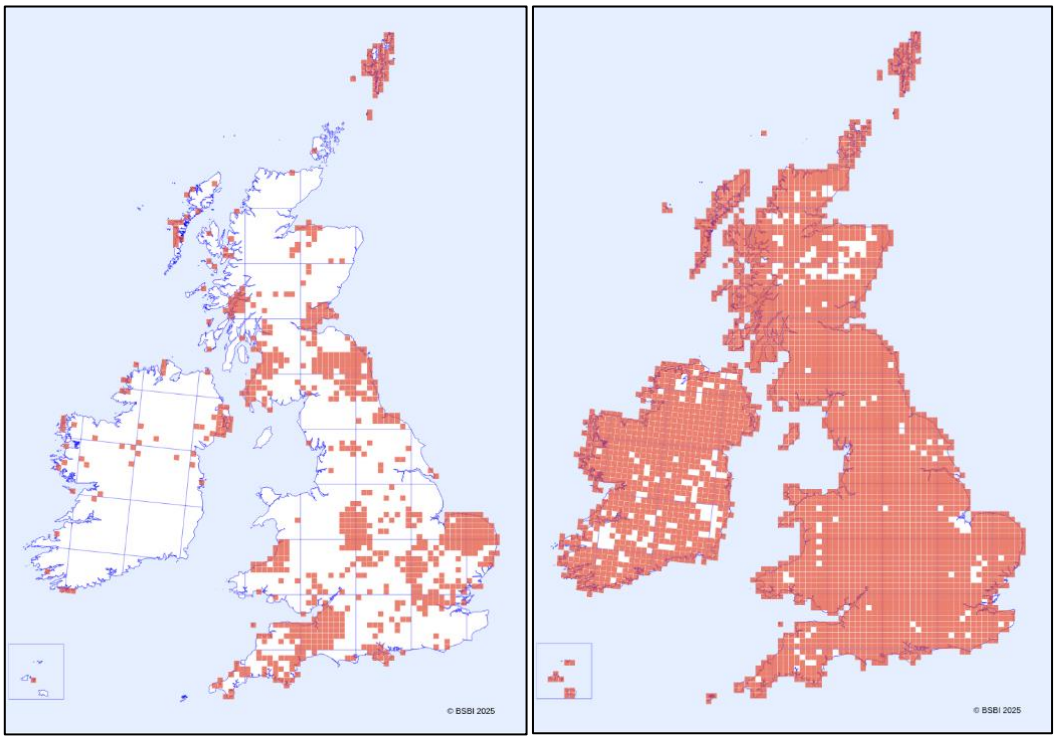


Figure 1. BSBI records for the UK distribution of *Eleocharis palustris* subsp. *waltersii* and of *Eleocharis palustris* (unassigned to subspecies) between 1987 and 2025. Records presented at the tetrad level.

Kaplan et al. (2015) based distribution maps of the two subspecies of *E. palustris* occurring in the Czech Republic entirely on revised herbarium material, distinguished using ripe fruit characters and stomatal length. A comparable revision of Italian material (Lastrucci et al., 2020) confirmed stomatal length as the most reliable character for separating the subspecies in *Eleocharis*. In that study, measurement required removal of a mid-culm stem section to prepare material for microscopic examination. Where access to large herbarium collections is required, the development of non-destructive methods is therefore desirable.

Trials showed that stomata are readily measurable in dried, unprepared *Eleocharis* material at ×200 magnification using top illumination, allowing large numbers of specimens to be examined rapidly. This approach also has the potential

to be enhanced through focal stacking to produce publication-quality images (Cobecore, 2018).

Methods

Herbaria were visited, and all sheets ascribed as *Eleocharis palustris* were examined, regardless of subspecies notation. The herbaria included: Cambridge University Herbarium (**CGE**), Fielding-Druce Herbarium Oxford (**OX**), Kew (**K**), Natural History Museum (**BM**), South London Botanical Institute (**SLBI**), & University of Reading Herbarium (**RGE**). For herbaria sheets, ×200 magnification was used with an objective lens ×20 PL L SP95M/200XM 160 mm, providing a long working distance for sufficient top illumination. Stomata were measured on the mid-culm section, working across the width of the culm, as stomata length varied along rows running down the stem. The length of the mid-spike glume was measured, along with the mid-culm width and the spike length. The material was assigned to subspecies based on stomatal measurements of Strandhede & Dahlgren (1968), where subsp. *palustris* stomata has been determined to be between 39 and 49 μm. Material on the cusp ($\geq$47 μm) left unassigned or considered to be subspecies *waltersii*. Geographical coordinates were obtained following the OS National Grid reference system using place names in conjunction with habitat descriptions and local knowledge from BSBI Vice-County Recorders. Results were plotted using QGIS onto the OS Open Rivers V3 (2023).

