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Biological flora of Central Europe – *Lupinus polyphyllus* Lindley

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ABSTRACT

The invasive herb *Lupinus polyphyllus* has been focus of a number of fact sheets worldwide but a comprehensive summary of the species' taxonomy and morphology, distribution, habitat requirements, and biology has been lacking. This paper gives a thorough account of the species' systematic position and taxonomy, highlighting the difficulties to delimit taxa, which is related to interbreeding among members of this genus. However, *L. polyphyllus* var. *polyphyllus* is apparently the taxon that has naturalized and is regionally invasive in temperate-humid climates worldwide. We also present an updated distribution map of *L. polyphyllus* in the native and invaded ranges, which highlights seven regions in the world where the species has been established. We show that the climatic niche of *L. polyphyllus* in the invaded range shifts towards higher summer precipitation and lower isothermality, probably because the invaded range includes subcontinental regions of eastern Europe and western Siberia. The habitats of *L. polyphyllus* range from rather dry to wet, have moderately acidic to strongly acidic soils, and the species' indicator values across Europe suggest that it occurs along a gradient from very nutrient poor sites to intermediate to rich sites from northern to southern Europe. The species shows high resistance to both drought and frost. In Central Europe, the species has a stronghold in alpic mountain hay meadows, abandoned meadows and pastures, low and medium altitude hay meadows, anthropogenic herb stands and temperate thickets and scrubs. In northern Europe, the species occurs in anthropogenic herb stands along roads and railroads as well as in abandoned pastures and fields. We also found some doubtful information about *L. polyphyllus* in the literature. This refers to its description as "rhizomatous perennial" although it lacks rhizomes; an apparently very high longevity of its seeds, which may only be true under artificial conditions in an ex situ seed repository; and a very deep rooting depth, which may not represent the average rooting depth but rather an extreme value. Knowledge about the interrelationships between the species' future population dynamics and spread and ongoing climate warming is lacking. Finally, our review points out that there is currently no evidence-based strategy for a cost-efficient management of *L. polyphyllus* although it is among the most problematic non-native plant species in Europe due to its environmental and socio-economic impacts.

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1. Introduction

Although the series Biological Flora of Central Europe explicitly embraces invasive species (Matthies and Poschlod, 2000), only few contributions have addressed non-native plants (Weber, 2000; Weber and Jakobs, 2005; Helsen et al., 2021) or native species that extended their range (Voss et al., 2012). The perennial herb *Lupinus polyphyllus* Lindl. (Garden lupine) is considered to be among the most problematic non-native plant species in Europe due to its environmental and socio-economic impact (e.g., Nehring et al., 2013; Tyler et al., 2015; Rumlerová et al., 2016; Nentwig et al., 2018) but it is, as yet, not included in the list of invasive alien species of Union concern (EU, 2019). Today, the species occurs in many European countries (CABI, 2020). The spread of *L. polyphyllus* in Central Europe has been very rapid during the last decades, considering that its status of naturalization was still unclear here in the late 80s and early 90s (e.g., Adolphi, 1987; Sebald et al., 1992). In Germany, the species is currently recorded in 81.2 % of all raster cells (of ca. 11 × 11 km; BfN, 2020). The Swedish Species Observation System (artportalen.se) contains ca. 40,000 records of the species. The average number of reports per year increased there from about 3 and 20 in the 60s and 70s, respectively, to about 280 between 1981 and 2010. Since 2017 there are > 1000 records per year, with a maximum of ca. 15,000 in 2019, when a new database on invasive species was launched. The increase in the number of records of *L. polyphyllus* thus reflects the ongoing spread of the species and the increasing awareness of people.

The latest broad account of the species' ecology was published in the framework of the European Network on Invasive Alien Species (NOBANIS) about 10 years ago (Fremstad, 2010) and there are other scattered data on the species compiled in fact sheets on the web (e.g., BfN, 2020; CABI, 2020; Naturvårdsverket, 2020). During the last years, many studies have contributed to new biological information and novel results through field and experimental studies. Therefore, we here strive to provide a comprehensive summary of the current knowledge on the taxonomy and morphology, distribution, habitat requirements, and the biology of *L. polyphyllus*. We will address the species' effects on other organisms, community structure and ecosystem processes, as well as discuss how to control the species at the local scale. Additionally, we will use this review to highlight important knowledge gaps concerning both the biology and management of the species since there seems to be currently no evidence-based, approved management approach for this species (e.g., Wissman et al., 2015; Tschan, 2018; Lennartsson et al., 2021).

2. Taxonomy and morphology

2.1. Taxonomy

L. polyphyllus has been described as "Large-leaved Perennial Lupine" by John Lindley in 1827 (Lindley, 1827). His description was based on material raised in the garden of the British Horticultural Society, originally collected by David Douglas in north-western North America. Other common names found in the literature are "Garden lupine" (e.g., Ramula and Kalske, 2020), "Bigleaf lupine" (e.g., Beuthin, 2012), "Washington lupine" (e.g., Aniszewski, 2001) or "Russell lupine" (Harvey et al., 1996); we will refer to Garden lupine throughout this paper. Common names in other languages than English are (Fremstad, 2010): "Vaste lupine" (B, NL), "Vielblättrige Lupine, Stauden-Lupine" (DE), "mangebladet lupin" (DK), "hulgalehine lupiin" (EE), "lupin vivace" (F), "komealupiini" (FI), "gausialapis lubinas" (LT), "daudzlapu lupīna" (LV), "hagelupin" (NO), "łubin trwały" (PL), "люпин Многолистный"(RU), and "blomsterlupin" (SE).

L. polyphyllus belongs to Fabaceae (Fig. 1), i.e., the third largest angiosperm family, which is composed of six subfamilies (Koenen et al., 2020). The subfamily Papilionoideae is divided into six major clades: the Genistoids, Dalbergioids, Mirbelioids, Millettioids, Robinioids and "IRLC", the Inverted Repeat Lacking Clade (Cronk et al., 2006). Within the Genistoids, *Lupinus* is part of the tribus Genisteae (core Genistoids) which is a sister tribus to Crotalarieae. Closely related are broom-like genera of the "Cytisus-Genista complex" (Genistinae), e.g., *Laburnum*, *Adenocarpus*, *Cytisus*, *Genista*, *Ulex*, or *Spartium*. The lupines form a distinct lineage (subtribe Lupininae (Hutch.) Bisby). This relationship is consistent with serological data (Cristofolini, 1989) and molecular-based phylogenies of the Papilionoideae (Doyle et al., 1997; Käss and Wink, 1997a, 1997b).

Lupinus represents a strongly supported monophyletic genus of approximately 280 species (Drummond et al., 2012) distributed into five main clades that are in general accordance with their geographical origin (Aïnouche and Bayer, 1999). The highest species diversity occurs in the Americas, and only 13 species originate from Europe and North Africa (Nevado et al., 2016). The most basic divergence between an Old World/Atlantic American group and a West New World group is corroborated by chemosystematics using quinolizidine alkaloids (Bermúdez-Torres et al., 2021). Phylogenetic studies based on nuclear DNA have shown that the western New World taxa form clade E, a large monophyletic, yet internally weakly resolved group (Ree, 2004). In the Andes, net diversification rates were found to be extremely high (Hughes and Eastwood, 2006), and seemingly still accelerating, suggesting an early explosive phase of radiation (Hughes and Atchison, 2015). The western North American perennials (NAP clade, appr. 60 spp.) from the Rocky Mountains, Great Basin, and Pacific Slope are only between 0.7 and 2.1 Mya old and are recently derived from a basally branching clade of annual plants endemic to the lower elevations of western North America (Drummond, 2008, Nevado et al., 2016).

2.2. Morphology

L. polyphyllus is a summer-green, semirosulate taproot-pleiocorm perennial hemicryptophyte with short adventitious shoots formed on the hypocotyl (Barneby, 1989; Jäger, 2017). As a pleiocorm (Jäger, 2017), it has "compact, perennial shoots (…) at the proximal end of the persistent primary root" (Klotz et al., 2002), and the overwintering caudex (rootstock) is situated close to or just below the soil surface (Barneby, 1989; Jäger, 2017). Using soil monoliths (30 × 30 × 30 cm) from the Czech Republic, Chmelíková and Hejcman (2012) showed that the species bears no rhizomes.

Shoot system – Numerous rosette leaves with long petioles form a basal leaf tussock, which across Central Europe may be about 40–90 cm high (Ludewig et al., 2022). Leaves are digitate and the lamina consist of 13–15 (Hegi, 1924), 9–12 (Sebald et al., 1992) or 5–12 (Barneby, 1989)

- Order Fabales
  - Family Fabaceae
    - Subfamily Papilionoideae
      - Clade Genistoids
        - Tribus Genisteae
          - Subtribus Lupininae
            - Genus Lupinus
              - West New World clade
                - NAP clade

Fig. 1. Systematic position of *Lupinus polyphyllus*.

leaflets, which are broadly to narrowly lanceolate, acute or obtuse, and ca. 0.5–2.5 × 3–15 cm in size (Barneby, 1989; Sebald et al., 1992), with appressed silky hairs on the upper surface or rarely glabrous. Each plant may have one to several erect stems with a basal diameter of about 12 mm (Rolf Lutz Eckstein, personal observation: 12 mm ± 2 mm, mean ± SD, min: 8 mm, max: 17 mm, 28 plants from Karlstad, Sweden) at peak flowering. The hollow stems are reddish, especially at the base, covered by ca. 2–4 mm long hairs and show an approximately pentagonal to roundish cross section. Each stem bears 3–5 stem leaves that become progressively smaller towards the top (Barneby, 1989). The stem ends in a single raceme of ca. (15)35–40(60) cm length at maturity (Sebald et al., 1992; Ludewig et al., 2022). Each raceme bears between 50 and 80 (Hegi, 1924) and ca. 120–130 zygomorphic flowers (Fremstad, 2010; Rolf Lutz Eckstein, personal observations: 127 ± 34, mean ± SD, min: 75, max: 210, 27 plants from Karlstad, Sweden). Later in the season, lateral inflorescences may originate from the axils of the stem leaves. Flowers are arranged in whorls of often 7–8 single flowers, but whorls become more indistinct when the inflorescence's axis elongates during flowering. Flower bracts are narrowly lanceolate and caduceus, they drop as soon as the petals become colored; pedicels usually 2–10 mm long (Barneby, 1989). The calyx is silky, 5–6(8) mm long at full flowering (Barneby, 1989; Vinogradova et al., 2012). The petals show various coloration, with either the same color or different colors of the standard and the wings (Vinogradova et al., 2012). The blue or purplish-blue flower morph is dominant over other colors such as pink and white (Bragdø, 1956). The standard is orbicular, glabrous, 8–13.5 mm long (Barneby, 1989), wings 4.5–7.5 × 10–15 mm, the keel is about as long as the wings, glabrous or ciliate and beaked. The pods are ca. 0.7 × 2.5–4.5(7) cm in size, each containing ca. 4–12 seeds (Hegi, 1924; Barneby, 1989; Sebald et al., 1992; Otte et al., 2002). A sample of 45 inflorescences from Sweden and Germany had on average 47 ripe pods (Rolf Lutz Eckstein, personal observation, range: 17–105). The valves of the pods are initially green, turning dark brown or black at maturity, and are densely covered by silky hairs. Seeds are rounded, oval-shaped, and have a size of ca. 4.3 × 3.2 × 2.7 mm (Aniszewski, 2001). Concerning the coloration of the seeds, several seed morphs (dark, patterned, gray, and light seeds) and testa ornamentations can be distinguished, which may be associated with different genetic lineages (Aniszewski, 2001).

Root system – Young plants develop an unbranched taproot. According to personal communication with Nijolė Lapinskinė (as cited in Volz, 2003: 12), the rooting depth in substrates that are easy to penetrate by roots may be up to 180 cm. This value has subsequently been cited in a number of papers (e.g., Otte and Maul, 2005) but most likely represents an extreme value close to the maximum rooting depth. In compacted soils such as in road verges, in habitats with very poor subsoils or in coarse rocky substrates, rooting depth is often much lower (Saba, 2017; Eckstein RL, own observation). Saba (2017) found an average taproot length of 22.3 cm ± 11.5 cm (mean ± SD, n = 33) in plants from the Rhön region (Germany), and 33 % of all excavated plants did not show a distinct taproot at all. Instead, the root system may also branch and spread vertically, but generally, it will remain relatively simple and sparsely branched (Fig. 2). The finest young roots are whitish and have a diameter of ca. 1 mm. Roots of older plants are tenacious and characterized by a yellowish root cortex, old roots become soft and swampy before they may disintegrate and die. The diameter of the root collar of large (old) plants may be ca. 30–40 mm (Eckstein RL, own observation). Root nodules are scarce to frequent and may have a diameter of between a few millimeters to up to a centimeter. Within the Genisteae, the genus *Lupinus* bears "lupinoid" nodules, which are characterized by two or more lateral meristems and uniformly infected cells in the central nodule tissue (Andrews and Andrews, 2017); lupinoid nodules may thus sometimes completely surround the root. Subterranean, short adventitious shoots may originate from the hypocotyl of older plants (Saba, 2017; Eckstein, RL own observation). The average length of these adventitious shoots is about 6–8 cm (Saba, 2017) with a range between 2 and 24 cm.

Fig. 2. Root system of a *Lupinus polyphyllus* plant from Karlstad (Sweden) harvested on 20 May 2021. The photo shows the main taproot, side roots with numerous nodules and some adventitious shoots originating from the hypocotyl. Photo: Rolf Lutz Eckstein.

3. Distribution and habitat requirements

3.1. Distribution

3.1.1. Native taxonomy and distribution

The delimitation of the natural geographic range of *L. polyphyllus* in North America is strongly dependent on the respective taxonomic circumscription and the intraspecific classification concept. Accordingly, the delimitation of the native range is treated quite differently. We follow the recent North American sources (Snow, 2009; Sholars and Riggins, 2020; Hitchcock and Cronquist, 2018 = FPNW) in adopting the wide taxonomic approach of Barneby (1989 = IMF) that includes several closely related taxa as varieties into a broad *L. polyphyllus*, yet neglecting the varieties *grandifolius* Lindl. ex J. Agardh and *pallidipes* A. Heller. Based on this, *L. polyphyllus* (s.l.) is native to western North America, from British Columbia in the west to western Alberta in the east, and western Wyoming, and south to Utah, New Mexico, and California. However, global compilations such as Plants of the World (POWO, 2022), WorldPlants (WPL, 2022), World Flora online (WFO, 2022), and the Leipzig catalog of vascular plants (LCVP, 2022) accept some taxa as distinct species, with probably mutually copied assignments (Table 1).

