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BIOLOGICAL FLORA*

Biological Flora of Britain and Ireland: *Polygonatum multiflorum*

No. 309

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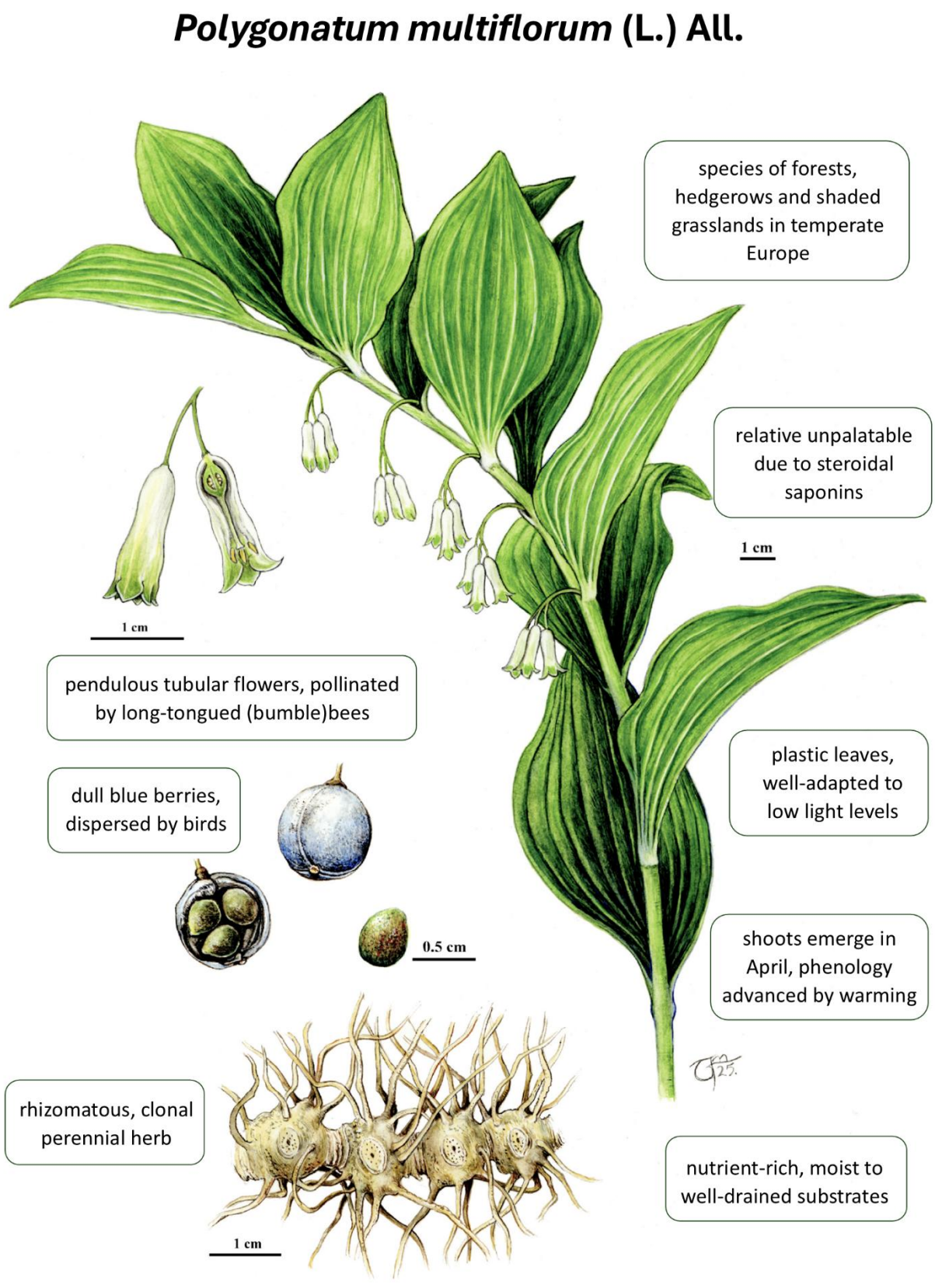
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Graphical abstract



Abstract

1. This account presents information on all aspects of the biology of *Polygonatum multiflorum* (L.) All. (Asparagaceae) , Solomon's Seal, 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 and conservation.

2. *Polygonatum multiflorum* is a rhizomatous, clonal perennial herb found in Britain and Ireland primarily in forests, but also in hedgerows and shaded grasslands. The native range consists of much of temperate Europe, extending into western Asia, and is typically associated with nutrient-rich, moist to well-drained substrates. The species is a characteristic component of semi-natural woodland understorey flora, often co-occurring with other shade-tolerant species such as *Mercurialis perennis* and *Anemone nemorosa*.

3. The flowers of *P. multiflorum* are pendulous, tubular, and creamy-white with green tips, arranged in axillary clusters along the arching stem. They are primarily pollinated by long-tongued bees and bumblebees. The resulting dull blue berries are dispersed by birds, contributing to the plant's spread across suitable habitats. Vegetative reproduction via rhizome extension is also common, leading to more or less distinct shoot clusters.

4. The species is relatively unpalatable to herbivores due to the presence of steroidal saponins, though it is sometimes browsed by deer and by insects such as the specialized Solomon's-seal sawfly (*Phymatocera aterrima*). It is also susceptible to fungal infections, which cause rust diseases. Recent studies have focused on the genetic fitness of populations under habitat fragmentation, on climate change effects on the species' phenology and on the vegetative and generative reproductive strategies that determine its dispersal dynamics.

5. Historically, *Polygonatum multiflorum* has been valued in herbal medicine for its purported wound-healing and anti-inflammatory properties. *P. multiflorum* is often associated with ancient woodland. While this species is currently not at risk of extinction, woodland management practices, habitat fragmentation, and climate change might cause population declines or range contraction.

KEYWORDS

conservation, ecophysiology, forest understoreys, geographical distribution, mycorrhiza, parasites and diseases, phenology, reproductive biology

Solomon's Seal**.** Asparagaceae (formerly Liliaceae), tribe Polygonacea, genus *Polygonatum* Mill. *Polygonatum multiflorum* (L.) All. is a long-lived, rhizomatous perennial herb, with arching, flowering stems emerging in spring from underground creeping rhizomes.

Rhizome horizontal, thick, with fibrous roots and annular scars from previous year's growth. Stems (20)25–80(90) cm, smooth, often glaucous, unbranched, and arching. Leaves usually 8-23, alternate, sessile to subsessile and sub-amplexicaul, elliptic to lanceolate, (4)5–12(15) cm × (2.5)3.5–4.5 cm, in two subdistichous rows; upper surface dark green, lower paler and nearly glaucous. Lower leaves ovate-oblong in shape, 3.5-4.5 cm wide, 5-12(15) cm long, whereas the upper often slightly smaller, 2.5-4 cm wide and 4-8 cm long, elliptical, obtuse at the apex, with entire margins and without stipules Leaf margins entire, veins parallel, slightly wider at mid-leaf. Inflorescence axillary, 3-8 nodding clusters, bearing 2–5(7) pendant flowers, borne on slender pedicels of 10-15 mm long. Flowers trimerous, actinomorphic, (10)12–18(25) mm, unscented, creamy-white with greenish tips, perigone a subcyindrical tube of 2-3 mm wide at the middle, slightly swollen at the base, consisting of 6 tepals in two whorls. Lobes (free part of the tepals), light-green, ovate-elongate, incurved outwards at the tip, the three external ones slightly longer and larger (ca. 2.9 × 1.8 mm) than the internal ones (2.6 × 1.6 mm). Stamens six, adnate to the perigone tube and inserted in its upper part at the same level, with filaments free for a short part and finely hairy. Anthers yellow, oblong and basifixed, reaching about the base of the lobes, with longitudinal and introrse dehiscence. Ovary superior, ovate, light green, tricarpellate, usually with three collateral locules, each including two ovules with axile placentation. Septal nectaries are present. The style is slightly shorter than the stamens, delicate, almost linear and white. The stigma is whitish and almost inconspicuous, formed by three lobes with dry-papillate surface. Fruit a globose, fleshy berry, initially green, ripening to dull blue with whitish waxes (pruine) on the external surface, 10-12 mm diameter. Seeds, usually up to two per locule, 2–5 mm, ovoid, smooth, with a hard greenish to dark brown coat at maturity, with yellowish chalaza. This information was compiled from various sources, including Cullen et al. (2011), Stace (2019), Fitter and Peat (1994), and Kew's Plants of the World Online (POWO) and Dahlgren et al. (1985).

Polygonatum multiflorum is closely related to *P. odoratum* (Mill.) Druce, but distinguished by its broader, sessile leaves and multiple-flowered inflorescences, compared to the narrower, petiole-like leaf bases and typically single-flowered inflorescences of *P. odoratum,* which has also a more upright growth and slightly fragrant blooms. The vernacular name "Solomon's seal" is used inconsistently across Europe and may refer to either *Polygonatum multiflorum* or *P. odoratum*. For clarification, *P. multiflorum* is sometimes called "common Solomon's seal", whereas *P. odoratum* is referred to as "angular" or "scented Solomon's seal" (GBIF, 2025). The vernacular names (in many languages) reflect the fact that the shape of the distinctive annular scars on the rhizomes are supposed to resemble

the seal of King Solomon. The genus *Polygonatum* is well known for its complex taxonomic history, with species often requiring detailed morphological and molecular analysis for accurate identification (Floden, 2014). Hybridization with other *Polygonatum* species has been reported in areas of sympatric distribution range.

Native to temperate woodlands of Europe and western Asia, *Polygonatum multiflorum* is typically found in (semi-)shaded, mesic ancient forests and hedgerows, preferring calcareous or nutrient-rich soils. Traditional uses of *P. multiflorum* include medicinal applications, particularly in herbal medicine for its purported anti-inflammatory and tonic properties. However, all parts of the plant, especially the berries, contain toxic saponins and are not suited for human consumption.

1 │ GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Polygonatum multiflorum is native to British woods, mostly on basic soils (Stace, 2019) and in the south, but is not native in Ireland (Fig. 1). It is locally frequent in England and Wales, and considered native only in ash woodlands and thickets over chalk and limestone, and less frequently over other, non-acidic substrates (Preston et al., 2002). It is naturalized elsewhere in the British Isles (Stace, 2019) and widely planted, e.g., in churchyards, parks and gardens, leading to escapes from cultivation. As a result, its native range is difficult to define with certainty (Preston et al., 2002; Stroh et al., 2020). In Britain, the species occurs naturally in 268 of the 2,805 10 km × 10 km grid squares (hectads), but in none of the squares covering the Channel Islands and Ireland, where it is considered a neophyte (Fig. 1; Hill et al. 2004; Preston et al., 2002; Stroh et al., 2020).

In continental Europe, *P. multiflorum* is representative of the European temperate floristic element (Preston & Hill, 1997) and occurs over much of the European continent from southern Scandinavia over the Baltic States to the Ural Mountains in Russia, southward to Basjkirostan (southern side of western Ural Mountains), south to the Caucasus and to Turkey, Greece, Italy and the Iberian Peninsula (Fig. 2). It is absent from the true Mediterranean climates in, for instance, Spain, Italy and Greece, where it is restricted to higher elevations. It is totally absent from Corsica, but present in a few sites on the mountains of Sardinia (F. Selvi, personal communication, May 2025). These Sardinian occurrences are not reported in GBIF (a global biodiversity database focused on species distribution data, www.gbif.org) and therefore not shown on the map (Fig. 2). In Europe, the species reaches its southernmost distribution limit in Sicily (Brullo et al., 1999). In central and western Europe such as in Belgium, France, Germany and the Netherlands, it is relatively frequent and occurs in woodland with mull humus, coppiced woods and shaded (riparian) banks (Lambinon et al., 1998; Duistermaat, 2020). In northeastern France, it also occurs in ancient hedgerows that can be more than 300 years old (i.e., hedgerows already mapped on Cassini's maps from 1725) (Lenoir et al., 2021).

In Scandinavia, it is occurring throughout the whole of Denmark but is native only up to c. 61°N in Norway, Sweden and Finland where it occurs in mixed and deciduous forests, coastal forests, mountain slopes, ravines, and overgrown meadows and pastures (Mossberg & Stenberg, 2012). The species is absent from Iceland (Kristinsson, 2013).

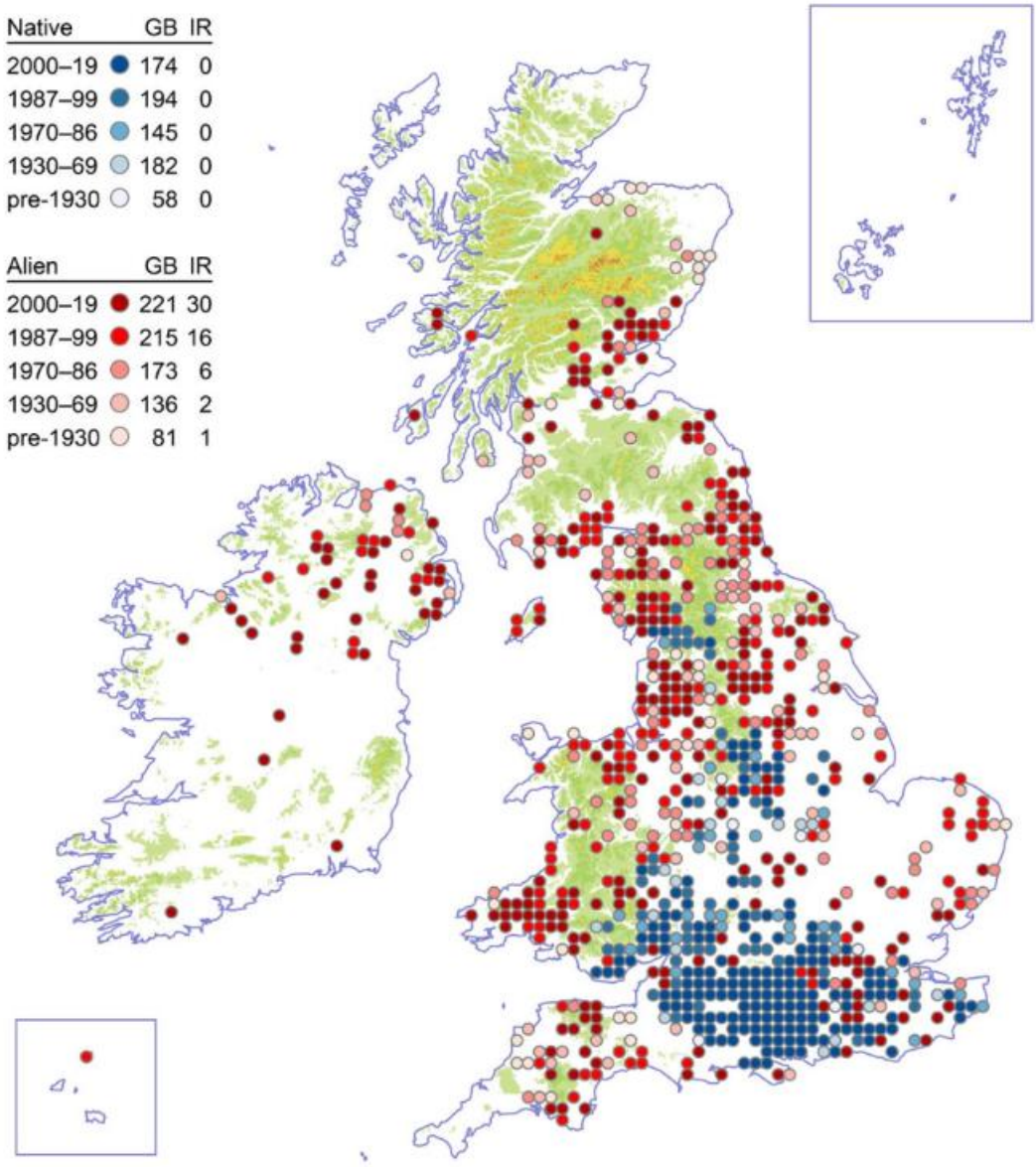


FIGURE 1 The distribution of *Polygonatum multiflorum* in the British Isles. Each dot represents at least one record in a 10-km2 of the National Grid. Colours represent status (native vs. alien) and hues represent time period of record. Map from the BSBI Online Plant Atlas (Stroh et al., 2020).

