



Monographs on Invasive Plants in Europe N°7: *Rhododendron ponticum* L.

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ABSTRACT

This report presents information on all aspects of the biology, ecology and invasion behaviour of *Rhododendron ponticum* L., particularly *R. ponticum* subsp. *baeticum* (Boiss. & Reut.) Hand.-Mazz. The main topics presented are: taxonomy, distribution, history of introduction and spread, ecology, biology, impacts, and management. The subspecies *baeticum* is native to the Iberian Peninsula, where it is close to extinction. This shade-tolerant evergreen shrub has been broadly introduced throughout Europe since the 18th century, mainly for ornamental purposes. The invasive taxon likely results from artificial introgressive hybridization with the Appalachian species *R. catawbiense* Minchx. It is now naturalized in many countries across western Europe and has become a serious invader in the British Isles. In continental Europe, it mostly invades forest ecosystems of the Atlantic domain, especially on acidic, nutrient-poor but moist soils. *R. ponticum* subsp. *baeticum* has perfectly adapted to the humid temperate climate of these regions. As a shade-tolerant species, it can spread out its dense canopy below tree canopies, thereby shading out most herb species and tree seedlings and saplings. Its thick litter likely impacts soil chemical and biological features and hence alters ecosystem processes. Though it produces thousands of seeds, the species mostly propagates vegetatively via layering and forms extended clonal thickets. Long-distance dispersal occurs via seeds, but those can only germinate on moss mats, decaying wood and bare soil and seedlings are very vulnerable to drought. The shrub is also known to be a reservoir for phytopathogenic oomycetes of the genus *Phytophthora*, including *P. ramorum* and *P. kernoviae*. *R. ponticum* subsp. *baeticum* invasion is an emerging threat to natural habitats and their associated fauna and flora in western continental Europe. Control is still challenging since management operations are not only expensive and time-consuming but also poorly effective due to vigorous resprouting from stumps after cutting and herbicide resistance.

KEYWORDS

Invasive alien species;
environmental impacts;
species distribution;
reproduction strategies;
management

Taxonomy

Names and classification

Scientific name: *Rhododendron ponticum* L. 1762

Synonym: *Azalea arborea* L., *Azalea lancifolia* (Moench) Kuntze, *Anthodendron ponticum* (L.) Rchb., *Hymenanthus pontica* (L.) H.F. Copel., *Rhododendron adansonii* E.-A. Bauman, *Rhododendron catesbaei* J.Forbes, *Rhododendron catesbaeum* Dum. Cours., *Rhododendron deciduum* Andrews ex Steud., *Rhododendron hyacinthiflorum* Steud., *Rhododendron lancifolium* Moench, *Rhododendron lowei* Loudon, *Rhododendron obtusum* P. Watson, *Rhododendron odoratum* Lodd. ex Steud., *Rhododendron ponticum* var. *obtusum* (P. Watson) G. Don, *Rhododendron speciosum* Salisb.

Subspecies:

- Scientific name: *Rhododendron ponticum* subsp. *baeticum* (Boissier & Reuter) Handel-Mazzetti 1909

Synonym: *Rhododendron baeticum* Boiss. & Reut. 1856, *Rhododendron ponticum* var. *baeticum* (Boiss. & Reut.) Wilk.

- Scientific name: *Rhododendron ponticum* subsp. *ponticum*

Taxonomic position (APG IV): Class: Eudicots, Order: Ericales, Family: Ericaceae, Tribe: Rhodoreae

Common names: adelfeira, loendro, loendreira [PT], azalea de Andalucia, jaranzo, ojaranzo [ES], rododendro [ES, PT], erroiz (Euskera), rododendron, rododendre pòntic (Catalan), rhododendron [FR, GB], Iberian rose bay, common rhododendron [GB], Pontian rhododendron [GB, NZ], Pontische Alpenrose [DE], Rhododendron des parcs, rhododendron pontique, rhododendron de la mer Noire [FR], Pontic rhododendron, wild rhododendron [NZ], kumar, kara kumar, kara komar, kara ağu [TR].

EPPO code: RHOPO (*Rhododendron ponticum*) and RHOPB (*Rhododendron ponticum* subsp. *baeticum*).

Morphological description

Species description

Rhododendron ponticum is a branching shade-tolerant shrub, reaching 2–8 m height, depending upon environmental conditions (wider spread in the shade or wet areas than in open or dry areas, where it forms more compact shrubs) (Cross 1975; Çolak et al. 1998). It particularly appreciates acidic soils and mild moist conditions (Barron 2007). It may grow to form individual shrubs or thick impenetrable thickets (Barron 2007).

This long-lived shrub is conforming to the architectural model of Scarrone (Tison and de Foucault 2014): its growth is first monopodial, and subsequently sympodial. The mature plant is composed of several major axes (Cross 1975) with a complicated branching (Nadezhkina et al. 2004). It spreads laterally rather than growing vertically. The weight of branches makes them collapse when not supported by neighbouring trees (Rotherham 1983).

The root system forms a dense and compact mat, mostly superficial, which may even be limited to the bryophyte mat in young plants, with much branched and fibrous roots (Cross 1975).

Rhododendron ponticum is a sclerophyllous, evergreen shrub, with alternate leaves, sometimes considered to be alternating spiral or lax whorl (Cross 1975; Sariyildiz and Küçük 2009), dark green on the top and lighter on the underside (Figure 1). Lauroid leaves (Mejías et al. 2002) are waxy with a thick cuticle (Yela 1997) and have an oblong shape with a slightly up-rolled margin (Esquivia 1993).

The attractive zygomorphic flowers are 6 cm width, pedicellate. They exhibit various shades of pink, from lilac pink to purple magenta, with a yellow spot on the upper petal. Corymboid terminal racemes of 7–21 flowers (Mejías et al. 2002) usually appear at the age of 10–12 years (Tabbush and Williamson 1987), but often earlier in the invasive range: 7 years (Erfmeier and Bruehlheide 2011) or even 3 years (Var and Dinçer 2012). Between 3,000 and 7,000 small seeds are produced per raceme, inside woody capsules (Barron 2007). Cross (1975) estimated that one shrub can produce over one million seeds. Seed production depends upon bush size and environmental conditions (Edwards 2006). Seeds are cylindrical, hairy at both ends, and reach 1.5 mm in length (Barron 2007).

Seedlings are 2–5 cm tall after the first growing season, with a simple root system (Barron 2007).

Distinguishing features

In the wild, several species can be mistaken for *Rhododendron ponticum*: *Prunus laurocerasus* which sometimes co-occurs (Maguire et al. 2008), but the latter has glossy leaves and its inflorescence is an elongated white raceme; and *Daphne laureola*, which

is a smaller shrub with greenish, small flowers at the axils of leaves. In the British Isles, *Rhododendron ponticum* can co-occur with other exotic *Rhododendron* species, such as *R. catawbiense* and *R. maximum*, both native from North America. Some horticultural varieties of *Rhododendron* can be mistaken for *Rhododendron ponticum* but they rarely escape from parks and gardens.

Variations at the infraspecific level

Rhododendron is a large genus belonging to the Ericaceae family that includes around 1200 species (Rotherham 1983). Within the species *Rhododendron ponticum*, several populations exist, due to its natural disjunct distribution. Two subspecies are currently recognized: *R. ponticum* subsp. *baeticum*, native to the Iberian Peninsula, and *R. ponticum* subsp. *ponticum*, native to the Black sea region (Pontic region), which distinguishes itself by its taller leaves (12 to 18–25 cm) with a smaller length-to-width ratio (Tutin et al. 1972), and its more or less glabrous raceme axes (Cross 1975; Hill and Hulme 2012). Invasive populations of *R. ponticum* in Britain and Ireland would derive from the Iberian taxon (Milne and Abbott 2000; Stout et al. 2015), a hypothesis supported by morphological characters such as absolute length of leaves, absolute width of leaves, length-to-width ratio of leaves and maximum leaf area (Erfmeier and Bruehlheide 2004).

Two wild varieties of *R. ponticum* have been described, one from Turkey with variegated leaves (var. *heterophyllum* = var. *variegatum*; CABI 2021a), the other from Lebanon (var. *brachycarpum*, Cox 1990). Many cultivars, sometimes referenced as “Hardy Hybrids” (Milne 1998), have been described, including var. “Album”, “Album multimaculatum”, “Angustifolium”, “Angustissimum”, “Atropurpureum”, “Aureomarginatum”, “Bullatum”, “Cassinefolium”, “Cheiranthifolium”, “Caerulescens”, “Contortum”, “Elegantissimum”, “Flore Pleno”, “Foliis Albis Variegatis”, “Foliis Argenteis”, “Foliis Aureis”, “Foliis Marginatis”, “Foliis Purpureis”, “Foliis Variegatis”, “Frondosum”, “Granulatum”, “Nazarethii”, “Obtusum”, “Ovatum”, “Pumilum”, “Punctatum”, “Roseum”, “Rotundifolium”, “Salicifolium” and “Vacciniifolium” (Cullen 2011).

There is evidence that hybridization is possibly at the origin of invasive *R. ponticum* populations of the British Isles. A historical analysis of the gardening literature of the 19th century (Dehnen-Schmutz and Williamson 2006) revealed that *R. ponticum* subsp. *baeticum* was made more hardy by artificial and natural selection and by hybridization with Appalachian species, especially *R. catawbiense* Minchx. This hypothesis is further supported by a genetic study (Milne and Abbott 2000), which suggests complex introgressive hybridization between Iberian material