On the other hand, most European publications follow the narrow concept (Starfinger and Kowarik, 2010; Fremstad, 2010; Vinogradova et al., 2012) and, according to all assessed sources (e.g., Mohlenbrock, 2014; Gilman, 2015; Angelo and Boufford, 2013), the non-native populations in eastern North America and Alaska (AKEPIC, 2011) are supposed to be *L. polyphyllus* s.str. (subspecies or variety *polyphyllus*). There are, however, speculations suggesting that the invasive populations of *L. polyphyllus* represent an anthopogenous ornamental taxon, which may have spread in the Pacific Northwest as a result of human activity. Dunn and Gillett (1966) have stated that var. *polyphyllus*, which occurs in both native and disturbed habitats, yet is confined to disturbed habitats in eastern North America, often escaping from cultivation.

Given these considerations, *L. polyphyllus* var. *polyphyllus* is most probably the taxon that is naturalized and regionally invasive in temperate-humid climates worldwide. Therefore, the following account provides a description of the distribution of the naturalizing *L. polyphyllus* s.str. (= var. *polyphyllus*). Nevertheless, we have decided to distinguish, compile and map all taxa of the *L. polyphyllus* complex *sensu*

Table 1

Taxonomic delimitation of the *Lupinus polyphyllus*-complex in different global to regional floristic treatments. Names under BASIC TAXON can be considered synonymized basionyms of described segregates and only names in **bold** are accepted in our treatment. The entities marked with an asterisk (*) are identified as parts of the complex *Lupinus polyphyllus* sensu lato in the respective sources.

BASIC TAXON	POWO	WPL	WFO	LCVP	FPNW	IMF
***polyphyllus* Lindl.**	subsp. *polyphyllus**	subsp. *polyphyllus**	var. *polyphyllus**	var. *polyphyllus**	var. *polyphyllus**	
grandifolius Lindl. ex J.Agardh	subsp. *p.* var. *grandifolius**	subsp. *p.* var. *grandifolius**	*L. polyphyllus**	"not found"		
pallidipes A.Heller	subsp. *p.* var. *pallidipes**	subsp. *p.* var. *pallidipes**	*L. polyphyllus**	*L. polyphyllus**	var. *pallidipes**	
***superbus* A. Heller**	subsp. *superbus**	subsp. *superbus**	*L. burkei*	*L. burkei*		var. *burkei**
***bernardinus* Abrams ex Eastw.**	subsp. *bernardinus**	subsp. *bernardinus**	*L. burkei*	"not found"		
***prunophilus* M.E.Jones**	*L. prunophilus*	*L. prunophilus*	var. *prunophilus**	var. *prunophilus**	var. *prunophilus**	var. *prunophilus**
***burkei* S.Watson**	*L. burkei*	*L. burkei*	*L. burkei*	*L. burkei*	var. *burkei**	var. *burkei**
***saxosus* Howell**	*L. saxosus*	*L. saxosus*	*L. saxosus*	*L. saxosus*	*L. saxosus*	var. *saxosus**
***ammophilus* E.H.Graham**	*L. ammophilus*	*L. ammophilus*	*L. ammophilus*	*L. ammophilus*		var. *ammophilus**
***humicola* A.Nelson**	*L. wyethii* subsp. *wyethii*	*L. wyethii* subsp. *wyethii*	var. *humicola**	var. *humicola**	var. *humicola**	var. *humicola**
***holmgrenanus* C.P.Sm.**	*L. wyethii* subsp. *wyethii*	*L. holmgrenanus*	*L. holmgrenanus*	*L. holmgrenanus*		var. *humicola**

Sources: POWO (2022): Plants of the world online, WPL (2022): WorldPlants, WFO (2022): World Flora online, LCVP (2022): Leipzig catalog of vascular plants, FPNW: Flora of the Pacific Northwest (Hitchcock and Cronquist, 2018), IMF: Intermountain Flora (Barneby (1989).

Barneby (1989) and Sholars and Riggins (2020) to provide a complete distribution map (Fig. 3 A-C).

The native range extends from the Californian Northern Coast ranges to south-western British Columbia approximately up to the Queen Charlotte Strait (Fig. 3A). Calder and Taylor (1968) showed that *L. polyphyllus* does not occur naturally in the Haida Gwaii (Queen Charlotte Islands) and is also absent from the adjacent coastal mainland. The main distribution is along the Coast Ranges to the Mountains of Vancouver Island and the western slopes of the Cascade Range. Occurrences further north along the Pacific coast (e.g., Calvert Island) as well in the interior are increasingly confined to ruderal habitats along roads, and within or close to settlements. This is in accordance with Hultén (1968), Rapp (2009) and AKEPIC (2011), where *L. polyphyllus* is considered a non-native, partly invasive species of the Alaskan flora. The same pattern can be observed in California, where occurrences south of the Coast Ranges are confined to settlements and urban areas. Beside the described main range, there are single collections across the range of the whole complex that are just labeled "*L. polyphyllus*" and some regional floras list these forms as native beside other named varieties (e.g., Lackschewitz, 1991; Culver, 1994).

In general, the New-World-species of the genus *Lupinus* lack strong genetic barriers to interbreeding, which is the reason for the difficulties of delimitation between many taxa (Dunn and Gillett, 1966). Especially the NW-American perennial lupines have long been recognized for their tendency to form interspecific hybrids (Phillips, 1957; Downey and Dunn, 1964; Barneby, 1989). *L. polyphyllus* s.str. probably produces hybrids with numerous closely related taxa, which either occur as delimitable elements of the complex or transitional states to more clearly characterized forms. Dunn (1965: 4) states: "*In short everywhere that L. polyphyllus has come into contact with another lupine, there has been some hybridization and subsequent introgression*". As putative partners Dunn (1965) lists *L. albicaulis* (revealing *L. p.* var. *pallidipes*), *L. latifolus* (revealing *L. p.* var. *superbus*), and an unknown crossing partner (revealing *L.p.* var. *prunophilus*). Furthermore, he suggested that *L. nootkatensis* Donn has evolved from introgression of *L. polyphyllus* with *L. arcticus*. A putatively backcrossing hybrid between *L. polyphyllus* and *L. nootkatensis* has been named *L.* ×*pseudopolyphyllus* Sm., yet is considered a synonym of *L. polyphyllus* by, e.g., Hultén (1968). Phillips (1957) reports experimental hybridization outcomes as part of taxonomic analyses. Accordingly, hybrid formations of *L. polyphyllus* with other perennial NW-American lupines were successful in all but one (*L. lepidus* Lindl.) cases. Kazimierski (1961) points out technical difficulties to exact hybridization trials (flowers sensitive to emasculation) and found hybridization with *L. mutabilis*, *hartwegii*, *burkei*, *truncatus*, and *douglasii* (*L. albifrons* var. *douglasii*) to be unsuccessful and only limited success in crossings with *L. arboreus*.

Keeping the above in mind, the most prominent hybridization involving *L. polyphyllus*, is *Lupinus* ×*regalis*, the group of so-called Russell hybrids (*Lupinus* ×*russellii* hort). These horticulturally produced forms, which differ from the wild type mainly by diverse flower colors and somewhat denser inflorescences, are suggested to form the bulk of the neophytic-expansive stands in summer-cool oceanic regions like the UK, Norway or New Zealand (Fremstad, 2010; Stace, 2010). Nevertheless, it seems not reasonable to assume that these cultivars dominate the secondary, synanthropic distribution. The origin and quantitative composition of Russell "hybrids" is by no means clearly documented. The potential parental species listed beneath *L. polyphyllus* differ strongly between undocumented sources. "*Russell carried out crosses. between North, Central, and Southern American species*" (Wolko et al., 2011: 169), "*Some cultivars may well contain genes of other lupin species, including L. nootkatensis, L. mutabilis and L. hartwegii*" (Preston et al., 2002). Gladstones (1970) points out that clear influences from e.g., *L. arboreus* are hardly recognizable and that the majority of "Russell lupines" parental material is rather that of *L. polyphyllus* with minor contributions from *L. arboreus* and *L. nootkatensis*. Clearly documented crossing attempts, e.g., Kazimierski (1961), show how difficult it is in practice to achieve targeted hybridizations. Observations from Russian-speaking countries also indicate that the proportion of horticultural hybrids in invasive populations is very small or hardly noticeable (Tkacheva, 2011; Vinogradova and Kuklina, 2012; Vinogradova et al., 2012).

3.1.2. Non-native taxonomy and naturalized distribution

For the non-native range, all naturalized Garden lupine records were subsumed under the name *L. polyphyllus* (Fig. 3 A-C). This also includes populations and occurrences described as being of hybrid origin *L.* ×*regalis*, *L.* ×*pseudopolyphyllus*), especially in the UK, Chile, and in New Zealand. The taxonomic delimitation of *L. polyphyllus* differs across the neophytic range. In the flora of the British Isles (Stace, 2010), the name *L. polyphyllus* is strictly applied to blue-flowered plants with unbranched inflorescences, while plants with branched inflorescences and blue, pink, purple or white flowers are called *L.* ×*regalis* Bergmans, which is supposed to be a hybrid of *L. polyphyllus* and *L. arboreus* Sims. According to Stace and Crawley (2015), and Stace et al. (2015) *L.* ×*regalis* is included in *L. polyphyllus* in the Netherlands. While in the British Isles most naturalized and casual lupines belong to *L.* ×*regalis* and different backcrosses, *L. polyphyllus* is the abundant taxon in Scandinavia. Similarly in New Zealand, the wild type seems to be more successful regarding naturalization (Scott and Tesfaye, 2000).

According to its wide distribution and local dominance, *L. polyphyllus* is recognized as a globally invasive plant species (Daehler, 1998; Valtonen et al., 2006). The non-native, synanthropic distribution range comprises roughly seven main areas of different size on all continents except Africa and Antarctica. These areas can be described as follows:

1. Western North America. The species has scattered lowland occurrences in and near settlements and urban areas throughout and around the native range (Fig. 3 A, 3 C-1). Probably often garden escapes

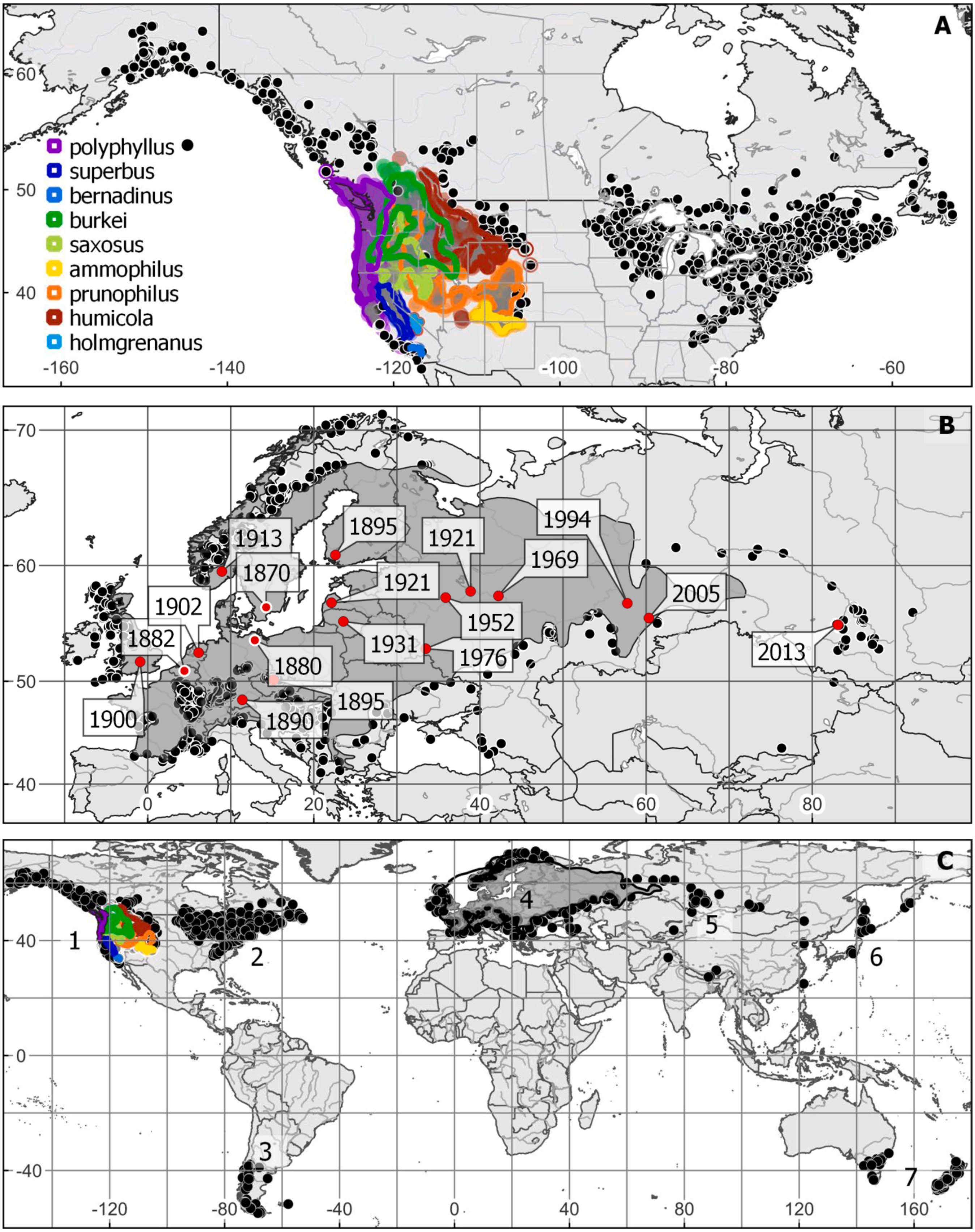

Fig. 3. Distribution of *Lupinus polyphyllus* s.l. (A) In North America, the native segregates in the west partly overlap in their distribution and are delimited by outlines according to the color scheme in the legend. Non-native, synanthropic occurrence locations are indicated by black dots. Distribution data based on digitally available herbarium specimen locations and county records (for data sources see Table 1). (B) In Europe, numbers give the first records for the species in different countries/ regions (cf. Table 6). (C) Numbers refer to the textual descriptions of the non-native naturalized distribution across the globe.

in urban green spaces, along irrigation channels, and drainage ditches. We also consider records given for NE Montana as synanthropic, as the data in Lackschewitz (1991), Mincemoyer (2013), and Montana Field Guide (2021a) suggest that - beside var. *burkei* and var. *humicola* - native *polyphyllus* populations are recorded only in W- and SW-Montana. Along the pacific coast, *L. polyphyllus* occurrences are reported mainly for Alaska's Pacific Maritime ecogeographic region northwards to Anchorage (AKEPIC, 2011; UAM, 2011).