Polygonatum multiflorum is not native to North America. Yet, it has been introduced into two distinct North American range clusters (Fig. 2) (GBIF.org, 2025). In the east, it has been reported in eastern Ontario, southern Quebec (these are the only occurrences reported in Kartesz, 2015) and several northeastern U.S. states. In the west, its distribution spans British Columbia, Washington and Oregon.

In both Canada and the U.S., the species is available for purchase in plant nurseries, which potentially caused the North American introductions. In Asia, the species has been observed in southeastern China and the Western Himalayas (Mehra & Pathania, 1960). It has also been documented in the highland forests of Northern Iran (Zare & Amini, 2022). Meusel and Jäger (1992) consider this region as well as part of Japan, as part of its native range (but occurrence in Japan is again not reported in GBIF, see above). In Oceania, *P. multiflorum* has been introduced as a garden plant and is found in New Zealand, as well as in Tasmania and around Melbourne.

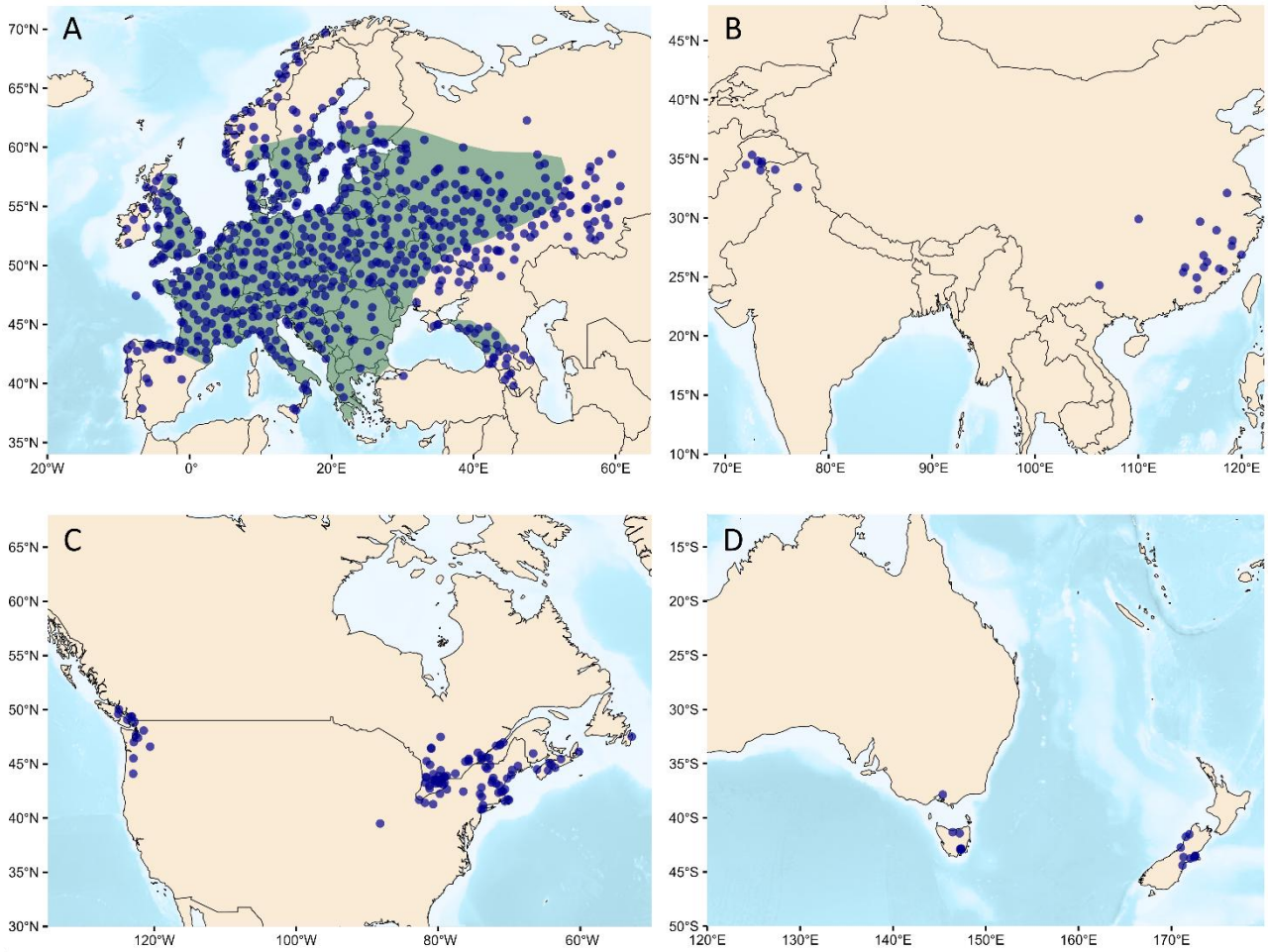


FIGURE 2 The distribution of *Polygonatum multiflorum* in (a) its native range, (b) Asia, (c) North America and (d) Oceania. The dark green polygon represents the estimated native distribution redrawn after Hultén and Fries (1986). The blue circles are reported occurrences from GBIF (GBIF.org, 2025) in March 2025, these occurrences were spatially thinned to 1 per 25 km2 (b–d) and to 1 per 2500 km2 for the native range (a).

In the British Isles, *P. multiflorum* occurs from sea level and up to 500 m above sea level (a.s.l.) in the Pennines Hills. In Scotland, it does not occur above 300 m. In western Europe, its elevational range stretches from around sea level, in France, Belgium, the Netherlands and England, and then up to 1500, 1350, 1320, 1290, and 920 m a.s.l. in the western Alps, northern Pyrenees, Massif Central,

western Jura and Vosges mountains, respectively (Lenoir et al., 2008). In the whole of Italy, the species ranges from 580 to 1675 m a.s.l. (Dainese et al. 2017) but at its southernmost limit, in Sicily, *P. multiflorum* occurs between 1400 and 1800 m a.s.l., in the Nebrodi and Madonie mountains (Brullo et al., 1999).

2 | HABITAT

2.1 | Climatic and topographical limitations

The distribution of mean annual temperatures across the distribution range of P. multiflorum ranges from 3°C to 14°C, with an optimum around 8°C (Vangansbeke et al. 2021). Mean annual precipitation ranges from 517 to 1158 mm, with an optimum around 700 mm. Hill et al. (2004) reported that monthly mean temperatures in January and July, and mean annual precipitation, in the 10-km squares occupied by P. multiflorum in the UK, are 3.6°C, 16°C and 829 mm, respectively. P. multiflorum is a shade-tolerant perennial herbaceous plant species commonly found in temperate deciduous forests.

Recent range shifts of P. *multiflorum* seem to be directed downward and equatorward, against the direction expected from climate warming. P. *multiflorum* shifted downslope at its optimum elevation in the Alps between 1981 and 2004 at a velocity of -37.1 m/yr (Bodin et al., 2013) and at a velocity of -0.9 m/yr throughout all mountain ranges in France (Lenoir et al., 2008). Yet, according to Dainese et al. (2017), its upper elevational margin shifted upslope at a velocity of +6.8 m/year between 1989 and 2009. Groom (2013) found an equatorward (southward) range shift at a velocity of -1.7 km/yr between 1978 and 2011 in Britain. In a European synthesis, *P. multiflorum*'s centroid across its baseline and current range shifted also to the south (to the south-southeast, with a bearing of 146.5°) by 6.83 km per decade during the last decades (Sanczuk et al., 2024). These range shifts could be explained by the negative impacts of nitrogen deposition or other drivers such as forests becoming increasingly shaded, having hitherto larger impacts than climate change thereby overriding the impacts of northward isotherm shifts (Sanczuk et al., 2024).

2.2 | Substratum

Polygonatum multiflorum is most common on moderately moist, nutrient- and base-rich, neutral to moderately acidic mull forest sites (Diekmann, 1994; Oberdorfer, 1994; Leuschner & Ellenberg, 2017). While being most frequent on mesic loamy soils, the species can be found on a wide range of other soil types, including relatively dry, sandy or rocky soils, as well as moist alluvial soils along streams and ravines. However, *P. multiflorum* does not tolerate permanently wet soils and is absent

from swamp and mire forests (Leuschner & Ellenberg, 2017). In England and Wales native populations of *P. multiflorum* are mostly associated with chalk and limestone, and less frequently with other, non-acidic substrates (Preston et al., 2002).

Ellenberg species indicator values for Central Europe are intermediate for the three edaphic variables: 5 for moisture (F), indicating a preference for fresh soils; 6 for pH (R), reflecting an optimum on weakly to moderately acid soils; and 5 for nitrogen (N), indicating a preference for moderately nitrogen rich soils (Ellenberg et al., 1992). In Sweden, Tyler et al. (2021) assigned an identical value for R (= 5), while the F score of 4 points to a main occurrence on slightly drier soils compared to Central Europe; the N score of 7 indicates a preference for sites with relatively high nutrient availability. In Great Britain, the species also appears to prefer more base- and nutrient-rich sites (R = 7, N = 6) than in Central Europe (Hill et al., 2004). Recently, Dengler et al. combined interregional indicator values to derive pan-European indicator values (EIVE) of niche position. For *P. multiflorum* these are 4.5 for moisture, 6.2 for reaction and 5.2 for nitrogen (Dengler et al., 2023). Among the ecological groups of forest floor plants in Central European broadleaved forests, Leuschner & Ellenberg (2017) assigned *P. multiflorum* to the *Galium odoratum* group characteristic for slightly dry to slightly damp and moderately acidic soils.

Available soil chemical data show that *P. multiflorum* has a wide amplitude in terms of soil acidity and no pronounced pH optimum, i.e. the species behaves differently from the response that is suggested by its indicator values for soil acidity (Fig. 3). This indicates at least that the niche optimum of the R indicator values is not very informative, given the species' wide niche width. In the three data sets for which extensive measurements of soil pH from forests were available (Germany, South Sweden and a transect across Europe from NW France to Estonia), the species can be found also on highly acidic soils with a pH around or even less than 3 and on soils exceeding a pH of 7 (Appendix 1). The mean pH varied between 4.2 and 5.0. The species' niche with respect to soil acidity, i.e. the range of soil pH values at which the species is able to occur, also varies along a latitudinal gradient in Europe, being narrowest in central regions and increasing towards the south and north (Reinecke et al., 2016).

P. multiflorum also shows a broad amplitude in its soil C / N ratio, varying between values of less than 10 up to 36.5 (means around 10 to 15) (Appendix 1). Most sites in which the species was present had values between 10 and 20, while the relative frequencies on soils with C / N ratios < 10 and > 20 were lower (Fig. 3). The concentrations of total phosphorus (P) in the mineral soil samples also varied widely (European gradient study: 8.6-123.6 mg 100 g-1 soil, mean: 34.3). Likewise, there were broad ranges in the values of plant available concentrations of P, Ca, K and Mg (data set from Germany,

Appendix 1). A study from southern Sweden on soil nitrogen mineralization in forest soils and temporal trends in various forest understorey species suggested that *P. multiflorum* has been largely stable in its frequency and is not favoured or disfavoured by low to moderate nitrogen deposition (Diekmann & Falkengren-Grerup, 2002).,

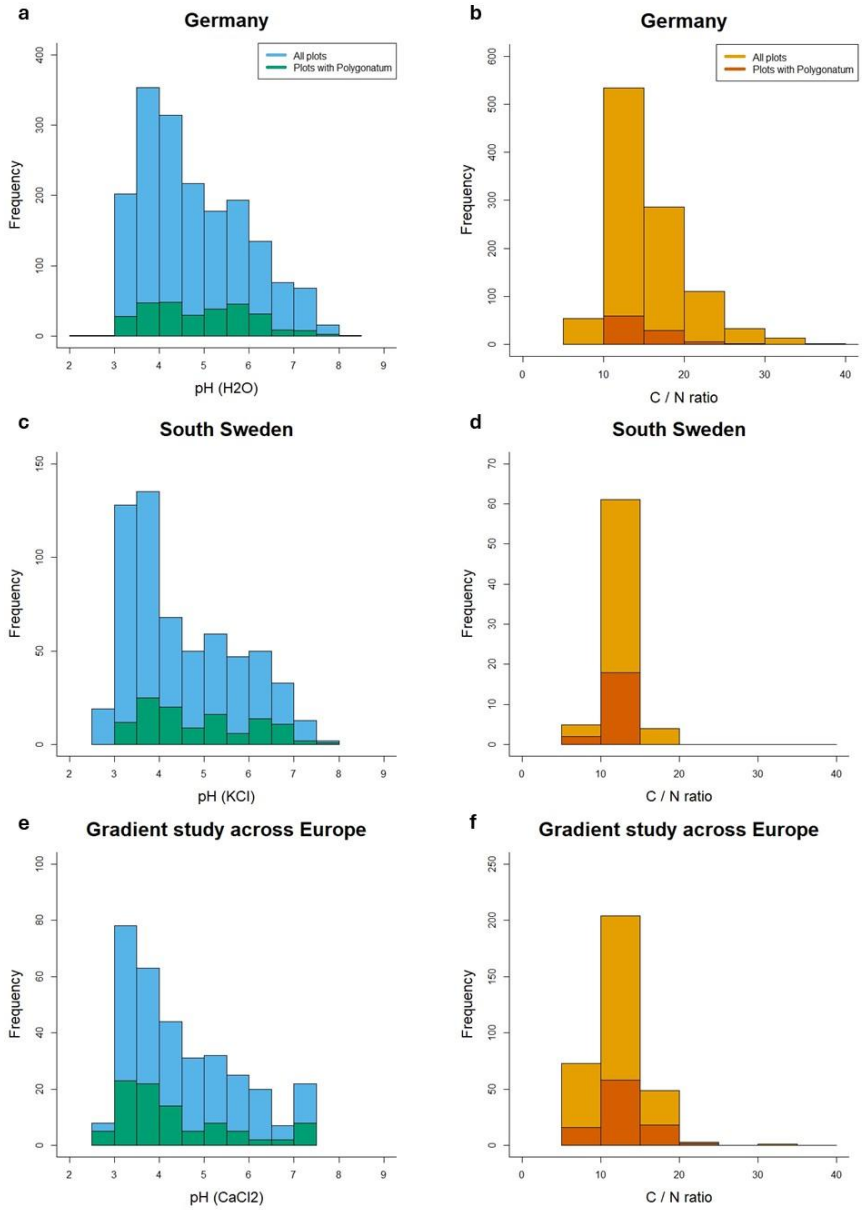


FIGURE 3 Frequency distribution of pH values (panels a, c, e) and C/N ratios (panels b, d, f) in the topsoil (0–5 cm) of data sets from deciduous forests in Germany (1755 plots, panels a, b), South Sweden (604 plots for pH, 70 plots for C/N, panels c, d) and along a transect from NW France to Estonia (330 plots, panels e, f). The blue or orange bars show all plots, the green or reddish bars depict the plots with occurrences of *Polygonatum multiflorum*. Note that the soil pH in the three datasets was measured in different solutions (H2O, KCl, CaCl2). Data sources: Germany (Gönnert, 1989; Heinken, 1995; Mast, 1999; Pannek et al., 2013; Pflume, 1999; Rüther, 2003; Wulf, 1992), South Sweden (Brunet, 1993; Depauw et al., 2019; Diekmann, 1994; Falkengren-Grerup, 1995), and Gradient study across Europe (Wei et al., 2023).

