

Review

The Impact of Life History Traits and Defensive Abilities on the Invasiveness of *Ulex europaeus* L.

Hisashi Kato-Noguchi *  and Midori Kato

Department of Applied Biological Science, Faculty of Agriculture, Kagawa University,
Miki 761-0795, Kagawa, Japan

* Correspondence: kato.hisashi@kagawa-u.ac.jp

Abstract

Ulex europaeus L. has been introduced into many countries as an ornamental and hedgerow plant, and it often escapes its intended location, establishing dense, feral thickets. These thickets threaten the structure and function of native flora and fauna in areas where the plant has been introduced. Because of its invasive nature, *U. europaeus* is considered one of the world's 100 worst alien invasive species. It exhibits rapid growth, and high biomass accumulation with a high nitrogen fixation ability. Its flowering phenology depends on local conditions and population. It produces a large number of viable seeds and establishes extensive seed banks. These seeds remain viable for a long time due to physical dormancy. *Ulex europaeus* produces elaiosomes on the seed surface that are likely used solely for seed dispersal by ants. *Ulex europaeus* has a high level of genetic diversity due to its allohexaploid chromosome sets. This allows the plant to adapt to different habitats and tolerate various climate conditions. It can survive in areas with limited sunlight beneath tall plant canopies. Its shade tolerance surpasses that of other shrub species. *Ulex europaeus* produces several compounds, including quinolizidine alkaloids, monoterpenes, flavonoids, and cinnamic acid derivatives. These compounds play a role in defensive responses to biotic stressors, including pathogen infections, herbivorous insects, and neighboring plants competing for resources. These life history traits and defensive abilities may contribute to the expansion of *U. europaeus* populations into new habitats, enabling the plant to thrive as an invasive species. This is the first study to examine the invasiveness of *U. europaeus* in terms of its growth, reproduction, ability to adapt to different conditions, and defensive responses to biotic stressors.

Keywords: adaptation; allelochemical; flowering phenology; herbivory; pathogen; reproduction; seed bank; plasticity



Academic Editor: Michael Wink

Received: 22 October 2025

Revised: 17 November 2025

Accepted: 17 November 2025

Published: 20 November 2025

Citation: Kato-Noguchi, H.; Kato, M. The Impact of Life History Traits and Defensive Abilities on the Invasiveness of *Ulex europaeus* L. *Diversity* **2025**, *17*, 805. <https://doi.org/10.3390/d17110805>

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1. Introduction

Ulex europaeus L. subsp. *europaeus* (hereafter referred to as *Ulex europaeus*), belonging to the Fabaceae family, is an evergreen perennial shrub, commonly known as gorse, whin or furze. It grows into a bushy shrub, that is usually 1–4 m tall. Its mature stems are brown and thick, with numerous spines up to 5 cm long, as well as and short branchlets that also end in spines. The leaves are alternate and attach directly onto the stems. They are initially trifoliate and replaced by greenish, 1–3 cm long narrow spine-tipped phyllodes with maturity. The bright yellow flowers are terminal clusters, that are 1.5–2.5 cm long. They have a pea-flower structure consisting of a banner (the large upper petal), wings (the two lateral petals), and a keel (formed by the fusion of the two lower petals). This structure

contains a single carpel and ten stamens. The fruits are typical legume pods. Immature pods are green and soft, growing to be 1–2 cm in length. They then turn dark brown and harden. The pods contain 1–6 brown seeds. The seeds are 3 mm long, and oval or heart shaped. *Ulex europaeus* has a shallow extensive root system. It forms impenetrable, dense thickets. The life span of the species has been recorded as between 30 and 45 years [1–5] (Figure 1).

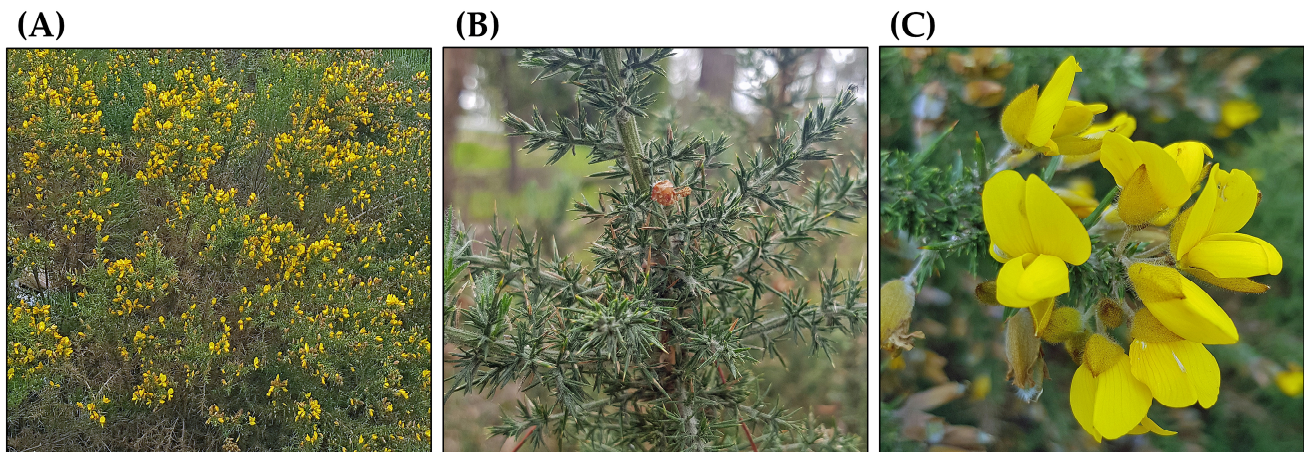


Figure 1. *Ulex europaeus*. (A): Stands, (B): Leaves, (C): Flowers. The photographs were gifted by Professor Singarayer Florentine.

