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Biological Flora of Britain and Ireland: *Geranium sylvaticum**

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Abstract

1. This account presents information on all aspects of the biology of *Geranium sylvaticum* L. (Wood Crane's-Bill) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of Britain and Ireland*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history, conservation and management.
2. *Geranium sylvaticum* is a perennial forb of woodland, semi-natural grassland, tall-herb vegetation, boreal dwarf shrub heaths and subalpine and subarctic scrub. In Britain and Ireland, it occurs in cool and moist northern-montane climates, in upland hay meadows, road verges, riverbanks, fens and mires, mountain rock ledges, crags and ravines and upland mixed ash forests.
3. *Geranium sylvaticum* is widespread in Scotland and northern England, with scattered native occurrences in Wales, central England and at the coast of County Antrim, Ireland. It has an extensive native range in Europe and Asia. At the north-eastern end of this range, *G. sylvaticum* can occur down to sea level, whereas in more southern range parts, it is limited to mountain habitats.
4. In Britain and Ireland, *Geranium sylvaticum* is a species mainly of neutral to moderately calcareous soils of intermediate fertility. In its continental Eurasian range, it also occurs on more acidic soils.
5. *Geranium sylvaticum* is gynodioecious, that is individual plants are typically female or hermaphrodite. Occasionally, individuals are gynomonoecious, producing both female and hermaphrodite flowers. Female flowers are usually smaller than the

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*Nomenclature of vascular plants follows Stace (2019) and, for non-British species, *Flora Europaea*.

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protrandrous hermaphrodite flowers. Flowers are visited by insects of the orders Hymenoptera, Diptera and Lepidoptera, as well as Coleoptera and Hemiptera.

6. Primary seed dispersal of *G. sylvaticum* is ballistic, that is seeds are ejected from fruits. The species has a transient soil seed bank persisting for less than 12 months. The seeds have physical dormancy, that is their seed coat is initially impermeable to water. The species has little capacity for vegetative spread.
7. In Britain and Ireland, *G. sylvaticum* underwent long-term distributional decline mostly before 1987. A marked recent increase in records has been observed in northern Scotland, due to either a slight northerly shift in its distribution and/or increased recording in previously underrecorded areas.

KEYWORDS
climate change, conservation, Eurasian Boreal-montane floristic element, genetic variation, grassland, gynodioecy, woodland

Wood Cranesbill. Geraniaceae. *Geranium sylvaticum* L. is a leafy, branched, perennial gynodioecious herb with compact rootstock.

Stem (15)30–70(95) cm, erect, with patent to retrorse eglandular hairs 0.5–2.0 mm long and sometimes patent, glandular hairs 0.2–0.8 mm long. Basal leaves in a ± deciduous rosette, stem usually with 1(–2) alternate stem leaves up to the first branch point of the inflorescence, this branch point with a pair of opposite leaves; sometimes a lateral branch arises from the node of the alternate leaf. Lamina (5.8)7.2–10.1(13.3) cm long, 7.8–16.3 cm wide; polygonal in outline and palmately divided ¾ to 6/7 into (5–)7(–9) ovate lobes up to twice as long as broad; base cordate. Petioles up to 30 cm, hairy, length diminishing rapidly upwards, with upper stem leaves being almost stalkless. Stipules 6.8–17.1 mm long and 1.1–5.2 mm wide, those of basal leaves ovate or oblong-ovate, those of stem leaves ovate-acuminate to lanceolate.

Inflorescence a dichasial cyme with 2-flowered cymules arranged solitary or in aggregates at the top of each branch. Peduncles (14)19–45(68) mm long, usually short or absent in cymule aggregates; bracteoles 1.8–6.1 mm long, 0.4–0.9 mm wide, lanceolate, whorled; pedicels (3.8)10–19(23.1) mm long, reflexed at the bud stage, upright at the flowering and fruiting stages.

Flowers actinomorphic, 22–30 mm in diameter, with female flowers typically smaller than hermaphrodite flowers, saucer-shaped; hermaphrodite flowers protandrous; some flowers of intermediate form with 1–9 functional stamens, along with non-functional stamens at various stages of regression. Sepals 5, (6.7)7.2–8.6(9.6) mm long, 2.4–3.7 mm wide, lanceolate, mucronate, mucro (1)1.5–2.2(3) mm long, abaxially with eglandular and glandular hairs, adaxially glabrous. Petals 5, (12.2)13–17.6(19.3) × (6.3)7.0–10.8(12.6) mm, usually violet blue with a white base, rarely pink or white, rounded or slightly notched at apex; base without claw, hairy adaxially and glabrous abaxially, ciliate on the basal margin. Stamens 10, in two whorls. Filaments pinkish, (7.2)7.6–8.8(10.5) mm long, arched outwards in female stage of flower; anthers bluish. Nectaries 5. Gynoecium 5.8–9.7 mm long, purple.

Fruit a dry five-celled schizocarp (22)26–30(36.8) mm long; immature fruit erect on erect pedicels; mericarps 3.4–5.1 mm long, 1.4–2.7 mm wide, not compressed at the apex, smooth, with adpressed eglandular hairs and patent glandular hairs; beak 16–27 mm long, with a narrowed apex (2.4)2.7–4.5(6) mm long. Seeds 2.7–3.4 mm long, 1.7–2.1 mm wide, dark brown, finely reticulate.

A recent monograph of the genus Geranium lists a total of 307 species (Aedo, 2023). In line with Yeo (2001), Aedo (2023) classified these into 28 informal taxonomic groups, acknowledging that more phylogenetic research is needed. Within this classification, the Sylvaticum Group, containing *Geranium sylvaticum* along with seven other closely related species, is located within the section Geranium which itself is located within the subgenus *Geranium* (Aedo, 2023). The other seven species in the Sylvaticum Group are *G. albiflorum*, *G. atlanticum*, *G. caeruleatum*, *G. endressii*, *G. pseudosibiricum*, *G. rivulare* and *G. schmidii* (Aedo, 2023). Detailed phylogenetic information for the Sylvaticum Group is not available. However, a phylogenetic parsimony tree for 85 taxa, including 83 members of the family Geraniaceae, and 34 member species of the genus *Geranium* confirms close relations between *G. sylvaticum* and *G. atlanticum* and *G. endressii*, the two other members of the Sylvaticum Group included in this tree (Fiz et al., 2008).

Previously, *G. rivulare*, *G. caeruleatum* and *G. pseudosibiricum* had been considered localised subspecies of *G. sylvaticum* (Webb & Ferguson, 1968). For *G. sylvaticum* itself, over 30 varieties and forms have been described (Aedo, 2023). In the British and Irish distribution range, notably, *G. sylvaticum* var. *wanneri* has been described from Cumbria, in hay meadows near Ravenstonedale, and west of Sedbergh (Halliday, 1997).

Using amplified fragment length polymorphism (AFLP) fingerprinting for the whole genome as well as cpDNA sequencing of the chloroplast genome, regional genetic variation in *G. sylvaticum* was studied in montane grassland populations in the Taunus region, Germany (Ernst et al., 2013). Sampling focused on 15 populations spread out across an area of approximately 150 km^2, with individual

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populations at least 500 m apart and separated by geographic barriers such as forest or urban areas. Based on results of the (AFLP) fingerprinting, the overall pairwise fixation index (FST) score (i.e. a measure of population differentiation due to genetic structure) across sites in the Taunus was 0.105 (range of individual pairs: 0.014–0.187) and statistically significant, indicating some flow but nonetheless marked population differentiation at the scale of the study. Pairwise genetic distances were correlated with geographic distances between populations, and average pairwise distances for each population were negatively correlated with altitude (Ernst et al., 2013), indicating greater genetic isolation of populations at lower altitudes, whereas populations in the centre of their local distribution range were genetically diverse and less differentiated. Overall gene diversity H_T was 0.32 and mean within-population diversity H_W was 0.28 (SE: 0.006). According to the authors, these values are high compared to those found in other species with a mixed breeding system (Ernst et al., 2013). Interestingly, within-population genetic diversity was independent of population size, which the authors put down to a late age of first flowering and a long potential individual lifespan.

The genetic diversity of 13 different *Geranium* species from across Iran including *G. sylvaticum* was measured by Shi et al. (2021). The nine investigated populations of *G. sylvaticum* were characterised by high genetic diversity, with isolation by distance and limited gene flow determining population structure. There was a significant correlation between genetic and geographic distances (Shi et al., 2021). Studies investigating the genetic diversity of wild *Geranium sylvaticum* populations were also carried out in England (Parfitt, 2000; Napper, 2003; both cited in Pacha, 2004).

Geranium sylvaticum is native to Britain and Ireland, being largely confined to the uplands where it is characteristic of dry and moist circumneutral grassland and some deciduous forest types.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Geranium sylvaticum is found in Scotland and England and is less common in Wales and Ireland (Stroh, Walker, et al., 2023; Stroh, Humphrey, et al., 2023; Figure 1). Northwards, it extends to about the Great Glen in Scotland, and southwards, its continuous native area extends to southwest Yorkshire and south Lancashire. Scattered native occurrences of *G. sylvaticum* can be found in central Wales, in central England, and in Ireland in County Antrim, where it is confined

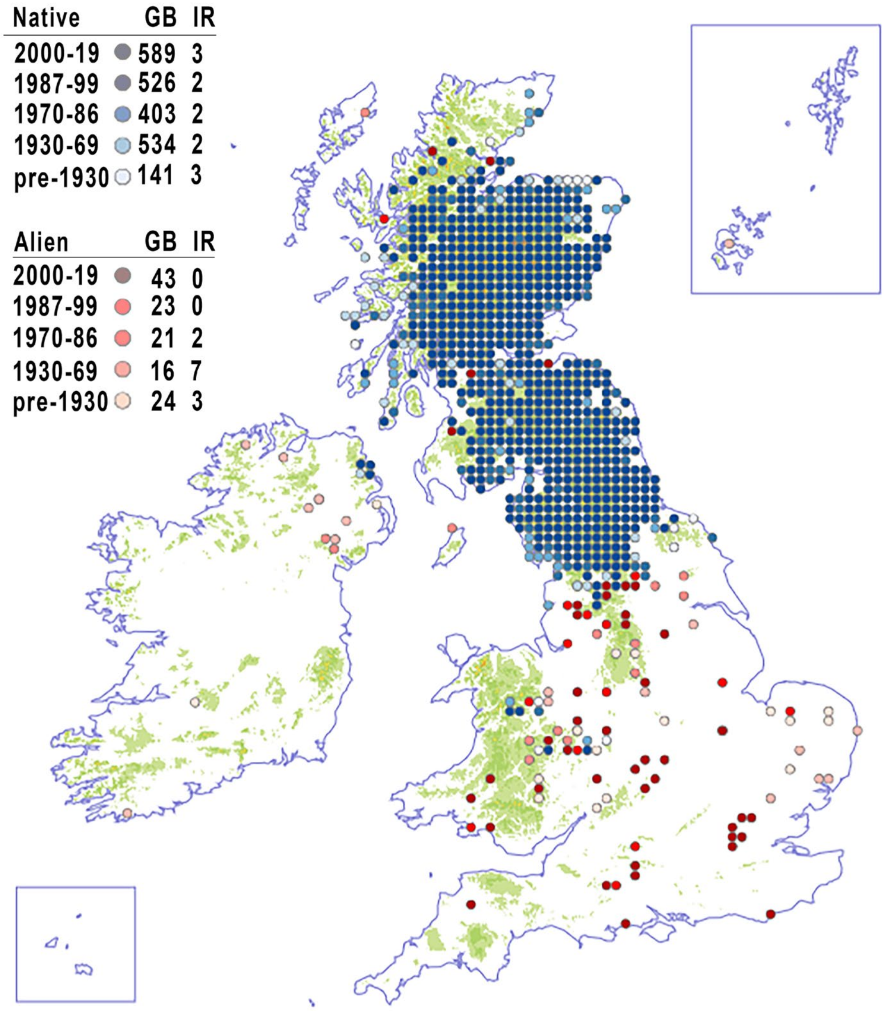

FIGURE 1 The distribution of *Geranium sylvaticum* in Britain and Ireland. Each dot represents at least one record in a 10 km square of the National Grid. Colour distinguishes native versus alien status, and shade indicates the date range of the most recent record. Figures for Great Britain (GB) and Ireland (IR) indicate total numbers of squares in each category. Source: Stroh, Humphrey, et al. (2023).

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to a coastal strip extending from Killyglen near Larne to Glenarm (Sell & Murrell, 2009; Stace, 2019; Stroh, Walker, et al., 2023; Yeo, 2001). The Scottish native range of the species also includes the islands of Mull and Eigg in the Inner Hebrides (Currie & Murray, 1983; Stroh, Walker, et al., 2023). Former populations on Skye, Lewis in the Outer Hebrides and Orkney were introduced (Crossley, 2019; Pankhurst & Mullin, 1991; Stroh, Walker, et al., 2023). Scattered introduced populations are found in Wales, southern England, and northern parts of Ireland (Figure 1), typically resulting from garden escapes (e.g. Boon & Outen, 2011; Sanford & Fisk, 2010; Trueman et al., 2013).

An analysis of biogeographical patterns in the British and Irish flora assigned *G. sylvaticum* to the '*Alchemilla glabra*' distribution type, comprising species that are 'often frequent in the uplands', 'have a distinctly easterly bias to their Scottish range' and 'extend southwards into England along the Pennine chain' whereas 'in Ireland they are northern' (Preston et al., 2013: 107). Biogeographically, *G. sylvaticum* belongs to the Eurasian Boreal-montane floristic element (Preston & Hill, 1997). In addition to Britain and Ireland, its native range is extensive, extending from the southern coast of Greenland, across Europe, including Scandinavia, the Baltic countries and European Russia and reaching into Asia as far east as the Yenisey Range in East Siberia (Gams, 1924; Sugorkina, 1995; Figure 2). It is native in most of continental Europe but is restricted to mountains in the south and absent from many islands (Webb & Ferguson, 1968). Northwards its distribution includes Fennoscandia and northern Russia, reaching northernmost Norway and Kolguyev Island (Wangerin, 1926), that is well above the arctic circle. Southwards its range extends to the mountains of the northern Balkan peninsula, and through the southern French mountains to the Pyrenees and Spanish mountains, and to the Calabrian Appenines (Gams, 1924; Wangerin, 1926); further east it reaches southwards into northern Asia Minor (Wangerin, 1926), and through the Caucasus into northwestern Iran (Gabrielian & Fragman-Sapir, 2008; Janighorban, 2009). Its native range also includes the Faroe Islands, Iceland and the south coast of Greenland (Aedo, 2001). Continental North American populations must be considered as introduced from cultivation (Aedo, 2001). This includes introduced populations in Quebec, Canada (Rousseau, 1968) that are now considered naturalised (van Kleunen et al., 2019). There are additional records for Illinois, Missouri and Wisconsin (all USA) and for Christchurch, New Zealand (GBIF Secretariat, 2023; see Figure 2).

In southern Europe, *G. sylvaticum* is a species of montane meadows but in northern and eastern parts of its range it occurs down to sea level (Yeo, 2001). In Britain and Ireland, it is mainly an upland species, recorded at altitudes from 200 m up to 1005 m, the latter recorded on Ben Lawers, Perthshire, Scotland (Preston et al., 2002; Stroh, Walker, et al., 2023). In other parts of its European range, *G. sylvaticum* reaches the alpine zone, with the altitudinal limit varying with geographical location. In the Alps, the species reaches 2650 m in the Engadin, 2500 m in Valais, 2400 m in Tyrol and 2200 m in the Bavarian Alps (Wangerin, 1926). According to Gams (1924), *G. sylvaticum* has an upper altitudinal limit of 2081 m in the Tatra Mountains, and in Scandinavia, the species reaches to the limit of the willow scrub vegetation. For Norway, Huxley (1986) gives an upper altitudinal limit of 1750 m. For northern Swedish Lapland, a maximum altitude of 1100 m has been reported, with *G. sylvaticum* occurring in forests below the tree line, in the transitional ecotone vegetation around the treeline and in dwarf shrub heath above the treeline (Sundqvist et al., 2008). In northern Norway, occurrences of *G. sylvaticum* above the treeline appear to be frequently linked to particularly nutrient-rich sites (Jon Moen, pers. comm.). While it is unknown to what extent this may apply to other mountain ranges, it may suggest that factors other than climate, for example

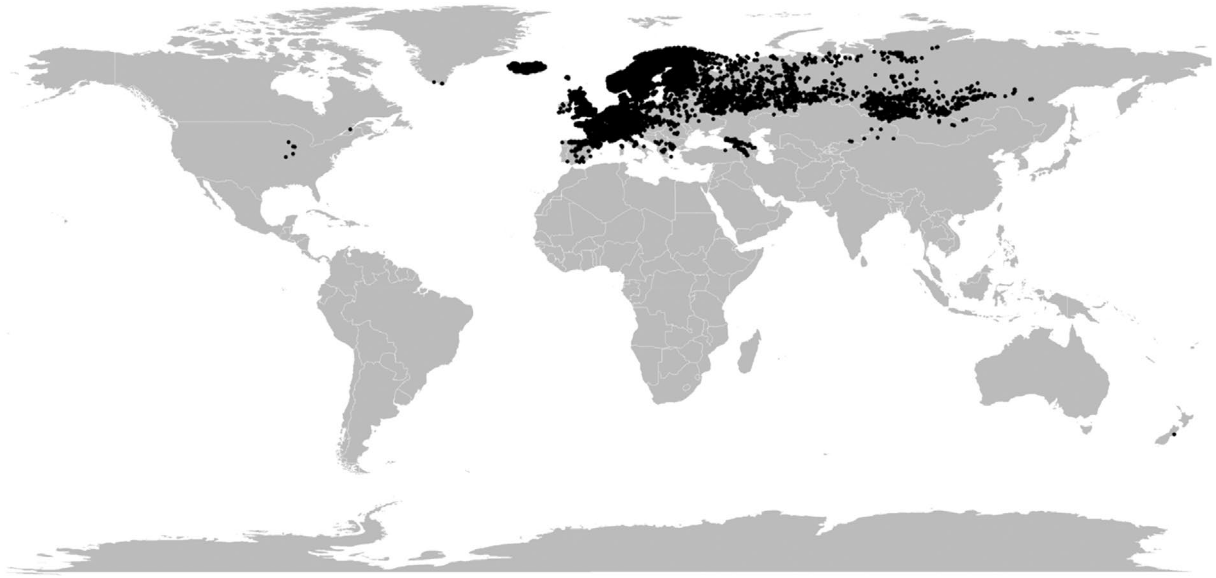

FIGURE 2 Global distribution of *Geranium sylvaticum*. Populations in Canada are naturalised, those in the USA and New Zealand are casual (see text). Data were obtained from the GBIF online repository (Global Biodiversity Information Facility, www.gbif.org) and mapped using R (R Core Team, 2025).

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nutrient availability, but also potentially herbivory (see Section 4), may co-determine altitudinal limits of the species locally. For Central Europe, the altitudinal preference of *G. sylvaticum* is also reflected by its Ellenberg temperature value of 4 (Ellenberg et al., 1991), indicating its occurrence mainly in high montane to montane habitats, its adjusted 'harmonised' Ellenberg temperature value of 3.4 across the European range (see Tichý et al., 2023 for an explanation of the harmonisation procedure), and its Swiss ecological indicator temperature value of 2+ (2+ = lower subalpine and upper montane stages) (Landolt et al., 2010).

Where *G. sylvaticum* and the closely related *G. pratense* co-occur, their altitudinal distributions tend to overlap, although *G. sylvaticum* is more restricted to upland habitats, and *G. pratense* is more restricted to lowland habitats (Stroh, 2019), reflecting their different climatic niches (as described in Section 2.1 here for *G. sylvaticum* and in Jefferson et al., 2023 for *G. pratense*). For example, in County Durham, the distribution patterns of the two species are almost inverse (Graham, 1988). Another example are the Harz and Thuringian Forest hill ranges in Central Germany, where *G. sylvaticum* mainly occurs as a component of yellow oat-grass (*Trisetum flavescens*) upland meadows, and *G. pratense* mainly occurs in false oat-grass (*Arrhenatherum elatius*) lowland meadows, with limited overlap (Ellenberg, 1996, based on data from Hundt, 1966).

Several studies in recent years have indicated that the upper altitudinal range limit of *G. sylvaticum* may be increasing. For example, a repeat vegetation survey carried out in 1999 by Virtanen et al. (2003) of the *Deschampsia flexuosa-Anthoxanthum odoratum* snow bed plant community on Mt. Sylfjellet, central Norway (63°00′N, 12°10E), replicating a previous survey by Nordhagen in the 1920s, found that in the intervening decades, the previously absent *G. sylvaticum* had colonised the community. In another study which investigated altitudinal shifts in a range of plant species in Dovrefjell-Sunndalsfjella National Park, Norway, *G. sylvaticum* was for the first time recorded in 2015 on the summit of Vesle Armodshøkollen mountain in the low-alpine zone at an altitude of 1161 m, after having previously not been recorded there in 2001 and 2008 (Vanneste, 2016; Vanneste et al., 2017). The lower-altitudinal limits of mountain populations may also be changing, possibly due to increased competition. In montane forest below the treeline in Russia's South Ural Mountains, *G. sylvaticum* has been observed to decline in mean cover between 2002 and 2014 (Gazol et al., 2017), possibly due to a denser forest resulting in more canopy shading or due to increased intra-specific competition in the forest understorey or a combination of both (Antonio Gazol, pers. comm.). In a transplantation experiment In the Central Alps, Italy, designed to simulate temperature increase as predicted under a changing climate, the frequency of occurrence *of G. sylvaticum*, determined via gridded quadrat counts in mountain meadow turf excavated to a depth of 25 cm and transplanted from an altitude of 2000 m to a new location at 1500 m altitude, declined by 45.6% over a 2-year period following transplantation (Niedrist et al., 2016). In the same study, in a monolith transplanted locally at 2000 m, frequency of *G. sylvaticum* increased to a level over six times as high as the initial value. While not specifically discussed by the authors, the observed decline of *G. sylvaticum* in the monolith transplanted downslope may have resulted from increased competition, since competitive grasses typically found at lower altitudes colonised the monolith following transplantation. The findings of both observational and experimental studies suggest that with climate change, both the lower and upper limits of the occurrence of *G. sylvaticum* might move upwards in mountain ecosystems. The results of environmental niche modelling of the response of *G. sylvaticum* to future climate change are discussed in Section 11.3.

2 | HABITAT

2.1 | Climatic and topographical limitations

Of the 13 European climate zones identified by Metzger et al. (2005), the core range of *G. sylvaticum* includes the Atlantic North, Alpine North, Boreal, Nemoral, Continental and Alpine South zones. Its range extends into the Mediterranean Mountains zone, but it is absent or largely absent from the Atlantic Central, Pannonian, Lusitanian, Anatolian, Mediterranean North and Mediterranean South zones.

In Britain and Ireland, *G. sylvaticum* is characteristic of cool and moist northern-montane climates (Figure 3). Average mean January temperature, average mean July temperature and average mean annual rainfall for British hectads (10 km × 10 km squares) with recorded *G. sylvaticum* populations (Preston et al., 2002) are 1.8°C, 13.0°C and 1339 mm, respectively, drawing on a 1961–1990 baseline (Hill et al., 2004). *Geranium sylvaticum* does not encounter its climatic cold limit in Britain and Ireland (Figure 3a), and its range extends into the alpine zone of European mountain ranges, into the far north of Europe and all the way east to Siberia. The fact that *G. sylvaticum* is mostly absent from southern lowland Britain, from most of Ireland, and the southern European lowlands, indicates that its realised climatic niche does not include such mild climates, although its fundamental niche does, given that *G. sylvaticum* individuals grow well under such conditions when in cultivation. Table 1 shows climate parameter values from the European part of the distributional range of *G. sylvaticum*, that is excluding its Siberian range east of the Urals (Vangansbeke et al., 2021). These indicate that British and Irish populations of *G. sylvaticum* tend to grow towards the warmer and wetter end of its range of climatic conditions.

A marked increase in the ground cover of *G. sylvaticum* over a 20-year period from 1987 to 2007 was observed in arctic alpine birch forest in northern Sweden, coinciding with an increase of 2.0°C in mean annual temperature (Wilson & Nilsson, 2009). In alpine grassland in Norway, ramet survival, growth and flowering probability were all positively related to July temperatures in the current year. Flowering probability was positively related to July temperature in the previous year, and growth was also positively related to the current year's total precipitation in July (Evju et al., 2011). Since these climatic variables reflect mid-summer conditions during a short alpine growing season (Evju et al., 2011), it appears plausible that near

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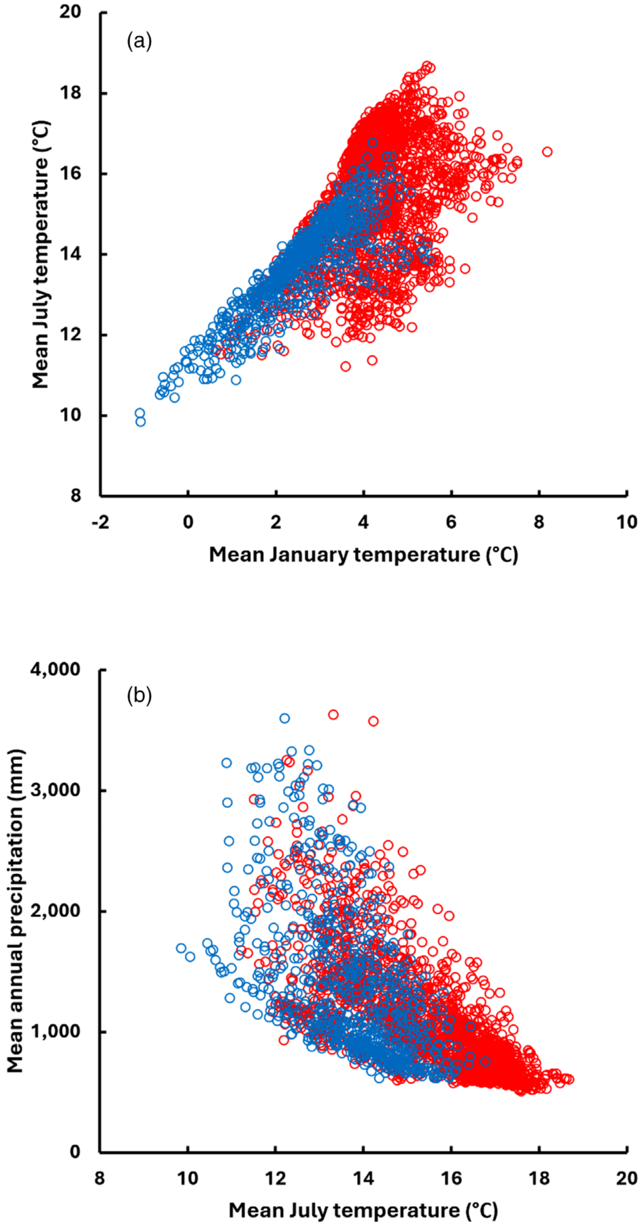

FIGURE 3 'Climate space' occupied by *Geranium sylvaticum* as represented by mean January and July temperatures and mean annual precipitation in hectads of the British and Irish National grids. Blue symbols represent hectads where *G. sylvaticum* is present; red symbols those where it is absent. Climate data (downloaded from Hill et al., 2004) and distribution data (downloaded from Stroh, Humphrey, et al., 2023) both supplied by Kevin Walker and BSBI. (a) July temperature plotted against January temperature; and (b) annual precipitation plotted against July temperature.

the 'cold edge' of this species' climate envelope, interannual climatic variation can exert significant influence on individual and population performance.

On a nine-point scale for snow cover species 'preferences' in southern Norway mountain vegetation, *G. sylvaticum* has a snow indicator value of 4, indicating the species to be slightly chionophobous, that is slightly snow-avoidant (Odland & Munkejord, 2008). Species in this category are characterised by an ecological maximum of occurrence in plots where in 2004, when the data underlying these indicator values was collected, the snow had completely melted around Julian day 122–127, that is around 2nd to 7th of May. As with classic Ellenberg values, this snow indicator value must be considered specific to the region for which it was derived.

2.2 | Substratum

Parent materials for soils that support populations of *G. sylvaticum* include superficial deposits resulting from glacial, aeolian, riverine or other mass movement processes, sedimentary rocks (limestone sandstones and shales) and both metamorphic and igneous rocks, particularly where the latter are base-rich, such as basalt, gabbro and dolerite. However, *G. sylvaticum* is generally absent where parent material gives rise to very acid soils, for example, over acid igneous rocks such as granite, or where, irrespective of geology, climatic factors give rise to extensive rainwater-fed peat formation resulting in raised or blanket bogs.

In Britain and Ireland, *G. sylvaticum* is a species mainly of neutral to moderately calcareous soils of intermediate fertility (Stroh, 2019). Major soil groups on which it occurs (using the soil classification of Avery (1990) with soil groups in parentheses where known), are brown soils (alluvial brown soils, calcaric brown soils), lithomorphic soils (rankers, rendzinas), gley soils (alluvial gley soils) and some less acid peat soils, notably groundwater-fed rich-fen soils (Rodwell, 1991a, 1991b, 1992).

In Germany, in the (north) western parts of the Eifel low-mountain range, Poschlod and Schumacher (2006) found populations of *G. sylvaticum* to occur consistently on loamy to sandy-loamy, low-base (silicate) to high-base (limestone) brown earths and stagnogley brown earths. In northern Russia, spruce forest populations of *G. sylvaticum* have been described on humic-illuvial podzol soils (Orlova et al., 2012), with a humus content in the B horizon of more than 3% (Stolbovoi, 2000), and boreal birch forest populations have been described on pararendzina soil (Koptsik et al., 2001). In such northern part of its Eurasian range, where *G. sylvaticum* is a frequent component of the field layer of boreal and hemiboreal forests (see Section 3), the soils are often derived from Quaternary glacial or glaciofluvial deposits and are mostly acidic or mesotrophic and range from nutrient-poor to nutrient-rich. The main soil types there are various types of podzols, brown soils, gleysols and organic soils with the hydrological characteristics ranging from very moist to dry (Kucherov & Kutenkov, 2021; Thiffault, 2019).

In Britain and Ireland, *G. sylvaticum* is assigned an Ellenberg value of 5 for moisture by Hill et al. (2004) and thus is most abundant on moist soils of average dampness. On the original Central European Ellenberg scale for soil moisture, the species is accorded a slightly higher value of 6, indicating an occurrence also on moist, but not wet, soils (Ellenberg et al., 1991). Similarly, for the Swiss flora, the species has been accorded a value of 3.5 on a five-point moisture indicator scale (Landolt et al., 2010). An extension into slightly wetter habitats

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TABLE 1 Climate means for the European part of the distributional range of *G. sylvaticum*, not including its Siberian range parts (after Vangansbeke et al., 2021).