Results

Herbarium sheets from 38 locations were clearly assigned subsp. *palustris* (Fig. 2).

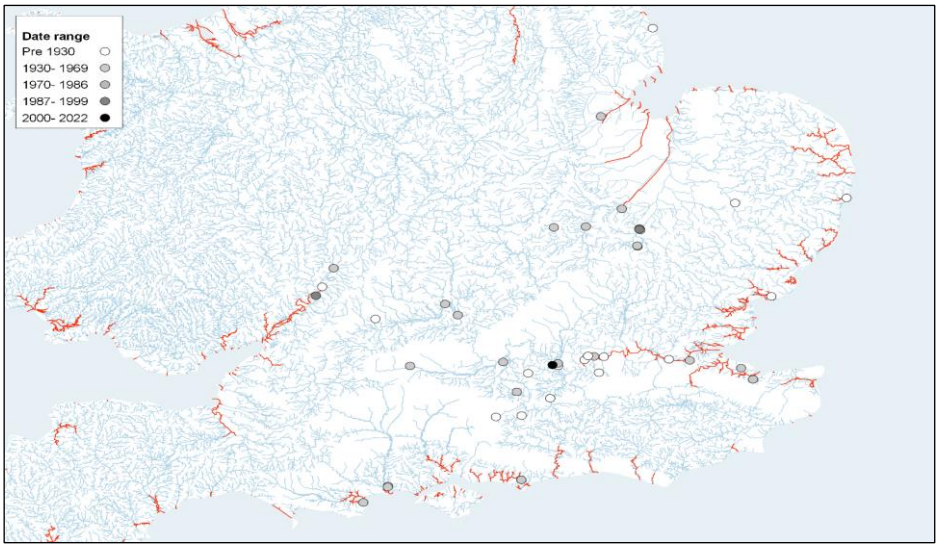


Figure 2. The UK distribution of *Eleocharis palustris* subsp. *palustris* from herbaria material. These are viewed in the context of the river systems. Red indicates tidal portions of rivers (OS Open Rivers V3, 2023)

All other sheets examined were assigned subsp. *waltersii*. Although the total number of sheets examined across all herbaria was not recorded, the low frequency of

subsp. *palustris* is illustrated by the detailed count at BM (see below). Assignments could not be made for four sheets. On specimens determined as subsp. *palustris* by stomata length (Fig. 3), all had glumes which were ≤3.5 mm in length. Achenes were available for viewing in only a handful of specimens. Observationally subsp. *palustris* had finer stems and smoother outlines of the flowering spikes due to its smaller glumes. Stems with a robust, "chunky" appearance were more likely to be subsp. *waltersii*.

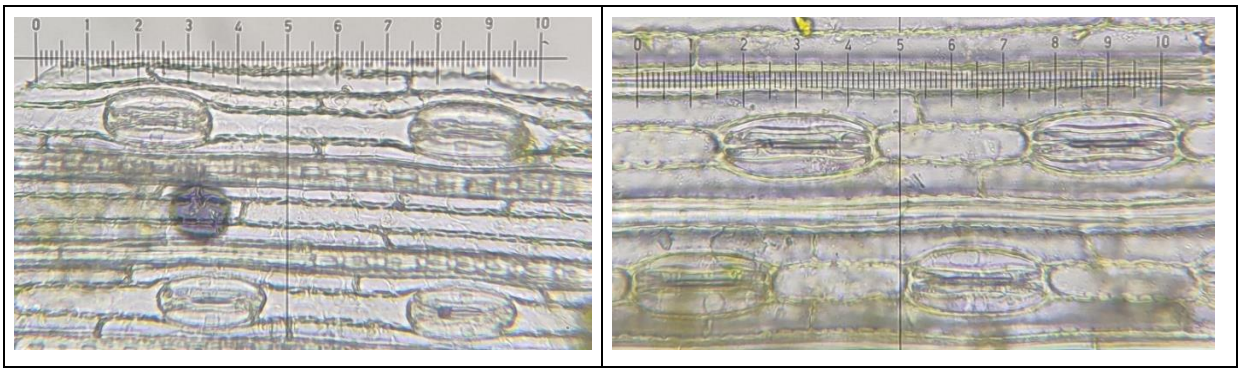


Figure 3. Fresh epidermal peels showing stomata from subsp. *palustris* (a) & subsp. *waltersii* (b). One division is 2.5 µm