2. Eastern North America, in a triangle between Minnesota, Newfoundland, and Maryland (Fig. 3A, 3C-2). Many records have been reported from eastern Minnesota to northern Wisconsin. Here the species has been deliberately seeded along roads (Minnesotawildflowers, 2022) and is spreading rapidly. Particularly dense and large populations are reported from the north shore of Lake Superior between Duluth and Thunderbay (Minnesotawildflowers, 2022). Another, more densely populated area stretches along the east coast, from New York City to Prince Edward and Cape Breton Islands. The active propagation of the species in the New England States has already found its way into literature in the character of Miss Rumphious (Cooney, 1982). While this range part currently seems to be roughly limited to the south by a Washington DC - Pittsburgh - Cleveland - Chicago line, *L. polyphyllus* spreads further south in the cooler climatic conditions and shallower soils of the Appalachian Mountains as far as northern Georgia.

3. Central & South America. Citizen-science-based observations for Mexico (iNaturalist, 2021) seem to be erroneous or refer to cultivated plants. Recent studies dealing with Mexican lupine species do not report occurrences of the *L. polyphyllus*-complex for this country. *L. polyphyllus* is established as a non-native species in Western South America along the Andes of Chile and Argentina (Fig. 3 A, 3 C-3) between 40° and 65°S (Domínguez et al., 2006; Quiroz et al., 2009). Invasive stands of *L. polyphyllus* along roadsides, lakeshores, and rivers often include colorful populations of partly hybrid origin (Wikimedia, 2021).

4. Europe. From Scotland to northern Spain (Pyrenees), northern Italy, eastwards to Croatia, Bulgaria, northern Ukraine, Samara, and Bashkortostan across the Ural Mountains to Tyumen'. From here westwards via Sverdlovsk, Arkhangelsk, and Murmansk to Scandinavia (Figs. 3B, 3C-4). In Europe, *L. polyphyllus* is specifically considered invasive in Norway (Fremstad, 2010), Sweden (Tyler et al., 2015), Finland (Valtonen et al., 2006), Lithuania (Vyšniauskiené et al., 2011), Germany (Kowarik, 2003), the Czech Republic (Hejda et al., 2009), Switzerland (InfoFlora, 2020), Ukraine, and Central Russia (Vinogradova et al., 2009). Due to historic and recent propagation for soil improvement at roadsides and in coniferous forests (e.g., Volz, 2003), the European area has become the largest range part worldwide. Larger gaps in this continuous distribution are confined to the coldest alpine mountain elevations (Scandinavian Mountain Range, Alps), regions with clayic, base-rich soils (e.g., Upper Rhine valley, Thuringian basin), and areas of calcareous and carbonate outcrops (e.g., Swabian Alb, Champagne).

5. Altay region/West Siberia. Many successfully established garden escapes and active cultivation resulted in another small non-native range part where the species is considered invasive also in semi-natural and natural habitats mainly in the region between the cities Novosibirsk, Tomsk, Novokuznetsk, and Barnaul (Figs. 3B, 3C-5). Further, isolated range patches are situated at the southern shore of Lake Baikal and in Northern Mongolia (Yakovlev et al., 1996; Vinogradova, 2016).

6. Pacific Far East region. *L. polyphyllus* is considered invasive for Hokkaido Island, Japan (Hokkaido Blue List, 2010), where it is certainly underrepresented in the available distribution data. The species occurs also on the adjacent southern Sakhalin Island and in the surroundings of Petropavlovsk in the southeast of the Kamchatka peninsula (Fig. 3C-6).

7. Australia and New Zealand. According to ALA (2021) and Williams and West (2000), *L. polyphyllus* is widespread in the alpine regions of SE Australia (Victoria and New South Wales). Well-known is the dramatic situation in some areas of the South Island of New Zealand where *L. polyphyllus* is seriously invasive in South Canterbury (Fig. 3C-7), especially along gravelly, braided riverbeds, and road verges (Howell, 2008; Caruso et al., 2013). The species has been actively sown in the past by road management companies and private persons and cultivation as a rangeland species is still promoted by agricultural research institutions (Scott and Tesfaye, 2000).

Other regions where *L. polyphyllus* has probably spread and is locally invasive, but has been less well documented are mountainous regions of Western Asia like e.g., Kashmir Himalaya (Sandilyan and Vairvel, 2020).

3.2. Habitat

The habitat requirements of plant species in situ can be characterized by indicator values, which usually are based on expert knowledge. In the invaded range, *L. polyphyllus* has been assigned indicator values for abiotic habitat requirements (light, nutrients, soil reaction, moisture, salinity); these refer either to Central Europe (Ellenberg, 2003) as a whole or to single countries such as Switzerland (Landolt et al., 2010), Italy (Domina et al., 2018), and Sweden (Tyler et al., 2021). The description of habitat requirements based on indicator values differs across Europe (Table 2), indicating that the main habitat types occupied by the species may vary between different regions in the non-native range. However, there may also be inconsistencies in the exact definitions of indicator value levels among countries.

In Switzerland, the Garden lupine mainly occurs in forestry-related habitats such as in clearcuttings and scree slopes (Lauber et al., 2018), and its habitats are described as half-shady, mesic to moist, acidic and moderately nitrogen (N) poor to moderately N-rich (Landolt et al., 2010). The species occurs also along forest fringes, in open forests and in clearcuttings in Germany (Sebald et al., 1992; Jäger, 2017), the Czech Republic (Slavík et al., 1997) and Finland (Ramula and Pihlaja, 2012). However, it may also develop dominant stands in different types of open mountain grasslands in Germany (e.g., Volz, 2003; Otte and Maul, 2005; Klinger et al., 2019; Hansen et al., 2021) and Poland (Pruchniewicz, 2017) with a wide range of nutrient availabilities. Consequently, the species is considered indifferent with respect to nutrient availability in Central Europe (Ellenberg, 2003), while it grows on intermediate to relatively N-rich soils in Italy (Domina et al., 2018). In Northern Europe, the species has its main stronghold in relatively nutrient-poor acidic grassland vegetation (Tyler et al., 2021), specifically open linear habitats along managed road verges (e.g., Ramula and Pihlaja, 2012; Wissman et al., 2015; Mossberg and Stenberg, 2019; Tschan, 2018). These habitats are mostly open and sunny to half-shady, dry to mesic, moderately to strongly acidic and very N-poor to moderately N-poor (Tyler et al., 2021).

As a legume with N-fixing root nodules, *L. polyphyllus* can establish in nutrient-poor habitats such as sand pits, landfills and along road verges (Tyler et al., 2021). Since N-fixation comes with a cost of higher energy demands, the species' growth benefits from high availability of phosphorous (P) (Tyler et al., 2021). The low P-availability at higher soil pH may be one explanation for the species' general preference of acidic soils; it is reportedly being less frequent and less dominant in regions with calcareous bedrock (e.g., Wissman et al., 2015). Another reason may be iron deficiency in calcareous soils, which adversely affects the growth of various species in the genus *Lupinus* (Tang et al., 1993a). High soil pH per se may also cause root surface disintegration (Tang et al., 1993b) with negative effects on root elongation as shown for *L. angustifolius*.

In its native range (see Section 3.1.1), *L. polyphyllus* s.str. occurs in wet mountain meadows and along streams (Hejda, 2013). Interestingly, wet montane to sub-montane grasslands are also a typical habitat of the species in the Czech Republic (Hejda, 2013), whereas wet grasslands are much less invaded than dry to mesic mountain grasslands in central Germany (Klinger et al., 2019). Ecological experiments using rainout-shelters (Vetter et al., 2019) showed that *L. polyphyllus* is comparatively drought tolerant and shows high water use efficiency

Table 2

Description of habitat preferences of *Lupinus polyphyllus* in different regions in Europe (ordered from north to south), expressed by indicator values for light, moisture, nutrients (nitrogen) and salinity. In brackets the numeric value given by the respective source, but note that the range of possible values may vary between indicator value systems.

Light	Moisture	Soil pH	Nutrients (N)	Salinity	Region	Source
Sun – half-shade (5)	Dry – mesic (3)	Moderately acidic – strongly acidic (2)	Very N-poor – moderately N-poor (2)	Not salt tolerant (1)	Sweden	Tyler et al. (2021)
Sun – half-shade (7)	Dry – moist (5)	Weakly acidic –acidic (4)	Indifferent (X)	Not salt- tolerant (0)	Central Europe	Ellenberg (2003)
Half-shade (3)	Mesic – moist (3)	Acidic (2)	Moderately N-poor – moderately N-rich (3)	n/a	Switzerland	Landolt et al. (2010)
Sun – half-shade (8)	Moist (5)	Weakly acidic –acidic (4)	Intermediate – N-rich (6)	Not salt- tolerant (0)	Italy	Domina et al. (2018)

after 54 days of experimental water shortage. Although the species may also tolerate temporarily wet soils, stagnant water and waterlogged conditions (low oxygen availability) may reduce N-fixation, root growth and nodulation in the genus *Lupinus* (Dracup et al., 1998; Malik et al., 2015). Also in its non-native range in the southern hemisphere, *L. polyphyllus* has established in at least temporarily wet, but probably well drained, riparian habitats such as braided riverbeds on the South Island of New Zealand (Harvey et al., 1996) as well as gravel bars in riverbeds in Chile (Meier et al., 2013).

Most sources categorize *L. polyphyllus* as being not salt-tolerant (Ellenberg, 2003; Domina et al., 2018; Tyler et al., 2021), i.e., avoiding even weakly saline habitats. This is contradicted by its widespread occurrence along the verges of even larger roads in Northern Europe, which are sites that receive high amounts of de-icing salts during winter. Evidence from a growth chamber experiment shows that high seed germination of the species (95 % and 79 %) occurs at sodium chloride (NaCl) concentrations of ca. 0.15 and 0.22 mol/L, respectively, which correspond to osmotic potentials of − 0.6 and − 0.9 MPa (Geni Zanol & Rolf Lutz Eckstein, unpublished data). Additionally, potted seedlings survived for four weeks when watered with NaCl solutions (−0.6 MPa: survival 100 %; −0.9 MPa: survival: 85.7 %) in the laboratory (Geni Zanol & Rolf Lutz Eckstein, unpublished data). These results suggest some salt tolerance of at least these early phases of the life cycle.

3.3. *Communities*

As an invasive species, *L. polyphyllus* does not belong to the native vegetation of Central Europe. After introduction, its abiotic habitat requirements, and the outcome of biotic interactions with native species determined in which native plant communities the species could establish. *L. polyphyllus* is therefore not included in comprehensive works covering the native vegetation of Central (Ellenberg and Leuschner, 2010) and Northern Europe (Dierßen, 1996). Older floras (e.g., Oberdorfer, 1990; Sebald et al., 1992) assign the species to communities of forests clearings, such as *willowherb and foxglove clearings* (EUNIS code G5.841; Chytrý et al., 2020; see Table 3), and *temperate thickets and scrub* (F3.1), which may be related to the initial sowing of *L. polyphyllus* for soil amelioration in forestry and along roads (e.g., Volz, 2003). A modern flora of Central Europe (Jäger, 2017) assigns the species to a number of communities, including *poor fens and soft-water spring mires* (D2.2), *low and medium altitude hay meadows* (E2.2), *alpic mat-grass swards and related communities* (E4.31), *anthropogenic herb stands* (E5.1), and *temperate thickets and scrub* (F3.1).

One of the most comprehensive documentations of communities invaded by *L. polyphyllus* in Central Europe, based on > 150 vegetation relevés, comes from the UNESCO biosphere region Rhön in Germany (Volz, 2003; Otte and Maul, 2005; Hansen et al., 2021). Here, the species occupies large proportions of mesic and wet *alpic mountain hay meadows* (E2.31) as well as mesic and wet *alpic mat-grass swards* (E4.31) (Klinger et al., 2019) but also occurs in *abandoned pastures* (E2.13) and abandoned meadows (Otte and Maul, 2005). In northern Europe, *L. polyphyllus* has a stronghold in *anthropogenic herb stands* (E5.1) along

Table 3

Plant communities with *Lupinus polyphyllus* in Europe. We refer to the names and codes of communities and habitats according to the EUNIS habitat classification (EUNIS, 2022). Table entries are sorted according to the EUNIS code. Additionally, we give the names for references communities / habitats used in the original sources. In square brackets: habitat types and codes listed in the EU Habitat directive. Superscript numbers link reference communities with the respective source.

EUNIS communities / habitats	EUNIS code	Reference communities / habitats named in the sources	Source
Poor fens and soft-water spring mires	D2.2	*Caricion fuscae*[1] *Caricion nigrae*[2]	[1]Otte & Maul (2005) [2]Jäger (2017)
Abandoned pastures	E2.13	Fallow phase of *Geranio-Trisetetum*[3]	[3]Otte & Maul (2005)
Low and medium altitude hay meadows	E2.2	*Arrhenatheretalia elatioris*[4] [Fenno-Scandian boreal and sub-boreal meadows – 6270][5] Meadow[6]	[4]Volz (2003) [4]Jäger (2017) [5]Eckstein RL, own observations [6]Ramula and Pihlaja (2012)
Alpic mountain hay meadows	E2.31	*Geranio-Trisetetum*[7] [Mountain hay meadows – 6520][8]	[7]Volz (2003) [7]Otte & Maul (2005) [8]Klinger et al. (2019)[8] Hansen et al. (2021)
Alpic mat-grass swards and related communities	E4.31	*Polygalo-Nardetum*[9] *Violion caninae*[10] [Species-rich *Nardus* grasslands, on silicious substrates in mountain areas – 6230][11]	[9]Otte & Maul (2005) [10]Jäger (2017) [11]Klinger et al. (2019) [11]Hansen et al. (2021)
Anthropogenic herb stands	E5.1	*Arction*[12] Road verges and railways[13] Wasteland[14]	[12]Oberdorfer (1990) [12]Jäger (2017) [13]Valtonen et al. (2006)[13]Ramula and Pihlaja (2012) [13]Wissman et al. (2015) [14]Ramula and Pihlaja (2012)
Temperate thickets and scrub	F3.1	*Sambuco-Salicion*[15] *Epilobio-Salicetum capreae*[16] Forest[17]	[15]Oberdorfer (1990) [15]Jäger (2017) [16] Sebald et al. (1992) [17]Ramula and Pihlaja (2012)
Willowherb and foxglove clearings	G5.841	*Epilobio-Digitalitetum*[18]	[18]Sebald et al. (1992)
Road networks	J4.2	Road verges[19]	[19]Valtonen et al. (2006) [19]Ramula and Pihlaja (2012) [19]Wissman et al. (2015)

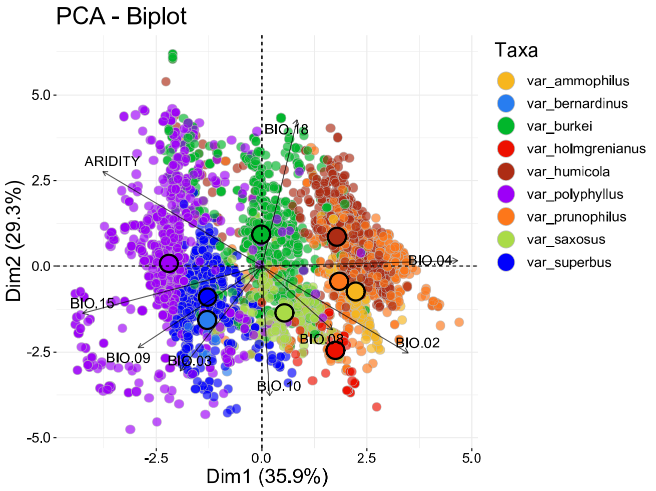

Fig. 4. PCA biplot showing the occurrences of the *Lupinus polyphyllus* segregate taxa as points in 2-dimensional multivariate climate space formed by the PCAs first two principal components (Dim1, Dim2, 65.2 % of total variance “explained”) and superimposed original variables as vectors (arrows) defined by the respective loading vector. Large symbols represent the mean position of the respective taxon in this climatic niche space.