Climate parameter	Median (mean)	5th percentile	95th percentile
Mean annual temperature (°C)	4.2 (4.0)	−2.0	9.6
Minimum annual temperature (°C)	−0. 1 (−0.1)	−6.0	5.4
Maximum annual temperature (°C)	7.9 (8.0)	2.0	14.9
Annual precipitation (mm)	610 (673)	485	1132

Note: Calculations were based on the distribution of the species between 15° W (Atlantic Ocean) and 60° E (Ural Mountains) and between 25° N (Sahara) and 75° N (Arctic Ocean) (Vangansbeke et al., 2021).

in some continental European habitats may also be indicated by some of the literature. According to Hegedüšová et al. (2012), *G. sylvaticum* is found across Europe in humid areas with long lasting snow cover in winter and rich rainfall in the summer. In the Harz mountains in Germany, the species has been observed on wet soil in small-sedge fens, although plants there were characterised by stunted growth (Harm, 1990). And in the subalpine zone of the Pyrenees, *G. sylvaticum* is indicative of more humid conditions that are more prevalent on their northern side that is more exposed to moisture-bearing winds from the Atlantic Ocean, compared to the southern slopes in the rain shadow of the Pyrenees (Gruber, 1981). A potentially wider realised ecological niche on the continent with respect to moisture may also be indicated by *G. sylvaticum*'s index value of 53–87 on the Russian Ramensky scale (Ramensky et al., 1956; Sugorkina, 1995), indicating a relatively wide range of occurrence, covering both dry and moist grassland and forest and wet grassland.

The species is characteristic of sites exhibiting moderate variability in soil moisture. This has been noted by Sugorkina (1995) for forests in the Moscow region, where locally adapted populations of *G. sylvaticum* displayed the highest vitality when growing under conditions of moderately variable moisture. It is also reflected in an intermediate indicator value of 2 on a three-point scale for alternating moisture for the Swiss flora (Landolt et al., 2010).

On the nine-point Ellenberg scale for soil-reaction, *G. sylvaticum* has been assigned a value of 6 for the floras of Britain and Ireland (Hill et al., 2004) and of Central Europe (Ellenberg et al., 1991), indicating that the species mostly grows on soils ranging between moderately acid and weakly basic (see also Table S1, which lists mean values and value ranges of soil chemical characteristics including pH, both in Britain and Ireland and in other parts of its native distribution range). In British upland hay meadows and lowland grassland mean pH values of about 6 have been reported for plant communities containing *G. sylvaticum* (Critchley et al., 2002; Smith, 1985). At the basic end of its soil-reaction range in Britain and Ireland, Grime and Hutchinson (1967) observed lime chlorosis in the leaves of *G. sylvaticum* plants growing in the calcareous Derbyshire Dales, indicating intolerance of basic soil conditions, and separating this species from the prevailing calcicolous species there. Mild chlorosis of seedlings of *G. sylvaticum* was also observed under experimental conditions when pot-grown and watered daily in a black protorendzina soil obtained from Winnatt's Pass, Derbyshire (pH = 7.2) (Hutchinson, 1967). Throughout its Eurasian distribution range, a wider range of pH values of 3.8–7.5 has been observed at sites supporting populations of *G. sylvaticum* (Table S1). A range almost as wide (pH 4.2–7.1) was found in the western German Eifel mountains, with populations of *G. sylvaticum* occurring both on soils originating from siliceous or calcareous parent materials (Poschlod & Schumacher, 2006). In the siliceous mountain ranges of Central Germany, where acidic soils prevail, grassland supporting *G. sylvaticum* is typically characterised by comparatively low pH values (Hundt, 1964; Waesch, 2006; see also Table S1).

Collecting data on vegetation composition and soil chemistry across 119 Finnish boreal forest sites, Närhi et al. (2011) found that the soil of those sites with *G. sylvaticum* was characterised by relatively low C:N ratio and Al, Pb, S, Ti and Zn concentrations, and relatively high-electrical conductivity, pH and Ca, Co, Mg, Mn, Ni and Sr concentrations, compared to soil from those sites from which the species was absent. Soil pH in their study ranged from 3.8 to 6.3, and Al concentrations ranged from 77 to 5050 mg Al per kg of soil. As indicated by projection of all soil variables in multivariate ordination space, soil pH and Al concentrations were negatively correlated with each other, suggesting that observed correlations between the occurrence of *G. sylvaticum* and various chemical element concentrations may have at least partly been driven by increasing aluminium toxicity with decreasing soil pH (Jarvis, 1986).

On the nine-point Ellenberg nitrogen scale, the recalibrated value of 5 for *G. sylvaticum* assigned by Hill et al. (2004) for Britain and Ireland differs by two units from the original value of 7 for Central Europe (Ellenberg et al., 1991). Ellenberg nitrogen values are now considered indicators of site productivity, rather than of soil nitrogen content or availability (Hill & Carey, 1997; Wagner et al., 2007). The reasons for this difference in two units between different range parts are not obvious. It could simply be due to different methodologies used in the calculation and assignment of nitrogen indicator values. There is also a possibility that this could reflect different climatic realities in different parts of the species' distributional range, which in turn might affect the realised niche of the species in terms of soil fertility. As noted in Section 2.1, the realised climatic niche space occupied by *G. sylvaticum* in Britain and Ireland represents a subset of the space occupied across its Eurasian range, with the species not reaching its cold limits in Britain and Ireland. One possibility is that potential negative effects of unfavourable climatic conditions on the persistence of *G. sylvaticum* could be alleviated by high-nutrient availability. Alternatively, higher nutrient availability may result in the competitive exclusion of *G. sylvaticum* when climatic conditions are particularly favourable, but not so much when they

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are unfavourable. Both these potential mechanisms could explain how occupation of climatically less favourable habitat in the Central European part of the species range could have simultaneously resulted in an overall tendency to occur in somewhat more fertile habitats in this part. In line with such a possibility of interacting realised niche dimensions, observations made in northern Norway indicate that under the climatically unfavourable conditions prevailing above the treeline, the occurrence of *G. sylvaticum* appears to be limited to nutrient-rich microhabitats (Jon Moen, pers. comm.).

In the Bavarian Alps, a part of the Northern Limestone Alps, *G. sylvaticum* is a positive indicator species for 'folic histosols' (Olleck et al., 2020), soils occurring mostly at montane and subalpine altitudes and characterised by a >15 cm thick organic soil layer (O horizon) directly overlaying poorly weathered bedrock (C horizon), with mineral (A and B) soil horizons absent. The finding suggests that under the conditions prevailing at such altitudes, *G. sylvaticum* has a requirement for a sufficiently developed humus layer. Such an interpretation is also in line with the observations made in northern Norway (Jon Moen, pers. comm.; see also Section 4).

3 | COMMUNITIES

3.1 | Britain and Ireland

In Britain and Ireland, *G. sylvaticum* is found in a range of grazed and ungrazed plant communities in upland hay meadows, road verges (Figure 4), riverbanks, fens and mires, mountain rock ledges, crags and ravines and within the field layer of upland mixed ash forests. It generally prefers more open vegetation but is somewhat shade tolerant (see Section 5.2). As a 'mesophilic species from stream-banks and woodland' (Smith, 1911: 317), *G. sylvaticum* did likely spread from such primary natural habitats into secondary semi-natural habitats such as managed grassland, after these had been created through woodland clearance.

The large number of habitats in which *G. sylvaticum* occurs is reflected in the number of National Vegetation Classification (NVC) communities in which the species is found (Table 2). It is one of the constant species in the typical mesotrophic MG3 *Anthoxanthum odoratum*-*Geranium sylvaticum* upland hay meadow NVC grassland community. MG3 grassland has frequent grasses combined with abundant broad-leaved herbs. The abundance of *G. sylvaticum* can be used as an indicator for species-rich upland hay meadow habitat and the species can occasionally account for 90% cover (Rodwell, 1992; Starr-Keddle, 2022). The *Bromus hordeaceus* subsp. *hordeaceus* subcommunity (MG3a) is the least species-rich MG subcommunity, with greater grass abundance and isolated patches of *G. sylvaticum* (O'Reilly, 2011). The *Briza media* subcommunity (MG3b) is the most species-rich, having an average of 35 species per 4 m^2. This community is found on sites characterised by long management continuity and contains other northern-montane species such as *Cirsium heterophyllum* and *Trollius europaeus* alongside *G. sylvaticum* (O'Reilly, 2011; Rodwell, 1992). The *Arrhenatherum elatius* subcommunity (MG3c) occurs in unmanaged areas such as steep banks, road verges and riverbanks, with a coarser sward of tussocky grasses alongside *G. sylvaticum* and *Geranium pratense*

FIGURE 4 *Geranium sylvaticum* in some common habitats in northern England. Top: On a road verge near Raisbeck, Cumbria, UK (photo: Richard Jefferson; centre: Along the edge of upland hay meadow in Teesdale, UK (photo: Ruth Starr-Keddle); bottom: In a species-rich bank in Lunedale, North Pennines, UK (photo: Ruth Starr-Keddle).

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TABLE 2 NVC plant communities in which *Geranium sylvaticum* has been observed in Britain and Ireland and their relationship to European vegetation classifications (JNCC, 2008; Rodwell, 1991a, 1991b, 1992; Strachan, 2017; *Jeanette Hall, pers. comm.).

NVC community code	NVC community name	UK BAP priority habitat	EUNIS type	Annex I
Mesotrophic grasslands				
MG2	*Arrhenatherum elatius*—*Filipendula ulmaria* tall-herb grassland	Lowland meadow	E2.21 Atlantic hay meadows	None
MG3	*Anthoxanthum odoratum*—*Geranium sylvaticum* grassland	Upland hay meadow	E2.3 Mountain hay meadow	6520 Mountain hay meadows
MG8	*Cynosurus cristatus*—*Caltha palustris grassland*	Upland hay meadow	E2.2 Low and medium altitude hay meadow; E3.4b moist or wet mesotrophic pasture; E2.3 mountain hay meadow	6520 Mountain hay meadows
Calcicolous grasslands				
CG14	*Dryas octopetala*—*Silene acaulis* ledge community	Upland calcareous grassland	E4.4 Calcareous alpine and subalpine grassland	H6170 Alpine and subalpine calcareous grasslands
Calcifugous grasslands and montane communities				
U4	*Festuca ovina*—*Agrostis capillaris*—*Galium saxatile* grassland	Upland dry acid grassland	E1.7a Lowland to submontane *Nardus* grassland	H6230 Species-rich Nardus grasslands, on silicious substrates in mountain areas (and submountain areas in continental Europe)
U16	*Luzula sylvatica*—*Vaccinium myrtillus* tall-herb community	Inland rock outcrop and scree habitats	E5.5 Subalpine moist or wet tall-herb and fern stands	None
U17	*Luzula sylvatica*—*Geum rivale* tall-herb community	Inland-rock outcrop and scree habitats	E5.5 Subalpine moist or wet tall-herb and fern stands	H6430 Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels
Fen meadows				
M26	*Molinia caerulea*—*Crepis paludosa fen meadow*	Purple moor grass and rush pasture	E3.5 Moist or wet ologotrophic grassland	H6410 Molinia meadows on calcareous, peaty pr clayey-silt laden soils
M27	*Filipendula ulmaria*—*Angelica sylvestris* fen meadow	Lowland fen	E5.42 Tall-herb communities in humid meadows	None
Woodlands				
W7*	*Alnus glutinosa*—*Fraxinus excelsior*—*Lysimachia nemorum* woodland	Wet woodland	G1.21 Riverine *Fraxinus*—*Alnus* woodland, wet at high but not at low water	H91E0 Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incnae, Salicion albae)
W9	*Fraxinus excelsior*—*Sorbus aucuparia*—*Mercurialis perennis* woodland	Upland mixed ash woodland	G1.A Woodland with chestnut, hornbeam, lime or rowan; G1.B mixed deciduous woodland	H9180 Tilio-Acerion forests of slopes, screes and ravines
W19*	*Juniperus communis* ssp. *communis*—*Oxalis acetosella* woodland	Upland heathland	F3.16 *Juniperus communis* scrub	H5130 *Juniperus communis* formations on heaths or calcareous grasslands

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(O'Reilly, 2011; Rodwell, 1992), with the two *Geranium* species potentially co-occurring where their ranges overlap (see Section 1). Where MG3 meadows have been neglected, ploughed or re-seeded, or had inorganic fertiliser applied, the meadows transition to the *Lolium perenne-Cynosurus cristatus* community (MG6) (Rodwell et al., 2000). *Geranium sylvaticum* can be found occasionally in MG6 meadows; however, it is more likely that the MG3 indicator species such as *G. sylvaticum*, *Sanguisorba officinalis* and *C. heterophyllum* are found around the field edges, suggesting that the flower-rich vegetation of *Rhinanthus minor*, *Euphrasia* spp. and *Trifolium pratense* in the main sward is an impoverished type of historically present MG3 grassland (O'Reilly, 2011; Rodwell et al., 2000). In Northern Ireland, where *G. sylvaticum* occurs very sparsely (see Section 1), it has been recorded in one hay meadow in County Antrim, with the sward composition aligning more closely to the lowland *Cynosurus cristatus-Centaurea nigra* (MG5) hay meadow community (Rodwell et al., 2007). In the North Pennines, there are occasionally transitions from drier MG3 meadows to species-rich, wet *Cynosurus cristatus-Caltha palustris* (MG8) grasslands (O'Reilly, 2011; Rodwell et al., 2000). There, *G. sylvaticum* can also be found at low frequencies in MG8 meadows, especially in the uncut banks of wet meadows (Ruth Starr-Keddle unpublished data). While such occurrences are not reflected in the floristic table describing MG8 grassland in Rodwell (1992), this has subsequently been acknowledged in the description of four additional MG8 subcommunities by O'Reilly (2011), all of which can contain *G. sylvaticum*, including as occasional in the species-rich subcommunity MG8n. In contrast, no reference to *G. sylvaticum* can be found in the description of MG8 subcommunities devised by Wallace and Prosser (2017).

Historically, MG3 hay meadows are likely to have originated from *Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis* (W9) upland mixed ash woodland after clearance of the woody vegetation and establishment of an annual hay cut (Pigott, 1956). W9 communities are found on calcareous moist soils on undulating, exposed situations in the upland fringes and highlands of northwest Britain. The community ranges from well-developed high-forest canopies to scrubby woodland with only a few scattered trees. The understorey has prominent ferns, bryophytes and grasses, with a variable ground flora. In the typical subcommunity (W9a) which is often grazed, *G. sylvaticum* is found rarely, whereas in the typically ungrazed species-rich *Crepis paludosa* subcommunity (W9b), *G. sylvaticum* and other taller northern-montane forbs are found more frequently (see also Section 4 on grazing). Transitions between the two subcommunities are related to steepness, which in turn affects grazing pressure, with flushing also thought to contribute to the distinctive character of the *Crepis paludosa* subcommunity. Thus, both substrate instability and increased soil moisture may jointly prevent development of a denser tree cover in this subcommunity and facilitate tall forbs including *G. sylvaticum* (Rodwell, 1991a). Fragments of ancient woodland are found in Upper Teesdale, where relics occur by cliffs next to the river Tees, with an understorey of species characteristic for MG3 grassland (Bradshaw, 2018). There is also a remarkable resemblance between MG3 upland hay meadows and the ‘Park meadows’ of Scandinavia that are found in clearings in the herb-rich, open birch and spruce woodlands (Gamble & St. Pierre, 2010; Moen & Oksanen, 1998; Pigott, 1956). Another NVC mesotrophic grassland community in which *G. sylvaticum* can be found is MG2 *Arrhenatherum elatius-Filipendula ulmaria* grassland (Rodwell, 1992). Other NVC woodland communities in which *G. sylvaticum* is at least occasionally encountered include W7 (*Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum* woodland) and W19 (*Juniperus communis* ssp. *communis-Oxalis acetosella* woodland) (Jeanette Hall, pers. comm.).

Geranium sylvaticum has also been found to colonise NVC communities typical of other habitat types, particularly where the more typical communities containing *G. sylvaticum* transition into other communities. For example, although *G. sylvaticum* is not officially listed in the original floristic table for *Filipendula ulmaria-Angelica sylvestris* (M27) mire vegetation, a species-poor tall-herb fen vegetation (Rodwell, 1991b), in Scotland it is found in ranker stands of MG3c grassland with frequent *F. ulmaria*, which can transition to M27 tall-herb fen (see e.g. Williams, 2008). To reflect this, where frequent *G. sylvaticum*, *C. heterophllum*, *C. majus*, *Meum athamanticum* and *T. europaeus* co-occur, a new subcommunity of M27 should be recognised (Rodwell et al., 2000).

Similarly, although not listed in the table for M26 mire vegetation in the original NVC (Rodwell, 1991b), in Upper Teesdale, *G. sylvaticum* is found in low frequencies in mire vegetation within the edges and banks of meadows that is transitional between this community and MG3b grassland, growing alongside other northern-montane species (O'Reilly, 2011). This is also reflected in Pigott's (1956) description of a ‘turfy marsh’ dominated by *Molinia caerulea*, with swampy patches occupied by clumps of *T. europeaus* and *G. sylvaticum* in a pasture grazed by cattle.

Furthermore, although *G. sylvaticum* is not listed in the floristic tables for *Festuca ovina-Agrostis capillaris-Galium saxatile* (U4) species-rich acid grassland in Rodwell (1992), there are examples of species-rich *Lathyrus montanus-Stachys betonica* (U4c) found on the banks of MG3b meadows with occasional *G. sylvaticum*, plus *Viola lutea* and *Lathyrus linifolius* (O'Reilly, 2011). In western Scotland, there is a distinctive form of this grassland with an abundance of tall forbs such as *G. sylvaticum*, *F. ulmaria*, *C. heterophyllum* and *A. sylvestris*. The intensity of grazing varies, but where it is heavier, these tall herbs are mostly reduced to short, non-flowering plants (Rodwell et al., 2000). This vegetation prepresents a potentially new subcommunity of U4, found on steep, moist but well-drained north-facing slopes (Rodwell et al., 2000).

In addition to the plant communities already mentioned, *G. sylvaticum* is found in several tall-herb communities on inaccessible rock ledges, gullies, crags and ravines in the cold, wet uplands of northwest Britain which are protected from grazing and burning. These typically occur on more sheltered ledges with deeper soil, allowing the assembly of such tall-herb communities (Ratcliffe, 1960; Smith, 1911). The *Luzula sylvatica-Vaccinium myrtillus* (U16) tall-herb community is dominated by *Luzula sylvatica*, frequent *Vaccinium myrtillus* and occasional willow scrub and saplings. *Geranium*

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sylvaticum is scarce but occasionally found in the *Dryopteris dilatata-Dicranum majus* (U16a) subcommunity. The *Luzula sylvatica-Geum rivale* (U17) tall-herb community is predominantly found in the Scottish Highlands, where it occurs in the subalpine zone with moderate snow cover, on open cliff tops and summits of mountains. However, there are also stands of U17a in Cumbria and in North Wales (Averis et al., 2004). *Geranium sylvaticum* is particularly characteristic of the *Geranium* subcommunity (U17b), with species such as *T. europaeus*, *Heracleum sphondylium* and *Alchemilla glabra*. U17b communities are restricted to the Grampians on the steepest and most inaccessible ledges, which is comparable to the subalpine and low-alpine tall-herb communities of northern Europe (Table 2). The *Dryas octopetala-Silene acaulis* (CG14) ledge community comprises luxuriant mixtures of dwarf shrubs, arctic willows, tall herbs such as *G. sylvaticum*, sedges and grasses among a carpet of small arctic-alpines and bryophytes. This fragmented community is confined to calcareous crags, ledges and rocky outcrops, mostly in the high-altitude montane regions of Scotland. Often there is the percolation of calcareous water over the soils. There are a few small examples of this community found on Helvellyn in the Lake District. There can be a transition to grazed calcicolous vegetation where the topography becomes smoother and the vegetation changes to habitats represented by arctic-alpines tolerant of grazing. These habitats share several characteristic northern-montane species of MG3b, MG3c and M26 upland communities (Rodwell, 1992).

Geranium sylvaticum also occurs on both wooded and open limestone pavements in the North Yorkshire Dales (Stevens, 2023, 2025; Ward & Evans, 1976; Willis, 2011), but very likely not elsewhere in Great Britain (Stevens, 2023, 2025; Ward & Evans, 1976). Limestone pavement is a complex of habitats, and as such does not easily fit within the NVC system (Rodwell et al., 2000). Using plant species presence data from 30 limestone pavements containing *G. sylvaticum* (Stevens, 2023), including 17 from Ward and Evans' (1976) original 1972–1975 survey and 13 from Stevens' 2017–2022 repeat survey, we tentatively NVC-matched these 30 sampling units using RMAVIS version 1.1.4 (Marshall et al., 2024). As expected, similarities with NVC communities were generally low, ranging from 0.10 to 0.16 even for the top matching NVC communities. These included the already discussed MG2 grassland (25 of the 30 analysed pavements were top matched with MG2 and its subtypes) and W9 woodland (2 samples) but also OV38 (*Gymnocarpium robertianum—Arrhenatherum elatius* fern vegetation) and CG9 (*Sesleria albicans—Galium sterneri* grassland) (one sample each). For one sample, the analysis returned CG8 grassland as the top matching NVC community, but this is exclusively a community of the Durham Magnesian limestone (Rodwell, 1992), where there are no limestone pavements. As already noted, similarities with NVC communities were generally quite low, so this analysis should be more considered to identify top affinities with various NVC communities, rather than a formal classification of limestone pavement vegetation in line with the NVC. Nonetheless, W9, OV38 and CG9 have all been listed by Rodwell et al. (2000) as typically associated with limestone pavement vegetation elements, with the field layer of W9 woodland vegetation essentially found in deeper grikes (i.e. natural cracks), OV38 found in shallower grikes, and CG9 found in shallow soil-filled grikes. And in the case of MG2 grassland, an affinity of limestone pavement vegetation to such grassland was previously identified by one of us based on personal experience of the habitat and examination of the floristic table and description of this community in Rodwell (1992; Richard Jefferson, personal observation).

Across the full range of NVC communities in which *Geranium sylvaticum* is known to occur, the species is commonly associated with the grasses *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Agrostis capillaris*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Festuca rubra*, *Poa pratensis* and *Holcus lanatus* and the broadleaf herbs *Alchemilla* spp., *Cirsium heterophylum*, *Conopodium majus*, *Filipendula ulmaria*, *Sanguisorba officinalis*, *Trolllius europaeus*, *Anthriscus sylvestris*, *Rhinanthus minor*, *Euphrasia* spp., *Trifolium pratense*, *Silene flos-cuculi*, *Crepis paludosa*, *Succisa pratensis*, *Veronica officinalis*, *Ranunculus acris* and *Leontodon hispidus* (O'Reilly, 2010, 2011; Rodwell, 1991a; Rodwell, 1991b; Rodwell, 1992; Rodwell et al., 2000). In upland hay meadows in the Yorkshire Dales National Park, Chi-squared association analysis based on a sample of 1 m × 1 m survey quadrats revealed that in this habitat, *G. sylvaticum* was positively associated with *Alchemilla glabra*, *Conopodium majus*, *Poa trivialis* and *Ficaria verna* (Pacha & Petit, 2008).

3.2 | Eurasian range

Across its Eurasian range, *Geranium sylvaticum* occurs in a wide range of plant communities across a range of vegetation types. These are summarised in Table S2. There is a very large literature on the various vegetation types with which *G. sylvaticum* is associated in Eurasia and Table S2 gives the sources of information providing more detailed information on specific plant communities.

To provide a general synthesis, where possible, the phytosociological units in which *G. sylvaticum* has been recorded have been cross-referenced to the overarching hierarchical floristic classification of Mucina et al. (2016). This classification has been instructive in compiling the following more detailed descriptions of the broad vegetation types.

3.2.1 | Forests, woodland and wood pasture

Boreal and hemiboreal forests

In the northern part of its Eurasian range, *G. sylvaticum* is a frequent component of the field layer of boreal and hemiboreal forests that are sometimes referred to collectively as western taiga (European Commission, 2013). These forests may be coniferous, deciduous or mixed. Typical canopy species include conifers, *Pinus sylvestris*, *Picea abies*, *Picea obovata*, *Larix sibirica* and *Abies sibirica*, and broad-leaved trees, *Populus tremula*, *Betula* spp. and *Sorbus aucuparia*. Typical species of the shrub layer include *Betula nana*, *Salix* spp. and *Juniperus communis*. The ground flora associates of *G. sylvaticum* and the

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species richness of the vegetation vary according to canopy dominants and soil type. In many cases, dwarf shrubs including *Vaccinium* spp., *Calluna vulgaris* and *Empetrum nigrum* are dominant. Other common associates include herbaceous vascular plant species such as *Convallaria majalis*, *Anemone nemorosa*, *Maianthemum bifolium*, *Oxalis acetosella*, *Lysimachia europaea*, *Melampyrum sylvaticum*, *Rubus saxatilis*, *Rubus chamaemorus*, *Saussurea alpina*, *Deschampsia flexuosa* and *Aconitum septentrionale*, the mosses *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum* spp. *and* lichens of the genus *Cladonia*. Bryophytes and lichens are often abundant.

Boreal and hemiboreal (Fennoscandian) wood pastures

Geranium sylvaticum can occur in lightly grazed, wooded grassland pastures (European Commission, 2013; Oldén, 2016). This is a vegetation mosaic in which the tree layer varies from sparse forest to small copses of trees and shrubs and patches of open grassland maintained by a long historical continuity of grazing. The tree layer consists of deciduous broad-leaved species such as *Quercus robur*, *Fraxinus excelsior*, *Tilia cordata*, *Betula* spp., *Populus tremula*, *Corylus avellana*, *Alnus incana* and conifers (principally *Picea abies*, *Pinus sylvestris*) or a mixture. In wooded pastures, the vegetation is dominated by grassland species such as the grasses *Agrostis capillaris*, *Anthoxanthum odoratum*, *Festuca ovina* and broadleaf species including *Antennaria dioica*, *Botrychium* spp., *Campanula persicifolia*, *Dactylorhiza viridis*, *Fragaria vesca*, *Prunella vulgaris*, *Ranunculus polyanthemos*, *Succisa pratensis*, *Veronica chamaedrys* and *V. officinalis*.

3.2.2 | Temperate zone and azonal forests

Pine forest on calcareous soils—Alvar forest

In the Baltic Sea islands of Sweden and Estonia in the nemoral zone, *G. sylvaticum* is a common component of the field layer flora of forest dominated by *Pinus sylvestris* on calcareous rendzina soils (Paal et al., 2015, 2017).

Alluvial and riparian forest

Geranium sylvaticum has been recorded from alluvial and riparian forests of the class Alno glutinosae-Populetea albae P. Fukarek et Fabijanic 1968 across its Eurasian range (Pielech, 2015; Smirnova, Bobrovsky, Khanina, Zaugolnova, Shirokov, et al., 2017). This vegetation usually occurs on nutrient-rich soils in riparian situations from the lowlands to the mountains. Typical canopy species are *Alnus glutinosa*, *A. incana*, *Salix fragilis* and *Fraxinus excelsior*.

In Poland, alluvial forest of the Alnetum incanae Lüdi 1921 association occurs at altitudes of 450–670 m along medium and large mountain rivers. Species of mountain tall-herb communities are the most characteristic part of the field layer, including *G. sylvaticum* which is diagnostic for this plant community (Pielech, 2015). Similarly, *G. sylvaticum* occurs as a dominant in the field layer on steep slopes of river valleys and ravines in European Russia. However, Mucina et al. (2016) suggest this forest type might be better placed in the Carpino-Fagetea, especially in central and northern Europe.

Mesic deciduous and mixed forests of temperate Eurasia

Geranium sylvaticum has been recorded from the field layer of a variety of deciduous and mixed forests on mesic or basic soils within temperate Europe and Asia including the montane belt of the sub-Mediterranean region. These forests fall within the class Carpino-Fagetea sylvaticae Jakucs ex Passarge 1968. The forests include *Quercus* and *Carpinus* forests (Novák et al., 2023), *Fagus sylvatica*-*Abies alba* forest and mixed montane forest communities such as in the Carpathians (Ujházyová et al., 2021) and the eastern Austrian Alps (Kerschbaumer & Kurz, 2021), subalpine beech forest in the Slovenian Alps (Polysticho lonchitis-Fagetum association) (Dakskobler & Rozman, 2021). In addition, in the nemoral zone in northwest Russia and, extending eastwards to the southern Urals, broad-leaved and mixed forests with *Quercus robur*, *Tilia cordata*, *Ulmus glabra* and *Pinus sylvestris* on deep-nutrient soils may support *G. sylvaticum* (Smirnova, Bobrovsky, Khanina, Braslavskay, et al., 2017). *Geranium sylvaticum* also occurs in the field layer of thermophilous *Acer*-*Tilia* forests (alliance Tilio-Acerion Klika 1955) on scree slopes, for example, in northern Spain (Zukal & Biurrun, 2022) and in beech forest with *Quercus* spp. in Denmark (Lawesson et al., 1998). In the cool-temperate regions of European Russia, *G. sylvaticum* is frequent in the field layer of two mesophytic oak forest alliances—the Lathyro pisiformis-Quercion roboris Solomeshch et Grigoriev in Willner et al. (2016) which occurs on fertile dark grey soils (Kozhevnikova & Prokhorov, 2021) and the Lathyro nigri–Quercetum roboris Bulokhov et Solomeshch 2003 (Semenishchenkov, 2017).

These alliances fall within the Quercetea pubescentis Doing-Kraft ex Scamoni et Passarge 1959, a separate class of cool-temperate *Quercus* spp., mixed deciduous and conifer forest.

Montane and subalpine conifer forests

Geranium sylvaticum is diagnostic for vegetation that falls within the broad category of montane calcareous relict pine forests such as the *Pinus cembra* forests in the Italian Alps (Pinetum cembrae Bojko 1931) (Sburlino et al., 2006) and forests of the class Erico-Pinetea (Carici albae–Pinetum sylvestris association) in the Caucasus (Ermakov et al., 2020). *Geranium sylvaticum* also occurs in *Picea abies*-*Larix decidua* forests in the Austrian Alps (Exner et al., 2002; Morton, 1927) (Adenostylo glabrae-Piceetum Zukrigl 1973) (Willner & Zukrigl, 1999), and in *Pinus peuce* forests on nutrient-poor soils over limestone in North Macedonia (Mandžukovski et al., 2022).

3.2.3 | Scrub

Geranium sylvaticum occurs as a characteristic species of species-rich subalpine, subarctic, boreo-alpine willow and alder scrub and birch krummholz (stunted, deformed shrubs and trees shaped by continual exposure to strong, freezing winds) across its Holarctic range, including in the Alps, the Carpathians, the Urals, the Balkans, the Caucasus and other associated massifs and, more generally in Northern Europe and Greenland. Typical willow species include *Salix*

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lapponum, *S. lanata*, *S. arbuscula* and *S. myrsinites*. Associated herbs may include *Potentilla crantzii*, *Bartsia alpina*, *Geum rivale*, *Cirsium heterophyllum* and *Angelica archangelica*.

