

Ecological consequences of Douglas fir (*Pseudotsuga menziesii*) cultivation in Europe

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Abstract Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) was first introduced to Europe from North America more than 150 years ago, was then planted on a large scale and is now the economically most important exotic tree species in European forests. This literature review summarizes the current knowledge on the effects of Douglas fir on soil chemistry, plants, arthropods and fungi. Douglas fir shapes its abiotic environment similarly to native tree species such as Norway spruce, silver fir or European beech. In general, many organisms have been shown to be able to live together with Douglas fir and in some cases even benefit from its presence. Although the number of species of the ground vegetation and that of arthropod communities is similar to those of native conifer species, fungal diversity is reduced by Douglas fir. Special microclimatic conditions in the crown of Douglas fir can lead to reduced arthropod densities during winter with possible negative consequences for birds. The ecological impacts of Douglas fir are in general not as severe as those of other exotic tree species, e.g., *Pinus* spp. in South Africa and *Ailanthus altissima*, *Prunus serotina* and *Robinia pseudoacacia* in Europe. Nonetheless, Douglas fir can negatively impact single groups of organisms or species and is now regenerating itself naturally in Europe. Although Douglas

fir has not been the subject of large-scale outbreaks of pests in Europe so far, the further introduction of exotic organisms associated with Douglas fir in its native range could be more problematic than the introduction of Douglas fir itself.

Keywords Biodiversity · Co-introductions · Ecosystem services · Forest ecosystems · Invasion biology

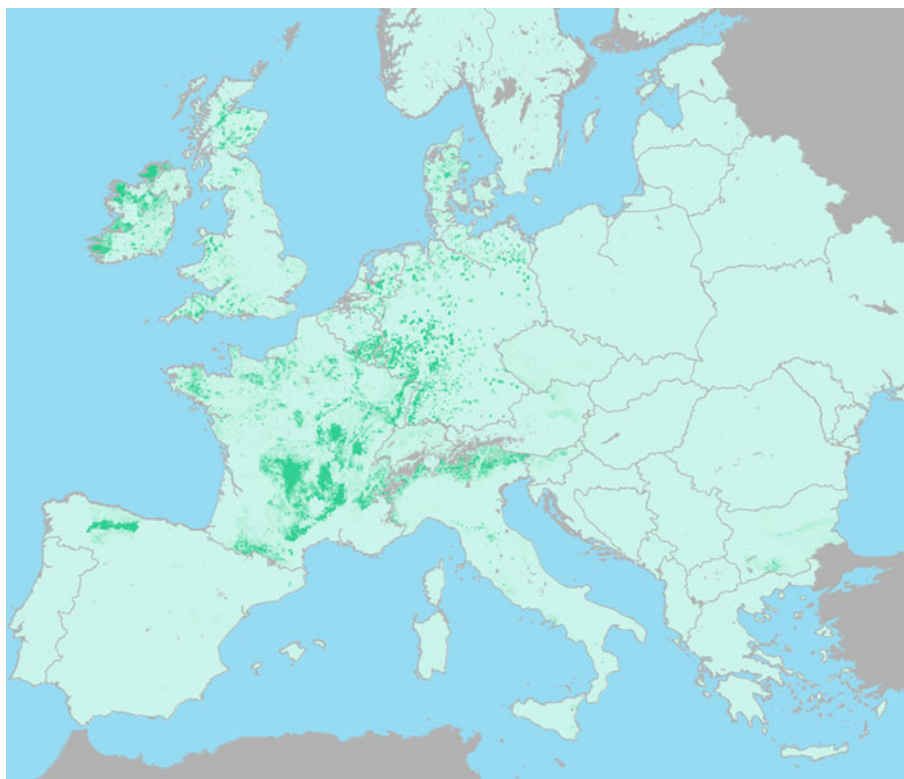
Introduction

Human beings have shaped forest ecosystems in Central Europe since prehistoric times, thus reducing the extent of forests to gain space for agriculture, thereby changing tree communities by cultivating the most useful tree species (Engelmark et al. 2001; Carnus et al. 2006; Essl et al. 2011). One example is Norway spruce (*Picea abies* (L.) H. Karst.), which has been planted on a large scale due to its wood quality and fast growth, and is now one of the most important tree species for forestry in Central Europe. Norway spruce has thus reached a population size much bigger than natural processes would have allowed (Schlyter et al. 2006). But large-scale mortality due to wind throw and bark beetle infestations showed that forestry with Norway spruce, especially in pure stands, bears considerable risks and is not an adequate solution in the face of climate change (Zebisch 2005, p. 86). During the search for alternatives with lower risk and higher yield, foresters have grown non-native tree species from all over the world, including tree species that have then become problematic due to their invasive potential (in Europe, e.g., *Ailanthus altissima*, *Prunus serotina* and *Robinia pseudoacacia*).