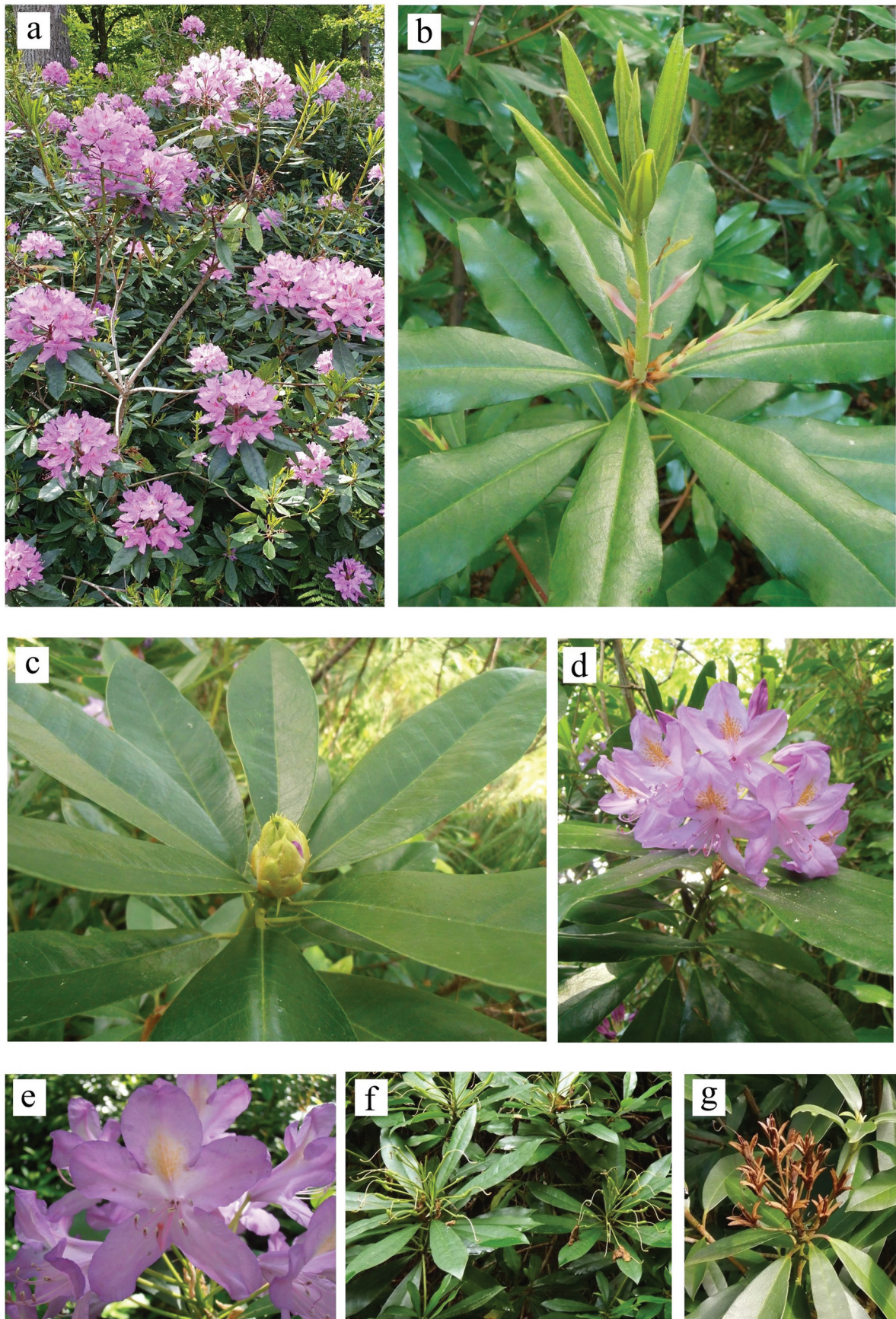


Figure 1. Morphology of *Rhododendron ponticum* subsp. *baeticum*. (a) flowering thicket. © Guillaume Decocq. (b) one-year shoot with laurel-type leaves. (c) flower bud. (d) raceme. (e) flower. (f) fruit development. © Marion Casati. (g) open woody capsules. © Maude Levilain.

of *R. ponticum* and other North American species of *Rhododendron*, including *R. catawbiense* and *R. maximum* L. Cullen (2011) proposed the name *Rhododendron x superponticum* for this complex of hybrids (*R. ponticum* x *R. catawbiense*, *R. maximum* and/or *R. macrophyllum* G. Don) (Cullen 2011). Hybridization could explain the niche shift between British invasive and Spanish native populations of *R. ponticum* (Manzoor et al. 2020). However, a more recent genetic study found no evidence for hybridization in Irish invasive populations (Erfmeier et al. 2011) so that the authors rejected the “genetic shift” hypothesis (Erfmeier and Bruelheide 2005, 2010). Instead, they considered that the invasiveness of Irish *R. ponticum* populations is due to more effective germination and growth than in the native range.

Finally, Spanish and Irish *R. ponticum* populations show some genetic differences but little genetic diversity, with the greatest proportion of genetic variation contained within rather than between populations (Erfmeier and Bruelheide 2011; Stout et al. 2015). Erfmeier and Bruelheide (2011) found a higher genetic diversity within the Georgian populations of *R. ponticum* than within Irish and Spanish populations. However, these results must be treated with some caution, given the limits of the markers used (AFLP markers in Erfmeier and Bruelheide 2011, AFLP markers

from *R. metternichii* var. *hondoense* in Stout et al. 2015). No studies use SSR markers specific of *R. ponticum*.

Distribution and status

Native range

Rhododendron ponticum has a disjunct distribution, at the origin of the two sub-species (*baeticum* and *ponticum*) (Mejías et al. 2002, 2007) (Figure 2). However, palaeological studies of interglacial deposits revealed a wider distribution in the past, with occurrences in the Austrian, French and Italian Alps (Depape and Bourdier 1952), Bulgaria, and even in northern Ireland (Çolak et al. 1998; Milne 1998). Its distribution area has contracted during the late Tertiary and Pleistocene in response to climate fluctuations (Cross 1975). It is thus likely that at some point in time both subspecies formed a single one, extending from Turkey to Portugal, as proposed by Çolak et al. (1998) and Milne (1998).

Rhododendron ponticum subsp. *baeticum* is endemic to the Iberian Peninsula, but its distribution is restricted to small, isolated areas of South-West Spain, central and southern Portugal (Rotherham 1983; Almeida et al. 2005). It is considered as an endangered relict species (Mejías et al. 2002, 2007), mainly because seedlings hardly establish, resulting in a virtual lack of

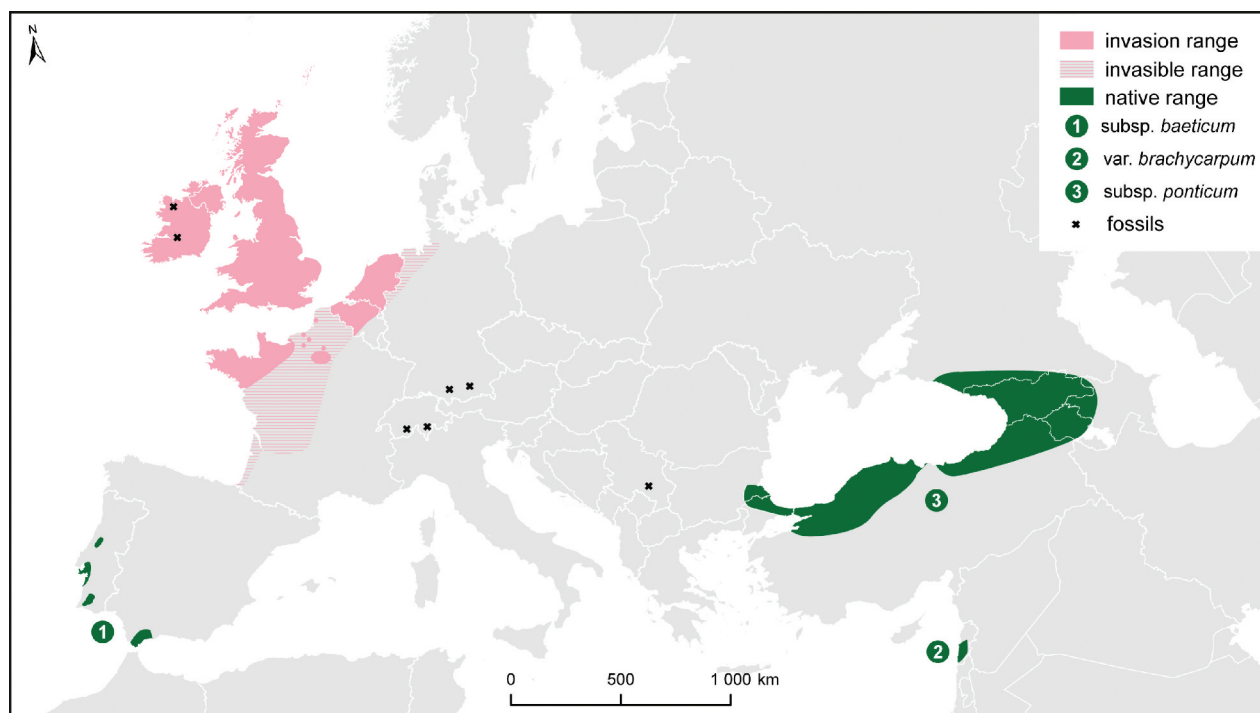


Figure 2. Distribution of *Rhododendron ponticum* in Europe and the Pontic area. The map was drawn using a number of sources, including regional and national Atlas and GBIF database. It highlights the regions to which the species is native (in green), invasive (in plain pink), and potentially invasive (in hatched pink; i.e. where the species is present and meets its ecological requirement, but without truly spreading). The map omits artificial plantations outside these areas. Fossils are pollen retrieved in sediments. © Emilie Gallet-Moron.

sexual reproduction. For this reason, *in vitro* culture has been implemented for the sexual and agamic propagation of the species (Cantos et al. 2007). Since 1971, the taxon is protected by law in the Botanical Reserve of Cambarinho, Portugal (Portuguese Decr. 364/71) (Almeida et al. 2005), and in Andalucía it is considered as threatened (Spanish Decr. 104/94) (Almeida et al. 2005) and as such is red-listed, both at the regional (Blanca et al. 1999) and national (Moreno 2011) levels.

Rhododendron ponticum subsp. *ponticum* occurs over a large part of the Black Sea Region, including South-East Bulgaria, North Turkey and the Taurus Mountains in South Turkey, Georgia and south-western most part of Russia (Cross 1975; Çolak et al. 1998). While the species is vulnerable in North-West Turkey and Bulgaria, it is abundant in the north-eastern part of its range so that it is sometimes considered as a weed (Rotherham 2001) or an “invasive” shrub that needs to be controlled (Eşen et al. 2004; Vacek et al. 2020).

Rhododendron ponticum var. *brachycarpum* forms an isolated, relict population close to the Lebanese coast (Cox 1990).

Introduced range

Rhododendron ponticum has been introduced in several European countries, where it is widely naturalized in temperate forests (Milne and Abbott 2000; Erfmeier and Bruelheide 2004). It is listed on the Observation List of invasive alien plants (EPPO 2012). *Rhododendron ponticum* is particularly invasive in the British Isles: it has spread throughout Ireland (Kelly 1981), where it is considered as one of the two most widespread invasive species (Barron 2007), and the most

humid west side of Scotland, England and Wales (Cross 1975). It invades indigenous forests as well as coniferous plantations, meadows, dune heaths, heathlands and peat bogs (Cross 1981; Stephenson et al. 2006) and, exceptionally, riverbanks and salt marshes (Dehnen-Schmutz et al. 2004). The Atlantic oak woodlands of western Scotland are considered particularly threatened (Edwards 2006) and registered in Annex I of the EC Habitat Directive (Maclean et al. 2017a).