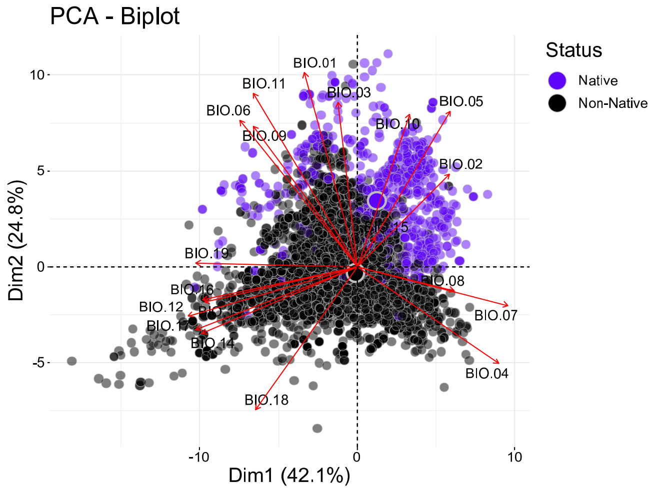

Fig. 5. PCA biplot showing the occurrences of the *Lupinus polyphyllus* native (purple) and non-native (black) occurrences as points in 2-dimensional multivariate climate space formed by the PCAs first two principal components (Dim1, Dim2, 67.0% of total variance “explained”) and superimposed original variables as vectors (arrows) defined by the respective loading vector. Large symbols represent the mean position of the respective group in this climatic niche space.

road verges and in the *road network* (J4.2) (Valtonen et al., 2006; Ramula and Pihlaja, 2012; Wissman et al., 2015), but it may also occur in *low and medium altitude hay meadows* (E2.2) (species-rich Fenno-Scandian boreal and sub-boreal meadows) and *abandoned pastures* and fields (Rolf Lutz Eckstein, personal observations).

Abundance of *L. polyphyllus* may range from very low (∼ 1 %) to very high cover (> 90 %), depending on light and water availability in different habitats (Volz, 2003; Otte and Maul, 2005; Hansen et al., 2021). On small spatial scales, the species may show patchy cover within the invaded meadows, ranging from 5 % to carpet-forming 90 % cover within a few meters (Otte and Maul, 2005). Across numerous relevés from the Rhön Mountains (Germany), the average cover of *L. polyphyllus* is 39 % (Hansen et al., 2021; Ludewig et al., 2021). Often populations in the non-native range can form dense stands with mean lupine cover exceeding 60 % (Valtonen et al., 2006; Ramula and Pihlaja, 2012; Hejda, 2013; Chytrý, 2016; Hansen et al., 2021) and the same was true also in the native range (Hejda, 2013). On road verges and clearance cairns it might form linear distributions with covers ranging between a few plants and > 70 % (Valtonen et al., 2006; Klinger et al., 2019). It might also be very abundant in riverbeds (Holdaway and Sparrow, 2006). The lowest cover values (1–2 %) or occurrences of single plants have been observed along forest edges (Otte and Maul, 2005).

3.4. Response to abiotic factors

In the native range, the different segregates of the *L. polyphyllus*-complex (see Section 3.1.1, Fig. 4) are climatically separated. The climatic conditions at the various sites were extracted from climate grid layers provided by CHELSA (Karger et al., 2017). A random forest classification approach (Liaw and Wiener, 2002) based on climate data and taxonomic grouping revealed that temperature seasonality (BIO.04, for a definition of the bioclimatic variables, see CHELSA, 2022) and the humidity-aridity-gradient are discriminating variables that differentiate the infraspecific taxa. A PCA biplot visualization (Fig. 4) based on the R-package “factoextra” (Kassambara and Mundt, 2020) shows that the taxa *L. polyphyllus* s. str. and *superbus* occupy the humid and oceanic part of the niche, whereas *prunophilus* and *humicola* are situated in the climatically most continental, and *holmgrenianus* in the most arid niche parts. However, this putative niche differentiation does not necessarily represent evolved physiological differences in tolerance to abiotic factors. Since the taxa are geographically separated, the differences might also be caused by spatial autocorrelation of climatic conditions.

A similar approach was taken to compare the climatic niche of the native *L. polyphyllus* var. *polyphyllus* with that of the plant in its non-native range (Fig. 5). Interestingly, here temperature seasonality (BIO.04) and winter cold (BIO.06) were the most conserved climatic variables with the strongest overlap between native and non-native niche parts. Summer precipitation (BIO.18) and isothermality (BIO.03) are discriminating variables that most strongly distinguish the native vs. non-native range parts. This is based on non-native occurrences in subcontinental regions of Eastern Europe and Western Siberia, where summer precipitation is predominant and isothermality is low. While clearly confined to humid conditions (Fig. 5, lowest aridity and precipitation seasonality = BIO.15), native *L. polyphyllus* s.str. apparently tolerates a wide range of mean temperatures during the warmest quarter (BIO.10). The extracted climatic conditions in the native range of both *L. polyphyllus* s.str. and of the *L. polyphyllus*-complex can be found in Table 4.

Non-native niche – The climatic tolerance limits that can be derived from the worldwide non-native occurrence localities of *L. polyphyllus* are ranging from MAT − 1.2–11.5 °C and MAP 181–1393 mm (Table 4). Judged from this range of values, the non-native climatic niche is clearly wider than that of native *L. polyphyllus* s.str., yet largely within the limits of the whole *L. polyphyllus*-complex.

Despite being adapted to mesic habitat conditions, adult individuals of *L. polyphyllus* can tolerate prolonged seasonal drought (Robson et al., 2008). In an experiment by Vetter et al. (2019), 44 days of drought had no effect on the survival of adult *L. polyphyllus* plants, but reduced the survival of 4-week-old seedlings by 29 %. However, drought negatively affected the performance (earlier senescence, lower number of leaves, and lower leaf size) of both adult plants and seedlings, but had no effect on seed production (Vetter et al., 2019). Compared to some grassland species native to Central Europe, *L. polyphyllus* is characterized by a higher water use efficiency under drought, which may partly explain its competitive success in drier habitats (Vetter et al., 2019). Fluctuating precipitation (2 weeks drought followed by intensive watering) did not affect survival of 4-week-old *Lupinus* seedlings or 12-month-old individuals (Vetter et al., 2019).

L. polyphyllus is also resistant to frost. Frost events of − 5 °C did not affect the performance of adult *L. polyphyllus* plants in an experiment (Plarre and Porsche, 1961); the same was found by Vetter et al. (2019).

Table 4
Climatic niche limits of native vs. non-native *Lupinus polyphyllus*. Abbreviations: MAT - mean annual temperature; MAP - mean annual precipitation; LQ - lower quartile (25th percentile); MED - median; UQ - upper quartile (75th percentile); IQR - inter quartile range).

Group	native *L. polyphyllus* s.str.		native *L. polyphyllus* s.l.		non-native *L. polyphyllus*	
Variable	MAT (°C)	MAP (mm)	MAT (°C)	MAP (mm)	MAT (°C)	MAP (mm)
LQ-(1.5 ×IQR)	2.6	287	-1.9	110	-1.2	181
LQ	7.8	1089	3.9	407	3.5	628
MED	10.2	1316	6.4	618	5.1	721
UQ	11.4	1698	8.7	978	6.7	934
UQ+ (1.5 ×IQR)	16.8	2596	15.8	1830	11.5	1393

Following simulated frost treatments of − 10 °C in an incubator, seedlings of *L. polyphyllus* showed 100% mortality, whereas adults showed 50 % mortality (Vetter et al., 2019). This is in line with findings cited in Volz (2003) that *L. polyphyllus* seedlings survive down to − 6 °C, whereas flowering shoots are susceptible to frost. Gavelienė et al. (2022) showed in a growth chamber experiment that elevated temperatures simulating climate warming (25 vs. 30 °C) affected root formation of *L. polyphyllus* through disturbing gravitropic orientation of initial roots and decreasing the cell division of root apical meristems. This led to a smaller root system of 30-day old seedling at 30 °C than at 25 °C and the authors argue that temperature effects on root development may alter the invasiveness of *L. polyphyllus*.

The species prefers low pH values and thus persists mainly on acidic soils (Cullen et al., 2011). In an experiment by John (1931), plants performed similarly on soils with pH-values between 4 and 7. Otte and Maul (2005) found *L. polyphyllus* on sites with pH-values between 4.1 and 4.6. Despite some interspecific differences, species of the genus *Lupinus* frequently perform poorly on alkaline soils. Besides negative effects of high pH values per se, low growth and survival may be attributed to factors such as low availability of iron (Longnecker et al., 1998), high HCO_3^- concentrations, or calcium toxicity (Dracup et al., 1998).

The availability of several mineral nutrients can affect the nitrogen fixation and thus the performance of *L. polyphyllus* (Longnecker et al., 1998). Nodulation and N-fixation can be reduced by high available soil nitrogen (Atkins, 1984). Due to the high phosphorous demands of nodulation and N-fixation, the species has a high need of P, and the growth of agriculturally used lupines is often limited by the availability of P (Longnecker et al., 1998). However, in a fertilizer experiment (Davis, 1991), yields of *L. polyphyllus* decreased with increasing P fertilization but this effect may have been caused by competition through resident legumes and grasses.

4. Life cycle and biology

4.1. Life cycle

L. polyphyllus is a short-lived, polycarpic perennial hemicryptophyte (Klotz et al., 2002), with a lifespan of usually at least three years (Beuthin, 2012). The database of Timmins and Mackenzie (1995) states that “50 year old plants” are known from New Zealand. However, since it remains unclear where and how this information was obtained, this number has to be considered uncertain. The life cycle can be divided into different developmental stages, such as the seed bank, seedlings, vegetative and flowering plants of various sizes (Ramula, 2014; Fig. 6). Sexual reproduction by seed dominates (Timmins and Mackenzie, 1995; Ramula, 2014; Li et al., 2016a), although vegetative propagation via underground adventitious shoots is possible (Rapp, 2008; Fremstad, 2010), with clonal shoots typically emerging near the base of the mother plant (Satu Ramula, personal observation). In both native and non-native ranges, individuals flower in their second year at the earliest (Beuthin, 2012; Jauni and Ramula, 2017), while in New Zealand, plants may flower already in their first year (Timmins and Mackenzie, 1995). In Finland, average annual survival for vegetative plants varies between 50 % and 90 % and for flowering plants between 80 % and 90 % depending on, e.g., the habitat type (Ramula, 2014), and retrogression (i.e., shrinkage) to smaller sizes is common (Ramula, 2017). Seedling survival tends to be low and less than 10 % of newly established seedlings survive to the next year (Jauni and Ramula, 2017; Satu Ramula, unpublished data). In general, vital rates (survival, growth, flowering probability, seed production) increase with increasing plant size (Ramula, 2014). Individuals are able to resprout when damaged or mown (Scott and Tesfaye, 2000; Ramula, 2020). Based on a common garden study, plants originating from non-native Finnish populations were larger but flowered less frequently and with fewer flowering shoots than conspecifics from the native range at least during their first year (Ramula and Kalske, 2020).

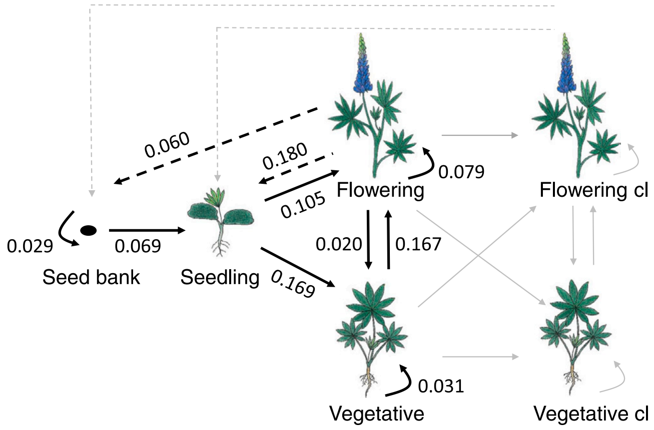

Fig. 6. Life cycle of *Lupinus polyphyllus* in which individuals can flower in their second year as earliest. The arrows represent annual transitions between life stages and dashed lines refer to sexual reproduction. Uncertain transitions involving potential clonal stages (cl) are indicated in gray. Numbers show elasticities for the non-clonal stages; elasticities for the clonal stages are omitted due to their small values (< 0.026), see Table S1 for details. Drawings by Martina Spenner.

Finite rates of population growth (λ) estimated from structured population models may greatly vary across non-native populations from projected rapid population increases to rapid population declines independent of habitat type and population size (range for λ: 3.198–0.520; Ramula, 2014). Population growth rate tends to be most sensitive to proportional changes in plant survival (measured as elasticities), and particularly the survival of the largest individuals is critical for the viability of declining populations (Ramula, 2017). However, the sensitivity of λ to proportional changes in plant survival decreases, while sensitivity to proportional changes in fecundity increases with increasing λ (Ramula, 2017). For a growing population from Finland (Fig. 6; based on data in Ramula, 2014; for details see Table S1) the largest elasticities were related to sexual reproduction (0.180, flowering plants producing seedlings), seedling growth (0.169, seedlings growing into vegetative plants) and the transition of vegetative to flowering plants (0.167).