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Fig. 1 Distribution map of Douglas fir in Europe with a resolution of 1×1 km, reprinted with permission from Brus et al. (2011)



Today, the most abundant non-native tree species cultivated in Central European forests is Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), which was first introduced in 1827 from western North America (Knoerzer and Reif 2002; Essl 2005). This conifer of the family Pinaceae is one of the eight existing species of *Pseudotsuga* according to Hermann (1982). The genus *Pseudotsuga* is thought to have originated in North America (with two currently existing species, *P. macrocarpa* and *P. menziesii*) and to have expanded into Eastern Asia through the Bering land bridge during the early Oligocene, currently with one species in Japan (*P. japonica*) and Taiwan (*P. wilsoniana*), and four species in mainland China (*P. brevifolia*, *P. forestii*, *P. gaussenii* and *P. sinensis*), although there is some debate about whether the Chinese species are really distinct (Wei et al. 2011). In its native range, *P. menziesii* covers a wide range of environmental conditions with a north-to-south extension of 4,500 km (between 19° and 55°N latitude) (Gugger et al. 2011; Wei et al. 2011). Douglas fir reaches maximum heights of over 100 m and yields of 28 m³/(ha*a) in managed forests (Russell et al. 1990). In contrast to the inland variety *P. menziesii* ssp. *glauca*, the coastal variety *P. menziesii* ssp. *menziesii* was found to be exceptionally suitable for European forests. High growth rates as well as rapid wound closure, good wood properties, resistance against the fungal pathogen *Rhodocone pseudotsugae* Syd. and a low number of pests and diseases are factors that have contributed to the large present-day

distribution of the coastal variety in European forests (Bußler and Blaschke 2004). Douglas fir was also supposed to be more resistant to wind throw than Norway spruce, but a study from Southwest Germany suggests that the two species are equally vulnerable to storm damage under current management conditions (Albrecht et al. 2013). However, storm susceptibility could be lower in case of a more complex forest structure (Schütz and Pommerening 2013). In 2008, Douglas fir acreage covered approximately 3 % of the total ideal forest area in France (427,000 ha), 2 % of the total ideal forest area in Germany (241,000 ha) and additional areas in the Netherlands (16,000 ha), Poland (4,852 ha), Austria (1,000 ha), Denmark (5,690 ha), Switzerland (2,540 ha) (Kownatzki et al. 2011), the British Isles (45,000 ha) (Smith and Gilbert 2003) and Sweden (Felton et al. 2013) (see also Fig. 1). In the future, the area of forests with the presence of Douglas fir in Europe is expected to increase further and, at least in Germany, Douglas fir is likely to become the third most important conifer in forests after Norway spruce and Scots pine (*Pinus sylvestris* L.) (Höltermann et al. 2008).

From an ecological point of view, cultivation of Douglas fir in Europe is likely to have significant impacts on forest ecosystems (Essex and Williams 1992; Peterken 2001; Felton et al. 2013), particularly in case of stands of pure Douglas fir and with high density of this species over large areas. Douglas fir plantations are particularly deleterious from a nature conservation point of view when they replace

species-rich and threatened ecosystems such as forest glades and heathlands (Fagúndez 2013). The introduction of Douglas fir can also be considered as a replicated large-scale experiment in the assembly of novel ecosystems (Seastedt et al. 2008; Hobbs et al. 2009; Pearse and Altermatt 2013), which could become important if assisted migration (the artificial translocation of plant species to enable them to cope with rapid climate change) will be adopted as a conservation strategy (Iverson and McKenzie 2013; Schwartz and Martin 2013). Several cases in the past have shown that exotic and invasive organisms can alter ecosystems, landscapes and ecosystem services (Knight et al. 2001; Richardson and Rejmánek 2004; Benesperi et al. 2012; Dodet and Collet 2012). In the United States, invasive exotic species cause costs of about \$120 billion per year (Pimentel et al. 2000, 2005). Globally, exotic species are considered one of the main reasons for the loss of biodiversity (IUCN 2000). The *Pinus* species introduced to South Africa show that trees are no exception to such threat. Beside economic and aesthetic benefits, the replacement of grass- and shrublands by pine forests reduced the freshwater run-off, increased the intensity of fires as well as the loss of soil due to subsequent erosion. Finally, the introduction of exotic pines reduced the population of 90 bird species of which half are endemic (van Wilgen and Richardson 2012). Tree species should therefore be introduced into new areas with caution and together with research to detect and prevent deleterious consequences.