In France, *R. ponticum* is a proven invasive species in several regions experiencing an oceanic climate (Brittany, Normandy, Hauts-de-France, and Île-de-France), where it mostly invades coniferous plantations, broadleaved or mixed forests, rarely heathlands (Bousquet et al. 2016; Quéré and Geslin 2016) (Figure 3). Elsewhere, close to the Atlantic coast or more inland, it is rather considered as a non-invasive naturalized species (e.g. Pays de la Loire; Dortel and Le Bail 2019), or as an emerging invasive species (e.g. Centre region; Desmoulins and Emerau 2017). Its actual distribution indeed comprises many spots on the entire metropolitan territory due to the fact it has been widely planted as an ornamental in many parks and gardens without escaping in the wild.

In Belgium, the species occurs in Flanders and in the northern part of Wallonia (Branquart et al. 2011), mostly in forests, especially in mixed Scots pine and pedunculated oak forests (Nadezhdina et al. 2004). *Rhododendron ponticum* is reported in the A2 (i.e. high impact and restricted range) black list based on ISEIA risk assessment (Branquart et al. 2011). Furthermore, *R. ponticum* is also considered as a potential threat to several Natura 2000 habitats, such as heathlands (Branquart et al. 2011).

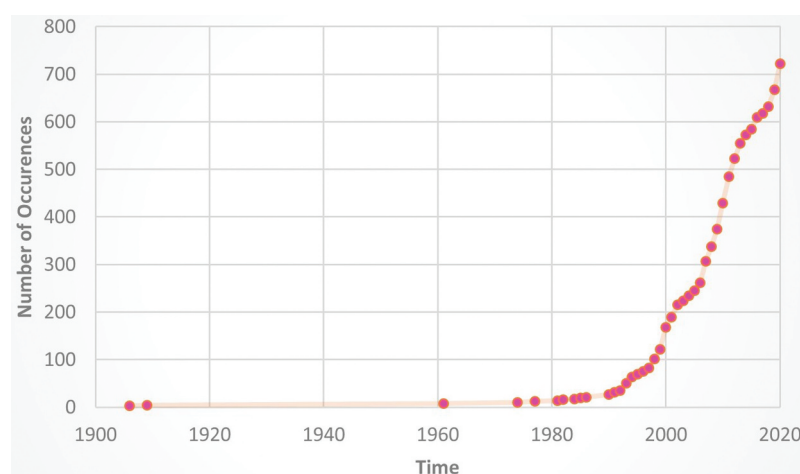


Figure 3. Invasion curve of *Rhododendron ponticum* L. in France based on databases of the INPN, the botanical conservatories, the IGN and information obtained from the ONF, the CRPF and via a participatory survey. Undated data and data with no location or with a precise location outside a forest environment were not considered. Total cumulative number of occurrences is given in the y-axis.

Rhododendron ponticum is also reported in the Netherlands and North-West Germany, where its invasion potential is recognized (Erfmeier and Bruelheide 2004). In Germany, it is registered on the blacklist of invasive species (Nehring et al. 2013).

Elsewhere in Europe, it occurs occasionally in West Norway, South Sweden, Poland, and Slovakia (Manceau 2015). Outside Europe, it has been introduced in New Zealand, where it is listed on the National Pest Plant Accord since 2008, and thus prohibited from sale, propagation, and distribution, though it is not yet widely naturalized (New Zealand Government 2020). It is also naturalized in South-East Australia, in the Blue Mountains (New South Wales) and the Dandenong Ranges (Victoria) and in western Tasmania.

History of introduction and spread

Few studies have attempted yet to reconstruct the invasion history of *R. ponticum* (Cross 1981). Its first introduction in the British Isles dates back to 1763 at Kew Gardens from “Levant and Gibraltar”, by the nurseryman Conrad Loddiges (Cronk and Fuller 1995). It was introduced first in England (Elton 1958) and, by 1800, in Ireland (Doyle 1999; Barron 2007). By 1803, it was being sold on London markets as a pot-plant and was planted throughout England mainly as an ornamental, rootstock for hybrid varieties of *Rhododendron*, game cover, and recreative purposes. This has led to multiple foci of introduction (Griffin 1994). Material from both the Iberian Peninsula and Turkey was originally introduced, for example, at the Royal Botanical Garden of Edinburgh (Milne 1998), but genetic studies suggest that only the subspecies *baeticum* from the Iberian Peninsula has escaped from gardens to spread in the wild. Its intensive planting in the 19th century, in particular as game cover, facilitated the colonisation of natural habitats (Dehnen-Schmutz et al. 2004). The first mentions of self-sown plants in Britain date back to 1829 (but the species' identity is uncertain), 1841 and 1849 (Dehnen-Schmutz and Williamson 2006; Parrott and MacKenzie 2013), especially in neglected large Victorian estates (Tabbush and Williamson 1987) where it was widely planted since 1765 (Eşen et al. 2006). It was first reported as an invasive species in 1943 (Thomson et al. 1993; Gritten 1995). Rotherham (2003) indicates that the rate of spread of *R. ponticum* patches has accelerated over the past five years as a likely consequence of increased

disturbance of natural ecosystems, but that its distribution is now considered stable since it has not been detected in new 10 km² squares.

In France, *R. ponticum* has been mainly introduced for ornamental purposes and game cover, often in castle parks. It has been first introduced in parks by Tournefort in 1703 (Baltet 1882). Interestingly, none of the regional floras of the late 19th century mentions *R. ponticum* in the regions where it is currently invasive. The first mentions appear in herbaria, which indicate some naturalized spots of *R. ponticum* in woodlands in the 20th century (e.g. in Apremont by Jovet, 1928; in Saint-Léger-en-Yvelines by Bouby, 1967; in Rochechouart by Bouby, 1975), as well as in a supplementary to Coste's French flora from 1977. Little information is available on the spread of *R. ponticum* in France but the increasing number of occurrences since the beginning of the 21st Century tends to confirm the status of “emerging invader” in France (Figure 3) and the species is more and more often reported as an emerging problem by forest managers (Office national des Forêts, Centre national de la propriété forestière, pers. com.). The species has indeed acclimatized to the Atlantic climate to the point of escaping from gardens, and thrives in the understory of nearby forests.

In Belgium, *Rhododendron ponticum* was mentioned in a natural area for the first time in Lippelo (Flanders) in 1920 (Groom 2010). It is now considered a threatening species due to its capacity to form monospecific bushes in forests, and its dispersal ability and environmental impact (Branquart 2012).

Ecology

Climate

According to the Köppen-Geiger Climate Classification (Kottek et al. 2006), the two subspecies of *R. ponticum* occur under contrasted climate conditions. In the Iberian Peninsula, the subspecies *baeticum* is found under a hot summer Mediterranean climate (class Csa), but it may cope with the effects of the dry season by growing along streams and where the topography creates more humid microclimatic conditions. In the Black Sea region, the subspecies *ponticum* mostly grows under oceanic climate conditions, with no dry season (class Cf) and a warm (Cfb) or hot (Cfa) summer. Towards the western most part of its range (North-West Turkey, Bulgaria) it is found under a hot summer Mediterranean climate (class Csa), whilst in the eastern part (North-East Turkey, Georgia, Russia) it occurs under a warm summer humid continental climate, with no dry season (class Dfb). Outside its native

range, in Europe, *R. ponticum* is exclusively found under oceanic climate conditions, with no dry season and a warm summer (Cfb). A dry season seems to be the main limiting factor since seeds and seedlings are intolerant to drought (Tabbush and Williamson 1987), in contrast with cold since the species is considered to be resistant to -20°C (CABI 2021a).

Substratum

Rhododendron ponticum can grow in a wide range of soils, but it thrives especially on podsol sandy soils (Rotherham 1983) and well-drained soils, more rarely and less vigorously on brown soils (Esquivia 1993). Favourable conditions such as a moss mat, a high moisture and light at the forest floor, are necessary for seed germination and seedling establishment, but once established, seedlings and saplings can cope with a wide range of conditions (Cross 1975, 1981) and survive several years while waiting for optimal conditions to grow up (Rotherham 1983).

Soil moisture, salinity and nutrients

Soil moisture and aeration are crucial environmental factors for the growth of *R. ponticum* (Eşen 2000; Eşen et al. 2004). The species avoids dry sites where its growth is reduced (Çolak et al. 1998). It has been considered as an indicator of very wet sites (Tashev et al. 2016), but it hardly grows on waterlogged soils (Cross 1975). Topography and microtopography play a role in soil drainage, with sometimes a close relationship between slope and *R. ponticum* occurrence (Thomson et al. 1993), which has been attributed to a greater stone content and thus a better soil drainage (Eşen 2000).

Rhododendron ponticum is resistant to salty soils but prefers soils with a high organic matter content (Cross 1975; Var and Dinçer 2012; Haffenden 2015).

Soil pH

The shrub is usually observed on acidic soils, with a pH ranging from 3.3 to 6.4. The optimal pH for its development lies between 4.5 and 5.5 (Var and Dinçer 2012), but Cross (1975) indicates a more effective germination of seeds when the pH is close to 4.0. Above a pH of 5.0 fewer seedlings are observed and growth is limited (Cross 1975). The species can grow in pockets of leached soil on stretches of limestone pavement (Kelly 1981).

Light

Rhododendron ponticum is a shade-tolerant species. It presents different adaptation strategies, such as a low metabolic rate, plasticity in leaf area in response to light intensity, and the ability to photosynthesize even in winter because being evergreen (Barron 2007). This

allows two main periods of growth, in late spring and mid and late summer (Yela 1997). Furthermore, its leaves present an additional layer of upper epidermis and thicker adaxial epidermal cells, which may allow leaf photoprotection against total light and UV in winter (Wang 2009). To germinate, the seeds require a certain amount of light, but once established saplings grow better under cover than in an open situation (Eşen 2000; Harris et al. 2011). Light availability plays a major role in the flowering of *R. ponticum*, and thus for its sexual reproduction, with a number of floral buds, which increases with light availability (Harris et al. 2011).

Response to biotic factors

The spread of *R. ponticum* is limited by the availability of suitable sites for recruitment. Seedlings are weakly competitive: although they can survive for years under unfavourable conditions, they are readily outcompeted by other plants and litter (Cross 1975). Disturbance can provide windows of opportunity for seeds to germinate, for example, by creating small gaps with bare soil. Forest management often contributes to the spread of *R. ponticum* by leaving bare wheel tracks or tree stumps covered with moss mats (Stephenson et al. 2006). Fire also facilitates the establishment of *R. ponticum* in the absence of superior competitors (Cross 1975).

Grazing of *R. ponticum* by rabbits, sheep and sika deer has been reported. Sheep grazing impedes the establishment and spread of *R. ponticum* (Thomson et al. 1993). The impact of grazing on seedlings can be positive or negative (Milne 1998), depending on the grazing pressure and the level of invasion. Grazing animals can promote invasion by reducing competition from other plants (Cross 1981). Grazing has little or no effect on mature plants (Cross 1975; Thomson et al. 1993) since, compared to most native species, *R. ponticum* is little consumed because of its low palatability. This is likely because leaves exhibit high concentrations of phenolic compounds and polycyclic diterpenes (grayanotoxins) (Cross 1981; Judd and Rotherham 1992).