If *P. multiflorum* grows in hedgerows, it apparently prefers less acidic and more base-rich soils than in forests (Wehling & Diekmann 2009a), possibly as a consequence of the addition of fertilizers on neighbouring fields. The hedgerow sites also offer different light conditions, with a mean value of 21% relative irradiance compared to only 2.2% in the studied closed forests.

3 │ COMMUNITIES

In the British Isles, *P. multiflorum* is often planted or discarded from gardens into the wild (Stroh et al., 2020). It is presumably a native species only in ashwoods and scrubs, developing on chalk and limestone and less frequently on other non-acidic substrates. According to the national vegetation classification system (Rodwell et al., 1991), it is a common component of the *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland community (W8). This community predominantly occurs in lowland Britain over moderately moist, base-rich soils derived from calcareous parent materials. In contrast, it becomes sparse in cooler and wetter climates on the northwestern uplands. *Polygonatum multiflorum* is present in the *Primula vulgaris-Glechoma hederacea* (W8a), *Anemone nemorosa* (W8b), and *Geranium robertianum* (W8e) sub-communities (Rodwell, 2006). Although the field layer of the *Fraxinus-Acer-Mercurialis* community is very variable, the most frequent species, apart from *Mercurialis perennis*, associated with *P. multiflorum* include *Hyacinthoides non-scripta, Circaea lutetiana, Geum urbanum, Arum maculatum, Viola reichenbachiana* and *V. riviniana* (Rodwell et al., 1991).

In northern Europe, *P. multiflorum* is predominantly associated with deciduous forests from the *Querco-Fagetea* class, present on relatively moist, moderately acid to highly alkaline, nutrient-rich humus soils, including the *Alno-Ulmion, Carpinion betuli, Fagion sylvaticae,* and *Tilio platyphyllis-Acerion pseudoplatani* alliances. Among those vegetation units it reaches the highest constancy and abundance, up to 25%, in eutrophic elm-ash forests (*Ulmus minor-Fraxinus excelsior community*), developing in the most fertile and moist soils of the boreo-nemoral zone. Frequent occurrence of *P. multiflorum* was also reported in eutrophic alder-ash forests, mesotrophic mixed deciduous forests with linden, although less abundant than in the elm-ash woodlands (Diekmann, 1994), and in beech forests on meso- and eutrophic soils (Diekmann, 1999). *Polygonatum multiflorum* is also mentioned in the European Habitat Directive interpretation manual (EUR27, 2007) as a characteristic species of Fennoscandian hemi-boreal, natural, old, broad-leaved deciduous woodlands (*Quercus, Tilia, Acer, Fraxinus* or *Ulmus* spp.), which are rich in epiphytes (9020). In some regions, it has been reported to occur in herb-rich *Pinus sylvestris* forests and on relatively dry, sandy soil in both mixed and coniferous forest. In addition, the species grows in abandoned, overgrown wooded meadows, pastures and old farmsteads, park environments, shady roadside ditches, path edges and at stone fences. The

species is also frequently found in woody corridors such as hedgerows and tree lines (Litza et al., 2022, McCollin et al., 2000). *Polygonatum multiflorum* is also less commonly found in herb-rich *Picea abies* forests, preferably on calcareous substrates, stream valleys, and in small rocky woodland islets located in an agricultural matrix. It is cultivated in some regions as an ornamental plant (Tyler et al., 2007; Jonsell & Aronsson, 2010).

In western Europe, *P. multiflorum* is regarded as an early summer flowering, relatively acid-tolerant, moisture-demanding species associated with shady, broadleaved forests, especially from *Fagetalia sylvaticae* order *Carpinion betuli* alliance, where it grows on slightly dry to slightly damp, moderately nutrient-rich, humus-rich clay soils. It is widespread in the herbaceous layer in brown mull beech forests (*Galio odorati-Fagetum*) and in lime- and oak-hornbeam forests (*Tilio cordatae-Carpinetum betuli*) (Leuschner & Ellenberg, 2017; Oberdorfer, 1995). It is common in floodplain riparian forests on nutrient-rich alluvial soils from the *Alno-Fraxinetalia excelsioris* order. It is also reported from mixed-oak forests, mixed conifer forest communities, deciduous and fir forests, tall herbaceous meadows, ancient hedgerows and shrublands in the mountains, and roadside embankments as a gregarious semi-shade species (Cordes et al., 2006).

In central and eastern Europe, the species occurs in a broad spectrum of deciduous forest communities from the *Querco-Fagetea* class, including the *Potentillo albae-Quercion petraeae, Alno-Ulmion, Carpinion betuli, Fagion sylvaticae,* and *Tilio platyphyllis-Acerion pseudoplatani* alliances. Occasionally, it also grows in mixed oak-pine forests (*Querco roboris-Pinetum*). However, it is predominantly reported from oak-hornbeam (*Tilio cordatae-Carpinetum betuli*), where in the most moist and fertile community variants it reaches cover up to 25% (Kącki & Śliwiński 2012, Matuszkiewicz & Matuszkiewicz 1996), and from beech forests, especially from *Dentario glandulosae-Fagetum* and *Dentario enneaphylli-Fagetum* communities, where it attains high constancy but low abundance, usually not exceeding 5% cover. According to the recent syntaxonomic revision of oak-hornbeam forests of Central Europe (Novák et al., 2020), although *P. multiflorum* frequently occurs in a broad range of other communities, it is recognized as a diagnostic species of the mesophytic Illyrian oak-hornbeam forests (*Epimedio-Carpinetum* community), occurring on calcareous soils, typical of the south-eastern Alps and Dinarids, confined to Carinthia (southern Austria). *Polygonatum multiflorum* also grows in alluvial forests, and sub-continental thermophilous oak forests. Rare occurrence of the species is observed in tall mesic and xeric scrub communities, early successional stages of oak-hornbeam forests and their secondary communities, with Scots pine in the stand, in *Corylus avellana-Sorbus aucuparia* thickets developing on coastal cliffs of the Baltic Sea, in herbaceous vegetation of forest clearings and *Rubus* scrub, and thermophilous forest fringe and tall-herb vegetation of the *Trifolio-Geranietea sanguinei* class, and sporadically in acidophilous

beech forests (Chytrỳ & Rafajová, 2003; Kącki & Śliwiński, 2012; Leuschner & Ellenberg, 2017; Riznychuk et al., 2023).

In southern Europe, *P. multiflorum* grows mostly between 200 and 1800 meters above sea level, in mesotrophic hornbeam and turkey oak woodlands, as well as beech forests on deep, fresh, neutral to slightly acidic soils, moderately rich in nitrogen. In Italy, *P. multiflorum* is primarily found in several communities of the *Fagion* alliance (Pignatti, 2017), with frequency ranging from 2% to 71%. In Natura 2000, it is considered as a species of habitats 9130 (*Asperulo-Fagetum* beech forests), and 9210* (Apennine beech forests with Taxus and Ilex), south of 42°N. In the mountains of Sicily, where it reaches its southern distribution limit, it grows in Mediterranean beech forests of the *Geranio versicoloris-Fagion* (Pignatti, 1998). It also occurs in Sardinia in a few isolated populations in mesic and shady humid sites of mountain forests. Other communities where it can be found in southern Europe are the mesotrophic forest communities of the alliance *Tilio-Acerion,* the lowland forests with *Quercus robur* and *Carpinus betulus* of the *Carpinion betuli* alliance and the mature stages of the Illyrian oak-hornbeam forests of Habitat 91L0, often with *Querucs petraea*.

According to the European Habitat Directive interpretation manual (EUR27, 2007), *P. multiflorum* is considered a typical species of Dobrogean Beech forests (91X0) – a relict beech forest of the Macin Mountains (Romania) of very insular distribution, isolated from the central beech regions of the Carpathians. Here it grows in stands with *Fagus sylvatica, F. taurica* (syn. *F. taurica* var. *dobrogica), Tilia tomentosa, T. cordata, Carpinus betulus, Populus tremula,* and *Ulmus glabra*

In the European Forest Plant Species List (EuForPlant), *P. multiforum* has been consistently recognized and classified as a species occurring mainly in closed forests - 1.1 species (Heinken et al., 2022). In the EUNIS habitat classification it is regarded as a diagnostic species of the T1E Carpinus and Quercus mesic deciduous forest and T1F Ravine forest, and a constant species of S37 Corylus avellana scrub, T17 Fagus forest on non-acid soils, T1E Carpinus and Quercus mesic deciduous forest, and T1F Ravine forest (Chytrỳ et al., 2020). In the syntaxonomic classification for Europe, it is a diagnostic species for the CA (FAG) *Carpino-Fagetea sylvaticae* and CL (GER) *Trifolio-Geranietes sanguinei* classes (Mucina et al., 2016).

4 │ RESPONSE TO BIOTIC FACTORS

Competitive ability and response to competition.

Polygonatum multiflorum is a clonal, rhizomatous perennial that thrives in shaded woodlands by forming long-lived colonies through slow lateral rhizome spread. Its cylindrical shoots, reaching up

to 80 cm in height, provide a competitive advantage in dim understorey habitats (Tulik et al., 2018). In dense oak-hornbeam forests, where light availability is significantly reduced, typically receiving only 2–5% of incident light, *P. multiflorum* invests in shoot elongation as an adaptive response to low light levels, enabling it to overtop smaller ground flora and access limited sunlight. This strategy enhances its ability to compete in light-limited environments but also makes it vulnerable to shading by taller vegetation when canopy conditions shift (Tulik et al., 2018; Karpavičienė & Mlečkaitė, 2019). Allometric relationships between shoot length and diameter support this adaptation. Tulik et al., (2018) reported strong positive correlations between shoot length and reduced diameter (Pearson's r = 0.96 at the basal section, 0.92 in the central region, and 0.85 in the apical part), reflecting a consistent strategy to maximise height with minimal structural investment. This pattern is reinforced by internal stem architecture: in *P. multiflorum,* turgor pressure from the inner parenchyma cells inside the sclerenchyma cylinder provides mechanical reinforcement, enabling the plant to grow taller and more slender in shaded conditions without structural failure (Tulik et al., 2018). These traits represent both physiological and competitive adaptations that support persistence in low-light environments. Despite its persistence in stable woodlands, *P. multiflorum* is a weak competitor in nutrient-rich or disturbed environments. Under high soil fertility conditions, particularly in forests affected by nitrogen deposition, it is frequently outcompeted by fast-growing ruderal species such as *Calamagrostis spp*. and *Digitalis purpurea* (van Dobben & de Vries, 2017). This vulnerability is even more pronounced in open or heavily disturbed habitats, where ruderal competitors such as *Rubus spp., Urtica dioica, Galium aparine* dominate the understorey layer (Decocq et al., 2005). In such contexts, *P. multiflorum* tends to decline or disappear altogether, highlighting its reliance on stable canopy cover and moderate nutrient regimes.

In its native broadleaf woodland habitat, *P. multiflorum* primarily competes for light and space rather than soil nutrients. It does not exhibit allelopathy but competes indirectly by shading smaller plants with its broad leaves (Karpavičienė & Mlečkaitė, 2019). Research on populations growing in open pastures found that plants were stunted, with 20–50% lower leaf and flower production compared to those in partial shade, suggesting that *P. multiflorum* is adapted to intermediate light conditions (Karpavičienė & Mlečkaitė, 2019). While performance declines in fully open, disturbed sites, *P. multiflorum* can maintain similar reproductive output in moist, semi-open habitats such as hedgerows, where partial shade and stable microclimatic conditions support growth (Wehling & Diekmann, 2009). Thus, the species appears sensitive not to openness per se, but to the interaction of light, competition, and drought.

Experimental studies confirm that *P. multiflorum* modifies its morphology in response to competition (Tulik et al., 2018). In shaded habitats, individuals develop taller, more slender stems with a reduced

shoot diameter, an adaptation that enhances light capture under competitive understorey conditions (Tulik et al., 2018). Along light gradients, plants in semi-open woods produce the tallest shoots and largest leaves, while those in deep shade or open fields remain smaller, indicating strong phenotypic plasticity constrained by the species' shade-adapted physiology (Karpavičienė & Mlečkaitė, 2019). The latter is further corroborated by experimental work from Blondeel et al. (2020) demonstrating that the specific leaf area (SLA) of *P. multiflorum* significantly decreases after artificial light addition under a closed canopy. The species thus has the ability to adapt its leaf morphology and develop a higher SLA when grown under low-light conditions to further optimize light absorption and carbon gain (Evans & Poorter, 2001). Indeed, the recent Ecological Indicator Value for Europe classification (EIVE scaled between 0-10, sensu Dengler et al., 2023) shows that; while the niche position of *P. multiflorum* for light is on the low side of the scale (EIVE-L = 2.5), the associated niche width for light is comparably very high (EIVE-Lnw = 6.0) emphasizing its remarkable plasticity to varying light conditions.

Effect of silvicultural practices

Forest management practices such as thinning, selective cutting, or traditional coppicing directly affect *P. multiflorum* by altering light availability, disturbance regimes, and competitive dynamics in the forest understorey. While the species is strongly shade-adapted, it can benefit from moderate increases in light - particularly under partial canopy opening - when competition from aggressive, ruderal species remains low. As a forest specialist sensu Heinken et al., (2022), *P. multiflorum* is typically found in long-established, semi-natural woodlands with structurally stable canopies and low anthropogenic disturbance. Coppice-with-standards is a traditional silvicultural system in which most of the stand is coppiced on long cycles (~ 30 years), while a smaller proportion of trees (the standards) are left uncut for much longer (e.g. 50–100 years). This system creates heterogeneous light regimes that might benefit *P. multiflorum* by providing intermittent canopy openings while retaining overall structural continuity (Decocq et al., 2005). According to Decocq et al. (2005), the species is more frequently found in traditional coppice-with-standards systems than in selectively cut stands, where disturbance occurs more frequently (e.g. thinnings every 4 years and fellings every 8 years). Riznichuk (2017) similarly found the lowest morphometric values (e.g. shoot length and number of flowers per shoot) in *P. multiflorum* individuals growing in full-light environments such as pastures, compared to those in forest interiors or edges. This suggests that *P. multiflorum* thrives under intermediate canopy openings, where moderate light penetration stimulates flowering and shoot elongation, while still providing shelter from temperature extremes and soil desiccation.

Overall, *P. multiflorum* functions as a competitive subdominant in forest understoreys: it can persist in shaded, low-disturbance woodlands and may achieve local dominance under favorable conditions, but is typically excluded by fast-growing, light-demanding or disturbance-tolerant species in more open or fertile habitats. Its adaptive strategies, including shoot elongation, reproductive suppression, and morphological plasticity, allow it to survive but constrain its spread in highly competitive environments (Tulik et al., 2018). The interplay between competition, silvicultural practices and other stressors, such as atmospheric pollution and herbivory, ultimately determines its long-term success in forest ecosystems.