Geranium sylvaticum also occurs in willow scrub on riverbanks with alluvial loamy-sandy soils in the lowland to submontane nemoral and continental belts of Europe such as in the Hercynian mountains of Germany where *Salix viminalis* and *Salix triandra* are the dominant willow species (Passarge, 1981, 1986).

Geranium sylvaticum is a differential species for the Sorbo chamaemespili-Pinetum mugo association (Poldini et al., 2004). This belongs to the Erico-Pinion mugo Leibundgut 1948 alliance, a subalpine calcareous pine krummholz (or pine scrub), sometimes considered as forest, of the Central and Eastern Alps and Carpathains (Mucina et al., 2016). The vegetation consists of a mix of acidophilous and calcicolous species over sediment-covered limestone.

3.2.4 | Dwarf shrub heaths

Geranium sylvaticum occurs in heaths of the boreal zone, often at low altitudes, and in the alpine and subalpine zones of the mountains of Eurasia. These heaths are dwarf or prostrate shrub formations dominated by ericaceous species (*Calluna vulgaris*, *Vaccinium* spp., *Erica* spp., *Empetrum* spp., *Arctostaphylos* spp., *Rhododendron* spp.) along with *Genista* and *Ulex* species. Most heath types occur on acidic siliceous substrates, but a few types occur on calcareous skeletal soils such as in the Alps, the Apennines (Italy) and the Dinaric Alps. As mentioned in Section 2.2, *G. sylvaticum* is found both on siliceous soils and on calcareous soils; however, during our literature search, we were unable to identify any occurrences of *G. sylvaticum* in heath on calcareous skeletal soils.

The heaths fall within two main phytosociological classes—Calluno-Ulicetea Br.-Bl. et Tx. ex Klika et Hadac 1944 (at lower altitudes) and Loiseleurio procumbentis-Vaccinietea Eggler ex Schubert 1960.

Of the former, in the French Massif Central, *G. sylvaticum* occurs in heathland of the suballiance Vaccinienion myrtillo-uliginosi subass. nov. hoc loco on volcanic soils which are not strongly oligotrophic (Thébaud et al., 2021). This type of heathland is dominated by *Vaccinium myrtillus* and *V. uliginosum* together with many herbaceous species, including chionophilic (i.e. cold-adapted) species and species more typical of mesotrophic soils. Characteristic species include *Euphorbia hyberna*, *Campanula scheuchzeri*, *Lilium martagon*, *Persicaria bistorta*, *Meum athamanticum*, *Poa chaixii* and *Hypericum maculatum*.

In mountain tundra in the Caucasus, *G. sylvaticum* occurs in a subalpine silicicolous low *Juniperus communis* community on siliceous soils (Aconito nasuti-Juniperion communis) and a *Rhododendron*-dominated ericaceous low scrub (Vaccinio myrtilli-Rhododendrion caucasici Vural 1996 nom. Dubium) (Onipchenko, 2002), both of which are communities within the class Loiseleurio procumbentis-Vaccinietea Eggler ex Schubert 1960.

3.2.5 | Wetlands

As described in Section 2.2, while being a moist-site indicator, occurring mainly on fresh soils of average dampness, *G. sylvaticum* is occasionally a component of certain types of wetland vegetation across its range. It can occur particularly in the drier parts of meso-eutrophic fens, fen-grassland ecotones and transition mires in the temperate, boreal and arctic zones in northern Europe, especially Scandinavia and Asia and in the Caucasus. Such vegetation is rich in sedges and rushes, mosses (especially *Sphagnum* species), dwarf shrubs such as *Calluna vulgaris* and the grass *Molinia caerulea*. The vegetation falls within the alliance Scheuchzerio palustris-Caricetea fuscae Tx. 1937 (Laitinen et al., 2021; Mucina et al., 2016).

Geranium sylvaticum may also occur sporadically in freshwater springs in shady forest habitats in submontane and montane areas of Central Europe such as in Poland (Svobodová, 2021) and Switzerland (Seiler et al., 2021). This vegetation falls within the Montio-Cardaminetea Br.-Bl. et Tx. ex Klika et Hadac 1944, an alliance covering European freshwater spring vegetation (Mucina et al., 2016).

3.2.6 | Open and ruderal habitats

There are references in the literature to the sporadic occurrence of *G. sylvaticum* on scree or talus slopes and stone mounds in the Caucasus and in central Europe (Onipchenko, 2002; Wangerin, 1926). *Geranium sylvaticum* is generally rare or absent from nitrophilic anthropogenically disturbed or ruderal vegetation. However, it has been documented as occurring in semi-ruderal tall-herb nitrophilous vegetation of disturbed forest margins and clearings on neutral soils in the Czech Republic (Kopecký, 1974). This vegetation belongs to the Aegopodion podagrariae Tx. 1967 nom. conserv. propos. alliance (Mucina et al., 2016). This vegetation is typically dominated by tall herbs such as *Anthriscus sylvestris*, *Urtica dioica*, *Dipsacus pilosus* and *Chaerophyllum aromaticum*.

3.2.7 | Tall-herb vegetation

Across its Eurasian range, *G. sylvaticum* is a constant species of certain types of hydrophilous tall-herb communities. These tall-herb communities can occur from sea level to montane areas of the boreal, temperate and sub-Mediterranean regions of Eurasia. The moist, usually eutrophic soils range from moderately acidic to calcareous. The tall-herb communities fall within the class Mulgedio-Aconitetea Hadac et in Klika et Hadac 1944 (Mucina et al., 2016). The vegetation is typically species-rich and supports a wide range of tall herbaceous species such as *Aconitum napellum*, *Adenostyles alliariae*, *Cicerbita alpina*, *Cirsium heterophyllum*, *Filipendula ulmaria*, *Geum rivale* and *Rumex alpinus*, and grasses such as *Calamagrostis arundinacea* and *Deschampsia cespitosa*.

As in the North Yorkshire Dales (Section 3.1), *G. sylvaticum* is also found in limestone pavement in south-eastern France (Gaudillat, 2008), where the species is found in stands of tall-herb vegetation.

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3.2.8 | Semi-natural grassland

Geranium sylvaticum occurs in a range of semi-natural grassland types across its Eurasian range. It is strongly associated with neutral grasslands of the class Molino-Arrhenatheretea and particularly with montane and supramontane meadows of the alliance Triseto flavescentis-Polygonion bistortae Br.-Bl. et Tx. Ex Marschall 1947 (mountain hay meadow; short: Triseto-Polygonion) on fertile mineral-rich soils, also referred to in the literature synonymously as Polygono bistortae-Trisetion flavescentis (or short: Polygono-Trisetion), that is with the order of the two eponymous species of the alliance inverted (Mucina et al., 2016). These Triseto-Polygonion meadows have clear affinities to MG grassland in Britain (Rodwell, 1992). Typical associates include *Trisetum flavescens*, *Cirsium heteropyllum*, *Persicaria bistorta*, *Meum athamanticum*, *Phyteuma* spp., *Sanguisorba officinalis* and *T. europaeus*.

It can also occur in meadows at lower altitudes in parts of its range, for example in species-rich mesotrophic wet meadows on mineral soils of the Calthion palustris Tx. 1937 (e.g. Raehse, 2001) that occur in sub-oceanic western and subcontinental central Europe. In the forest-steppe landscapes of the plains of western and central Siberia, *G. sylvaticum* is a component of moist mesophytic meadows often on rarely flooded river terraces. These temperate continental forest-steppe meadows belong to the order Carici macrourae-Crepidetalia sibiricae (Ermakov & Maltseva, 1999; Korolyuk & Tishchenko, 2020; Korolyuk et al., 2016; Lashchinskiy et al., 2014; Tishchenko, 2017, 2022; Tishchenko & Korolyuk, 2020). The meadows result from the anthropogenic clearance of hemiboreal forests followed by mowing and grazing (Ermakov & Maltseva, 1999). Differential species include widespread forest herbaceous species including *Aegopodium podagraria*, *Crepis sibirica*, *Hieracium umbellatum*, *Lilium pilosiusculum* and *Pulmonaria mollis*.

Alpine and subalpine calcareous grasslands of the European mountain ranges within the class Elyno-Seslerietea Br.-Bl. 1948 in the synthesis of Mucina et al. (2016) may also support *G. sylvaticum*. In the Carpathian Mountains in Romania, *G. sylvaticum* is a diagnostic species of the Seslerio rigidae-Festucetum carpaticae association. This subxeric plant community occurs on shallow soils atop basic rock formations, at elevations between 1400 and 1600 m where snow often persists. Associated species include *Festuca carpatica*, *Sesleria tatrae*, *Swertia alpestris* and *Primula carpatica* (Bělohlávková & Fišerová, 1989). In the Austrian Alps, *G. sylvaticum* occurs on supramontane to alpine calcicolous meso-hygrophilous sedge swards of the Caricion ferrugineae G. Br.-Bl. et Br.-Bl. in G. Br.-Bl. 1931 (Grabner, 1997).

4 | RESPONSE TO BIOTIC FACTORS

4.1 | Biotic effects of fertiliser application

Geranium sylvaticum is a competitive–stress tolerant–ruderal (CSR) strategist (Pierce et al., 2017). Accordingly, in semi-natural agricultural grassland, at least to an extent, *G. sylvaticum* can often successfully cope with the effects of fertiliser or manure application, particularly with the associated potential increase in competition for light resulting from increasing aboveground biomass production. Such an outcome is supported by both experimental and observational studies.

A 5-year management trial in montane meadows in the Swiss Alps found that application of either 75 kg or 150 kg mineral fertiliser N per hectare per year did not cause a reduction in the relative contribution of *G. sylvaticum* to total standing biomass, compared to a control treatment without N fertilisation (Thomet et al., 1989). And a 7-year experiment in a montane meadow in the Belgian Ardennes found that annual application of composted manure resulted in higher *G. sylvaticum* cover, compared to that found in an unfertilised control treatment (Luxen et al., 2008). Furthermore, two observational studies carried out in the Alps found higher occurrence of *G. sylvaticum* following an increase in fertiliser use with management intensification. In the Swiss Alps, frequency of occurrence of *G. sylvaticum* within studied regions and its abundance within swards as determined by quadrat and yield fraction methods were higher in resurveys of sites previously surveyed 17 to 29 years earlier, not just in nutrient-poor semi-natural grassland (Peter et al., 2009), but also in fertile permanent grassland (Peter et al., 2008). These increases were attributed to increased fertiliser use with management intensification (Peter et al., 2008, 2009). Another study, investigating land use transitions in the central French Alps (Quétier et al., 2007), found substantial colonisation by *G. sylvaticum* after the introduction of regular farmland manure application on previously unfertilised subalpine hay meadows. In the Alps, *G. sylvaticum* has also been reported from areas within grassland where livestock rest, that are characterised by a high fertility from dung deposition, with the resultant lush vegetation being referred to in German as 'Lägerflur' (Wangerin, 1926).

Less clear results were found in a 12-year two-factorial experiment in grassland in Krkonoše National Park, Czech Republic, that combined fertiliser application versus no fertiliser and management by cutting with removal vs. cutting without removal (i.e. mulching; Pourová et al., 2010). In this study, fertiliser application resulted in an increase in the frequency of *G. sylvaticum* in only one of three experimental replicate blocks. However, in this study, compost was used and was only applied every other year, which would have had only limited effects on nutrient availability compared to a more regular application, for example of manure or artificial fertiliser.

In German montane grassland, Wagner et al. (2007) found that across a fertility gradient ranging from low-yielding species-rich grassland to high-yielding species-poor grassland, covering a gradient of dry standing biomass from 130 to 620 g per m^2 as determined by the beginning of June, *G. sylvaticum* performed best at intermediate levels of productivity, but was absent from the most productive sites. It stands to reason that in grasslands already characterised by rather high-soil fertility, where the sward is already mainly composed of competitive species, *G. sylvaticum* would be negatively affected by fertiliser application.

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4.2 | Hay cutting and livestock grazing

4.2.1 | Grazing versus cutting

Geranium sylvaticum is considered moderately tolerant to mowing, but susceptible to livestock grazing and associated trampling (Dierschke & Briemle, 2002). Accordingly, in a large-scale observational survey in the Swiss Alps, Rudmann-Maurer et al. (2008) found that *G. sylvaticum* performed better in meadows than in pastures. In fertilised grassland, mean *G. sylvaticum* cover was highest (3.8%) in grassland traditionally cut for many years, but lower (1.3%) in grassland where management had shifted from cutting to grazing and lowest (0.7%) in long-term pasture. In unfertilised grassland, mean covers of *G. sylvaticum* of 0.9%, 0.8% and 0.2% in the cut, recently grazed and long-term grazed grassland similarly indicated a preference of cutting over grazing (Rudmann-Maurer et al., 2008). Similarly, in an observational study of dry grassland vegetation in the Russian Middle Urals, *G. sylvaticum* was characteristic of sites predominantly managed by hay cutting with occasional aftermath grazing but absent from more intensively grazed sites (Gorchakovskii & Abramchuk, 1996). An intolerance of *G. sylvaticum* to grazing was also invoked by Losvik (1988) to explain its patterns of occurrence in western Norway's Hordaland region. Its reduced presence there in oceanic districts compared to more continental districts was attributed to suppression by more frequent winter grazing in oceanic districts. A contrasting result was found in a long-term grassland management experiment in southern Sweden, where *G. sylvaticum* was more frequent in grazed plots than in annually cut plots (Wahlman & Milberg, 2002). One reason for this may the that in this study, very low-stocking densities were applied to grazed plots.

Studies investigating livestock diet composition in relation to relative plant species abundance in grazed grassland have found that the relative contribution of *G. sylvaticum* to livestock diet can vary. Svensk (2023) found for Swiss alpine pastures that *G. sylvaticum* was incorporated in the diet of cattle in proportion to its occurrence in the vegetation of feeding places. On the other hand, in wooded meadows in Åland, southwest Finland, examination of the diet of sheep and cattle found that *G. sylvaticum* was either not eaten or only consumed in very small amounts (Haeggström, 1990). In contrast, *G. sylvaticum* is considered preferred forage for reindeer (Warenberg et al., 1997 in Bråthen & Oksanen, 2001). This positive selection of *G. sylvaticum* by reindeer could be due to reindeer typically grazing in harsher environments than the agricultural grasslands in which the food preferences of sheep and cattle had been investigated, with the vegetation made up of less palatable species in reindeer grazing lands.

Given that there appears to be no positive selection of *G. sylvaticum* as a food plant by cattle or sheep, the negative impacts on the species regularly observed in in pasture habitats grazed by such livestock are likely due to factors other than positive grazing selection.

4.2.2 | Management intensity

Cutting frequency

Given its moderate tolerance to cutting, *G. sylvaticum* generally tends to perform better under more relaxed cutting regimes. In a 5-year management experiment in Swiss montane hay meadows, *G. sylvaticum* (Thomet et al., 1989) achieved higher biomass under a traditional regime involving two cuts followed by aftermath grazing, whereas a move to a more intensive cutting regime involving three cuts annually, including an earlier first cut, resulted in lower biomass contribution to the sward (Thomet et al., 1989). *Similarly*, *G. sylvaticum* achieved higher cover in various Central and Northern European grasslands when cutting regimes were relaxed from cutting annually to cutting once every 2 or 3 years (Aune et al., 1996; Dierschke & Peppler-Lisbach, 2009; Toivonen et al., 2013).

Grazing intensity

Given its susceptibility to grazing livestock, as with cutting frequency, a negative correlation can also be expected between intensity of livestock grazing and performance of *G. sylvaticum*. There is some evidence that complete abandonment of grazing management typically, at least initially, results in an increase in performance aspects such as *G. sylvaticum* abundance or cover (Section 'Management abandonment'). Roughly speaking, grazing intensity is a product of several aspects of grazing, notably stocking density during grazing events, as well as duration and frequency of grazing events. Published information on how these aspects individually affect performance of *G. sylvaticum* is scarce. We know of only one experimental study reporting the effects of different pasture stocking densities on *G. sylvaticum*. This experimental study was carried out in southern Norwegian alpine grassland interspersed with shrubs, and compared three treatments, including 'high-density' sheep grazing at a stocking density of 80 sheep per km^2, 'low-density' sheep grazing at 25 sheep per km^2, and an ungrazed control, that were arranged in a randomised block design ($N=3$) (Evju et al., 2006, 2011; Maurset, 2015; Steen et al., 2005). Notably, even the 'high' stocking density in this experiment was low compared to stocking densities typically used in more productive semi-natural grassland elsewhere. After 2 years, a higher mean (±SE) percent relative abundance of *G. sylvaticum* was recorded in plots grazed for approximately 2 months in the summer at low density (9.9% ± 1.6) or at high density (8.1% ± 1.2) than in the ungrazed control (5.1% ± 0.6) (Steen et al., 2005). In the second and third year, with increasing stocking density, a higher proportion of *G. sylvaticum* plants were grazed, but neither plant height nor flowering frequency was significantly affected (Evju et al., 2006). Based on a 6-year dataset, the relatively low-grazing pressure in both grazed treatments was sufficient to reduce *G. sylvaticum* growth compared to the ungrazed treatment, but stimulated the rate of new shoot formation, with shoot survival and flowering rates unaffected (Evju et al., 2011). Since *G. sylvaticum* can regenerate from buried rhizome fragments with substantial reserve stores (Sections 6.1 and 6.5) that can be quickly mobilised, this might give plants a certain tolerance to grazing (Hellström et al., 2006; Rodwell, 1992, 2015). Observations

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from this Norwegian study align with studies of *G. sylvaticum* shoot survival and new shoot production following grazing by voles in greenhouse experiments involving excavated turf from boreal forest floors (Ericson & Oksanen, 1987; Moen et al., 1996) that indicated high capacity for regeneration from rhizomes (Section 9.1).

As already stated, both stocking densities in this experiment in Norwegian alpine grassland were low in comparison to densities typically used in more productive semi-natural grassland. Furthermore, *G. sylvaticum* plants do not grow as tall in such alpine grassland, compared to climatically more favourable British and Irish habitats (Figure 5). Thus, it is possible that grazing of taller species in the community may have freed *G. sylvaticum* plants from competition for light, also potentially compensating for any direct effects of grazing on individuals. Interestingly, according to Evju et al. (2011), the effects of grazing on individual *G. sylvaticum* plant growth appeared to be particularly pronounced in dry summers, that is when sward productivity would have been lower, and plants would have been less able to compensate for being grazed. More recent results appear to suggest that, while initially, frequency of abundance of *G. sylvaticum* was higher in the low- and high-grazing density treatments compared to the ungrazed control treatment (Steen et al., 2005), this was partly reversed after 12 years, with *G. sylvaticum* relative abundance by then having been found to have increased in the ungrazed control treatment, compared to the high-grazing density treatment (Maurset, 2015). There was also some evidence that this increase was more pronounced at elevations below 1150 m (Maurset, 2015). Thus, the longer-term effects of grazing observed in this experiment appear to align more with a reported sensitivity of G. sylvaticum to grazing livestock (Dierschke & Briemle, 2002). The fact that such alignment was only observed after several years of experimental grazing management illustrates the importance of longer-term experimental studies, also cautioning for careful interpretation of short-term (e.g. 2- to 3-year) studies.

A decline in recent decades of *G. sylvaticum* cover in fertile herb-rich boreal forests documented by a 2013–14 resurvey of northern boreal forests previously surveyed between 1957 and 1981 has been linked with increased grazing pressure from reindeer, which could have been due to *G. sylvaticum* being a preferred forage plant of reindeer (Warenberg et al., 1997 in Bråthen & Oksanen, 2001) and/or with its particular sensitivity to trampling due to its tall stature (Moen & Oksanen, 1998). However, atmospheric deposition, for example of sulphur, and climate change may have also played a role (Maliniemi et al., 2019). Between the original surveys and resurveys, the understory vegetation of the studied boreal forests generally shifted from herb-dominated to more grass-dominated (Maliniemi et al., 2019). According to observations made in British broad-leaved woodland, *G. sylvaticum* is similarly sensitive to deer grazing (Kirby, 2001), which could again also be due to trampling in addition to being grazed.

Management abandonment

In line with its comparatively late-seasonal phenology (Section 7), both management cessation and its seasonal timing (Section 4.2.3) in semi-natural grassland in which *G. sylvaticum* occurs can be expected to affect resident populations of the species. The evidence for these management aspects is discussed here from an ecological perspective, to be revisited again in Section 11 in the context of species conservation. Evidence from multiple studies indicates that in semi-natural grassland, usually, at least initially, *G. sylvaticum* benefits from management cessation. For example, a 15-year multi-site experiment in subalpine grassland in the Austrian Central Alps comparing fenced-off plots with continually cattle-grazed plots found that *G. sylvaticum* benefited more than any other species from management cessation (Mayer & Erschbamer, 2017). In another experiment, exploring the effects of management resumption in restored grassland in northern Finland (Huhta et al., 2001; see also Section 4.2.3) over a period of 10 years, following a previous 8-year abandonment, *G. sylvaticum* cover in continually unmanaged control plots increased from 4% at the outset of the experiment in 1993 to a maximum to 8.5% in 2001, followed by a marked decline in the final 2 years of the study (2002: 3.5%; 2003: 4.9%; Hellström et al., 2006). A similar marked decline was not observed in any of the treatments involving annual cutting, suggesting that even though *G. sylvaticum* initially responds positively to

FIGURE 5 Comparison of *G. sylvaticum* individuals growing in a hay meadow bank near Bowber Head, Cumbria, UK (left; photo: Richard Jefferson) and in low-alpine zone grassland on a south-facing hillside in Hol municipality, Buskerud county, southern Norway (right; photo: Courtesy of Marianne Evju ©). The plants at Bowber Head, UK, were 90 cm tall, whereas the plants in Norwegian low-alpine grassland reached a height of 20 cm.

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agricultural abandonment, in the longer term, ongoing vegetation succession will result in less favourable conditions for the species. Management abandonment also appeared to be conducive to higher *G. sylvaticum* cover in a survey of Swiss Alps grassland (Rudmann-Mauer et al., 2008; see also Section 4.2.1), with higher mean cover found in abandoned unfertilised grassland both in previously grazed sites (1.2%) and in previously mown sites (1.3%), compared to recently managed unfertilised grassland (0.2%–0.9%). Similarly, in a comparison of regularly mown Estonian wooded meadows with previously managed but now abandoned ones, *G. sylvaticum* was among a group of 'mowing-suppressed' species that expanded after regular mowing ceased (Otsus et al., 2014). In a study comparing the vegetation of both mown and abandoned Finnish meadows, *G. sylvaticum* was similarly classified as an indicator of management abandonment (Huhta & Rautio, 1998). An increase in the abundance of *G. sylvaticum* after the abandonment of sheep grazing was also observed in Iceland (Einarsdóttir, 2006, cited in Marteinsdóttir et al., 2017), where *G. sylvaticum* was also generally less abundant in extensively sheep grazed areas than in corresponding ungrazed areas (Valdimarsdóttir & Magnússon, 2013, cited in Marteinsdóttir et al., 2017). In Finland, Pykälä (2005), in a survey of three types of cattle grazed and abandoned grassland, found that mean percent cover of *G. sylvaticum* was 0.1%, 0.5% and 1.1% in old pastures, new pastures and abandoned grassland, respectively, with grassland type being marginally non-significant. Differences in sample plot frequency of occurrence followed a similar marginally non-significant trend, with 11.0%, 19.5% and 33.5%, respectively, for the same three grassland types. Monitoring in montane grassland in northern Finland 6 and 9 years after the initiation of long-term exclusion of summer-grazing reindeer found much increased flower production by *G. sylvaticum*, particularly when this had been combined with annual application of NPK fertiliser (Johanson et al., 2025). Renewed abandonment following the reinstatement of summer sheep grazing in previously abandoned montane grassland allowed *G. sylvaticum* abundance to recover after having previously been reduced when grazing had been reinstated (Krahulec et al., 2001).

Suggested reasons for the frequently (at least initially) positive response of *G. sylvaticum* to management abandonment in grassland include its relative competitiveness (see Section 4.1) and hence positive adaptation to changes in soil fertility and moisture regimes associated with abandonment (Mayer & Erschbamer, 2017), and its comparatively high shade tolerance (Mayer & Erschbamer, 2017; see also Section 5.2). Another reason may be its ability to develop comparatively high levels of shoot thrust (Campbell et al., 1992; Kingsbury, 2008), enabling regenerating shoots to penetrate a litter layer frequently developing after abandonment. This ability is also reflected in its response to the practice of mulching, that is cutting with cuttings left in place, from which *G. sylvaticum* typically benefits, in comparison to a traditional practice of cutting with removal, at least in the absence of fertiliser application (Dierschke & Peppler-Lisbach, 2009; Pourová et al., 2010).

4.2.3 | Seasonal timing of management

In a 5-year grassland restoration experiment in northern Finland lasting from 1993 to 1998, comparing continued management abandonment ($N=10$ plots) with restorative late mowing in August ($N=30$ plots) reinstated 8 years after cessation of previous management, late mowing by scythe with removal of cuttings and ongoing abandonment were similarly conducive to stable populations of *G. sylvaticum*, further underlining the compatibility of this species with seasonally late annual mowing (Huhta et al., 2001). An additional treatment involving early mowing was introduced in a 5-year continuation of the experiment from 1998 to 2003. The original 30 experimental late-mowing plots were split into three separate treatments, including a continuation of the original late-mowing treatment, with two additional treatments involving late mowing with added annual ground disturbance, and a move to early mowing in in late June (all three treatments $N=10$ experimental plots), with the original ten experimental plots representing ongoing management abandonment continued (Hellström et al., 2006). In this modified experiment, late mowing in August without additional soil disturbance resulted in a percentage cover of *G. sylvaticum* at the end of the experiment up to three times as high as that observed in the other three experimental treatments (14.5% vs. 4.9%–5.7%), including the early cut in late June with otherwise identical management. It appears likely that the undisturbed late-mowing regime did boost seed set of *G. sylvaticum*, as well as allowing plants to relocate at least some aboveground resources into belowground plant parts prior to mowing (Hellström et al., 2006). Differences with the late-mowing treatment including disturbance are discussed in Section 4.4.

Conversely, the authors of a German study have suggested that very early mowing in May, before the flower buds emerge, should affect the performance of *G. sylvaticum* less than a typical hay cut in June (Happel & Nowak, 2000). While they did not experimentally test this proposition, evidence that this may be the case for grazing is provided by an experiment carried out in an MG3b upland hay meadow in Cumbria (Smith & Rushton, 1994). This experiment compared a range of spring and autumn grazing treatments, finding that, in the spring grazed treatment, in which sheep were restricted to the meadow throughout April and early May and then removed for growth of the hay crop, *G. sylvaticum*, *Sanguisorba officinalis and Cirsium heterophyllum* all increased in abundance (Smith & Rushton, 1994). As with mowing, the effects of seasonal grazing on *G. sylvaticum* populations may also depend on seasonal timing. Reinstatement of annual summer sheep grazing from the end of June in previously abandoned montane grassland in the Krkonoše Mountains, Czech Republic, reduced the abundance of *G. sylvaticum* by one third over the first 3 years (Krahulec et al., 2001). In contrast, reinstatement of late-seasonal sheep grazing in abandoned grassland in northern Finland from the end of July had little effect on *G. sylvaticum* compared to a fenced-off unmanaged control treatment (Hellström et al., 2003), which, according to the authors was due to plants by then having already flowered and begun to reallocate

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resources to their root system. This means interference from management with the growth and reproduction of *G. sylvaticum* (as described in Section 7), would have been reduced, much the same way as with late mowing.

4.3 | Wild mammal grazing

The effects of small mammal grazing by microtine rodents on arctic-alpine vegetation including *G. sylvaticum* were investigated in an exclosure experiment carried out in arctic-alpine tundra in northern Norway (Moen & Oksanen, 1998; Olofsson et al., 2002). Ramets of several species including *G. sylvaticum* were transplanted into open plots and into exclosure plots, both in tall-herb meadow vegetation at lower altitude of which *G. sylvaticum* was a natural component, and further up above the treeline in snow bed vegetation, of which *G. sylvaticum* was not a natural component. In the lower-altitudinal tall herb meadow, mean survival of *G. sylvaticum* plants after 7 years was high (73–87%) regardless of plot type. In contrast, in the snow bed plots which were characterised by a shorter growing season, survival of *G. sylvaticum* was 100% in exclosure plots, but only 33% in open plots (Moen & Oksanen, 1998), indicating that grazing had a much larger impact on plant survival in the harsher snow bed environment than in that of lower altitude tall-herb vegetation. Mean annual growth rates of *G. sylvaticum* from 1987 to 1994 followed a similar pattern. Biomass sampling carried out in 1998 in both open and exclosure snow bed plots showed that *G. sylvaticum* had the third highest gain among all species in response to mammalian grazer exclusion (Olofsson et al., 2002). Work on other species has indicated that the expansion of lowland plant species to higher altitudes with warming may be hampered by mammalian herbivory (Kaarlejärvi et al., 2013). However, as *G. sylvaticum* was also observed in some nutrient-rich sites above the treeline (Jon Moen, pers. comm.), the upper altitudinal limit of the species in the region may be determined by an interaction between climate, mammalian grazing and soil fertility. Mediating effects of grazing on altitudinal shifts were, however, suggested by Speed et al. (2012), who based this suggestion on findings from the grazing density experiment in southern Norwegian alpine grassland described above in Section ‘Grazing intensity’ (Evju et al., 2006, 2011). In the ungrazed treatment there, the median altitude of *G. sylvaticum* plants recorded in 50 cm × 50 cm permanent plots went up by 35 m over 8 years, whereas in the high-sheep density treatment it went down by 6 m (Speed et al., 2012).

4.4 | Disturbance

Geranium sylvaticum is sensitive to many kinds of ground disturbance, in addition to trampling (see Section 4.2), both in grassland and forest habitats. In restored grassland in northern Finland, the additional introduction of annual ground disturbance to an existing regime of late-seasonal mowing, with the soil surface broken by a spade to achieve ca. 25% bare ground, reduced *G. sylvaticum* cover over time, compared to a treatment without added disturbance (Hellström et al., 2006). Over 5 years, mean *G. sylvaticum* cover on plots with added disturbance decreased from 8.5% to 5.7%, whereas without added disturbance, mean cover more than doubled from 6.5% to 14.5% (Hellström et al., 2006). Negative effects of ground disturbance were also evident in a hay meadow in the French Jura Mountains, in which the occurrence of *G. sylvaticum* was positively associated with areas characterised by only low levels of disturbance by montane water voles, *Arvicola scherman* Shaw 1801 (Nicod et al., 2020).

Sensitivity to ground disturbance has also been invoked as explanation for the finding that *G. sylvaticum* was one of several species whose frequency of occurrence was reduced in the vicinity of nests of the ant *Formica aquilonia* Yarr. in a forest area in Novosibirsk Oblast, Russia, but increased with increasing distance from the ant nests (Bugrova & Karakulov, 2010). However, in this case, the observed patterns could also be explained by other mechanisms, for example seed predation by ants.