Ulex europaeus is native to central and western Europe, including the British Isles, where it is prevalent in heathland and shrubland plant communities. This species also plays a role as a pioneer species in the early stages of plant succession. It has been planted in hedgerows to define boundaries, and as a ground cover plant. It has also been cultivated as fodder [1,6,7]. During the 19th and 20th centuries, *U. europaeus* was introduced into several other European countries, as well as into North America, South America, Oceania, Asia, and southern Africa and it was used as a hedgerow and as an ornamental plant. It has subsequently spread to over 50 countries [1,2,8–13]. A worldwide distribution map of *U. europaeus* was available [3,13].

Ulex europaeus was introduced to the Canterbury Plains in New Zealand for the purpose of creating hedgerows and windbreaks. These hedgerows and windbreaks were estimated to exceed 300,000 km in total length [14]. Due to its invasive nature, *U. europaeus* has spread beyond its original planting sites. It forms dense thickets along roadsides, in farmlands, grasslands, recently harvested woodlands, tree plantations, and in other disturbed areas, including national parks and protected areas [1–3,7]. Several sources of information are available for estimating the extent of its invasion. For example, it has spread to over 23 million hectares in Australia; 900,000 hectares in New Zealand; 100,000 hectares in Chile; 14,000 hectares in Oregon, USA; and 8000 hectares and 6000 hectares on the islands of Hawaii and Maui, respectively [1–3,15]. Additionally, *U. europaeus* has reduced agricultural areas on the South Island of New Zealand by 3.6% [16]. The annual management cost of *U. europaeus* was estimated to exceed 47 million U.S. dollars in New Zealand [3].

Feral colonies of *U. europaeus* have been reported to reduce the abundance and diversity of native plant communities, and to alter their species composition [1,2,17,18]. In the lowlands of New Zealand, *U. europaeus* replaced *Kunzea ericoides* (A.Rich.) Joy Thomps., the dominant native woody species that forms early-successional vegetation. Communities dominated by *Kunzea ericoides* have a different species composition and greater species diversity than communities dominated by *U. europaeus*. Several native plant species were

less abundant or absent in the *U. europaeus* community than in the *Kunzea ericoides* community. These differences persisted over time [19]. Native plant species did not become established until 25 to 30 years after the *U. europaeus* infestation, given that this species has an average lifespan of 25 to 30 years [20]. The *U. europaeus*-dominated community contains several naturalized woody plants, including *Sambucus nigra* L., *Crataegus monogyna* Jacq., *Cytisus scoparius* (L.) Link, and *Rubus erythrops* Edees & A. Newton. In the *U. europaeus* community on the South Island of New Zealand, the most frequent understory species were naturalized grasses and herbs, such as *Dactylis glomerata* L., *Agrostis* spp., *Anthoxanthum odoratum* L., and *Hypochaeris* spp. [20]. *Ulex europaeus* infestations significantly decreased the abundance of native plant species in forest-grassland mosaics of southern Brazil, including the protected shrub species *Daphnopsis racemosa* Griseb. and the protected grass species *Axonopus fissifolius* (Raddi) Kuhlm. (reported as *A. affinis*) and *Paspalum notatum* Flügge. The understory beneath *U. europaeus* canopies was less diverse and more homogeneous than in uninfested areas [21]. The *U. europaeus* infestations threaten the Garry oak (*Quercus garryana* Douglas ex Hook.) ecosystem in British Columbia, Canada. This ecosystem is home to several rare species, including *Triteleia grandiflora* Lindl. (reported as *T. howellii*), *Castilleja levisecta* Greenm., and *Balsamorhiza deltoidea* Nutt. [22,23]. *Ulex europaeus* infestations also threaten the endemic flora of the Hakalau Forest National Wildlife Refuge on the island of Hawaii [24].

The infestation of *U. europaeus* alters the population and species diversity of birds [25,26], reptiles [27], and insects [28], as well as small mammals, such as mice (*Mus musculus*) [25], by changing food availability, movement opportunities, nesting sites, and predator pressure. Although some populations of mammals and birds are larger in habitats infested with *U. europaeus*, the presence of this plant disrupts the ecological balance of these ecosystems, affecting the food chain and trophic levels. Replacing native vegetation with *U. europaeus* thus affects the structure and function of both the flora and fauna.

Like many other members of the Fabaceae family, *U. europaeus* fixes nitrogen. This nitrogen is released into the soil during the decomposition of its litter. This increases the nitrogen concentration in the surrounding soil [29,30]. Soil under *U. europaeus* stands has a higher nitrogen concentration than soil under non-nitrogen-fixing trees [31,32]. On average, invasive Fabaceae plants have been shown to increase soil nitrogen mineralization and nitrification by over 50% [33]. Some nitrogen dissolves into groundwater and is carried downstream by water flows [17,34–36]. An increase in nitrogen concentration has environmental implications. It alters ecosystem function [37,38]. *Ulex europaeus* modifies the fire regime by increasing the flammability of available fuels in an ecosystem. This occurs through enhanced fire ignition and spread, as well as increased fuel loads [39–43]. Therefore, *U. europaeus* infestations affect biotic processes by reducing plant diversity and richness, as well as altering food chains and trophic levels of organisms within ecosystems. *Ulex europaeus* infestations also impact abiotic processes by increasing nitrogen levels and altering the fire regime. Due to its invasiveness and impact, the International Union for Conservation of Nature (IUCN) has listed *U. europaeus* as one of the world's 100 worst invasive alien species [44].

Several reviews are available on management strategies for *U. europaeus*. Control measures include biological, ecological, physical, and chemical methods [1–3,45–47]. Additionally, the review examines the impact of *U. europaeus* on native ecosystems, agriculture, and the economy in areas where it has been introduced [18]. The life history traits of *U. europaeus*, including reproduction, growth, and adaptation to different environmental conditions, have been extensively investigated. Its ability to defend itself against herbivory and pathogen infection, as well as its allelopathic properties, have also been documented.