Although over 150 years have passed since Douglas fir was introduced in Europe and although its cultivation has been intensified during the past century, there is still the lack of a comprehensive compilation of valuable studies about the ecological impacts of Douglas fir in Central Europe. This review aims thus to summarize and discuss the current knowledge regarding effects of Douglas fir on soil chemistry, plants, arthropods, as well as fungi. The literature was searched systematically at the end of 2012 using as keywords “Douglas fir”, “*Pseudotsuga menziesii*”, “Douglasie”, “sapin de Douglas”, “Douglasia” and “abete di Douglas” and as search tools “Web of Science” and “Google Scholar”. Since several studies on this topic were published in languages other than English (see Meyer 2011; Budde 2006; Knoerzer 1999; Utschik 2006), the review also aims to make this literature accessible beyond linguistic borders. Because there has been little attention to the effects of Douglas fir on vertebrates in Europe, this issue is not considered here (but deserves research; Kolb 1996). Only deer browsing and buck rubbing has been reported occasionally and the impact is similar or higher on Douglas fir compared to Norway spruce (Wezel 2008; Metzler 2010; Kownatzki et al. 2011).

Effects on soil chemistry

Soil chemistry is shaped by the canopy-forming tree community. For instance, litter fall and root exudates link the tree with other organisms connected with the soil, including arthropods, the ground vegetation and microorganisms (Binkley and Giardina 1998). In the following, the impact of the introduction of Douglas fir on soil chemical characteristics is summarized to evaluate the impact of this foreign tree species on soil biota and nutrient cycling.

Prietzl and Bachmann (2012) studied 18 sites with former plantations of Norway spruce (16 sites) and Scots pine (2 sites) which had been transformed into Douglas fir and European beech (*Fagus sylvatica* L.) stands between 33 and 123 years ago. The study areas cover a wide range of environmental conditions and are expected to be representative of forest sites in Central Europe (Prietzl and Bachmann 2012). Humus form, soil organic carbon (concentration and stock), C/N ratio and nitrogen (concentration and stock) showed significant differences among different stand types. Specifically, the replacement of Norway spruce and Scots pine by Douglas fir and European beech led to C/N, OC and N stock decreased within the organic litter. However, concerning the other layers (topsoil 0–10 cm, and subsoil 10–30, 30–50 and 50–80 cm), a less uniform picture was detected. Such a non-unidirectional impact of Douglas fir was also shown on forest soil chemistry (Malchair and Carnol (2009) and on the rhizosphere chemistry (Calvaruso et al. 2011; Mareschal et al. 2010; Turpault et al. 2005, 2007). This complexity is not surprising, considering that tree species is only one factor out of many that influence forest soil chemistry, from bed rock to climate conditions, ground vegetation or stand history (Ganssen 1972). Unless more time is needed to perceive the effects of Douglas fir on the lower soil horizons, it appears that Douglas fir is not creating chemical soil properties completely divergent from those observed with native Central European tree species (Augusto et al. 2002, 2003).

Nonetheless, Douglas fir maintains a high fine root density from the surface to a depth of 23 cm, whereas fine roots of oak (*Quercus petraea* (Matt.) Liebl.), Norway spruce and European beech concentrate in the topmost soil layer (Calvaruso et al. 2011). High fine root densities in deeper soil layers might help reduce interspecific competition for nutrients with other tree or shrub species and can be interpreted as niche separation. Such a vertical differentiation of the fine root system has been shown for Douglas fir in mixed stands with Norway spruce (Lei et al. 2012) and also in mixed Douglas fir–European beech stands (Hendriks and Bianchi 1995).

To summarize this section, the indirect effects of Douglas fir on soil chemistry seem to be similar to those of

native tree species and might allow coexistence with the organisms living on and in the soil. This hypothesis needs to be further tested in a wider variety of regions and soil conditions, e.g., at metal-polluted sites (Van Nevel et al. 2013), and with long-term monitoring of soil functions, e.g., nitrification rates (Mareschal et al. 2013) and N re-translocations (Wang et al. 2013). Moreover, the general assumption that Douglas fir is harmless from the point of view of soil conditions disregards more specific interactions at the molecular level, e.g., allelopathy, which could have an impact on soil organisms even if the general chemical soil properties are suitable for them (Steinlein 2013; Prescott and Grayston 2013).

Effects on plants

Species diversity of plants

Budde (2006) compared the understory vegetation of at least 50 years old pure (European beech, Scots pine and Douglas fir) and mixed forest stands (Douglas fir–Norway spruce, Scots pine–European beech, Douglas fir–European beech) in the course of the growing season 2003. The study sites were located in the north-western lowlands of Germany with mainly oceanic climate (mean annual precipitation 650–800 mm, mean annual temperatures 8.4–8.9 °C) and soils classified as secondary podzols. In this study, no plant or moss species was exclusively present in a single-stand type, although preferences were detected. In terms of the species diversity of plants and mosses in the underlayer and ground cover, Douglas fir and Douglas fir–Norway spruce stands displayed the highest species numbers whereas pure European beech and mixed European beech–Scots pine stands exhibited the lowest species numbers. A similar pattern was identified by Augusto et al. (2003) when they studied the impact of six tree species on vegetation and soil properties at 26 locations within the northern half of France. Although a reduced vegetation cover within Douglas fir stands was detected for some comparisons, these authors found no reduction in species richness, but even an increase when Douglas fir stands were compared to European beech stands. This pattern could be caused by differences in the light supply, which was severely reduced in European beech stands over summer compared to Douglas fir and Norway spruce stands (Budde 2006). The low light supply in European beech stands impeded plant growth in the understory and allowed only a small number of species to grow. Concerning the functional species groups (dispersal strategies, life forms after Raunkiaer and preferred ecosystems, e.g., open land inhabitants), no pattern was detected separating the ground vegetation in Douglas fir stands from that in native tree