Habitats and syntaxonomy

In both native and invasive ranges, *R. ponticum* is primarily a woodland species, though it can occur in open habitats, such as heathlands and disturbed habitats. In the invasive range, it invades habitats that have been disturbed by forest management, grazing animals (Rotherham 1983) or forest fires (Eşen et al. 2006).

Native range

In the native range, *R. ponticum* subsp. *baeticum* commonly occurs in riparian shrublands and woodlands, mixed woodlands and cork oak stands (Almeida 2003). It is almost restricted to the margins of permanent or intermittent watercourses (Mejías et al. 2007), but sometimes occurs in mountain ravines and slopes experiencing frequent fogs (Cantos et al. 2007). It characterizes two thermo-meso-Mediterranean vegetation types in moist to damp, acidic, nutrient-poor soils and under hyperhumid (micro-)climate conditions (Rivas-Martínez et al. 2001):

- forest communities of the meso-mediterranean association *Rhododendron baetici-Alnetum glutinosae* (Rivas Goday & Rivas-Martínez in Rivas-Martínez 1965, Rivas-Martínez & Sánchez-Mata 2001), or, more rarely, of the thermomediterranean association *Arisaro proboscidei-Alnetum glutinosae* Martínez-Parras & Peinado 1987, both associations belonging to the *Osmundo regalis-Alnion glutinosae* alliance (*Salici purpureae-Populetea nigrae* (Rivas-Martínez & Cantó ex Rivas-Martínez, Bascónes, T.E. Díaz, Fernández-González & Loidi) Rivas-Martínez, Fernández-González, Loidi, Lousã & Penas 2001 class). They form either gallery forests or the mantle of alder riparian forests in narrow gorges and valleys;
- shrub communities of the *Rhododendrenion baetici* Rivas-Martínez et al. 2001 sub-alliance (*Quercetea ilicis* Br.-Bl. ex A. & O. Bolòs 1950 class), which grow at the outer edge of streams or as the mantle of riparian oak (*Quercus canariensis*, *Q. suber*) and alder (*Alnus glutinosa*) forests. Those include the *Scrophulario laxiflorae-Rhododendretum baetici* A.V. Pérez, Galán & Cabezero 2000 em. Rivas-Martínez et al. 2001 association in Spain; and the *Campanulo primulifoliae-Rhododendretum pontici* Vila-Viçosa, J.C. Costa, Quinto-Canas & Pinto-Gomes 2012 and *Calluno vulgaris-Rhododendretum baetici* Honrado, P. Alves, Lomba, Torres & B. Caldas 2007 associations in South and Central Portugal, respectively.

In all these Iberian syntaxa, the vegetation is typically ombrophile, with many ferns and bryophytes, and several “Tertiary relicts” of subtropical origin (Loidi 2017). In particular, *R. ponticum* subsp. *baeticum* co-occurs with other evergreen, lauroid shrub species, such as *Laurus nobilis*, *Nerium oleander*, *Phillyrea latifolia*, *Daphne laureola*, *Viburnum tinus*, *Arbutus unedo*, *Prunus lusitanica*, for example.

In the Black Sea region, *R. ponticum* subsp. *ponticum* is typically a species of the Pontic beech forest, which extends from North-West Anatolia to Georgia

and Russia (Eşen 2000), mostly in lowlands (<500 m). It often co-occurs with other (laurel-leaved) evergreen shrub species such as *Prunus laurocerasus*, *Ilex colchica* and *Daphne pontica* that are considered as “Tertiary relict” (Tzonev et al. 2006; Korkmaz et al. 2008; Tunçkol et al. 2020). Syntaxonically, *R. ponticum* is considered a characteristic species of the order *Rhododendro pontici-Fagetalia orientalis* Quézel, Barbéro & Akman 1980. As such, it occurs in a number of forest plant associations dominated by beech (*Fagus orientalis*; e.g. the *Rhododendro pontici-Fagetum orientalis* Stefanov ex Tzonev et al. 2006 in Bulgaria and North-West Turkey, the *Cardamino impatiendis-Fagetum orientalis* Arslan 2008 in Central Anatolia, the *Ilici colchicae-Fagetum orientalis* Quézel, Barbero et Akman 1980 in Central and North-East Turkey, and Georgia), oak (*Q. hartwissiana*, e.g. the *Rubocaucasici-Quercetum hartwissianae* Korkmaz, Yalcin, Kutbay, Berk and Bilgin 2008 on shallow brown soils in Anatolia), chestnut (*Castanea sativa*; e.g. the *Hedero helici-Castaneetum sativae* Yurdakulol, Demirors and Yildiz 2002 on humic brown soils in Anatolia) and poplar (*Populus tremula*; e.g. the *Carpino betuli-Populetum tremulae* Korkmaz, Yalcin, Kutbay, Berk and Bilgin 2008 on calcareous soils in Anatolia). It can form a dense shrub layer in the understory of these forests. Interestingly, the floristic composition of these forests shares most genera and many species with European deciduous forests, so that they belong to the same *Quercus robur-Fagetum sylvaticae* Br.-Bl. & J. Vlieger in J. Vlieger 1937 class.

In the Colchic region (North-East Turkey and Georgia), *R. ponticum* subsp. *ponticum* can be found at higher altitudes (1300–1800 m) together with other rhododendron species (e.g. *R. luteum*, *R. caucasicum*, *R. smirnowii*), on mountain slope forests of the *Quercus ponticii-Betuletum medwediewii* Eminagaoglu & Kutbay 2006 association (*Pino sylvestris-Piceetalia orientalis* Quézel, Barbero & Akman 1980 order), which grows on acidic, mesic soils under a humid climate. In North Anatolia, *R. ponticum* occurs in the mediterraneo-oceanic maquis of the *Calluno vulgaris-Arbutetum unedonis* Korkmaz et al. 2008 association (Korkmaz et al. 2008).

In Lebanon, *R. ponticum* var. *brachycarpum* is restricted to a few alder (*Alnus orientalis*) gallery forests established on headwaters and stream banks in the sandstone mountains (Chouchani et al. 1975).

Invasive range

In the introduced range, *R. ponticum* can cope with a broad range of light, soil and temperature conditions, but tolerates neither basic soils nor drought. It occurs in different habitat types as long as the climate is humid and the soil is acidic, with an optimum on more or less sandy moist soils, similarly to the edaphic

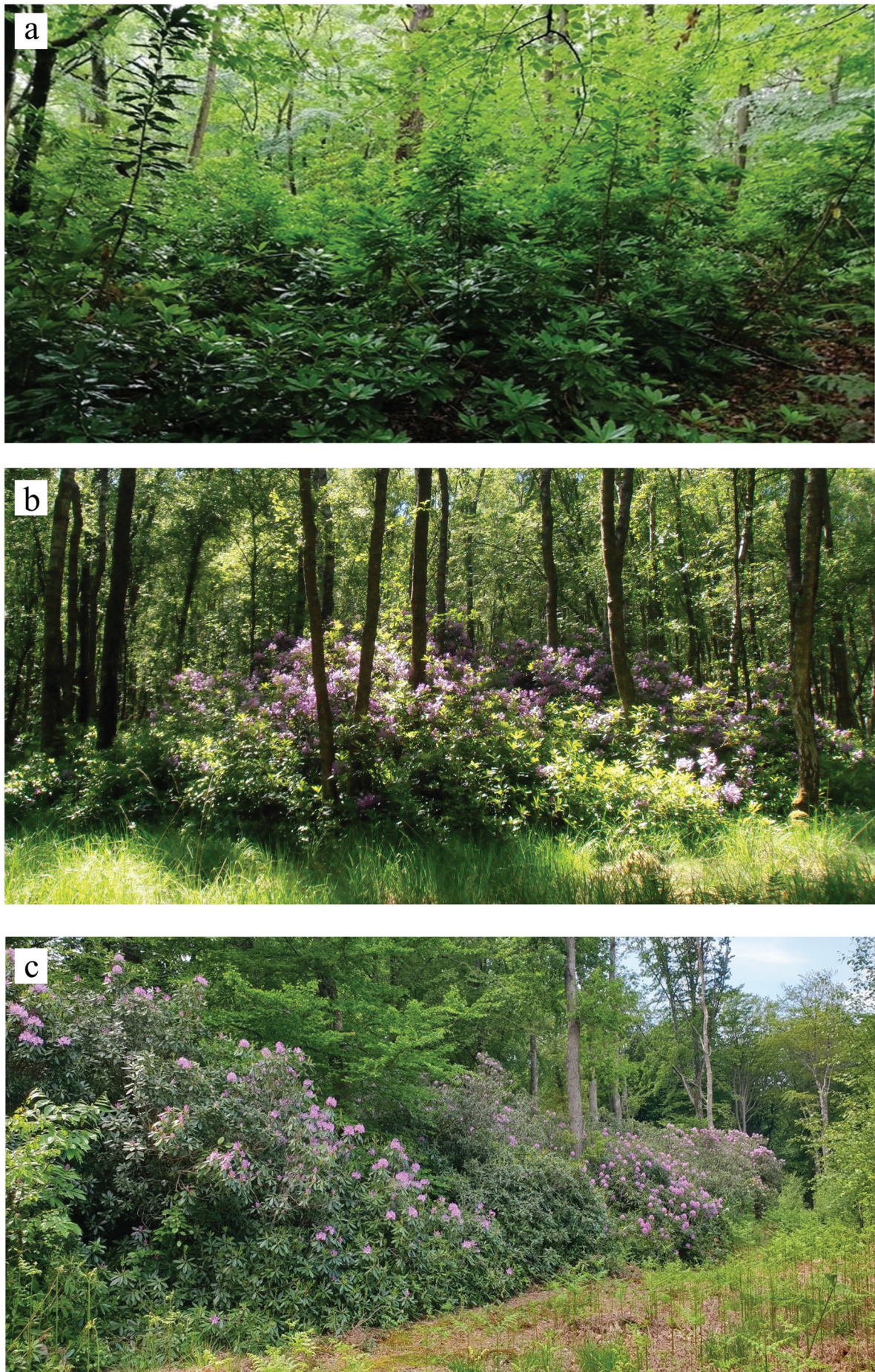


Figure 4. Forest stands invaded by *Rhododendron ponticum* in north-western France (a) In the understory of a closed-canopy forest. (b) A pioneer individual below an open-canopy forest. © Marion Casati. (c) Invasion of an edge following a clearcut. © Guillaume Decocq.