However, no review has focused on these characteristics of the species. This is the first review to address these characteristics.

2. Criteria for Selecting Literature

A combination of online search engines was used to search the literature: Scopus, ScienceDirect, and Google Scholar. The following terms were searched in relation to *U. europaeus*: adaptation, allelopathy, botany, climate, control, fauna, flora, flowers, fire, habitat, herbivory, impact, invasiveness, genetic diversity, growth, pathogens, plasticity, reproduction, seed banks, seed dispersal, soil, stress tolerance, sprouting, and temperature. We included these research papers as thoroughly as possible. However, we excluded those with unclear methods.

3. Growth

Sixty-four days after germination, *U. europaeus* reached a height of 11.7 cm and a dry weight of 24.7 g [48]. *Ulex europaeus* juveniles exhibited a higher early growth rate than other Fabaceae species, including *Acacia longifolia* (Andrews) Willd and *Cytisus grandiflorus* DC. [49]. Juvenile plants typically have trifoliate leaves that are replaced by narrow, spine-tipped phyllodes as the plants mature (Figure 1B). The plant undergoes rapid extension growth and frequent branching when it begins producing the phyllodes [50,51]. In New Zealand, the annual increase in stem diameter was 5 mm, and the annual increase in height was 20 cm. In 15 years, *U. europaeus* grew to heights ranging from 1.2 to 6 m and diameters ranging from 13 to 22 cm. The trees reached maximum heights of 7 m and maximum stem diameters of 22 cm [7,20]. The annual mean dry matter accumulation was 15,000 kg per hectare for the first 4–5 years and 10,000 kg per hectare for the next 7–10 years [52]. Twenty-five years after the infestation, the area contained 60,000 stems and a basal area of 51 m² per hectare. Very few native species were observed in areas infested with *U. europaeus* [20]. In Oregon, USA, the initial growth of *U. europaeus* was slow. After two to three years, its growth accelerated vertically and laterally, reaching heights of 2 m within 8–10 years [7].

Ulex europaeus establishes a mutualistic relationship with nitrogen-fixing rhizobia, including *Bradyrhizobium* spp. [24,53,54]. All *U. europaeus* plants, including those younger than six months, were found to be nodulated with rhizobia in the rhizosphere on Hawaii Island. The endemic Fabaceae species of Hawaii, *Acacia koa* A.Gray, also mutualizes with *Bradyrhizobium* spp. However, the population density of *Bradyrhizobium* spp. was much higher in the *U. europaeus* rhizosphere than in the *Acacia koa* rhizosphere [24]. The estimated annual rate of nitrogen fixation is 100–200 kg per hectare [52]. *Cytisus scoparius* is known to be an effective nitrogen fixer. It fixes 111 kg of nitrogen per hectare annually [55]. Therefore, the nitrogen fixation capability of *U. europaeus* is similar to or greater than that of *Cytisus scoparius*.

Ulex europaeus exhibits rapid growth and high biomass accumulation. It also has a high colonization rate of rhizobia and exhibits high nitrogen fixation. This ability to fix nitrogen may contribute to its rapid growth and high biomass accumulation. Rapid growth also requires effective photosynthesis [56,57]. However, information about the photosynthetic ability of *U. europaeus* is unclear.

4. Reproduction

4.1. Seed Production and Dispersal

Ulex europaeus reaches reproductive maturity two to three years after germination [1–3]. Flowering phenology varies by region and population. In its native range, it flowers from September to June, with a peak in April in Brittany, France. Flowering durations range from

one to six months within and among populations. Spring flowers produce a large number of seeds, while winter flowers produce a smaller number. However, seed predators attack spring seeds more intensely than winter seeds. This polymorphism in flowering time and duration is thought to be caused by high genetic variation of the species among populations [58,59]. In the UK, it flowers year-round, with the most flowers appearing in April and May [60]. In its introduced range, *U. europaeus* blooms year-round in Sri Lanka [61]. In Hawaii and Réunion, an island in the Indian Ocean, it primarily blooms in winter [62,63]. In New Zealand, flowering occurs between autumn and spring [64]. In Brazil, it flowers between autumn and winter or year-round [65]. In Australia, flowering occurs between spring and early summer, as well as between autumn and early winter [66]. In temperate climate regions, the number of pollinators, such as bees and bumblebees, decreases in winter months. Flowers remain open longer to increase pollination opportunities [67]. Its ability to adjust its flowering period in relation to local conditions may explain how it is able to invade different regions.

Ulex europaeus produces a large number of viable seeds. Its flower structure prevents it from producing seeds without pollination by honeybees and similar insects (Figure 1C) [65,68]. This species produces viable seeds through insect-mediated self-compatibility. However, outcrossing produces more viable seeds than self-pollination in both native and introduced ranges. Nevertheless, plants from introduced ranges produce more seeds than those from native ranges [68].

The seeds are contained within leguminous pods. Dehiscent pods can eject seeds up to 5 m from the mother plant [69]. Wind gusts can carry pods containing seeds up to 50 m away [70]. *Ulex europaeus* produces a white tissue, called an elaiosome that adheres tightly to one end of the seed surface [2,4]. Elaiosomes are rich in lipids and proteins, which attract ants that carry the seeds to their nests. This contributes to the secondary dispersal of the seeds [65,71,72]. Photos of elaiosomes can be found in the literature [2,4]. Seeds of *U. europaeus* are carried short and long distances by birds and small mammals, such as mice (*Mus musculus*), as well as by water flow, vehicles, agricultural equipment and humans [7,25,69].

The flowering phenology of *U. europaeus* varies depending on local conditions and population. The plant produces a large number of viable seeds primarily through outcrossing. These seeds are dispersed by the dehiscent nature of the pods, as well as by wind, water, ants, birds, mammals, and human activity. This occurs over short and long distances.