species stands. In general, the results suggest that pure and mixed Douglas fir stands can host a diverse understory vegetation, which, in species number and composition, is not much different from the understory vegetation in native conifer stands. The differences in species diversity are expected not to be the result of the canopy-forming tree species alone but of different light conditions, which are mainly shaped by stand age, stand composition and stand structure. Therefore, contrasts in species diversity arise rather between pure conifer and pure broadleaf stands than among species of the same group (Budde 2006).

At two different locations in western Bavaria in Germany, Leitl (2001) compared the vegetation in a pure Douglas fir stand with two pure stands of Norway spruce and European beech as well as mixed stands of two forest reserves with the presence of Norway spruce–European beech and oak (*Quercus robur* L.)–European beech. Surprisingly, the forest reserves exhibited the lowest and the two Norway spruce and the Douglas fir stands exhibited the highest species diversity. The high diversity of ground vegetation in the Norway spruce stand could be due to the co-occurrence of still present relict species typical of European beech stands. Other explanatory factors include the species characteristics of Norway spruce stands and their higher spatial heterogeneity due to wind throw gaps and skidder trails. The high diversity in the Douglas fir stand is a consequence of the infiltration of ruderal species from a forestry road and skidder trails. One further remarkable observation is the epiphytic growth of an undetermined fern on Douglas fir stems up to a height of 10 m, which was enabled by the coarse bark structure of Douglas fir.

Are the reported effects of Douglas fir on plant diversity the result of its function as a physical ecosystem engineer? Physical ecosystem engineers control the availability of resources for other organisms (Jones et al. 1997). In particular, the impact of tree species on the light supply in the understory is important for the understory vegetation (Barbier et al. 2008). Nonetheless, there is no competition for light between a mature tree and the understory vegetation but rather a top-down regulation of this resource. Douglas fir appears to influence the light regime similarly to the effect of native tree species. Analogously to soil chemistry, the overall soil, light, water and probably temperature conditions in Douglas fir stands are not much different from those of native tree species (Voloscuk 2012). Therefore, relatively many plant species manage to live in pure and mixed stands of Douglas fir. However, differences in species composition have been documented, with species of the natural forest community rarely present in Douglas fir stands (Leitl 2001). Consequently, the species number alone is not a sufficient indicator of near-natural conditions, and species composition should be taken into

account in future studies of the ecological impacts of Douglas fir on plant diversity. This situation of a different community composition despite similar abiotic conditions might be the result of allelopathic interactions causing the absence of some plant species (Chou 1993; Rice 1979). Secondary plant compounds of Douglas fir tissues were analysed several times (e.g. Kuiters and Sarink 1986; Dellus et al. 1997; Oh et al. 1967; Zou and Cates 1995), but the few available studies including effects on vegetation focused rather on allelopathic inhibition of Douglas fir seedlings by other plant species than vice versa (Del Moral and Cates 1971; Rose et al. 1983; Tinnin and Kirkpatrick 1985).

The two studies of Budde (2006) and Leitl (2001) furthermore showed some problems faced by research on the ecological impacts of exotic tree species. It is difficult to uncouple the effect of a single tree species on its environment from the effect of other factors such as stand age, history and structure, as well as temporal variations between seasons and years. Most studies of ecological effects of Douglas fir are to be taken with caution due to such confounding factors. Moreover, it is not easy to set the standard for comparisons. In many parts of Europe, Douglas fir is used as an alternative to its nearest relative in Europe (Norway spruce) and a comparison seems to be reasonable (Goßner 2008). But in many European forest sites, Norway spruce has been grown outside of its natural range and is not part of the assumed natural tree species community. Thus, the conservation potential of a change from conifers to forestry with autochthonous deciduous tree species is disregarded when Douglas fir is only compared with Norway spruce (Bürger-Arndt 2000). A way out of this impasse would be a comparison of Douglas fir's impacts on biota in pure and mixed conifer as well as broadleaved stands as it has been implemented in several studies.