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

As a consequence of its clonal propagation through rhizome branching (section 6.3), *P. multiflorum* builds more or less distinct shoot clusters. These clusters may comprise both vegetative and flowering shoots (Kosiński, 2015). In an attempt to explore how flowering shoots are distributed across clusters, Feigs et al. (in prep.) counted the number of flowering shoots in all 2135 shoot clusters present across nine forest patches in East Germany. They defined a cluster as a group of at least partly flowering shoots with a distance of < 30 cm among adjacent shoots. The number of flowering shoots ranged from 1 to 269 with most clusters comprising less than 10 flowering shoots (Fig. 4).

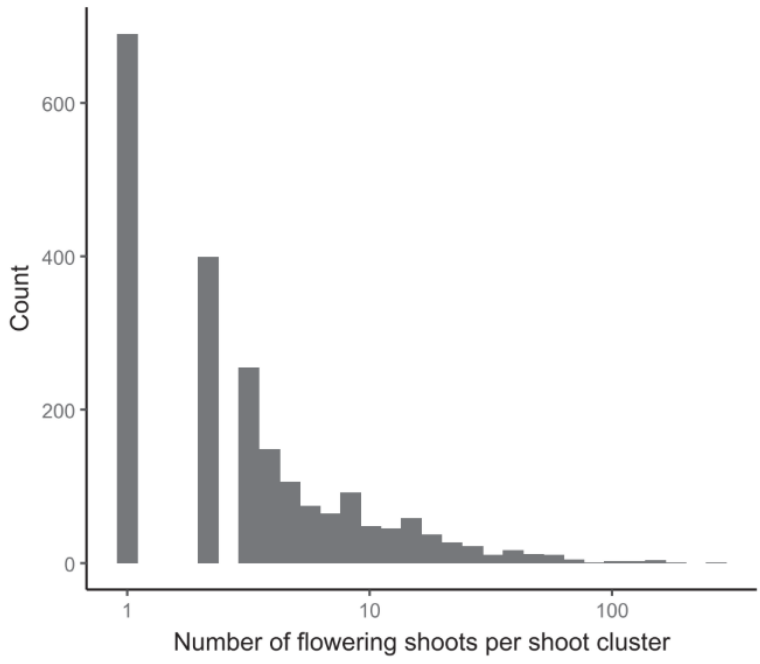


FIGURE 4 Frequency distribution of the size of 2135 flowering shoot clusters sampled across nine forest patches (24–693 clusters per forest patch) in East Germany (Feigs et al., in prep). Gaps in the distribution are the result of the log-transformed x-axis.

Although growing in clusters is a result of rhizome branching, apparent shoot clusters are not necessarily monoclonal. Feigs et al. (in prep.) sampled 59 shoot clusters of various sizes ranging from 2 to 190 flowering shoots with the aim to explore their clonal structure. From each shoot cluster, they collected leaf samples from some flowering shoots so that all remaining shoots were within 30 cm reach of a sampled shoot. They sampled between 2 and 25 flowering shoots from each cluster, in total 249 flowering shoots. Of these, 245 could be genotyped successfully based on seven microsatellite markers. Among the genotyped samples, there were 144 multilocus genotypes (i.e. different genets). Only 26 of the 59 clusters (42.4%) were monoclonal. The proportion of monoclonal clusters decreased with cluster size from 62% in clusters with ≤5 flowering shoots over 48% in clusters with 6 to 20 flowering shoots to 24% in clusters with >20 flowering shoots. Thus, different genets with several shoots are often intermingled with each other, which fits the observation that recruitment from seed occurs regularly within established stands (Kosiński, 2012; section 6.3).

Populations may be very small with only a few flowering shoots, but can also comprise many thousand shoots. In 43 populations distributed across temperate Europe, Naaf et al. (2021) found that the average density of flowering shoots across the entire population area ranged between 0.2 and 200 flowering shoots (median 5.5) per 100 m². Within clusters, the density of flowering shoots is also variable with a median and maximum of 8.5 and 32.3 flowering shoots per m², respectively (Feigs et al., 2022).

5.2 | Performance in various habitats

In northwest and central Europe, *P. multiflorum* is traditionally considered an ancient woodland indicator species and several comparative studies show significantly higher frequencies in ancient than in post-agricultural woodlands (Bossuyt et al., 1999; Brunet et al., 2011; Hermy et al., 1999; Honnay et al., 1998; Kimberley et al., 2013; Kirby, 2006; Orczewska, 2010; Wulf & Heinken, 2008). Nevertheless, several studies also provide evidence against this: Verheyen et al. (2003) evaluated 12 field studies from eight European countries and found no consistency in the preference of *P. multiflorum* for ancient forests. *Polygonatum multiflorum* has a colonizing capacity index of 15, indicating a moderate association with ancient forests on a scale ranging from -100 (strongly associated with recent forests) to +100 (strongly associated with ancient forests) (Verheyen et al., 2003). The species is colonizing recent woodlands (70 years or younger) adjacent to ancient woodland regularly (Dzwonko & Gawronski, 1994; Dzwonko, 2001; Verheyen & Hermy, 2001), but usually at low rates ranging from ca 0.2 m to 2 m per year (Bossuyt et al., 1999; Dzwonko, 2001; Orczewska, 2010; Brunet et al., 2012). Colonization of spatially isolated recent woodlands is relatively rare (Brunet, 2007; Butaye et al., 2001), but was observed in some isolated young forests

(up to 36 years old). A study on genetic diversity in isolated populations revealed no significant influence of forest age (range: 18 - 338 years) on allelic richness (range: 2.5-10.19) or expected heterozygosity (range: 0.53 - 0.79), a positive influence of forest age on observed heterozygosity (range: 0.50 - 0.88), and a negative influence of forest age on inbreeding coefficient (range: -0.25 - 0.24) (Huang et al., 2024). Based on a vegetation resurvey in Southern Sweden, *P. multiflorum* was found to be an indicator species of low management intensity (i.e. no or limited signs of recent canopy thinnings) (Depauw et al., 2019).

A meta-analysis by Litza et al. (2022) on the influence of management, landscape and climate on herbaceous forest specialist plants in hedgerows showed that *P. multiflorum* is one of the most frequent forest specialists to occur in woody corridors such as hedgerows and tree lines across Europe. The species occurred in 28% of the plots in the north-eastern lowlands of Germany and 22% of the plots in the Atlantic region of France (Picardy) (frequencies corrected for plot size). This was mainly attributed to the species' ability to disperse via zoochory (e.g. via birds), but also its preference for moist soils (i.e., hedgerows are often bordered by small creeks or channels). In addition, *P. multiflorum* appears to perform equally well in terms of plant size and reproductive output in forests and hedgerows, as shown by Wehling and Diekmann (2009a).

To assess the effect of four habitat characteristics on the probability of occurrence of *P. multiflorum*, we used occurrence data collected in 2012 from seven European regions across a latitudinal gradient from Northern France to Central Sweden. These four habitat characteristics were forest size, forest age, and abiotic and biotic heterogeneity of the forest. Abiotic heterogeneity was approximated by the topographic variability of the patch. Biotic heterogeneity was defined as the total woody species diversity within the patch (see Vanneste et al. (2019) for further details on the calculation of these variables). From this analysis, we can conclude that *P. multiflorum* has a preference for larger and older forest patches, and that also abiotic and biotic heterogeneity of forest patches increase the probability of occurrence of *P. multiflorum* (Fig. 5). For these same seven study regions, Naaf et al. (2021) found that larger forest patches resulted in higher genetic diversity for *P. multiflorum*. The species is therefore sensitive to habitat loss and fragmentation.

Polygonatum multiflorum is generally found in low-light environments (e.g. in the understorey of oak-hornbeam forests), and its shoots are better adapted to compete for light than those of other *Polygonatum* species such as *P. odoratum* (Tulik et al., 2018). Furthermore, experimental work by Blondeel et al. (2020) demonstrated that the specific leaf area (SLA) of *P. multiflorum* significantly decreased after light addition under a closed canopy. The species thus has the ability to adapt its leaf morphology and develop a higher SLA when grown under low-light conditions to further optimize

light absorption and carbon gain (Evans & Poorter, 2001). This is further corroborated by the Ecological Indicator Value for Europe classification (EIVE scaled between 0-10, *sensu* Dengler et al., 2023); while the niche position of *P. multiflorum* for light is on the low side of the scale (EIVE-L = 2.5), the associated niche width for light is comparably very high (EIVE-Lnw = 6.0) emphasizing its remarkable plasticity to varying light conditions. Furthermore, the experiment by Blondeel et al. (2020) also showed that individuals of *P. multiflorum* grow taller on high fertility soil with high pH compared to sandy or intermediate fertility soil with lower pH, whereas experimental warming and nutrient addition did not affect any of the species' traits.

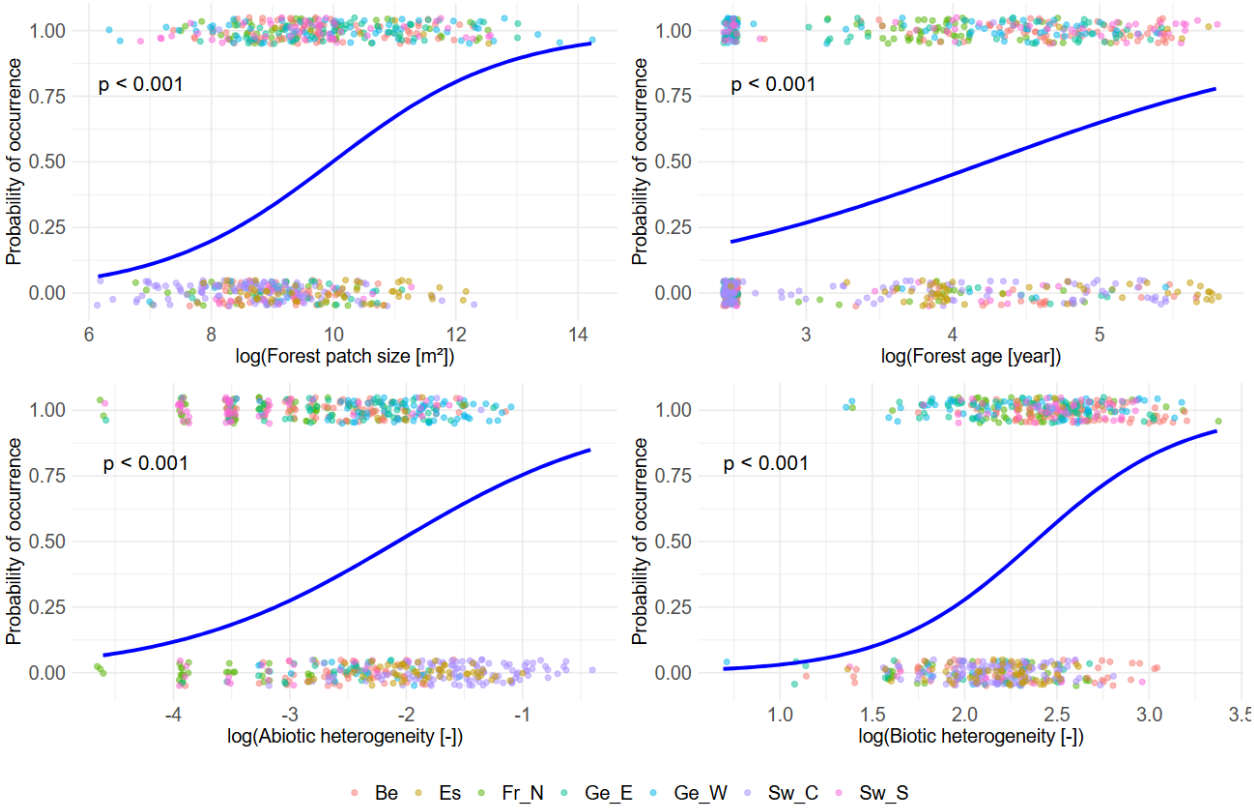


FIGURE 5 Probability of occurrence of *Polygonatum multiflorum* as a function of different habitat characteristics: Forest patch size, forest age, abiotic heterogeneity (calculated as topographic variability) and biotic heterogeneity (calculated as total woody species diversity) (see Vanneste et al., 2019 for further details on the calculation of these variables). We applied binomial logistic regression models to fit occurrence data from seven European regions: Belgium (Be), Estonia (Es), Northern France (Fr_N), Eastern Germany (Ge_E), Western Germany (Ge_W), Central Sweden (Sw_C), and Southern Sweden (Sw_S). We used presence–absence data as response, one of the four habitat characteristics as predictor, and region as random effect.

5.3 | Effect of frost, drought and other abiotic stressors

Polygonatum multiflorum can suffer from stress related to frost and salinity under cold climates. In a Norwegian experiment using rain gardens (Laukli et al., 2022), shallow depressions in greenspaces meant to store rainwater in winter while being (usually) dry in summer (Vike & Clewing, 2020), *P. multiflorum* showed necrosis and high mortality, which was attributed to a combination of strong frost in the growing season and adverse effects from de-icing salt accumulated in the soil along paths in the greenspaces (Laukli et al., 2022). In addition, the species is known to be sensitive to flooding (Van Landuyt et al., 2006). When *P. multiflorum* suffers from abiotic stress, the proportion of single-leafed juvenile individuals in the population can increase, leading to less foliage in the population during the years after (Karpavičienė & Mlečkaitė, 2019; Kosiński, 2012).

The morphology of *P. multiflorum* could contribute to drought tolerance. The species has a relatively low SLA compared to co-occurring species, which points towards a lower sensitivity to drought stress (Blondeel et al., 2020; Poorter et al., 2009). The rhizomes of *P. multiflorum* are a reserve for carbohydrates that can be used to mediate and recover from drought stress (Lubbe et al., 2023), and the directional growth of the rhizomes is not affected by soil moisture content (Raunkiaer, 1904). However, since the topic of drought tolerance is understudied for this species, there are contradictions in the literature which mainly consists of gardening guides. According to Chatto (1982), *P. multiflorum* is drought tolerant as long as there is enough humus in the soil, but Huxly (1992) claims that *P. multiflorum* is intolerant to drought. More scientific research is thus needed.

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Polygonatum multiflorum is a perennial herb with sympodially branching rhizomes, usually developing at 3-106 cm of depth in the soil; they are 9-15 mm thick, fleshy and starch-rich (nutrient-storing), up to c. 30 cm long, horizontal and creeping (Fig. 6). The rhizomes are whitish to pale brown, sub-cylindrical with alternately swollen and constricted segments, sometimes dentate, with annular scars of the aerial stems of the previous years on the swollen segments, and a delicate scent of elder. The root system is fasciculate with numerous roots provided with a multi-layered velamen; the roots are fibrous more or less isodiametric, sinuous and developing in all directions. The aerial stems arise from the end of each rhizome branch generation, unbranched and erect but gracefully arching above, usually glaucous, terete and weakly striate-angular in the upper part, often with scarious scale-like leaves sheathing the underground part.