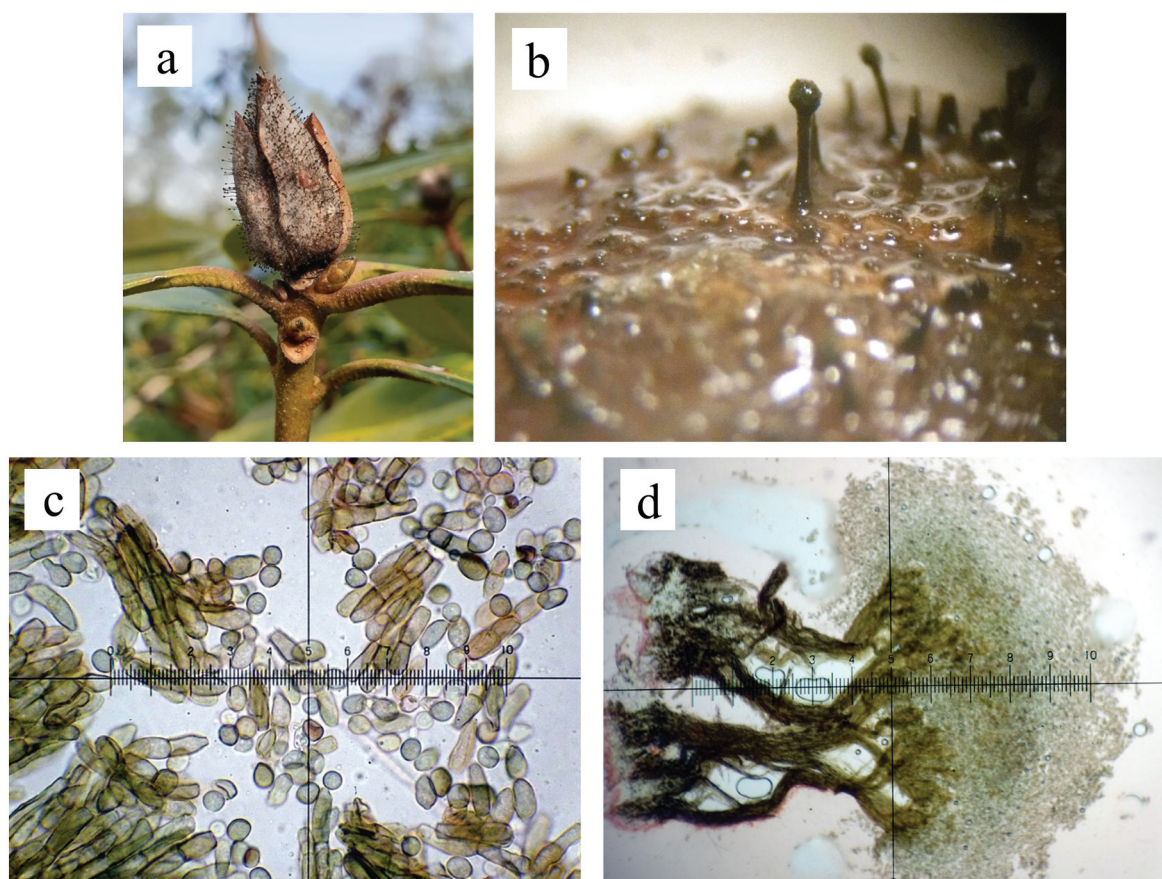


Figure 5. Details of *Pycnostysanus azaleae* (a) In a flower bud of *Rhododendron ponticum*. © Guillaume Decocq. (b) Microscopic observations at magnification 20. (c) Observation of conidia at magnification 100. (d) Observation at magnification 1000. © Abel Flahaut.

and climatic conditions experienced in the Iberian native range. *Rhododendron ponticum* mostly invades acidophilous oak (class *Quercetea robori-petraeae* Braun-Blanquet & Tüxen ex Oberdörfer 1957) and beech (alliance *Ilici aquifoliae-Fagion sylvaticae* Braun-Blanquet 1967) forests, as well as their edges and clearings, especially when the natural vegetation is disturbed (e.g. forest management, storms and overgrazing by deer) or replaced by pine plantations (Figure 4). In the British Isles, *R. ponticum* also frequently invades heathlands (alliance *Ericion cinereae* Böcher 1940), and even bogs (alliance *Osmundo regalis* – *Myricion gale* Julve ex B. Foucault & J.-M. Royer 2014) (Foley 1990; Doyle 1999). Other habitats that are less frequently invaded include shrublands, grasslands, sand dunes and urban areas.

Ecological interactions

Herbivory

Being evergreen, *R. ponticum* is a potential feeding resource for herbivores (Yela 1997), especially in areas where few other woody species retain their leaves in winter, as in Atlantic Europe (Judd and

Rotherham 1992). However, few insect species have been reported to feed on the plant in the invasive range (Elton 1958; Yela 1997). Most are generalist species (Judd and Rotherham 1992), which feed only occasionally or accidentally on *R. ponticum*, such as, for example, caterpillars that fell from neighbouring trees (Yela 1997). In the British Isles, Elton (1958) reported that some insects attack rhododendron, but without impacting its development. These insects include two weevils (*Otiorhynchus singularis* and *Otiorhynchus sulcatus*) and a few moths of the Tortricidae family, some of which eat the leaves or roll up inside to become nymphs. Elton also reported the presence of other moths and some native beetles, as well as four exotic insect species (the moth *Gracilaria azaleella* from Japan; an Aleyrodid “fly”, *Dialeurodes chittendeni* from Himalaya; a Tingid bug, *Stephanitis rhododendri* and a Jassid bug, *Graphocephala coccinea*, both from North America). This low rate of invertebrate herbivory has been attributed to the high phenolic concentrations in the tissues (Rotherham 1983). Similarly, in the native range, few

phytophagous insects are associated with *R. ponticum*, with the notable exception of the lepidopteran caterpillar *Cosmia* sp., which, combined with a fungal infection by *Gloeosporium* sp., damage up to 8% of the total leaf area (Blanca et al. 1999).

Plant pathogens

Both in native and invasive ranges, *R. ponticum* leaves are colonized by phytopathogenic oomycetes of the genus *Phytophthora*: *Phytophthora hedraiaandra* (Moralejo et al. 2009), *Phytophthora kernoviae* and *Phytophthora ramorum* (Purse et al. 2013) among others, which are responsible for the sudden oak death (Williams et al. 2010). Characteristic symptoms of the infection are brown spots on the leaves and black necrosis of the stem tips (Desprez-Loustau et al. 2018).

Several phytopathogenic fungi (e.g. *Cercoseptoria handelii* in the UK; Hedger and George 2004) are also associated with *R. ponticum* (Cross 1975), but

without particular consequences on its development, except for *Pycnostysanus azalea*, which can cause bud blast (Cross 1975; Hedger and George 2004). This species is present in most of the countries where *R. ponticum* occurs (as in France, pers. obs.: Figure 5), except in Portugal and Spain (CABI 2021b).

Epiphytic species

Two species of epiphytic fungi have been identified on the leaves of *R. ponticum* in the UK: *Coleophoma empetri* (on dead fallen leaves), and *Coleophoma fusiformis* (on living leaves) (Wu et al. 1996).

Mycorrhiza

Rhododendron ponticum can form associations with dark septate endophytes (Cross 1975; Mitchell and Read 1981) and ericoid mycorrhizae (Harley and Harley 1987; Vohník and Albrechtová 2011), which are thought to promote their invasiveness (Rotherham 1983). So far, symbiotic fungi seem to be poorly documented.

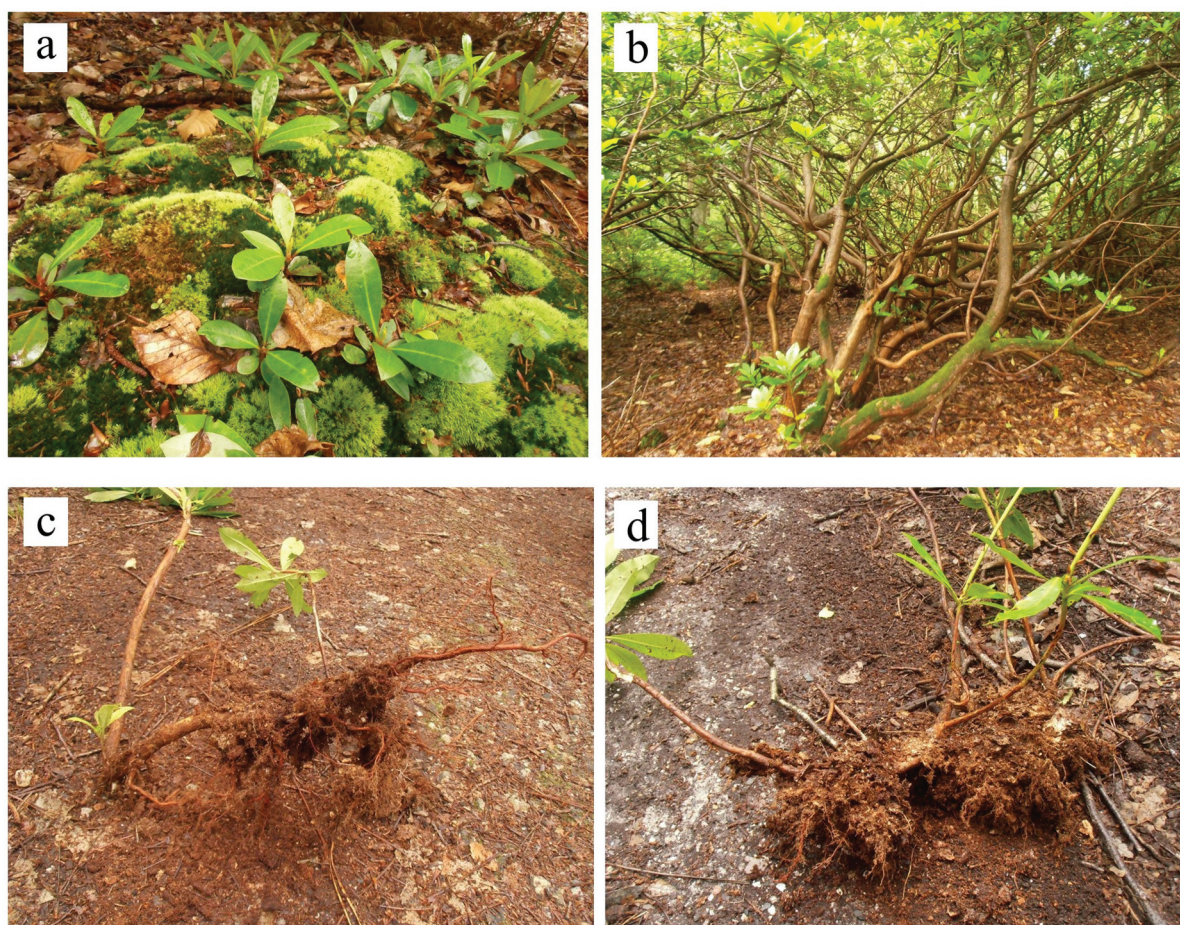


Figure 6. Propagation means of *Rhododendron ponticum* in the exotic range. (a) seedling establishment on moss mats covering a decaying stump. (b) stump resprouts. (c) uprooted individuals revealing branch layering. (d) uprooted individuals revealing root suckering. © Marion Casati.

