Supplementary Material

Risk is in the eye of the assessor: comparing risk assessments of four non-native tree species in Germany

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Literature review of the four non-native tree species red ash (*Fraxinus pennsylvanica* Marsh.), princess tree (*Paulownia tomentosa* (Thunb. ex Murray)), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and red oak (*Quercus rubra* L.)

The literature collection is divided into the following sections for each non-native tree species: (1) Native range, (2) Pathways of introduction, (3) Distribution, (4) Soils, climate, light, (5) Natural regeneration, (6) Dispersal pathways, spreading mechanisms, dispersal distances, (7) Impacts (8) Potential future effects (9) Invasive history elsewhere, (10) Available control measures, and (11) Further research requirements. The review of this literature collection is presented in Tables 1-4. Data collected includes all relevant articles related to the topic. However, the collected articles are of variable quality; for example, major conclusions or statements in the literature may be based on the authors' perceptions or qualitative indicators, rather than reliable evidence. Note: if a literature source that was cited in another source was unavailable, we used the following citation: Schenk 1939 as cited in Vor 2015.

Table 1 Red ash (*Fraxinus pennsylvanica* Marsh); Ra=Red ash.

Category	Information
Native range	Eastern North America (Vor 2015)
Pathways of introduction	Red ash ('Ra') was deliberately introduced to Europe at the end of the 19 th century. In Germany it was primarily used as an ornamental tree species, but was initially used between 1870 and 1892 for timber production (Schenk 1939 as cited in Vor 2015). The importance of Ra for forestry purposes decreased over time. However the species was continuously cultivated as an ornamental tree and was used to protect river banks from erosion until the 20 th century (Drescher and Prots 2016, Vor 2015).
Distribution	The current distribution of Ra in Europe is still unclear because: (1) the species may have been widely overlooked and often not well differentiated from the white ash (<i>Fraxinus americana</i> L.) (Prots et al. 2011) and (2) no detailed distribution maps for this species exist for individual European countries (Drescher and Prots 2016). The highest density of Ra stands in Europe can be found in north-east Germany (Reichhoff and Reichhoff 2008 as cited in Prots et al. 2011), in floodplain forests along the Tisza river in Hungary and along parts of the lower Danube in Romania (Drescher et al. 2003, Prots et al. 2011).
	In Germany it is a facultative wetland species, common in alluvial forests and

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Information

marshes (Zacharias and Breucker 2008). The majority of Ra stands are situated along the river Spree and Havel in the area of Berlin and Brandenburg and along the Mittlere Elbe biosphere reserve in Saxony-Anhalt (Schmiedel 2010).

Natural regeneration has been reported in Germany, particularly in the biosphere reserve 'Mittlere Elbe' (Schmiedel 2010, Zacharias and Breucker 2008) and in northern Germany in Bremen, where at least two new generations have become established (Albrecht et al. 2014).

Soils, climate, light

Ra is described as a pioneer species which grows on alluvial soils along rivers which are typically flooded once or twice a year. However, this species is able to grow under different site conditions and can also form part of a climax forest community (Schmiedel 2010). In its native range Ra is distributed over a large area with average annual rainfall in the range of 500-1800 mm and an average annual temperature between 6 and 21 °C.

In Germany Ra is relatively undemanding in terms of its soil and nutrient requirements on alluvial sites (Vor 2015). Unlike native European ash (*Fraxinus excelsior* L.) in Germany Ra can grow throughout long periods of wet or dry conditions (Arndt 2009, Wright 1965 as cited in Vor 2015) and in soils with low or high pH (McComb 1949 as cited in Schmiedel 2010).

The major factors that regulate the establishment of Ra in Germany are: (1) light, (2) water and (3) species composition (see also 'Impacts'). Ra seedlings need sufficient light and moisture to establish themselves (Vor 2015). Seeds can even germinate in flooded conditions (Schmiedel 2010). Ra is considered a less shade-tolerant tree species (Kennedy 1990 as cited in Vor 2015). It is very light demanding and can spread rapidly in forest gaps (Prots et al. 2011). This species has high light requirements, particularly in the seedling phase (Schmiedel 2010). With increasing age the need for light decreases, thus the competitiveness of Ra decreases (see also 'Impacts') (Vor 2015). These characteristics allow this species to settle quickly in free stands and migrate into more or less dense woodlands (Prots et al. 2011), but not into closed forest stands (Vor 2015).

In its native range Ra can establish itself in climax forests, however its percentage of forest cover decreases with increasing forest stand age (Gucker 2005).

Case study

Mittlere Elbe

In the Mittlere Elbe biosphere reserve successful natural regeneration is more common in cleared and open habitats compared to closed forest sites (Schmiedel 2010). Regeneration is particularly successful on cleared and open habitats, on very moist stands with nutrient-rich soils in regularly flooded areas (Schmiedel 2010, Zacharias and Breucker 2008).

Ra regeneration is marginal in well-established forest stands with continuously closed canopies, dominated by (fast growing) native tree species, which cover different age classes, such as dry formations of the Querco-Ulmetum forest stands (e.g. pedunculate oak (*Quercus robur* L.), fluttering elm (*Ulmus laevis* Pall.), field elm (*Ulmus minor* Mill.) (Zacharias and Breucker 2008)).

Regeneration potential

Red ash reproduces both vegetatively through coppice shoots and regrowth from root material and via seeds. Ra starts fructifying at 6-7 years old and produces around 280,000 seeds per tree (Schmiedel 2010).

Information

Dispersal pathways, spreading mechanisms and dispersal distances

Pathways

Ra has been introduced both intentionally through forestry and ornamental cultivation, and unintentionally by humans, e.g. via the transport of top soil by car for river channelization. Establishment of this species can be indirectly encouraged through the creation of open micro-sites and by eliminating riparian vegetation (Prots et al. 2011). Further spread is possible via wind and water (Schmiedel et al. 2013, Schmiedel and Tackenberg 2013).

Spreading mechanisms and distances

Ra spreads in the form of seeds (both anemochorous and hydrochorous) and also vegetatively via coppice shoots and regrowth from root material. The seeds are dispersed by wind and can be carried distances over 100 m in their native range. In native ranges vegetative regeneration is typically coupled with periodic disturbances such as drought, fire or logging (which increases light availability) (Gucker 2005). A simulation by Schmiedel and Tackenberg (2013) demonstrated possible spreading (anemochory) distances of 120-250 m in Germany. In a city forest in Bremen an average seed dispersal distance of 100 to 140 m to the mother tree was measured by Albrecht et al. (2014). Natural regeneration and establishment of Ra is likely in areas within a radius of <50 m from the seed source (Schmiedel et al., 2013). Water is considered to be the most important secondary pathway for long-distance dispersal: the seeds, which float well, can be transported several kilometres in water (Schmiedel and Tackenberg 2013). Since the majority of Ra stands in Europe are probably connected by river corridors, hydrochory (the dispersal of seeds by water) may be an important factor explaining the successful spread of Ra in central European floodplain forests (Schmiedel and Tackenberg 2013).

Impacts

Summary

Reports on the invasiveness of Ra in central Europe are mainly based on its ability to spread (quickly) in alluvial forests. The negative long-term impacts of this species on biodiversity are mainly presumed and have yet to be scientifically proven (but see its invasive history in Austria).

Competition

Ra has spread in typical alluvial near-natural floodplain forest communities in eastern Germany and has established dominant stands at sites where these trees were planted in the past (Schmiedel et al. 2013). Competitive advantages are likely in very light or very humid areas (flood areas) of the hardwood alluvial forest in the 'Mittlere Elbe' Germany (Schmiedel and Schmidt 2010). Ra is considered to develop into the dominant tree species on light and regularly flooded sites (i.e. floodways) in hardwood alluvial forests. This is thought to particularly occur within Phalaris arundinaceae sub-communities of oak-elm forests, where for example the field elm is no longer present and the loss of typical species compositions is considered likely (Schmiedel 2010). The tolerance of Ra to flooding seems to enable this species to persist in very wet alluvial sites, which are no longer suitable for the reestablishment of native broadleaf tree species (Vor 2015). The impact Ra could have on native biodiversity, e.g. whether the species is able to compete with native tree species in older forest stands, is not yet known (Schmiedel 2010, Vor 2015). The presence of Ra may negatively impact the natural regeneration of pedunculate oak seedlings (Schmiedel & Schmidt, 2010). However Ra seems to be less competitive on drier sites with older forest stands in Germany and this species will most likely not be able to persist under such site conditions (Müller 2011, Vor 2015).

Category Information Ecosystem In vitro experiments revealed that Ra has an allelopathic potential, meaning the alteration ability to inhibit the germination or growth of neighbouring plants through the (abiotic and release of substances into the surrounding environment. However this effect has yet to be proven under field conditions (Csiszár 2009). biotic) The excessive growth of this species in sunken hardwood alluvial forest sites e.g. sinks or floodways causes: (1) long-term structural habitat changes to sites, which were originally treeless and (2) the loss of natural boundaries (Schmiedel and Schmidt 2010). For such sites a decline in the typical plant species composition of the herb layer would also be expected (Schmiedel and Schmidt 2010). Potential See 'Competition' above. impact in near-natural ecosystems To date, pathogen transmission has not been proven in Germany (Vor 2015). Transmission of pathogens Although likely not co-introduced, Ra is a potential host of the emerald ash borer or parasites (co-(Agrilus planipennis Fairmaire) in Europe. Emerald ash borer, native to Asia, is now introduction) rapidly spreading in European Russia threatening European ash as well as introduced Ra. However, until now the majority of emerald ash borer infestations have only been observed on introduced Ra trees (Musolin et al. 2017, Orlova-Bienkowskaja 2014, Valenta et al. 2016). In Serbia (Bieńkowski and Orlova-Bienkowskaja 2018, Petrović-Obradović et al. 2007) and Spain (Hidalgo and Durante 2012) Ra was recently identified as the first initial host of the woolly ash aphid (Prociphilus fraxinifolii (Riley)), which is native in the U.S., Canada, and Mexico. Whether this aphid could also be a threat to European ash or other species is unknown. According to Hałaj and Osiadacz (2017) the aphid has already spread over a large area in Europe and will soon enter Germany. Since this aphid has only recently been detected it is unlikely to have been co-introduced with Ra. So far, this aphid species is considered harmful to European ash (Hałaj and Osiadacz 2017) and is potentially more widely distributed in Europe due to its use of Ra as a host plant (Hidalgo and Durante 2012). Hybridization Ra does not hybridize (Schmiedel 2010). Potential According to Schmiedel et al. (2013) Ra will continue to establish in European future effects floodplains because the natural regeneration of this species is more tolerant to flooding than the recruitment of native species such as European ash. Ra will create novel habitats where this tree species was absent in the past. Ra is mainly reported to grow at elevations of 98-199 meters above sea level in the Ukraine - global warming, increased tourism and industrial activity may contribute to shift in the distribution range to higher elevations (Prots et al. 2011). Large scale forestry plantations could encourage future expansion of Ra. The straightening of Transcarpathian river systems can result in increased amounts of fine sediment and nutrient deposition in areas further downstream. These soil changes make areas very suitable for the establishment of Ra and make natural riverine habitats vulnerable to invasion by Ra, including riverine forests (Prots et al. 2011).