There was substantial variation in size and appearance between samples, and both species can exhibit reduced forms, likely under varied environmental conditions. Sheets are typically comprised of a few stems, but the rhizome portion had been collected in some. The small number of stems, combined with high phenotypic plasticity, prevented the collection of meaningful morphological data. Some sheets showed robust stems that had been grazed. The regrowth of these had much finer stems and a smaller flower spike. Reduced forms of both subspecies produced fewer flowers per spike. The mid-spike glume length appeared to be the most consistent field characteristic for separating the subspecies. However, the sample size was prohibitively small, with often a few spikes per sheet, and samples may have originated from regrowth.

An example of the recording effort across the UK, representative of voucher dates in herbaria collections, was counted at BM, with a total of 357 vouchers examined; 13 were assigned as subsp. *palustris*, from ten locations, 342 were assigned as subsp. *waltersii*, and two remain unassigned (Table 2), indicating that subsp. *palustris* comprises only a small proportion of herbarium material. Approximately 2/3 of the vouchers were collected before 1930. There were only 17 vouchers from 1970 to 2022.

Habitats were grouped into categories based on their location descriptions and site history. 17 locations were associated with coastal grazing marshes or the tidal portions of rivers, 16 with inland grazing marshes, floodplains, and upper-reach habitats, and five were associated with fens.

Table 2. Herbarium vouchers at BM with collection year noted, and their assignment into subspecies. Two vouchers remain unassigned

Date classes	*E. palustris* subsp. *palustris*	*E. palustris* subsp. *waltersii*
Pre-1930	9	214
1930-1969	4	112
1970-1986	0	8
1987-1999	0	2
2000 onwards	0	6
Total	**13**	**342**

United Kingdom distribution of *E. palustris* subsp. *palustris* using herbarium material

Herbarium sheets of subsp. *palustris* from across the UK were examined, and a clear pattern of a southern England distribution emerged, most closely associated with reclaimed coastal grazing marshes and river floodplains. Records are tabulated in Appendix 1.

VC7, North Wiltshire

A voucher at BM from Poulton, made by T.A. Preston (25/06/1885), and identified by S.M. Walters. Preston taught at Marlborough College, and it appears likely that the record relates to the nearby Poulton Farm (Grose, 1957), with floodplain meadow associated with the River Kennet, an upper tributary of the River Thames. Another voucher by H.J. Killick (15/05/1948) also places subsp. *palustris* at a marsh near Knighton, Ramsbury, again associated with the River Kennet.

VC9, Dorset

A single voucher at RGE for Studland Heath, likely associated with coastal wetland. Submitted by E.C. Wallace (19/06/1933).

VC11, South Hampshire

M.C.F. Proctor (May 1952) had a voucher at CGE for Winkton Meadows, Christchurch, which S.M. Walters (1952) confirmed based on glume and stomata length. Winkton Meadows is associated with the floodplain of the River Avon, above where it meets the River Stour at Christchurch, flowing into Christchurch Harbour. At RGE, a voucher for Fleet Pond by J.E. Lousley, det. S.M. Walters (May 1953). The pond and surrounding wetland are associated with the Basingstoke Canal, converging with the River Wey, a main tributary of the River Thames.

VC12, North Hampshire

A voucher at OX from Alton, made by Canon J. Vaughan (08/06/1888), was likely associated with the floodplain of the River Wey, a Thames tributary.

VC13, West Sussex

A voucher at BM from Manhood End, by E.C. Wallace (12/01/1905), was once an area of salt marsh bordering the Chichester Channel. Further vouchers from RGE confirm the plant by E.C. Wallace (06/08/1939) and J.E. Lousley, det. S.M. Walters (May 1953). The voucher by E.C. Wallace additionally gave the Chichester Canal as a location. The marshes of the Manhood Peninsula are atmospherically described in Rudyard Kipling's poem "Eddi of Manhood End" (1913).