In a forest in southern Finland, ground disturbance by annual litter raking and removal in autumn over a 25-year period did not appear to affect the frequency of occurrence of *G. sylvaticum* along a transect of 1 m^2 plots, which was similar both in the raked area and in an adjacent unraked area in virgin forest, but *G. sylvaticum* mean cover in transect plots and its mean biomass contribution in harvested central 25 cm × 25 cm subplots were lower within the raked area (Lindholm & Nummelin, 1983), suggesting on average smaller plants.

The effects of human recreational activities more generally and of general anthropogenic pressures on forest populations of *G. sylvaticum* are less clear. The abundance of *G. sylvaticum* in forests in Russia's Altai region was lower in areas with higher human recreational activity (Sokolova, 2019). In contrast, a Polish study of forest ground flora found *G. sylvaticum* to be neither indicative of undisturbed conditions nor indicative of anthropogenic disturbance, suggesting that it can tolerate some such disturbance (Fornal-Pieniak et al., 2021). Accordingly, *G. sylvaticum* has been variously considered a species favoured by forest management (Esseen et al., 1997) or a character species of near-natural forest (Sepp & Liira, 2009).

Heavy disturbance by clearcutting sharply reduced *G. sylvaticum* occurrence in the ground vegetation of grassy spruce taiga forest in Russia's Arkhangelsk region (Rai et al., 2012) although reduced shading through tree removal has been found to promote *G. sylvaticum* in other contexts (see Section 5.2). The latter is also evident in the fact that *G. sylvaticum* is a frequent coloniser of tree clearings produced by windfall, for example in fir forest in the Pyrenees (Álvarez-Asension & Puigdefábregas-Tomás, 1986). Increased light availability may have facilitated colonisation, although the authors did also point out that soil disturbance and subsequent nutrient release caused by the uprooting of windfall trees could also have played a role, boosting the growth of colonising *G. sylvaticum* plants (Álvarez-Asension

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& Puigdefábregas-Tomás, 1986; see also Section 2.2). A reverse process of increasing canopy closure in mountain woodland in the South Urals, resulting from a lack of canopy-level disturbance, has been linked with the disappearance of G. *sylvaticum* from the understorey vegetation (Gazol et al., 2017), reflecting its light requirements (see Section 5.2).

Geranium sylvaticum appears to have a certain resistance to burning, although this may depend on seasonal timing. Accordingly, a quick recolonisation of sites by *G. sylvaticum* was noted for bonfire sites in nature reserve grassland in Norway, where site management included the in situ burning of brash and herbage piles (Arnesen, 1999). The author hypothesised that recolonisation was initiated by surviving rhizomes, possibly at the edge of the burned area, giving rise to new fertile plants and recolonisation via seed dispersal (Arnesen, 1999). Incidentally, a similar observation was made after a widespread spontaneous forest fire of the Aletsch Forest in Switzerland in late May and early June 1944. There, *G. sylvaticum* was one of several species resprouting after just a few weeks and present in high numbers the next year in areas where the soil surface was still blackened from the fire (Lüdi, 1946).

4.5 | Plant–plant interactions

A study carried out in dry grassland on Konevets Island in the Leningrad region of Russia (Lebedeva et al., 2009) found that within the canopy of *G. sylvaticum*, the cover of forbs was lower than that of grasses, compared to outside the canopy. Two possible and not mutually exclusive explanations are that (1) levels of competition may be higher with architecturally more similar forbs than with grasses and (2) grasses are better at colonising the space underneath *G. sylvaticum* canopies due to stronger clonal spread.

In a grassland mesocosm experiment in which 11 sown perennial species were sown in mixture, *G. sylvaticum* attained a biomass about four times higher in mesocosms with the added annual hemiparasite *Rhinanthus minor*, compared to the control without *R. minor* (Bardgett et al., 2006). The presence of *R. minor* also resulted in a reduction in the biomass of perennial ryegrass, *Lolium perenne*, a preferred host of *R. minor* (Westbury, 2004 and references therein), by about two thirds (Bardgett et al., 2006), suggesting that the benefits to *G. sylvaticum* were indirect, resulting from a reduction in interspecific competition.

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Geranium sylvaticum plants can be found as solitary individuals (Starr-Keddle, 2018), patch-forming (Fitter & Peat, 1994) or in big clumps (Pacha, 2004). An occurrence in clumps has also been noted by Pigott (1956) for turfy marsh vegetation in Upper Teesdale. Gams (1924) describes *G. sylvaticum* growing in dense, tight clusters, often with individuals closely packed together in tall herbaceous meadows and scrubby habitats in central Europe.

A typically clumped occurrence of *G. sylvaticum* (Kingsbury, 2008) may be due to its limited ability for vegetative spread, which is achieved by short, unbranched rhizomes (3–10 cm), with meristems on the rhizome giving rise to clonal offspring (Ågren & Willson, 1994; Evju et al., 2011; Fitter & Peat, 1994; Klimešová & Klimeš, 2019; Salomonson et al., 1994; Sugorkina, 1995). The rhizomes grow slowly and remain attached to the originating plants (Klimešová & Klimeš, 2019), gradually expanding the populations under suitable management regimes, but not at great distances (Ernst et al., 2013; Klimešová & Klimeš, 2019). Sugorkina (1995) describes the process of rhizome fragmentation in older plants as 'particularisation', resulting in two to four genetically identical 'particulars' (plants) growing close by to each other.

5.2 | Performance in various habitats

Depending on various factors such as soil and climate conditions, light availability and the presence and intensity of grazing, the height of *G. sylvaticum* individuals is variable, ranging from 15 to 95 cm (Aedo, 2023; Evju et al., 2011; Nilsson, 1986; Stroh, 2019; Yeo, 2001). Figure 5 illustrates the variability in size of *G. sylvaticum* individuals in different parts of its native range.

The performance of *G. sylvaticum* in habitats in relation to light availability has been variously explored. While being shade tolerant, it can be found both underneath forest canopies and in open vegetation, often reaching high abundance in intermediate situations such as forest clearings (Sugorkina, 1995). This wide ecological amplitude is also reflected in the 'Plants for the Future' database, which lists *G. sylvaticum* as tolerating full shade (deep woodland), semi-shade (light woodland) or no shade (Fern, 1997). Its Ellenberg light value of 6 in Britain and Ireland (Hill et al., 2004) and in Central Europe (Ellenberg et al., 1991) similarly marks out *G. sylvaticum* as a species that can grow both in semi-shade and in more well-lit conditions. Across the European range, Tichý et al. (2023) calculated a higher adjusted value of 6.7, potentially indicating a propensity to occur in slightly better-lit habitats in some parts of its European range.

Populations of *G. sylvaticum* in Russia's Moscow region had reduced densities under forest canopies (1.9–4.7 individuals per 0.25 m^2), compared to adjacent meadow populations (4.1–17.1 individuals per 0.25 m^2) (Sugorkina, 1995). In a management experiment in southern Sweden, clearance of woody plants from a wooded meadow, either by herbicide application or mechanically, resulted in an increase in the abundance of *G. sylvaticum*, possibly due to increased light availability (Hansson & Fogelfors, 2000). In a controlled experiment where *G. sylvaticum* was grown from seed for 20 weeks under four combinations of light and nutrients, number of leaves produced and biomass accumulation were higher under high-light conditions (Salomonson et al., 1994). *Geranium sylvaticum* responded positively to light in combination with both low as well as high nutrient supply, although low-nutrient supply slowed the

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rate of leaf production (Salomonson et al., 1994). Mean (±SE) relative growth rate was almost twice as high under good availability of both nutrients and light ($79.4 \pm 11.2\,\mathrm{mg\,g^{-1}\,day^{-1}}$) compared to high nutrients but low-light levels ($42.3 \pm 1.9\,\mathrm{mg\,g^{-1}\,day^{-1}}$). At low nutrient levels, increased light availability did not boost growth rate, which was $24.0 \pm 1.8\,\mathrm{mg\,g^{-1}\,day^{-1}}$ at low light availability and $26.1 \pm 1.6\,\mathrm{mg\,g^{-1}\,day^{-1}}$ at high light availability. High nutrient availability also positively affected shoot meristem growth under low- and high-light treatments, although effect of light changed substantially through the growing season. Leaf to root allocation of biomass depended more on nutrients than on light; however, the light effect was changing during different phenological stages. Overall, increased light availability increased plant growth in both low- and high-nutrient treatments (Salomonson et al., 1994).

In a boreal *Picea abies* plantation planted in 1967 that included experimental 50 m × 50 m plots with and without fertiliser application since 1987, the abundance of *G. sylvaticum* in the forest floor vegetation was much higher in fertilised plots with *P. abies* stands that had been thinned in 2003 and 2004 than in control and fertilised plots with no additional thinning (Hedwall et al., 2013), indicating that with increasing forest canopy cover, its occurrence in forests is limited by decreasing light availability. One explanation for this is that the maintenance cost of large amounts of meristematic rhizome tissue due to an associated high-respiration rate may be too high for the species to persist in more shaded forest floor habitats (Moen et al., 1996). A preference of *G. sylvaticum* plants for less shaded habitats was also observed in an abandoned dry meadow in Russia's Leningrad region, where *G. sylvaticum* occurred at higher frequency away from solitary pine trees compared to directly under their crowns (Zhuraleva et al., 2012). In Swedish wooded meadows continuously managed for decades by mowing or grazing, *G. sylvaticum* occurred at higher frequency in more shaded conditions and in less dense vegetation (Einarsson & Milberg, 1999).

The effects of light availability on flowering and seed set of *G. sylvaticum* have been variously investigated. For example, Korhonen et al. (2004), over a period of 2 years in northeastern Finland, compared flowering, relative seed set per plant and average seed mass in five populations each both from low-light sites (range: 2.2–12 klux light illuminance) and from high-light sites (range: 95–106 klux). *Geranium sylvaticum* produced about 35% fewer flowers in low-light sites than in high-light sites, and plants growing in the former had lower relative seed set than plants growing in the latter, averaging 5% and 9% of relative seed set per plant, respectively, equating to just 0.3 and 0.5 seeds per fruit (see Section 8.3). Average seed mass was unaffected by high- vs. low-light environment (Korhonen et al., 2004). Plants from low-light sites showed higher arbuscular mycorrhizal and dark septate fungal colonisation compared to plants from high-light sites, which the authors interpreted as a prioritisation of mycorrhizal symbiosis by plants growing in low-light sites, at the expense of seed production (see Section 6.2).

In northern Sweden, experimentally unmanipulated plants growing at a meadow site began to flower earlier and produced more flowers and on average about four times as many seeds than unmanipulated plants growing at a forest site, where light levels were considered lower (values not reported) (Ågren & Willson, 1994). Mean seed production per plant (±SE) equalled 32.6 ± 2.4 for meadow plants ($N = 70$) and 7.4 ± 1.0 for forest plants ($N = 60$). With average total leaf biomass of meadow plants 30% lower than that of forest plants, differences between habitats were even more accentuated for mean seed mass to leaf mass ratio, which was 0.40 for meadow plants and 0.06 for forest plants. This means that, for a given plant size, meadow plants produced over six times as many seeds as forest plants. Both mean flower production and percentage fruit set were markedly higher in the meadow population than in the forest population (Ågren & Willson, 1994). The authors concluded that lower light conditions, and possibly lower nutrient supply in the forest habitat impacted flower production and seed-set (Ågren & Willson, 1994). It was concluded that *G. sylvaticum* plants required more photosynthetic tissue to support a given level of seed production under low-light conditions than under high-light conditions (Ågren & Willson, 1994). Similar results for fruit set were obtained in a study from Western Siberia, Russia, where hermaphrodite *G. sylvaticum* plants produced on average 1.6 times as many fruits in a meadow population under high-light conditions than in a forest population under low-light conditions (Gordeeva, 2025). Comparable results were also obtained in western Norway, in a study investigating growth and seed production parameters of *G. sylvaticum* plants in low-alpine willow scrub, both underneath the canopy of *Salix lapponicum* and outside its canopy (Totland & Esaete, 2002). While plants growing under *S. lapponicum* were characterised by a larger size and greater numbers of leaves, they produced similar numbers of seeds of similar average seed weight as plants growing away from canopies (Totland & Esaete, 2002). In a natural meadow population in northeast Finland, using experimental shading of one set of plants, and comparing performance of this set with that of an unshaded control set of plants, experimental shading (90% light availability reduction during fruiting) resulted in 57% lower mean seed production per plant (Varga et al., 2015). As in other studies (Korhonen et al., 2004; Totland & Esaete, 2002), shading did not affect mean seed mass, nor in this study seed phosphorus content (Varga et al., 2015). An early study documenting 48% fruit set in a damp grove meadow, as opposed to 34% in '*Melica-Lathyrus*' pine forest, and 10% in '*Hepatica-Oxalis*' pine forest, appears to suggest that reduced seed production in shaded habitats is at least partly the result of reduced fruit set (Perttula, 1941). As with shading, removal of photosynthetic tissue through simulated herbivory also affects seed production. In abandoned grassland in northeast Finland, the effects of simulated herbivory on *G. sylvaticum* plants were studied in a field experiment with randomised complete block design, also comparing female and hermaphrodite plants. Half of the plants had all rosette leaves and 50% of the leaf area of each stem leaf removed, with the remaining plants having no leaves removed (Varga et al., 2009). Experimental defoliation resulted in reduced fruit set, reduced seed set per fruit and reduced total seed output per plant, with female and hermaphrodite individuals equally strongly affected (Varga et al., 2009). Overall, the findings of various studies in terms of flower production

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and seed set are in line with Sugorkina's (1995) observation that population regeneration from seed is most successfully achieved under conditions of good lighting.

In relative terms, shading may be less detrimental for *G. sylvaticum* individual performance at the warmer end of its native distributional range. In a mesocosm transplant study involving twelve forest plant species including *G. sylvaticum*, the effects of forest edge vs. forest interior habitats and of open forest vs. dense forest habitats on the survival, growth and flowering probability of 12 forest plant species, including *G. sylvaticum*, were investigated in relation to habitat microclimate, and contrasting such effects with those of a large-scale macroclimatic gradient along a 1750 km long trans-European transect including five regions ranging from central Sweden to Italy (Wei et al., 2024). One finding was that *G. sylvaticum* individual survival and percentage ground cover attained by individuals were higher in open forests than in dense forests, but at the warmer end of the macroclimatic gradient, both percentage cover and survival were more strongly reduced in open forest than they were in dense forest, indicating a potential role of habitats with favourable microclimate in alleviating negative warming effects (Wei et al., 2024; see also Section 11.3). *Geranium sylvaticum* had the lowest survival rate across the 12 study species, and only 6% of the originally 240 planted individuals were alive after 3 years (Wei, 2023). Physiological responses to shading by *G. sylvaticum* plants are discussed in Section 6.5.

A study in Yorkshire, UK, compared the morphological and phenological characteristics of *G. sylvaticum* in upland hay meadows and nearby road verges (Slack, 2003, in Pacha, 2004). The plants in the road verges were double the height and width of those in the meadows, with a greater number of closed buds, open flowers and unripe fruit (Pacha, 2004). Pacha (2004) interpreted this finding as indicative of road verges being more suitable habitats for *G. sylvaticum* than meadows. One potential explanation could be that road verges may be less intensively managed than meadows (see Section 4).

5.3 | Effect of frost, drought, etc

Geranium sylvaticum is highly frost tolerant and cold adapted. It is found in a range of habitats with long lasting snow cover (November to May) and high rainfall in the summer (Hegedüšová et al., 2012). The ‘Plants for the Future’ database lists *G. sylvaticum* as hardy in USDA hardiness zones 4–8 (zone 4 = cold climate with minimum winter air temperatures ranging from −34.4 to −28.9°C; zone 8 = cool climate, −12.2 to −6.7°C) (Fern, 1997). In two southern Norwegian mountain areas, *G. sylvaticum* occurred in nine plant communities whose average minimum soil temperatures in winter ranged between −7.7 and +0.3°C but was absent from five communities characterised by even lower average minimum soil temperatures in winter, ranging between −19.8 and −11.5°C (Reinhardt & Odland, 2012). It has been surmised that low-winter temperatures prevent respiratory use of the carbohydrate and protein reserve in the bulky rhizome and that this store is utilised once the temperature rises above the threshold for growth in early May (Rodwell et al., 2007).

Numerous references describe the higher-elevation habitats that *G. sylvaticum* is found in, often above 200–450 m in upland Britain and across Europe, with frequent snow cover (Hegedüšová et al., 2012; Moen & Oksanen, 1998; Molau & Larsson, 2000; Olofsson et al., 2002; Rodwell, 2015; Sugorkina, 1995; Wei et al., 2024; Yeo, 2001; see also Sections 1 and 2.1). In the UK, it is found in areas where the winters are cold, wet and windy with up to 50 to 55 days average observed snow in the northern Pennines at 450 m (Manley, 1936, 1940). In its native British range, *G. sylvaticum* has a short growing season where growth normally begins in late April to early May, but late frosts are frequent, and temperatures can remain below the base temperature for plant growth at this time (Pigott, 1956; Rodwell, 2015). In Northern European alpine vegetation, length of the snow-free growing season may also play a role in limiting colonisation (Jon Moen, pers. comm.). However, with a warming climate, previously unsuitable high-alpine habitats may now become more suitable (see Section 11.3).

Experimental studies have indicated that *G. sylvaticum* is at least moderately drought tolerant, but that its growth is reduced following more severe drought. The effects of moderate drought were investigated experimentally in an eight-week potted-plant experiment involving both a standard and a reduced watering regime, with average soil water contents of 27.2% v/v and of 19.3% v/v, respectively. Above- and belowground biomass production and flower production remained unaffected by reduced watering (Wagg, 2012). The effects of a 1-month experimental drought in early summer were explored in a mesocosm study in a hay meadow in the Austrian Central Alps (Karlowsky, 2018). Drought was simulated using transparent rain exclusion shelters and followed by rewetting (watering). Folllowing the drought treatment, aboveground accumulated biomass was similar between drought-exposed experimental plants and control plants. However, following rewetting, experimental *G. sylvaticum* plants recovered much slower than control plants, resulting in reduced shoot biomass. For observations of the response of physiological parameters in this study see Section 6.5.

The effects of elevated ozone levels on *G. sylvaticum* were investigated in an 8-week potted-plant experiment combining four different background ozone levels ranging from 30.4 to 65.5 ppb with two levels of watering (Wagg, 2012). The second-lowest ozone level of 39 ppb represented an unmanipulated control. Increased ozone resulted in delayed flowering and reduced aboveground biomass in *G. sylvaticum* individuals, although for aboveground biomass, most of the reduction appeared to occur between the lowest and second-lowest ozone level, indicating a certain tolerance to further ozone level increases within the range tested (Wagg, 2012). Belowground biomass remained unaffected by background ozone levels (Wagg, 2012). Such delayed flowering could potentially interact with the effects of different timings of grassland management actions such as hay cutting (see also Section 4) and may make the species more susceptible to cutting or grazing earlier in the season. Wagg (2012) also found that the response of various physiological parameters in *G. sylvaticum* plants differed between watering treatments. A reduction in stomatal conductance was observed in

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plants receiving reduced watering, but not in well-watered plants (Wagg, 2012). Similarly, with increasing ozone levels, xylem sap abscisic acid concentrations increased, and pH decreased only in plants under reduced watering, but not in well-watered plants (Wagg, 2012). Hůnová et al. (2011) reported no ozone-induced damage in *G. sylvaticum* plants naturally growing with a mean ozone concentration of 37 ppb, that is towards the lower end of the concentrations experimentally tested by Wagg (2012).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Geranium sylvaticum is a herbaceous plant with perennial, sympodial rhizome branching from four to seven orders (Sugorkina, 1995). The rhizomes are short, epigenous, carrying up to 19 buds at soil depths of up to 10 cm (Chytrý et al., 2021). All branches of the rhizome bear numerous perennial adventitious brown roots that are 10–15 cm long and up to 2 mm in diameter; the main root typically remains functional for about 10–12 years (Sugorkina, 1995). In a Czech montane meadow, the distribution of *G. sylvaticum* root biomass within the topmost 12 cm of the soil profile was fairly even; of a total of 13 species whose root profiles had been characterised, only two other species, *Leontodon hispidus* and *Ranunculus acris* had such a more or less even vertical root distribution, with nine other species having most of their root biomass concentrated in the top four cm of soil, and one species, *Nardus stricta*, having most of its root biomass in the top 12 cm of soil concentrated at a depth of 8–12 cm below the soil surface (Herben et al., 2018). Thus, *G. sylvaticum* appears to be one of the more deep-rooting species in this type of grassland (Herben et al., 2018).

For the first 6–7 years after germination, sometimes up to 10 years, only rosette shoots are formed before the first semi-rosette shoot develops, carrying a basal rosette of 3–4 leaves and a stem with leaves and inflorescence. As described for Russia's Moscow region, an adult plant of *G. sylvaticum* typically has one to five vegetative rosette shoots, and one to three flowering semi-rosette shoots 30–80(100) cm tall, that are all connected by the rhizome (Sugorkina, 1995). The petiole of rosette leaves is up to 30 cm long, with the blade 8–12(15) cm in diameter and deeply cut into 7 toothed lobes. The number of teeth on the lobes increases during ontogenesis from 3–5 in juvenile up to 11–24 or occasionally more, in adult plants (Sugorkina, 1995). The leaf arrangement is alternate in the rosette, becoming opposite on a flowering stem. The lower stem leaves have short petioles, while the upper leaves are sessile, with the upper-most having only 3–5 lobes, and being much smaller than rosette leaves (Boswell et al., 1864). The stipules are lanceolate, pointy, 15–20 mm long, light brown in colour (Sugorkina, 1995). Information on the value range observed in *G. sylvaticum* for two leaf morphological parameters characterising the level of investment by plants in leaves as their primary photosynthetic structures—specific leaf area (SLA) and leaf dry weight (LDW)—is given in Table S3.

The lower part of the stem below the first branching is covered by eglandular hairs of variable lengths, with a few glandular hairs appearing on an upper part of the stem among eglandular hairs (Troshkina, 2018). The stem, peduncles, petioles and leaves are covered with unicellular and bicellular sharp-pointed conical hairs as well as with glandular hairs (Trembalya Ya et al., 2018; Troshkina, 2019) that are, respectively, 0.2–0.5 mm and 0.2 to 0.9 mm long (Aedo, 2023). *G. sylvaticum* is predominantly hypostomatous, that is stomata are more numerous on the lower leaf surface, with much fewer on the upper surface. This is a typical feature of species of shaded habitats, where CO_2 is unlikely to limit photosynthesis (Bucher et al., 2017; Peat & Fitter, 1994). The stomata are anomocytic, that is their guard cells are surrounded by cells resembling the remaining epidermis cells (Trembalya Ya et al., 2018).

The flowering stem bifurcates at the first node (Sugorkina, 1995). The inflorescence structure is classified as a closed thyrsus (Kuznetsova et al., 1992), with main axis growing until it terminates in a terminal flower. The *G. sylvaticum* thyrsus is composed of monochasial cyme modules, which have both main and lateral axes terminated in a flower each. The pedicels remain erect at all stages of flower and fruit phenology (Sugorkina, 1995; Troshkina, 2019; Yeo, 2001). Flower morphology somewhat varies depending on whether plants are female or hermaphrodite (see taxonomic description and Section 8.1).

The pollen grains of *G. sylvaticum* are large relative to those of other *Geranium* species, with a polar axis of 74.3–88.2 μm and diameter of 69.0–84.5 μm, tricolpate, colpi long (32.29 μm) and narrow (11.37 μm) (Troshkina, 2017, 2018). Exine surface semitectate (continuous in places), coarsely reticulate-clavate. Clavae are ovoid or roundish, variable in sizes 1.0–2.1 μm. Clavae with 2, 3, rarely 4 tips cross-connected by furrows (Figure 6, adapted from Troshkina, 2018). Smaller size of pollen was reported for specimens from Eastern Azerbaijan (Wang et al., 2021), with polar axis length 56–75 μm and equatorial diameter 55–78 μm and from Albania (Kallajxhiu et al., 2014, with length 58–65 μm and equatorial diameter 57–69 μm.

The fruit is a dry schizocarp with an apical beak (Chytrý et al., 2021). Each fruit locule typically contains one seed or occasionally two seeds (see Section 8.3). The mericarps are covered by both eglandular and long glandular trichomes with tiny, unicellular heads (Aedo, 2023; Troshkina, 2022).

The seeds are dark brown, smooth or faintly punctate, oblong, 2.4–3.8 mm long and 1.3–1.9 mm wide, with lateral hilum. Tokarski (1972) reported seed size dimensions for *G. sylvaticum* as follows: length (2.4–)2.5(–2.8) mm; width (1.6–)1.8(–1.9) mm; thickness (1.4–)1.7(–1.8) mm. Seed coat cells are polygonal, with shallow, thick undulate anticlinal walls (Moghadam et al., 2015).

6.2 | Mycorrhiza

Geranium sylvaticum routinely grows in association with arbuscular mycorrhizal (AM) fungi in its roots (e.g. Eriksen et al., 2002; Harley

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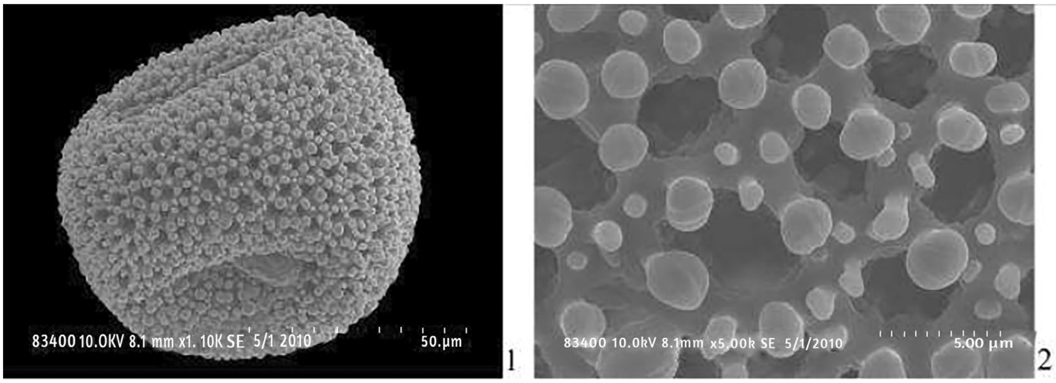

FIGURE 6 Pollen grain of *Geranium sylvaticum*: 1—general view (scale 50 µm); 2—sculpture of the exine surface (scale 5 µm) (adapted from Troshkina, 2018).

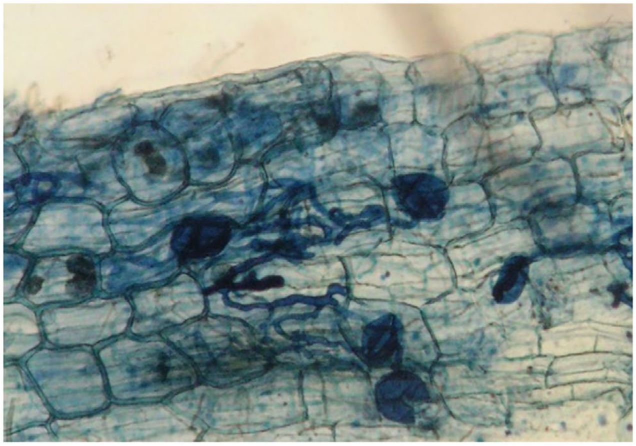

FIGURE 7 Intraradical hyphae and vesicles within the root of a *G. sylvaticum* plant experimentally colonised with *Glomus hoi*.

& Harley, 1987). One exception was a study in Swedish forest tundra, in which plants were determined non-mycorrhizal (Michelsen et al., 1998). Typically, a high proportion of root length is colonised by AM fungal structures (e.g. Akhmetzhanova et al., 2012; Eriksen et al., 2002; Kruger, 1961; Varga et al., 2009), that become visible after staining with trypan blue or another suitable dye (Figure 7). AM fungal colonisation of *G. sylvaticum* seedlings tends to occur relatively fast. In a pot experiment, Varga et al. (2015) showed that seedlings were colonised within 2 months following germination. However, while beneficial effects of AM fungi for adult plants, including those of *G. sylvaticum*, have been commonly reported (see below), the study by Varga (2015) showed that the presence of AM fungal spores in the soil decreased *G. sylvaticum* seed germination, whereas seedling survival was unaffected, and seedling establishment was enhanced.

In a mesocosm experiment, the level of *G. sylvaticum* root colonisation by AM fungi was highest at 8.7% of root length colonised in a low-fertility soil corresponding to a soil P-index of 0, whereas at higher residual soil fertility corresponding to P-index values of 1 and 2, only 4.1% and 5.1% of root length were colonised (Bardgett et al., 2006). In the same study, mean tissue P concentrations in *G. sylvaticum* were highest at higher residual soil fertility, and lowest in the low-fertility soil, and as a result, inversely correlated to the extent of AM fungal colonisation (Bardgett et al., 2006). Much wider variation of AM fungal root colonisation in *G. sylvaticum* has been documented in a mycorrhiza-focused Russian database covering a wide geographical range of ecosystems across the former Soviet Union (Akhmetzhanova et al., 2012). Levels of AM fungal colonisation were reported for 21 samples of *G. sylvaticum*, covering a wide geographic site range, spreading from the Polar Ural Mountains in the north to the Caucasus mountains in the south. In addition to a single sample from a meadow for which zero colonisation was reported, three more samples (two from woodland and one from a meadow) reported a very low frequency of colonisation at 2%. Most commonly, frequencies of colonisation were in the range of 40%–80%, with a maximum value of 90% recorded in a sample from a spruce forest (Akhmetzhanova et al., 2012). Overall, there was no clear difference in the intensity of mycorrhizal colonisation in *G. sylvaticum* between woodland and meadow habitats.

The effect of light availability on mycorrhizal colonisation during the growing season was investigated at 10 study sites in northern Finland (Korhonen et al., 2004), with the prediction that in low-light habitats, plants would be more carbon-limited and thus, the level of AM fungal colonisation would be lower than in high-light habitats. All roots from 300 plants sampled were heavily colonised by AM fungi. In the sites with high-light availability, AM fungal colonisation decreased from 41% on 26th June to 35% on 16th July and in August. Under low-light availability, colonisation remained at about 46% throughout of the growing season. Throughout the experiment, and contrary to expectations, mean AM fungal colonisation levels were between 5% and 11% higher in the low-light habitats than in the high-light habitats (Korhonen et al., 2004). This led to the conclusion that allocation to the fungal symbionts was of higher priority than allocation to reproduction (Korhonen et al., 2004).