4.2. Seed Bank and Germination

Ulex europaeus forms large seed banks. In New Zealand, the average seed bank density was 5446 seeds per m², ranging from 133 to 20,742 seeds per m². Mean seed densities were recorded as 1357 seeds per m² in France, 2140 seeds per m² in Sri Lanka, and 19,960 seeds per m² in Réunion [61,73,74]. Large plants produced a relatively large seed banks [74]. Over 90% of the seeds were found within the top 6 cm of soil [73]. Seed viability decreases over time after deposition. Seed banks had higher viability when seeds were buried deeper in the soil. Ten and 20 years later, 10% and 1% of the seeds buried 5 cm deep remained viable, respectively [75]. However, considering the density of the seed bank, even 1% is sufficient for the regeneration of *U. europaeus*. Following the complete removal of *U. europaeus* stands, regeneration occurred through germination from the seed banks. The regeneration rate was 200 and 350 seedlings per m² at 3 and 15 months after the removal, respectively [76].

The seeds of *U. europaeus* have hard, impermeable seed coats and exhibit physical dormancy. This suggests that the seeds have the potential to persist in the seed bank. Germination rate increased with mechanical and chemical scarification, as well as thermal shock treatments [7,77–79]. The germination rate of scarified seeds from both France

(the native range) and Réunion (the introduced range) was over 90%. In contrast, the germination rate of unscarified seeds from France and Réunion was 0–10% and 10–60%, respectively. Seeds from Réunion also exhibited higher germination velocity [79]. The difference in germination patterns between the native and introduced ranges is primarily due to the interaction between genetic and environmental factors [80,81]. The hard seed coats of *U. europaeus* also protect the seeds from predators. Their physical dormancy contributes to the dispersal, persistence, and establishment of this invasive plant species over time and space [82–85].

Thermal treatments at temperatures between 60 and 100 °C stimulated the germination of *U. europaeus* seeds. These seeds can survive thermal treatments up to 150 °C [74]. The temperature of wildfires consuming bush and grass is usually around 200 °C. Severe fires can reach temperatures as high as 800 °C [86,87]. During a wildfire in the forest of Susa Valley, Italy, the maximum soil surface temperature was 165.5 °C. In contrast, the maximum temperatures 2 cm and 6 cm below the soil surface were 69.7 °C and 65.4 °C, respectively [88]. During fires in *U. europaeus* stands, temperatures 10 cm above the soil surface ranged from 300 °C to 1000 °C. In contrast, temperatures below a 4 cm soil depth remained below 100 °C [89]. Therefore, wildfires may stimulate germination in seed banks rather than killing *U. europaeus* seeds. Fifteen months after a wildfire in southern New Zealand, *U. europaeus* seedlings grew to 65 cm in height. This post-fire growth rate was faster than that of other native shrub species, including *Coprosma ciliata* Hook.f., *Leptospermum scoparium* J.R.Forst. et G.Forst., and *Ozothamnus leptophyllus* (G.Forst.) Breiwt. & J.M.Ward [70]. Due to its high oil content, *U. europaeus* increases flammability, fire development, and fuel loads, thereby modifying the fire regime. Wildfires involving this plant can significantly damage existing plant communities and often leave behind bare fields [40–43,90]. As previously mentioned, wildfires stimulate the germination and growth of *U. europaeus*. Therefore, wildfires may contribute to *U. europaeus* becoming the dominant species in post-fire vegetation [91].

Ulex europaeus forms a large seed bank. The seeds exhibit physical dormancy, which protects them and enables them to survive for extended periods. This dormancy also promotes the plant dispersal and establishment over time and space. Wildfires stimulate germination and enhance its dominance in post-fire vegetation.

4.3. Resprouting

Ulex europaeus sprouts from its stem tissue when its above-ground parts are damaged by fire or mechanical means, such as cutting [1,2,7]. Cutting treatments of *U. europaeus* result in sprouting from the remaining basal parts of the stems within three weeks [92]. One year after cutting, 84% of *U. europaeus* produced sprouts. Their aerial dry biomass ranged from 55 to 3500 g per plant [93]. Within four months after a wildfire, *U. europaeus* also sprouted from the remaining basal parts of its stems. Ten months after the fire, 46% of the plants produced sprouts [89]. These sprouts reached heights of 30 and 90 cm at 10 and 15 months after the fire, respectively, in southern New Zealand. This growth rate was higher than that of other native shrub species [70]. The annual biomass accumulation was 246 and 137 g per m² in the first and second years after the fire, respectively. These values represented 90% and 85%, respectively, of the total annual biomass accumulation of all plant species in burned areas during the first and second years. The annual accumulation of the sum of nitrogen, phosphorus, and potassium in *U. europaeus* accounted for 90–92% and 86–88%, respectively, of the total annual accumulation of the sum of these nutrients in all plant species during the first and second years [94]. Therefore, most biomass accumulation and nutrient uptake after the fire was due to *U. europaeus*. Thus, wildfires contribute to landscapes dominated by *U. europaeus* through sprouting from remaining stems.