VC15, East Kent

There are three vouchers for Graveney Marshes, near Whitstable. This area now corresponds with the Seasalter Levels, sited behind sea defences on the Thames Estuary and managed as grazing marsh by the RSPB. They are all made by S.M. Walters and consist of the Holotype at BM, and the Isotype (16/09/1946) at CGE, referred to in the publication in *J Ecol* 37, 194 (1949). The isotype is described as coming from a wet ditch, and the voucher at BM is described in Latin, translating to a "wet grassland ditch". Both were reported to have a chromosome count of $2n = 16$.

A voucher found at RGE records the plant on the Isle of Sheppey by an unknown recorder (20/07/1947), pond in marshes, SW corner. This corresponds with Elmley Nature Reserve, a grazing marsh managed by the RSPB.

VC16, West Kent

Four vouchers again link two sites to the Thames Estuary. At Swanscombe Marshes, there is a voucher in SLBI by W.H.G. (22/08/1901) and three at BM: E. and H. Drabble (19/06/1903), J. Roffey (10/07/1938), and J. Braybrooke Marshal (10/07/1938). The most closely related current site is named Botany Marsh. S.M. Walters (04/08/1949) lodged a voucher at CGE from Higham Marshes. Higham is managed by the RSPB as a large area of grazing marsh sited behind flood defences.

VC17, Surrey

Three herbaria vouchers were found associated with the River Thames in West London. The first at Battersea was made by E.B. Bangerter (June 1838) and is in the Kew collection. In the "mud by the Mall" at Richmond, a voucher collected by G. Moggeridge (July 1865) was lodged at OX.

The first voucher from Kew was found at the SLBI and was made by W.R. Sherwin (July 1905). Later, the Kew Herbarium interestingly provided a series of herbarium vouchers from the Thames, which unusually consisted of a large tangle of rhizomes and a few stems. These were made by W.B. Turrill (13/07/1928), who worked at Kew at that time. The fact that so many sheets were made places this as a significant shoreline feature.

A voucher at SLBI provided by C.E. Britton (14/08/1911) is from a pond in Lower Morden, near the Pyl Brook, a Thames tributary in South London. Two further herbaria vouchers are likely associated with the floodplain of the River Wey, a main tributary of the River Thames. A voucher at BM for Woodbridge from Moore (20/01/1905) and duplicate vouchers at CGE and SLBI for Frensham Great Pond from E.S. Marshal (16/07/1888).

Two vouchers document the presence of subsp. *palustris* at Runnymede, the first by W.H. Beeby (05/07/1885) in a pool by the Thames and then 123 years later,

an RBG Kew Herbarium Wild Voucher by T. Heller and O. Rigby (27/08/2008) of a population at Langham Pond, Runnymede. Neither sheet had been taken to the subspecies level. The pond results from an abandoned river loop from the Thames and a well-known botanical hotspot for rarities.

VC19, North Essex
A voucher at BM was found for a population at St Osyth, Essex, collected by R.S. Standen (10/06/1897). This is likely related to the tidal estuary at Brightlingsea and the coastal grazing marshes.

VC21, Middlesex
Staines provided two vouchers, the first lodged at **K** by J. Fraser (12/07/1885) and the second at Staines Moor, a sheet at BM provided by D.H. Kent (28/04/1947). Staines Moor is exposed to the dynamic effects of the River Colne just before its confluence with the River Thames.

VC22, Berkshire
RGE vouchers documented two occurrences: first, near Reading, in "water behind Earley Power Station" by A. Gridland (20/05/1956), another Thames-associated location; and second, at South Hinksey by H.J.M. Bowen, det. S.M. Walters (02/08/1964), which describes an area of marsh at the convergence of Hinksey Stream and the River Thames.

VC23, Oxfordshire
The higher Thames reaches provided vouchers by C.E. Hubbard and W.B. Turrill (14/06/1944), lodged at Kew and RGE, for Cassington, from an area described as "wet sand in old river gravel pits".

VC25, East Suffolk
Two vouchers were found. The first, lodged with OX and found at Southwold by C.E. Palmer (09/07/1890), is from a coastal location, likely in a grazing marsh associated with the tidal creeks. A voucher at BM from Bradwell, collector unknown (10/01/1905), marks the easterly extent of a fenland population documented in VC29 and VC30.