According to Prots et al. (2011) Ra will likely spread in natural ecosystems in the

long term, with or without human intervention.

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Invasive history elsewhere

According to Prots et al. (2011) Ra is one of the most rapidly spreading introduced woody species in central Europe of the last 25 years. The spread from cultivated sites to new locations has been reported in several European countries, e.g. in the Czech Republic (Möllerová 2005), Croatia (Kremer et al. 2006b), Serbia (Batanjski et al. 2015), Austria (Essl et al. 2002), Ukraine (Prots et al. 2011), Hungary (Török et al. 2003), Romania (Drescher and Prots 2016) and Poland (Sienkiewicz et al. 2001 as cited in Schmiedel 2010). The spread of this species has also been reported outside of Europe in Russia (Borisova 2011), Brazil (Kalesnik and Aceñolaza 2008) and Kenya (Mullah et al. 2014).

More details

- This species is established in Croatia (Kremer and Čavlović 2005). On heavy and wet sites Ra demonstrates increased growth rates compared to native tree species (Kremer et al. 2006a). Since the start of the 20th century Ra has been planted in swamps in the Danube basin and along the river Drava, where the European ash could not survive. From here it has spread to many other locations; seeds were likely spread via flood water (Kremer et al. 2006b).
- Classified as invasive in the Czech Republic (Pergl et al. 2016, Pyšek et al. 2002), Ra has been identified as one of the most expansive and invasive non-native species in the Czech Republic (Möllerová 2005).
- Ra is spreading increasingly in fragile wet habitats in Serbia, it has established stable populations in riparian habitats in a nature reserve, with an average cover of 95 %. These habitats are considered to develop into a Ra dominated forest, further preventing the growth and regeneration of natural forest communities (Batanjski et al. 2015). Ra is considered to be invasive in the forests of Belgrade (Nikolić et al. 2010). Ra individuals were recorded in a protected natural area of Mt. Avala in several different forest communities (i.e. Rusco-Quercetum frainetto-cerris, Rusco-Querco-Carpinetum, Conifer plantations and Meadow vegetation (Glišić et al. 2014). Note: here the species is not differentiated from white ash.
- Ra is considered an invasive tree species in **Austria** that poses a conservation threat as it invades natural and semi-natural habitats, where it competes with and replaces native species (Essl et al. 2002). Ra is established and spreading in the Danube-Auen National Park. This spread is likely further promoted by the clear cutting of Salix-Populus stands and general deforestation, but also by the presence of poplar hybrids which increase light availability (Prots et al. 2011). In the protected near-natural old growth forest 'WWF –Schutzgebiet Marchauen Marchegg' Ra will likely spread further. It has already replaced old pedunculate oak, flattering elm, silver poplar (*Populus alba* L.) individuals over the last 25 years and it has almost outcompeted narrow-leaved ash (*Fraxinus angustifolia* Vahl) in the lower age classes (Drescher et al. 2005 as cited in Prots et al. 2011). Naturalized populations are present in urban areas of Vienna, particularly along the Danube and the Danube canal, as well as on ruderal sites (Essl and Stöhr 2006). A few naturalized individuals have been observed in upper Austria, close to cultivated trees (Essl and Hauser 2005).
- In the **Ukraine** Ra has been reported in urban railway areas (Denisow et al. 2017) and in floodplain habitats (Prots et al. 2011). In the Transcarpathian region Ra

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was planted in forests and used as an ornamental tree in cities. Ra escaped into nearby floodplain habitats four to seven years after planting and is now well established and still spreading. This species is expected to further expand in riverside channels and damp roadside habitats. Active management is only possible at the early stage of invasion and only feasible at a small scale (Prots et al. 2011).

• Ra is considered a problematic invasive species in Hungary because it has spread into nature reserves (i.e. floodplains, gallery forests, disturbed bogs and marshes) (Török et al. 2003). Ra has been recorded in several types of habitat including: marshes, eu-and mesotrophic wetlands and sedge beds, dry and semi-dry closed grasslands, riverine shrublands and woodlands (where >10% of the habitat is endangered by Ra), mesic deciduous woodlands in the lowland, and steppe woodlands (Botta-Dukát 2008). Ra is the dominant tree species in tree layer of riverine forests along the river Tisza where it successfully regenerates and has established in the shrub and herb layer of the forests (Drescher, et al. 2003).

In a 80 year old unmanaged riparian forest reserve, within a National park, native tree species were preferably used by the native Great spotted woodpecker, compared to Ra, which was almost not used (Ónodi and Csörgő 2013). According to Ónodi and Csörgő (2013), Ra reproduces faster and occurs more frequently than native tree species in the National Park. Ra influences chemical soil traits and establishes under the canopy of native tree species, seedlings thus shade the ground and prevent the establishment of saplings of native tree species. As a result there are very few saplings of native ash species in the study area. These (increasing) ecosystem changes will have an effect on Great spotted woodpeckers, which play a key role in alluvial forest communities.

- Ra is considered invasive in Romania (Third National Report to the UNCBD 2005
 as cited in Preda et al. 2017). It has spread and continues to spread in the fluvial
 delta in the biosphere reserve Danube Delta (Drescher and Prots 2016).
- The spread of Ra is considered to be connected with the decrease of native species in alluvial forests in **Poland** (Sienkiewicz et al. 2001 as cited in Schmiedel 2010).
- Ra is increasing in its occurrence in **Moldova**, particularly along roads, railways and ruderal areas (Sîrbu and Oprea 2010).
- Ra forms dense thickets in anthropogenic habitats and in natural communities in Russia in the upper Volga region (Borisova 2011).

Available control measures

The cultivation of this species is no longer recommended (Vor 2015).

The eradication of Ra from floodplain habitats is considered impossible at its current state of occurrence in central Europe, however the need to control its spread in areas of high conservation value is recognised (Drescher and Prots 2016).

Any form of risk management can only be effective at the early stage of invasion, or when dealing with a low number of individuals (Prots et al. 2011). Eradication measures are however challenging since the species can regenerate from tree stumps after felling (Zacharias and Breucker 2008). The following measures are recommended to avoid the further spread of Ra when new floodplain areas are

Category	Information
	planted: (1) the promotion of native tree species and (2) the maintenance of a high canopy cover in the tree layer, with several native tree species which cover all ages classes (Zacharias and Breucker 2008).
Further	Long-term monitoring of the impact of Ra on native biodiversity and habitats in
research	alluvial hardwood forests is necessary, alongside research on the possible future
requirements	spreading of this species (Schmiedel 2010).

Table 2 Princess tree (Paulownia tomentosa (Thunb. ex Murray) Steud.); Pt=Princess tree.		
Category	Information	
Native range	Central and western China (Stimm et al. 2015).	
Pathways of introduction	Princess tree ('Pt') was deliberately introduced to Europe as an ornamental plant at the beginning of the 19 th century. In Germany the tree was/is tested in trials for its potential use as a source of biomass for energy production and high valuable timber (Stimm et al. 2015).	
Distribution	This species is distributed throughout Europe and natural regeneration has been recorded in Austria, Switzerland, France, Italy, Romania, Bulgaria, the Czech Republic and Spain (Essl 2007, Gyuleva et al. 2012, Jeanmonod and Schlussel 2006, Nagodă et al. 2014, Pyšek et al. 2002, Wittenberg et al. 2006). In Germany Pt was first recorded as having naturalized in 1925 (Kiermeier 1977 as	

In Germany Pt was first recorded as having naturalized in 1925 (Kiermeier 1977 as cited in Stimm et al. 2015). It is currently established in the German states of Baden-Württemberg, Hessen, Nordrhein-Westfalen and Saxony; with spontaneous occurrences recorded in Berlin, Bavaria, Niedersachsen and Rheinland-Pfalz (Buttler and Thieme 2018). Naturalized populations in Germany have increased since the 1970s and 1980s particularly in the warmer regions, in the states Rheinland-Pfalz and Baden-Württemberg (Kiermeier 1977 as cited in Stimm et al. 2015). Here this species is predominantly present in urban areas, industrial wastelands and across railways, mainly due to the relatively warm temperatures in cities in general, but also because Pt is mainly planted in urban areas (Richter and Böcker 2001).

Soils, climate, light

Pt is a pioneer species with a wide physiological range: in its native range it is able to tolerate temperatures ranging from -25°C to 40 °C and precipitation ranging from 500 to 2,500 mm per annum. However, younger plants are threatened by frost and can only tolerate extreme temperatures of -10°C (Stimm et al. 2015). Pt prefers moist and fertile, base-rich soils, however it can tolerate high soil acidity, drought and low soil fertility (Innes 2009). Seedlings grow well within a pH range from 7.0 to 4.0, but little or no growth was observed in garden experiments at a pH of 3.0 (Melhuish et al. 1990).

In Germany established Pt populations are often found in urban areas, particularly in the warmest regions, with minimum annual average temperatures of 9-10 °C (Richter 2002). Key limiting factors for the invasive success of this species are winter minimum temperatures as well as early and late frosts (Richter and Böcker 2001). Ideal conditions for the establishment of Paulownia species comprise sites with aerated sandy soils, without wind and with sufficient sunlight (Schweiger 2009 as cited in Stimm 2013). Dense leaf litter prevents germination. Seedlings require exposed mineral soil with little to no leaf litter (Kuppinger 2008) for

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germination and full sunlight for both germination and growth; thus Pt frequently establishes after disturbances which create such conditions. Pt is not able to establish in forest systems as it cannot persist where the canopy is too dense to regenerate. Stimm et al. (2015) considered Pt as shade intolerant and therefore not present in dense forests, whereas Longbrake and McCarthy (2001) considered this species to establish populations even in low light conditions.