5. Adaptivity

5.1. Genetic Variation

The *Ulex* genus comprises over 15 species. Most *Ulex* species are only found on the Iberian Peninsula. This area is believed to be the primary center of diversification for the genus [95]. The *Ulex europaeus* species consists of two subspecies: *Ulex europaeus* subsp. *europaeus* and *U. europaeus* subsp. *latebracteatus* (Mariz) Rothm. *Ulex europaeus* subsp. *europaeus* is an allohexaploid species with $2n = 96$ chromosomes. In contrast, *U. europaeus* subsp. *latebracteatus* is a tetraploid species with $2n = 64$ chromosomes [96–98]. *Ulex europaeus* subsp. *europaeus* is the only invasive species in the genus of *Ulex* species. *Ulex europaeus* subsp. *latebracteatus*, on the other hand, is only found in Spain, Portugal, Madeira, and France, and is not considered an invasive species [99]. The allohexaploid of *U. europaeus* subsp. *europaeus* evolved from the hybridization of two distinct lineages between *U. europaeus* subsp. *latebracteatus* and *Ulex minor* Roth, a diploid species with $2n = 32$ chromosomes, over the past one to two million years. *Ulex europaeus* subsp. *europaeus* (hereafter again referred to as *Ulex europaeus*) exhibits a high level of genetic diversity due to its allohexaploid chromosome sets. These chromosome sets originated from two different species, and each of its six chromosomes can carry up to six different alleles at each locus. This genetic diversity may contribute to the invasive nature of the species, including its ability to adapt to different climates and habitats [96–98]. Allopolyploidy provides high environmental tolerance and makes the species invasive [100–103].

Within its native range, the neutral genetic diversity of *U. europaeus* decreases from Spain to France, and from France to Scotland. Its naturalization in northern Europe has also been accompanied by a decrease in the neutral genetic diversity [97,98]. This south-to-north gradient suggests that the Iberian Peninsula is the origin of species of *U. europaeus* [95]. With the exception of Chilean populations, the introduced populations are genetically closer to the French and Scottish populations than to the Spanish populations. The populations in New Zealand, California, and the islands of Hawaii and Maui are also genetically similar [104]. These genetic similarities may reflect the origins of these populations. For instance, the British introduced *U. europaeus* to New Zealand before 1835 and to the West Coast of the USA before 1912. The Chilean population may have multiple origins, including Spain and Germany [105–108]. These populations, including the Chilean population, still exhibit high levels of genetic diversity, comparable to those in France, Scotland, UK, Spain and Germany [97,98]. This suggests that most introduced populations have not undergone a significant population bottleneck [109,110]. Therefore, the evolutionary potential of the introduced populations may be similar to that of the native populations [97,98]. This high evolutionary potential of the introduced populations is consistent with the high degree of phenotypic plasticity described in Section 5.2.

5.2. Habitats and Climate

Ulex europaeus thrives in open and/or disturbed areas, such as overgrazed pastures, abandoned crop fields, roadsides, and post-fire communities. It also grows in coastal grasslands, dunes, heathlands, forest understories and edges, and on hillsides [111–114]. Riparian and ravine areas, where water flow carries its seeds are also suitable habitats [113]. *Ulex europaeus* was often used to create hedgerows and windbreaks. Since then, it has spread into surrounding areas, including pastures, crop fields, and roadsides [1,6,7]. *Ulex europaeus* is found at low elevations. However, its range extends from sea level to 400 m in California [115]; 800 m in New Zealand [116]; 1000 m in Chile [117]; 2300 m in Hawaii [35]; and 4000 m in the Colombian Andes [118].

The suitable annual mean temperature range for *U. europaeus* is from 4 °C to 22 °C [7,119]. However, it is found in areas where the mean maximum temperature of

the hottest month exceeds 32 °C and the mean minimum temperature of the coldest month is below −6 °C [7,46,119,120]. The plants sustained severe frost damage during a winter when temperatures dropped below −20 °C. They fully recovered within two years [1]. The suitable annual precipitation range for *U. europaeus* is 300 mm to 1500 mm [7,46,119]. However, the species can tolerate dry conditions. Its ability to withstand periods of reduced precipitation due to two features: its narrow spine-tipped phyllodes (Figure 1B), which reduce the leaf surface area and perspiration; and its shallow, extensive root system, which allows for efficient water absorption [1,119,120]. *Ulex europaeus* grows in various soil types, including sandy, clay, and loam soils, as well as nutrient-poor soils [1,7]. It tolerates a pH as low as 3.5 to 4.5 [24,121,122]. It thrives in well-drained soils, and can tolerate areas with a high water table, such as riparian zones [114].

Ulex europaeus is a light-demanding pioneer shrub species [20]. These pioneer woody shrubs are among the first plants to become established in forests during the process of plant succession. Most pioneer shrubs disappear when successional tall plants occupy the forest canopy and decrease sunlight penetration [123]. However, *U. europaeus* can survive in these successional forests, where shrubs have less access to light [124,125]. Under 40% and 4% full-light conditions, *U. europaeus* seedlings survived at rates of 98% and 80%, respectively. The mean photosynthetic photon flux was measured at 2210 $\mu\text{mol}/\text{m}^2/\text{s}$ at midday under full-light conditions during the experiments. The photosynthetic photon flux at 4% of full-light was only 353 $\mu\text{mol}/\text{m}^2/\text{s}$. The survival rates of other Fabaceae shrub seedlings under 4% of full-light condition were 2% for *Retama sphaerocarpa* (L.) Boiss., 10–15% for *Spartium junceum* L., *Genista scorpius* (L.) DC., and *Cytisus scoparius* (L.) Link, and 40% for *Coronilla juncea* L. [126]. Thus, *U. europaeus* has much higher shade tolerance than other species of Fabaceae shrubs. These six species, including *U. europaeus*, exhibited variation in the ratio of leaf-to-total photosynthetic area (including leaves and green stems). In deep shade conditions, increasing the ratio of leaf-to-total photosynthetic area is necessary for survival. Under these conditions, *U. europaeus* seedlings increased this ratio much more than other species [126].