4.2. Spatial distribution of plants within populations

Populations of *L. polyphyllus* typically consist of hundreds or thousands of individuals (Otte and Maul, 2005; Ramula, 2014), in which average plant densities (including seedlings) vary from 5 to 121 individuals m^{-2} (Ramula, 2014). Small individuals, which usually represent either seedlings or small vegetative plants, tend to be more abundant in populations than large flowering individuals (Ramula,

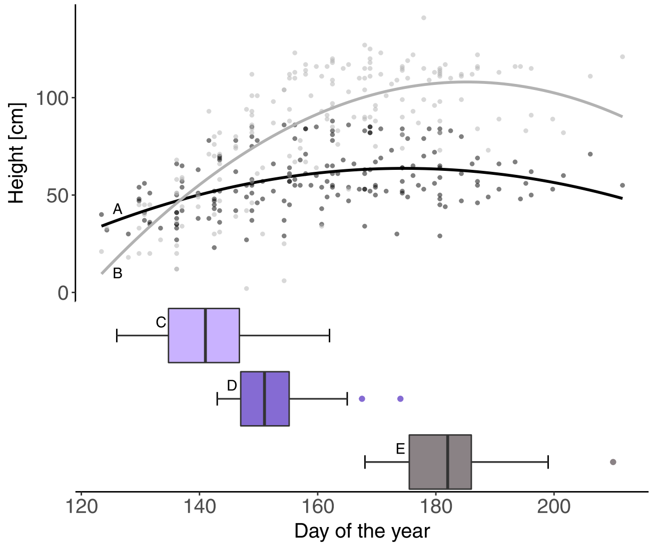

Fig. 7. Phenology of *Lupinus polyphyllus* in 21 populations across Europe (ranging in latitude from 49.8°N to 63.4°N) in 2019 (data from Ludewig et al., 2022). Height (cm) to the top of the highest basal leaf (A), height to the top of the main inflorescence (B), day first flower opened (C), day of half of the length of the inflorescence with open flowers (D), and day first fruit was ripe (E).

2014). Single individuals and low- or medium-density patches contribute considerably to the rapid spread of local lupine stands (Volz, 2003) and to changes in lupine distribution patterns in mountain meadows (Klinger et al., 2019). Dense stands may be partially due to short dispersal distances because seeds are dispersed ballistically up to a few meters from the mother plant (Volz, 2003; Jantunen et al., 2005). Moreover, vegetative propagation via underground adventitious shoots (Rapp, 2008; Fremstad, 2010) may contribute to high plant densities. High plant density leads to a reduction of seed production, survival and flowering probability of plants (Ramula, 2014).

4.3. Phenology

Seeds of *L. polyphyllus* germinate in spring (March-April in Central Europe) and cotyledons remain green and alive until June/July. *L. polyphyllus* shows rapid growth of leaves, usually building distinct roundish cushions in April to May, which may give the species a head start over many co-occurring plants. *L. polyphyllus* reaches its maximum vegetative height between the end of May and the end of June (Ludewig et al., 2022) (day 150–180, Fig. 7).

The species is most noticeable during flowering, which occurs from May to early September in the native range (Dunn, 1965). In Europe, the first flowers within the inflorescence open between early May in the south (49.8°N) and early June in the north (63.4°N) (Ludewig et al., 2022). The main flowering period is from May/June to August/September (Sebald et al., 1992; Klotz et al., 2002; Fremstad, 2010; Jäger, 2017; Mossberg & Stenberg, 2019; Ludewig et al., 2022). Based on an analysis of > 3500 photos from GBIF (gbif.org), the main flowering time (>50 % flowering probability) is between May 1 and July 31 in Central Europe; it is about 15 days shorter for populations at 60°N compared to those at 50°N (Yves Philippe Klinger, unpublished data). Because of the long inflorescences and progressive flowering from the base to the top of the raceme (Haynes and Mesler, 1984), single individuals may flower for several weeks. The average flowering duration of the species is ca. 3 months (Klotz et al., 2002), but individuals may flower much later in the season. Compensatory flowering can often be observed in road verge populations that have been mown late in July or August (Rolf Lutz Eckstein, personal observation). Depending on site and weather conditions, in Germany flowering individuals can be observed until November (Yves Philippe Klinger, personal observation). There is additional temporal spread of flowering among individuals within populations and among populations along a latitudinal gradient across Europe. In a phenology study, the day of the year for different flowering phases (e.g., first open flower, half of inflorescense length with open flowers, first ripe pod) increased 1.3–1.8 days per degree of latitude across Europe (Ludewig et al., 2022). It takes from end-May to end-June until half of the length of the inflorescence bears open flowers, and the first ripe pods appear between mid-June and late-July across Europe (Fig. 7; data from Ludewig et al., 2022). The time lag between flowering and seed production is 26.6–39.1 days (Ludewig et al., 2022). Fruiting (>50 % probability of ripe fruits on plants) starts between July 1 and July 15 in Central Europe (Yves Philippe Klinger, unpublished data).

4.4. Reproduction

Flowers of *L. polyphyllus* exclusively produce pollen but no nectar (Haynes and Mesler, 1984), although diffuse information on this matter can be found in popular literature. Pollen grains are approximately 40 × 20 μm in size depending on a color morph (Vinogradova et al., 2012). Pollen fertility is > 95 % but varies between main and side inflorescences at least for a pink color morph in Russian populations (Vinogradova et al., 2012). The pollen is presented on the stigma using a pumping mechanism, which is described by Haynes and Mesler (1984) as follows: “*During floral development the set of smaller anthers pushes the pollen mass into the tip of the keel, beyond the stigma and its circlet of forward-pointing hairs. When a bee manipulates a flower by bracing its head against the banner, pushing the wing petals down with its hind legs, and sliding the keel down over the style with its forelegs, the stigma, with the aid of the circlet of hairs, scoops pollen out through the aperture of the keel and up against the bee. The same downward pressure causes the small anthers to force more pollen towards the tip of the keel. When the pressure is released, the orientation of the hairs allows the stigma to slip back through the pollen mass in the tip of the keel so that the next time the mechanism is worked, the stigma can again carry pollen out of the aperture*”. Upper flowers usually produce more pollen than lower flowers, and lower flowers may often completely lack pollen (Haynes and Mesler, 1984). Since flower color does not change after pollination, pollinators may not be able to visually assess the pollen status of flowers (Haynes and Mesler, 1984).

Cross-fertilization is more frequent than self-pollination (Aniszewski, 2001). Pollinators of *L. polyphyllus* are mostly bumblebees and solitary bees (Pohtio and Teräs, 1995; Jakobsson and Padrón, 2014; Van der Kooi et al., 2016). Across the native range of *L. polyphyllus*, the following bumblebee species have been reported as pollinators of the species or the genus: *Bombus vagans*, *B. bifarius*, *B. centralis*, *B. fervidus*, *B. flavifrons*, *B. frigidus*, *B. huntii*, *B. melanopygus*, *B. mixtus*, *B. nevadensis*, *B. rufocinctus*, *B. sylvicola*, *B. sitkensis*, *B. occidentalis*, *B. pensylvanicus*, *B. bimaculatus*, *B. griseocollis*, *B. impatiens*, and *B. kirbiellus* (Montana Field Guide, 2021b). In the non-native range, the most frequent pollinating bumblebee of *L. polyphyllus* is *B. terrestris* in the Netherlands (Van der Kooi et al., 2016). In Sweden, the bees *Anthophora quadrimaculata*, *Megachile analis*, and the bumblebees *B. distinguendus*, *B. hortorum*, *B. humilis*, *B. jonellus*, *B. lapidarius*, *B. lucorum*, *B. pascuorum*, *B. soroeensis*, *B. subterraneus*, and *B. terrestris* have been observed as pollinators (Pettersson et al., 2004; Boström, 2020). Large bumblebee species like *B. subterraneus* and *B. terrestris* but also the queens of many of the other species activate the pollen dispensing mechanism of *L. polyphyllus* using their hind legs and abdomen, while smaller species like *B. jonellus* and the workers of some of the larger species use vibration pollination, after “diving” into the flowers (Boström, 2020).

Self-pollination may also be possible in *L. polyphyllus* (Kirchner, 1905). In the related *L. perennis*, self-pollination decreased fruit set from 24 % when open-pollinated to 11 % when self-pollinated, which led to a lower fruit and seed production per inflorescence and less seeds per fruit (Shi et al., 2005). Following self-pollination in *L. perennis*, offspring biomass was reduced by 25–35 %. In Swedish and Finnish populations, *L. polyphyllus* plants with natural access to pollinators produced significantly more seeds and had more seeds per pod than plants, in which pollinators were excluded through netting (Hauhia, 2018; Boström, 2020).

However, not all flowers become seed pods, and abscission rates of up to 65 % have been observed in Icelandic populations of the related *L. nootkatensis* (Greipsson and El-Mayas, 2003). At maturity, the seed pods of *L. polyphyllus* burst and spread the seeds ballistically over distances of up to 5.5 m from the mother plant (Volz, 2003). Each plant can produce up to 2500 seeds (Aniszewski, 2001), but on average, less seeds are produced (326–2093 seeds per plant, according to the LEDA Database, Kleyer et al., 2008).

The capacity for vegetative spread of *L. polyphyllus* individuals is limited. However, Rapp (2005) assumed, based on very low ratios of flowering plants to vegetative plants, that the species spreads vegetatively through rhizomes (see also Fremstad, 2010). In contrast, Chmelíková and Hejcman (2012) stated that the species lacks rhizomes and also Jauni and Ramula (2017) did not find this type of propagation. Volz and Otte (2001) report vegetative spread through polycormons of ca. 0.2 m per year. Clonal growth organs are described as 'epigeogeneous stems' and 'root splitters' in the CLO.PLA database (Klimešová et al., 2017). The plant is capable of resprouting after disturbance events (Brobäck, 2015), and even very short (≥3 cm) shoot fragments can successfully do so (Saba, 2017). Resprouting may allow the plant to persist under a variety of disturbance regimes (Elliott et al., 2011).

4.5. Germination

L. polyphyllus produces orthodox seeds, i.e. seeds that survive drying to low moisture contents (Royal Botanic Gardens Kew, 2021). The seeds show intermediate to high germination rates, ranging between 19 % in a greenhouse (Sõber and Ramula, 2013) and 69 % in a common garden (Klinger et al., 2020). In several greenhouse or climate chamber experiments, germination was as high as 98 % (Volz, 2003), or up to 100 % (Royal Botanic Gardens Kew, 2021) but only when seedcoats were scarified. Similarly, seed viability rates determined using tetrazolium tests were as high as 98.3% (Volz, 2003). Germination was found to vary considerably between source regions (19–25.8 %; Sõber and Ramula, 2013) but also between neighboring populations (by 10 %; Volz, 2003). Generally, larger seeds of *L. polyphyllus* are characterized by higher germination rates than smaller ones (Sõber and Ramula, 2013). It is still unclear if there is a trade-off in the number of produced seeds and their size in *L. polyphyllus* (Aniszewski, 2001; Sõber and Ramula, 2013). As in many legumes, seeds of *L. polyphyllus* become hard-seeded during seed formation and thus express physical dormancy (PY). The percentage of seeds expressing PY was 19 ± 7 % (Elliott et al., 2011) but may vary between populations and individual plants of the same population. Depending on the expression of PY, germination of *L. polyphyllus* takes place either in autumn after seed shed or in spring of the following year (Klinger et al., 2020). Germination rates ranged between 63.2 % and 69 % for fully ripened seeds after winter stratification in a common garden experiment (Klinger et al., 2020).

When not pre-treated, seeds of *L. polyphyllus* are characterized by asynchronous germination patterns, probably due to varying levels of PY (Klinger et al., 2020) and a hard seed coat. In laboratory experiments, cold-wet stratification or scarification were found to increase the germination of several Great-Basin *Lupinus* species (Jones et al., 2016). Soaking the seeds for five minutes in concentrated sulfuric acid increased germination rates in hard seeds of the related *L. nootkatensis* (Greipsson and El-Mayas, 2003). Cold stratification (at 5 °C) for six weeks followed by alternating temperatures (15 °C/7 °C) lead to increased germination rates in *L. polyphyllus* compared to no pre-treatment (Elliott et al., 2011). Very high germination rates (99%–100%) have also been observed following the partial removal of the seed coat using a scalpel (Royal Botanic Gardens Kew, 2021). Exposure to heat (37 °C/47 °C) and heat shock treatments (80 °C) did not affect the germination of *L. polyphyllus* (Elliott et al., 2011). Emergence of *L. polyphyllus* was found to be rather insensitive to soil pH of 5.5–7.6, although seeds from forest habitats showed higher emergence in neutral and basic soil compared to acidic soil (Sõber and Ramula, 2013). Burial depth had a significant effect on the germination of *L. nootkatensis* with seeds buried in > 3 cm depth having lower germination rates than seeds buried between 1 and 3 cm (Greipsson and El-Mayas, 2003). Several studies found that alternating temperatures simulating fall or spring conditions led to the highest germination rates (Volz, 2003; Elliott et al., 2011). *L. polyphyllus* seeds from southern Germany were characterized by consistently high germination rates under a variety of experimental climate conditions following storage at 0 °C and given regular watering (Arfin-Khan et al., 2018). In the same experiment, germination of *L. polyphyllus* failed under 11/− 5 °C and 36/9 °C day/night temperature regimes (Arfin-Khan et al., 2018). Seeds of *L. polyphyllus* can be stored over long periods under standardized, artificial conditions such as those found in a genebank. For example, Harrington (1972) found 75 % germination after 49 years storage at room temperature. In an attempt to improve viability equations used for estimation of seed longevity under various storing conditions in genebank facilities, Sapra et al. (2003) calculated seed longevities of 79 and 208 years at − 10 °C and − 20 °C, respectively (5 % seed water content). Unfortunately, these estimates, which may represent some type of seed quiescence under highly artificial conditions conducive to seed viability, are quoted by various reports and species information pages as representing seed dormancy in situ. However, this is most probably not the case (Tobias Donath el al., unpublished data).