Regeneration potential

Pt can reproduce from seeds or vegetatively, via regrowth either root or stem material. It is considered one of the world's fastest growing tree species (with increments of >1m in height per year), however only under specific conditions (see above 'Climate, soils and light'). Pt forms new shoots at an early age and when regenerating vegetatively from coppices, in such cases growth of up to 5 m per year is considered possible (Bean & McClellan 1996 as cited in Innes 2009). A single tree is capable of producing an estimated twenty million seeds (Pier 2005) at the age of 3-5 years old (Rebeck 2012) and forms a persistent seed bank (Longbrake 2001). According to Innes (2009) seeds remain viable for 2-3 years whereas others have estimated viability up to 15 years (Lovenshimer and Madritch 2017).

Dispersal pathways, spreading mechanisms, dispersal distances

Pathways

The only current significant pathway of introduction in Germany is ornamental planting. Pt mainly spreads in urban areas where it is planted as an ornamental tree, but it is also capable of spreading long distances along railways from the urban sites where trees are originally planted (Stimm 2013, Stimm et al. 2015).

Spreading mechanisms and distances

Pt can propagate vegetatively. Seedlings are able to spread from 4 weeks after germination (Innes 2009) and shoots can grow more than 4 m in a single season (Pier 2005), which enables the species to persist after disturbance. This species has seeds that are easily transported long distances by wind and water (Pier 2005). In the U.S. seeds have been recorded to disperse up to 3.5 kilometres from mature individuals (Anjozian 2010, Kuppinger 2008). In urban areas in Germany, the majority of seedlings are found within 200 m of the mother plant (Richter and Böcker 2001). The uncontrollable spread of this species in Germany via root suckers is considered unlikely under forest conditions. Spreading due to light seed weights is estimated to play a more important role, but most likely only outside of forests (Bork et al., 2015).

Impact

Summary

Almost no information on the impact of Pt on native biodiversity in Europe is available. Overall, any potential effects of Pt in Germany need to be differentiated into effects on forest sites and effects on open habitats. In forest areas with dense canopies Pt is unlikely to successfully establish and spread. Consequently, in such conditions the loss of native biodiversity is unlikely (Stimm et al. 2015). However, in open sites spread of this species and therefore impacts on native biodiversity are possible (see 'Competition' and 'Invasive history in other countries' in the U.S.).

Competition

The formation of adventitious root buds give Pt competitive advantages and it can thus be a successful pioneer in newly disturbed areas (Hu 1959 as cited in TodoroviĆ et al. 2010) where it can form monocultures (CABI 2017). Furthermore, Pt seedlings can grow quickly and create sufficient leaf surface area to suppress the development of species in lower layers of the forest through shading

Category Information (Beckjord et al. 1983 as cited in Innes 2009). Therefore Pt may be a component of early successional communities following disturbances in forests, but would likely be subsequently outcompeted by other tree species that grow taller (Stimm et al. 2015). So far, Pt is mainly found to occur on ruderal sites where only few other native species are found, e.g. in urban areas (Essl 2007, Richter and Böcker 2001). Ecosystem It is estimated that the large amount of leaf litter produced by Pt can change site alteration specific nutrient availability due to the high nitrogen concentration in the leaves (abiotic and (CABI 2017), which can prevent the establishment of other species but also of Pt biotic) itself (Stimm et al. 2015). Potential Unknown. impact in So far, Pt has not spread in natural ecosystems in Germany (Stimm et al. 2015). semi-natural According to Kowarik (2010) Pt has established within natural vegetation of rock ecosystems formations at the southern edge of the alps, however any spatially explicit information in the publication is lacking. Transmission Pt could potentially serve as host for the invasive stink bug (Halyomorpha halys of pathogens (Stål)) from East Asia, which was first reported in Switzerland and has already or parasites spread to an enormous extent in the U.S. (Wermelinger et al. 2007). Note: this bug (cois probably not co-introduced and a range of host species are possible, including for introduction) example Ailanthus altissima (CABI 2019). Pt is known to hybridise with fortunes paulownia (Paulownia fortunei (Seem.) Hybridization Hemsl.) in its native range (CABI 2017). Seeds of the hybrid *P. tomentosa x fortunei* were used in a trial in Germany, but they were derived form a nursery in the U.S. (Stimm 2013). There is a lack of native congeneric species in Germany and as such no information on hybridization with native tree species is available. **Potential** The ecological effects of Pt could become more important in the future because future effects predicted climate change might allow Pt to spread beyond its current distribution range (Essl 2007, Vicsnjic 2003). The likely extension of cultivation areas for this species in central Europe could increase the potential impact on native populations particularly in marginal sites (Stimm et al. 2015), as has been demonstrated for other introduced species (Kowarik 2003). In order to reduce unforeseeable risks, the expansion of cultivation areas of this species are not recommended (Stimm 2013, Stimm et al. 2015). For example, in open habitats there are indications for a potential invasiveness (Stimm et al. 2015). It is possible that Pt could prove invasive in Europe where it is continuously introduced and cultivated (CABI 2017). **Invasive** Pt is classified as invasive in North America and New Zealand (CABI 2017). In the history U.S. invasion seems to be connected to fire, however, fire is not mandatory for elsewhere successful recruitment (Lovenshimer and Madritch 2017). More details In Austria the number of sites with Pt has increased exponentially since the 1960s. It behaves as a pioneer species and mainly colonizes disturbed areas,

such as synanthropic habitats (habitats associated with humans/human uses) in urban spaces. The invasion of Pt is not yet a nature conservation issue, however further spread into more natural habitats should be carefully

monitored (Essl 2007).

- Pt is subspontaneous (i.e. first generation growing in the wild after having been introduced) in Corsica, **France** (Jeanmonod and Schlussel 2006) and in Paris in urban areas (Muratet 2007).
- Pt is reported to occur rarely (Pyšek et al. 2002) and is listed on a watch list in the **Czech Republic** (Pergl et al. 2016).
- So far, Pt is classified as non-invasive in **Bulgaria**. However, in order to prevent potential negative consequences, further risk assessments for all soil types and climates need to be conducted, and the species requires careful monitoring (Gyuleva et al. 2012).
- In **Romania** Pt is considered as potentially invasive in the future (Nagodă et al. 2014).
- Pt is classified as subspontaneous in Switzerland (Wittenberg et al. 2006).
 Although the species prefers urban areas it has also established in forest clearings (Richter and Böcker 2001). For example, Pt is reported to form forest stands in the coppice forest at lake Lugano (Langdon & Johnson 1994 as cited in Richter 2002) and to rapidly colonize disturbed forest stands after fire in the Swiss Alps (Maringer et al. 2012).
- Pt is classified as an invasive species in **New Zealand** (CABI 2017).
- Pt is classified as invasive in the U.S. in Georgia, Tennessee, Oregon, and Kentucky (CABI 2017). It was originally brought to the U.S. for ornamental purposes in around 1844, but escaped cultivation and has naturalized particularly in the eastern half of the U.S. It has become a permanent part of the landscape and can be found along roadsides, riverbanks, and forest edges; Pt is reported as invasive species in 26 American states (Ding et al. 2006). Measures have been recommended to prevent the further spread of this species (Snow 2015).

Invasion seems to be particularly connected to fire in forests of the eastern U.S. (e.g. Dumas et al. 2007, Hagan et al. 2015, Lovenshimer and Madritch 2017), however fire is not mandatory for successful recruitment (Lovenshimer and Madritch 2017). The post-fire invasive potential can be explained at the germination level since many components of fire stimulate germination of Pt seeds. Nevertheless, post-fire spreading is complex and also depends on habitat conditions (TodoroviĆ et al. 2010).

Pt seems to be able to spread and form forests in disturbed, light sites based on a single introduction (Lovenshimer and Madritch 2017) by forming colonies from prolific root sprouts (Langdon and Johnson 1994). However, it is considered unlikely that Pt will persist beyond the early stages of invasion except in xeric sites (Kuppinger et al. 2010) as it is an early successional species which is often outcompeted by more shade tolerant species in a later stage of succession. Thus, Pt is not able to invade intact forest systems as it cannot persist where the canopy is too dense to regenerate (Neel 2012). Pt can develop into a dominant species in dry and nutrient poor sites since such extreme site conditions exclude most other species (Kuppinger 2008).

Information

Competition

Overall, outcompeting native species is rare; exceptions are xeric sites with naturally exposed and nutrient-poor soils and sunny aspects such as cliffs and rocky outcrops, which can be inhabited by specialized native flora. For example, Pt displaced two rare and endangered native plant species on such sites in the Great Smokey Mountains National Park (Kuppinger 2008 as cited in Innes 2009).

Species richness and Shannon diversity of sampled vegetation decreased in invaded plots compared to non-invaded plots across burned areas in the ecological important region 'Linville Gorge Wilderness Area' in North Carolina (Lovenshimer and Madritch 2017). When Pt seedlings grow fast they can create sufficient leaf surface area to suppress the growth of smaller seedlings due to shading (Beckjord et al. 1983 as cited in Innes 2009). Pt competes with native tree species in disturbed forest areas (Williams, 1993; Langdon and Johnson 1994; Johnson, 1996 in Simberloff 2000); for example it replaces native pines in Great Smoky National Park where natural fires have returned (Simberloff 2000).

Ecosystem integrity

Pt is very susceptible to herbivory in the U.S. (Longbrake 2001) and flowers of Pt are pollinated in North America by a variety of nectar- and pollen-feeding insects (Innes 2009).

Comparison to Europe

According to Stimm et al. (2015) two factors may lead to the greater invasive success of Pt in the U.S. compared to Europe. The first is its large cultivation area in the 1970s and 1980s (Innes 2009) and the second is its invasion of large areas after large-scale disturbances, such as fire (Williams 1993). Disturbances on such a large scale are far more seldom in Europe.

Available control measures

To prevent any ecological risks, Pt should not be cultivated on a larger scale, particularly it should not be cultivated nearby open habitats of high conservation value (Essl 2007, Stimm et al. 2015).