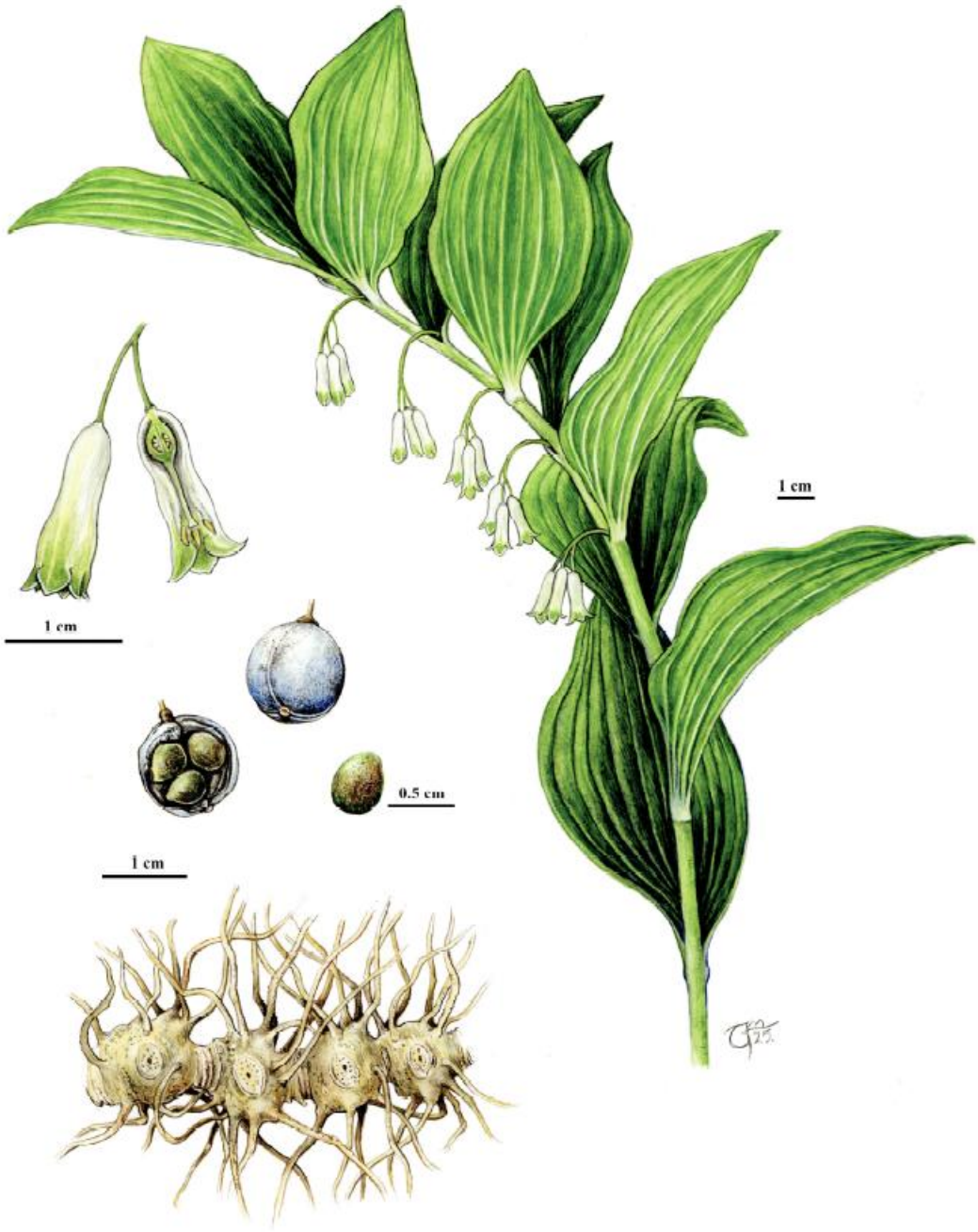


FIGURE 6 Colour plate showing the most important morphological characteristics of *Polygonatum multiflorum*, with details of the flower, the fruit and the rhizome. Artwork by Laura Vivona.

The inflorescence is a raceme, approximately occupying the upper third of the stem. Flowers are trimerous and actinomorphic, normally bisexual (but dioecious variants are present in the Mediterranean region, described from Sicily as P. broteri Guss.). The leaf size is variable depending on site conditions, with smaller leaves being produced on less fertile soils with water limitation. The stomata are anomocytic. There is limited information available on the water relations of *P. multiflorum*, but Salisbury and Oliver (1928) showed an increasing number of stomata per area for leaves from the base towards the upper part of the plant, from 53 per mm² for the lowest leaves up to 91 per mm² for the top leaves. This was described as a general pattern also found in many other herb

species related to the variation in the level of humidity individual leaves are exposed to (Salisbury & Oliver, 1928).

6.2 | Mycorrhiza

Despite its ecological importance, the mycorrhizal symbiosis in *P. multiflorum* is not entirely understood, in part because existing original observations are scarce, outdated, methodologically limited, rarely reported in English, and/or difficult to retrieve. However, the genus *Polygonatum* as a whole has been recently considered to be predominantly arbuscular mycorrhizal (AM), based on at least 67% consistency of species diagnoses with AM within the genus (Soudzilovskaia et al., 2020). As this genus is relatively small, the assignment of AM status to *P. multiflorum* is likely correct. Yet, earlier work considered the species to be more of a facultatively AM plant rather than an obligate one (Harley & Harley, 1987; Wang & Qiu, 2006), based on three reports supporting the AM and two reports supporting the non-mycorrhizal status (as cited in Harley & Harley, 1987).

The assignment of AM symbiosis is primarily determined by microscopic observations of endophytic fungal colonization by AM fungi inside root fragments of the host plant, while the non-mycorrhizal status results from the observation of a consistent absence of mycorrhizal fungi in the roots (Cosme et al., 2018). A facultative AM plant is therefore one that is found in nature sometimes with an AM status and other times with a non-mycorrhizal one. One recent study on a number of species of temperate forests including *P. multiflorum* added further support to the AM status of this species (Rożek et al., 2019), in line with the genus' status (Soudzilovskaia et al., 2020). These authors went further to document the occurrence of the *Arum* type of AM (Rożek et al., 2019). The *Arum* type is one of the two major morphological classes of AM symbiosis (the *Paris* type being the other; Cosme et al., 2018) and is characterized by the formation of intercellular hyphae linked to intracellular arbuscules and inter- or intracellular vesicles, primarily located inside the tissues of the root cortex (Dickson, 2004). Despite their contribution to clarifying the mycorrhizal status, these morphological assignments do not allow for distinguishing the different fungal species that can associate with *P. multiflorum*.

While recent advances have expanded our understanding of AM fungal diversity (Lutz et al., 2025), at present, virtually nothing is known about the diversity of mycorrhizal fungi that can inhabit the root tissues of *P. multiflorum*. Similarly, studies examining the multifunctional role of AM fungi in *P. multiflorum* are lacking. The role of AM fungi in their host plants can range from parasitism to mutualism (Johnson et al., 1997), and they can influence not only plant growth but also various host traits related to nutrition, fitness, defence against pathogens and herbivores, and tolerance to abiotic

stresses (van der Heijden et al., 2015; Cosme, 2023). Given these knowledge gaps, and the species' botanical, ecological and ornamental importance, further research is warranted to fully understand the symbiotic functioning of *P. multiflorum* in mycorrhizas.

6.3 | Perennation: reproduction

Polygonatum multiflorum is classified as a geophyte (Dierschke, 2013). Each year, a new segment is added to the rhizome (Fig. 7b). Each rhizome segment extends from one scar of the aerial shoot to the next one (Fig. 7; Kosiński, 2015). The aerial shoot lasts from May to September within a single year, while the lifespan of a rhizome segment is approximately eight to ten years (Kosiński, 2015).

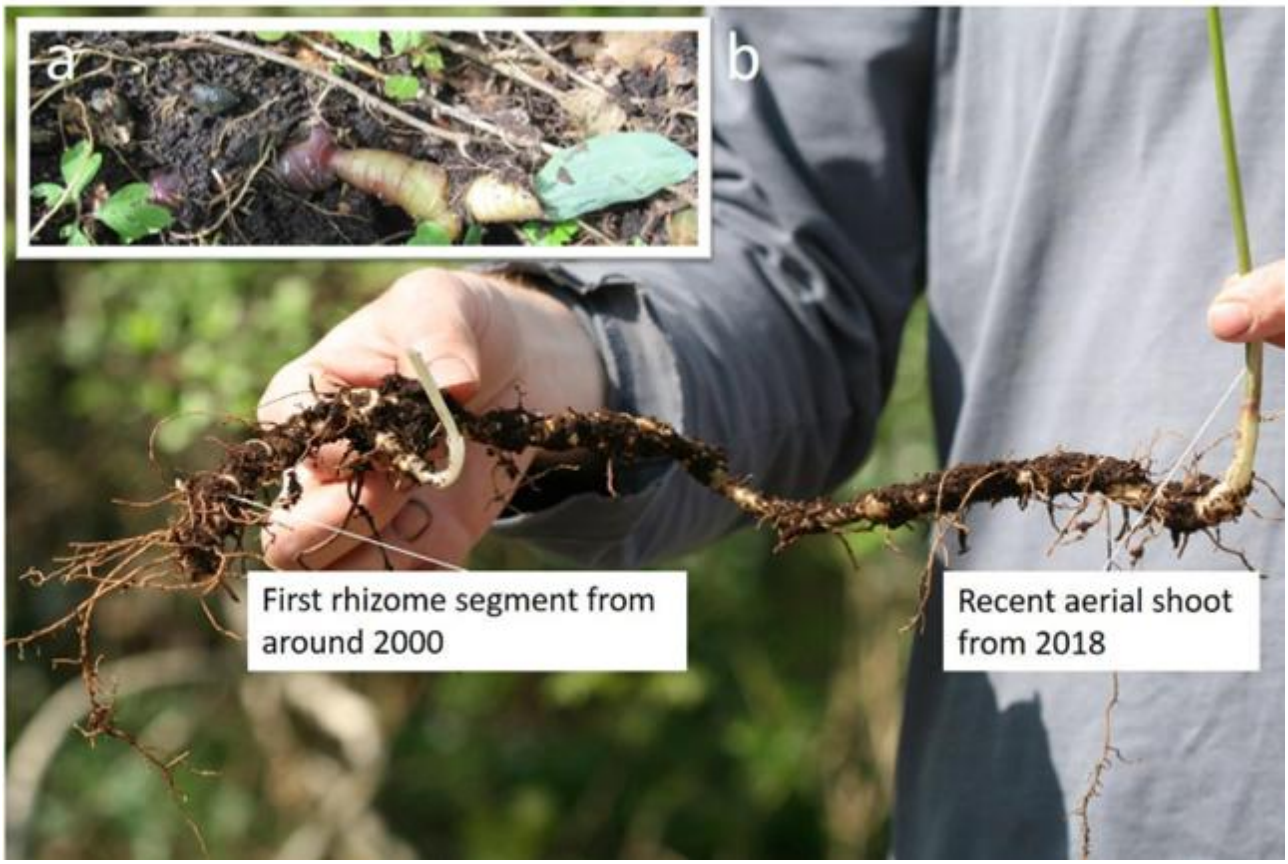


FIGURE 7 (a) Fresh leaves are growing out of a rhizome segment of *Polygonatum multiflorum* in May 2018, (b) Rhizome segments and aerial shoots of a multiple year old individual of *P. multiflorum* in May 2018. Photos a and b: Jannis Till Feigs.

Over the course of a year, the rhizome segment increases in length by 2-3 cm (Kosiński, 2015). Rhizome growth begins at the seedling stage (see section 8.5 on seedling morphology; Kosiński, 2015) and branching starts in the fourth year (Kosiński, 2015). While the main rhizome produces generative shoots no earlier than the seventh year, lateral rhizomes can form generative shoots from the fifth year on (Kosiński, 2015). The majority of generative shoots develop from the tenth year

onward (Kosiński, 2015; Labutina et al., 2019). Once generative maturity is reached, generative shoots emerge annually, producing flowers and seeds (Kosiński, 2015). Under controlled conditions, around 50 percent of individuals survive for at least eleven consecutive years (Kosiński, 2015). Individual longevity of up to 35 years has been reported (Ernst, 1979).

While rhizome segments of younger individuals grow both plagiotropically (horizontal direction) or orthotropically (vertical direction), the rhizome segments of older individuals tend to exhibit plagiotropic gowth (Kosiński, 2015). The relative contribution of both plagiotropic or orthotropic growth can change in response to environmental factors, such as variation in light conditions (Persson, 1975).

6.4 | Chromosomes

Polygonatum multiflorum has been widely investigated for chromosome number. As many as 54 published sporophytic counts are currently reported in the Chromosome Counts Database (CCDB; Rice et al. 2015). The numbers reported here are 2n = 18, 20, 22, 24, 28, 29, 30, and 36; the number 2n = 32 is also cited in Flora Europaea, vol. 5 (De Filippo, 1980). These numbers suggest a wide infraspecific karyological variability and presence of distinct chromosome races, although some erroneous counts cannot be excluded. Overall, the number 2n = 18 is most frequently observed and is apparently the more stable, being determined in plants from most of Europe, including the British Isles (Maude 1939, Clapham et al. 1987, pg. 534). Also Therman (1953) describes the chromosome number of European *P. multiflorum* as 2n = 18 and points out that at the time of writing it was the only *Polygonatum* species with a chromosome number that was not a multiple of 10. Therman (1953) thus suggested that the haploid number 9 is a derivative of the original basic haploid chromosome number n = 10. The ideogram drawn by Therman (1953) shows six longer and three shorter chromosomes.

The numbers 2n = 36, 22, 28 and 29 were reported mainly in plants from the eastern parts of the species range; for example Mehra and Pathania (1959) reported that all studied specimens from the west Himalayas had 2n = 22, with five long chromosome pairs and six short chromosome pairs. Abramova (1990) reported 2n = 28 and 29 in plants from the former Soviet Union.

Descending dysploidy may have been the possible process by which the most common haploid number n= 9 originated from n=10, followed by polyploidization to 2n = 36 in some populations and again by descending dysploidy events that led to origin to lower somatic numbers such as 2n=32, 30, 29, 28, and the others.

The *P. multiflorum* and *P. odoratum* hybrid, *Polygonatum x hybridum* has a chromosome number of 2n = 19 (Therman, 1953).

Few studies of population genetic variability have been carried out on *P. multiflorum*, but Szczeciska et al. (2006) reported higher levels of polymorphism in Polish *P. multiflorum* than in *P. odoratum* and *P. verticillatum* when analysing the species for the same genetic markers.

On the other hand, DNA sequencing in *P. multiflorum* has been performed for several genomic regions, especially nuclear or chloroplast, and used for reconstructing the phylogeny of the genus and species divergence patterns (e.g., Qin et al, 2024). In 2021, the complete sequence of the chloroplast genome, consisting of about 154564 base-pairs, was deposited in NCBI (Xia et al., 2022).

6.5 | Physiological data

Only a few studies have focused on the response to shade of *P. multiflorum* and photosynthetic characteristics. Topchiy et al. (2020) measured several photosynthetic parameters after subjecting *P. multiflorum* plants to varying light levels. Plants were collected at two sites differing in light availability, soil moisture and nutrient content of the soil. The plants were then subjected to a level of photon flux density similar to their natural shady environment of 80 µmol m^{-2} s^{-1} and to a significantly higher level of 800 µmol m^{-2} s^{-1}. *P. multiflorum* plants were compared with two other herb species (*C. majalis, A. europaeum*) and with three shrub species (*Prunus padus, Corylus avellana, Euonymus europaeus*). They found that, under the low light treatment, the plants collected from the lowland sites with an adequate supply of moisture and nutrients, were characterized by more efficient functioning of the photosynthetic apparatus (higher maximum and effective quantum yields in photosystem II, lower non-photochemical quenching). Under the high light treatment, plants from the two different sites showed similar efficiency. Under the high light treatment, *P. multiflorum* plants showed a significant decrease in photochemical quenching (qP) (from 0.8 to 0.6), but no photoinhibition (values below 0.6), which was the case for *Convallaria majalis* and for *Asarum europaeum*. *Polygonatum multiflorum* was thus found to be more resistant to high light intensities. In general, this study confirms the pattern that *P. multiflorum* is well adapted to shade, but benefits from a slight increase in light availability up to intermediate light levels (sections 4 and 5.2).