Natural regeneration

The natural regeneration of Douglas fir in Europe is not a local and recent phenomenon: it has already been reported from Austria, Bulgaria, France, Germany, Switzerland, the UK (Knoerzer 1999), Italy (Avolio and Bernardini 2000) and the Czech Republic (Bušina 2007) since the 1950s, as well as outside of Europe in Argentina, Chile and New Zealand (OECD 2008). Recently, natural regeneration of Douglas fir was reported in Mediterranean mountain forests in Spain (Broncano et al. 2005; Carrillo-Gavilán et al. 2012). The ability to regenerate naturally is important because it provides the possibility for Douglas fir to increase its local abundance and regional distribution in Europe, thereby changing the tree species composition independently and multiplying the ecological impacts of this tree species. Knoerzer (1999) determined the natural

regeneration of Douglas fir in the Black Forest in Germany as representative for the soil acid mid-range mountains in Central Europe. In this dissertation, the author detected natural regeneration of Douglas fir in a large set of locations and stand types in the Black Forest in Germany. Douglas fir seedlings were able to establish among and compete successfully with other common tree species such as silver fir (*Abies alba* Mill.), European beech and Norway spruce, especially on sites with acid soils and a good light supply. In Bavaria, Douglas fir occurs in 27 out of 160 forest reserves, but natural regeneration within closed forests was rarely observed (Endres and Förster 2013). These results imply that Douglas fir is no longer dependent on human plantings but can now regenerate independently and establish successfully in neighbouring stands. In Germany and neighbouring countries, natural regeneration of Douglas fir has become a matter of debate in nature conservation (Kaiser and Purps 1991; Walter et al. 2005; Zerbe 2007; Fischer 2008; Walentowski 2008; Meyer 2011; Konnert and Fussi 2012). To maintain the *Q. petraea* (Mattuschka) Liebl. stands on acidic soil with their high number of rare and endangered species, natural regeneration of Douglas fir has to be removed regularly (Knoerzer 1999). Conversely, a study from the Netherlands reported spontaneous regeneration of native tree species in monotonous conifer plantations, including those of Douglas fir (Jonášová et al. 2006). Regeneration of Douglas fir depends also on the resident soil microbial community (Haugo et al. 2013) and co-introductions of suitable mycorrhizal fungi can enhance its invasiveness (Dickie et al. 2010). Although Douglas fir stands seem to create conditions similar to those created by native conifers (as seen in “Effects on plants” and “Arthropod species diversity” sections), this exotic tree could change habitats distinctly, given that Douglas fir invades deciduous tree stands (Fischer 2008). Further research is needed on whether the ecological impacts (or lack thereof) of Douglas fir plantations are similar to those of Douglas fir stands established naturally.

Effects on arthropods

Arthropod species diversity

In Europe, at least 87 phytophagous insect species have been recruited by Douglas fir, which is about one-third of the number of species observed on this tree species in its native North American range (Goßner and Bräu 2004; Roques et al. 2006). Many of these recruited species are polyphagous (42 %) and feed on more than one plant family. The relative high proportion of monophagous insects (30 %) on Douglas fir may be based on the definition of monophagous, which here includes species feeding or fulfilling their larval stage

within a single plant genus. But this number seems to indicate that the chemical or mechanical defence system of Douglas fir allows even several specialized species to cope with it. This has been attributed to the taxonomic closeness of Douglas fir to native tree species (the closest relative in Europe is Norway spruce) as well as to the generally low diversity of secondary plant compounds of gymnosperms (Tahvanainen and Niemelä 1987). This argument is supported by the observation of Roques et al. (2006) that all monophagous arthropods recruited by Douglas fir in Europe have conifers (mainly Norway spruce) as primary hosts and by the observation of phylogenetic conservatism in the assembly of the phytophagous fauna on Douglas fir in Bavaria (Goßner et al. 2009). The results of Goßner and Simon (2002) support these assumptions as their survey detected no difference in the species number as well as only slight differences in the community structure of crown-dwelling beetles between six Norway spruce and Douglas fir trees, respectively. Concerning the relative proportion of species in each insect order as well as the guild structure, arthropod communities on Douglas fir do not differ significantly between Europe and North America (Roques et al. 2006). Although there are some insect families which have not yet been found feeding on Douglas fir in Europe in contrast to North America and vice versa, recruitment has taken place on a broad taxonomic and functional scale (Roques et al. 2006).

Arthropods and the physical environment provided by Douglas fir

A large part of Douglas fir's impact on the biota in a forest ecosystem can be ascribed to its function as a physical ecosystem engineer (Jones et al. 1997). In the following section, the resulting impacts of the physical influences of Douglas fir trees on arthropod communities are compared with those of native trees.

Ziesche and Roth (2008) studied the distribution of soil-dwelling spiders of two pure stands (Norway spruce and Douglas fir) and two mixed stands (European beech–Norway spruce, Oak (*Q. robur*)–European beech) within four age classes between 15 and 112 years at a small spatial scale (10 m distance between pitfall traps). Correlations were tested with canopy-forming tree species and habitat parameters such as temperature, air humidity, soil characteristics and vegetation features. It was shown that many spider species were not randomly distributed and especially the Douglas fir and mixed oak–European beech stands possessed some specific spider assemblages. Concerning the link between the canopy-forming tree species and the spider assemblage, a seasonal pattern was observed. In spring, there was a distinct difference in species composition between the conifer and deciduous tree stands. This can be explained by

the different abiotic conditions between conifer and deciduous tree stands in this season of the year. In the course of the growing season, the environmental parameters in conifer and broadleaved stands became more similar to each other and the spider assemblage was not clearly correlated with tree species in summer and fall. The most important parameters for the prediction of the species distribution were litter type, canopy closure, temperature, grass and moss cover as well as soil moisture. This suggests that the ecological impact of Douglas fir as physical ecosystem engineer changes with season and stand age and is to a large extent dependent on forest management.