Spread is unlikely in the majority of the forest sites since Pt will not be able to compete against shade tolerant species in the course of succession. Where necessary, seed production can be avoided by girdling (Stimm et al. 2015).

Once the species has established it is recommended to eradicate Pt by pulling out seedlings, removing the entire root by hand before the taproot is well developed, felling the tree close to the ground and repetitive spraying of the remaining stump with herbicides is also recommended (Remale 2005).

Further research requirements

- Careful monitoring of future spread of Pt is recommended by several authors (see above).
- To assess future risks to biodiversity, factors which limit spread of Pt into areas
 of high conservation value should be analysed (Essl 2007).

Table 3 Douglas fir (Pseudotsuga menziesii Mirb (Franco)); Df=Douglas fir.		
Category	Information	
Native range	West and north U.S., south-west Canada (Spellmann et al. 2015).	
Pathways of introduction	Douglas fir ('Df') was deliberately introduced to Europe in 1827. In Germany it was used as an ornamental tree around 1830 and it has been used in forestry since the middle of the 19 th century (Spellmann et al. 2015).	
Distribution	Df is distributed throughout Europe today and it is reported to cover 830,707 ha of forest within Europe (plantations or species presence in a mixed forest) (Hasenauer et al. 2017, Pötzelsberger 2018). The largest areas of Df cultivation are found in France, Germany and the United Kingdom (Bastien et al. 2013 as cited in Da Ronch et al. 2016). In terms of cultivated area it is the most important introduced	

Soils, climate, light

Pfalz (BMEL 2014).

The establishment of Df is mainly regulated by: (1) its limited seed dispersal distance, (2) site conditions, (3) competition with other tree species, and (4) browsing by deer (Knoerzer 1999a, Spellmann et al. 2015).

coniferous tree species in Germany, covering 217,604 ha, i.e. 1.9 % of the total forest area (NFI, 2012) (Figure 1). Areas on which Df is cultivated in Germany (2012) have increased by 19 % since 2002. The proportion of Df in forests varies throughout the federal states in Germany, where it comprises 0.8 % of forest cover in Bavaria, 3.3 % in Baden-Württemberg, 3.6 % in Hessen and 6.4 % in Rheinland-

Df is a semi-shade tree species and seedlings require sufficient light in the early stages of natural regeneration. Therefore, sites with low canopy density and an absent shrub layer are appropriate for germination and establishment. Seedlings need mineral soils, thus suitable sites are those with limited needle litter, surfaces with soil wounding (for example from harvesting timber), but also locations with several stone blocks, or areas on which boulder movements regularly clear the soil surface.

Optimal initial conditions for natural regeneration are found in open coniferous forest sites. Establishment is particularly successful on base-poor and acidic soils with sufficient light availability (e.g. Oak forest in Baden-Württemberg) (Spellmann et al. 2015). In general Df seedlings need sufficient light for successful growth. Thus, management practices such as clearing gaps, thinning or opening the tree canopy and disturbing the soils is beneficial for the naturalization of Df (e.g. Broncano et al. 2005, Jonášová et al. 2006).

Forest areas with a closed canopy, a shrub or herbal layer of vegetation and wet or calcareous soils provide unsuitable conditions. The likelihood of successful establishment of Df decreases with increasing nutrient and water levels. Df is able to tolerate water shortages, but does not tolerate excess water, i.e. (periodically) wet sites. Df is highly sensitive to drought in the germination and establishment stage but once established this species is able to adjust well to extreme droughts (Rigling et al. 2016).

Success of natural regeneration of Df in mixed broadleaf forests is low, particularly in forest areas with dense European beech (*Fagus sylvatica* L.) trees in the understory or in the intermediate layer (Spellmann et al. 2015), or in unmanaged forest reserves, which are often characterized by a closed canopy (Bindewald and Michiels 2018, Endres and Förster 2013).

Information

Case studies

Lower Saxony, Lüneburger Heide (Appelfelder 1999)

- Successful establishment of Df in light coniferous forests (medium success in deciduous forests) in the national park (NP) Lüneburger Heide.
- An increased area of natural regeneration and further spread of Df is expected in the NP in the future as the majority of adult Df trees are not yet fructifying.

Bavaria (Eggert 2014, Endres and Förster 2013)

Based on Bavarian forest inventory data natural regeneration of Df is negligible in state forests: the actual area where Df is naturally regenerating is rather small and has hardly increased between two inventories. Natural regeneration is particularly scarce in closed forest sites and unmanaged forest reserves.

Baden-Württemberg (Bindewald and Michiels 2018, Knoerzer 1999b)

- Successful establishment of Df on base poor and acidic soils with sufficient light availability.
- Negligible natural regeneration, particularly in closed forests (e.g. European Beech stands) and unmanaged forest reserves.
- Natural regeneration has been recorded for two generations of Df in Southwestern Germany (Knoerzer 1999a): In the south of the Black Forest a 30-40 year old Df stand had established through natural regeneration from an adjacent old Df stand and had itself produced fertile seeds.

City forest of Freiburg (Steinmetz and Bauhus 2016)

Although Df is the dominant tree species in the study area and natural regeneration is encouraged by forest management, natural regeneration of Df is limited to a few sites and decreased from 1999-2009 (based on regional forest inventory data).

Regeneration potential

Df only reproduces via seeds and starts fructifying at an age of about 30 years (Appelfelder 1999). The tree produces a mast (many more seeds than normal) on average every 14 years. Df does not establish a long-term seed bank (Starfinger and Kowarik 2011a), as the seeds do not survive more than 3 years in the ground and the majority of seeds die after 1-2 years (M. Karopka, unpublished data, FVA). It is estimated that Df produces 300-3000 viable seedlings per tree per year in Germany (based on a germinating rate of 40-80% of seeds) (M. Karopka, unpublished data, FVA). This value can change considerably when the tree produces a mast.

Dispersal pathways, spreading mechanisms, dispersal distances

Pathways

The major pathway of Df propagation is through forestry: the spread of this species into areas of high conservation value is only possible in the vicinity of cultivated Douglas fir stands (Bindewald and Michiels 2018).

Spreading mechanisms and distances

Df seeds are only dispersed by wind (Spellmann et al. 2015). The majority of the seeds fall within a distance of 100-240 m from the mother tree (Dick 1955, Eggert 2014, Mair 1973 in Jonášová et al. 2006), although in rare cases seeds have travelled 2000 m (Dick 1955). How far Df seeds can be dispersed in central Europe is not yet known as seed dispersal data are not yet available. Note: The dispersal distances reported by Dick (1955) in the U.S. are based on seed dispersal measurements. Seed dispersal distances from other studies in Europe are based on National Forest Inventory (NFI) data or estimates (e.g. Eggert 2014).

Information

Impact

Summary

Based on the current literature, the true extent of the current or future ecological risks of Df is highly uncertain (Felton et al. 2013, Höltermann et al. 2008, Schmid et al. 2014, Tschopp et al. 2015). The ecological consequences of the establishment of Df seem to be negligible but could still pose a risk in the future (Schmid et al. 2014). A variety of studies analysed the interaction of Df with native biota but the results are diverse and occasionally contradicting. Many organisms appear to live together with Df and may benefit from its presence. At the same time there are also cases where Df can have a negative impact on single groups of species. There appears to be a shift of species composition and species dominances towards generalists rather than specialists in fungi, arthropod, bird and vascular plant species in Df stands. The indirect effects of Df on soil chemistry seem to be similar to those of native coniferous species and may therefore allow coexistence with other species (see reviews for further information, Schmid et al. 2014, Tschopp et al. 2015). The authors criticize that the majority of existing studies are not representative of the general situation in Europe, as they were conducted in a limited set of locations or on a small number of individuals, or only short-term data (e.g. one growing season) was collected (Schmid et al. 2014), other studies did not differentiate between different proportions of Df in forest mixtures (Tschopp et al. 2015). In particular, there are substantial gaps in the knowledge about the long-term effects of Df on typical native species communities of protected forest communities, and on rare species such as red list species (Bindewald and Michiels 2018, Tschopp et al. 2015).

Competition

Df exhibits a superior growth rate compared to native tree species in many cultivated forest sites. In these sites natural regeneration is often desired and encouraged. If no specific management is applied at the majority of forest sites in Germany the establishment of Df is limited by shade-tolerant companion tree species such as European beech (Fagus sylvatica L.) (Spellmann et al. 2015). However, on more open dry acidic forest sites Df could develop to be the dominant tree species (Bindewald and Michiels 2018) (see below 'Potential impact in seminatural ecosystems').

Ecosystem integrity (biotic and abiotic)

Biotic properties

Several studies have investigated the ecological effects of Df cultivation (Schmid et al. 2014), however results are not consistent (Spellmann et al. 2015).

Examples

Arthropods

Studies on arthropod species and composition connected with Df vary depending on the studied species, tree species mixture and season (Tschopp et al. 2015):

- There is no significant difference between beetle fauna in the tree crowns of Norway spruce (*Picea abies* (L.) H. Karst.) and Df (Gossner and Simon 2002) but there appears to be reduced activity of red list beetle species on dead wood of Df compared to Norway spruce (Gossner 2004b).
- A reduction in the number of arthropods in Df crowns in winter leads to reduced activity of wintering birds (Gossner and Utschick 2004).
- The introduction of exotic species can in some cases increase the associated biodiversity, as new species increase the structural and temporal diversity of the forest (Kjaer et al. 2014). For example Df mixed with native European beech trees can lead to an increase in the richness of tree-dependent arthropod communities (Gossner and Ammer 2006).

Category Information

- A comparison of pure Df plantations with a plantation of sessile oak (Quercus petraea (Matt.) Liebl.) of the same age in the same country revealed that afforestation with Df plantations leads to conspicuous changes in epigaeic invertebrate communities. Communities of ants and carabids were impoverished in the Df plantation, however the activity of diplopods for example was higher (Finch and Szumelda 2007).
- Potentially due to a lack of native congener in Europe, Df recruited only 33.9 % of the number of arthropod species that are associated with Df in the native range (Roques et al. 2006).

Fungi

A comparison of different stands in Bavaria revealed that pure Df stands exhibited the lowest total species richness of fungi compared to the other stand types. Pure Df stands also had the lowest number of endangered fungi and fungi which are indicators of near-natural habitats. The diversity and relative proportion of fungal guilds (mycorrhiza, saprotrophic fungi and others) was most similar to that observed in Norway spruce (Utschik 2001).