VC29, Cambridgeshire
Cambridgeshire provides several locations associated with a formerly more dynamic fenland landscape. S.M. Walters had identified five locations from his time as curator of the CGE, all within easy walking distance of the botanic gardens on the southern side of Cambridge. Coe Fen (02/06/1911 and July 1949), and the voucher from 1911 was confirmed in 1950 with the stomata length noted. Vicars Brook (05/06/1946 and 05/08/1949) with the voucher from 1949 described as from a wet meadow, cited with a chromosome count of $n = 9$. Lastly, a voucher was described (28/07/1998) as in Grantchester in a Skating Meadow along a route from Newnham Croft. Further afield, he identified a voucher at Swavesey (25/05/1955), a grazing marsh maintained by the RSPB.

Two vouchers by G. Crompton (August 1951 and July 1957) were also lodged at CGE, with the 1957 location corresponding with Thriplow Meadows SSSI.

VC30, Bedfordshire
Two occurrences were associated with the Great River Ouse, a once highly dynamic fenland river with a tidal influence. Both vouchers at CGE, the first from Eaton Socon, are described as water meadows with no named recorder (19/08/1949). The second was by J. Dony (10/06/1957) at Moor End, Felmersham.

VC33, East Gloucestershire
Three vouchers were found from sites along the Severn, up to Upper Lode, the highest point at which tidal influence occurs. These were a voucher at BM from Maisemore Ham by J.W. Staines (June 1915), two vouchers at Kew, one from Upper Lode, described as above the lock by C.C. Townsend (07/08/1951), and another in the marshy pasture at Elmore by E. Milne-Redhead (22/06/1987).

VC36, Herefordshire and VC39, Staffordshire
Two vouchers in the CGE collection, one from a location described as the Herefordshire Beacon, collector unknown (July 1837) and another from Tamworth, again collector unknown, with the same date. Herefordshire Beacon may refer to a wider area of botanical search. The second appears likely to be associated with the River Glenn, before the confluence with the River Welland and the fenland-to-Wash transition.

VC53, South Lincolnshire
A voucher at CGE from Surfleet by E.J. Gibbons and S.R. Amner (July 1954). It is again a population associated with the River Welland and likely associated with the wider, formerly more dynamic fenland landscape.

VC54, North Lincolnshire
S.C. Stow and E.A. Woodruff-Peacock created a voucher lodged at **BM** from Trusthorpe (03/07/1903). Noted on marine silts, likely coastal marsh, this represents the most northerly extent of the UK distribution but still within the Wash area.

Discussion
This study presents a revised UK distribution for *Eleocharis palustris* subsp. *palustris* based on the examination of herbarium material verified using stomatal measurements. The subspecies shows a predominantly southern and eastern distribution in Britain, most frequently associated with coastal grazing marshes and river floodplains, with fewer inland records. The following discussion considers these patterns in relation to habitat association, rarity, ploidy-linked traits, and processes influencing the range margin.

Habitat and distribution patterns
Considered as a whole, the verified herbarium material shows that *Eleocharis palustris* subsp. *palustris* in Britain occurs within a limited but coherent range of lowland wetland landscapes. Many records derive from coastal grazing marshes and the tidal portions of rivers, particularly around the Thames Estuary, the Wash, and

the tidal Severn. Several of these coastal and estuarine localities are represented by repeated voucher collections spanning many decades, including material from the type locality, indicating long-term persistence within these landscapes rather than isolated or transient occurrences.

Coastal grazing marshes and tidal portions of rivers

The greatest concentration and most consistent records are associated with coastal grazing marshes and the tidal reaches of rivers. These environments are characterised by dynamic hydrological conditions, including periodic inundation and saline influence, and by long histories of grazing that maintain open vegetation structure. Such conditions appear to provide stable habitat for subsp. *palustris*, with repeated voucher collections indicating persistence over extended periods. The prevalence of records from these landscapes suggests that they represent core habitat for the subspecies within Britain.

Inland grazing marshes and river floodplains

Further inland, records occur along the same river systems, notably within the Thames catchment and the fenland margins of eastern England, where plants were associated with grazing marshes and floodplain meadows. These inland sites are generally more scattered and are represented by fewer repeated collections, but they share broadly similar landscape characteristics, including open vegetation structure and a history of grazing or periodic disturbance. The continuity between coastal, estuarine, and inland floodplain records suggests occupation of a connected set of lowland wetland environments; however, this pattern does not imply a specific mechanism of connectivity or dispersal, which remains unresolved.