Goßner and Ammer (2006) studied the tree-specific arthropod communities of Douglas fir and Norway spruce in three stand types (Norway spruce, European beech and Douglas fir) in two study sites in Bavaria (Germany) over three consecutive vegetation periods (March–October) on the stem as well as in the crown. In the stem, Douglas fir revealed lower species diversity compared to Norway spruce (in European beech-dominated and Norway spruce-dominated stand types). This is assumed to be the result of a different bark structure of Douglas fir representing a less suitable pathway for stratum changing arthropods than the less structured bark of Norway spruce (Goßner and Ammer 2006). Differences in bark might explain the low species numbers detected on Douglas fir in the studies of Glatz et al. (2003), Winter (2001), Winter et al. (2001) and Kohlert and Roth (2000). This special, less suitable bark structure was also assumed to have an effect on arthropods in the crown. If the colonization of Douglas fir crowns over the stem is constrained for some arthropod species, colonization from neighbouring trees becomes necessary and the general stand composition and structure gain in importance. Goßner and Ammer (2006) assumed that the higher Norway spruce to Douglas fir distance in European beech-dominated stand types was the reason for the relatively low arthropod species number in Douglas fir crowns compared to that of Norway spruce in this stand type. In general, the diversity of arthropod communities in the tree crown of Douglas fir was significantly higher (in Douglas fir- and Norway spruce-dominated stand types) or the same (in European beech-dominated stand types) as compared to Norway spruce, but fluctuated strongly with years and observed guild. Goßner and Ammer (2006) assumed that Douglas fir and Norway spruce crowns differ in their microclimatic conditions, which are the result of (1) Douglas fir's higher canopies [the species already reaches heights over 50 m in Europe; Kownatzki et al. (2011)], (2) horizontal and not pendulating twigs and thus (3) a more open structure. These factors probably lead to warmer conditions in the Douglas fir crown during summer and support the additional establishment of thermophilous species. In contrast to summer time, Goßner and Utschik (2002) showed for the same study site that in

winter 2000 and February 2001 almost no arthropods (on two examined trees) and no foraging birds (in a 6.25 ha large area) could be found on Douglas fir crowns. This might be the result of unfavourable microclimatic conditions during winter in the crown of this tree species.

These results show that Douglas fir can possess special abiotic habitat conditions compared to Norway spruce as a result of divergent bark and crown structures, thus exhibiting different arthropod communities. Although these differences were observed only during a short period of the year and affect only specific groups of organisms, cascading effects on lower or higher trophic levels can be expected and should be the object of further research.

Douglas fir as food resource for arthropods

The chemical composition of wood, bark and needles is crucial for herbivorous and decomposing arthropods. Secondary plant compounds are thought to act as a chemical defence against consumption by herbivores and decay by decomposers (Horner et al. 1988; Haslam 1994; Schowalter et al. 1986).

The decomposer communities of European beech, Norway spruce and Douglas fir were compared at two sites in Bavaria (Engel 2001). While European beech stands were characterized by high individual numbers concerning the macro-fauna (Isopoda, Diplopoda and Lumbricidae), Norway spruce was rather dominated by the meso-fauna (Collembola, Acari and Nematoda). Douglas fir was in an intermediate position between these two tree species. However, the study gives no information on species numbers, guild structure or temporal patterns. The litter decay rate of Douglas fir was similar to that of the native conifers Norway spruce, silver fir and European larch and was thus rather slow compared with native broad leaved species such as common hornbeam (*Carpinus betulus* L.) or sycamore maple (*Acer pseudoplatanus* L.). Unless the result is due to differences in site conditions, this finding would suggest that the secondary plant compounds of Douglas fir are similar to those of the studied native conifers, thus allowing detritivores to use Douglas fir needles as food source. There are also reports of higher quality of the leaf litter (and thus higher biomass of detritivores) for Douglas fir compared to Norway spruce, because, contrary to Douglas fir, the needles of *P. abies* cause acidification of the litter (Pontégnie et al. 2005).