Spiders

In a tree species experiment, spider biomass and abundance was negatively affected by Df (compared to European beech, sessile oak and spruce). These impacts persisted even in stands were Df was present in diverse tree species mixtures (Schuldt and Scherer-Lorenzen 2014).

Epiphytes

- The bark of conifers is generally acidic and the dense foliage reduces light levels at the tree trunk, therefore coniferous trees like Df do not provide suitable conditions for epiphytes (Alexander et al. 2006).
- The broad buckler-fern (*Dryopteris dilatata* (Hoffm.) A. Gray) prefers the trunks of Df compared to those of European beech (Kühnel 1995).
- One study identified a lower quantity and diversity of epiphytic mosses on Df compared to European beech (Kühnel 1995).

Understory layer

- Comparison of Df stands (where >85% top tree crown layer was Df) with European beech stands (where >85% top tree crown layer was European beech) in the State of Baden-Württemberg (Kühnel 1995):
 - Higher percentage cover was observed in the herbaceous layer in European beech forests
 - Lower average diversity of herbal vegetation in Df stand types (species numbers were similar for European beech and Df, but frequency distribution differed (lower evenness values): there was a shift of species dominances with a tendency of fewer competitively weak (and rare) plants and a dominance of more common species in Df stands
- The results of comparisons of the understory of 50 year old pure (European beech, Scots pine (*Pinus sylvestris* L.) or Df) and mixed forest stands (Df-Norway spruce, Scots pine-European beech, Df-European beech) in north-western lowlands in Germany suggested that pure and mixed Df stands have similarly diverse understory vegetation compared to native conifer stands. However, species of natural forest communities are rarely present in Df stands (Budde, 2006).

Information

 The acidic nature of Douglas firs needles and their high density of foliage decreases light availability and soil pH, which tends to restrict the growth of understory herbs but favors mosses (Felton et al. 2013).

Biodiversity and structural diversity

Total number of species in the tree, shrub, herb, and moss layer as well as structural diversity is higher in old pure and mixed Df stands compared to near-natural European beech-hornbeam-oak, European beech-pine and spruce-European beech-mixed stands of a similar age in two nature reserves (Vor and Schmidt 2006).

Abiotic properties

The effects of Df on soil chemistry seem to be similar to those of native coniferous species and may facilitate coexistence with other species – depending on the habitat type (Schmid et al. 2014).

Examples

Comparison of Df with native coniferous species

- Df may have different abiotic habitat conditions compared to Norway spruce, as a result of their different bark and crown structure, however the chemical composition of secondary plant compounds in the needles of both tree species are similar (Schmid et al. 2014).
- The rate of litter decay in Df is similar to those of Norway spruce, European silver fir (*Abies alba* Mill.) and European larch (*Larix decidua* Mill.) (Engel 2001) and even exceeds those of other cultivated tree species in Germany (Burschel and Huss 1997).
- Microbial litter decomposition under stands of Df and under native tree species
 was compared in the lowlands of north-west Germany. There was no significant
 difference of microbial parameters under Df compared to Scots pine, European
 beech or Norway spruce (Mindrup et al. 2001).

Comparison of Df to native broadleaf tree species

Plantations of pure Df and sessile oak of the same age were compared. Higher
moss cover and needle litter resulted in higher soil acidity in the Df plantations
compared to the sessile oak plantations (Finch and Szumelda 2007).

Potential impact in protected ecosystems

<u>Case study in the State of Baden-Württemberg</u> (Bindewald and Michiels 2016, Bindewald and Michiels 2018)

Natural regeneration has been reported in several protected forest types of high conservation value in southwestern Germany (approximately 0.01 % of total forest area in the region), such as natural formations (i.e. habitats that cover only very small areas, where e.g. acidic open rocky heaps, acidic rock formations, are present), rare near-natural forest habitats located in the sessile oak (*Quercus petraea* (Matt.) Liebl.) forest communities on dry sites with acidic soils, and habitats characterized by mixed-broadleaf forests (*Deschampsia flexuosa-Acer pseudoplatanus* community) situated on rocks or steep slopes on nutrient-poor sites.

Potential effects in special sites of high conservation value

• The establishment of Df in the understory in specific (protected) sites (see above) will likely change the typical site conditions such that light is limited and the pH is lowered (Felton et al. 2013, Knoerzer 1999b): (1) shade will increase

Information

with an increasing number of Df individuals (of increasing age) having a negative impact on heliophilous species; (2) rising needle fall, thus acidification of deeper soils and the accumulation of nitrogen may increase nitrophilous species (Knoerzer 1999b). The typical flora and fauna of such specific sites may be threatened by a decrease in species diversity, also affecting red list species (Blings 1998 as cited in Knoerzer 1999b). Df changes the typical vegetation structures on treeless rock formations (Knoerzer et al. 1996) and highly specialized thermophilous and heliophilous flora and fauna are considered likely threatened by such changes (Knoerzer 1999b).

- If no risk management is applied, Df may overtake native oak species and develop to be the dominant tree species as is the case in oak forests in California (Cocking et al. 2014, Engber et al. 2011). In California Df grows faster than oak, reaching greater heights and its branches suffer less mechanical damage from competition. Df emerges from the understory through the canopy, replaces the original dominant oak tree species and is considered to cause rapid ecosystem change (Hunter and Barbour 2001). The conversion of Californian oak forests to shade-tolerant conifers is one direct outcome of fire exclusion. In Germany native oak regeneration is regularly suppressed by the high browsing pressure posed by deer. On rocky sites with nutrient-poor soils which would naturally form sessile oak forest communities, oak cannot regenerate and compete and Df seem to be less attractive for browsing (Knoerzer et al. 1996).
- In near-natural birch-oak forests Df reaches the assured stage of regeneration (>1.3 m), outcompetes the native tree species and is estimated to be the dominating canopy species in the final forest stage (Knoerzer 1999a).

Transmission of pathogens or parasites (cointroduction)

Df is the secondary host of the Sitka-spruce gall aphid (*Gilletteella cooleyi* (Gillette)) (Gossner 2004a, Hartmann et al. 2007 as cited in Spellmann 2015). No further knowledge on the transmission of other pathogens by Df is available (Spellmann et al. 2015), but future risks are considered likely (Felton et al. 2013).

Hybridization

Df has no native congeners (Czaja 2000) and, thus, does not hybridize (Felton et al. 2013).

Potential future effects

In the future, an increase in the spread and establishment of Df is expected in Germany (Appelfelder 1999) since the majority of adult Df trees in Germany are not yet fructifying (NFI 2012). The spread of Df is expected to marginally increase as a result of climate change (Kleinbauer 2010). Df is considered to have potential significant impacts on forest ecosystems, particularly when planted over large areas and in high densities (Da Ronch et al. 2016).

Invasive history elsewhere

In Germany, classification of Df as an invasive species is controversial (Nehring et al. 2013, Vor et al. 2015). Elsewhere: According to Richardson and Rejmánek (2004) Df is considered a serious conifer invader¹ which has escaped after cultivation in Argentina, Austria, Bulgaria, Chile and Great Britain. Spread from cultivation areas in adjacent habitats in Europe has been reported in several countries, e.g. in Spain (Broncano et al. 2005, Carrillo-Gavilan et al. 2012), Austria (Essl 2005) and southwestern Germany (Bindewald and Michiels 2018, Knoerzer 1999b); outside

¹ 'Invasive' taxa produce reproductive offspring, often in large numbers, at considerable distances from parent plants

Category Information

Europe in Argentina (Orellana and Raffaele 2010, Simberloff et al. 2010, Simberloff et al. 2002), Chile (Pauchard et al. 2015) and New Zealand (Ledgard 2002). According to Wagner et al. (2017) Df is one of the ten most common introduced tree species invading (i.e. spread into) acidophilus Quercus woodland in Europe, but information on the particular extent of established populations in the different ecosystem types is not provided.

More details

- In **Austria**, Df has established in the Bohemian Massif. Here, Df has mainly colonized open-conifer forests, acidic European beech forests (Luzulo-Fagetum), and near-natural acidophilus oak forests (Sorbo torminalis-Quercetum) (Essl 2005).
- In the Montseny Natural Park in **Spain** the establishment of Df seedlings started 15 years after planting. Df seedlings were able to spread into adjacent areas 100 m from the plantation in less than 30 years after planting (Broncano et al. 2005). However, the probability of successful Df establishment decreased along the early life-cycle stages in all studied sites, i.e. European beech and helm-oak forest and heathlands (Carrillo-Gavilan et al. 2012).
- In a study in **Switzerland** no stands with strong Df spread were found and only few Df stands were located nearby nature reserves. Accordingly, no potential (future) negative effects of this species could be detected (Hafner and Wohlgemuth 2017).
- Douglas fir frequently established outside of plantations in native forests in Argentina where it is considered to be invasive (Orellana and Raffaele 2010, Simberloff et al. 2010, Simberloff et al. 2002). Df seeds are described to reach several hundred meters from their propagule source in open and disturbed areas (e.g. ridge tops, roadsides and remnant pastures), however, almost all large Df individuals (i.e. > 10 m in height) were growing in remnant pastures within 200 m of the mother tree (Simberloff et al. 2002). Df interferes with the pollination and sexual reproduction of native wind-pollinated conifers, and thus may decrease their long-term population viability in Argentina (Martyniuk et al. 2015).
- According to a study by Pauchard et al. (2015) Df is naturalized and invasive in
- In **New Zealand** Df is more shade-tolerant than pines and there is a risk that this species spread into open native forest, shrub lands and grasslands. The frequency of Df spreading into open shrub lands and grasslands is already increasing, particularly following disturbances (Ledgard 2002). Df is assumed to adversely impact native tree seedlings and soil communities through modifications of the microenvironment both above and below the ground (Dehlin et al. 2008).

Native range

• Df seedlings established successfully in open grasslands in British Columbia, **Canada** (Bai et al. 2000)

Information

• In the **U.S.** native oak forest are being encroached upon in California: Df outgrows native oak species, resulting in oak mortality (this is the direct outcome of fire exclusion in north coast oak woodlands) (Cocking et al. 2014, Engber et al. 2011, Hastings et al. 1997). *Note: whether such competition patterns are applicable to Germany is unknown*.