Biology

Phenology

In Spain, flowering can occur from January to June (Almeida 2003), while in the invasive range the flowering period lasts 2 months (Mejías et al. 2002), usually from May to June (Cross 1975). The flowering can occur earlier some years, with favourable meteorological conditions, in April (pers. obs.) or even in February (Cross 1975). Flowering in late summer and scattered flowers during autumn-winter can also be observed (Cross 1975; pers. obs.).

Physiology

Temperature

Rhododendron ponticum can tolerate a wide range of temperatures, from -17°C to 26°C (Esquivia 1993). It is commonly considered more tolerant to low temperatures in the invasive than in the native range, which has been attributed to introgressive hybridization with frost-resistant North American *R. catawbiense* and *R. maximum* (Milne and Abbott 2000). Leaves can acclimatize to cold conditions via structural adaptations, such as thicker leaf blades and a waxy cuticula (Wang 2009). It is a non-thermonastic species (i.e. the movements of the leaves are not caused by temperature variations), unlike other *Rhododendron* species such as *R. catawbiense* (Nilsen 1991; Wang 2009). Cold acclimation in *Rhododendron ponticum* involves an increased content in several proteins conferring higher resistance to frost and drought, at the expense of several proteins involved in photosynthesis (Die et al. 2017).

Shade tolerance and response of leaves to light availability

Rhododendron ponticum exhibits several characteristics of shade-tolerant shrubs, such as a low metabolic rate, a high resistance to disease, and a high capacity to increase leaf area in response to a reduction in light intensity (Barron 2007). Furthermore, *R. ponticum* is an evergreen shrub so that it can continue to photosynthesize in winter, unlike deciduous plants. Compared to the native evergreen *Ilex aquifolium*, which often shares the same habitats, *R. ponticum* exhibits a higher photosynthetic nitrogen use efficiency, a larger investment of nitrogen in chlorophyll, and a larger leaf area, but equal photosynthetic potential and light-harvesting efficiency (Niinemets et al. 2003). Furthermore, mean leaf-level phenotypic plasticity was greater in the invasive (Belgium) than native (Spain) populations.

Allelopathy

Several secondary compounds are found in *R. ponticum*'s tissues, in particular free phenolic compounds and short-chain aliphatic acids (Simons 1988). Those vary in quantity depending upon plant organ and age. They are also present in the litter and topsoil beneath rhododendron canopies (Rotherham 1983), where they can inhibit the growth of common grasses, such as *Festuca ovina* (Rotherham & Read 1988, Parrott and MacKenzie 2013). These allelopathic effects towards seed germination and leaf emergence are species-dependent and concentration-dependent (Davis 2013). Allelochemicals also affect the soil decomposer community (Sariyildiz and Küçük 2009). Which secondary compounds are responsible for these allelopathic relationships remains unclear, but some proven allelopathic terpenes such as taraxerone and taraxerol have been suspected to contribute to the invasiveness of the species (González-Pérez et al. 2011).

Reproductive biology

Floral biology

Rhododendron ponticum is a monoecious shrub with an entomogamic pollination (Cross 1975). The flowers provide an abundant sugar-rich nectar (Dietzsch 2009), which is attractive to several generalist pollinators both in the native and exotic ranges (Stout et al. 2006). However, among the many insects visiting flowers, only a few ensure pollination. Common bumblebees are the main pollinator (Stout 2007a); in Spain, it is mainly pollinated by *Xylocopa violacea* and *Bombus terrestris* (Mejías et al. 2002).

Reproductive strategies

Rhododendron ponticum is a clonal species with a high-regenerating capacity, which reproduces both sexually and vegetatively (Erfmeier and Bruelheide 2004; Barron 2007) (Figure 6). The dominant mode of reproduction of the plant is debated. Though it produces a huge number of wind-dispersed seeds, few are deposited in suitable microsites for effective germination and, when germination is successful, many seedlings are killed by summer drought. Vegetative reproduction is much more successful but hardly allows long-distance dispersal except by forestry vehicles (pers. obs.). It occurs via layering (when horizontal branches in contact with the ground form roots) (Tabbush and Williamson 1987), root suckering (Griffin 1994), and lignotuber resprouting (Mejías et al. 2002), making it more important than sexual reproduction (Tabbush and Williamson 1987). The prevalence of one mode of reproduction over the

Table 1. List of EUNIS habitats where *Rhododendron ponticum* occurs in Europe and the Pontic area (after Branquart et al. (2011) and Rodwell (1991) for the invasive range; Korkmaz et al. (2008), Tunçkol et al. (2020) and Tzonev et al. (2006) for the Black Sea region; and Loidi (2017) and Rivas-Martinez et al. (2001) for the Iberian Peninsula). Dark grey and light grey indicate usual and occasional habitats, respectively.

EUNIS Habitats	Iberian Peninsula	Black Sea region	Invasive range
T. Forest and other wooded land			
T1. Broadleaved deciduous forest			
T1-4. Mediterranean and Macaronesian riparian forest			
T1-4B11. Iberian meso-Mediterranean alder galleries			
T1-4B2. <i>Rhododendron</i> – <i>Alnus</i> galleries			
T1-7. <i>Fagus</i> forest on non-acid soils			
T1-7C. Pontic <i>Fagus</i> forests			
T1-8. <i>Fagus</i> forest on acid soils			
T1-82. Atlantic acidophilous <i>Fagus</i> forests			
T1-B. Acidophilous <i>Quercus</i> forest			
T1-B1. Atlantic <i>Quercus robur</i> – <i>Betula</i> forests			
T1-B2. Atlantic acidophilous <i>Fagus</i> – <i>Quercus</i> forests			
T1-B3. Atlantic <i>Quercus petraea</i> forests			
T1-B4. Aquitano-Ligerian <i>Quercus</i> forests on podsols			
T2. Broadleaved evergreen forest			
T2-1. Mediterranean evergreen <i>Quercus</i> forest			
T2-11. <i>Quercus suber</i> forest			
T2-112. South-western Iberian <i>Quercus suber</i> forests			
T2-2. Mainland laurophyllous forest			
T2-21. Mediterranean-Atlantic <i>Laurus</i> – <i>Quercus</i> forest			
T3. Coniferous forest			
T3-L. Coniferous planted forests of non-native trees			
T4. Lines of trees, small anthropogenic forests, recently felled forest, early-stage forest and coppice			
T4-6. Early-stage natural and semi-natural forests and regrowth			
T4-7. Coppice and early-stage plantations			
T4-8. Recently felled areas			
S. Heathland, scrub and tundra			
S4. Temperate shrub heathland			
S4-1. Wet heath			
S4-2. Dry heath			
S4-23. Atlantic <i>Erica</i> – <i>Ulex</i> heaths			
S9. Riverine and fen scrubs			
S9-3. <i>Salix</i> fen scrub			
S9-4. Mediterranean riparian scrub			
S9-41. <i>Nerium oleander</i> , <i>Vitex agnus-castus</i> and <i>Tamarix</i> galleries			
D. Mires, bogs and fens			
D1. Raised and blanket bogs			
D1-1. Raised bogs			
D1-14. <i>Myrica gale</i> scrub on raised bogs			
B. Coastal habitats			
B1. Coastal dunes and sandy shores			
B1-6. Coastal dune scrub			

other likely depends on environmental conditions, in particular humidity (Mejías et al. 2002). For example, in Ireland, the species actively reproduces by seeds while vegetative spread is limited (Cross 1981), whilst in the Pontic and Iberian native ranges, it hardly reproduces sexually due to the failure of seedling establishment (Erfmeier and Bruelheide 2004) but successfully reproduces via branch-layering (Eşen et al. 2006). In France, very few *Rhododendron ponticum* seedlings are found on the forest floor (except in microhabitats, such as bare organic soil, moss mats and decaying stumps), while branch-layering is very active, especially on wet soils (pers. obs.).

Seed production and dispersal

Reproduction is an important issue in the Iberian native range, where the species hardly self-maintains (Almeida et al. 2005) compared to at least part of the

invasive range (Erfmeier 2004). Seeds are ripe in winter (sometimes earlier in autumn in the Iberian native area; Mejías et al. 2002) and subsequently progressively released until June (Cross 1975). Seed dispersal is mainly ensured by wind, but dispersal by animals is also reported (Cross 1975, 1981). Wind-dispersed seeds are mainly disseminated within 10 m around the mother plant, a tiny fraction travelling more than 50 m away (Stephenson et al. 2007). Seeds being very light (0.063 mg; Edwards 2006), it is assumed that they can travel over a longer distance, up to 1 km (Rotherham 1983). Consistently, Harris et al. (2009) indicate that expansion of the invasion front is due more to seeds produced by older, taller plants than to seeds released by recently matured plants.

No dormancy has been reported for seeds (Milne et al. 2003; Daly et al. 2014). The lifespan of seeds does not seem to exceed 1 year (Cross 1975), up to 160 days

according to Barron (2007). Thus, they do not incorporate the permanent soil seed bank (Maclean et al. 2018a). Under favourable conditions, seeds can germinate within 5 to 6 days (Barron 2007), mostly during spring and summer (Cross 1981). Seeds and seedlings require a suitable microhabitat to successfully germinate and establish, respectively. Short moss mats, decaying fallen logs and tree stumps, and compacted bare grounds (e.g. wheel tracks) provide optimal humidity conditions (Cross 1975, 1981; Stephenson et al. 2006). Bryophyte mats in particular appear to facilitate the establishment of *R. ponticum* seedlings (Eşen 2000; Barron 2007). Under hyperhumid microclimatic conditions, seedlings can even establish as epiphytes (Cross 1975).

Impacts

Positive and negative effects on biodiversity are reported, depending upon the degree of invasion of a site (isolated bushes in managed parks vs. monospecific bushes in the understories).

Uses and positive impacts

Due to its spectacular flowering, *R. ponticum* has long been widely used as an ornamental, like many other rhododendron species (Dehnen-Schmutz and Williamson 2006). Other uses in the exotic range, which explain its multisite introduction, include shelter for game and rootstock. It can provide shelter for certain species, such as badgers and many bird species (Rotherham 2001), including regionally rare species such as the nightingale (Rotherham 1983).

Rhododendron ponticum is used as firewood in Turkey, and locally in Britain and Ireland (Çolak et al. 1998). In Turkey, rhododendrons are used to provide biomass as an alternative raw material for medium density fiberboard manufacturing (Akgül et al. 2012). *Rhododendron ponticum* can also be used for producing a pulp with short fibres to make paper (Birinci et al. 2020). An appropriate process further allows the production of biofuels, such as bioethanol (Hennequin et al. 2021).