This palatability of the secondary plant compounds is not only acknowledged by the severe damages arising from the large pine weevil *Hylobius abietis* (Linnaeus, 1758) (Wallertz and Malmqvist 2013), but is also supported by the colonization of Douglas fir by several bark beetle species. Bertheau et al. (2009) reported eight indigenous bark beetle species, Laufhütte (1997) detected 24 species

on Douglas fir in Europe, and Bringmann (2001) reported 14 bark beetle species which used Douglas fir for their larval stage (as reported in Goßner 2004). But in contrast to the native tree species, Douglas fir in Europe has so far not been the subject of large-scale outbreaks of an insect herbivore. After the cyclone “Lothar” in December 1999, only 2.6 % of the Douglas fir trees surveyed in France had been attacked by bark beetles in autumn 2000 (versus 36 % of Norway spruce) and only 6 % by autumn 2001 (versus 72 % of Norway spruce) (Roques et al. 2006). Although bark beetles can breed more or less successfully on Douglas fir, some chemical properties of Douglas fir seem to constrain their fitness.

Gruppe and Goßner (2006) studied the eating habits of black arches larvae (*Lymantria monacha* (Linnaeus, 1758)), a polyphagous palearctic lepidopteran, providing the caterpillars a choice between Norway spruce and Douglas fir needles. The test showed that black arches prefer Douglas fir needles compared to Norway spruce needles. The authors argued that high contents of fructose and glucose could act as feeding-stimuli favouring Douglas fir consumption. But the consumption of Douglas fir needles led to reduced larval weights which might be caused by high concentrations of organic acids (quinic and shikimic acid) and procyanidins increasing the energy demand for metabolizing Douglas fir needles and thus hindering carbon assimilation. In contrast to black arches, larvae of the great spruce bark beetle (*Dendroctonus micans* Kugel.) feeding on Douglas fir bark had the lowest survival rate compared to individuals feeding on four further conifer species’ bark (Japanese larch (*Larix kaempferi* Sarg.), grand fir (*Abies grandis* (Dougl.) Lindl.), Norway spruce and Serbian spruce (*Picea omorika* (Panc.) Purk.), and a successful completion of the lifecycle of the bark beetle is unlikely (Wainhouse and Beech-Garwood 1994).

On the whole, the chemical composition of Douglas fir tissues seems to be similar to the one of Norway spruce. This comparability might be the result of the taxonomic closeness and a low degree of specialisation in conifer insect herbivores (Roques et al. 2006; Tahvanainen and Niemelä 1987; Goßner 2004). However, there seems to be some distinct incompatibilities, as even polyphagous herbivores such as black arches cannot cope well with this diet. A detailed chemical analysis would be necessary to clarify this inference.

Co-introduced exotic arthropods on Douglas fir in Europe

From their native habitat in western North America, three parasites followed Douglas fir to Europe, namely the Douglas fir woolly aphid *Gilletteella (Adelges) cooleyi* as well as *Gilletteella coweni* and the seed cone wasp *Megastigmus spermotrophus* (Goßner 2004). In the following,

ecological impacts caused by these co-introduced insect species from the native range are listed.

Goßner et al. (2005) compared the aphidophagous insect community of Douglas fir and Norway spruce in Douglas fir-, European beech- and Norway spruce-dominated stand types in south-western Bavaria (Germany) from March to October 2000, using flight interception traps. Although no measurements were conducted, the authors assumed that the aphidophagous insect community on Douglas fir relies almost solely on Douglas fir woolly aphid because native aphids have not been reported to reach higher densities on Douglas fir. The aphidophagous insect community on Douglas fir exhibited significantly higher numbers in specimens and species compared to Norway spruce in all stand types. This indicates that a broad range of aphidophagous insects, including species with different demands and degrees of specializations, have the ability to use this exotic species at least as secondary food resource, even profiting from it and thus increasing their population sizes. For forestry, a beneficial effect can be expected when the antagonists of aphids are supported to increase their population size, thereby exerting a stronger control of the aphid communities on indigenous trees. But not all insects feeding on aphids are able to use this new resource. Goßner mentioned in his dissertation that in the book of Gösswald (1990), ants are reported to refuse Douglas fir woolly aphids and decrease in their abundance in Douglas fir stands.

Auger-Rozenberg and Roques (2012) sampled seeds from Douglas fir in seed orchards in south-western France over almost two decades to survey the population of *Megastimus spermatrophus*, a seed chalcid introduced to Europe at the end of the nineteenth century. They reported a wide distribution, abundance and impact of *M. spermatrophus* in and on Douglas fir seeds. It can be assumed that this exotic insect occupied the whole niche of cone and seed insects because of missing competitors until the arrival of exotic seed bugs (*Leptoglossus* sp.) in 2008. Although no switch to native tree species has been reported for *M. spermatrophus*, such a host jump has been reported for *Megastimus schimitscheki* in France (Auger-Rozenberg and Roques 2012). It is possible that other organisms introduced from western North America or other regions could make this step and cause widespread ecologic and economic problems in the future (Kirichenko et al. 2013).