Available control measures

- The designation of buffer zones around susceptible habitats has been suggested
 to limit the spread of this species (Ammer et al. 2016, Bindewald and Michiels
 2018). With buffers ranging from 300 m according to regional forest guidelines
 (ForstBW 2014), to 1-2 km according to Walentowski (2008). These buffers
 should contain Df within the cultivated forest area and avoid any further spread
 into sensitive areas.
- Where necessary, forest management can decrease the establishment and spread potential of Df by planting competitive native tree species and by early removing of single trees before they produce seeds (Spellmann et al. 2015).
- Any undesired occurrence of Df can be mechanically removed with low effort since the tree does not regenerate by regrowth from root material or via coppice shoots (Spellmann et al. 2015).

Further research requirements

Further areas of research to fill gaps in the current knowledge, some examples:

- Comparison of Df's impact on biota in pure and mixed coniferous stands as well as broadleaf stands (Schmid et al. 2014).
- Assessment of the ecological impact of Df plantations in comparison to Df stands which establish naturally (Schmid et al. 2014)
- Fungal interactions of Df (Schmid et al. 2014)
- Ecological integration: Comparing Df and silver fir (Schmid et al. 2014)
- Assessment of the influence of Df on native biodiversity in different mixtures
 particularly with European beech along a gradient, to determine the threshold at
 which negative effects become evident (Tschopp et al. 2015)
- Assessment of the influence of Df on rare and red list species, e.g. on lichen, and species of national priority (Tschopp et al. 2015)
- Assessment of the ecological (long-term) effects on near-natural forest sites and their native species communities (Bindewald and Michiels 2018)
- Investigating the frequency of natural regeneration and particularly the spreading potential of Df in different semi-natural (forest) ecosystems throughout Europe (Tschopp et al. 2015)

Table 4 Red oak (Quercus rubra L.); Ro=Red oak.

Category	Information
Native range	Northeastern US, southeastern Canada (Nagel 2015).
Pathways of	The first documented introduction of red oak ('Ro') to Europe was in Switzerland in
introduction	1691 (Badoux 1932 as cited in Nagel 2015). Cajander (1922) mentioned the 16 th and
	17 th century as the first main period of introduction to Europe. Ro was initially used
	in parks. From the mid-18th to 19 th century Ro was used in silvicultural trials. After
	positive trial evaluations, the tree was intensively cultivated in eastern Germany in
	the 1950s - 1960s (Nagel 2015). In terms of cultivation area Red oak is now the most
	economically important introduced broadleaf tree species in Germany (BMEL 2014).

Distribution

Ro is widely distributed in Europe with the largest areas of Ro cover in Germany, France, Belgium and the Netherlands (Nagel 2015). In Germany, Ro is cultivated on approximately 55,000 ha, i.e. 0.5 % of the forested area of Germany (NFI 2012), often on restored open-cast mines. Ro occurs mostly in planted stands in Germany and successful spread and establishment can be only found in isolated cases on nutrient-poor, dry soils with little browsing pressure (Nagel 2015). Natural regeneration is frequent on sites where the potential natural vegetation includes the species *Galio odorati-Fagetum* or *Luzulo-Fagenion*, which constitute two major vegetation types in Bavaria (Winter et al. 2009).

Examples of the percentage of forest area covered by Ro outside of Germany

- 0.2 % in the Czech Republic, based on national forest inventory data (Bednář et al. 2016)
- 0.03% in Slovenia (Kutnar and Pisek 2013)
- 0.9% (from the number of tree trunks, 3% basal area and 0.08% in regeneration) in Italy, based on inventory data (Rizzo and Gasparini 2011)

Soils, climate, light

Ro is well-adapted to large climatic variability in its native range (Kölling 2013). It is relatively drought tolerant as an adult tree (Desmarais 1998 as cited in Nagel 2015) and seedling (Miltner and Kupka 2016). Ro is periodically shade tolerant, particularly up to the age of 10 (Vor 2005). Therefore, Ro is able to persist below a dense canopy for a certain period of time (Johnson & Major as cited in Nagel 2015).

The establishment of Ro in Germany is mainly regulated by soil and light conditions, seed predation and browsing pressure (Nagel 2015). Seedlings are relatively independent from limiting soil nutrient resources due to their large seed size (García and Houle 2005). Ro is resistant to storms, fire, frost, drought and emissions (Nagel 2015).

Favorable conditions

- Ro has a preference for calcium-deficient soils and south-facing ledges and ribs (Dreßel and Jäger 2002).
- Natural regeneration of Ro is most successful on nutrient poor, dry and warm sites (Vor 2005)
- Ro occurrence and natural regeneration has been recorded in Poland, mostly on poor soils with high C/N-ratios, typically occupied by coniferous forests (Chmura 2014).
- Ro regenerates easily in light pine forests in Belgium (Vansteenkiste et al. 2005).
- Ro occurs in the medium and late successional stages of shady forests after disturbances like clear cutting, fires or storms. After fires, Ro can easily regrow in its native range (Foster 1992 and Elliot et al. 1998 as cited in Dreßel and Jäger 2002).
- Greatest growth rates of seedlings where light availability is high, but Ro is also competitive under semi-shade and periodical shade conditions. It is termed a 'gap specialist' (Major et al. 2013).

Appropriate conditions

- Natural regeneration is successful even on a thick layer of humus (Bachmann et al. 2009).
- Ro seeds can emerge even under thick leaf litter (Kostel-Hughes et al. 2005).

<u>Unsuitable conditions</u>

• Soils with high calcium content >1.5%.

• Light suppression: in mixed forest with European beech Ro seedlings grow slower in height than seedlings of European beech under closed canopy conditions (Nagel 2015).

Case studies

Saxonian Swiss National Park (Dreßel and Jäger 2002)

- Successful natural regeneration of Ro on south-facing, rocky sites.
- Light availability was correlated with the number of surviving seedlings.
- Browsing damage was of secondary relevance; mainly trees <50 cm were affected.

Managed hardwood forests of southwestern Germany (Major et al. 2013):

- Prolific natural regeneration of Ro, even under closed canopy conditions. Higher number of individuals than native tree species. Sustainable regeneration with a significant number of trees entering the mid storey.
- Especially prolific on nutrient-poor soils, less abundant on sites with elevated soil calcium levels.
- Establishment of Ro was strongly connected to seed trees due to limited seed dispersal.
- Ro is promoted by periodic selective harvesting which maintains a disturbed state of mid-succession, allowing Ro seedlings to persist in canopy gaps.

Comparison of natural regeneration and dispersal in three forested sites (Vor 2005)

- Highest abundance of natural regeneration in warm, nutrient-poor and dry stands without browsing pressure (conditions were advantageous for Ro compared to other species.)
- Lower density of Ro seedlings in stands with lower temperature, high nutrient and moisture conditions.
- Poor regeneration on sites where nutrient, water and temperature conditions were on average in between of the two other sites (could be related to age differences)

Comparison between different European countries (Merceron 2016)

Ro regeneration was most successful where Ro was dominant in the tree layer, but also under native oaks in France, Spain and Wallonia or under coniferous stands in Spain and Germany (Data based on forest inventories).

Regeneration potential

Ro starts fructification from the age of 25 (Meloni et al. 2016) and produces a mast every 2-5 years (Nagel 2015). Vegetative regeneration of red oak is confined to stumps as it does not grow from root material. Although vegetative reproduction by regrowth from the stump is possible (Bachmann et al. 2009), it has not played an important role in Germany so far, since shoots are often browsed by wild animals (Nagel 2015).

Dispersal pathways, spreading mechanisms, dispersal distances

Pathways, vectors

Small mammals such as mice and birds are the main vectors of seed dispersal in Ro (Bieberich et al. 2016). Furthermore, the Eurasian jay (*Garrulus glandarius* (Linnaeus)) can transport Ro seeds over long distances (Bachmann et al. 2009). The jay has been shown to prefer native oak acorns over Ro acorns (Dreßel and Jäger 2002), because Ro acorns have a thicker pericarp (Bieberich et al. 2016). Nonetheless, Ro is still effectively dispersed which has resulted in dominant Ro stands in the understory vegetation of forests in Poland (Myczko et al. 2014). In

Wallonia in Belgium Ro acorns are dispersed by wood mice, red squirrels, rats and wild boar, although native oak acorns are also preferred by these mammals. Results suggest that Ro is gradually crossing the natural dispersal barrier, without human intervention (Merceron et al. 2017a).

Spreading mechanisms and distances

Restricted seed dispersal is the main factor influencing the spatial distribution of Ro recruits. According to Nagel (2015), jays can transport seeds up to 4 km, however they are usually transported a maximum of 150 m. Dreßel and Jäger (2002) reported high densities of Ro seedlings (i.e. 700 seedlings / ha) 700 m from the nearest old Ro stand and single seedlings at a distance of 1.5 km. Riepõas and Straigytë (2008) found considerable seedling densities 500 m from Ro plots and single seedlings up to 1.5 km from the nearest Ro stand. The highest densities of seedlings were found on relatively fertile soils.

Overall, the spreading potential of this species is considered to be limited by ineffective seed dispersal vectors, a lack of vegetative reproduction and a high browsing pressure at the majority of forest sites in Germany (Major et al. 2013, Nagel 2015).

Impact Summary

It is considered challenging to assess ecological impacts as many Ro stands are still rather young and effects on native species vary for different species groups. For example, a negative impact on bryophytes (Woziwoda et al. 2017) or ferns has not been detected so far (Zarzycki et al. 2015), however negative impacts on native species richness and dominance of Ro in the regeneration compared to e.g. native oaks have been observed in Poland (Woziwoda et al. 2014a).

Competition Shade tolerance

- Ro is more shade tolerant and competitive than native oak species in all developmental stages, but its height increment is slower than that of European beech regeneration under closed canopy conditions (Strathmann & Warth 1987 as cited in Nagel 2015).
- In the early regeneration stage, Ro can compete with native shade-tolerant tree species such as sycamore (*Acer pseudoplatanus* L.) and common hornbeam (*Carpinus betulus* L.) (Major et al. 2013).
- In Poland, Ro has a higher establishment success but lower dispersal rates than pedunculate oak (*Quercus robur* L.) (Myczko et al. 2014).
- Nagel (2015) suggests though, that the situation in Germany is not comparable
 to that of Poland for example, since European beech is more competitive and
 shade-tolerant and thus would outcompete Ro in the long-term.