Linked to the sexual dimorphism in this plant (see Section 8.1), it was investigated whether the association between *G. sylvaticum* and AM fungi is gender-specific (Varga et al., 2009; Varga & Kytöviita, 2010a), providing ample evidence that the different plant genders may differ in their association with AM fungi and in

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the benefit derived by the plant. Seasonal trends in AM fungal colonisation were investigated in a field experiment in an abandoned meadow in northeastern Finland to measure the effects of simulated herbivory on plant and fungal traits. Root colonisation by AM fungi was overall high, increasing from 70% in July to 85% in August, coinciding with the fruiting period (Varga et al., 2009). Whereas defoliation did not affect fungal colonisation intensity as expected, seed production decreased by half in both genders. In a separate pot experiment, Varga and Kytöviita (2010a) measured the mycorrhizal benefit that the three sexual phenotypes obtained from two different species of AM fungi. During the study, hermaphrodites suffered most from the lack of AM symbiosis as the proportion of flowering plants was dramatically reduced by the absence of AM fungi (from 66% and 58% of the plants flowering when growing in association with *Claroideoglomus claroideum* and *Glomus hoi*, respectively, to 17% in non-mycorrhizal condition). Both intermediate and female plants benefited from the symbiosis with AM fungi relatively more than hermaphrodites in terms of higher P acquisition, demonstrating that the interactions between AM fungi and plants can be gender-specific.

There is some indication that the identity of the mycorrhizal partner might affect seed set in plants. In an experiment, both total seed set and individual seed mass in *G. sylvaticum* were affected by the identity of fungal mycorrhizal partners, with experimental inoculation of plants with the AM fungus *G. hoi* resulting in both lower seed set per plant and in lower average seed mass compared to inoculation with *C. claroideum* and in lower seed mass also compared to non-inoculated control plants (Varga & Kytöviita, 2014). Total seed production per plant in non-inoculated control plants was intermediate between that measured in the two inoculation treatments, but did not differ significantly from either (Varga & Kytöviita, 2014). Recent research indicates that mycorrhization may also affect flower visitation by pollinators, with pollinators visiting more flowers on mycorrhizal plants, and spending more time on such plants, compared to non-mycorrhizal plants (Tuorila, 2025). However, this investigation did not include potential subsequent effects also on seed set.

According to the MarjaAM database (Öpik et al., 2010), at least 21 different 'virtual' taxa (i.e. phylogroups of AM fungus that could be interpreted as species, delineated from each other through their different, in this case small subunit (SSU) rRNA, gene sequences) have so far been recorded on *G. sylvaticum*. Most such species belong to the family Glomeraceae, but members of the Gigasporaceae, Acaulosporaceae and Archaeosporaceae have also been identified. It remains to be tested whether the genders of this gynodioecious plant differ in their root AM fungal communities.

The mycorrhiza of *G. sylvaticum* can be classified as *Paris*-type due to an intracellular localisation of fungi in cortical cells. Giesemann et al. (2021) found some evidence suggesting that *G. sylvaticum*, among 30 other species with *Paris*-type AM mycorrhiza, might be partially mycoheterotrophic, that is able to access photosynthates produced by other plants through hyphae. They measured that 42%–66% of carbon gain in *G. sylvaticum* significantly differed in stable isotope enrichment factors ε^{13}C from neighbouring non-mycoheterotrophic species (Giesemann et al., 2021).

6.3 | Perennation: Reproduction

This perennial hemicryptophyte (Hill et al., 2004) has individuals that can live for over 20 years (Evju, 2009; Klimešová & Klimeš, 2019; Sugorkina, 1995). Reproduction is mainly by seed, with little or no vegetative spread (Hill et al., 2004), although limited vegetative spread of *G. sylvaticum* through its epigeogenous stem or rhizome has been indicated by Klimešová and Klimeš (2019). According to Sugorkina (1995), the ramets of old generative plants tend to fragment. This limited vegetative spread can result in a clumped distribution of individuals (see Section 5.1). Evju et al. (2011) found in Norwegian dwarf shrub—grass vegetation that clonal reproduction, that is ramet formation, gets stimulated by sheep grazing (see also Section 4).

Individuals in the wild typically start flowering 7–10 years after germination (Salomonson et al., 1994; Sugorkina, 1995). Accordingly, *G. sylvaticum* individuals resulting from a multi-species sowing experiment in alder-birch forest had not yet reached the flowering stage 6 years after sowing (Perttula, 1941). However, the length of the juvenile stage in the various forest herbs investigated could be shorter in regions with longer vegetation periods and a more favourable climate (Perttula, 1941). Container-grown, seed-sown *G. sylvaticum* plants have been observed to start flowering after as little as 4 years (Ruth Starr-Keddle, personal observation). A dependence of flowering on plant size was documented in Norwegian low-alpine grassland, for which a threshold of 128 mg dry mass per ramet was determined above which 13% of *G. sylvaticum* plants were found flowering, whereas at a lower range from 32 to 128 mg, dry mass, only 0.3% of plants achieved flowering status (Evju et al., 2011). According to Salomonson et al. (1994), young plants have one perennial shoot meristem that overwinters, from which a varying number of leaves are initiated in the following spring.

6.4 | Chromosomes

Forty-two out of 46 records of chromosome numbers for *G. sylvaticum* listed in Aedo (2023) are $2n=28$ or $n=14$ (Aedo, 2023). The other four records in Aedo (2023) were either $2n=24$ or $n=12$, including $n=12$ for pollen samples from a white-flowered *G. sylvaticum* individual from the province of Dalarne in Sweden (Tjebbes, 1928). For British specimens of *G. sylvaticum*, $2n=28$ was confirmed by Van Loon (1984; in Aedo, 2023), and for samples from Lancashire by Montgomery et al. (1997). More recently, $2n=28$ was also reported from Turkey (Martin et al., 2022), and from cultivated plants both in the Netherlands (Zonneveld, 2019) and Belgium, in the latter case for the cultivated variety *G. sylvaticum* 'Album' (Akbarzadeh et al., 2021). According to Van Loon (1984), chromosome numbers for *G. sylvaticum* different from $2n=28$ would need further confirmation. More

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recently, in Catalonia, Spain, $2n=56$ has been reported (Petrova & Stanimirova, 2001), which according to Martin et al. (2022) is most likely due to dysploidy. In samples from Düzce in Turkey (altitude 413 m), *G. sylvaticum* was shown to possess relatively low intrachromosomal and interchromosomal asymmetry (Martin et al., 2022).

6.5 | Physiological data

6.5.1 | Photosynthesis

Geranium sylvaticum employs the C3 photosynthetic pathway (Fitter & Peat, 1994). The maximum net photosynthetic rate for *G. sylvaticum* in Finland was $12.1 \pm 1.4\,\mu\text{mol}\,\text{m}^2\,\text{s}^{-1}$ for plants growing in high-light habitats and $6.7 \pm 1.4\,\mu\text{mol}\,\text{m}^2\,\text{s}^{-1}$ for plants growing in low-light habitats, with a light compensation point (i.e. light intensity value where the rate of photosynthesis equals respiration) of $54\,\mu\text{mol}\,\text{m}^2\,\text{s}^{-1}$ (Varga & Kytöviita, 2017a).

6.5.2 | Water relations

The response of *G. sylvaticum* to extreme drought was investigated using a mesocosm approach on a hay meadow in the Austrian Central Alps (impacts on biomass were discussed in Section 5.3; Karlowsky, 2018). SLA was used as a proxy for plant resource strategy and the species was classified as exploitative (sensu Grime, 1977), as experimental plants at peak drought were characterised by lower SLA (mean ± SE: $15.0 \pm 3.1\,\text{m}^2\text{kg}^{-1}$) than non-stressed control plants ($22.4 \pm 0.6\,\text{m}^2\text{kg}^{-1}$), with the response thought to be an adaption to water stress. Exploitative species have a higher nutrient acquisition rate, leading to higher leaf N concentration and SLA. They are expected to be more sensitive to extreme drought than conservative species, but recover their biomass faster after disturbance (Grime, 1977). Average leaf N concentration during recovery from drought stress was non-significantly higher in plants that had experienced drought ($16.8 \pm 0.8\,\text{mg N g}^{-1}$) than in control plants ($14.6 \pm 0.3\,\text{mg N g}^{-1}$; Karlowsky, 2018).

6.5.3 | Inorganic nutrition

Belowground nitrogen accumulation (organic N, proteins, nitrate and total N) in nine boreal understorey species including *G. sylvaticum* was studied in northern Sweden, comparing plants in unfertilised control plots and plants grown in plots fertilised with $75\,\text{Kg N ha}^{-1}$ (Nordin & Näsholm, 1997). As in most studied species, total N concentration increased in *G. sylvaticum* rhizomes and roots in response to fertilisation (Table S4). Most of this N was stored as insoluble proteins and in the form of the free amino acid arginine. The authors noted that very low nitrate concentrations were recorded in all samples (Nordin & Näsholm, 1997).

Nitrate assimilation in *G. sylvaticum* plants was measured in a swamp forest in Central Sweden (Högbom & Ohlson, 1991). Current and maximally induced (i.e. the maximum amount of activity after giving a surplus of nitrogen) nitrate reductase activity was determined as $0.01 \pm 0.01\,\mu\text{mol NO}_2^-\,\text{g}^{-1}\text{h}^{-1}$ and $0.34 \pm 0.15\,\mu\text{mol NO}_2^-\,\text{g}^{-1}\text{h}^{-1}$, respectively. Seasonal variation was further investigated in the same site in 1993. Peak nitrate reductase activity was observed at the end of June (Ohlson & Högbom, 1993).

6.6 | Biochemical data

Besides fundamental biochemical constituents such as amino acids and proteins, carbohydrates and minerals, the biochemical composition of *G. sylvaticum* also includes terpenes and terpenoids (i.e. essential oils), phenolics (i.e. phenolic acids, flavonoids and tannins) and heavy metals. Essential oil composition was reported by Kahriman et al. (2010), who identified 78 different components, with murolene and linalool as major essential oils of the leaves.

The phenolic profiles include 12 phenolic acids, 14 flavonoids and five types of tannins present in different proportions within the different organs of the plant (Tuominen, 2013; Tuominen et al., 2013). It was suggested that the organ-specific polyphenolic profile found was related to the diverse biotic and abiotic factors the different organs are subjected to, as many of these secondary metabolites act as defensive compounds against herbivores and pathogens. This suggestion agrees with the observation that the total phenolic content in *G. sylvaticum* leaves increased with a simulated herbivory treatment (Saetnan & Batzli, 2009). In contrast, in the short-lived petals, tannins function mainly as co-pigments and not as herbivore deterrents (Tuominen et al., 2015).

Ivancheva and Petrova (2000) characterised the flavonoids in flowers of 11 *Geranium* species, including *G. sylvaticum*. They reported a flavone (luteolin) and three flavonols (kaempferol, quercetin and myricetin). These flavonols have been also reported from foliar trichome exudates (Harborne & Williams, 2002). *G. sylvaticum* contains both hydrolysable (i.e. gallotannins and ellagitannins) and condensed (i.e. proanthocyanidin) tannins (Tuominen, 2013; Tuominen et al., 2013), which act as herbivore deterrents. A very high level of oxidative activity in *G. sylvaticum* relates to extremely high levels of geraniin in the plant tissues (Vanhakylä & Salminen, 2023). Both hydrolysable tannins ($85.0 \pm 1.5\,\text{mg g}^{-1}$ dry matter; $N=10$ individuals) and biologically active quinic acid derivatives ($8.4 \pm 0.2\,\text{mg g}^{-1}$ dry matter; $N=10$) in *G. sylvaticum* were found at levels higher than intermediate compared to other species (in both cases normalised values >0.6, with normalisation based on a database containing values for >3500 plant species worldwide) (Vanhakylä & Salminen, 2023). *G. sylvaticum* showed high (normalised values >0.8) protein precipitation capacity (PPC) ($56.9 \pm 3.0\,\text{mg g}^{-1}$ dry matter; $N=10$). However, only slightly more than half of hydrolysable tannins were involved in PPC, possibly because of their structures being non-optimal for PPC (Vanhakylä & Salminen, 2023).

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Petal colour is defined by malvidin 3-(6-acetylglucoside)-5-glucoside—a dominant (85%) anthocyanin in the flowers of *G. sylvaticum* (Andersen et al., 1995). Four minor anthocyanin glycosides were also isolated from the flowers: 3,5-diglucosides of malvidin and cyanidin, and the 3-glucosides of cyanidin and delphinidin, which give the characteristic pink-lilac colouration (Andersen et al., 1995). Sylvatiins, four acetylglucosylated hydrolysable tannins acting as co-pigments, have also been isolated from the petals of *G. sylvaticum* (Tuominen et al., 2015). The amount of sylvatiins affects flower colour: deep purple petals contain more A and C sylvatiins in comparison with lighter coloured petals (Tuominen et al., 2015).

The amino acid composition in the leaves and stems of *G. sylvaticum* was studied by Razarenova et al. (2012). The compounds identified were as follows (amounts given in $\mathrm{mg\,g^{-1}}$ dry biomass): asparagine ($0.36\,\mathrm{mg\,g^{-1}}$), glutamine ($0.58\,\mathrm{mg\,g^{-1}}$), *o*-proline ($0.09\,\mathrm{mg\,g^{-1}}$), serine ($0.12\,\mathrm{mg\,g^{-1}}$), glycine ($0.17\,\mathrm{mg\,g^{-1}}$), histidine ($0.18\,\mathrm{mg\,g^{-1}}$), arginine ($1.32\,\mathrm{mg\,g^{-1}}$), alanine ($1.21\,\mathrm{mg\,g^{-1}}$), proline ($4.00\,\mathrm{mg\,g^{-1}}$), tyrosine ($0.22\,\mathrm{mg\,g^{-1}}$), valine ($0.36\,\mathrm{mg\,g^{-1}}$), iso-lecithin ($0.48\,\mathrm{mg\,g^{-1}}$), lecithin ($0.07\,\mathrm{mg\,g^{-1}}$), phenylalanine ($0.08\,\mathrm{mg\,g^{-1}}$), lysine ($0.16\,\mathrm{mg\,g^{-1}}$), cystine plus cysteine ($0.16\,\mathrm{mg\,g^{-1}}$), methionine ($3.48\,\mathrm{mg\,g^{-1}}$), tryptophan ($0.037\,\mathrm{mg\,g^{-1}}$) (Razarenova et al., 2012). In the pollen of *G. sylvaticum*, the concentration of free and protein-bound amino acids was 48.47 and $40.25\,\mathrm{\mu g\,mg^{-1}}$, respectively (Weiner et al., 2010).

Carbohydrates in *G. sylvaticum* and the closely related *G. pratense* and *G. palustris* were analysed by Razarenova et al. (2014). Monosaccharides detected in aboveground parts of *G. sylvaticum* include mannose, glucose, galactose, rhamnose and arabinose, with no relative amounts reported. However, in belowground parts of the plant, glucose is the predominant monosaccharide, indicating a key role in energy storage (Razarenova et al., 2014). Water-soluble polysaccharides found in all parts of the plants were composed of the monosaccharides mentioned, with the addition of xylose and galacturonic acid (Razarenova et al., 2014). Both in above- and belowground plant parts, the highest levels of monosaccharides were found at the stage of flower bud development, whereas water-soluble polysaccharides had their highest concentrations at the beginning of the flowering stage, especially in roots and rhizomes, where their amounts more than doubled compared to the bud development and end of flowering stages (Razarenova et al., 2014).

Seasonal variation in the chemical composition of *G. sylvaticum* plant parts in line with plant phenology (see Section 7) has also been observed for other compounds. Nordin and Näsholm (1997) documented late-seasonal nutrient storage in the belowground structures of *G. sylvaticum*, which contained much higher concentrations of nitrogen in various forms in September than in June (Table S4). This nutrient storage function of belowground structures is also obvious from the fact that belowground organs of *G. sylvaticum* contain higher concentrations of minerals than aboveground parts (Table S5). In fact, *G. sylvaticum* stores significantly larger amounts of iron, manganese and zinc than *G. pratense* or *G. palustre* (Razarenova, 2013). Seasonal and ontogenetic variation of polyphenols have been observed in the different organs of *G. sylvaticum* (Tuominen & Salminen, 2017). Geraniin concentration was highest in leaves, with a maximum observed in basal leaves after flowering, although remaining rather constant throughout the growing season. Some minor polyphenols such as ascorgeraniin and chebulagic acid increased during the growing season, while the concentrations of others peaked in May. In flowers, most of the polyphenols reached maximum levels during buds' development and gallotannins in flower pistils peaked during the fruiting phase (Tuominen & Salminen, 2017).

7 | PHENOLOGY

Plants overwinter as a short, unbranched rhizome from which new leaves first emerge in mid-May and then continue to form throughout the season. According to Steeves and Sussex (1989), this species possesses sympodial deciduous shoots and internodal elongation only occurs during flowering. The main flowering period of *G. sylvaticum* in the British Isles occurs between June and August (Fitter & Peat, 1994). The flowering phenology of *G. sylvaticum* was studied in detail from 1 June 1988 to 21 August 1988 for a population in the Pennine Dales in Northern England, in a 'northern' hay meadow at Bowber Head (Smith & Jones, 1991). Flowering ended by the 5th of July, and fruiting occurred between 5th June and the 16th of August. Seed shed peaked on 12th July, with the bulk of *G. sylvaticum* seed having been shed over the period of haymaking (Smith & Jones, 1991). A slightly later seed set in the North Pennines was observed by Starr-Keddle (2022), who noted that there, the species typically sets seed after a prescribed annual cut date on 15th July. Work carried out in the Yorkshire Dales appears to suggest that flowering and seed set might occur somewhat earlier in road verge populations than in meadow populations (Slack, 2003, in Pacha, 2004), likely because of different selective pressures due to different management regimes, such as, an absence in road verges of grazing livestock in the spring.

In the Vogelsberg region in Hesse, Germany, flowering typically starts between mid-May and early June, with the main flowering time in the second half of June (Happel & Nowak, 2000). In this region, plants fruit as early as the end of June, and typically, the main fruiting time is in the second half of July (Happel & Nowak, 2000). Perttula (1941) found that Finnish populations studied in 1933 shed their seeds mostly during the period between 15 July and 31 July. Peak biomass in Finnish populations occurred at the beginning of September (Törmälä & Raatikainen, 1976). In Russia's Moscow region, *G. sylvaticum* plants usually resume growth in early May with the formation of rosette leaves, with reproductive shoot elongation taking place around the end of May (Sugorkina, 1995). Flowering typically takes place from early June to early July. Slightly earlier flowering has been observed in the northeast German lowlands, where the species is often in full bloom at the end of May (Wangerin, 1926). Flowering is generally later and its duration shorter in higher mountainous areas of Central Europe where it is typically limited to August (Wangerin, 1926). After fruiting, existing reproductive shoots die back to the renewal zone of the rhizome (Sugorkina, 1995).

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From these various studies, geographic trends in the phenology of G. sylvaticum appear to be less obvious than those observed for the closely related *G. pratense* (Jefferson et al., 2023), which may be due to its lower-altitudinal distribution with increasing latitude (see Section 1), potentially offsetting at least some of the otherwise expected latitudinal climatic variation that would lead to marked phenological variation.

After flowering, plants produce the second generation of rosette leaves (Sugorkina, 1995). Throughout its range, reflowering occurs often in response to mowing and occasional flowering outside the main flowering season has been reported, for example in Germany (Happel & Nowak, 2000), Russia (Solovjev et al., 2019) and Finland (Sandra Varga, personal observation). Flowering in autumn has been reported for alpine valley meadows after mowing in spring (Kerner von Marilaun, 1902). Work by Evju et al. (2011) carried out in Norwegian alpine grassland appears to suggest that individual ramets can go dormant for one or several growing seasons.

There is some evidence that environmental change affects the phenology of *G. sylvaticum*. Bolmgren et al. (2013), using long-term citizen science phenological records collected by a farmer in southern Sweden, found that from 1980 onwards, the first flowering date of *G. sylvaticum* had significantly advanced, compared to the mid-1950s. Over the whole time series, first flowering date was significantly linked to mean monthly morning temperature in the month preceding first flowering, suggesting that this advancement of first flowering was linked to a warming climate (Bolmgren et al., 2013). On the other hand, Wagg's (2012) finding of delayed flowering in response to experimentally increased ozone levels (see Section 6.5) suggests that long-term changes in ground-level ozone concentrations could also potentially impact flowering phenology.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Populations of *G. sylvaticum* are usually gynodioecious, having both female (i.e. male-sterile) and hermaphrodite individuals in different proportions. However, some individuals are gynomonoecious (i.e. they have both female and hermaphrodite flowers, the latter with 10 functional stamens distributed into two whorls, within the same plant). Some plants may also produce partially male-sterile flowers with a reduced number of functional anthers, with 1–9 fertile stamens per flower rather than the usual 10. Such partially male-sterile flowers often contain 5 fertile stamens, with one whorl producing only fertile stamens, and one whorl producing infertile staminodes instead (Gordeeva, 2025), but any number from 1 to 9 fertile stamens in a flower is possible. Gynomonoecious phenotypes, regardless of whether they additionally produce some partially male-sterile flowers alongside female and hermaphrodite flowers, are also referred to as intermediate phenotypes (Gordeeva, 2025; Putrament, 1962; Varga & Kytöviita, 2010a). The three types of flowers are shown in Figure 8. It has been suggested in older literature that, at least occasionally, a reduction of the female function of stigmas can occur. Müller (1881), in one population in the Swiss Alps, observed large-flowered plants whose flowers had reduced and barely functional or non-functional stigmas. Schulz (1890; cited in Wangerin, 1926) observed functionally male flowers with reduced stigmas on otherwise hermaphrodite plants.

The reported frequency of female, intermediate and hermaphrodite phenotypes in Finnish and Central/Eastern European natural populations varied widely between different studies (Table 3). Moreover, sex change (i.e. gender diphasy) has been documented in this species in response to changes in availability of resources such as, for example light (Varga & Kytöviita, 2016). For example, Varga and Kytöviita (2016) performed a reciprocal transplantation experiment involving three different sites in Finland, transplanting a total of 374 plants between habitats differing in the amount of light that the plants received. Plant sexual expression was monitored for all flowering plants for four consecutive years. Throughout the 4-year study period, expression in 49% of the plants was labile, and this was related to the amount of light the plants received in their new habitats. Light availability has also been hypothesised to affect the frequency of hermaphrodite plants forming at least some partially male-sterile flowers, which was more than twice as high in a meadow population under high-light conditions than in a forest population under low-light conditions (Gordeeva, 2025). Potential links between sex expression and soil conditions—notably soil moisture and soil pH— have been hypothesised by Volkova et al. (2007), but since their study did rely on examination of only one flower per plant, more research may be required.

Sexual dimorphism in floral and non-floral characteristics has been extensively reported in this species (Table 4). Much such research has been carried out in the context of exploring how the female morph in gynodioecious plant species can persist while being seemingly disadvantaged in fitness terms compared to the hermaphrodite morph, as female plants have just one way to pass on their genes to the next generation, via seed production, whereas hermaphrodite plants can also do so via pollen production (Dufay & Billard, 2012). In the context of non-floral characteristics, while results are also summarised in Table 4, findings are discussed further within relevant sections (see, e.g. Section 8.3 for seed production characteristics).

Hermaphroditic flowers are larger than female flowers (Table 4). Pollen-producing flowers are protandrous, a mechanism that has been hypothesised to contribute to female advantage in this species (Elzinga & Varga, 2017). By measuring the individual floral lifespan in the absence of pollination on 122 female, 129 hermaphrodite and 111 intermediate flowers, Elzinga and Varga (2017) showed that the stigmas of female flowers had a lifespan more than twice as long as those of partially male-sterile and hermaphrodite flowers, and female flowers stayed open for longer. In pollen-producing flowers, the five stigmatic lobes remain tightly closed during the pollen presentation phase, which may last from 30 min to often 6 h or longer depending on the weather conditions (Varga, Nuortila, & Kytöviita, 2013). After

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FIGURE 8 Different flower types produced by *Geranium sylvaticum*. Top: Female flower without stamens; centre: Intermediate flower with six functional stamens; bottom: Hermaphrodite flowers with ten functional stamens (photos: Sandra Varga).

this non-receptive female phase, the five papillate stigmatic lobes start opening at the top, curling downwards. Flowers remain in the female phase between one and a half hours and often 6h or even longer, before the stigma lobes close again and the petals shrivel and drop. This translates to an early opening of the stigma in female flowers compared to the protandrous hermaphrodite ones (Elzinga & Varga, 2017).

All flowers usually offer nectar from five nectaries located at the base of the flowers (Varga, Nuortila, & Kytöviita, 2013). Nectar secretion patterns in Finnish *G. sylvaticum* populations were studied by Varga, Nuortila, and Kytöviita (2013), showing that hermaphroditic flowers produce more sugar than female flowers (Table 4), and observing nectar reabsorption in the former. According to Percival (1961) and Käpilä (1978), the nectar produced by *G. sylvaticum* flowers contains sucrose, fructose and glucose.

The species is self-compatible, even though protandry seems to strongly decrease the chance of self-pollination as reported by Lefebvre et al. (2019). Asikainen and Mutikainen (2005b) examined the effects of supplemental hand pollination on *G. sylvaticum* to determine whether the species was pollen and/or resource limited, showing that supplemental hand pollination and fertilisation increased fruit set by 28% and 32%, respectively.

The flowers of *G. sylvaticum* are insect-pollinated and visited for pollen and nectar by a range of generalist insect species (Table 5). In Finland, most visits are made by Diptera, followed by bumblebees and other hymenopterans (Soininen & Kytöviita, 2022; Varga & Kytöviita, 2010b). In general, female flowers are visited less frequently than hermaphroditic ones (Asikainen & Mutikainen, 2005a; Soininen & Kytöviita, 2022; Varga & Kytöviita, 2010b), which may be at least in part due to the fact that hermaphroditic flowers produce more sugar than female flowers. Detailed studies on plant-pollinator interactions for this species have been done recently. Lefebvre et al. (2019) assessed the pollination effectiveness of dipterans north of Mercantour National Park, France. They reported that in this subalpine area, where bumblebees are scarce, almost 81% of the visits were made by Diptera, followed by Hymenoptera (18% of visits) and butterflies and beetles. Baumann et al. (2021) assessed the pollination service of wild bees and hoverflies on *G. sylvaticum* plants in Hesse, Germany and reported that seed set was significantly and positively associated with hoverfly abundance. Within the 20 populations investigated, Baumann et al. (2021) reported visits by 34 different species of wild bees and 32 species of hoverflies. Lastly, Soininen and Kytöviita (2022) recently examined pollinator-flower interactions using video cameras and concluded that *Bombus* spp. were the most efficient pollinators, followed by syrphid flies and honeybees *Apis mellifera* (L.). Autogamous pollination (i.e. self-pollination) only occurred by *Bombus* spp. and authors estimated that about 5% of visits to hermaphrodites could have potentially resulted in autogamous pollination.

8.2 | Hybrids

No spontaneous hybrids of *G. sylvaticum* are known from the British and Irish flora (Stace et al., 2015). From cultivation, Yeo (2001) reported three different hybrids, including *G. sylvaticum* x *G. albiflorum*, *G. sylvaticum* x *G. palustre* and *G. sylvaticum* x G. *rivulare*, with

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TABLE 3 Contribution of different sex morphs to Finnish and Central/Eastern European natural populations of *G. sylvaticum*. n/a: No information given for this morph.

Countries	Females (%)	Intermediate (%)	Hermaphrodite (%)	Study unit	*N*	Source
Poland, Slovakia	3.3–24.8	4.1–15.6	59.6–92.2	Populations	12	5
Finland	1.8–22.2	0.0–3.1	77.8–98.2	Regions	9	6
Finland	0.4–27.2	n/a	n/a	Populations	23	1
Russia	3.2–12.3	n/a	n/a	Years (single population)	3	2
Russia	9.4	n/a	n/a	Single population	1	3
Russia	4.7–7.4	0.8–1.6	92.1–93.7	Populations	2	4

Sources: 1. Asikainen and Mutikainen (2003), 2. Demyanova (2013a), 3. Demyanova (2013b), 4. Gordeeva (2025), 5. Putrament (1962), 6. Vaarama and Jääskeläinen (1967).

the latter one also mentioned by Gams (1924). A cross between *G. sylvaticum* x *G. endressii* has also been documented (Akbarzadeh et al., 2021). According to Gams (1924), a possible cross between *G. sylvaticum* x *G. phaeum* [var. *lividum*], was 'very doubtful'. A sterile hybrid *G. sylvaticum* x *G. pratense* has also been reported (Yeo, 2001), but this cross could not be replicated artificially (Akbarzadeh et al., 2021).

8.3 | Seed production and dispersal

In *Geranium* species, typically only one of the two ovules per carpel develops into a seed, that is the whole fruit, consisting of five carpels, typically produces up to five seeds (Boesewinkel & Been, 1979). This has also been noted for *G. sylvaticum* (Sugorkina, 1995). However, occasionally, both ovules in a carpel abort or a single mericarp can produce two much-flattened seeds in superposition (Boesewinkel & Been, 1979). Such production of two seeds per locule may be genotype-specific (Sandra Varga, personal observation). Averages of 4.28 and 4.92 ovules in ripe fruit were reported for a lowland and an alpine plant community, respectively, in Norway (Lázaro & Larrinaga, 2018). Under field conditions, most *G. sylvaticum* flowers typically produce fewer than five seeds, even when five embryos are formed inside the flower. Söyrinki (1939), who studied three populations in the then Petsamo Province, Finland (now Pechengsky District, Russia) without distinguishing between different sex morphs, reported averages (±SE) of 3.3 (±0.3), 3.3 and 2.3 (±0.3) seeds per fruit for each respective population ($N = 20$ for all populations, with standard errors calculated from raw data listed by the author for two of the three populations), with individual values ranging from zero to five seeds per fruit. Evju et al. (2011) reported 2.35 seeds per fruit for a Norwegian population. Similarly, studies separating different sex morphs of *G. sylvaticum* have typically found fewer than five seeds produced per flower (Table 4).

At the level of whole plants, on average, female plants produce more seeds than hermaphrodite plants, thus enabling female plants to compensate for their inability to also reproduce via pollen (see Section 8.1; Table 4). This was also found in studies that controlled their analysis for potential size differences between sampled female and hermaphrodite individuals (Ramula & Mutikainen, 2003; Varga et al., 2009). Asikainen and Mutikainen's (2005b) study, while not experimentally controlling for potential differences in plant size between sex morphs, produced similar findings. This larger seed production seems to be mostly the result of female plants having higher fruit set than hermaphrodites, rather than from females producing more overall flowers or more seeds per fruit (Table 4). Some studies have looked at several populations simultaneously and for consecutive years. For example, a 2-year study involving the repeated sampling of 11 *G. sylvaticum* populations across Finland over two consecutive years confirmed higher seed production per flower by female plants compared to hermaphrodite plants in both years, and higher fruit set in the former in the second year of the study, in the only year this latter parameter was also measured (Asikainen & Mutikainen, 2003). Specifically, seed set per flower was 1.2 and 1.7 times as high in female plants compared to hermaphrodite plants in years one and two of the study, respectively, and fruit set in year two, the one year when this was also studied, was 1.4 times as high in female plants as in hermaphrodite plants (Asikainen & Mutikainen, 2003). However, the effect of gender morph on seed production per flower varied between populations and was not consistent across all combinations of population and year. Another 2-year study, covering three populations of *G. sylvaticum*, and involving a comparison between open-pollinated plants and plants also receiving supplemental hand pollination, similarly found markedly higher seed higher fruit set and seed set per fruit in female plants than in hermaphrodite plants (Asikainen & Mutikainen, 2005b). In this study, annual mean fruit set in a population in open-pollinated plants ranged from 29% to 71% in females and from 18% to 49% in hermaphrodites. Similar patterns were observed for annual mean seed set, which ranged from 1.5 to 2.4 seeds per fruit in females and from 1.1 to 1.9 seeds per fruit in hermaphrodites. While any fitness benefits conferred to hermaphrodite plants by their additional male function are extremely difficult to quantify under field conditions, the observed higher levels of seed set in female plants may offset such benefits. Early results by Vaarama and Jääskeläinen (1967) contrasted with the findings from later studies, but it should be noted that the units studied by these two authors were *G. sylvaticum* shoots, rather than whole plants. Moreover, they also did not control for plant size, and having themselves noted a trend in their population for

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TABLE 4 Sexual dimorphism in natural (i.e. non-experimental) *G. sylvaticum* plants.