4.6. Response to competition

4.6.1. Competition and disturbance during the establishment phase

Some of the habitats of *L. polyphyllus* s.str. in its native range are characterized by regular disturbance of the soil, and the species has also spread to anthropogenic, disturbed habitats, such as road verges (e.g., Hejda, 2013; Electronic Flora of British Columbia, 2022). Disturbed habitats are particularly prone to being invaded by *L. polyphyllus* outside of its native range (Fremstad, 2010; Jauni et al., 2015), and may support highly competitive populations of *L. polyphyllus* with high densities of plants (Meier et al., 2013).

The success of *L. polyphyllus* on disturbed soils is mainly due to high rates of establishment of new plants from seed. The correlation between cover of bare soil and establishment success is, however, not straightforward. Bastl et al. (1997) found establishment to be highest in intermediate successional stages in sand pits (10 yrs after ground disturbance), not at early stages with highest cover of bare soil and lowest competition, probably due to too dry topsoil conditions on newly disturbed ground with open sand. At later successional stages (20 yrs after disturbance), establishment was reduced by competition. In contrast, on more moist soils (peat bog) establishment of *L. polyphyllus* was highest on bare soil, and decreased with successional age and increasing vegetation cover and competition (Bastl et al., 1997). Ramula et al. (2015) found no increased establishment (established seedlings per sown seed) when the small-scale cover of bare soil was doubled from ca. 15 % to ca. 30 % in 50 × 50 cm plots. Also in this study, reduced soil moisture may have reduced seedling survival on bare soil. The success of *L. polyphyllus* during the establishment phase may thus partly be determined by an interplay between availability of low-competition microsites, e.g., bare soil, and soil moisture sufficient for seedling survival.

Bare soil seems to favor seedling survival, whereas initial seedling establishment is less affected. An intense disturbance event (vegetation and litter removal before seed sowing) increased seedling survival by 15 % but had no effect on seedling establishment in a seed sowing experiment (Jauni and Ramula, 2017). In contrast, a mild disturbance event (breaking the soil surface mechanically before seed sowing) increased seedling establishment in the following spring by a few percentage points. Large seeds and the species' capacity for nitrogen fixation further contribute to rapid establishment on bare soil and soils with low nutrient status (e.g., Che, 2018).

4.6.2. Competition and adult plants

At young stages, *L. polyphyllus* is susceptible to competition from tall native vegetation (Vetter et al., 2019), but once established, the species rapidly grows into a tall plant with a high leaf area. Where establishment conditions are favorable (see previous section), the plants often occur in dense stands. Therefore, *L. polyphyllus* is probably among the most competitive plant species in grassland communities. The high competitive capacity of *L. polyphyllus* is reflected by reduced abundance or exclusion of other species in dense stands, and reduced species richness following *L. polyphyllus* invasion (e.g., Valtonen et al., 2006; Thiele et al., 2010; Meier et al., 2013; Rapp, 2005; Hansen et al., 2021; Knudsen, 2021). However, even an intermediate cover of lupine (about 35%) can reduce plant species richness in semi-natural grasslands (Prass et al., 2021).

The effects of *L. polyphyllus* on the native flora are mainly due to competition for light, as indicated by larger effects on low-growing than on taller plant species (e.g., Thiele et al., 2010). For example, Valtonen et al. (2006) showed that both the abundance and number of low-growing species were reduced, whereas medium-sized species were reduced only in their abundance and tall species not at all. Consequently, the functional composition of the invaded plant community shifts towards community-weighted trait means characteristic for competitive species (Hansen et al., 2021), and species associated with early successional habitat types are particularly affected by the invasion of *L. polyphyllus* (Thiele et al., 2010).

The competitive effect of *L. polyphyllus* on plant communities is similar to that of other tall competitive species (Hejda, 2013; Czarniecka-Wiera et al., 2019). However, *L. polyphyllus* is a problematic invasive alien plant because it may colonize nutrient-poor disturbed habitats at early successional stages (e.g., Magnússon et al., 2004; Thiele et al., 2010; Hejda et al., 2009). Here, the native flora is dominated by low-growing pioneer species and *L. polyphyllus* is among the few, often the only, competitive tall pioneer species. Resistance to drought (through water storage in adventitious shoots and a high capacity of resprouting after drought damage) contributes to making *L. polyphyllus* a strong competitor on dry soils (Vetter et al., 2019). Adult plants of *L. polyphyllus* appear to be highly resistant to competition from native vegetation (e.g., Thiele et al., 2010; Lauterbach and Nehring, 2013).

4.7. Herbivores and pathogens

4.7.1. Herbivores

Species in the genus *Lupinus* produce quinolizidine alkaloids, which are important defense compounds. In its native range, several herbivorous species are adapted to tolerate or even take advantage of these chemicals, such as the aphid *Macrosiphon albifrons*, which may not only feed on the plant but also accumulate chemicals for its protection against predators (Wink, 1986). Summarizing results of several herbivory experiments, Wink (1988) showed that an alkaloid content of > 0.7 mg g^{-1} fresh weight in several lupines (*L. polyphyllus* had >1 mg g^{-1} fresh weight) almost eliminated herbivory by rabbits, leaf miners, and generalist aphids. However, the aphid *M. albifrons* preferred the plants with high alkaloids contents and avoided the ones with low concentrations of these chemicals. This suggests that *L. polyphyllus* has an effective chemical defense against generalist herbivores. Nevertheless, seeds inside the pod are consumed by the larvae of the weevil *Tychius lineelus* (Babcock et al., 1993). Other herbivores observed in the native range include lepidopteran caterpillars, leaf miners, the western flower thrips *Frankliniella occidentalis* (during flowering), and the seedcorn maggot *Delia lupini* (Babcock et al., 1993).

The two root weevils *Charagmus gressorius* (syn. *Sitona gressorius*) and *Ch. griseus* (syn. *S. griseus)* are known to be a pest in foremost eastern Europe in arable fields of Narrow-leaved lupine (*L. angustifolius*) and White lupine (*L. albus*) but they are also known to feed on both the leaves and roots of *L. polyphyllus* (Hanavan et al., 2008; Ströcker et al., 2011). The two weevil species can use a wide range of plant species but seem to prefer species of *Lupinus*. The beetles' larvae feed on roots, causing the plant to suffer from a decreased efficiency of their symbiotic nitrogen fixation system. They also utilize the leaves as adults in spring, which may have severe effects on young plants (Piedra-García and Struck, 2021). However, potential impacts on *L. polyphyllus* at the population level are unknown. In Finland, leaves of *L. polyphyllus* are consumed by generalist herbivores, primarily by the land snail *Arianta arbustorum* but also by some lepidopteran caterpillars, while pods are occasionally consumed by the gorse shieldbug *Piezodorus lituratus* (Hemiptera) that has specialized on legumes (Satu Ramula, personal observation).

4.7.2. Pathogens

An anthracnose was first diagnosed in 1939, but descriptions of similar damages to species of *Lupinus* had been reported as early as 1912 (Talhinhas et al., 2016). The organism causing the anthracnose is the ascomycete *Colletotrichum gloeosporioides*. However, *C. gloeosporioides* is rather a complex of at least 22 species that may cause problems to various plant species such as vegetables and fruits including e.g., citrus, yam, papaya, avocado, coffee, eggplant, sweet pepper, and tomato (Weir et al., 2012). *C. gloeosporioides* may infect at least 1000 plant species either primarily or as a secondary infection of already damaged plant tissue (Phoulivong et al., 2010). In nurseries of the *Lupinus ×russellii* hybrid of *L. polyphyllus* (see Section 3.1.1), outbreaks of *C. gloeosporioides* have resulted in the death of young plants and bent and crooked adult plants with leaf spots (Elmer et al., 2001). Reports of these outbreaks are from various places in the world e.g., Australia, Canada, England, New Zealand, and Poland (Reed et al., 1996; Herms and Mattson, 1992; Elmer et al., 2001). Moreover, *L. polyphyllus* can be infected by a powdery mildew in both the native and introduced ranges (Smith and Wheeler, 1969; Bradshaw et al., 2021). This fungal disease is caused by different *Erysiphe* species, including *E. intermedia, E. lupini*, and *E. trifoliorum* (reviewed in Bradshaw et al., 2021). The infection begins on older leaves with the fungus forming a white powdery cover, followed by brown spots (cleistothecia).

4.8. Symbionts

Among vascular plants the vast majority of species (ca. 85 %) shows some kind of mycorrhiza (Brundrett and Tedersoo, 2018), with arbuscular mycorrhiza (AM) being the most common type (72 %). While the type of mycorrhiza is mostly consistent within a family (Brundrett, 2017), the genus *Lupinus* represents an exception to this rule (Oba et al., 2001). Fabaceae are generally known as hosts for an AM symbiosis with relatively high levels of root colonization (Oba et al., 2001). When 36 species of *Lupinus* were inoculated with AM fungi, 33 species (incl. *L. polyphyllus*) showed at least external hyphal growth (Oba et al., 2001). A review of Shi et al. (2017) showed that 35 of 43 lupine species showed colonization by AM fungi but root colonization rates were always low. Thus, the mycorrhizal association seems to be weak and probably non-functional since none of the species showed the formation of arbuscules in the root, and shoot dry mass did not differ between inoculated and non-inoculated plants (Oba et al., 2001). Consequently, although there have been some field observations of AM fungi in *L. polyphyllus* (O'Dell and Trappe, 1992; Wurst et al., 2010), the genus *Lupinus* as a whole is considered non-mycorrhizal (Oba et al., 2001; Lambers et al., 2013).

Almost all of the tested species in the tribe Genisteae (Fabaceae), to which *L. polyphyllus* belongs, have the ability to fix atmospheric nitrogen with the help of symbiotic bacteria (diazotrophs) in root nodules (Stępkowski et al., 2018). The most frequent diazotroph symbionts of the tribe belong to the genus *Bradyrhizobium* (Andrews and Andrews, 2017; Stępkowski et al., 2018; Dung, 2020), which is also the most common symbiont within the genus *Lupinus* (Stępkowski et al., 2007). In

New Zealand, 22 rhizobial isolates could be extracted from ten roadside populations of *L. polyphyllus* (Ryan-Salter et al., 2014); all isolates were identified as *Bradyrhizobium.* In inoculation experiments (Ryan-Salter et al., 2014; Black et al., 2015), all bacterial isolates formed functional nodules on *L. polyphyllus*, indicating that diazotroph symbionts that nodulate the species are widespread in the South Island of New Zealand. The fact that also *Bradyrhizobium* isolates gained from roots of other invasive species of the Genisteae tribe (*Ulex europaeus*, *Cytisus scoparius* and *Chamaecytisus palmensis*) with similar nodA gene sequences made root nodules on *L. polyphyllus* in the laboratory suggests that several invasive legumes may share a "*common pool of rhizobia*" (Black et al., 2015). Studies on root nodules of *L. polyphyllus* from Belgium identified *Bradyrhizobium japonicum* and *Rhizobium leguminosarum* (De Meyer et al., 2011) as well as *Bosea lupini* sp. nov. (De Meyer and Willems, 2012) as diazotroph endosymbionts.

4.9. Physiological data

L. polyphyllus has been the object of a number of studies on the geotropism of seedlings in the past (Brain, 1933, 1952). These studies showed that a geotropic response to a stimulus, i.e., plants being laid horizontally for 20 min, varied among seasons and declined during winter (Brain, 1952). Other physiological studies on the species focused on the amounts, the biosynthesis and the transport of alkaloids (e.g., Karlsson Strese, 1981; Wink and Hartmann, 1982; Mende and Wink, 1987). Wink and Hartmann (1982), studying purified chloroplasts from leaves of *L. polyphyllus*, found that two important enzymes linked to the biosynthesis of quinolizidine alkaloids are localized in the stroma of the chloroplasts. Mende and Wink (1987) studied the uptake of the quinolizidine alkaloid lupanine into protoplasts and isolated vacuoles, using cell suspension cultures of *L. polyphyllus* and six other plant species. They concluded that the uptake of lupanine by vacuoles is driven by a specific transport protein and could thus rule out passive diffusion of lupanine across the tonoplast.

Information on the amounts and types of alkaloids in *L. polyphyllus* (e.g., Karlsson-Strese, 1981; Buzuk et al., 2002) as well as other physiological studies focusing on seed germination (e.g., Elliott et al., 2011) are treated comprehensively in Sections 4.5 and 4.10, respectively.

4.10. Biochemical data

Within the family Fabaceae, the tribe Genisteae, to which *L. polyphyllus* belongs, is chemo-taxonomically characterized by quinolizidine alkaloids (QA) (Wink et al., 1995; Wink, 2013). Since legumes have access to atmospheric nitrogen through their root symbionts, they produce more nitrogen-containing secondary metabolites (e.g., non-protein amino acids, glucosinolates, amines, and alkaloids) than non-nitrogen fixing plants (Wink, 2013). These nitrogen-containing secondary metabolites, which accumulate in the seeds, may have a double function, i.e., serve as defense compounds as well as compounds for nitrogen storage from which nitrogen can be remobilized during germination and seedling growth (Wink and Witte, 1984).

L. polyphyllus has already early after its introduction to Europe been used as green manure, for soil amelioration in forestry (e.g., Fruwirth, 1914, 1921; Lent, 1934), and as feed for domestic animals and game (on food plots) (Fruwirth, 1914). However, animals often avoided the species because of its high alkaloid contents (especially QA) and high contents of QA have even led to poisoning of domestic animals (Karlsson Strese, 1981). Consequently, since the 1930 s, much research into the biochemical composition of *L. polyphyllus* and other lupines has been done, aiming at reducing the content of QA and using the species as industrial crops or for animal and human nutrition (e.g. Karlsson Strese, 1981; Aniszewski, 1993a; b, 1998; Kaiser et al., 2020). There have been attempts to breed and cultivate alkaloid-poor lines of *L. polyphyllus* (Aniszewski, 1993a). Although total alkaloid contents of seeds of this alkaloid-poor line (variety SF/TA) were relatively low (226 – 366 µg g^{-1}) and there was no significant increase in alkaloid contents between successive years (1992–1994; Aniszewski, 1998), which would make the variety increasingly bitter, this breed was unsuitable for human nutrition without prior processing (Aniszewski, 1993a). With the successful development and cultivation of "sweet lupine" varieties of *Lupinus albus* L. (Mediterranean), *L. angustifolius* L. (Australia), *L. luteus* L. (Europe), and *L. mutabilis* L. (South America) with significantly lower QA content that their wild types (reviewed in Kaiser et al., 2020), further attempts to breed sweet varieties of *L. polyphyllus* have been abandoned.