Ulex europaeus shrubs located in shaded areas under *Pinus pinaster* Aiton forests had longer green stems and thinner branches, containing spine-tipped phyllodes. These green stems, branches and phyllodes comprise the main photosynthetic tissue of the mature plants. Under deep shade conditions, the species reduces pod and seed production and allocates more biomass to photosynthetic tissues than to other tissues [124,125]. During the seedling stage, *U. europaeus* increases the ratio of leaf-to-total photosynthetic area under deep shade conditions. As the species matures, it allocates more biomass to produce longer, green stems and thinner branches with phyllodes under these conditions. *Ulex europaeus* leaves are trifoliolate during the seedling and juvenile stages. They become narrow, spine-tipped phyllodes with maturity (Figure 1B). These morphological alterations enable the species to adapt to deep shade conditions.

These investigations revealed that *U. europaeus* exhibits high genetic diversity due to its allohexaploid nature. This diversity persists in introduced ranges. *Ulex europaeus* exhibits high plasticity in response to various environmental conditions, including temperature, precipitation, soil types, and light availability. It is a light-demanding pioneer shrub species. However, it tolerates light-limiting conditions and survives in successional forests.

6. Defensive Response to Biotic Stressors

Biotic stressors interfere with the germination, growth and reproduction of host plants. These stressors also force significant selective pressure on the distribution, abundance, and survival of host plants. These stressors include pathogens, herbivores, and neighboring plants that compete for resources [127–133]. Several noxious invasive plant species have

been reported to exhibit defensive responses to biotic stressors. These responses may contribute to their invasive nature [134,135]. *Ulex europaeus* has also been reported to respond defensively to biotic stressors and to contain related defensive compounds.

6.1. Defensive Compounds Protect Against Pathogens and Herbivores

Ethanol and ethyl acetate extracts from the leaves and branches of *U. europaeus* suppressed the growth of the pathogen bacteria; *Pectobacterium carotovorum* and *Rhizobium radiobacter*, and pathogen fungi; *Botrytis cinerea* and *Phytophthora cinnamomi* [136]. *Pectobacterium carotovorum* and *Rhizobium radiobacter* cause soft rot and crown gall diseases, respectively, in a wide range of host plant species [137,138]. *Botrytis cinerea* causes gray mold disease in over 200 host plants [139]. *Phytophthora cinnamomi* is distributed worldwide and causes dieback and root rot diseases in a wide variety of host plants [140]. This fungus is also listed as one of the world's 100 worst invasive alien species by the IUCN [44]. The main compounds in these extracts are lupeol and β -amyrin (both triterpenes), neophytadiene (a diterpene), sitosterol (a phytosterol), and *dl*- α -tocopherol (vitamin E) [136]. These compounds have been reported to exhibit pharmacological activity. However, they may not be responsible for the defensive response [140–144].

Ulex europaeus contains several quinolizidine alkaloids, including lupanine (compound 1 in Figure 2), cytisine (compound 2), anagyrine (compound 3), 5,6-dehydrolupanine (compound 4), *N*-methylcytisine (compound 5), *N*-acetylcytisine (compound 6), *N*-formylcytisine (compound 7), rhombifoline (compound 8), and baptifoline (compound 9) [144–147].

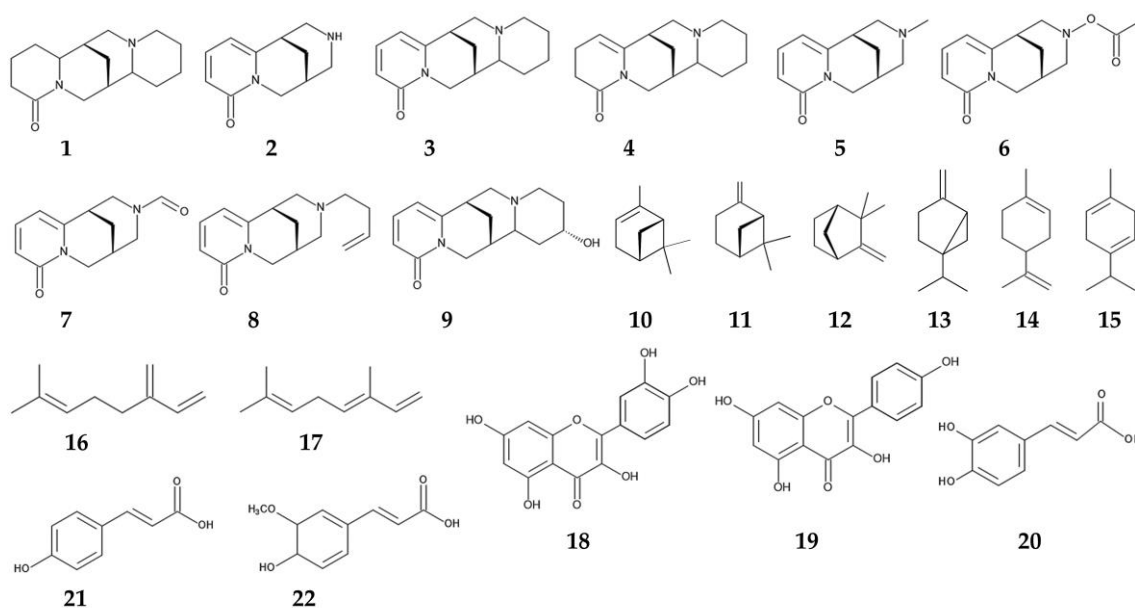


Figure 2. Compounds involved in defense functions of *Ulex europaeus*. Quinolizidine alkaloid; 1: Lupanine, 2: Cytisine, 3: Anagyrine, 4: 5,6-Dehydrolupanine, 5: *N*-Methylcytisine, 6: *N*-Acetylcytisine, 7: *N*-Formylcytisine, 8: Rhombifoline, 9: Baptifoline. Monoterpene; 10: α -Pinene, 11: β -Pinene, 12: Camphene, 13: Sabinene, 14: Limonene, 15: γ -terpinene, 16: Myrcene, 17: *trans*-Ocimene, Flavonoid; 18: Quercetin, 19: Kaempferol. Cinnamic acid derivatives; 20: Caffeic acid, 21: Coumaric acid, 22: Ferulic acid.