Fen locations

A smaller number of records originate from fen habitats, including several sites within the Cambridgeshire fens. These locations are typically represented by isolated or infrequent collections and are more difficult to interpret ecologically than the coastal and floodplain records. Their occurrence may reflect the persistence of remnant populations within landscapes that have undergone substantial historical modification. Nevertheless, these records indicate that subsp. *palustris* is not confined exclusively to coastal or floodplain environments, while emphasising the fragmented and potentially relic nature of some inland occurrences.

Rarity of subsp. *palustris* in Britain

Only four herbarium vouchers of subsp. *palustris* were found dating from after 1960, compared with material from 37 localities before this date. Despite the much larger number of *E. palustris* vouchers in herbaria from before 1960, we can nevertheless be confident that subsp. *palustris* is rare in the UK. Material at **BM** indicates that it comprised <4% of all specimens collected as *E. palustris* both before 1930 and between 1930 and 1970. Although a greater number of vouchers exist in herbaria from before 1960, these derive from relatively few confirmed localities, and it can therefore be inferred that subsp. *palustris* has always been scarce in Britain. Representation of the subspecies within herbaria may be elevated relative to its true frequency in the field, as collection effort is likely to favour atypical plants and peak during periods of focused taxonomic study, notably during the mid-twentieth

century. Following this period, interest appears to have waned, in part owing to the difficulty of subspecific identification.

When considering present-day rarity, it is likely that subsp. *palustris* now occurs at fewer sites than are represented in the historical herbarium record. Many of the habitats described are likely to have undergone substantial change through flood defence works, drainage, urban expansion, river modification, and changes in agricultural practice, notably the cessation of grazing at some sites; loss of ponds may also have contributed locally. Nutrient inputs associated with intensive agriculture have further affected many remaining waterbodies. Collectively, such losses of habitat extent and quality are likely to reduce population size, site availability, and the potential for recolonisation. Nevertheless, some populations may persist within habitats covered by the UK Biodiversity Action Plan Priority Habitat of Coastal and Floodplain Grazing Marsh.

Predicting habitat preference in relation to ploidy level

There are reported differences in both distribution and ecological association between the two subspecies of *Eleocharis palustris* (e.g. Kaplan et al., 2015; Julve, 2019). Variation in ploidy level is an important heritable trait that is commonly accompanied by changes in genome size, which can influence basic cell dimensions and traits such as stomatal size and density. Across diverse angiosperms, larger genome sizes are significantly correlated with larger guard cell (stomatal) length and reduced stomatal density, consistent with widely reported relationships between genome size and cell size in plants (Beaulieu et al., 2008).

It should be noted, however, that *Eleocharis*, as a member of the Cyperaceae, possesses holocentric chromosomes, in which kinetochore activity is distributed along the length of the chromosome rather than localized (Håkansson, 1958). This condition is known to influence chromosome behaviour and may affect the stability and consequences of polyploidy. As a result, relationships between genome size, cell size, and ecological traits in *Eleocharis* may differ in subtle ways from those observed in taxa with monocentric chromosomes, although this remains poorly understood.

Genome size is also increasingly recognised as a factor influencing ecological and phenotypic variation in plant taxa at landscape scales (Henniges, 2023). These general cytogenetic and morphological relationships provide a plausible context for interpreting ecological differences between the subspecies.

Genome size variation is reflected in stomatal traits that are directly relevant to plant water relations, as stomatal size and density influence rates of gas exchange and transpiration through their effects on maximum stomatal conductance. Stomatal size also influences the speed at which stomata open and close in response to environmental change, with smaller stomata opening and closing more rapidly than larger stomata (Drake et al., 2013). Across angiosperms, variation in genome size is associated with differences in stomatal traits that influence plant performance under water stress, suggesting potential effects on water-use efficiency (Faizullah et al., 2021).

In this context, the smaller stomata characteristic of subsp. *palustris* could plausibly confer greater tolerance to environmental stress relative to subsp. *waltersii*, consistent with ecological observations reported from continental Europe (Kaplan et al., 2015; Julve, 2019). Together, these considerations provide a plausible

mechanistic framework for interpreting the observed ecological associations of subsp. *palustris*, without implying direct causal determination.

The occurrence of two ploidy levels within *Eleocharis palustris* is therefore likely to have ecological consequences that contribute to differences in distribution and habitat association between the subspecies. The revised UK distribution presented here indicates that subsp. *palustris* is most frequently associated with coastal grazing marshes, river floodplains, and other wetland habitats of relatively low competitive intensity, while subsp. *waltersii* is more widespread across a broader range of environments. These contrasting patterns suggest that ecological filtering, acting on traits linked to ploidy level, contributes to shaping the realised distributions of the two subspecies.