In the Black Sea region, *R. ponticum* is used as a traditional medicine for its analgesic and anti-inflammatory properties, for example, to soothe toothache and rheumatic pain (Qiang et al. 2011). These effects are attributed to the presence of flavones in the leaves (Erdemoglu et al. 2008). Antimicrobial activity, as well as antitumoral properties on prostate epithelial cancer cells have also been advocated (ManiKumar et al. 2011). A recent study has shown in the pollen collected by bees the presence of amino acids and phenolic compounds of medicinal interest (Ecem Bayram 2021).

Negative impacts

Effects on biodiversity

Rhododendron ponticum is a long-lived shrub, able to form dense monospecific bushes in suitable conditions, which shade out native plant species of the understories (Milne 1998). Even in the native range, in Turkey, native tree species (including beech) hardly regenerate and grow below rhododendron canopies (Eşen 2000; Eşen et al. 2004; Vacek et al. 2020). In the invasive range, only 2% of the daylight can reach the ground so that most herb species die and natural regeneration fails (Barron 2007). It has been shown that even bryophytes and lichen are threatened by *R. ponticum* in Atlantic oak woodlands of the west coast of Great Britain (Long and Williams 2007), which are also of international conservation value and listed in Annex I of the EU Habitats Directive (Maclean et al. 2017b). In Lundy (British Isles), the invasion by *R. ponticum* is a threat to the endemic Lundy cabbage *Coincya wrightii*, which is listed on the UK Biodiversity Action Plan, as well as to its associated insect fauna (Compton et al. 1998). It is also a threat for other plant communities, as well as for archaeological features associated with quarries that are damaged by the extent of the root system. Other habitats threatened by *R. ponticum* are listed in Table 1.

Bird species richness and abundance are negatively impacted (Hope Jones 1972; Rotherham 1983). By modifying the understory structure and associated microhabitats, *R. ponticum* can also impact bat populations, especially the large and most agile species *Nyctalus noctula*, *Eptesicus serotinus*, and *Nyctalus leisleri*. Smaller species like *Myotis* spp. and *Pipistrellus pygmaeus* appear not affected by the presence of *R. ponticum* and occasionally use sites where it is present for commuting and roosting activities (Beason et al. 2020).

Rhododendron ponticum has been associated with an increased abundance of some native mammals, such as the wood mice, that can enhance seed predation on native species and provide some parasites like ticks with more hosts (Malo et al. 2012).

The nectar of *R. ponticum* flowers is toxic to many pollinators (Tiedeken and Stout 2015), such as solitary bee and honeybee species native to the British Isles, but not to a common bumblebee species (Tiedeken et al. 2016). This has been attributed to the high concentrations of grayanotoxins (Tiedeken et al. 2014), including grayanotoxin I (Tiedeken et al. 2016). The replacement of native species by this invasive shrub can thus negatively affect pollinators by reducing their food resource (Tiedeken et al. 2016).

The rhizosphere diversity of testate amoebae communities has been found to be positively impacted by *R. ponticum* in Spain (Vohník et al. 2012) but negatively in the UK (Sutton and Wilkinson 2007).

Soil invertebrates (including earthworms) are similarly negatively affected, likely because of allelochemicals present in *R. ponticum* leaf litter (Cross 1975). Consistently, Malo et al. (2012) reported lower invertebrate biomass in invaded forest stands, as well as a lower tick density.

Effects on ecosystems

Rhododendron ponticum can significantly impact ecosystem functioning, by altering abiotic factors, such as light arrival at the forest floor and soil properties (Cross 1975). In particular, *R. ponticum* produces a thick, recalcitrant litter (Horuz et al. 2014), which decomposes slowly (Sariyildiz and Küçük 2009), alters the dynamics of degradation of the organic matter, and lowers soil pH (Jones et al. 2019a). This results in a mor humus (Esquivia 1993), which can form a baker crust inhibiting the recruitment of other plant species (Cross 1975), ultimately contributing to soil podsolization (Rotherham 1983). However, Maclean et al. (2017a) indicate that the invasion of *R. ponticum* does not affect soil pH, C:N ratio and nutrient concentrations (N, P, K, Ca, and Mg). Even after rhododendron removal, soil respiration hardly recovers (Jones et al. 2019a).

In riparian ecosystems, the dense shade and low litter quality provided by *R. ponticum* can alter detritic food webs and lower algal production and consumption (Hladyz et al. 2011). Leaves accumulate in freshwaters as native species do not consume it much (Doherty-Bone et al. 2018), thereby altering habitat structure and benthic food web (Hladyz et al. 2011). The aquatic ecosystem can even shift towards a “novel ecosystem” since some invasive alien crustacean species, such as *Pacifastacus leniusculus* and *Eriocheir sinensis*, consume dead leaves (Doherty-Bone et al. 2018).

Since *R. ponticum* acts as an intermediate “foliar” host for the phytopathogenic oomycetes *Phytophthora ramorum* (see above), it acts as a reservoir of the “sudden oak death” disease in invaded forests (Williams et al. 2010). It can thus facilitate the wind-mediated infection of several tree species such as oaks, larches, chestnut or beech (Desprez Loustau et al. 2018). This oomycete was first reported in 1990 in Europe and severely damaged larch plantations in the UK (Grünwald et al. 2019). Several cases have been reported in France over the last decades, mainly in the Finistère department (Desprez Loustau et al. 2018). There, *Phytophthora ramorum* was detected for the first time in 2017 on Japanese larch (*Larix kaempferi*) (Schenck et al. 2018). From 27% of the trees infected in May 2017, the proportion reached 42% in September 2017, motivating the clear-cutting of approximately 50 hectares of Japanese larches (Saintonge et al. 2020). The western (i.e. coastal zone along the English Channel) and southern parts (e.g.

Montagne Noire and Cévennes) of France appeared to be both climatically favourable to *P. ramorum* and to contain sensitive forest species, such as larch and chestnut (Desprez Loustau et al. 2018).

Succession

Rhododendron ponticum invasion can stop the natural forest succession by drastically reducing the seed germination and seedling recruitment of native trees and shrubs (Stephenson et al. 2006; Stout et al. 2006). For example, in their study Vacek et al. (2020) indicate that the natural regeneration of Turkish beech forests is limited by a dense understory of *R. ponticum*. Even decades after *R. ponticum* removal, the understory plant communities did not recover their original composition, possibly due to seed limitation and the rapid formation of a bryophyte layer (Maclean et al. 2017a, 2018b), but also because of the re-invasion by *R. ponticum*. For example, in Killarney National Park, despite active controlling operations undertaken since the 1990s, 10 hectares of forest are still invaded.

Health

Honey made with *R. ponticum*'s nectar is toxic and has been called “Mad honey” or “deli bal” in Turkish (Mermoz 2015). Mad honey poisoning was first described in 401 BC by Xenophon, after his soldiers (the 10000) have suffered from vomiting, diarrhoea and hallucination after eating rhododendron honey (Gunduz et al. 2011). In 65 BC, 1000 Roman soldiers of general Pompey were killed by Persian villagers after being rendered inert by the Mad honey they ate. These symptoms are attributed to grayanotoxins, which cause neurotoxic and cardiovascular disorders (Jansen et al. 2012; Yaylaci et al. 2014; Küçük et al. 2018). Few cases of poisoning have been reported in the invasive range, probably because bees are unable to reach the nectar, unlike long-tongued bumblebees (Elton 1958). The poisoning by grayanotoxins is lethal to cattle and pets, but not to humans.

Economic impacts

The main economic impact of *R. ponticum* invasion concerns forestry, through direct decreased regeneration and recruitment (Barron 2007; Vacek et al. 2020) and indirect effects via tree mortality induced by *Phytophthora ramorum* (Grünwald et al. 2019), of which *R. ponticum* is a recognized host-producer (Higgins 2008). Management operations that aim at eradicating the species from invaded stands (woodlands and protected natural areas) also represents a huge cost. A positive impact has been suggested, through entrance fees in parks during the flowering period of the species (Dehnen-Schmutz et al. 2004). Furthermore, *R. ponticum* can be a marginal source of income, via, for example, the sale of wood, chippings, and seedlings (Dehnen-Schmutz et al. 2004).

Legislation

Rhododendron ponticum is listed under Schedule 9 to the Wildlife and Countryside Act 1981 with respect of England and Wales. According to Section 14 of the Act, it is an offence to plant or otherwise cause this species to grow in the wild. In Ireland, *R. ponticum* is one of the 35 invasive plant species mentioned under the Third Schedule of the European Communities (Birds and Natural Habitats) Regulations 2011, which lists non-native species subject to restrictions under regulations 49 (Prohibition on introduction and dispersal) and 50 (Prohibition on dealing with and keeping this species). In Scotland, the Wildlife and Countryside Act 1981 (amended by the Wildlife and Natural Environment (Scotland) Act 2011) makes it an offence to sell any listed invasive species, including *R. ponticum*. In France, there is no regulation for *R. ponticum*, but the National Botanical Conservatory of Brest (France) advises against planting it near forested areas on acidic soils.

Since 2012, *R. ponticum* is on the EPPO Observation List of invasive alien plants. Although it is regarded as a threat and an invasive alien plant in several countries, *R. ponticum* is currently not

considered by the Regulation (EU) no. 1143/2014 on the prevention and management of the introduction and spread of invasive alien species.

However, an emergency legislation was introduced in 2002 (Decision 2002/757/EC, last amended by 2013/782/EC and 2017/728/EU) to prevent the introduction and the spread of *Phytophthora ramorum* within the EU, an oomycete responsible for the sudden oak death and larch dieback, and for which *R. ponticum* is a foliar host (Purse et al. 2013; Desprez Loustau et al. 2018; see above).

Management

The management of *R. ponticum* is debated in the public opinion since its aesthetic bloom makes it attractive to people (Bremner and Park 2007). Several control methods have been experimented, but with a relatively low rate of success since post-clearance re-invasion is frequent due to seedling recruitment from the soil seed bank or seed rain, and resprouting from stumps or suckering from roots (Cross 1981; Compton et al. 1998). Removal of *R. ponticum* is costly and time-consuming, so it

Table 2. Suggested priority and control options based on *Rhododendron ponticum* development and invaded site conditions. Adapted from Edwards (2006) and Long and Williams (2007).