Fowden (1959) studied the nitrogen (N) content in different tissues of *P. multiflorum* at different growth stages and found that the amount of N in the roots varied between 15. 5.5 and 26.4 mg N g^{-1} dry weight of tissue, in the rhizome between 13.7 and 23.6 mg N g^{-1} dry weight of tissue and in the shoot between 27.5 and 76.5 mg N g^{-1} dry weight of tissue, with the lowest values reported at the end of the growing season in August and the highest values in mid-April. *P. multiflorum* was identified

as a N conservative species in an experimental N uptake study in which 15N was traced in pulse additions of $15NH_4$-$15NO_3$. Less than 1% of the pulse additions was taken up by *P. multiflorum* plants (Blondeel et al., 2019). Luwe (1995) studied the uptake of macro- and micronutrients and heavy metals by *P. multiflorum* and the content in different organs. He found that Ca and Mg were highest in the shoots, whereas other elements accumulated in the roots (K, Fe, Mn, Zn, Cu, Pb, Cd, Ni, Al) (Luwe, 1995). However, the rhizome contents of Ca, Mg, K, Fe, Zn, Al and Pb increased significantly with increasing age of the rhizomes. For Zn and Cd, the study found that the contents in below- and aboveground organs were correlated and indicated translocations of these elements within *P. multiflorum* plants. Additionally, the study reported significant positive correlations (correlation coefficient $r > 0.7$) between several nutrients and heavy metals contents in the plant organs (Ca, Zn, Cu, Cd and Ni) and the NH_4Cl-exchangeable cation fraction of the upper mineral soil, but no correlations with the total element contents in mineral soil or organic litter, nor with the NH_4Cl-exchangeable cation contents in organic litter. This data thus indicated a substantial uptake of nutrients and heavy metals by *P. multiflorum* from the NH_4Cl-soluble cation fraction of the upper mineral soil, which was dependent on the soil pH (Luwe, 1995).

6.6 | Biochemical data

The *Polygonatum* genus is known for containing many secondary metabolites in its organs; primarily saponins, phytohormones, glycosides, flavonoids and alkaloids are reported (Khan & Rauf, 2015). *Polygonatum multiflorum* specifically is a rich source of steroidal glycosides (Gvazava et al. 2019), anthraquinones and other phenolic compounds and has a long history of use in traditional medicine (Lu et al. 2007). In a comparative study of rhizomes of three *Polygonatum* species in the Indian Himalayans, *P. multiflorum* was found to have significantly higher flavonoids and total antioxidant activity (ABTS assay) in comparison with *P. verticillatum* and *P. cirrhifolium* (Suyal et al., 2021). Most studies identifying secondary metabolites from species of the *Polygonatum* genus focus on extracts from the rhizomes and roots (Zhao et al., 2015), however seeds have also been studied for different *Polygonatum* species (Qi et al., 2022). Specifically for *P. multiflorum*, Chopin et al. (1977) studied flavonoids extracted from the plant's fresh leaves; no specific study could be found on the comparison of metabolite content between different organs of the species.

7 | PHENOLOGY

Polygonatum multiflorum is a perennial spring geophyte with rhizomes that survive underground to store water and nutrients during winter (Karpavičienė & Mlečkaitė, 2019). It emerges from this dormant state in spring to capitalize on high light availability under the still open tree canopy. Leaf

flush onset for *P. multiflorum* in Great Britain has been recorded in April, maintaining its aboveground biomass until October (Taylor, 2023; Poland & Clement, 2020). The flowering period is significantly shorter, between May and June in Great Britain and Ireland (Taylor, 2023; Sell & Murrell, 1996). It flowers earlier in warmer conditions and later in brighter conditions (Lorer et al., 2023).

The phenology of *P. multiflorum* strongly responds to spring warming (i.e. changes in the mean temperature in March and April). Observational data (Schnitzler and Carbiener, 1991; Nordt et al., 2021) has shown that flowering onset advances on average between 5 and 6 days per degree warming in spring (see Appendix 2 for details). Also in experimental settings, similar sensitivities to spring warming with open top chambers have been observed (Lorer et al., 2024). A new analysis method (Landuyt et al., 2025), applied on data from the same experiment, even showed that temperature within a very short time window in spring (between 14 March and 3 April) best explained differences in the timing of flowering phenology between plants that were growing inside open top chambers and plants that experienced no experimental warming. Based on this short forcing time window, temperature sensitivity of flowering phenology was estimated to amount up to ca 9 days advance per degree warming. Data on the sensitivity of vegetative phenology to warming are rare, but generally confirm advances across early (e.g. leaf unfolding) and late phenological stages (e.g. senescence onset), with later phenological stages advancing at a lower rate, leading to prolongations of the growing season as a response to spring warming (PhenObs network). Using experimental data from Lorer *et al.* (2024), and additional growth measurements in the same experiment (see Fig. 8), we find that growth onset is on average advanced while senescence and dormancy are notably delayed under warmer conditions. Complete population dormancy (i.e. the moment when all individuals have disappeared aboveground), on the other hand, happens earlier under warming. Fig. 8 also shows that the flowering period is clearly shorter and earlier in warmed plots.

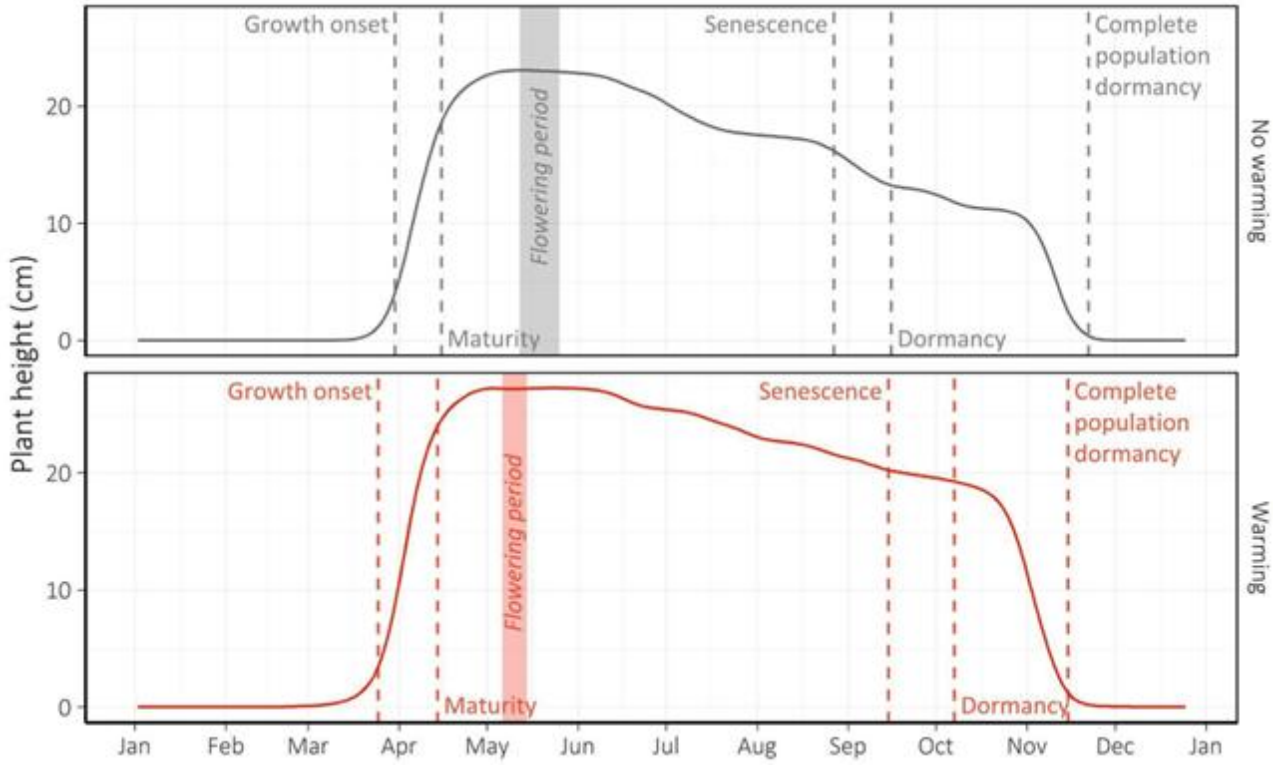


FIGURE 8 Growth and flowering phenology of *Polygonatum multiflorum* in an understorey warming mesocosm experiment in lowland Belgium (Lorer et al., 2023; and additional measurements in the same experiment). For control plots (n= 21, top) and warmed plots (with open-top chambers n= 18; bottom), the mean intra-annual plant height curves, measured in 2023, are shown. Growth events extracted from these curves are indicated with dashed vertical lines: mean growth onset, maturity, senescence and dormancy, and complete population dormancy (i.e., the moment when all individuals have disappeared above-ground). The flowering period is indicated with the vertical bar.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

Polygonatum multiflorum is an outcrossing, self-incompatible species (Kosiński, 2012). It is insect-pollinated (Corbet et al., 1988; Kosiński, 2012), particularly by long-tongue bumblebees (e.g. *Bombus pascuorum* and *B. pratorum*), but occasionally pollinated by hoverflies and solitary bees (Naaf et al., 2021; Feigs et al., 2022 in Germany, Fig. 9). Its pollen has also been detected in honeybee honey (de Vere et al., 2017). The number of flowering shoots varies among populations (e.g. 22% to 79%, Labutina et al., 2019).

Plants reach their generative maturity and flower from the seventh year, but mostly at age ten-to-fifteen years (Kosiński, 2015; Labutina et al., 2019). Flowers are in clusters of 2–5. Flowers form up to 15 inflorescences per shoot (Karpavičienė & Mlečkaitė 2019). The number of flowers varies, with

an overall average 10–26 flowers per shoot (Kosiński, 2012; Karpavičienė & Mlečkaitė, 2019; Labutina et al., 2019), but the number ranges from 1 to 51 between specimens (Karpavičienė & Mlečkaitė, 2019) and between years (Labutina et al., 2019). The flowering continues for at least 10 days up to a few weeks; the flowering is sequential from the bottom to the top of the shoot, mostly by three flowers at the time (Kosiński, 2012; Labutina et al., 2019).

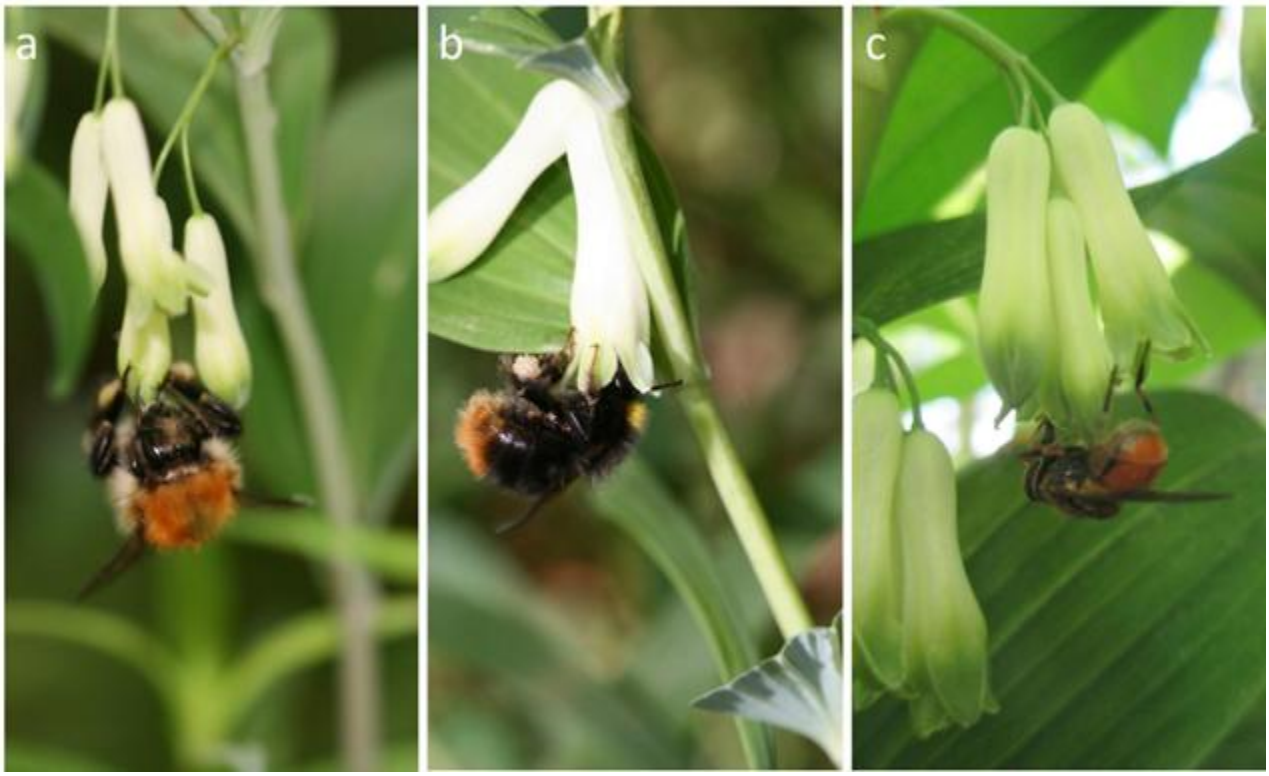


FIGURE 9 Pollinators on *Polygonatum multiflorum* flowers: (a) *Bombus pascuorum*, (b) *B. pratorum*, and (c) the hoverfly *Rhinigia campestris*. Photos a–c: Jannis Till Feigs.

The flowers are mostly hermaphrodite and consist of 6 stamens and a pistil of three fused carpels (Kosiński, 2012). Flowers have a structural dimorphism in the form of heterostyly or dichogamy, sometimes andromonoecy). Usual hermaphrodite flowers have a stigma located at the level of the anthers, but in some flowers, a carpel has a short style as a stigma is below the anthers and ovules have not been developed (Kosiński, 2012). Some flowers can have only male properties – they have an atrophied carpel and no ovules in the ovary. Along the shoot, typical hermaphrodite flowers occur in the lower and middle positions and others are common at the top part of the shoot, male flowers mostly at the top (Kosiński, 2012). Flower dimorphism occurs within most plants, only some shoots have all flowers with well-developed carpels, and a smaller proportion has flowers only with atrophied styles (e.g. 67%, 23%, 10% respectively in the study of Kosiński, 2012). The number of ovules varies between the proximal and the distal position of the stem, but also between populations (Kosiński, 2012).

8.2 | Hybrids

The only known hybrid is *P. multiflorum* and *P. odoratum* = *Polygonatum x hybridum* Brügger 1886 (syn: *P. x intermedium* Boreau 1857, *P. x mixtum* K.Richt. 1890, *P. x officinaloides* H. Lév. 1917, *P. multiflorum* subsp. *intermedium* K.Richt. 1890) , 2n=19 (see section 6.4). It is likely a hybrid of garden origin as it has been rarely observed in the wild (Lambinon et al., 1998) and went extinct in several historical localities (Tison & de Foucault, 2014). It is mostly cultivated as an ornamental in parks and gardens, especially in the UK (Stace, 2019), from where it has escaped and naturalized in woodlands. It differs from *P. multiflorum* by its more robust aspect (up to 1 m high), its ridged to slightly angular stems, and the longer perianth (15-25 mm instead of 9-20 mm) of the flowers grouped by 2-3. Flowering is followed only rarely by berry production. Published cytological or germination studies confirming fully fertile sexual reproduction are lacking. Its establishment under wild conditions therefore may depend predominantly on vegetative propagation (rhizome spread) rather than regular seed recruitment.