Populations at the range margin

Towards the edge of its distribution, subsp. *palustris* is confined to relatively few and often isolated sites, which may increase the influence of population size and connectivity on its long-term persistence. Experimental and field studies have shown that hybridisation can occur between the two subspecies and that backcrossing proceeds predominantly towards subsp. *waltersii* (Lewis & John, 1961; Strandhede, 1966). Where the subspecies occur sympatrically, this asymmetry raises the possibility that populations of subsp. *palustris* may be progressively assimilated through hybridisation, particularly where populations are small or geographically isolated. This process is consistent with genetic swamping, whereby repeated hybridisation coupled with asymmetric backcrossing leads to the progressive loss of the rarer taxon's genetic integrity in favour of a more widespread or competitively dominant relative. The combined effects of ecological filtering and asymmetric hybridisation may therefore help to explain both the restricted distribution and apparent rarity of subsp. *palustris* in Britain. Together, these interacting processes provide a plausible framework for interpreting the current distribution pattern observed in the UK.

Although *E. palustris* is highly effective at vegetative spread once established, seed is likely to be the more significant source of dispersal into higher catchment locations, where colonisation depends on longer-distance transport rather than local clonal expansion. Observations that newly dug ponds and ditches are readily colonised by *E. palustris* suggest that fruit set and dispersal are not necessarily limiting at the species level, although it remains uncertain whether sufficient observations exist to substantiate this specifically for subsp. *palustris*.

Seed-bank studies have shown that *E. palustris* forms a persistent and moderately dense seed bank, but no distinction has been made between subspecies, and the influence of the smaller seed size of subsp. *palustris*, the survival and persistence of which remain unknown. Where hybridisation has occurred, seed banks may therefore contain a mixture of genotypes, which may reduce the likelihood of persistence or re-emergence of pure subsp. *palustris* populations following disturbance. The extent to which this process operates in natural populations remains uncertain.

The subspecies is not climatically limited, as its European range extends into northern Scandinavia, indicating that factors other than temperature are responsible for its restricted British distribution. Dispersal distance, population fragmentation, and post-disturbance persistence may therefore act in combination to constrain

further expansion at the range margin. A recent UK Red List assessment has classified *Eleocharis palustris* subsp. *palustris* as Data Deficient (Stroh et al., 2025), reflecting continuing uncertainty in its distribution and status.

Future work

Fieldwork to assess the current status of populations identified from herbarium vouchers is ongoing and continues to yield new information on both historical and extant sites, including observations made in 2025. Several previously documented localities have been revisited, and additional sites have been identified, contributing to a clearer picture of persistence and current distribution. Genetic study of populations at these locations has the potential to clarify several of the outstanding questions discussed above, particularly with respect to hybridisation and population continuity. Continued survey of historical localities, combined with targeted searches informed by habitat characteristics, will further refine understanding of the British range of the subspecies.

Conclusions

Herbarium vouchers of *Eleocharis palustris* in Britain were successfully examined using a non-destructive method based on stomatal measurements taken directly from specimens with a long-working-distance lens. This approach enabled efficient examination of a large number of vouchers and allowed reliable reassessment of material irrespective of previous determinations. Reassessment of herbarium material resulted in the resolution of previously unassigned specimens and, in some cases, reassignment of material determined to subspecies level, highlighting the difficulty of consistent identification using morphological characters alone, and the value of stomatal measurements in resolving subspecific identity.

Application of this method has resulted in a revised UK distribution for subsp. *palustris*, demonstrating a predominantly southern and eastern distribution, most frequently associated with coastal grazing marshes, river floodplains, and related lowland wetland landscapes. Verified records indicate long-term persistence at a small number of locations, alongside a broader pattern of rarity within Britain.

Interpretation of these distributional patterns in relation to ploidy-associated traits provides a plausible ecological framework for understanding differences between the two subspecies, although the present study does not directly test physiological mechanisms. At the edge of its European range, the restricted distribution of subsp. *palustris* in Britain is likely to reflect a combination of ecological and historical factors acting on a limited number of sites.

The work presented here establishes a robust baseline for assessing the current status of subsp. *palustris* in Britain and provides a foundation for future field and genetic studies aimed at refining understanding of its distribution, persistence, and ecological differentiation.

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