In particular, lupanine, increased the mortality of the larvae of the gorse seed weevil *Exapion ulicis* and the gorse pod moth *Cydia succedana* [146,148]. This compound also suppressed the infestation by the rust fungal pathogen *Uromyces genistae-tinctoriae* [146]. Cytisine increased the mortality of the fall webworm moth *Hyphantria cunea* larvae, the mustard aphid *Lipaphis erysimi*, and the vetch aphid *Megoura japonica* [149–151]. Anagyrine

causes crooked calf disease in sheep and cattle [152,153]. Other quinolizidine alkaloids; 5,6-dehydrolupanine, *N*-methylcytisine, *N*-acetylcytisine, *N*-formylcytisine, rhombifoline, and baptifoline are also toxic to mammals, and may deter herbivory by them as well [154–157]. Quinolizidine alkaloids are toxic to fungi and herbivores. They act as neurotoxins that can bind to either the acetylcholine receptor or the muscarinic acetylcholine receptor [155–157]. Therefore, they can serve as defensive compounds against herbivores. The concentration of anagryrine was highest in *U. europaeus* shoots, and followed by *N*-acetylcytisine, cytisine and lupanine [146]. However, the concentrations of these quinolizidine alkaloids varied within and among *U. europaeus* populations, and did not differ significantly between the native (Brittany and Scotland) ranges and introduced (New Zealand and Réunion) ranges of *U. europaeus* [146]. Thus, the sensitivity of herbivore populations in the native and introduced ranges should be investigated in the future.

Ulex europaeus emits several monoterpenes as volatiles, including α -pinene (compound 10), β -pinene (compound 11), camphene (compound 12), sabinene (compound 13), limonene (compound 14), γ -terpinene (compound 15), myrcene (compound 16), and *trans*-ocimene (compound 17) [158,159]. Total monoterpene emissions ranged from 0.15 mg of carbon per m² per hour in November to 0.89 mg of carbon per m² per hour in July. These emissions were measured in hill grassland in Wray, and in coastal heathland in Kelling Heath, both of which are located in England. The main monoterpenes emitted from *U. europaeus* in both areas were α -pinene and *trans*-ocimene [159]. These volatile monoterpenes are known to be emitted in response to attacks by herbivorous insects and to induce defensive responses such as increased cell wall strength and the production of toxic substances through the jasmonic acid pathway [160–162]. *Ulex europaeus* also contains several flavonoids, including quercetin (compound 18) and kaempferol (compound 19) [163]. These flavonoids have been reported to act as defensive compounds against pathogen infection [164–166]. Therefore, these quinolizidine alkaloids, monoterpenes and/or flavonoids can protect against insect and mammal attacks, as well as pathogen infections. These defensive compounds may contribute to the distribution, abundance, survival, and invasive nature of the species. However, these investigations were primarily conducted under laboratory conditions. The defensive responses of *U. europaeus* in the field remain unclear.

6.2. Defensive Compounds Protect Against Competing Plant Species

Plants compete with neighboring plants for resources, such as nutrients and water. Allelopathy is a mechanism that gives plants a competitive advantage over neighboring plants. This function involves releasing allelochemicals into the rhizosphere soil and surrounding atmosphere. These released allelochemicals suppress the germination and growth of the competitive plants, while giving host plants an advantage in acquiring resources [167–172]. Several invasive plant species have been reported to exhibit allelopathy by releasing allelochemicals [173–176]. These plants produce and store allelochemicals in the various parts, including leaves and flowers, which makes them extractable [177–180].

Aqueous extracts from the above-ground parts of *U. europaeus* suppressed the growth of three woody plant species *Quillaja saponaria* Molina (Quillajaceae), *Peumus boldus* Molina (Monimiaceae) [181], and *Cryptocarya alba* (Molina) Looser (Lauraceae) [182]. Leaf leachates and aqueous extracts of leaf litter from *U. europaeus* suppressed the germination of *Lactuca sativa* L. (Asteraceae) and *Abutilon theophrasti* Medic. (Malvaceae), respectively [183,184]. This inhibitory activity of the leaf leachates was determined using a sandwich method with two layers of agar [185]. Aqueous extracts of flowering branches, as well as the soil mixed with chopped flowering branches, of *U. europaeus* suppressed the growth of *Amaranthus retroflexus* L. (Amaranthaceae) [186,187]. Volatile compounds from flowering

U. europaeus also suppressed the growth of *Amaranthus retroflexus* and *Digitaria sanguinalis* (L.) Scop. (Poaceae) [188,189]. These findings suggest that *U. europaeus* is allelopathic and contains allelochemicals.

The leaves, flowers and flowering branches of *U. europaeus* contain cinnamic acid derivatives, including caffeic acid, coumaric acid, and ferulic acid [163,188,189]. These derivatives are synthesized from phenylalanine through the shikimic acid pathway. These compounds have been identified in a wide variety of plant species [190,191], and have been reported to act as allelochemicals [192–194]. They alter the plasma membrane structures, and reduce the transmembrane electrochemical potential of plant cells. These compounds also suppress the activity of enzymes involved in essential metabolic processes, such as cell division, photosynthesis, respiration, protein synthesis, and phytohormone synthesis [195–197]. As described in Section 6.1, *U. europaeus* contains flavonoids; quercetin and kaempferol, and emits monoterpenoids as volatiles; α -pinene, β -pinene, camphene, sabinene, limonene, γ -terpinene, myrcene, and *trans*-ocimene [158,159,163]. These flavonoids and monoterpenes have been reported to act as allelochemicals in various plant species [198,199], including several invasive plant species [200–205]. Therefore, the compounds identified in *U. europaeus* may act as allelochemicals, suppressing the germination and growth of neighboring plants and providing *U. europaeus* with a competitive advantage. However, allelochemicals only work after they are released into the rhizosphere soil and surrounding atmosphere. The concentrations of these compounds in the rhizosphere soil and surrounding atmosphere are unclear.