According to Tison & de Foucault (2014) a locally-reported clonal mutant (*P. multiflorum* var. *bracteatum*) is characterised by a branched stem and foliated bracts and under favourable conditions may form locally abundant patches. Given the clonal nature of the spread of this form, its occurrence may reflect stable, low-disturbance woodland microsites with limited seedling recruitment, which in turn may have implications for genetic diversity and long-term resilience of such stands.

8.3 | Seed production and dispersal

After flowering, 21% - 66% of flowers produce fruits, ca 3-15 fruits per shoot (Labutina et al., 2019). The fruit ripening period of *P. multiflorum* lasts from May to September (Labutina et al., 2019). The fruit is a spherical, dark blue, juicy berry. A mean weight of 0.466 g, a water content of 83.5 % and the following dry weight contents have been measured: nitrogen 1.48%, lipids 1.2%; carbohydrates 43.6% (Eriksson & Ehrlén, 1991). For the round-oval seeds, a mean weight of 28.6 mg (Eriksson & Ehrlén, 1991), and a length of up to 3.8 mm has been measured (Labutina et al., 2019). The fruit/flower ratio (fruit set) per ramet amounted to 24.5% (note, 20 flowers per shoot) and was very variable (coefficient of variation, CV = 84.6%). The long-term dynamics of the fruit set played an important role in this variability. However, the fruit-set variation was higher among populations than among years (Kosiński, 2012). The proportion of flowers that set fruit was higher on the lower and middle positions than on the upper ones. The substantial dynamics of the fructifying shoots usually resulted from damage caused by grazers or parasites. The initial fruit/flower ratio (for young fruits)

was on the average twice as high as the final fruit set (for ripe fruits) and was calculated at 45.7% as compared to 20.8%.

The fruit type of *P. multiflorum* indicates vertebrate dispersal. Its spherical, blue-black berries have been categorized as "ingested" because these traits are typical of bird-dispersed species, suggesting potential for long-distance dispersal (Schaumann & Heinken, 2002; Ehrlén & Eriksson, 1993; Ehrlén & Eriksson, 2000; Müller-Schneider, 1986). Additionally, landscape genetic analysis of isolated *P. multiflorum* populations within agricultural landscapes provided indirect evidence suggesting woodland birds as seed dispersers (Naaf et al., 2022). Ungulates also regularly feed on *P. multiflorum* (see Chapter 9.1), which could result in seed dispersal. However, studies have not recorded seeds of *Asparagaceae* (including *P. multiflorum*) in marten faeces (Schaumann & Heinken, 2002), suggesting that martens may not disperse these seeds. Overall, long-distance seed dispersal appears to be a rare event, and multiple authors have described *P. multiflorum* as having a slow colonizing capacity (Bossuyt et al., 1999; Dzwonko, 2001; Orczewska, 2010; Brunet et al., 2012). Identifying seed dispersers and assessing the strength of seed dispersal remains a significant knowledge gap.

8.4 | Viability of seeds: germination

The germination of *P. multiflorum* begins after cold-wet stratification, typically under moist and dark conditions at 20°C, with radicles emerging after two weeks and full germination occurring after approximately eight weeks (Feigs et al. in prep.; Cooly, 1895). The process includes an early phase of rhizome formation lasting around five weeks (Feigs et al. in prep.). The seed itself is hard and spherical, with a large endosperm rich in cellulose that contains oil and protein but lacks starch or sugar (Cooly, 1895). The embryo, although small, consists of a cotyledon that surrounds the future stem tip and a tiny hypocotyl (Cooly, 1895).

Prior to germination, the embryo of *P. multiflorum* remains dormant—similar to other temperate woodland herbs such as *Convallaria majalis* (Vandelook et al., 2019). As the seed absorbs water, it softens and swells, starting the germination process.

P. multiflorum seems to be able to attain high germination. Using 1442 seeds from 87 mother plants spread across nine forests in north-eastern Germany, the overall mean germination was 70%, varying between 56 and 80% between the different forest populations (Feigs et al., in prep.). Seeds underwent a cold stratification period (6 weeks at 5 °C on wet filter paper) and were subsequently subjected to a constant 20 °C in a dark environment. First radicles emerged (i.e., germination) after two weeks. In a seed-sowing and survival experiment reported by Ehrlén and Eriksson (2000) and Ehrlén et al. (2006), 90 seeds (mean weight of 28.6 mg) of *P. multiflorum* were sown in each of four 0.5 m x 0.5

m subplots, replicated in each of 48 forest patches where the species was either present (5) or absent (43) in a 50 m radius around each experimental plot. Two and three years after seedling emergence, 100% of emergent *P. multiflorum* seedlings were still present in the already occupied forest patches. In the forest patches previously not occupied by the species, post-emergence seedling survival was markedly lower, with only 81% and 56% survival two and three years after seed sowing, highly comparable to germination and survival for other forest species of similar life-histories such as e.g. *Convallaria majalis* which were equally sown in this study. Crucially, these results pinpoint that a high number of unoccupied sites were suitable habitat for *P. multiflorum*. Finally, the abiotic environment had no impact on seedling emergence and survival of the species up to three years post-sowing. Ehrlén and Eriksson (2000) demonstrate by comparison with the other forest species in the study (*Convallaria majalis, Actaea spicata, Dentaria bulbilifera, Paris quadrifolia, Campanula latifolia* and *Lathyrus vernus*) how the large seed mass of *P. multiflorum* is a likely driver behind the high survival and colonization rate of the species in unoccupied patches, while simultaneously causing the species to be dispersal limited. This is even true within the species, as seed weight strongly and positively affects germination rate (Fig. 10).

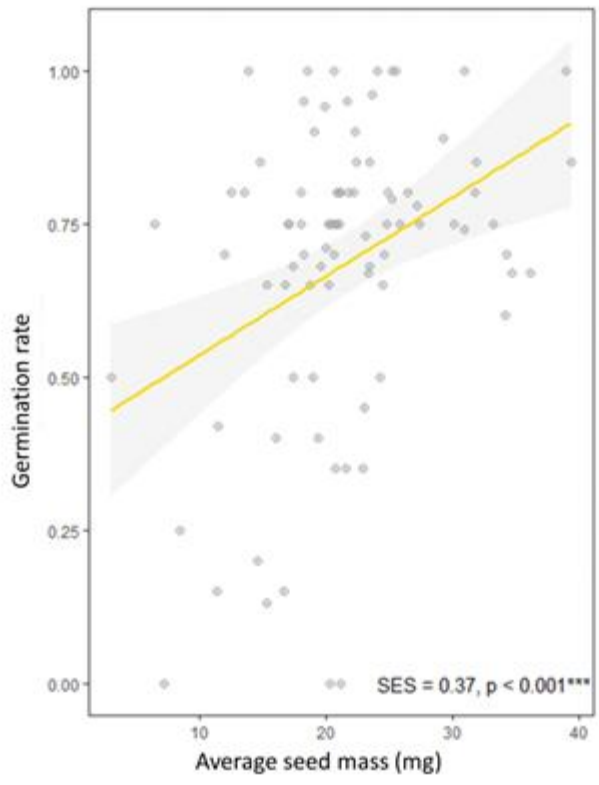


FIGURE 10 Germination (proportion of seeds) in *Polygonatum multiflorum* in relation to average seed mass (mg), based on germination of 1442 seeds from 87 mother plants distributed across nine forest stands in north-eastern Germany (Feigs et al., in prep).

Seedling mortality of *P. multiflorum* was less than reported for the other species in the experiment of Ehrlén et al. (2006) (for more in-depth details, see Ehrlén & Eriksson 2000 and Ehrlén et al. (2006)). Eleven years after seed sowing, the species was still present in 18 out of 43 (41%) previously unoccupied forest patches. In a similar seed sowing experiment in 24 plateau forests in Flanders (Belgium), Baeten et al. (2009) illustrate how seed sowing density (18, 140 or 560 seeds/ 0.5 x 0.5m2 plot) as well as litter removal positively affected recruitment of *P. multiflorum* two years post-sowing. There are no indications that *P. multiflorum* forms a persistent seed bank, at least it was never found in germination trials from deciduous forest soils (Eriksson, pers. obs.).

8.5 | Seedling morphology

Seedling emergence in *P. multiflorum* takes two years (Kosiński, 2015). In the first year, germination is restricted to the growth of a primary root and a bulb-like rhizome, which is about 4 mm long, has several adventitious roots, and ends with an orthotropic terminal bud (Fig. 11a). When seeds are germinated on moist filter paper in Petri dishes kept at 20°C in the dark, a small radicle emerges two weeks after a cold-wet stratification. A small rhizome will have developed after five weeks (Feigs et al., in prep.).

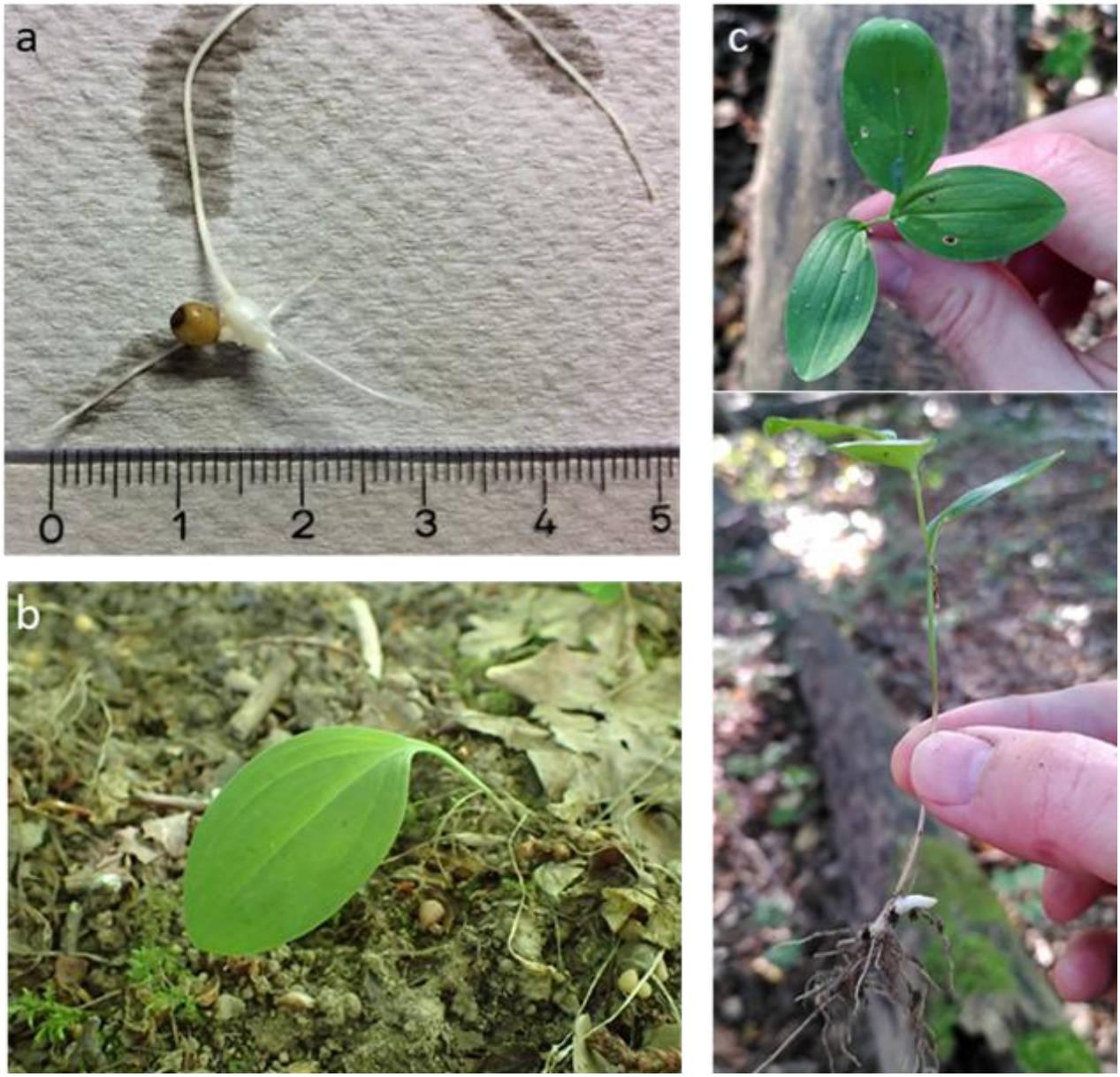


FIGURE 11 Stages of germination and seedling development in Polygonatum multiflorum. (a) Seed with developed rhizome, primary root, adventitious roots and a terminal bud 7 weeks after cold-wet stratification. (b) First above-ground shoot with a single leaf. (c) Juvenile individual with three leaves and small rhizome, from which the new increment is growing. Photos a, c: Tobias Naaf. Photo b: Krzysztof Ziarnek (Creative Commons Attribution-Share Alike 4.0 International).

In the second year, a first aerial shoot with a single leaf grows from the terminal bud (Fig. 11b). At its base, a new rhizome increment develops, from which a new aerial shoot will grow in the following year. In a comprehensive seed sowing experiment, Kosiński (2012) found the aerial shoots in the third and fourth year after sowing to have one to three leaves (Fig. 11c). In the following years, the number of leaves per shoot increased up to more than 20 leaves in some individuals, however, up to the 11th year, most shoots still had five or less leaves (Kosiński, 2015). Rhizome branching may start in the fifth year, although by the 11th year, most individuals (94%) still showed a simple unbranched

rhizome (Kosiński, 2015). Individuals may reach sexual maturity in the seventh year and then produce two to four flowers (Kosiński, 2012). However, most individuals (≥95%) remained in an immature state even after 11 years.

Seedlings of *P. multiflorum* occur relatively frequently within established populations. Riznychuk et al. (2023) classified between 3% and 12% of the shoots encountered in Precarpathian forests as first-year above-ground seedlings. However, distinguishing juvenile plants grown from seeds from young ramets originating from rhizome branching is difficult and only possible by exhuming the plants (Kosiński, 2012).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

Various tissues of *P. multiflorum*, including leaves, fruits, seeds, and roots, contain toxins (Zhao et al., 2018; Ehrlén & Eriksson, 1993). Among these toxins saponins and lectins have been identified (Zhao et al., 2018; van Damme et al., 2000), with the seeds having higher concentrations than the pulp (Ehrlen & Eriksson 1993). Despite its toxicity various mammals (including roe deer *Capreolus capreolus* (Linnaeus) and mouflon *Ovis musimon* Pallas), as well as mollusks and insects, feed on *P. multiflorum* (Marchand et al., 2013; Kosiński, 2012), often causing significant damage to the plants (Fig. 12a; Kosiński, 2012). As the saponins reduce palatability, but do not guarantee immunity against herbivory, *P. multiflorum* is considered relatively unpalatable, but the degree of herbivory depends on the environmental context. A study by Řepka et al. (2021) compared Holedná game reservoir in the Czech Republic, which has high densities of fallow deer (*Dama dama* (Linnaeus)) and mouflon, with the surrounding forest. In this study, *P. multiflorum* was found in 20% of the forest plots but was absent within the reserve. In regions with ungulate overabundance, deer preferentially graze young emerging shoots in spring, leading to shoot loss before flowering can occur. This phenomenon has been widely documented in European forests, where selective browsing by deer reduces reproductive success in perennial herbs by eliminating flowering stems before seed set (Řepka et al., 2021).