Growth

Ro exhibits fast growth, especially in trunk diameter. The height growth of young trees is comparable to sycamore and superior to native oaks and European beech, both when comparing planted monocultures in open areas (Schober 1987 as cited in Nagel 2015) and mixed plantations in open areas (Göhre & Wagenknecht 1955 as cited in Nagel 2015).

- In southwestern Germany Ro grows faster than native oak species (20% more growth in height and 40% in volume) and just as fast as *F. sylvatica* (Klädtke 2016).
- There is an area of successful natural regeneration of Ro on a study site in southwestern Germany (Kuehne et al. 2014). Ro seedlings can develop a fairly

large leaf area. This likely makes the net carbon gain and total photosynthesis of Ro seedlings superior to other species, both in large openings and under closed canopies, with strong competition for light. Due to these qualities, Ro seedlings can outperform pedunculate oak as well as shade-tolerant species such as sycamore.

• In the National park 'Sächsische Schweiz' European beech is competitive and more successful than Ro on 'average sites', however Ro is just as successful as European beech on xerothermic sites where larger beech trees have been logged. In the long run, Ro is expected to dominate on dry and acidic sites, since pioneer species like Scots pine (*Pinus sylvestris*) and birch (*Betula spec.*) are already being outcompeted on these sites (Dreßel and Jäger 2002).

Gap specialist

- Phototropic growth allows Ro to occupy gaps in the forest canopy (Nagel 2015).
- In open spaces, in gaps or in areas with less dense canopies Ro even competes with European beech (Vor & Lüpke 2002, Mews 2012 as cited in Nagel 2015), yet Ro is inferior to beech under dense forest canopies (Nagel 2015).

Pathogen exposure

- Ro is less susceptible to pathogens and seed predation than native tree species (Nagel 2015).
- The absence of major parasites has released selection pressures and led to genetic differentiation in Ro since its introduction. Ro may have advantages compared to native oak species as it has no known pathogens in Europe (Daubree and Kremer 1993).

Other aspects of competition

In a review Miltner and Kupka (2016) argue that fast growth, drought tolerance and resistance to fungal diseases could lead to natural dominance of Ro on dry, acidic sites in Bohemia in the Czech Republic.

Ecosystem alteration (abiotic and biotic)

There are a great number of studies on the ecological integration of different species groups with Ro but with partly inconsistent results:

Soil microorganisms

- Lower microbial activity was observed in soils of Ro plantations compared to sessile oak (*Quercus petraea* (Matt.) Liebl.) plantations of the same age (Nicolini and Topp 2005).
- Fewer soil microorganisms are present in Ro leaf litter compared to pedunculate oak leaf litter (Riepðas and Straigytë 2008).

Arthropods

- Arthropods that are strongly specialized for European oak species cannot simply migrate to Ro (Van Nieukerken et al. 2012).
- There is a smaller spectrum of herbivorous insects on Ro compared to native oak trees (Gossner and Simon 2005 as cited in Nagel 2015).
- Certain species occur on Ro but prefer native oaks (Gossner and Bräu 2004)
- Some integration has been identified: e.g. more species have been found on Ro than on European beech and even protected deadwood beetles have been identified on Ro (Nagel 2015).
- Soil arthropods in red oak stands: no significant differences were observed for spiders, rove beetles and myriapoda compared to native oak stands (Balkenhol

- 2006 as cited in Nagel 2015).
- Rove beetle communities in reforested areas of eastern Hungary were found to be less diverse and less abundant in Ro plantations than in plantations of native pedunculate oak. Understory vegetation, soil temperature and pH were found to most strongly influence rove beetle diversity (Nagy et al. 2015).
- Insect communities in the crowns of Ro stands differ in comparison to those in stands of native oaks (Gossner 2004b).
- Pre-dispersal seed predation in Ro: Predation by moths is low and similar to sessile oak species. Predation by weevils (beetle) is high among sessile oak species but very low in Ro (Bogdziewicz et al. 2017).
- Heteroptera abundance and biodiversity on Ro is significantly lower (25-50%) than on pedunculate oak and generalist species dominate the diversity of Heteroptera found on Ro (Gossner and Bräu 2004).
- The abundance and diversity of Sawflies (*Symphata*) on Ro in Bavaria was found to be lower than that of native tree species (Gossner et al. 2007).
- Mite communities in Ro stands in Poland differed significantly from pedunculate oak stands. Species composition was marginally different and overall mite abundance was significantly higher in Ro leaf litter. This is probably due to the thick Ro leaf litter layer, which is a result of the higher litter production (Kohyt and Skubała 2013).
- Larvae of the chestnut tortrix moth (*Cydia splendana* (Hübner)) and beech moth (*Cydia fagiglandana* (Zeller)) in Poland use Ro acorns as a foraging substrate and can thus stabilize their trophic niches in years where native oak species produce few acorns (Myczko et al. 2017).
- Lower densities of collembola and mites were found in Ro plantations when compared to sessile oak plantations of the same age on former lignite open-cast mines (Nicolini and Topp 2005).
- The great capricorn beetle (*Cerambyx cerdo* (Linnaeus)) avoids Ro and is exclusively found on pedunculate oak in a Natura 2000 site in Poland. However, the studied Ro had a smaller trunk diameter than the native oaks, which could be a confounding factor in that study (Oleksa and Klejdysz 2017).
- The number of insect species found on Ro in Britain was lower than the number found on pedunculate oak and Turkey oak (*Quercus cerris* L.) (Welch 1981).

Fungi

- Ro deadwood decomposed faster than deadwood of native oak species (Möller 1998 as cited in Nagel 2015).
- Over 120 species of deadwood fungi were found on Ro including rare and protected species (Sammler et al 2011 as cited in Nagel 2015).
- No significant difference was found between mycorrhiza associated with Ro and native oak species (Gebhardt et al 2006 as cited in Nagel 2015).
- Ro stands have been colonized by several macromycetes in Brandenburg, Germany. However, due to its shorter lifespan Ro is less suitable for some species than sessile and pedunculate oak (Sammler 2004).
- The diversity of ectomycorrhizal fungi on a 35 year old Ro in Poland was much lower than what would be expected on pedunculate oak. The ectomycorrhizal fungal community on Ro was also dominated in another study by one very abundant species (Sousa et al. 2014, Trocha et al. 2012).

Birds

 Increased number of non-forest bird species, mostly synanthropic species, were observed in forest patches with Ro compared to natural forest in a park in Poland (Grzędzicka et al. 2017).

• Ro is considered a good food source for woodpeckers (Gatter 1972).

Plants

- Increased numbers of non-native plant species were observed in forest patches with Ro compared to natural forests (Grzędzicka et al. 2017).
- Differences in the vegetation structure and species composition of forests containing Ro and pedunculate oak were compared in Lithuania. The percentage cover of the second tree and herb layer was lower in Ro stands than native oak stands, while the percentage cover of the shrub layer was higher. Species diversity was overall lower in Ro stands (Marozas et al. 2009).
- The biodiversity in Scots pine pedunculate oak forests in Poland is reduced when Ro is present in the stand. The presence of Ro also results in a reduction of the herbal plant community and a shift in species compositions towards more shade tolerant species (Woziwoda et al. 2014a).
- In secondary forests on former agricultural land in Poland, admixture of Ro increases the diversity of epiphytic bryophytes. Ro is a better 'bryophyte host' than native oaks. However, this is counteracted by a negative effect on the understory diversity (Woziwoda et al. 2017).
- Fern populations in forest stands (mixed broadleaf forest, acidophilous oak forest and acidophilous European beech forest) dominated by Ro where compared with the same forest types without Ro in southern Poland. Fern species in Ro dominated forests in Poland are bigger and have larger ground coverage than in control forest patches, whilst percentage coverage of herb species and species diversity were higher in forest stands lacking Ro (Zarzycki et al. 2015).

Studies on abiotic properties

Litter decomposition

- The slow litter decomposition of Ro is often described as a problem but requires site-specific consideration, since slow decomposition only occurs on nutrientpoor soils (Nagel 2015). Although Ro produces a high amount of litter, Ro leaf litter decomposition is faster than that of native oaks and contains less nitrogen, resulting in a higher initial C/N ratio. Over time, a faster decomposition of the higher amount of leaf litter compensates for its lower N content (Straigytë et al. 2009).
- Leaf litter decomposition in Ro is slightly slower than decomposition of leaf litter for European beech but faster than decomposition of European larch (*Larix decidua* Mill.) in Lithuanian plantations. Total litter mass of Ro was 30 % higher than in other species (Ciuldiene et al. 2017).
- Litter decomposition within the native range of Ro functions differently, as litter-burying earthworms are absent. Introduced European *Lumbricus* species avoid Ro leaf litter due to its low calcium content and prefer leaf litter of other tree species (Holdsworth et al. 2008, Holdsworth et al. 2012). The consequences in European forest ecosystems e.g. for soil chemistry are so far unknown.

Nutrient immobilization in the soil

 Bonifacio et al. (2015) tested the effects of over 50 years of Ro cultivation on well-developed, nutrient-poor soils, originally covered by native pedunculate oak. Ro sites showed a different humus form caused by a higher tannin and alkyl content of the leaf litter. Ro leaf litter was less easily degradable, cation biocycling was inhibited and in particular phosphorus and calcium retention led to lower availability of these elements in the mineral soil.

These results match the findings of Riepðas and Straigytë (2008) who found that due to slow litter decomposition, soils in Ro stands in Lithuania contain more K but less P, Ca and other nutrient trace elements than soils in comparable pedunculated oak stands.

Soil acidification & leaching

- Ro causes soil acidification on the upper forest soil layers (Finzi et al. 1998 in Dreßel and Jäger 2002, Miltner et al. 2016). Soil properties of sessile oak forests were compared with Ro forest sites. Total carbon and nitrogen in the upper soil levels were lower compared to native oak forest (Nicolini and Topp 2005).
- Ro dominated forests are not prone to leaching nitrogen into the groundwater, due to the high C/N ratio in the soil (Lovett et al. 2002). Low levels of NO3-leaching is due to the higher N-deposition of Ro, compared to other species in the native range (Crowley and Lovett 2017).
- Red oak leaf litter leaks high amounts of tannin into leachate during decomposition which may affect the development of aquatic organisms (e.g. tadpoles in pools of water) due to tannin toxicity when growing in or around freshwater ecosystems. This effect has been demonstrated on tadpoles under laboratory conditions (Earl et al. 2012, Earl and Semlitsch 2015). Ro leaf litter has a high tannin content compared to other North American tree species, however studies comparing Ro leaf litter tannin content to native oak species leaf litter in Europe is lacking.
- The chemical composition of Ro leaf litter is similar to native broadleaf species (Skorupski et al. 2012). Note: Ro leaf litter was not compared to other oak species leaf litter but to a mixture of leaf litter from different deciduous tree species in this study.