7. Synthesis

According to the existing literature, *U. europaeus* was introduced to many countries as a hedgerow and ornamental plant. However, it often escapes these locations and becomes established impenetrable, dense thickets in surrounding areas, such as pastures, crop fields, and roadsides. It has also spread to coastal vegetation, riparian zones, heathlands, and forest understories. The infestation of *U. europaeus* threatens the structure and function of native flora and fauna as a noxious invasive species.

Table 1 shows the main characteristics of *U. europaeus* invasiveness and includes relevant references. *Ulex europaeus* exhibits rapid growth, and high biomass accumulation, as well as a high nitrogen fixation ability. It reaches reproductive maturity early. The flowering phenology of *U. europaeus* depends on local conditions and populations. This species produces a large number of viable seeds, which establish a substantial seed bank. The seeds exhibit a physical dormancy and remain viable for an extended period. *Ulex europaeus* produces elaiosomes that it attaches to the surface of its seeds. These elaiosomes stimulate the seed dispersal by ants. Seeds are also dispersed by birds, small mammals, water flow, and human activity. *Ulex europaeus* establishes more quickly in a post-fire community than other native plants due to its ability to germinate and resprout after a fire. It also alters the fire regime by increasing flammability, fire development, and fuel loads.

Ulex europaeus has very high genetic diversity and significant evolutionary potential due to its allohexaploid chromosome sets. It can adapt to the different habitats and tolerate various climate conditions, including low temperatures and drought. *Ulex europaeus* is a light-demanding pioneer shrub species. However, it can tolerate light-limiting conditions, such as those under the canopy of successional tall plants. Its shade tolerance exceeds that of other native shrub species. The morphological alteration of trifoliate leaves into narrow, spine-tipped phyllodes may enable the species to adapt to deep shade and drought conditions.

Table 1. The mechanisms of *Ulex europaeus* contribute to its invasiveness.

Characteristic	Reference
Growth ability	
➤ Rapid growth and high biomass accumulation	[7,20,48–51]
➤ High nitrogen fixation with high mutualism with nitrogen-fixing rhizobia	[24,52]
Reproduction	
➤ Early reproductive maturity	[1–3]
➤ Different flowering phenologies in different conditions and populations	[58–67]
➤ Production of a large number of viable seeds	[65,68]
➤ Production of elaiosomes only for seed dispersal by ants	[2,4]
➤ Large seed bank	[61,73,74]
➤ Seed longevity due to physical dormancy	[73–79]
➤ Alteration of the fire regime and rapid establishment in post-fire communities	[39–43,70,73,91–94]
High adaptability to different conditions	
➤ High genetic diversity due to its allohexaploidy	[95–98]
➤ Wide range of habitats	[1,6,7,35,111–118]
➤ Tolerance to low temperatures and drought	[1,7,46,119,120]
➤ Tolerance to shade conditions	[124–126]
➤ Morphological leaf alterations with maturity	[1–3,50]
High defense ability against pathogens, herbivory, and competitive plant species	
➤ Protection against pathogens and herbivory	[136,145–147,157,159,163]
➤ Protection against competitive plant species	[158,159,163,182–184,186–189]

Ulex europaeus produces compounds involved in the defensive responses to biotic stressors, such as pathogens, herbivores, and neighboring plants that compete for resources. The quinolizidine alkaloids; lupanine and cytisine increase the mortality of herbivorous insects, and protect against infection by pathogenic fungi. Other quinolizidine alkaloids are toxic to herbivorous mammals. *Ulex europaeus* emits several monoterpenes as volatiles to protect against herbivorous insects. The plant also produces flavonoids to protect against pathogen infection. *Ulex europaeus* produces several cinnamic acid derivatives as allelochemicals (Figure 2). The aforementioned monoterpenes and flavonoids also act as allelochemicals. These compounds suppress the germination and growth of neighboring plants, which gives *U. europaeus* an advantage in acquiring resources.

In summary, this species exhibits high growth and reproductive rates. It is highly adaptable to different habitats, climates, and forest undergrowth. It also exhibits defensive responses against herbivory, pathogens, and competition for resources with other plants. These characteristics may contribute to the expansion of the *U. europaeus* population in the introduced ranges. Other noxious invasive plant species, such as *Arundo donax* L., *Bidens pilosa* L., *Imperata cylindrica* L., *Lantana camara* L., *Leucaena leucocephala* (Lam.) de Wit, *Mikania micrantha* Kunth, and *Mimosa pigra* L. also exhibit a high growth and reproductive capacities, high adaptability to different habitats, high defensive abilities against herbivory, pathogens, and neighboring plants [169,173,175,176,192–194]. Therefore, these characteristics may be important to be invasive plant species. Additionally, most invasive plant species grow alongside other plant species in their native ranges without endangering them. These invasive plants may share a coevolutionary history with these plant species. However, they threaten native plant species in their introduced ranges because they lack a coevolutionary history, as described in relation to invasive plants and herbivores [206–208].

This review may provide insight into effective eradication methods within ecosystems. *Ulex europaeus* escapes cultivation, and establishes dense thickets. Therefore, its invasive nature should be considered when handling it. Many investigations have been conducted on the life history traits of *U. europaeus*. However, information on its defensive response to biotic stressors under field conditions is limited. Further research should investigate the concentrations of putative allelochemicals in the rhizosphere soil and surrounding atmosphere should be investigated. The defensive responses of *U. europaeus* have primarily

been investigated under laboratory conditions. These responses should also be investigated under field conditions.

Funding: This research received no external funding.

Institutional Review Statement: Not applicable.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Conflicts of Interest: The authors declare no conflicts of interest.

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