Biochemical production of alkaloids is localized in the leaves (chloroplasts) (Wink and Hartmann, 1982). The translocation of alkaloids within the plant occurs through the phloem and they are mainly stored in epidermal cells and in the seeds (Wink et al., 1995), which therefore show the highest QA concentrations of all plant parts. The total alkaloid concentrations of green parts of *L. polyphyllus* from three populations in Germany and Poland (Karlsson-Strese, 1983) ranged from 20 to 46 mg g^{-1} (average: 32.3 mg g^{-1}) whereas seeds from ten populations showed concentrations between 13 and 55 mg g^{-1} (average: 38.9 mg g^{-1}). Populations of the cultivated sweet variety of *L. polyphyllus* (Plarre and Porsche, 1961) had much lower total alkaloid concentrations (green parts: 0.20 mg g^{-1}, excluding one outlier; seeds: 0.24 mg g^{-1}; Karlsson-Strese, 1983). Seeds of *L. polyphyllus* from the Vitebsk oblast, Belarus (Buzuk et al., 2002) showed total alkaloid concentrations ranging between 17.5 and 32.3 mg g^{-1} (average: 23.4 mg g^{-1}).

QAs act as neurotoxins that may affect acetylcholine receptors and block sodium channels (Wink, 2013). Therefore, it is interesting to note that some Native American tribes allegedly have used *L. polyphyllus* as medicine or tonic (Moerman, 2003; Beuthin, 2012), while others considered the species as toxic. However, in a list of plants used by Native Americans of Vancouver Island (Chapman Turner and Bell, 1971), *L. polyphyllus* is denoted with a question mark. Given the lack of genetic barriers in the genus *Lupinus*, which leads to hybridization and introgression (e.g., Dunn, 1965; see Section 3.1.1), it appears to be unclear exactly which taxon has been used by Native American tribes.

QAs, specifically sparteine, which also occurs in *L. polyphyllus* (Wink et al., 1995), has antibiotic effects against bacteria and fungi at concentrations that can be found in wild plants (Wink, 1984a). In feeding trials, QAs had mollusc-repellent properties (Wink, 1984b; Kalske et al., 2022a). The mollusc-repellent effects were substance-specific though (Wink, 1984b), with the QAs cytisine and N-methylcytisine having larger effects on the generalist molluscs *Helix pomatia* and *Arion rufus* than lupanine. However, lupanine found in pollen of different crop lupine species can reduce the fitness of the generalist bumblebee *Bombus terrestris* (Arnold et al., 2014). Buzuk et al. (2002) studied the regulation of metabolism of alkaloids through different elements based on correlation analyses. These authors suggest that a large part of the variation in alkaloid contents in lupine seeds is related to the variation of potassium (K) and nickel (Ni) concentrations, while variation in the alkaloid contents of leaves was due to variation in the concentrations of K, calcium (Ca), zinc (Zn), copper (Cu), and vanadium (V). Potassium exerted a negative effect on the production and accumulation of alkaloids, which, as Buzuk et al. (2002) speculate, could be due to a K-induced stimulation of protein biosynthesis, leading to competition for lysine, a precursor of both alkaloids and proteins.

In wild populations of *L. polyphyllus* from the non-native range (Germany), 29 different QAs have been detected and characterized in leaves and hypocotyls using nuclear magnetic resonance spectroscopy (Veen et al., 1992) and 38 QAs have been reported from leaves and seeds by using capillary gas-liquid chromatography (Wink et al., 1995). The main QA in leaves is lupanine (Wink et al., 1983; Kalske et al., 2022a). Since these alkaloid profiles are often species-specific, they may represent an "*alkaloid fingerprint*" (Wink et al., 1995). Kalske et al. (2022a) identified 23 QAs or alkaloid isomers in six native (USA) and 16 non-native (Finland) populations, with concentrations ranging from trace amounts to up to 7.26 mg g^{-1} leaf. Comparisons between native

Table 5

Concentrations (mg g^{-1}) of nitrogen (N), phosphorus (P) and potassium (K) in different plant fractions of *Lupinus polyphyllus* and seasons. Data from Volz (2003).

Element	Plant fraction	Concentration (mg g^{-1})	Season
N	Roots	28.0	Spring
		15.0	Summer
	Above-ground vegetative	48.0	Spring
		22.0	Summer
		18.0	Fall
	Seeds	60–70	
P	Roots	2.4	Spring
		1.2	Summer
	Above-ground vegetative	4.5–5.3	Spring
		1.8–2.3	Summer
		1.2–1.4	Fall
	Seeds	3.2–3.5	
K	Roots	7.5	Spring
		2.5	Summer
		5.0	Fall
	Above-ground vegetative	17.0	Spring
		2.0	Summer

and non-native populations showed that leaf alkaloid composition differed significantly between regions; native populations showed a more diverse alkaloid composition than populations from Finland, whereas alkaloid richness and the total concentrations of QAs did not differ between regions (Kalske et al., 2022a).

Inhibitory allelopathic effects of *L. polyphyllus* vary across herbaceous species, being most pronounced early in life. Mixtures of QAs showed allelopathic effects on other plant species in a laboratory experiment, significantly inhibiting the germination of seeds of *Lactuca sativa* (Wink, 1983). Moreover, leaf litter leachates of *L. polyphyllus* reduced the germination and root growth of native grasses and forbs and delayed their germination (Loydi et al., 2015). However, these negative effects ceased soon after germination (Loydi et al., 2015). Aqueous leachate from shoots was usually more allelopathic than leachate from roots in terms of inhibiting germination of co-occurring native herbs from three families (Kalske et al., in press). Based on activated carbon addition experiments, the presence of *L. polyphyllus* slightly reduced the germination of the perennial herb *Plantago lanceolata* (Wurst et al., 2010) and the biomass of the perennial herb *Anthriscus sylvestris* (Lyytinen and Lindström, 2019).

Akritidu et al. (2013) identified 20 different organic acids in the roots of *L. polyphyllus* collected in Kharkiv Oblast (Ukraine). There were ten carboxylic, two phenolic, and seven fatty acids, which varied in concentrations between 22 and ca. 6400 µg g^{-1}. Of the carboxylic acids, malic acid, hepta-2,4-dienoic acid, malonic acid, and citric acid were most abundant. In a later study, Boinik et al. (2015) analysed the phenolic compounds of *L. polyphyllus* roots from the same region, showing that the roots contained mostly condensed tannins such as epicatechin, catechin, and epigallocatechin.

Volz (2003) did nutrient analyses (N, P, K, and other elements) of *L. polyphyllus* from meadow populations in the Rhön area. He found that seeds had much higher concentrations of N and P than above-ground vegetative biomass and roots (Table 5). Concentrations varied between seasons and considerably decreased from spring to summer and fall, probably due to translocation between plant organs and/or dilution through growth.

Kalske et al. (2022b) analysed volatile organic compounds (VOCs) emitted from the leaves of *L. polyphyllus* based on five native (USA) and five invasive (Finland) populations. They found that the VOC emissions were similar for plants from both origins and contained 22 different compounds, with green leaf volatiles being most abundant.

4.11. Genetic data

Common chromosome number of *L. polyphyllus* is 2 n = 48 (Tuschnjakowa, 1935; summarized in Rice et al., 2015) with a single record of 2 n = 96 from British Columbia. The species is usually described as a polyploid; either a tetraploid (Klotz et al., 2002; Kubešová et al., 2010; Jeelani et al., 2011, 2017) or an octoploid (te Beest et al., 2011), having the basic chromosome number of x = 12 (Klotz et al., 2002). However, it is sometimes also referred to as a diploid (Šmarda, 2018). Estimates of nuclear genome size (2 C-value) vary from 1.62 to 1.70 pg (Naganowska et al., 2006; Zonneveld, 2019).

Table 6

First dates of recorded/published findings of naturalized stands of *Lupinus polyphyllus* outside its native range.

Date	Region	Source
1870	Skåne/Sweden	Hylander (1971)
1880	Mecklenburg/Germany	Fukarek (2006)
1882	Belgium	Invasive species in Belgium (2022)
1890	Bavaria/Germany	Hegi (1924)
1895	Czech Republic	Pyšek et al. (2012)
1895	Finland	Elven and Fremstad (2000)
1900	UK	Preston et al. (2002)
1902	The Netherlands	Nederlands Soortenregister (2022)
1913	Norway	Rask-Jensen (2018)
1921	Latvia	Gudžinskas (2000)
1921	Russia/Yaroslavsk	Vinogradova et al. (2009)
1931	Lithuania	Gudžinskas (2000)
1941	Russia/Tomsk	Ebel et al. (2016)
1950	Poland	Tokarska-Guzik (2003)
1952	Russia/Moscow	Vinogradova et al. (2009)
1957	Russia/Kaluga	Vinogradova et al. (2009)
1969	Russia/Vladimir	Vinogradova et al. (2009)
1976	Russia/Brjansk	Vinogradova et al. (2009)
1980	Russia/Tver	Vinogradova et al. (2009)
1990	Russia/Krasnoyarsk	Ebel et al. (2016)
1994	Russia/Bashkortostan	Muldashev et al. (2014)
1996	Russia/Altai	Ebel et al. (2016)
2004	Russia/Kemerovsk	Ebel et al. (2016)
2005	Russia/Chelyabinsk	Kulikov (2005)
2011	Russia/Irkutsk	Ebel et al. (2016)
2013	Russia/Novosibirsk	Ebel et al. (2016)

Studies on intraspecific genetic variation are scarce and currently limited to three countries in the non-native range. These studies revealed significant genetic differentiation among ten Lithuanian populations based on six RAPD markers (Vyšniauskiené et al., 2011), among 84 Russian populations based on RAPD, ISRR and REMAP markers (Osipova et al., 2021), and among 51 Finnish populations based on 13 microsatellite markers (Li et al., 2016a). Moreover, genetic variation (measured as the number of unshared alleles between pairs of individuals) was positively associated with lupine population size and seedling establishment (Li et al., 2016b; Ramula, 2016; Osipova et al., 2021). Despite significant genetic differentiation among non-native populations, most of the genetic variation still occurs among individuals within populations rather than among populations within countries (Vyšniauskiené et al., 2011; Li et al., 2016a). In Finland, genetic differentiation of the populations was not associated with latitude, which suggests human-mediated spread of the species with multiple introductions from different sources (Li et al., 2016a). In Russia, the genetic variation tended to increase with invasion history, being higher for older populations (introduced some decades ago) than for more recent populations (ca. five years old; Osipova et al., 2021).

5. History of invasive spread

The colonization history of *L. polyphyllus* is well documented (Fig. 3B, Table 6). It was introduced in 1826 to Great Britain as an ornamental plant (Goethe, 1893) and soon afterwards nurseries and botanical gardens offered a variety of color forms (Lehmann, 1833; Krausch, 2003). In the late 19th and in the 20th century, the species was also promoted for undersowing as green manure by north-western European forestry administrations, especially in regions with acidic,

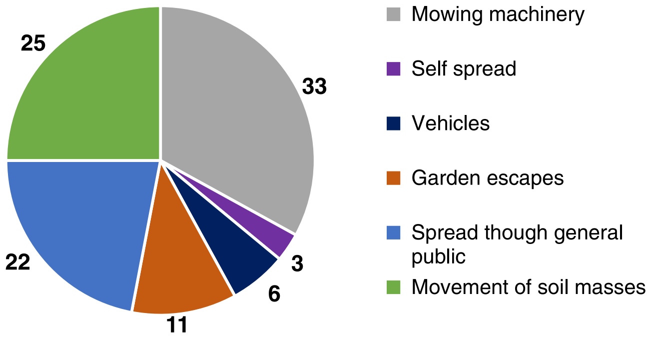

Fig. 8. Main vectors of dispersal of *Lupinus polyphyllus* in Sweden according to interviews with experts (from Wissman et al., 2015).

nitrogen depleted soil. Additionally, it was sown as game-fodder by hunters and foresters. In Scandinavia, *L. polyphyllus* was apparently actively distributed along roads and highways as part of re-cultivation measurements after road construction works (Elven & Fremstad, 2010; Rask-Jensen, 2018). In Russia, agricultural cultivation is still in practice. Based on interviews with experts from the Swedish Transport Administration, the Swedish Environmental Protection Agency, the Swedish Board of Agriculture, Country Administrative Boards and municipalities (Wissman et al., 2015), the most common current vectors of spread in Sweden are mowing machinery, movement of soil fill for road construction and deliberate or undeliberate spread of the species though the public (Fig. 8). In contrast, self-spread, escapes from gardens or transport by vehicles is considered to play a minor role in the current stage of invasion (Wissman et al., 2015).

Outside Eurasia, *L. polyphyllus* also started to naturalize after introduction into commercial trade. In New England, the first introductions probably arrived from England instead of the North American native range. Naturalized occurrences in Massachusetts were first reported in 1948 (Sorrie, 2005). The partially intentional seed dispersal by humans has even entered the world of literature in person of the semi-fictitious Miss Rumphius (Cooney, 1982). Seemingly inspired by this narrative, also people in New Zealand are reported to have scattered lupine seeds along roadsides, e.g., in the Tekapo region (Scott, 1993; Wardle, 2016). To add even more poetry, it is reported that tour bus drivers deliberately spread seeds to promote colorful roadside vegetation for tourists. Additionally, in NZ there are large-scale lobbying and research activities supported by the Merino industry to establish the evidently invasive species in sheep pastures (Scott and Tesfaye, 2000). The first reports of naturalized stands date from 1958 (Webb, 1980).

The cultivation and spread of the species increased from 1900 onwards and it started to escape from cultivation approximately at the same time (Fig. 3B, Table 6). Given the different usages and pathways for dispersal, the rapid, large-scale colonization process of *L. polyphyllus* in Eurasia and worldwide is clearly driven by direct, intentional dispersal by humans and only locally by its own, probably quite limited dispersal (Rask-Jensen, 2018). Areas with currently large-scale increasing colonization and establishment are Eastern Europe, Northern Asia, W-Himalaya, and extratropical Andean S-America.