Characteristic	Females	Hermaphrodites	Significance	Additional information	Source
Floral characteristics					
Anthers/flower	0	10	—		8
Nectar sugar accumulation (μg per flower per 24 h)	80.6 ± 22.3	186.4 ± 40.8	n.s.	Measured during the female phase	10
Petal length (mm)	11.6 ± 0.2	18.0 ± 0.1	***		8
	10.8 ± 0.1	17.3 ± 0.1	***	Average of 11 populations	2
	9.7 ± 0.4	14.7 ± 0.7	***		5
Pistil mass (mg)	1.6 ± 0.1	1.7 ± 0.1	n.s.	Forest population	7
	1.3 ± 0.1	1.4 ± 0.1	n.s.	Meadow population	
Pollen grains/anther	n/a	1414.5 ± 29.9	-	Average of 10 populations	1
Other characteristics					
Flowers per plant	27.6 ± 2.9	39.7 ± 3.6	*		8
	30.0 ± 1.4	38.7 ± 2.0	†	Average of 13 populations, year 2000 taken	1
	56.8 ± 2.4	69.1 ± 7.5	n.s.	High-light population	12
	15.4 ± 2.4	34.1 ± 4.2	*	Meadow population	6
Fruits per plant	12.6 ± 2.0	20.6 ± 2.6		Meadow population	6
Fruit set (%)	57 ± 5	40 ± 3	***	Average of 8 populations, year 2001	1
	57 ± 6	49 ± 4	***	Karariinanlaakso population, 2001	3
	46 ± 6	40 ± 4		Karariinanlaakso population, 2002	
	53 ± 4	28 ± 4		Paimio population, 2001	
	30 ± 4	18 ± 4		Paimio, population 2002	
	74 ± 6	40 ± 5		Seili I population, 2001	
	62 ± 5	46 ± 4		Seili I population, 2002	
	81 ± 3	62 ± 4	***		9
	90.7 ± 2.3	74.4 ± 4.8	n.s.	Naturally pollinated plants	4
Plant height (cm)	47.7 ± 1.4	48.7 ± 0.9	n.s.		9
Stems per plant	2.3 ± 0.2	2.2 ± 0.2	n.s.		9
Seed mass (mg)	4.4 ± 0.2	5.2 ± 0.2	n.s.	Average of 11 populations, year 2000 taken	1
	4.5 ± 0.2	4.4 ± 0.2	n.s.	Forest population	7
	4.7 ± 0.2	4.6 ± 0.2	n.s.	Meadow population	
	5.5 ± 0.1	5.2 ± 0.1	n.s.	Naturally pollinated plants	4
	5.5 ± 0.1	5.7 ± 0.2	n.s.	Control plants, year 2002	11
Seeds per fruit	2.0 ± 0.2	2.1 ± 0.1	n.s.	Seeds per flower	8
	1.1 ± 0.1	0.9 ± 0.1	*	Average of 11 populations, year 2000	1
	1.3 ± 0.1	0.8 ± 0.1	*	Average of 10 populations, year 2001	
	3.4 ± 0.2	3.2 ± 0.2	n.s.	Forest population	7
	3.8 ± 0.2	3.4 ± 0.3	n.s.	Meadow population	
	2.0 ± 0.2	2.0 ± 0.1	**	Karariinanlaakso population, 2001	3
	1.6 ± 0.3	1.1 ± 0.2		Karariinanlaakso population, 2002	
	2.0 ± 0.2	1.8 ± 0.2		Paimio population, 2001	
	1.5 ± 0.2	1.2 ± 0.1		Paimio, population 2002	
	1.7 ± 0.2	1.6 ± 0.1		Seili I population, 2001	
	2.1 ± 0.2	1.8 ± 0.1		Seili I population, 2002	
	3.2 ± 0.2	2.2 ± 0.2	***		9
	2.7 ± 0.2	2.1 ± 0.1	0.026	Naturally pollinated plants	4
	2.9 ± 0.3	3.8 ± 0.2	**		5

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TABLE 4 (Continued)

Characteristic	Females	Hermaphrodites	Significance	Additional information	Source
Seeds per plant	54.1 ± 8.0	84.1 ± 9.8	*	Values are per shoot, not per plant	8
	31.0 ± 9.5	103.2 ± 22.0	***	Forest population	7
	48.0 ± 5.2	59.7 ± 6.9	n.s.	Meadow population	
	54 ± 11	48 ± 8	***	Karariinanlaakso population, 2001	9
	33 ± 8	19 ± 4		Karariinanlaakso population, 2002	
	52 ± 10	21 ± 4		Paimio population, 2001	
	20 ± 5	9 ± 2		Paimio, population 2002	
	60 ± 16	27 ± 6		Seili I population, 2001	
	74 ± 15	39 ± 8		Seili I population, year 2002	
	115.3 ± 30.2	70.1 ± 10.5	***		9
	95 ± 21.6	64.5 ± 12.0	***	Control plants, year 2002	11
	31.9 ± 4.0	32.6 ± 4.0	n.s.	High light taken	12

Note: Some of the data presented is from unmanipulated control plants in studies involving experimental manipulation involving other individuals in the population. Means ± SE are shown. Significant differences between the two sex morphs as indicated by *p*-values from statistical analyses in source publications are indicated as follows: ***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$; †$0.05 < p \leq 0.10$; n.s.: $p > 0.10$; —: Not tested. Additional information is provided on source populations and timing of measurements.

Sources: 1. Asikainen and Mutikainen (2003), 2. Asikainen and Mutikainen (2005a), 3. Asikainen and Mutikainen (2005b), 4. Barlow (2012), 5. Elzinga and Varga (2017), 6. Gordeeva (2025), 7. Ramula and Mutikainen (2003), 8. Vaarama and Jääskeläinen (1967), 9. Varga et al. (2009), 10. Varga, Nuortila, and Kytöviita (2013), 11. Varga et al. (2015), 12. Varga and Kytöviita (2017a).

hermaphrodite plants to produce larger and sturdier shoots than female plants (Vaarama & Jääskeläinen, 1967), this mostly consistent difference in size between the two sex morphs represents the most likely explanation for their contrary findings.

There appears to be no trade-off between seed production and stamen formation at the level of individual flowers growing on hermaphrodite plants, that is seed production per flower appears to be independent from the number of functional stamens (Varga & Kytöviita, 2017b). Furthermore, the fact that observed seed set per flower is generally markedly lower than the typical maximum of five seeds per fruit indicates that seed production is usually constrained by external factors such as nutrient or light availability (for a discussion of the latter aspect see Section 5.2) and/or pollen limitation.

Several studies have measured the impact of nutrient limitation on reproductive output. In an investigation of the effects of nutrient availability and of supplemental pollination on reproductive output in three natural populations of *G. sylvaticum*, fertiliser application and supplemental hand pollination both increased fruit set in plants (Asikainen & Mutikainen, 2005b). Both seed set and overall seed production were boosted by fertiliser application, but not by supplemental hand pollination, indicating that both these components of reproductive output were predominantly nutrient-limited rather than pollen-limited. Fertiliser application also resulted in an increase in average seed mass of 6.6% across all three populations (Asikainen & Mutikainen, 2005b), reflecting an increase in seed quality. Regardless of whether a plant was female or hermaphrodite, supplemental hand pollination as well as fertiliser application appeared to produce similar benefits to reproductive output (Asikainen & Mutikainen, 2005b), although, as suggested by Varga et al.'s (2015) reassessment of these data, in the absence of supplemental hand pollination, hermaphrodite plants may have benefited more strongly than female plants from fertiliser application. Positive effects of supplemental hand pollination, resulting in a significant increase of current year seed production by 29%, were also documented by Toivonen and Mutikainen (2012).

The fitness costs of reproduction for *G. sylvaticum* plants were investigated by Ågren and Willson (1994; see also Section 5.2). Seed set was compared between unmanipulated control plants and plants prevented from setting seed by excising the stigmas at flower opening in two populations, including a meadow population and a forest population (Ågren & Willson, 1994). Permitting seed production in the year of the experimental manipulation did exact a cost in terms of the probability of plants to flower in the next year, both in the meadow population (in which 75% of the manipulated plants flowered again in the following year compared to only 53% of unmanipulated control plants) and in the forest population (40% vs. 23%) (Ågren & Willson, 1994). Lower percentages at the forest site may have been due to reduced light and potentially also lower nutrient availability (Ågren & Willson, 1994). Plant survival, vegetative growth as characterised by the number of leaves produced per plant, and number of flowers produced by floral plants appeared to be unaffected by suppression of seed set in the previous year (Ågren & Willson, 1994). The relatively short growing season of about 3 months for the studied northern Swedish populations and the resulting temporal overlap between vegetative growth and reproductive growth may have been conducive to the observed marked reproductive (flowering) cost. Such cost might be lower or absent in more southern populations.

The effects of increased seed production from supplemental hand pollination of plants in one year on the expression of reproductive parameters in the following year have been found to differ between female and hermaphroditic plants (Toivonen & Mutikainen, 2012). A decrease in flowering probability at the level of whole plants was observed for hermaphrodites but not for females

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TABLE 5 Insects recorded as flower visitors of *G. sylvaticum*. Species recorded as visitors in Britain and Ireland in bold.

Order	Family	Species
Diptera	Anthomyiidae	***Delia nigrescens*** Rondani[15]
	Empididae	***Empis diagramma*** Meigen**[15]**, *Empis pandellei* Daugeron[4,14], ***Empis punctata*** Meigen[15], ***Empis tessellata*** Fabricus[14,15], *Empis variegata* Meigen[4], ***Empis vitripennis*** Meigen[15], *Rhampomyia* Meigen sp.[4]
	Muscidae	***Drymeia hamata*** Fallén[15], *Phaonia alpicola* Zetterstedt[6], ***Phaonia angelicae*** Scopoli[15], *Phaonia hybrida* Schnabl[6], ***Phaonia incana*** Wiedemann[15], *Phaonia lugubris* Meigen[6], ***Spilogona solitariana*** Collin[15], ***Stomoxys calcitrans*** L.[15], *Thricops aculeipes* Zetterstedt[6], *Thricops cunctans* Meigen[6], *Thricops nigretellus* Zetterstedt[6]
	Syrphidae	*Cheilosia illustrata* Harris[5], *Cheilosia impressa* Loew[5], *Chrysotoxum elegans* Loew[5], *Chrysotoxum fasciatum* Müller[5], *Chrysotoxum fasciolatum* De Geer[9], ***Dasysyrphus tricinctus*** Fallén[1,5,9], *Didea intermedia* Loew[5], ***Episyrphus balteatus*** De Geer[1,5], ***Eriozona syrphoides*** Fallén[1], ***Eristalis arbustorum*** L.[15], *Eristalis nemorum* L.[5], *Eristalis pertinax* Scopoli[5], *Eristalis rupium* Fabricius[9], *Eupeodes corollae* Fabricius[5], *Eupeodes luniger* Meigen[5], *Helophilus pendulus* L.[3,5,9], *Helophilus trivittatus* Fabricius[5], *Lapposyrphus lapponicus* Zetterstedt[5], *Leucozona inopinata* Doczkal[5], *Leucozona lucorum* L.[9], *Melanostoma mellinum* L.[5], *Menalostoma scalare* Fabricius[5], *Merodon equestris* Fabricius[5], *Microdon* Meigen sp.[3], *Platycheirus albimanus* Fabricius[5,9,10], ***Platycheirus clypeatus*** Meigen[15], *Platycheirus complicates* Becker[2], *Platycheirus europaeus* Goeldlin, Maibach & Speight[5], *Platycheirus jaerensis* Nielsen[2], *Platycheirus kittilaensis* Dušek & Láska [2,5], *Platycheirus laskai* Nielsen[2], *Platycheirus latimanus* Wahlberg[2], ***Platycheirus manicatus*** Meigen[1,9,15], *Platycheirus naso* Walker[2], *Platycheirus nielseni* Vockeroth[2], ***Platycheirus peltatus*** Meigen[5,15], *Platycheirus scutatus* Meigen[5], *Rhingia campestris* Meigen[1,5,10,15], *Scaeva selenitica* Meigen[5], *Sericomyia bombiformis* Fallén[5], *Sericomyia lappona* L.[5], *Sericomyia silentis* Harris[5], *Sphaerophoria infuscata* Goeldlin[14], *Sphaerophoria scripta* L.[3], ***Sphegina verecunda*** Collin[1], *Syritta pipiens* L.[5], *Syrphus ribesii* L.[3], *Volucella bombylans* L.[5,9,14]
Hymenoptera	Andreniidae	***Andrena bicolor*** Fabricius[1], *Andrena cineraria* L.[5], ***Andrena coitana*** Kirby[15], ***Andrena dorsata*** Kirby[1], *Andrena fucata* Smith[5], *Andrena gravida* Imhoff[5], *Andrena haemorrhoa* Fabricius[5], *Andrena hattorfiana* Fabricius[5], *Andrena helvola* L.[5], *Andrena rufricus* Nylander[9], *Andrena subopaca* Nylander[5], ***Andrena wilkella*** Kirby[1]
	Apidae	***Anthophora furcata*** Panzer[1,5,9], ***Apis mellifera*** L.[1,3,4,14,15], *Bombus balteatus* Dahlbom[12], *Bombus barbutellus* Kirby[5], *Bombus bohemicus* Seidl[3,5,12], *Bombus cryptarum* Fabricius[5], ***Bombus distinguendus*** Morawitz[1], ***Bombus hortorum*** L.[1,5,9,12,15], ***Bombus humilis*** Illiger[5,15], ***Bombus hypnorum*** L.[1,3,5,10], ***Bombus jonellus*** Kirby[5,7,9,12,13,15], ***Bombus lapidarius*** L.[1,3,5], *Bombus lapponicus* Fabricius[9], ***Bombus lucorum*** L.[1,3,5,7,15], ***Bombus monticola*** Smith[7,15], ***Bombus muscorum*** L.[1,7,15], *Bombus norvegicus* Sparre-Schneider[5], ***Bombus pascuorum*** Scopoli[1,3,5,7,15], ***Bombus pratorum*** L.[1,3,5,7,10,15], *Bombus soroeensis* Fabricius[3,5], *Bombus sporadicus* Nylander[3], *Bombus subterraneus* L.[5], *Bombus sylvarum* L.[5], *Bombus sylvestris* Le Peletier[5], ***Bombus terrestris*** L.[1,3,5,15], *Ceratina* Latreille sp.[4], *Eucera longicornis* L.[5], ***Nomada ferruginata*** L.[15]
	Cimbicidae	*Corynis obscura* Fabricius[3,4]
	Colletidae	*Hylaeus confusus* Nylander[5], ***Hyaelus hyalinatus*** Smith[1]
	Halictidae	***Halictus*** Latreille **sp.**[15], *Lasioglossum calceatum* Scopoli[5], *Lasioglossus costulatum* Kriechbaumer[5], *Lasioglossum lativentre* Schenck[5], *Lasioglossum rufitarse* Zetterstedt[5], *Sphecodes ephippius* L.[5]
	Megachilidae	***Chelostoma campanularum*** Kirby[1], ***Megachile centuncularis*** L.[1], ***Megachile maritima*** Kirby[1], ***Megachile versicolor*** Smith[1], ***Megachile willughbiella*** Kirby[1,5], ***Osmia bicornis*** L.[1]
	Megalodontesidae	*Megalodontes* Latreille sp.[4]
	Melittidae	***Melitta haemorroidalis*** Fabricius[1]
Lepidoptera	Hesperiidae	***Ochlodes sylvanus*** Esper[1], *Ochlodes venatus* Bremer & Grey[11], ***Thymelicus sylvestris*** Poda[1]
	Lycaenidae	**Celastrina argiolus L.**[1], *Glaucopsyche alexis* Poda[11], *Lycaena hippothoe* L.[11], ***Lycaena phlaeas*** L.[1], ***Polyommatus icarus*** Rottemburg[1,11]
	Nymphalidae	*Aglais io* L.[3], ***Aglais urticae*** L.[1], *Araschnia levana* L.[3], **Lasiommata megera L.**[1], ***Maniola jurtina*** L.[1], ***Pararge aegeria*** L.[1], **Pyronia tithonus L.**[1], ***Vanessa atalanta*** L.[1,3]
	Pieridae	***Anthocharis cardamines*** L.[1,3], ***Gonepteryx rhamni*** L.[1], ***Pieris brassicae*** L.[1,15], **Pieris napi L.** [1,11], ***Pieris rapae*** L.[1]
Coleoptera	Byturidae	*Byturus ochraceus* Scriba[8]
	Cerambycidae	*Brachyta interrogationnis* L.[4]
	Curculionidae	*Zacladus geranii* Paykull[3]
	Oedemeridae	*Oedemera virescens* L.[14]
Hemiptera	Correidae	*Coreus marginatus* L.[3]
	Pentatomidae	*Dolycoris baccarum* L.[3], *Pentatoma rufipes* L.[3]
	Rhopalidae	*Corizus hyoscyam* L.*i*[3]

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(Toivonen & Mutikainen, 2012). An opposite effect was observed for total seed production of plants which was lower in the year after supplemental hand pollination in females, but not in hermaphrodites, compared to open-pollinated plants of the respective same sex. Calculating a multiplicative 'seed fitness' index combining two ratios between hand-pollinated and open-pollinated plants for the probability of flowering and for the total numbers of seeds produced per plant, respectively, seed fitness in the following year after supplemental hand pollination was reduced by 56% in female plants, and by 39% in hermaphrodite plants, indicating that the future cost of current seed production on the female function of reproduction is higher in females.

Mean seed mass ranges from 3.97 mg (Varga, Vega-Frutis, & Kytöviita, 2013) to 6.68 mg (SER et al., 2023). The Seed Information Database contains six entries for *G. sylvaticum*, ranging between 5.10 and 6.68 mg and averaging 6.12 mg (SER et al., 2023). Mean seed mass values of 5.9 and 6.1 mg were obtained by Korhonen et al. (2004) for a northern Finnish population sampled in 1999 and in 2000, respectively, with Varga et al. (2015) reporting a mean value of 5.7 mg for the same population when resampled in 2002. Bruun and Ten Brink (2008) measured a mean seed mass of 5.33 mg. Naturally, a wider range of observed seed mass values can be expected for individual seeds, compared to the above ranges of mean seed mass based on seed lots. Accordingly, in an experimental study, observed individual seed mass ranged from 3.3 to 7.35 mg (Varga, 2014). In Asikainen and Mutikainen's (2003) comparative study of 13 populations involving repeat measurements for most populations in two consecutive years, mean population seed mass in a particular year ranged from 4.3 to 5.7 mg for seeds produced by female plants and from 4.6 to 6.1 mg for seeds produced by hermaphrodite plants. Statistical analysis indicated significant variation with year, population, and for the interaction between these two factors, but not for maternal gender (i.e. female vs. hermaphrodite plants) or its interaction with year and/or population (Asikainen & Mutikainen, 2003). These results are in line with other studies which found that, contrary to total seed production per plant, mean seed mass appears to remain similar between female and hermaphrodite plants (Table 4). Experimental manipulation of light availability also appears not to affect seed mass, nor seed phosphorus content (Varga et al., 2015).

Seed mass remained similarly unaffected by degree of root colonisation both by arbuscular mycorrhizal fungi and by dark septate fungi in Korhonen et al.'s (2004) study. However, in Varga and Kytöviita's (2014) common-garden experiment, seed mass was affected by mycorrhizal inoculation treatments. Plants inoculated with the AM fungus *G. hoi* produced seeds of lower average mass (4.0 mg) than plants inoculated with *G. clarioideum* and non-mycorrhizal plants (both 4.6 mg).

Primary seed dispersal in *G. sylvaticum* is ballistic (Gams, 1924). At maturity, the fruit splits into the five mericarps which detach at the bottom from the central column of the fruit (Müller-Schneider, 1977). Initially, the seed is held back by a cluster of bristles at the lower end of the carpel orifice, but as the carpel tissue dries out further, the carpellary beak also detaches from the central column of the fruit and coils up (Figure 9), and the seed is ejected by the explosive recurvature of the awns and the resulting centrifugal force; after seed ejection, the tops of the carpellary beaks remain attached to the central column of the fruit (Müller-Schneider, 1977; Sauer, 1933). This specific type of dispersal has also been referred to as the 'Geranium pratense type' (Wangerin, 1926; Yeo, 1984; see also Jefferson et al., 2023), in distinction from mechanisms described for other species within the genus *Geranium*.

The seeds of *G. sylvaticum* lack specific appendages (Tokarski, 1972), and in the Pladias database for the Czech flora and vegetation (Chytrý et al., 2021), seed dispersal of the species is listed as being primarily autochorous, that is external dispersal vectors are assumed to play a minor role. However, secondary anthropochorous seed dispersal has been documented by Auffret and Cousins (2013), who found that *G. sylvaticum* is dispersed in the clothes of meadow managers after hay cutting. Another pathway of anthropochorous dispersal, seed transport with cut hay, which has also been discussed for the closely related *G. pratense* (Hundt, 1975; Jefferson et al., 2023), typically depends on the timing of the hay cut in relation to species phenology (Wagner et al., 2021). Accordingly, hay cut between 5th and 12th July 1999 from six meadows at Piper Hole Meadows, Cumbria, did not contain any seeds of *G. sylvaticum*, despite a relatively high frequency of occurrence of 41%–60% of this species in the vegetation, based on a recorded 24 quadrats of 0.25 m^2 across the six meadows (Edwards & Younger, 2006). According to Edwards (2003), the reason for this absence of *G. sylvaticum* seed from the hay was that the cut took place prior to ripe seed having been produced. The timing of the annual cut of traditionally managed hay meadow typically requires suitable weather conditions (Rodwell, 2015; Smith & Jones, 1991), and a later hay cut in some years should facilitate dispersal of *G. sylvaticum* seeds with hay (Edwards, 2003).

Secondary dispersal of hay-dispersed seed might occur via farmland manure from livestock fed with such hay (Edwards & Younger, 2006). While Edwards and Younger (2006), due to the early cutting of the hay in their cattle feeding trial were unable to detect *G. sylvaticum* seeds in cattle manure, endozoochory by cattle has been confirmed through detection of germinable *G. sylvaticum* seeds in cow pats collected from a Swiss alpine pasture (Salzmann & Schenker, 1946 in Ernst et al., 2013). Secondary dispersal of *G. sylvaticum* seeds by flowing water, for example along streams or rivers, likely occurs only across small distances, due to the limited buoyancy of the seeds. Romell (1938), classifying species of the Swedish flora based on the maximum time their seeds can float, assigned *G. sylvaticum* to the category least adapted to floating on water characterised by a 'maximum floating time of less than one hour'. Given the limited capacity of *G. sylvaticum* for (particularly non-anthropochorous) secondary dispersal, it is no surprise that Liira and Paal (2013), modelling the occurrence of forest-dwelling plant species along 'woody corridors' using transect data, classified the species as 'forest-restricted', that is unable to disperse along 'woody corridors' such as hedgerows (even though the species also occurs in non-forest habitats such as grassland, see Section 3).

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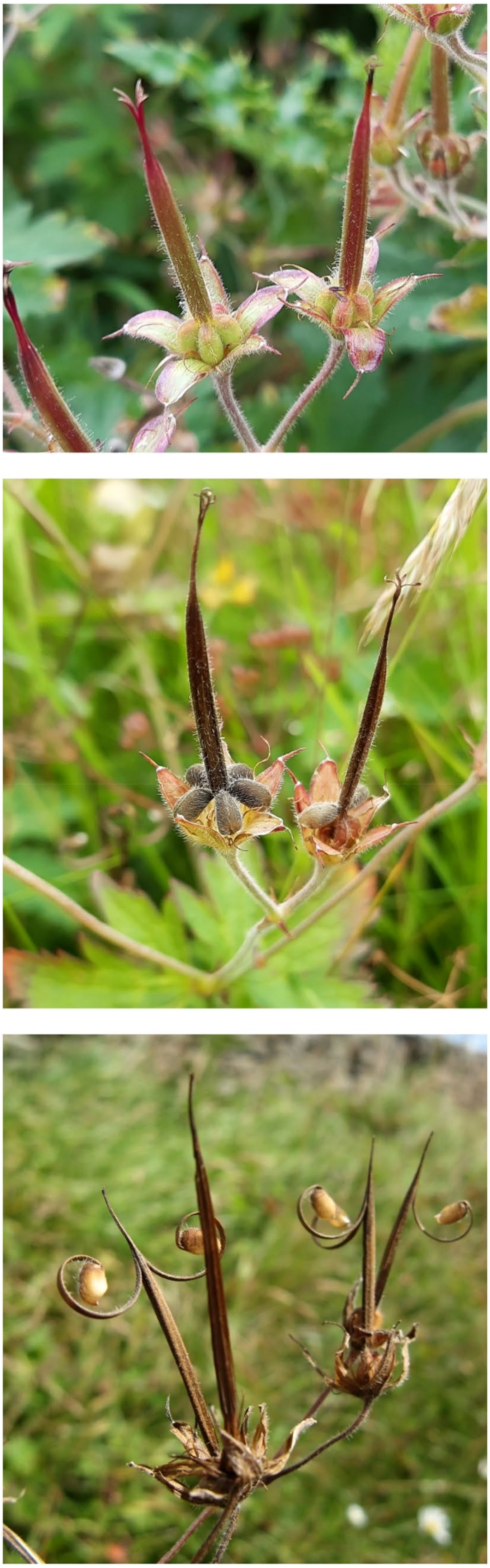

FIGURE 9 Different stages of seed-head development of *Geranium sylvaticum*. Top: Initial seed-head developing, with green casing; centre: Seed-head developing over time, with casing turning brown and beginning to lift; bottom: Seed-head has catapulted the seeds out of the casings (photos: Ruth Starr-Keddle).

8.4 | Viability of seeds: Germination

Soil seed bank studies indicate that *G. sylvaticum* tends to form a transient soil seed bank sensu Thompson et al. (1997), with seeds typically persisting for less than 12 months. Studies in which soil was sampled in spring or early summer, that is before the current year's seeds have been dispersed from their mother plants, have mostly failed to detect the species (Granström, 1982; Jankowska-Błaszczuk et al., 1998; Waesch, 2006) or have found only a few sporadic seedlings emerging from samples (Milberg, 1992). Seed bank studies that involved sampling in summer or autumn, that is after the current year's crop of seeds should had been shed from their mother plants, have occasionally detected viable seeds. Edwards (2003), studying the soil seed banks of five grassland sites at Piper Hole Meadows, Cumbria, England with soil sampling in early September, recorded the emergence of seedlings of *G. sylvaticum* from soil representing the 0-5 cm depth layer of three out of fifteen core samples to a depth of 10 cm, whereas no seedlings were detected to emerge from any of the samples from the lower (5–10 cm) depth. However, several other studies involving late-seasonal sampling failed to record germination from *G. sylvaticum* (Kiirikki, 1993; Molau & Larsson, 2000; Smith et al., 2002). *G. sylvaticum* was also not detected in the seed bank of Triseto flavescentis-Polygonion bistortae grassland in Germany, which had been sampled both in spring and in autumn (Von Borstel, 1974).

Fresh mature seeds of *G. sylvaticum* are unable to absorb water. In a 10-day test of water permeability of fresh seeds on moist filter paper, Meisert (2002) found that 96% of seeds of *G. sylvaticum* remained impermeable to water throughout the test. In line with this initial non-permeability of the seed coat, Söyrinki (1939) observed only slow and intermittent germination of non-scarified intact seeds from three source populations of *G. sylvaticum* over a period of 11 to 13 months, at which point practically full germination of 96%–100% had occurred. Much accelerated germination of seeds was reported in response to mechanical scarification involving partial removal of the seed coat (Kontuniemi, 1932), providing clear evidence of physical seed dormancy, even though in another study, sulphuric acid scarification had resulted in only a small stimulatory effect (Kallio & Piiroinen, 1959). In the same study, exposure to gibberellic acid did not stimulate seed germination (Kallio & Piiroinen, 1959), but when sulphuric acid scarification preceded exposure to gibberellic acid, an unspecified 'very high proportion of seeds germinated' (Kallio & Piiroinen, 1959: 1831). These findings suggest that, apart

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from physical dormancy due to seed coat impermeability, *G. sylvaticum* seeds may also additionally display physiological dormancy, that is combinational seed dormancy sensu Baskin and Baskin (2004). Physiological seed dormancy in *G. sylvaticum* alongside a mechanism of physical seed dormancy has also been suggested by Hill (2001; as cited in Rodwell, 2015) and by Vandvik et al. (2017). No information was available on how cold stratification was carried out in Hill's (2001; as cited in Rodwell, 2015) experiments. However, results obtained by Vandvik et al. (2017) after 2 months of seed exposure to moist chilling in darkness indicate that in their study, cold stratification resulted in the induction of secondary dormancy, rather than in dormancy alleviation. They found much higher final germination of 45% after treatment of seeds with gibberellic acid (GA3) than after cold stratification at just 17% final germination. Moreover, the final germination percentage of fresh seeds was closer to that of GA3-treated seeds than to that of cold-treated seeds, indicating that the significant difference between GA3-treated and cold-treated seeds may have been at least as much caused by a depression of germination by cold stratification treatment as by an actual stimulation of germination by the gibberellic acid. Overall, while physical dormancy appears to be ubiquitous in seeds of *G. sylvaticum*, an additional component of physiological dormancy might be less so. Within-species variation in physiological dormancy has been commonly observed in other species, due to various causes (Baskin & Baskin, 2014), and the same might apply for *G. sylvaticum*. It is possible that in some situations, seed coat impermeability (i.e. physical seed dormancy) may be the sole cause of seed dormancy, whereas in other situations, a component of physiological seed dormancy might also be present. More research will be needed to ascertain if and how regularly the seeds of *G. sylvaticum* might have a physiological component of seed dormancy in addition to physical dormancy. The physical seed dormancy ascertained for the species is compatible with its formation of only a transient soil seed bank, as seed dormancy is neither a necessary nor sufficient condition for the accumulation of a persistent seed bank (Thompson et al., 2003), with many species characterised by physical seed dormancy similarly characterised by only a short-lived soil seed bank (Thompson et al., 1997).