Invasion stage	Invasibility	Active layering	Fertility	Visual aspect of rhododendron population	Priority for treatment	Treatment (version de base)
No plant	Low (no rhododendron nearby, low habitat suitability)	-	-	No visible individual	Very low	None
	High (fertile rhododendron nearby and presence of regeneration microsites: moss mats, bare organic soil, decaying stump)	-	-		Low	Monitoring and manual control (hand pulling) if seedlings are present
Colonisation (<1.3m high, <1.5m radius)	Low to high	no	no	Isolated individuals or small bushes	Low	Avoiding canopy openings and soil mechanical disturbances.
	Low to high	no	yes	Small bushes	Low to medium	Manual control (hand pulling) or, whenever impossible, herbicide control (foliar herbicide treatment)
	Low to high	yes	yes or no	Rapidly extending bushes	Medium	
Growing populations (>1.3m high, no access to individual stems)	Low to high	no	yes or no	Isolated bushes	Medium	Manual control (manual cutting) and herbicide control (stem injection, cut stump treatment, or foliar herbicide treatment)
	Low to high	yes	yes or no	Coalescent, extended bushes	High	
Mature populations (>1.3m high, stem basis diameter >3cm diameter)	Low to high	no	yes or no	Isolated bushes	Medium	Mechanical control (grubbing, mechanical flailing, lever and mulch)
	Low to high	yes	yes or no	Rapidly extending bushes	High	
Regrowth from stumps and roots	Low (no rhododendron nearby, low habitat suitability)	-	-	Resprouts or root suckers	High	Mechanical control (grubbing)
	High (fertile rhododendron nearby and presence of regeneration microsites: moss mats, bare organic soil, decaying stump)	-	-		High	Manual control (manual cutting) and Herbicide control (foliar herbicide treatment for old cut stumps or stump herbicide treatment for freshly cut stumps)

Invasibility refers to both habitat suitability and propagule pressure. Fertility refers to the production of viable seeds.

is difficult to treat large areas. The method must be chosen carefully, according to the intensity of the invasion and constraints imposed by the invaded site. Decision tools have been elaborated in order to help land managers (Edwards 2006; Long and Williams 2007) (Table 2). For example, newly cut stumps are considered as a priority target for treatment, before resprouts reach sexual maturity and become seed sources for the invasion of adjacent areas (Edwards 2006). Overall, the monitoring of established populations is recommended to estimate their tendency to spread. Seedlings and saplings can be easily uprooted. Non-mature bushes (i.e. individuals of short stature that do not reproduce sexually) can be manually or mechanically extirpated or alternatively chemically treated, especially when the habitat is vulnerable to invasion. Mature extended bushes can be cut down, but chemical treatment of stumps is often needed to prevent from resprouting.

Prevention and early detection

First, given the appreciated aesthetic value of *R. ponticum* by people, it is essential to prevent new sources of introduction, and thus encourage the use of alternative plants (Long and Williams 2007). Second, since *R. ponticum* is a particularly difficult species to eradicate once established, early detection is crucial to avoid the need for extensive and costly future control operations (Thomson et al. 1993). The vulnerability of seedlings to competition and drought is an asset for managers (Cross 1975). Prevention relies on the identification of sites vulnerable to *R. ponticum*. This can use niche-based species distribution models (SDM) and GIS-based decision support (Edwards and Taylor 2008). A recent study has focused on the current and future distribution of *R. ponticum* in Wales, taking into account land cover and land use data, in association with climate data (Manzoor et al. 2021). The amount of suitable habitat for *R. ponticum* is likely to decrease or increase by 2030, depending on the scenario of climate change and future land cover and use considered. For example, an increase in forest cover would favour the expansion of *R. ponticum*, whilst a decrease in forest cover and the conversion of coniferous to deciduous forests would prevent it. Several studies used simulation models to assess the spread of *R. ponticum* and its drivers, as well as the different control strategies (Griffin 1994; Stephenson et al. 2006, 2007; Harris et al. 2009, 2011; Purse et al. 2013; Haffenden 2015; Manzoor et al. 2018, 2020). These models can be used for management, especially to identify the most vulnerable habitats. Such models

may help managing not only the invasion of *R. ponticum* but also the spread of *Phytophthora ramorum* and *P. kernoviae* (Purse et al. 2013).

Manual removal

Manual removal by cutting is a costly and time-consuming method with limited effectiveness on mature individuals (Eşen 2000), and further stimulates active resprouting from stumps (Rotherham 1983). However, this method minimizes soil and seed bank disturbance, thus favouring the regeneration of forests (Vacek et al. 2020). It is recommended to remove mature individuals first (Edwards 2006), to prevent flowering and seed production (Stout 2007b). Removal of the flower heads after flowering of sexually mature individuals prevents seed dispersal and thus the establishment of new populations (Barron 2007).

Manual methods can be combined with herbicide application, to avoid resprouting (Compton et al. 1998; Dehnen-Schmutz et al. 2004). In the British Isles, burning is commonly combined with cutting methods to avoid resprouting (Eşen et al. 2006).

For young individuals, hand pulling is a cheap method that allows access to areas inaccessible to machinery and avoids the costs and collateral damage associated with the use of herbicides, but it may be labour extensive and is limited by the size of the plant and soil conditions as it requires the complete removal of plant which may otherwise regenerate (Higgins 2008).

Mechanical control

Different techniques, such as brush raking and brush lading, winching, excavating, chopping, grubbing and flailing with machinery are used for the control of *R. ponticum* in the British Isles but also in Turkey (Tabbush and Williamson 1987; Eşen et al. 2006). Mechanical removal can facilitate forest regeneration on the short term, but the long-term benefit is more questionable (Eşen et al. 2006). The passage of heavy machines across forests may affect the regeneration and growth of trees (e.g. due to soil compaction, pollutant emission, formation of ruts and puddles). Furthermore, the low accessibility of some sites (e.g. on steep slopes or remote areas) and the cost must be considered with this method. Mechanical scarification of the topsoil by bulldozers has been proposed, but exposes to soil erosion and challenges the long-term maintenance of forest productivity (Eşen et al. 2006).

Herbicide application

Herbicides, mainly glyphosate, imazapyr and triclopyr, have been widely used to control *R. ponticum*. They are applied by foliage spray or stump treatments

(Tabbush and Williamson 1987). This application must be done on the entire foliage so that the bush dries out completely, or on as many stems as possible, and a regrowth treatment is usually necessary in the following years (Tabbush and Williamson 1987). Foliar application has proven effectiveness to control *R. ponticum* (Eşen and Zedaker 2004), despite the waxy cuticle of its leaves, which prevents the absorption of herbicides (Tabbush and Williamson 1987). Nevertheless, their toxicity and persistence in soils should be considered before application, and their use may damage other plants. Stump treatment has the advantage of being more targeted and to induce a slow death, allowing gradual changes in moisture and light conditions, which is believed less impacting on the native biota (Long and Williams 2007).

Biological control

Robinson (1980) suggests that planting trees with dense canopies can help limit or even eliminate *R. ponticum*. This seems, however, counterintuitive since the species is highly shade-tolerant.

Several mycoherbicides are being tested in the UK for biological control (Eşen et al. 2006, citing Evans 2003). Field trials using the fungus *Chondrostereum purpureum* to prevent resprouting returned no significant effect (Willoughby et al. 2015). *Cryptosporiopsis* sp., a fungus isolated on *R. ponticum* in Windsor Great Park, Berkshire, has been suggested for biocontrol (Seiser and Evans 2003).

In isolated areas such as Lundy, Compton et al. (1998) suggest the use of *Pycnostysanus azaleae* (bud blast disease; see above) and its vector to try to slow down the spread of *R. ponticum*.

Post-clearance monitoring and restoration

Rhododendron ponticum regenerates easily from root fragments and stumps (Jones et al. 2019b). Clearance may facilitate its recolonization by inducing suitable conditions for seed germination (Compton et al. 1998; Harris et al. 2009), such as bare ground with moss mats (Stephenson et al. 2006).

It is thus necessary to restore habitats following *R. ponticum* clearance to retrieve the original plant community, and a long-term plan must be considered, with active surveillance over more than 8 years (Jones et al. 2019b). Bryophytes and lichens can recover within a few years, as demonstrated for the epiphytic community of the Atlantic oak woodlands, which recovered about 15 years after *R. ponticum* removal, with similar or even greater total cover and species richness (Maclean et al. 2017b). The fungal community, on the other hand, hardly returns to its previous stage (Monk et al. 2014). The native understory plant community (and in particular forbs and grasses), fails

in general to return to its original composition, even after 30 years (Maclean et al. 2017a, 2019). Adding native seeds (Maclean et al. 2018a) combined with the creation of suitable germination sites (Maclean et al. 2018b) have been shown effective for restoring native vascular plant communities, but it requires a case-by-case assessment of each site where *R. ponticum* is controlled (Maclean et al. 2019). Adding activated carbon against allochemicals has no proven effect (Maclean et al. 2018b).

Side effects of control operations must also be considered, such as changes in light availability and humidity due to rhododendron extirpation and damages caused by the control method used (e.g. toxicity related to the use of pesticides, physical damage by machines) (Long and Williams 2007).

Control costs

Control campaigns are very expensive. First, the cost depends on the method used to control *R. ponticum* (manual, mechanical, chemical, other), the size and accessibility of sites to be treated, and their level of invasion (Stephenson et al. 2006). Second, the cost depends on the method of material removal (Dehnen-Schmutz et al. 2004). Third, post-clearance restoration and surveillance, and often re-treatment, further increase the costs for control (Jones et al. 2019b). Controlling *R. ponticum* has been estimated between £150 and £10,000 ha⁻¹ in the UK (Dehnen-Schmutz et al. 2004; Parrott and MacKenzie 2013). In their study, Williams et al. (2010) estimated that the annual cost of *R. ponticum* removal in the UK is just over £8.6 million. A study at Snowdonia National Park (Wales) in 1988 has estimated that the eradication would cost £30 million (Simons 1988).

Conclusion

Rhododendron ponticum has a long history of invasion in the British Isles but is now an increasingly successful invader in continental Europe. Consistently, many studies have focused on *R. ponticum* in the British Isles, but few elsewhere in Europe. Climate change, particularly mild, humid winters, seem to promote its success on acidic soils under oceanic climate conditions, which offer similar ecological conditions as in the native range. *Rhododendron ponticum* invasion severely impact forest dynamics and biodiversity, while significantly altering ecosystem functioning and services. Anticipating *R. ponticum* invasion is essential to prevent its further spread. For this purpose, it is necessary to avoid its direct introduction in or nearby acidophilous woodlands, which are the more vulnerable habitats. Where it is already present, niche-based models coupled with GIS tools can help in the early detection of spread, thereby allowing effective control measures

(Manzoor et al. 2020). Further work is needed to better document population dynamics, especially the circumstances under which recruitment is successful. The plant's ecophysiology requires further investigation, to test whether the species is better adapted than native shrubs and even "pre-adapted" to the developing climate conditions in Europe. Relationships with other biota in the recipient ecosystems remain largely unknown, though it is crucial to understand the impact of invasion on ecosystem functioning and thus to evaluate the relevance of effective control operations.

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