Potential impact in semi-natural ecosystems

Ro can cause conflicts with nature conservation (Dreßel and Jäger 2002, Kowarik 2002), as it is estimated that Ro could develop to be a dominant species on dry, acidic sites (Miltner and Kupka 2016). For example, Dreßel and Jäger (2002), found that red oak persists in natural vegetation on south-facing rocky sites with little browsing pressure in a national park in eastern Germany.

From the nature conservation point of view natural woodland borders and rock habitats are possibly prone to (further) invasion and thus would require Ro removal (Starfinger and Kowarik 2011b).

Transmission of pathogens or parasites (cointroduction)

There are very few records of pathogen transmissions and to date no proven cases of co-introductions with Ro. There are some cases of potentially harmful species introduced in the more recent past:

- Very few pathogens have been registered in association with Ro and no damaging effects have yet been recorded (Nagel 2015).
- The oak skeletonizer (*Bucculatrix ainsliella* (Murtfeldt)) a leaf eating moth is the first lepidopteran species to feed on Ro in Europe. It has spread in the Netherlands, Belgium and in parts of Germany however no damaging effects

- have been reported so far (Van Nieukerken et al. 2012).
- The fungus *Ceratocystis fagacearum* (T. W. Bretz) J. Hunt responsible for mass mortality among north American oaks ('oak wilt') has not yet been found in Europe, but poses a severe potential threat in the future (Koch et al. 2010, Johnson et al. 2002 as cited in Nagel 2015).
- The oak lace bug (*Corythucha arcuata* (Say)) is an insect native to North America, which can cause early leaf drop in cases of heavy infestation. Damage to European oak species are more severe (Bernardinelli 2006). This bug was first found in Europe in 2000 but it is not strictly a co-introduced species of Ro.
- The aphid Myzocallis walshii (Monell) was introduced to Europe in the 1990s (Doychev 2015). Only aesthetic damages by this species to ornamental Ro trees have been recorded until now (Doychev 2015). The first instance of this aphid in the Czech Republic was recorded in 2003 and it has so far only been observed on Ro (Havelka and Starý 2007).

Hybridization

Ro does not hybridize with European oak species (Nagel 2015).

Potential future effects

Both Ro and pedunculate oak in Lithuania have been extending their growing season since 1980 due to changing climatic conditions. However, while the pedunculate oak growing season extended by 22 days, the growing season of Ro has only extended by 11 days. Assuming continued warming, this could improve the competitive ability of native oak, but also entail higher risks due to late frost, to which Ro is more resistant (Sujetoviene and Sveikauskaite 2014).

Invasive elsewehre

Summary:

In Germany, the classification as an invasive species is controversial (Nehring et al. 2013, Vor et al. 2015). Elsewhere: Ro is considered invasive in natural and seminatural oak forests in the Czech Republic, Poland and Lithuania. In these forest types, the elimination of typical heliophilous herbal communities is particularly emphasized as a major detrimental effect of Ro (for further information see e.g. Nagel 2015). In Belgium, Ro is reported as invasive in light coniferous forests (Branquart et al. 2007, Vansteenkiste et al. 2005). In Spain and France, Ro regeneration has been reported on forest inventory plots without the presence of adult Ro (Merceron 2016).

More details

- Increases in the natural regeneration of Ro in light *Pinus* stands have been recorded in **Belgium** (Branquart et al. 2007, Vansteenkiste et al. 2005). The proportion of Ro present in forests is increasing due to lower seed predation for Ro than for native oak species (Vansteenkiste et al. 2005). Ro is considered invasive in the Liedekerke forest reserve on sandy loam soils, an area where an anthropogenic heathland was left unmanaged after WWII. A three to four fold increase in basal area was reported for Ro between 1986 and 2006. Ro comprised 20% of total basal area of the forest in 2006 (Vanhellemont et al. 2009).
- Increase in the natural regeneration of Ro has been recorded in light *Pinus* stands in the **Netherlands** (Oosterbaan & Olsthoorn 2005 as cited in Nagel 2015).
- Natural regeneration was recorded on plots without any adult Ro in **Spain** and **France** (Merceron 2016).

- In Northern Italy floodland oak-hornbeam forests of the plains and interior hills (EU Habitat 9160), sweet chestnut forests, mixed floodplain and alluvial forests of alder (Alnus spp.) and willow species are forest areas most threatened by Ro invasion (Meloni et al. 2016).
- Ro germinates and self-reproduces successfully in **Poland** and is considered invasive in the country. Populations of Ro are increasing since the number of reported occurrences of Ro are growing exponentially (Tokarska-Guzik 2005). This includes natural ecosystems such as the Bialowieza National Park. Ro occurs both in natural and semi-natural habitats in the Silesian upland, southwestern Poland where it is one of the three most common neophytes (Chmura 2004). It mostly occurs in stands between 20 and 80 years old in *Calamagrostio-Quercetum* communities where it covers about 75 % of the vegetation plots. Seedlings occur in all forest communities except *Molinio-Pinetum* and *Carici-Fagetum* (Chmura 2004). In northwestern Poland Ro mainly occurs in seminatural, low-disturbance habitats which include deciduous, coniferous and mixed forest types (Mysliwy 2014). In western Poland Oleksa and Klejdysz (2017) reported the occurrence of Ro in a Natura 2000 site.

Overall, detrimental impacts on biodiversity, protected areas, the landscape and the economy in Poland are expected as outcomes of an increased occurrence of Ro (Tokarska-Guzik 2005). Chmura (2013) considered Ro as a 'competitive species' both in regeneration and as a mature tree. The main impacts of Ro in the tree layer are a reduced cover and diversity in both the herb and shrub layer caused by light deficiency (Chmura 2013). Furthermore, the relatively thick leaf litter limits species diversity in invaded vegetation patches by inhibiting the growth of other species (Woziwoda et al. 2014a). Nagel (2015) suggests though, that the situation is not comparable to Germany where European beech is more competitive and shade-tolerant and thus would outcompete Ro.

Presence of Ro in Scots pine – pedunculate oak forests in Poland correlates with a reduced amount of saplings in the shrub layer, i.e. natural regeneration of other species is inhibited (Woziwoda et al. 2014a)

Ro acorn infestation by *Curculio* spec. beetles and the moth *Cydia fagiglandana* (Zeller) is significantly lower than among native pedunculate oak acorns in Poland. This could lead to higher germination rates and seedling fitness of Ro (Myczko et al. 2017).

- Riepõas and Straigytë (2008) classified Ro as invasive in Lithuania and consider it to be more competitive than European oak species. The authors describe a negative influence of Ro on ground vegetation: abundant Ro regeneration competes with native species in the herb layer and leads to a reduced species diversity. Straigytë et al. (2012) argue that exposure to fungal and viral diseases is lower than in the native range, leading to low disease infestation rates among Ro in Lithuania, increasing its fitness compared to native species.
- In the **Czech Republic**, Ro is frequently recorded in surveys and classified as an invasive species (Pergl et al. 2016). However, Hajzlerová and Matějček (2011) do not consider Ro a serious danger in their study area, the Tichá Orlice.

Available control measures

• Establishing buffer zones of 2 km around specific light, dry and acidic sites, such as rock biotopes is one suggested recommendation to prevent the spread of this species (Starfinger and Kowarik 2011b)

- Where necessary, planting shade-tolerant native species (e.g. beech) (Nagel 2015)
- Repeated spring or summer coppicing, and soil tillage can limit the spread of Ro (ECORICE 2015 as cited in Meloni et al. 2016).
- Mechanical removal of 1 -2 year old regeneration is possible, since Ro does not reproduce via growth from roots (Dreßel and Jäger 2002).
- Removal of older trees will inhibit seed production, but sites need to be revisited regularly (Oosterbaan and Olsthoorn 2005)
- Oosterbaan and Olsthoorn (2005) assess and compare four different methods for the control of invasive tree species: Chemical treatment is cheap but often not suitable for environmental reasons. Girdling is cheap and feasible for older trees. Uprooting of whole trees is expensive and just as effective as planting shade-tolerant tree species.

Further research requirements

Competition with F. sylvatica and climate change

- The hypothesis that 'Ro will be outcompeted by European beech in central Europe' (e.g. Nagel 2015) is not supported by data so far. For example, Klädtke (2016) questions this argument and suggests studying the competition between Ro and European beech regeneration.
- It is not yet known whether Ro would have an advantage compared to native species as a result of climate change (Bolte et al. 2009). This raises the question whether beech will still be more competitive with more frequent droughts.
- Genetic analysis suggests that introduced Ro originates from the northern end
 of their native range. It is not yet known whether this could have implications
 for future climate adaptation, e.g. in terms of drought tolerance (Merceron et
 al. 2017b)

Lack of long-term data

Reif et al. (2011) argue that the long time lag between the introduction and spontaneous spread of non-native tree species should be taken into account when estimating the species' potential risks. Therefore, they recommend that future research focusses on more long-term trial areas. It is particularly important to study how many generations are necessary for a species to reach optimal competitiveness. For example, most Ro stands in Poland are still very young and the maximum propagule pressure has not yet been reached (Woziwoda et al. 2014b). There is lack of available data on risks of older Ro stands.

Ecosystem impacts

- Studies on the spread and establishment of Ro in various ecosystem types including protected/natural ecosystems in Europe (pers. comment)
- Studies on pests, parasites & pathogens which are native to Europe and/or those
 which were introduced from the native Ro range and whether they are triggered
 by Ro and might affect other tree species in Europe in the future (pers.
 comment).
- Nutrient depletion on poor soils after 18 years has been proven by Nicolini and Topp (2005). What are the long-term effects of Ro on nutrient-rich soils?
- Investigate whether fast growth and slow litter degradation in Ro lead to an induced nutrient depletion in the soil (Anonymous as cited in Nagel 2015)

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