In laboratory germination experiments, germination of dry-stored non-scarified *G. sylvaticum* seeds remained low and was hardly affected by light and temperature cues (Vandvik et al., 2017). Germination began earlier, and final germination was slightly higher, at a constant temperature of 25°C than at a constant temperature of 10°C, but diurnal temperature fluctuation did not appear to boost germination in comparison to a constant temperature regime, and neither did full light for a photoperiod of 16 h per day result in higher germination than darkness (Vandvik et al., 2017). In the field, seed germination of *G. sylvaticum* typically takes place in spring (Kontuniemi, 1932; Perttula, 1941; Söyrinki, 1939; Sylvén, 1906), although some authors did observe some additional germination in autumn (Witte in Sylvén, 1906; Kontuniemi, 1932). In a field experiment involving autumn sowing of *G. sylvaticum* and of several other species into four different microhabitats in Norwegian subalpine grassland (uncut sward of ca. 20 cm height, cut sward of 5 cm height, cut sward of 0 cm height and bare ground gaps with both above- and belowground parts of plants removed), Vandvik et al. (2017) did not find any differences in seedling emergence. The authors linked this indiscriminate germination across different microhabitats with the already mentioned low responsiveness of seeds to light and temperature cues. However, subsequent seedling mortality was much lower in the gap and 0 cm treatments than in the 5 cm and uncut treatments, indicating a susceptibility to competition at the seedling stage. Individual mortality was 2.5 times as high in the second winter after sowing than in the following summer.

In a controlled greenhouse experiment, mycorrhizal status of the mother plant strongly affected seedling relative growth rate of *G. sylvaticum* in the first 2 months after germination, with mean rates of 29, 32 and 31 $\mu g\, mg^{-1}\, day^{-1}$ for seedlings grown from seeds produced by mother plants that are non-mycorrhizal, inoculated with *C. claroideum* and inoculated with *G. hoi*, respectively (Varga, Vega-Frutis, & Kytöviita, 2013). Seedling relative growth rate was also affected to a lesser extent by the mycorrhizal status of the pollen donor plant, whereas the sex of the mother plant being female or hermaphrodite did not play a role (Varga, Vega-Frutis, & Kytöviita, 2013).

In a field sowing experiment including three stands of Callunetum heathland and an agricultural grassland, each with a different type of soil, the effects of applying a combined N-P-K-Mg fertiliser on seedling establishment and subsequent performance were investigated for over 100 species of plant including *G. sylvaticum* (Miles, 1974). Seeds were sown into 1.5 m × 1.5 m experimental plots stripped of their vegetation prior to the experiment. Species performance was characterised by means of rooted frequency based on cell occupancy in a 1 m × 1 m quadrat gridded into one hundred 10 cm × 10 cm squares and placed centrally in experimental plots. No effect of fertiliser application on *G. sylvaticum* performance was observed in the agricultural grassland. In the Callunetum with the least fertile soil as determined by bioassays with a range of species, a peaty podsol, *G. sylvaticum* plants exclusively established in plots that had received fertiliser, achieving 15% rooted frequency, with the difference between the two plot types being highly significant. In contrast, in the Callunetum with the most fertile soil, a brown soil, initial establishment of *G. sylvaticum* was slightly higher without added fertiliser (23% rooted frequency) than with added fertiliser (17% rooted frequency). The continued persistence *G. sylvaticum* plants 3 years after sowing appeared to be related to innate soil fertility, with a steep drop in frequency of occurrence in the initially fertilised plots on peaty podsol, contrasting with a high level of persistence both in the agricultural grassland and in the Callunetum on brown soil (Miles, 1974).

8.5 | Seedling morphology

Figure 10 illustrates the developmental stages of *G. sylvaticum* seedlings from initial germination to the mature seedling stage. The following description has been assembled from direct observation of the seedlings and the descriptions in Muller (1978) and

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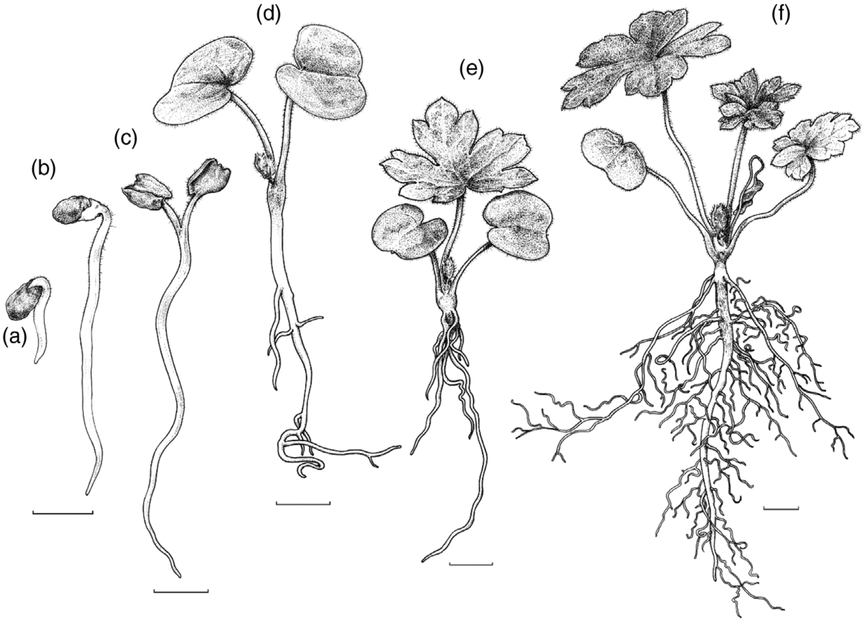

FIGURE 10 The development of *Geranium sylvaticum* seedlings from germination. Stages: (a) emergent radicle on 25 November 2023, (b) larger seedling root on 27 November 2023, (c) seedling with cotyledon on 29 November 2023, (d) appearance of first true leaf on 8 December 2023, (e) seedling with one fully grown true leaf on 21 December 2023 and (f) seedling at the four-leaf stage, with dicot leaves starting to die back, on 29 February 2024. Seeds were scarified, soaked in water for 1 h, and sown on 5 October 2023. Seedlings were grown from seed collected at Arla Burn farm near Middleton-in-Teesdale. As plantlets were uprooted, the age sequence is represented by different specimens. All scale bars indicate 5 mm. The seedlings were grown and drawn by Lucy Hulmes ©.

Sugorkina (1995). Germination is epigeal. The hypocotyl is 6–15 mm long, with short ordinary unicellular hairs towards the tip and slightly woody. The two herbaceous cotyledons are kidney-shaped and asymmetrically wider than long (mean length/width = 0.76), with a cordate base that is 14–16 mm wide and a tip that is emarginate cuspidate. Their petioles are 4–6 cm with unicellular ordinary and glandular hairs. An epicotyl is absent. True seedling leaves are alternate, have a 6–10 cm long petiole with chiefly ordinary unicellular hairs and adnate membranous stipules and are palmatipartite with seven rather wide lobed segments and a cordate base and a diameter of 0.5–3 cm. These leaves have mainly ordinary unicellular hairs and acuminate-cuspidate lobe tips.

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Geranium sylvaticum can occur in grasslands grazed by domestic herbivores including sheep and cattle (see also Section 4.2.1). In northern England, UK, hay taken from MG3 grassland meadows and containing *G. sylvaticum* is used as a winter feed for cattle and sheep (Jefferson, 2005). In Russia, *G. sylvaticum* is generally not preferred by livestock in green form but is consumed in hay (Grozdov in Sugorkina, 1995). Ellenberg (1952) considers *Geranium* spp. to be satisfactory fodder both in green and in dry form. *Geranium sylvaticum* is also consumed by various semi-domesticated and wild mammalian herbivores. In eastern Europe, it features on a list of plants consumed by the European bison (*Bison bonasus*) (Borowski et al., 1967). In northern European reindeer grazing lands, *G. sylvaticum* is considered preferred forage for reindeer (*Rangifer tarandus* L.) (Warenberg et al., 1997, in Bråthen & Oksanen, 2001). In a mosaic of coastal pine forest, birch scrub and heather near Trondheim, Norway, *G. sylvaticum* was present at 20% of the vegetation sampling sites, but it was found in just two of the rumens of 19 female red deer (*Cervus elephus* L.) shot in the area between May and September (Albon & Langvatn, 1992). The mean (±SD) percent volume of rumen content made up by *G. sylvaticum* was 0.3% ± 1.0%. In the central Italian Alps, Andreoli et al. (2016) studied the feeding ecology of alpine chamois (*Rupicapra rupicapra* L.) in autumn. Analysis of the rumen content of 35 samples revealed that families of monocotyledonous plants were most frequently represented in the diet. The mean (±SE) percentage volume made up of *G. sylvaticum* was exceptionally small (0.01% ± 0.01), indicating that it tended to be avoided by chamois. The dietary preferences of 11 captive mountain hares (*Lepus timidus* L.) in southern Norway were determined using cafeteria trials plus direct observations of radio-tracked individuals (Johannessen & Samset, 1994). In the cafeteria trials, *G. sylvaticum* was among the preferred species, with the 14th-highest mean preference index among the 54 plant species whose green parts had been offered to the hares. The diet composition of Norwegian lemming (*Lemmus lemmus* L.) and field vole (*Microtus agrestis* L.) was examined in various alpine habitats in central Norway, including willow meadows (meadows rich in tall perennial herbs and willow thickets), the habitat of *G. sylvaticum* (Saetnan et al., 2009). *Geranium sylvaticum*, which was infrequent in the study area compared to grasses and species of willow (*Salix* spp.), did occur

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in the stomach contents of both species at very low frequency, and appeared to have been selected against in their diets, based on the ratio of use versus availability (Saetnan et al., 2009). *Geranium sylvaticum* also was not significantly more damaged in the 'added *L. lemmus*' treatment of an enclosure experiment in a northern Norwegian tall-herb meadow, compared to a control treatment (Moen, 1990). On the other hand, significant damage in the form of clipped *G. sylvaticum* shoots was caused in another treatment included in the same experiment in which grey-sided voles *Craseomys rufocanus* (Sundevall) were added to enclosures (Moen, 1990).

Moen et al. (1993) created an artificial boreal forest floor community in a greenhouse to be grazed by four herbivorous vole species *M. agrestis* L., *Clethrionomys rufocanus*, *Clethrionomys glareolus* Schreber and *L. lemmus*. Calculation of Jacob's forage ratio showed that the two species of *Clethrionomys*, as indicated by positive values of this index, preferred *G. sylvaticum*. In contrast, *M. agrestis* and *L. lemmus* tended to avoid *G. sylvaticum*, as indicated by negative Jacob's forage ratio values, in agreement with Saetnan et al.'s (2009) findings. In a follow-up analysis of Moen et al.'s (1993) data, it was shown that *G. sylvaticum*, which, while non-toxic, had to be considered chemically defended due to its high content of digestibility-reducing tannins (Section 6.6), had suffered much higher shoot mortality than the toxic perennial *Actaea spicata* (Moen et al., 1996). This applied both when subjected to grazing by the more generalist herbivore *M. agrestis*, and when subjected to grazing by the more specialist *C. rufocanus*. However, as the experiment was only concluded when herbivores showed signs of significant nutritional stress or, in some cases, died (Moen et al., 1993), it is possible that the damage to *G. sylvaticum* was more accentuated in such an experimental setting that it would have been under field conditions where the animals would have been able to move on to other grazing patches. Despite high levels of shoot mortality in such controlled experiments, *G. sylvaticum* individuals were able to compensate for this by producing new shoots from meristematic rhizome tissue, thus replacing lost shoots by new growth (Ericson & Oksanen, 1987; Moen et al., 1996). Such capacity for regeneration has also been observed in southern Norwegian alpine grassland following sheep grazing (Section 'Grazing intensity').

The seeds of *G. sylvaticum* made up a small part of the diet of hazel grouse, *Tetrastes bonasia* L. near Arkhangelsk, Russia. An analysis of the crop contents of 268 birds collected throughout the year from 1981 and 1986 and again in 1988 indicated that in the autumn (September) diet of this species, the seeds of *G. sylvaticum* made up 0.2% in fresh weight of consumed plants (Borshchevsky, 2011).

Various studies have investigated invertebrate herbivory of *G. sylvaticum* and the effects on both the herbivores and the plants. For example, a litter decomposition laboratory experiment with the earthworm *Lumbricus rubellus* Hoffmeister, a key primary decomposer in alpine habitats in Austria, tested the impact of three aged litter types (an evergreen dwarf shrub, a perennial grass and the forb *G. sylvaticum*) plus a control of aged cow dung on various *L. rubellus* life history (fitness) metrics (Steinwandter et al., 2019). When *L. rubellus* fed on the *G. sylvaticum* litter type, all life history traits were affected positively, with the highest mean values observed for biomass increase, fertility and reproduction rate and the least number of days to reach pre-maturity, compared to the other three treatments. A cafeteria feeding experiment in microcosms combining various litter types, including that of *G. sylvaticum*, with a range of Austrian alpine soil macro-decomposers—two species of earthworm (*L. rubellus* and *Dendrobaena octaedra* Savigny; both Lumbricidae) and two millipede species (*Cylindroiulus fulviceps* Latzel and *C. meinerti* (Verhoeff), both Julidae, Diplopoda), found that the tested species were generalist or opportunistic feeders in that they fed on all offered litter types and qualities, resulting in few discernible food preferences and selections (Steinwandter & Seeber, 2020).

The seed-feeding larvae of the weevil *Zacladus geranii* (Paykull) are confined to feeding on larger species of *Geranium* in Britain and Ireland, including *G. sylvaticum* (Cawthra, 1957; Morris, 2008). They have been found to damage the seeds of *G. sylvaticum* in two ways, either via boring a small hole in the seed or by consuming part of the seed (Asikainen & Mutikainen, 2005a). In an experimental field population of *G. sylvaticum* in central Finland, *Z. geranii* caused pre-dispersal seed damage in 3.8% of 7107 seeds collected from 55 plants, with seed damage frequency neither affected by maternal gender morph type (female, intermediate, hermaphrodite) nor by flowering phenology (Varga, 2014).

Both the seedling and mature stages of *G. sylvaticum* appear to be unattractive to herbivorous slugs. A feeding experiment was carried out under controlled conditions in a heated greenhouse that involved the introduction of field slugs *Deroceras reticulatum* Müller to monocultures of seedlings of 23 grassland species (Barlow et al., 2013). It found that the seedlings of *G. sylvaticum* were the least damaged after 14 days of slug feeding, with very low mortality. Another study experimentally simulated the impact of various UK climate change scenarios with and without slug grazing (not identified to species) on a novel sown plant community consisting of 36 grassland forbs, including *G. sylvaticum*, grown in outdoor mesocosms (Alizadeh & Hitchmough, 2020). *Geranium sylvaticum* was one of the species whose biomass production was unaffected by slug grazing and was hence classed by the authors as unpalatable to slugs. In a '*cafeteria*' *style* experiment in which three different slug species (*Arion vulgaris* Moquin-Tandon, *Arion fuscus* (Müller), *Deroceras agreste* L.) were offered a free choice of leaf discs from mature individuals of various combinations of three out of 21 Central European montane meadow plant species, *G. sylvaticum* was consistently among the least preferred species in terms of leaf matter consumption (Scheidel & Bruelheide, 1999). In an additional experiment in which individuals of *D. agreste* were given a choice over a period of 24 h between a leaf disk from which leaf epidermal hairs had been shaved off, and a 'control' leaf disk from the same plant species with hairs left intact, the control leaf discs of *G. sylvaticum* remained untouched, and only a small amount of leaf matter had been consumed of the leaf discs which had their epidermal hairs shaved off (Scheidel & Bruelheide, 1999). This finding indicated that the low palatability of *G. sylvaticum* leaves was not just due to their morphology, but also potentially their chemistry (see Section 6.6).

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Palatability of *G. sylvaticum* was also found to be low in a feeding experiment involving first instar hatchlings of the grasshopper *Chorthippus parallelus* (Zetterstedt), a generalist insect herbivore (Unsicker et al., 2008). *C. parallelus* performed more poorly when reared on a single-species diet of *G. sylvaticum* leaves, compared to any of seven other single-species diets and compared to various combinations of three species or all eight species of grassland plant. On a *G. sylvaticum* only diet, no test individuals developed past the second instar, and 80% died in the first instar, indicating a very low level of palatability of *G. sylvaticum* leaves (Unsicker et al., 2008). In a field experiment carried out by Stein et al. (2010) in montane grassland in Germany, *G. sylvaticum* was among the species whose cover was unaffected by the combined application of aboveground and belowground insecticide, compared to unsprayed control vegetation. Its response contrasted on the one hand with species benefiting from application, mainly the highly palatable *Vicia cracca* and *Festuca rubra*, and with species negatively affected by application, that were either low-statured and hence likely prone to increased competition for light under reduced herbivory (*Ajuga reptans*, *Luzula campestris*) or that were known to be aromatic and hence likely to be chemically well defended against herbivory (e.g. *Achillea millefolium*, *Hypericum maculatum* and *Meum athamanticum*).

Various phytophagous arthropod species have been recorded as feeding on *G. sylvaticum* in Britain and Ireland (Table 6), including three sawflies, two beetles, two aphids and one mite. Two of these species are monophagous, four oligophagous and two polyphagous. The documented number of phytophagous insect and mites associated with *G. sylvaticum* is comparable to that of other robust perennial herbs that have a similar area of occupancy (number of 10 km squares present), biogeographic distribution (all boreal-montane species; Preston & Hill, 1997) and habitats in Britain & Ireland. *Cirsium heterophyllum* and *Trollius europaeus* occur in 592 and 580 10 km squares, respectively, whereas *G. sylvaticum* occupies 635 10 km squares. *C. heterophyllum* has eight species and *T. europaeus* has 11 (Collin, 1954; Ellis, 2023; Padovani et al., 2020; Pitkin et al., 2023; Redfern & Shirley, 2011; Spencer, 1972). In the Database of Insects and their Food Plants (DBIF) for Great Britain (Padovani et al., 2020), the same species have slightly lower numbers of associated insects listed, indicating that this database is not as comprehensive. *Geranium sylvaticum* has six herbivorous insect species listed alongside two mite species, whereas *C. heterophyllum* and *T. europaeus* have seven and three insect species, listed, respectively. That said, there are perennial herbaceous species that span a wider range of British climates and are less geographically restricted in Britain & Ireland, that have a greater number of phytophagous insects and mites such as *Pimpinella major* (618 10 km squares) with 17 species of insects and mites listed across the above sources, and nine insect species listed in the DBIF (Padovani et al., 2020).

No species of butterfly of the genus *Aricia* have yet been found feeding on *G. sylvaticum* in Britain & Ireland, although *Aricia agestis* (Denis & Schiffermüller), which has been found feeding on *G. sylvaticum* in Germany (Clarke, 2024), has been recorded in Britain and Ireland as feeding on *G. pratense* (Asher et al., 2001). In continental Europe, five widespread species of the family Lycaenidae—*A. agestis*, *Aricia nicias* Meigen, *Eumedonia eumedon* (Esper), *Cacyreus marshalli* Butler and *Aricia artaxerxes* Fabricius, subsp. *allous* Geyer—have all been recorded as feeding on *G. sylvaticum* (Clarke, 2024).

9.2 | Plant parasites

Eight species of parasitic fungi and oomycetes—including three types of mildew and two rusts—have been recorded from *G. sylvaticum*. These are listed and described in Table 7. Fifty-seven plurivorous species have also been recorded on mostly dead stems and leaves of *G. sylvaticum* (Fitter & Peat, 1994).

In a field survey in Sweden, it was investigated how well the rust fungus *Uromyces geranii* (DC.) G.H. Otth & Wartm. was able to naturally infect uninfected control plants and plants already infected with either one of two other fungi, *Puccinia geranii-sylvatici* Karsten or *Puccinia morthieri* Körn (Deng-Yi & Ericson, 2002). This was supplemented by an inoculation experiment in which the same three types of plant were deliberately inoculated with *U. geranii*. Both the field survey and inoculation experiment found *G. sylvaticum* plants already colonised by *P. morthieri* to be much more resistant to *U. geranii* than both healthy plants and plants already colonised by *P. geranii-sylvatici*. The authors also suggested that a more limited resistance to infection by *U. geranii* can result from prior infection with *P. geranii-sylvatici*, although in this case, not all measured parameters bore out such an interpretation (Deng-Yi & Ericson, 2002).

Korhonen et al. (2004) reported dark septate (DS) fungi colonising the roots of *G. sylvaticum* with a similar rate to AM fungi. DS colonisation in high- and low-light availability sites was consistently higher by about 20% in the shaded sampling locations. The role of DS fungi in plant physiology is not fully understood and seems to range from parasitic to mutualistic (e.g. Jumpponen, 2001). Korhonen et al. (2004) measured significantly lower flower production in the shaded locations, which might be linked to the high level of DS fungi; however, more specific research is required to clarify a role of DS fungi in the roots of *G. sylvaticum*.

9.3 | Plant diseases

A laboratory experiment by Dunbar and Stephens (1992) demonstrated that *G. sylvaticum*, inoculated at the 5-week-old seedling stage with the bacterial blight *Xanthomonas campestris* (Pammel) Dowson, possessed comparatively high resistance against this disease, as indicated by an 83% survival rate observed three weeks after inoculation, with under 50% of tissue blighted. This bacterial leaf spot is a serious disease of garden pelargoniums (*Pelargonium* x *hortorum*) but is also known to infect *Geranium* species.

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TABLE 6 Insect and mite species recorded in Britain and Ireland and recorded as feeding on *Geranium sylvaticum* (larva, unless otherwise specified) but excluding nectar and generalist pollen-feeding species.

Order/family/species	Plant part and feeding habit	Distribution & status	Source
Coleoptera			
Zacladus geranii Paykull	Larva—seeds/fruits Adult—flowers, leaves. Oligophagous on larger *Geranium* spp	Widespread (E, W) Rare (S)	1, 2, 3
Limobius borealis Paykull	On *Geranium* spp. Oligophagous	Scarce (E, W)	1, 4
Diptera			
Dasyneura geranii Kieffer[a]	Mines leaves of *Erodium* spp. and Geranium spp.	Very rare (E)	6, 9
Agromyza nigrescens Hendel[a]	Mines leaves of *Erodium* spp. and Geranium spp.	Rare (E, S, W)	9, 10, 11
Hymenoptera			
Tenthredinidae			
Fenella monilicornis Dahlbom	Mines leaves of *G. sylvaticum*	Very rare (S)	1, 5, 8
Ametastegia carpini Hartig	Larva free-living on *Geranium* spp. Oligophagous	Local (E, W, S & I)	1, 5
Macrophya albipuncta Fallén	Larva on *G. sylvaticum*	Local/uncommon (E, S)	1, 5
Hemiptera			
Aphididae			
Acyrthosiphon malvae Mosley	Flowers, leaves. Widely polyphagous	Local to widespread (E—southern)	6, 7
Aulacorthum solani Kaltenbach	Leaves. Widely polyphagous	Common and widespread (E, W, S, I)	7
Lepidoptera			
Amblyptilia punctidactyla Haworth[a]	Larva feeds on flowers and developing seeds of *Erodium* spp., *Geranium* spp. and a few other taxa. Oligophagous	Local (E, W, S & I)	1, 12
Acari: Eriophyoidea			
Aceria geranii Canestrini	Leaf gall On *Geranium* spp. Oligophagous	Scarce or underrecorded (E, W)	6

Species occurring in Britain and Ireland and recorded on G. sylvaticum in continental Europe

A *Dasyneura geranii* (Diptera: Cecidomyiidae) occurs on *G. sylvaticum* in continental Europe (Ellis, 2023) but has only been recorded on *Geranium sanguineum* and *Erodium cicutarium* in Britain and Ireland (Redfern & Shirley, 2011).

B *Agromyza nigrescens* Hendel, 1920 (Diptera: Agromyzidae) occurs on *G. sylvaticum* in continental Europe but has not been recorded on this species in Britain and Ireland. In Britain & Ireland there are general records for the species feeding on the *Geranium* spp. (Ellis, 2023; Pitkin et al., 2023; Spencer, 1972).

C *Amblyptilia punctidactyla* (Lepidoptera: Pterophoridae). The larva is a generalist seed predator and has been recorded feeding on *G. sylvaticum* in Sweden (Kolb et al., 2007). In Britain & Ireland there are general records for the species feeding on the Geraniaceae (Padovani et al., 2020).

Note: Key: E = England, W = Wales S = Scotland I = Ireland.

[a] Denotes species recorded as feeding on *G. sylvaticum* in continental Europe, but not yet in Britain and Ireland.

Sources: 1. Padovani et al. (2020), 2. Cawthra (1957), 3. Morris (2008), 4. Morris (2002), 5. Benson (1952), 6. Redfern and Shirley (2011), 7. Favret and Aphid Taxon Community (2025), 8. Liston (1995), 9. Ellis (2023), 10. Pitkin et al. (2023), 11. Spencer (1972), 12. Kolb et al. (2007).

10 | HISTORY

The only potential fossil record of *G. sylvaticum* for Great Britain in the Glacial and Post-glacial period appears to be a pollen grain recorded from Colney Heath (St Albans) dated to 13,560 B.P, which was noted as being either *G. pratense* or *G. sylvaticum* (Godwin, 1975). Based on the more northerly range of *G. sylvaticum* it was suggested to most likely be *G. sylvaticum*.

The first record of *G. sylvaticum* in Britain and Ireland documented in the literature is in the form of annotations made by T. Penny on C. Gesner's plant illustrations dated as by 1565 (Foley, 2006 in Pearman, 2017). The first herbarium record dates to 1670 (Ray in Pearman, 2017).

Observations of the flowers of *G. sylvaticum* provided the starting point and inspiration for fundamental investigations of the reproductive mechanisms of flowering plants carried out by the renowned

TABLE 7 Parasitic fungi and oomycota recorded as utilising the aboveground parts of *G. sylvaticum* in Britain and Ireland.

Species & Family	Type and location	Host(s)	Source
Plasmopara geranii-silvatici Săvulescu (Peronosporaceae) Oomycota	Downy mildew Forms yellowish to violet leaf blotches on the adaxial surface of the leaf and a white down on the abaxial side	Oligophagous on various *Geranium* species including *G. sylvaticum*	3
Plasmopara pusilla (de Bary) Schröter (Peronosporaceae) Oomycota	Downy mildew forms brown blotches on the adaxial surface of the leaf and a white down on the abaxial side	Oligophagous on various *Geranium* species including *G. sylvaticum*	1, 2
Podosphaera fugax (Penz. & Sacc.) U. Braun & S. Takam (Erysiphaceae) Ascomycota	Powdery mildew Forms hypophyllous colonies on leaves	Oligophagous on various *Geranium* species including *G. sylvaticum*	2, 3
Puccinia geranii-silvatici Karsten (Pucciniaceae) Basidiomycota	Rust fungus occurring aaaon the surface of the leaves and petiole	Oligophagous on various *Geranium* species including *G. sylvaticum*	3
Uromyces geranii (DC.) Fr. (Pucciniaceae) Basidiomycota	Rust fungus on the abaxial surface of the leaves. Uredinia are cinnamon brown and the aecia are orange and up to 2 cm in length	Oligophagous on various *Geranium* species including *G. sylvaticum*	1, 2, 3
Ramularia geranii (Westendorp) Fuckel (Mycosphaerellaceae) Ascomycota	Sac fungus (Ascomycetes). Forms brown spots on leaves	Oligophagous on various *Geranium* and *Erodium* species including *G. sylvaticum*	3
Venturia geranii (Fries) Winter (Venturiaceae) Ascomycota	Sac fungus (Ascomycetes). Forms spots on leaves with pycnidia (fruiting bodies)	Oligophagous on various *Geranium* species including *G. sylvaticum*	2
Pirottaea paupercula Nanff. (Dermateaceae) Ascomycota	Sac fungus (Ascomycetes) apothecium (fruiting bodies) scattered and erumpent on stems	Oligophagous on various *Geranium* species including *G. sylvaticum*	1

Sources: 1. Ellis and Ellis (1997), 2. British Mycological Society (2024), 3. Woods et al. (2024).

German naturalist and botanist Christian Konrad Sprengel (1750–1816), one of the founders of the discipline of pollination biology. In the introduction to his seminal book *Das Entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen* ('The discovered secret of nature in the structure and fertilization of flowers'; Sprengel, 1793), he remarked 'When in the summer of 1787, I carefully examined the flower of wood crane's-bill (Geranium silvaticum) [sic] flower, I found that the lower part of its petals was furnished with fine soft hairs, on the inside and on both margins' and concluded 'If one assumes that the five nectar droplets in the flowers, secreted by the same number of glands, are intended as food for certain insects, one might similarly not consider it unlikely there would also be provisions for this nectar not to be spoiled by rain, and that these hairs were present for this purpose'.

Historically, *G. sylvaticum* was at least sometimes considered a weed by farmers (Brenchley, 1920). The great vigour displayed by *G. sylvaticum*, particularly under fairly to highly fertile soil conditions, meant that when occurring in great abundance, in semi-natural grassland, it outcompeted other species of higher nutritional value to livestock. This was for example the case in East Lancashire after use of the chain harrow and roller had lapsed (Milburn, 1916), but also, in fertile subalpine grassland in the Alps (Gams, 1924).

10.1 | Medicinal and other uses

Geranium sylvaticum is listed as a medicinal herb in Iceland with use of the whole plant including the roots (Róbertsdóttir, 2016). It is known as an astringent, haemostatic and vulnerary (Róbertsdóttir, 2016). Halldórsson (1783, in Róbertsdóttir, 2016) states 'This herb heals sores, closes and draws together. It disperses clotted blood when applied externally. If it is boiled in wine and then taken in, it eliminates urinary retention and urinary stones. It also lessens women's menses. The juice of the herb is said to cure cancer in the female

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breast by drawing out all toxins there from. Similarly, it cleanses other sores'.

Geranium species contain geraniol, an essential oil and geraniin, a hydrolysable tannin (see also Section 6.6). Geraniol has antimicrobial properties (Pattnaik et al., 1997) and can also inhibit tumour growth (Burke et al., 1997). Geraniin has also been noted to inhibit tumour activity (Li et al., 2013), but also has other properties, including being antibacterial, antifungal and antiviral (Goahr et al., 2003; Yang et al., 2007). It also has anti-inflammatory properties (Jiang et al., 2016; Küpeli et al., 2007). Pronounced anti-inflammatory properties of *G. sylvaticum* root extracts were identified in a Norwegian study (Eltvik et al., 2025). Methanol extracts of *G. sylvaticum* from aerial parts of plants in Bulgaria indicated good antioxidant activity based on free radical scavenging activity (Nikolova et al., 2010). This has also been reported by Lin et al. (2008). IC$_{50}$ values (half-maximal inhibitory concentration, a measure of a drug efficacy and how much of the drug is needed) were less than $50\,\mu g\,ml^{-1}$ in standard antioxidant assays using DPPH radicals (Nikolova et al., 2010).