Besides herbivory, insects can also cause significant damage to *P. multiflorum* populations (Kosiński, 2012). Several insect species from the orders Diptera, Hymenoptera, Hemioptera, and Coleoptera parasitize the stems, leaves, and flowers of *P. multiflorum* (Table 1). Insects frequently damage the fruits, leading to premature fruit drop (Labutina et al., 2019). When drying berries were opened, numerous passages were found inside, leading to the drying of the fruits and damage to the seeds (Labutina et al., 2019). A share of 16% fruits attacked by non-disperser (invertebrate) frugivores has

been reported (Eriksson & Ehrlén, 1991). One species that shows a strong specialization for *P. multiflorum* is the sawfly *Phymatocera aterrima* (Klug), commonly referred to as the "Solomon-seal Sawfly" (Fig. 12c, b; Crowley et al., 2024). This species is widely distributed across Europe, including Austria and Germany (Altenhofer & Pschorn-Walcher, 2003), Poland (Kosinski, 2012), Wales and Scotland (Liston et al., 2014; Musgrove, 2023). It has been reported for England since 1839, where it was introduced together with *P. multiflorum* via gardens (Benson, 1952; Miles, 1962).



FIGURE 12 Herbivory patterns on *Polygonatum multiflorum* plants (a) by mammals and (b) by insect larvae. (c) Close-up of three sawfly (*Phymatocera aterrima*) larvae feeding *on P. multiflorum* leaves. Photos a, b: Jannis Till Feigs; Photo c: Tomas Pocius (via iNaturalist).

Adult *P. aterrima* are entirely black with tinted wings. Egg deposition primarily occurs inside the thin stems of young plants, with up to ten pale green eggs inserted into a shallow depression beneath the cuticula. At the oviposition site, the plant tissue turns red over an area of 1-2 cm. The larvae typically emerge in the second half of May and feed by creating elongated, irregularly serrated holes in the leaf blade (Fig. 12b). Shortly after hatching, the larvae prefer feeding on smaller plants, mostly during twilight. Initially, individuals from the same clutch feed together on a single leaf, but as they grow, they disperse and begin feeding on larger plants. They feed for up to eight hours per day. The

feeding period in the wild lasts about three weeks, during which the larvae frequently switch host plants due to the extensive damage they cause (Altenhofer & Pschorn-Walcher, 2003).

The long-term consequence of heavy browsing and herbivory is a gradual decline in clonal expansion and a demographic shift towards predominantly juvenile, vegetative individuals (Istomina et al., 2016). This suggests that *P. multiflorum* exhibits a compensatory response to shoot herbivory by allocating resources toward survival rather than reproduction, prioritizing the maintenance of its rhizomatous network over immediate generative efforts. The shift from reproductive to vegetative shoots has been observed in multiple studies and is a common strategy among perennial forest herbs subjected to recurrent defoliation (Heinken et al., 2022).

TABLE 1 Insects associated with *Polygonatum multiflorum*, grouped by group and family. The affected organ, the mode and the source of the information is also reported.

	Organ	**Mode**	**Source**
Coleoptera			
Chrysomelidae			
Lilioceris lilii	Leaf	Free	PPE (2025)
Diptera			
Cecidomyiidae			
Contarinia florum	Flower	Gall	PPE (2025)
Contarinia polygonati	Flower	Gall	PPE (2025)
Drosophilidae			
Drosophila suzukii	/	/	Kenis et al. (2016)
Scathophagidae			
Americina media	Leaf	Miner	PPE (2025)
Americina vittata	Leaf	Miner	PPE (2025)
Hemiptera - Sternorrhyncha			
Aphididae			
Aulacorthum speyeri	Leaf	Free	PPE (2025)
Myzus ascalonicus	/	/	Cox (1976)
Hymennoptera			
Tenthredinidae			
Phymatocera aterrima	Leaf	Free	PPE (2025)

9.2 | Plant parasites and diseases

Polygonatum multiflorum is generally regarded as having a low incidence of viral infection in horticultural settings, but it is susceptible to a wide range of fungal species, including both host-specific (monophagous) taxa such as *Passalora polygonate* (Dearn.) U. Braun*, Phyllosticta cruenta* Sacc.*, Stomatinia rapulum* (Fr.) Fuckel*, Cladosporium polygonate* Sawada*, Septocylindrium polygonate* Dearn. & House*, Septoria polygonate* Pass., and *Urocystis miyabeana* Syd. & P. Syd. and more polyphagous (plurivorous) species. Most of these pathogens primarily affect the foliage (Table 2). In addition, numerous saprotrophic fungi have been recorded in association with *P. multiflorum* (see Appendix 3). While most saprophytes colonize and derive nutrients from the entire senescent or dead plant, a subset appears to specialize on the decaying stems (Ellis & Ellis, 1997).

TABLE 2 Fungi associated with *Polygonatum multiflorum*. Main affected plant organ, group, family and source of the information (*species reported for the whole genus *Polygonatum*).

	Organ	**Mode**	**Source**
Ascomycota			
Cladiosporiaceae			
Cladosporium polygonati *	Leaf	Leaf spot	PPE (2025)
Dermateaceae			
Duebenia compta	/	/	Ellis and Ellis (1997)
Glomerellaceae			
Colletotrichum dematium	Leaf	Leaf spot	PPE (2025)
Leptosphaeriaceae			
Leptosphaeria gloeospora	Stems	/	PPE (2025)
Microascaraceae			
Cephalotrichum purpureofuscum	/	/	Ellis and Ellis (1997)
Mycosphaerellacea			
Passalora polygonate	Leaf	Leaf spot	PPE (2025)
Septocylindrium polygonati *	Leaf	Leaf spot	PPE (2025)
Septoria polygonati *	Leaf	Leaf spot	PPE (2025)
Periconiaceae			
Periconia cookie	/	/	Ellis and Ellis (1997)
Plectosphaerellaceae			

Verticillium albo-atrum	/	/	Ellis and Ellis (1997)
Verticillium dahlia	/	/	Ellis and Ellis (1997)
Phyllostictaceae			
Phyllosticta cruenta	Leaf	Leaf spot	PPE (2025)
Saccotheciaceae			
Aureobasidium microstictum	Leaf	Leaf spot	PPE (2025); Ellis and Ellis (1997)
Sclerotiniaceae			
Valdensia heterodoxa	Leaf	Leaf spot	PPE (2025)
Stromatinia rapulum	Root	Gall	PPE (2025)
Botrytis cinerea	Stems/ leaves/ flowers/ fruits	/	PPE (2025); Ellis and Ellis (1997)
Basidiomycota			
Pucciniaceae			
Puccinia sessilis	Leaf	Pustule	PPE (2025)
Urocystidaceae			
Urocystis miyabeana	Leaf	Gall/ stripe	PPE (2025)

10 │ HISTORY

Polygonatum multiflorum was first described by Linnaeus in his Species Plantarum (1753) under the name *Convallaria multiflora.* The type collection was included in the Linnaean Herbarium Savage (1945), and a photograph can be consulted online (Linnean Society of London, 2025). Linnaeus indicated that the species occurs on the cliffs and rocks of northern Europe ("Europae septentrionalis praecipitiis, rupibus"). The name *Polygonatum*, based on the character of its rhizome, was later suggested by Miller (1731), Ownbey (1944) and Allioni (1785).

Phylogenetic analysis based on chloroplast sequences placed *P. multiflorum* firmly within the *Polygonatum* section but suggested that the European *P. multiflorum* and Asian (Himalayan) *P. govanianum* (which had previously been included in *P. multiflorum*) indeed should be treated as separate species (Floden & Schilling, 2018). The molecular distinction of *P. multiflorum* and *P.*

govanianum is further supported by differences in morphology and chromosome number. A separate study, using nuclear DNA, failed to obtain a monophyletic clustering of *P. multiflorum* individuals but did not report the origin of the included individuals (Xia et al., 2022).

The species has long been recognized for its ornamental value, being a possible driver for its contemporary introductions outside of its native range in e.g. Canada and the USA and in Ireland where it is considered a neophyte. The species appears in the Fromond list, listing plants “necessary for a garden” in Britain from around 1525 (Harvey, 1989), and has been recorded in e.g. palace parks in Poland (16th century, Nowinska et al., 2016), Ukraine (Feofaniya park (Kiev); Matiashuk et al., 2021) and Russia (St-Petersburg, 18th century, Ignatieva & Konechnaya, 2004). Historically, *P. multiflorum* has been equally recognized for its medicinal use, dating as far back as the “Cruydeboeck” (“herbal book”) published by Rembrecht Dodoens (1554), who lists the species above- and belowground plant parts are unsuitable for internal use (acknowledging the species to be poisonous, See section 6.6). On the other hand, Dodoens (1554) states that roots (or their sap) placed on wounds or bruises help the healing process. In the Himalayas, the species’ rhizome is used as a blood purifier, nervine tonic and aphrodisiac (Kala, 2005).

11 │ CONSERVATION AND MANAGEMENT

Conservation status and legislation

A study of 1,220 semi-permanent plots across Europe recorded a 1.3% decline in *P. multiflorum* over intervals ranging from 12 to 67 years between resurveys (De Frenne et al., 2013). In Great Britain, population trends between 1930 and 2019 were largely stable, while Ireland saw a moderate increase over the same period. However, more recent data from 1987 to 2019 indicate a strong decline in Great Britain and a moderate to strong decline in Ireland, with these trends adjusted to account for differences in survey effort over time (Taylor, 2023). Regional resurveys of the flora in southern Sweden revealed an increasing frequency of *P. multiflorum* at the landscape level, probably related to increasing forest areas (Tyler et al., 2007; Jonsell & Aronsson, 2010). However, resurveys of sample plots in deciduous forests in both Germany and southern Sweden showed a decreasing local abundance of the species, probably as a result of soil acidification (Falkengren-Grerup, 1995; Leuschner & Ellenberg, 2017).

Polygonatum multiflorum has been classified as a species of "Least Concern" under IUCN criteria in ten European countries, including Great Britain, Austria, Belgium, Denmark, France, Germany, Luxembourg, Netherlands, Norway, Sweden and Switzerland (Lončarević et al., 2024; SLU Species Data Bank, 2025). Due to its widespread distribution in mainland Europe, Britain and Ireland, *P.*

multiflorum does not have any special protection status (Taylor, 2023). The species is officially listed as an introduced species in Ireland and Canada (Roy et al., 2020), with further introductions in countries such as USA, New Zealand, Australia and China (Section 1), likely due to its ornamental appeal and international trade (Saul et al., 2017). Despite its introduction in multiple regions worldwide, there are no reports of *P. multiflorum* being considered invasive, nor any documented evidence of significant negative impacts on native flora or the need for urgent management interventions.

The species is recognized as an indicator of ancient forest throughout northwestern Europe (Hermy et al., 1999, see section 5.2), including Great Britain (Kimberley et al., 2013) and is considered a forest specialist species across its native range (Heinken et al., 2022). However, the species is also frequently found to colonize recent woodlands (Verheyen & Hermy, 2001) and hedgerows in parts of its range in general (Wehling & Diekmann, 2009a; Litza et al., 2022), and the UK specifically (McCollin et al., 2000), forming viable populations unaffected by unique environmental conditions in these habitats.

Future threats and associated management for conservation

Polygonatum multiflorum is one of the most common forest species across its European distribution and although not exclusively, it is often associated with ancient forests (see 5.2). Nevertheless, like ancient forest species in the UK (e.g. *Paris quadrifolia*, Jacquemyn et al., 2008; *Primula elatior*, Taylor & Woodell, 2008; *Poa nemoralis*, Plue et al., 2020), it faces many environmental threats ancient forests experience. The foremost threat is habitat loss. With only 2.5% of the UK's land area covered by ancient forests, their continued decline (Rackham, 2008) presents a critical risk to the long-term survival of *P. multiflorum*. In addition, habitat degradation poses a significant challenge, particularly through acidification caused by nitrogen deposition, which can drastically reduce the species' occurrence and abundance (Falkengren-Grerup, 1995) due to negative impacts on growth (Govaert et al., 2021).

Climate change is another key factor influencing *P. multiflorum* populations. Warming temperatures may directly affect local population dynamics (Govaert et al., 2021), while altered canopy dynamics - such as increased light availability - could have indirect effects (Blondeel et al., 2019; Govaert et al., 2021). Although greater light availability has been linked to significant increases in species cover (e.g., a 72% increase over 25 months; Blondeel et al., 2019), the long-term implications remain uncertain. Moreover, forest management practices are likely to adapt to climate change, which could further influence canopy conditions and present an additional threat to the species. The spread of non-native tree species, planted or invaded in stands previously containing *P. multiflorum*, has already led

to severe declines and local extinctions of *P. multiflorum* in some regions. For example, *Ailanthus altissima* in France (Motard et al., 2011), *Quercus rubra* in Lithuania (Marozas et al., 2009), and *Robinia pseudoacacia* in Italy (Sitzia et al., 2018) have all contributed to significant losses of the species. Additionally, the decline of pollinators - particularly *Bombus* spp. - due to land-use changes, such as grassland loss, poses a critical risk to *P. multiflorum*. Pollinator declines could lead to genetic erosion, an otherwise less pressing concern in fragmented populations, precisely due to the high mobility of its key pollinator assemblage (Naaf et al., 2022).

In summary, safeguarding *P. multiflorum* requires maintaining the ecological integrity of its primary habitat: ancient forests. Given its limited dispersal ability (Section 8.3; Bossuyt et al., 1999; Brunet et al., 2021), creating new forests is most beneficial in close proximity to ancient ones (Bossuyt et al., 1999) or in connection to hedgerows with the species (Wehling & Diekmann, 2009b). However, ensuring the persistence and proper management of existing ancient forests remains the most viable approach to securing the future of *P. multiflorum*.

ACKNOWLEDGEMENTS

This work was supported by the Research Foundation – Flanders (FWO) by funding the scientific research network FLEUR (W000322N, www.fleur.ugent.be). The author group (Appendix 4) is connected through the FLEUR network and conceived the idea on an online network meeting. We would like to thank all the botanical gardens and people of the PhenObs network (https://www.idiv.de/de/web/phenobs.html) for collecting and providing data. We thank Bente Graae, Dr. Sarah Dalrymple and four anonymous reviewers for their constructive comments on an earlier version of this manuscript. We acknowledge funding for PhenObs from the German Science Foundation (DFG) via the German Centre for Integrative Biodiversity research (iDiv) enabling the development and coordination of this project. ED, FVM & PDF received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (ERC Consolidator Grant CanopyChange 101124948). Research Foundation Flanders (FWO) also supported LD (research project 1221523 N), DL (research project G098625N) and EL (research project G078921N; funding obtained by PDF and DL).

AUTHOR CONTRIBUTIONS

Pieter Vangansbeke and Pieter De Frenne conceived the study. All authors were involved from the start, collected and synthesized the existing literature, wrote the original draft, and contributed to review and editing. Pieter Vangansbeke guided the process and led the review and editing.

STATEMENT OF INCLUSION

This study was developed within the FLEUR network, which brings together researchers studying forest plant ecology across Europe. All researchers involved in the FLEUR network were invited to join the author team, irrespective of background, gender, or career stage.

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