6. Impact and management

6.1. Impact

In a study on 19 invasive and native dominants, Hejda et al. (2021) showed that *L. polyphyllus* had relatively small effects on species richness and diversity of abandoned meadows as compared to e.g. *Reynoutria* ×*bohemica* (invasive) or *Calamagrostis epigeios* (native). This may be because the species pools of some invaded habitats (such as abandoned meadows and pastures, anthropogenic herb stands, temperate thickets and scrub, and willowherb and foxglove clearings, see Table 3) contain a number of tall species that are unlikely to be outcompeted by *L. polyphyllus* (Hejda et al., 2009; Hejda, 2013). However, the impact of *L. polyphyllus* is much larger when the species invades communities such as alpic mountain hay meadows, alpic mat-grass swards but also nutrient-poor road verges in Europe or riparian terrasses in New Zealand (Hejda, 2013). In these communities, *L. polyphyllus* changes the vertical structure of the usually low-growing vegetation (Otte and Maul, 2005), leading to increased plant cover (as a proxy of biomass) higher up in the vegetation (30–70 cm above ground). Similarly, the community-weighted means (CWM) of canopy height increased with increasing cover of *L. polyphyllus* in plots of alpic mountain hay meadows and alpic mat-grass swards (Hansen et al., 2021). The CWMs of specific leaf area increased and of leaf dry matter content decreased as a response to the invasion with *L. polyphyllus* in alpic mat-grass swards (Hansen et al., 2021). Moreover, in a study along road verges in southern Sweden using a paired-plot design, Knudsen (2021) found that communities with dominant *L. polyphyllus* were higher and showed a larger CWM for plant height. The species has therefore a strong filtering effect on species composition of these invaded communities, suppressing small species (Otte and Maul, 2005; Thiele et al., 2010) and favouring large-stature tussock grasses such as *Poa chaixii* and *Deschampsia cespitosa*, as well as ruderal plants such as *Cerastium glomeratum*, *Galium aparine*, *Galeopsis tetrahit*, *Cirsium arvense*, *Urtica dioica*, and *Chamaenerion angustifolium* (Otte and Maul, 2005). Along road verges in Sweden, large grasses and nitrogen-demanding herbs such as *Arrhenatherum elatius* and *Anthriscus sylvestris* frequently occur together with *L. polyphyllus* (Wissman et al., 2015). In Germany, Schäfer (2021) found that *L. polyphyllus* increased the ecological novelty (i.e., the dissimilarity of an invaded ecosystem compared to its uninvaded state; Schittko et al., 2020) of invaded mountain meadows, although no negative effect on the functional diversity was found. Through these effects on species composition, *L. polyphyllus* exerts negative impacts on the species diversity of invaded communities (Valtonen et al., 2006; Thiele et al., 2010; Ramula and Pihlaja, 2012; Hansen et al., 2021; Knudsen, 2021) and may be a driver of the homogenization of community composition (Valtonen et al., 2006; Hansen et al., 2021; Knudsen, 2021). Additionally, a recent multisite mesocosm study indicated that the presence of *L. polyphyllus* may disrupt a positive richness–recovery relationship of semi-natural grasslands in the face of drought (Vetter et al., 2020).

In addition to its effects on vascular plant communities, *L. polyphyllus* can have cascading impacts on arthropod communities. In Finland, the number of arthropods was about 46 % smaller at invaded sites than at uninvaded sites during the peak flowering of *L. polyphyllus*, mainly due to the lower abundance of beetles, Diptera, Lepidoptera, and ants (Ramula and Sorvari, 2017). In contrast, bumblebees were about twice as abundant at invaded sites than at uninvaded ones, with *Bombus lucorum* being particularly abundant (Ramula and Sorvari, 2017). Similarly, a considerable increase in the number of bumblebees was observed at lupine-invaded sites in Sweden, leading to more pollinator visits to a native perennial herb compared to uninvaded sites (Jakobsson and Padrón, 2014). However, *L. polypyllus* had no effect on the species richness of Lepidoptera (Valtonen et al., 2006) and bumblebees (Ramula and Sorvari, 2017).

6.2. Management

6.2.1. Above-ground disturbance and vegetation management

L. polyphyllus is not typically occurring in shady habitats, such as forests. Bush and tree encroachment during the course of secondary succession may be delayed by environmental stress, such as drought and nutrient deficits in habitats of *L. polyphyllus*. However, *L. polyphyllus* shows considerable tolerance to both those factors. Open habitats may also be temporary and occurring in environments subject to regular disturbances. *L. polyphyllus* apparently is highly adapted to such conditions both in its native and non-native range. This is due to its high capacity to establish from seeds on disturbed ground and its adventitious shoots that are tolerant of disturbance and can resprout. A third type of factor maintaining habitat openness is regular vegetation disturbance such as grazing and mowing. *L. polyphyllus* is indeed invading also such habitats, and its tolerance of above-ground disturbance has been studied in order to understand how vegetation management can be used to control the species.

As *L. polyphyllus* is considered an invasive species in most European countries, it is actively controlled in many parts of Europe. Albeit the fact that there are many practitioners with long-term experience in managing *L. polyphyllus*, there is little peer-reviewed literature assessing the efficacy of different control measures. In general, depending on invasion stage and local context, control either aims at full eradication or at reducing the abundance of *L. polyphyllus*. Most commonly, mechanical control is performed either through manual removal of plants, e.g., by uprooting, or adapted mowing schemes. The latter can lead to a reduction of population viability and size, eventually resulting in local eradication. Control may also include reduction of dispersal capacity. This can be done either by reducing seed production, e.g., by the removal of inflorescences, or by reducing germination rates (e.g. through heat treatments). Finally, *L. polyphyllus* can be controlled effectively by targeted herbicide application. However, as the species invades many areas of high conservation value in Europe, herbicide application on a larger is scale is often not an option.

6.2.2. *Mowing*

There are several examples of mowing experiments with *L. polyphyllus*. Volz (2003) did a mowing experiment in a stand with > 50 % lupine cover testing combinations of different types and timing of mowing on *L. polyphyllus* in mountain meadows. The types of mowing were: (i) bar mower and removal of biomass; (ii) bar mower without removal of biomass; (iii) mulching without removal of biomass. The timing of mowing included (a) June (main flowering phase), (b) July or (c) in June and August. This experiment unfortunately lacked proper spatial replication, but it can still give some indication of management effects. Depending on the mowing type, an early mowing in June or July reduced biomass of *L. polyphyllus* to between 10 % and 50 % of the biomass at treatment start (Figs. 41–43 in Volz, 2003). Mowing the plots twice per summer reduced biomass to < 20 % of the biomass of 1998 in all three mowing types.

Blomqvist (2021) did a field experiment on the level of individual plants, testing the potential of *L. polyphyllus* for regrowth after cutting. Individuals of similar size in a road verge population in Karlstad (Sweden) were either cut (1) once (in May), (2) twice (in May + June), or (3) three times (in May + June + July). The mowing treatments significantly reduced the biomass of stems, inflorescences and total biomass but not leaf biomass (Blomqvist, 2021), which indicates that plants after mowing invest most strongly into leaf regrowth. Initial above-ground biomass was positively related to the potential of regrowth, i.e., larger plants were better able to compensate for biomass removal through mowing. However, based on a two-year study, Saarinen et al. (2010) reported that annual mowing (once or twice per summer) increased mean lupine cover in road verge habitats. In particular, mowing lupines once during the summer enhanced the production of flowering shoots (Saarinen et al., 2010), probably because of resprouting.

Valtonen et al. (2006) suggest regular early mowing, i.e., before the lupines have shed their seeds, together with the removal of the cuttings, to be the best management option. Annual biomass removal has been shown to reduce plant size, flowering probability, shoot and root biomass, plant survival and the number of flowering shoots in a common garden experiment (Ramula, 2020). As a result, a single biomass removal event considerably decreased the long-term population growth rate of Finnish populations (Ramula, 2020). Otte at al. (2002) showed that lupine density somewhat decreased after 3–5 years of continuous mowing. However, due to its ability to resprout after mowing, a second mowing event may be necessary to control the species in southern populations. The timing of mowing needs to be chosen carefully, as mowing machinery can contribute considerably to the dispersal of the species (Yves Philippe Klinger, unpublished results). The risk of unwanted dispersal during/after management depends on the development stage of seeds: in an experiment to test the germinability of seeds of *L. polyphyllus* in relation to cutting time, Klinger et al. (2020) found that germination patterns differed between seeds from plants that were cut at different dates. Germination of the green and soft seeds of plants cut early was low, whereas ~60 % of the dark and hard seeds of plants cut late germinated. Additionally, seeds of plants cut late expressed physical dormancy and were thus prone to germinate in spring (i.e., after winter stratification), which may lead to higher seedling survival (Klinger et al., 2020).

In summary, the results of mowing experiments are still ambiguous, which may be related to different locations, environmental conditions, and study durations. This highlights the need for further studies. However, the available results indicate that mowing plants over multiple years is necessary to reduce the abundance of lupines and early mowing seems to have significantly larger impact on lupines than mowing after the flowering phase.

6.2.3. *Grazing*

Although *L. polyphyllus* contains toxic alkaloids (see Section 4.10), it can be controlled via grazing. In the Biosphere Reserve Rhön (Germany), grazing by sheep and goats is used to reduce lupine cover in areas that cannot be mown or as aftermath grazing after mowing (Biosphärenreservat Rhön, 2022). Individuals of *L. polyphyllus* are particularly vulnerable to sheep grazing during their first year (Ryan-Salter, 2019). Cattle may be used to graze (and trample) areas invaded by *L. polyphyllus* (Otte et al., 2002). However, as with other control measures, grazing can result in the unwanted dispersal of *L. polyphyllus*. In a feeding experiment, Otte et al. (2002) found that up to 20.4 % of fully ripened, hard seeds of *L. polyphyllus* were defecated undigested by sheep. These seeds showed a germination rate of 46 %, meaning that 9.4 % of ingested seeds survived the gut passage. As the retention times in the gut can be > 4 days (Otte et al., 2002), migratory sheep may potentially disperse *L. polyphyllus* seeds over several kilometers. However, this could be avoided given adequate management, i.e., grazing before seed production. Thus, Klinger et al. (2021) found only one individual of *L. polyphyllus* in the dung of migratory sheep between July and September. Furthermore, night penning of sheep outside of conservation sites may reduce propagule pressure on these sites.

Albeit *L. polyphyllus* is considered invasive and should thus not be actively promoted, a recent thesis (Ryan-Salter, 2019) focused on the species' value as forage in the invaded range in New Zealand. The study concluded that *L. polyphyllus* may be a suitable forage option for dryland, high-country farmers in NZ, as it can be used to considerably improve the productivity of areas of low soil fertility. However, establishing the species needs careful management, including seedbed preparation and specific grazing regimes during the first season. Once established, *L. polyphyllus* may become a persistent dryland species that will produce significant spring forage on high-country farms.

6.2.4. *Other forms of management*

The use of biological control of *L. polyphyllus* (see also Section 4.7) is, to our knowledge, scarcely addressed in the literature (e.g., Harvey et al., 1996). Root weevils and pathogens might reduce the growth of the species, but under which conditions (if any) and for which areas these agents may be used is uncertain. Tests and analysis of the consequences for both native and cultivated plants have to be taken into account as well as the costs and efforts compared to other control measures.

In species of the genus *Lupinus*, bicarbonate reduces root elongation (Peiter et al., 2001) and therefore, a lime treatment might be used to increase soil pH and to suppress the growth of lupines. However, evidence for the efficiency of liming is limited. Although wood ash reduced the germination and seedling growth of *L. polyphyllus* under laboratory conditions, it had no effect under field conditions even when large amounts of granulated ash were used (Tuominen, 2020).

Recently, studies have addressed the use of different heat treatments to kill seeds of *L. polyphyllus* (e.g., Blomqvist, 2021; Bitarafan et al., 2021; Hassani et al., 2021). These studies showed that owing to their thick seed coat, seeds of *L. polyphyllus* are rather insensitive to heat. About 81 ± 7 % (mean ± SD) of the seeds were viable after incubation at 60 °C for 15 min in the laboratory (data from Blomqvist, 2021) and soil steaming for 3 min at 98 °C was necessary to inhibit germination (<5 % of seeds still viable; Bitarafan et al., 2021). These results are also corroborated by Elliot et al. (2011) who found that a pre-treatment at 80 °C for 7 min did not affect germination of *L. polyphyllus.* Moreover, Hassani et al. (2021) reported that about one third of seeds were able to survive a one-month long treatment in a composting plant. In an experimental biogas plant, survival of seeds of *L. polyphyllus* after fermentation for 35 days depended on hardseededness (Baltes, 2020): hard, dark brown seeds showed 6.6 % germination at 37 °C and 2.5% at 50 °C, whereas soft, green or brownish seeds did not germinate at all.

7. Conclusions

Our review of *L. polyphyllus* highlights the difficulties of delimiting closely related taxa within the genus, which is caused by the lack of strong barriers to interbreeding. However, there appears to be consensus that the taxon *L. polyphyllus* var. *polyphyllus* has naturalized and is regionally invasive in temperate-humid climates worldwide. Data on its global distribution show that the species has successfully established in seven regions worldwide. The climatic niche of *L. polyphyllus* in the invaded range shifts towards higher summer precipitation and lower isothermality as compared to the native range, largely because the invaded range includes subcontinental regions of eastern Europe and western Siberia. Overall, *L. polyphyllus* may grow under a wide range of habitat conditions, i.e. in rather dry to wet, and moderately acidic to strongly acidic soils. The species has apparently a high resistance to drought and frost. A comparison of the species' indicator values suggests that *L. polyphyllus* occupies a gradient ranging from very nutrient poor sites in northern Europe to intermediate to rich sites in southern Europe. Also the communities, in which *L. polyphyllus* occurs, vary across Europe. In Central Europe the species has a stronghold in various types of meadows, pastures, herb stands, temperate thickets and scrubs, while in northern Europe the species mainly occurs in anthropogenic habitats along roads and railroads.

During the research for this review, we encountered some doubtful information about *L. polyphyllus* that uncritically reiterates in several fact sheets, reports and webpages. One such erroneous piece of information refers to the apparently very high longevity of seeds, which was taken from a modeling study on seed longevity under optimal dry and cold storage conditions for ex situ conservation. Similarly, there is some uncertainty and large variation in the literature concerning the actual lifespan of the species. Another piece of doubtful information is the deep rooting depth of *L. polyphyllus*, which apparently originates from an unpublished source and may rather characterize a maximum than a representative average value. Finally, *L. polyphyllus* is sometimes considered a "rhizomatous perennial" although it lacks true rhizomes. These points highlight some critical knowledge gaps, which partly relate to aspects of the species' life cycle and morphology that may be either time-consuming or labor-intensive to study.

We conclude that there is currently no evidence-based strategy for a cost-efficient management of *L. polyphyllus*. The development of such control measures is necessary because *L. polyphyllus* is among the most problematic non-native plant species in Europe with respect to environmental and socio-economic impacts. The species has significant negative effects on community structure, composition, species richness and diversity, especially in nutrient-poor habitats such as alpic mountain hay meadows, alpic mat-grass swards but also nutrient-poor road verges or riparian terraces. Finally, we also see critical knowledge gaps concerning the interrelationships between the species' future population dynamics, spread and ongoing climate warming.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2022.125715.

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