The activity of acetylcholinesterase is a main target for the symptomatic treatment of Alzheimer's disease (Vecchio et al., 2021). Ethanolic extracts of aerial parts of Icelandic *G. sylvaticum* plants inhibited acetylcholinesterase activity in vitro, with IC$_{50}$ values of $3.56\,mg\,m\,L^{-1}$ (Sigurdsson & Gudbjarnason, 2007).

Anthocyanins are believed to have medicinal properties, and five anthocyanin glycosides have been isolated from the flowers of *G. sylvaticum* (Andersen et al., 1995, Section 6.6). The major anthocyanin identified was malvidin 3-O-(6-O-acetyl-fl-D-glucopyranoside) -5-O-fl-D-glucopyranoside. Minor anthocyanins were identified as 3,5-diglucosides of malvidin and cyanidin, and 3-glucosides of cyanidin and delphinidin (Andersen et al., 1995).

Demasi et al. (2021) analysed the phytochemical composition of 22 wild edible flowers including *G. sylvaticum*. *Geranium sylvaticum* possessed the highest relative antioxidant activity together with *Rosa canina*, *R. pendulina* and *Paeonia officinalis*.

Several medicinal uses for *G. sylvaticum* have been listed in the Russian-language literature, including for the treatment of rheumatism, bleeding, gastrointestinal illnesses (including diarrhoea, dysentery and enterocolitis), kidney stones, gout, angina pectoris and as an astringent, haemostatic agent, for the control of bleeding (Sokolov et al., 1988). The alcoholic extract of the aerial part has been found to inhibit the activity of acetylcholinesterase (Petrova & Budantsev, 2010). Furthermore, a high concentration in the plant of methionine, an amino acid essential to humans, means that 10 g of dry leaves and stems can supply 15% of human daily need in this amino acid (Brezgin, 1973).

According to Grossheim (1952), the roots of *G. sylvaticum* contain an ellagic acid that can be used as a tanning agent for leather. Also mentioned in the literature has been the use of the flowers of *G. sylvaticum* for dying fabrics blue (Gams, 1924; Grossheim, 1952). According to Gams (1924), in Iceland, this practice dates to pre-Christian times. Gams (1924) also mentions their use for dying Easter eggs in the Black Forest, Germany, and the production of a yellow colourant from the plant in Norway.

10.2 | Cultivation

According to Kingsbury (2016), *G. sylvaticum* was illustrated in *Hortus Eystettensis* (Besler, 1613), but it was only occasionally cultivated in the early modern period from *c.* 1500 to 1800; however, it received much more interest as an ornamental horticultural plant from 1946 onwards. Since then, various horticultural cultivars have been derived from wild colour-variants, including white, pink and deep blue cultivars (Yeo, 2001). In northern Scandinavia, cultural relict populations from early cultivation have persisted in the close surroundings of historical places such as monastery ruins, churches, castles and old farms and villages (Solberg et al., 2013).

11 | CONSERVATION AND MANAGEMENT

11.1 | Status

Geranium sylvaticum has been classified as of Least Concern under IUCN criteria in the GB vascular plant Red List (Stroh et al., 2025). However, in the England Red List (Stroh et al., 2014), it is listed as Near Threatened. In the Wales Red Data List (Dines, 2008), it is listed as Critically Endangered with fewer than 30 individuals extant across four locations. In Wales, the small populations are outliers as here, the species reaches the southern edge of its core range in Britain and Ireland. It is listed as Vulnerable in the Irish Red List (Wyse Jackson et al., 2016) and the entire Irish native population is confined to Northern Ireland. There, it is very rare, with native localities confined to an area between Larne and Glenarm, County Antrim (see Section 1). It is listed as a Northern Ireland priority species and a Northern Ireland Species Action Plan for it has been developed (Department of Agriculture, Environment, & Rural Affairs, 2005).

In the most recent vascular plant hectad Atlas for Britain and Ireland (Stroh, Walker, et al., 2023), Hill's (2012) Frescalo modelling approach was used to adjust trend estimates for differences in recorder effort across different time periods. For Great Britain, the results indicated a declining long-term trend in occurrence for the period 1930–2019 and a stable to moderately declining more recent short-term trend for the period 1987–2019. Similar long-term trends have been quantified also for England and for Northern Ireland (Stroh, Humphrey, et al., 2023). For England, the short-term trend for the period 1987–2019 indicates a more pronounced decline than for Great Britain as a whole, particularly since about 2005 (Stroh, Humphrey, et al., 2023). In contrast, for Scotland, the trend data suggests an increase since about 2005 (Stroh, Humphrey, et al., 2023), that may be due to an increase in records in northern Scotland, due either to better recording or possibly indicating a slight northerly shift in the distribution of the species (Stroh, Walker, et al., 2023). In Wales, the long-term trend for the period 1930–2019 was rather stable, whereas, as for Scotland, the short-term trend indicates some recent increases (Stroh, Humphrey, et al., 2023). However, change statistics based on hectad occupancy may not necessarily be a sensitive indicator for changes taking place at much smaller

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spatial scales, for example, in terms of the number of individual site-specific populations or of average population size within sites (Rich & Karran, 2006).

Geranium sylvaticum is identified as an indicator of high-value habitat. Walker (2018), for example, identified *G. sylvaticum* as an axiophyte (a species indicative of high-habitat quality) in 11 out of 12 (92%) British counties that have produced lists of axiophytes and where the species is present. Similarly, the Nature Conservancy Council's England Field Unit drew up lists of unimproved mesotrophic grassland indicator species and allocated *G. sylvaticum* to the category of a species highly characteristic of unimproved mesotrophic grasslands, though also occurring on mesic soils in other habitats such as mires and woodlands (Rowell & Robertson, 1994). The grassland indicators were allotted numerical scores depending on their level of affinity for high-value semi-natural grassland. The numerical values are on a 4-point scale (1, 2, 4 and 8) with *G. sylvaticum* assigned a value of 4. Plant species tolerant of higher nutrient status soils and that also occur widely in semi-improved grasslands scored 1 whereas species virtually confined to semi-natural mesotrophic grassland scored 8. The total scores for individual indicator species for grassland sites surveyed during the 1980s and 1990s were used as an aid to site evaluation for conservation.

Starr-Keddle (2022) used indicator species to evaluate the success of upland hay meadow restoration in the North Pennines. Grassland plant species were assigned an indicator score ranging from −2 through to +4. Positive indicator species were defined as plants that are typical of upland hay meadows. As a good indicator for high-quality MG3 upland hay meadow habitat, *Geranium sylvaticum* was given a +3 score.

Because in its semi-natural habitats, *G. sylvaticum* is almost always confined to good condition sites of high biodiversity, its presence can help to indicate desirable ecological conditions for certain habitats, for example in terms of soil fertility and moisture, as well as sward composition and structure. Not surprisingly, therefore, it has been used as a positive indicator or a desirable forb in the Common Standards Monitoring system (CSM) for tall-herb communities including MG2 *Arrhenatherum elatius*-*Filipendula ulmaria* tall-herb grassland and upland hay meadows (MG3 *Anthoxanthum odoratum*-*Geranium sylvaticum* grassland) (Robertson & Jefferson, 2000). The CSM system aims to determine the condition of habitats or interest features within Sites of Special Scientific Interest (SSSIs).

The British and Irish plant communities with which *G. sylvaticum* is associated (see Section 3 and Table 2), either form part of habitats listed on Annex I of the European Commission Habitats and Species Directive or are covered by the country-level lists of priority habitats or listed as communities of high-botanical value in the GB guidelines for selection of biological SSSIs (JNCC, 2024a, 2024b, 2024c). Special Areas of Conservation (SACs) designated for the Annex I habitats in the UK were already listed as Areas of Special Conservation Interest under the pan-European Emerald Network under the Bern Convention, prior to the UK leaving the EU. These sites will continue to be protected through existing domestic UK legislation (the Habitat Regulations) which implements and retains obligations from the Habitats Directive (JNCC, 2024d). One of the key Annex I habitats for *G. sylvaticum* in the UK are mountain hay meadows (EUNIS code: H6520) for which three SACs were originally designated, covering all the habitat notified as SSSI in England and Scotland (JNCC, 2024e). Of the habitats listed in Table 2 all but three are listed as either Vulnerable or Endangered in the European Red List of terrestrial habitats (Janssen et al., 2016). The exceptions are upland mixed ash woodland, upland calcareous grassland and the two inland-rock tall-herb communities listed in the table which are all Least Concern (LC).

One third (442 out of 1359) of the occurrences of *G. sylvaticum* recorded between 2010 and 2019 at the 100 m × 100 m scale within British and Irish map hectads in which the species is assumed to be native in Plant Atlas 2020 (and therefore excluding introductions) intersect or occur entirely within SSSI boundaries (Tom Humphrey and Kevin Walker, BSBI, pers. comm.), indicating that about one third of native populations benefit from statutory protection. The corresponding figures for the three individual countries are as follows: (England—160 out of 460 records, that is 35%; Scotland—279 out of 894 records, i.e. 31%; Wales—three out of five records, i.e. 60%). Percentages based on the longer period of records from 1970 to 2019 are rather similar (GB: 34%; England: 35%; Scotland: 34%; Wales: 58%). Not benefiting from statutory protection are populations on road verges such as in the north Pennines and Cumbria in northern England, although some of these may benefit from status as non-statutory Local Wildlife Sites or protected road verges, with these latter voluntary schemes usually being administered by local Wildlife Trusts and the the local highway authorities.

11.2 | Conservation

Studies on the conservation of *G. sylvaticum*, for example by ensuring favourable habitat management or habitat restoration and species re-introduction, have mainly focused on its semi-natural secondary habitats, such as upland hay meadows and road verges. Its primary habitats, such as riverine and woodland habitats, have been focused on by some studies investigating the impacts of climate change (Section 11.3).

11.2.1 | Traditional management

Long-term traditional management of MG3 upland hay meadows in the northern Pennines, Cumbria and Lancashire, that is of the key habitat for *G. sylvaticum* in England, is an ancient practice. It involves sheep grazing in spring, no grazing between late May to July (shut-up period), hay making from mid-July to August, autumn grazing with cattle, low applications of farmyard manure (maximum 12 t/ha/year) and occasional liming (Critchley et al., 2007; Jefferson, 2005; Rodwell, 1992). The process of hay making allows seeds to fall back to the soil and transfers seeds across meadows, facilitating dispersal (Pacha, 2004). Phenological studies from a meadow

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in Ravenstonedale, Yorkshire (see also Section 7), indicate that *G. sylvaticum* develops ripe seed around 12th July which corresponds with a mid-July cut date, allowing the seed to be shed during this time (Smith & Jones, 1991). Further experiments set-up by Smith et al. (Smith et al., 2000, 2003, 2008, 2017) found that *G. sylvaticum* favours a short spring grazing season, an early shut-up/closure of the meadows and a late cut date in August (see also Section 4). In the colder North Pennines, *G. sylvaticum* requires a 3-month growing season to flower and set seed (Starr-Keddle, 2018), thus benefiting from a long shut-up period, with spring grazing stopped before early May and preferentially a later cut date (Starr-Keddle, 2022).

In Central Europe, historically, semi-natural montane grasslands providing habitat for *G. sylvaticum* were regularly cut twice a year, with farmyard manure additions (Hegedüšová et al., 2012). In Finland, *G. sylvaticum* is a key component of meadows which were originally grazed with cattle, sheep or horses but are now often just mown (Hellström et al., 2006; Huhta & Rautio, 1998).

Road verges and uncut edges are important habitats for *G. sylvaticum* where fragments of MG3 upland hay meadow vegetation, including the MG3c subcommunity (see Section 3), can be found (Gamble & St. Pierre, 2010; O'Reilly, 2011; Pacha, 2004). The lack of grazing on road verges may allow earlier growth of *G. sylvaticum* so that plants are bigger and can flower sooner, isolating populations in meadows and road verges (Pacha, 2004). Road verge management should aim to emulate upland hay meadow management, with at least one late-July cut, and arisings removed if possible. Pasture and riverbank management should avoid high grazing intensity, aiming for low grazing intensity in early spring, late summer or autumn, but avoiding grazing during the flowering period in June and July (Gamble & St. Pierre, 2010; Stroh et al., 2019). In other near-natural and natural habitats of *G. sylvaticum*, such as, for example tall herb ledge communities, access by livestock would be inimical for many species, including *G. sylvaticum*.

11.2.2 | Management intensification

The recent widespread decline in meadow botanical diversity has been related to changes in management such as high stocking densities in spring, later shut-up dates, earlier cutting times, a shift from hay making to silage production, increases in soil fertility with inorganic fertiliser use, re-seeding with *Lolium perenne* and *Trifolium repens* and loss of meadows to pastures (Bradshaw, 2009; Critchley et al., 2007; Jefferson, 2005; Kirkham et al., 2014; Pacha & Petit, 2008; Rodwell et al., 2007; Smith et al., 2003, 2008, 2017; Starr-Keddle, 2014, 2018). In addition, even in the most traditionally managed meadows, several studies have shown that species richness is reduced with low applications of farmyard manure at the rate of 12 t/ha/year (Kirkham et al., 2014; Smith et al., 2003), the effects of which may be compounded by atmospheric nitrogen deposition (Tomlinson et al., 2021). Other studies have shown that traditional meadows are frequently spring grazed until the end of May and cut around the 15th of July which is a short growing period for *G. sylvaticum* (Critchley et al., 2007; O'Reilly, 2010; Pacha & Petit, 2008; Smith et al., 2017). Smith and Jones (1991) analysed past farmer diaries and found that the use of faster modern machinery reduced the duration of hay-making on individual Pennine Dale farms by 35–61% between the 1950s and the 1970s, which would have impacted flowering times and seed set.

A resurvey of 47 upland hay meadows in Yorkshire in 2003 previously surveyed in 1980 found a general decline in habitat quality characteristics and disappearance of *G. sylvaticum* from 40% of the fields (Pacha & Petit, 2008). Extinction was higher in some dales than others, with Ribblesdale (North Yorkshire) showing the sharpest decline, losing 80% of site populations of *G. sylvaticum* from its fields, followed by Wharfedale (60%) and Malhamdale (50%) (Pacha, 2004). Bradshaw (2009) undertook surveys in 1967 in Teesdale which were repeated in 2003/4. In Newbiggin / Holwick, *G. sylvaticum* had dropped from being previously found in 52 fields to being found in 44 fields during the repeat survey. Road verges and river margins were found to become increasingly important habitats for the species, especially in areas where the species had disappeared from adjacent meadow habitats, although the road verges were becoming dominated by coarser grasses (Bradshaw, 2009). Starr-Keddle (2014) compared surveys undertaken over a 30-year period in Upper Teesdale and showed that several characteristic MG3 species (Rodwell, 1992)—such as *G. sylvaticum*, *Alchemilla* spp., *Conopodium majus*, *Trollius europaeus* and *Sanguisorba officinalis*—had declined (Starr-Keddle, 2014). These studies concluded that the declines were caused by a combination of changes in grazing management, an increase in the use of inorganic fertilisers, decrease in lime application and a widespread shift from haymaking to silage production (Bradshaw, 2009; Pacha, 2004; Pacha & Petit, 2008; Starr-Keddle, 2014). The disappearance of *G. sylvaticum* from Cumbrian hay meadows was similarly attributed to excessive use of fertilisers and the shift from hay to silage production (Halliday, 1997). The latter shift tends to be associated not just with increased fertiliser use, but also with other changes to management, such as, for example a higher cutting frequency and faster grass crop removal allowing fewer opportunities for seeds being shed, all of which could have individually contributed to this disappearance.

Across Europe, montane meadows in the Triseto-Polygonion alliance have substantially declined due to shifts from traditional management practices to more intensive ones, and due to abandonment and subsequent scrub encroachment (Eriksson et al., 2002; Hegedüšová et al., 2012; Rodwell, 2015; Rodwell et al., 2007). In Scandinavia, meadows were once extensive, created through large-scale forest clearance across the countryside. After the 1940s, meadows were abandoned, converted to arable fields or planted with trees, resulting in a decline in their area extent by almost 90% (Eriksson et al., 2002). In the 1880s, in Finland, the area of semi-natural grassland peaked at 1.6 million hectares, but the meadows have steadily declined (Soininen, 1974). Huhta and Rautio (1998) compared two meadows that had regularly been mown in late June, with abandoned meadows where mowing and sheep grazing had stopped. *Geranium sylvaticum* was found in the abandoned meadows, growing

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alongside *A. odoratum*, *M. sylvaticum*, *R. acris* and *T. pratense*. They concluded that late June cut dates decreased diversity by reducing perennial, tall-growing species (Huhta & Rautio, 1998). In Finland, *G. sylvaticum* is found in wooded meadows that used to have cattle grazing but have since been abandoned (Hansson & Fogelfors, 2000; Kotiluoto, 1998). *G. sylvaticum* increased in areas where the tree cover was manually thinned (Hansson & Fogelfors, 2000), and where mowing and aftermath grazing was reintroduced (Kotiluoto, 1998).

11.2.3 | Conservation management

Since the late 1980s, farmers have been entering agri-environment schemes which aim to maintain high biodiversity within species-rich grasslands, by adopting low-intensity farming practices such as low applications of farmyard manure, a restriction on the use of inorganic fertilisers and a prescribed cut date of 8th July, 15th July or 22nd July, depending on location (Critchley et al., 2003, 2007; Rodwell et al., 2007). However, despite these schemes, the botanical diversity of semi-natural grasslands has continued to decline into the 21st century (Critchley et al., 2003, 2007; Rodwell et al., 2007). Several authors have commented on inflexible set prescriptions, citing the fixed dates for hay cutting, stocking rates, farmyard manure rates and shut-up periods as damaging to the species richness and diversity of upland hay meadow habitats (Rodwell, 2015; Rodwell et al., 2007; Starr-Keddle, 2022). The uniform cutting time seems to be favouring MG6 plant species such as *Rhinanthus minor* and *Trifolium pratense* which can regularly flower and set seed before the 15th of July cut date. In contrast, several MG3 species which typically set seed after the 15th of July, such as *G. sylvaticum*, *Cirsium heterophyllum* and *Sanguisorba officinalis*, are gradually disappearing from meadows, e.g. in the North Pennines (Starr-Keddle, 2022). These latter species may no longer be provided with at least occasional opportunities for seed set as would have previously been the case in bad weather years when farmers would have been forced to delay hay cutting. A survey of 33 meadows designated as SSSI in the North Pennines found a 48% decline in botanical quality (O'Reilly, 2010). As a result of the changes in meadow management as described above, plant communities in these meadows are shifting from NVC MG3 to NVC MG6 meadows (O'Reilly, 2010).

In the Yorkshire Dales, *G. sylvaticum* declined in meadows both inside and outside agri-environment schemes (Pacha, 2004); however, the rate of decline was more severe outside of schemes and in less strict AES options allowing still some application inorganic fertiliser and with more extended grazing. Overall, meadows in agri-environment schemes were characterised by greater habitat quality, with abundant *G. sylvaticum* particularly related to low grazing in the spring and autumn (Pacha, 2004). Hewins et al. (2005) showed that priority habitats within agri-environment schemes are more likely to be in favourable condition as those outside agreements, although in the case of upland hay meadows, only 7% overall (12% of sites inside of SSSI designation) were in favourable condition; the authors thought it unlikely that species-rich upland hay meadows existed in good condition outside of SSSI designation (Hewins et al., 2005). Critchley et al. (2007) resurveyed 116 Pennine Dales upland hay meadows in 2002 that had been previously surveyed in 1987, recording five 1 m × 1 m quadrats in meadows that had been in agri-environment schemes. Set prescriptions included a shut-up around 15th May and a cut date of 8th July, 15th July or 22nd July. Broad-leaved herbs such as *G. sylvaticum* favoured low-intensity spring grazing and a cut date after 22nd July. Results indicated that intense spring grazing and earlier cut dates should be avoided, with a preference for later cut dates after 22nd July (Critchley et al., 2007). In a study analysing baseline and repeat surveys of 98 meadows in Upper Teesdale, botanical diversity had declined over time, along with MG3 species such as *Alchemilla* spp., *G. sylvaticum* and *Sanguisorba officinalis*, both in meadows designated as SSSI, as well as in meadows in basic agri-environment schemes, although species richness and diversity were higher in SSSI meadows (Starr-Keddle, 2014). Overall, these various studies concluded that agri-environment schemes did protect the habitat in the most species-rich sites, despite a decline in habitat quality (Critchley et al., 2007; Hewins et al., 2005; O'Reilly, 2010; Pacha, 2004; Pacha & Petit, 2008; Starr-Keddle, 2014).

11.2.4 | Habitat quality and connectivity

Pacha and Petit (2008) surveyed meadows in the Yorkshire Dales and—using an index of habitat quality for *G. sylvaticum* based on the occurrence of a range of other species thought to be positively or negatively associated with the quality of its habitat—showed that the extinction rate of *G. sylvaticum* was higher in low-quality and isolated fields, with habitat quality also being linked to degree of isolation. The remaining upland hay meadows differed in size and spatial arrangement, with the potential to affect the continued floristic decline in these meadows (Pacha & Petit, 2008), although larger upland hay meadows may be protected from the consequences of fragmentation (Jefferson, 2020). The effects of spatial isolation have also been demonstrated by population genetic studies by Shi et al. (2021) on Iranian populations of *G. sylvaticum* and by Ernst et al. (2013) on German populations (see taxonomic description). These studies indicate genetic differences among populations, due to isolation by distance and limited gene flow. Such findings indicate that continued isolation of habitat patches would over time lead to a loss of genetic diversity by drift (Ernst et al., 2013).

Given the potential for future declines in upland hay meadow quality and connectivity, for example as some habitat may cease to be sympathetically managed, the conservation of ‘natural’ ecosystems supporting *G. sylvaticum* is also important. Such habitats include among others limestone woods, limestone pavements and montane rock outcrops, where ‘open’ conditions are maintained by natural processes such as droughts or rockfalls. The continued light management of road verges supporting populations of *G. sylvaticum* also deserves attention, as does the ecological restoration of suitable habitat and populations (discussed below in Section 11.2.5). Extant upland hay meadows, remnant tall-herb vegetation found

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in patches in isolated meadows, on banks and edges of improved fields, steep uncut banks, riverbanks, road verges and in woodland glades all strengthen connectivity between fragmented habitat patches, playing an important role for the survival of *G. sylvaticum* (Jefferson, 2020; Pacha, 2004; Pacha & Petit, 2008).

11.2.5 | Restoration

Several methods are available for restoring the botanical diversity of meadows, such as overseeding with purchased seed mixes, brush harvesting, green hay transfer from donor meadows or planting of wildflower plug plants (Kirkham et al., 2012; Smith et al., 2000, 2003, 2008; Starr-Keddle, 2018, 2022; Sullivan et al., 2020). In the North Pennines, Starr-Keddle (2022) harvested green hay from MG3b donor meadows with species such as *G. sylvaticum*, *Alchemilla* spp., *Conopodium majus* and *Sanguisorba officinalis and* spread seed onto 42 MG6 receptor meadows with good populations of *R. minor* and *T. pratense* (classed as 'second-stage enhancement'). Botanical data from monitoring surveys showed that *G. sylvaticum* slightly increased in 12 meadows with seed addition, with 28 meadows showing some shift from an MG6 community to an MG3b community (Starr-Keddle, 2022). Starr-Keddle (2018) explained that *G. sylvaticum* was harvested around the third to fourth week of July, but it was difficult to collect the seeds of *G. sylvaticum* as they needed to be harvested when completely ripe, but just before the seedhead 'pings' (Starr-Keddle, 2018). Starr-Keddle (2022) concluded that second-stage enhancement did not work well for characteristic MG3 plants such as *G. sylvaticum*, *Alchemilla* spp. and *Sanguisorba officinalis* (Starr-Keddle, 2022). This trend was also found in the Forest of Bowland and the Yorkshire Dales, where *Alchemilla xanthochlora* Rothm. and *G. sylvaticum* did not establish in 18 receptor meadows that had seed addition using green hay transfer, despite the target species being key indicators in the donor meadows (Sullivan et al., 2020). In Cumbria, an MG3b donor meadow with frequent *G. sylvaticum* was used to restore an MG6 meadow using green hay transfer; however, *G. sylvaticum* was not recorded in the receptor meadow during monitoring surveys (Kirkham et al., 2012). In a long-term grazing, cutting and seed addition experiment conducted by Smith et al. (2000, 2003, 2008) on an MG6 upland hay meadow at Colt Park, Yorkshire, UK, one-year-old plants of *G. sylvaticum* were planted into all plots that had received a seed mixture of various species including from commercial sources and seed collected from road verges. *Geranium sylvaticum* was recorded in a few plots with low-soil fertility and 21st July cut date, but the target MG3b community was hard to establish (Smith et al., 2000, 2003, 2008). Starr-Keddle (2018) collected seeds of species including *G. sylvaticum* and grew wildflower plug plants. Early monitoring has shown that some of the broad-leaved herbs planted into the edges of meadows have survived, with the larger plants of *G. sylvaticum* grown in bigger pots establishing better than smaller individuals (Starr-Keddle, 2018). These studies suggest that establishing *G. sylvaticum* into meadows is difficult and the focus should be on maintaining the species richness of existing species-rich upland hay meadows through traditional management practices (Pinches et al., 2013), including low levels of spring grazing until early May and a late summer cut after 21st July, alongside a plug planting regime.

11.3 | Climate change

In general terms, over land, the most recent climate change predictions for the UK—UKCP18 (Met Office, 2018) predict a move towards warmer, wetter winters and hotter, drier summers over the next 50 years. As a cold-adapted, boreal-montane species (Preston & Hill, 1997; Wei et al., 2024; see also Section 1), *G. sylvaticum* is potentially sensitive to such climate warming (McDonald, 1994). The climate parameters for its distribution (Section 2.1) suggest that under the above climate change scenarios, its range, distribution and abundance in Britain and Ireland may change. These changes are likely to involve contraction in range and reductions in abundance due to local extinctions, but also conceivably some local expansion to higher altitudes. Such altitudinal shifts have been reported from Scandinavia where previously unsuitable high-alpine habitats have become favourable for *G. sylvaticum* due to climate warming reducing the duration and extent of snow cover (Kullman, 2016; Niittynen et al., 2018; Vanneste, 2016; Virtanen et al., 2003).

Jansson et al. (2019) investigated the impact of changes in riverine flow regimes on the habitat extent of riparian plant communities from five sites in river reaches with low channel slope and baseflow on a boreal catchment in northern Sweden. In Europe, climate forecasts predict lower annual spring flood peaks and higher winter flows which would result in narrower riparian zones. Jansson et al. (2019) modelled the hydrological niche of riparian plant species based on the probability of occurrence along gradients of flood frequency and duration and used predicted future water-level fluctuations (based on climate models and IPCC emission scenarios) to calculate changes in flow-related habitat availability of individual species. The transects across the river included upland species where the upper elevational limit lies above the upper limit of the riparian zone, that is flood conditions did not determine the upper limit of occurrence. The predicted response of upland species was highly dependent on how far down into the riparian zone the species occurred, with upward shifts of the lower limit for the species with the longest elevational extent, to increasingly large downward shifts the higher up in the riparian zone the lower limits occurred (Jansson et al., 2019). For those species in the upland category, more than half are predicted to shift their lower limit further down in response to shorter flood durations. However, specifically in relation to *G. sylvaticum*, modelling predicted no significant changes in the lower elevational limit in these riparian situations (Jansson et al., 2019).

Berry et al. (2007) modelled the potential impacts of climate change on the future British and Irish distribution of 120 Biodiversity Action Plan species, including *G. sylvaticum* and 37 other vascular plant species, by characterising the bioclimatic envelopes of these species. Modelling was carried out using a 5 km

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resolution, comparing six UKCIP02 climate change scenarios covering the 2020s, 2050s and 2080s. The role of climate uncertainty was further investigated by applying 28 climate change scenarios to six species, again including *G. sylvaticum*, to explore uncertainties from three sources: future greenhouse gas emissions, imperfect understanding of climate science and modelling and natural climate variability (Berry et al., 2007). For *G. sylvaticum*, virtually no gains in potential suitable climate space were predicted under any of the scenarios, with a substantial reduction in the overall amount of potential suitable climate space for *G. sylvaticum* and losses occurring throughout England, Wales, Ireland and southern Scotland (Berry et al., 2007). As a result, the distribution would become centred on northern, western and central Scotland by the 2050s and 2080s (Berry et al., 2007). However, these predictions must be qualified in terms of a lack of consideration of the models for biotic interactions, dispersal capabilities and the possibility of rapid adaptation (Berry et al., 2007).

To assess species' responses to climate warming, Wei et al. (2024) set up a cross-continental transplant experiment involving five regions covering large macroclimate and microclimatic gradients across Europe (43° N–61° N), and the transplantation of 12 understory plant species common in European temperate forests, including *G. sylvaticum*. Transplant sites were in dense and open forests stands and at forest edges and in interiors. Over 3 years, they examined the effects of the warming tolerance of each species across all transplanted locations on local plant performance, in terms of survival, height, ground cover, flowering probabilities and flower number (see also Wei, 2023). Using species' upper thermal limits (the temperature at the warm limit of their distribution range) minus the local habitat temperature experienced at a given location, they calculated warming tolerance (ΔT_{niche}) as a species-specific thermal vulnerability index (Wei et al., 2024), as a predictor of how much more warming a given species can tolerate before negative impacts are expected to occur. For *G. sylvaticum*, performance indices for all five captured aspects performance showed consistently positive responses to ΔT_{niche} (Wei et al., 2024). This could be due to the presence of thermal regulatory and adaptive strategies and plasticity (Wei et al., 2024). However, it would be premature to conclude that *G. sylvaticum* is necessarily resilient to climate warming, with further long-term research required on within-species dynamics and their effects on plant performance in a warming climate (Wei et al., 2024). Overall, the weight of evidence, especially the outcomes from the modelling undertaken by Berry et al. (2007), suggests that the distribution and range of *G. sylvaticum* in Britain & Ireland is likely to contract with future warming.

AUTHOR CONTRIBUTIONS

Markus Wagner coordinated the writing of the manuscript. Markus Wagner, Richard G. Jefferson, Ruth E. Starr-Keddle, Sandra Varga, Irina Tatarenko and Duncan B. Westbury wrote sections of the manuscript, and Lucy Hulmes produced the seedling drawings for Section 8.5. All authors read and commented on all parts of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

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No data were used in this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Means or ranges of selected topsoil chemical characteristics for vegetation types and plant communities containing a regular component of *G. sylvaticum*.

Table S2. Broad vegetation types of *G. sylvaticum* across its Eurasian range.

Table S3. Leaf dry weight (LDW) and specific leaf area (SLA) information for *G. sylvaticum* from the literature.

Table S4. Concentrations of three forms of nitrogen and total nitrogen in belowground parts of *G. sylvaticum*.

Table S5. Concentration of minerals in above- and belowground parts of *G. sylvaticum*.

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