Effects on fungi

Fungal diversity associated with Douglas fir

Vacher et al. (2010) reported in their meta-analysis that the introduction status (exotic or native) of tree species

growing in France has no significant effect on the number of interactions with fungal species and concluded that exotic species are well integrated into the French tree–fungus network. However, they believe that studies which quantify the interactions might show a different picture. This result is consistent with the study of Strong and Levin (1975), who detected a similar number of fungal species associated with introduced tree species in Britain compared to native ones, when the distribution area of the tree was taken into account. Therefore, a lower fungal species number of exotic trees would be rather a result of a small distribution area than of exotic tree–fungus incompatibilities. Strong and Levin (1975) also proposed that exotic tree species reach their limit in species richness of fungi rather rapidly due to the good dispersal ability of fungi.

In the fungal database of the United States Department of Agriculture (Farr and Rossman 2013), 59 fungal species are listed for Douglas fir in Europe, as opposed to 1,423 species in North America. This distinct difference in species numbers is surprising and seems to contradict the general assumptions of Vacher et al. (2010) outlined above. But the data from Farr and Rossman (2013) have to be interpreted with caution as the numbers of detected fungi species in Douglas fir stands from Utschik (2001) and Buée et al. (2011) are higher than 59 species. Nevertheless, regarding the fungal species number of the closest congener in Europe Norway spruce with 1,074 listed species in Europe, we can conclude neither that this database is just focusing on North America nor that Europe is poor in fungi. Confounding factors to be considered here are the 2.5 times larger area and the currently one-third smaller human population of North America compared to Europe, so that there are probably more observers in Europe than in North America for unit area. To obtain an overview and compare Douglas fir with other native and exotic tree species, we plotted the fungal diversity for the most common tree species of Europe against the area covered by the tree species in Central Europe (Fig. 2). For Douglas fir, this figure seems to contradict the assumption of Strong and Levin (1975) that introduced tree species have a similar number of associated fungal species compared to native tree species. Native fungi might be to a great extent incompatible with Douglas fir so that negative impacts on fungal diversity are likely to result from its cultivation. It is, however, possible that, since the focus of fungal research and observation has not been on exotic species so far, the real number of fungal species hosted by Douglas fir might be higher than reported. Indeed, other exotic trees such as *R. pseudoacacia* and *Eucalyptus* spp. exhibit relatively high species numbers of fungi in Europe (Fig. 2).

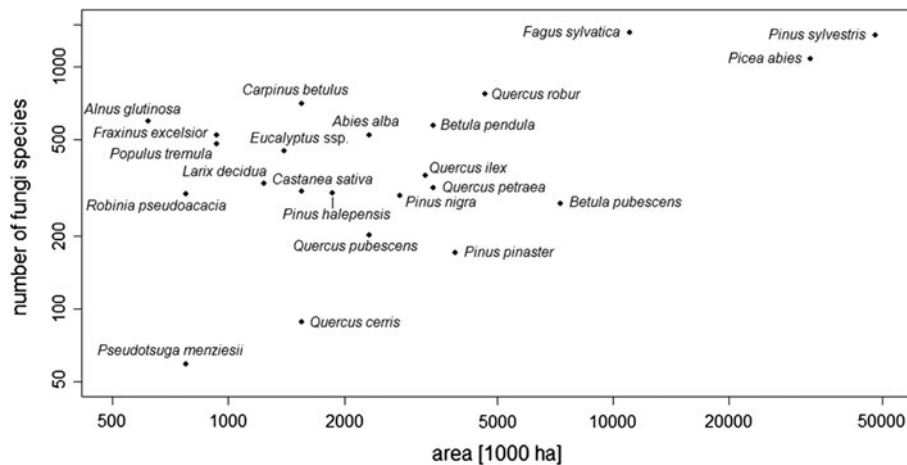


Fig. 2 Relationship between the area occupied by the most common tree species in Europe (Köble and Seufert 2001) and the number of fungi (Farr and Rossman 2013) associated with each tree species, including Douglas fir, in Europe plotted on logarithmic scales. The information on the total forest area of Europe derives from

EuropeanCommission (2013). The regression of logarithmically transformed number of fungi against logarithmically transformed tree range area is significantly positive ($n = 23$, $y = 0.275 + 0.360x$ (SE 0.127), $r^2 = 0.28$, $p = 0.01$)

Fungal diversity and temporal patterns

Parlade et al. (1995) studied the ability of 27 native fungi species from northern Spain to form ectomycorrhiza with Douglas fir seedlings in an artificial pure culture growth experiment to increase the fitness of Douglas fir seedlings after their out-planting. They found that 18 of the 27 species formed ectomycorrhiza with Douglas fir seedlings and eight of them colonized at least 50 % of the fine roots. This indicates a relatively high capability of Douglas fir seedlings to cooperate with native fungi under aseptic conditions and supports the general expectations derived from Vacher et al. (2010) and Strong and Levin (1975), although the low-studied species number and the artificial growth conditions make extrapolation difficult.

In contrast, the study of Utschik (2001) shows a different pattern. In the years 1999 and 2000, fungal fruit bodies were sampled in five different stand types (Douglas fir-dominated, Norway spruce-dominated, Norway spruce–European beech mixed stands, deciduous trees and nature reserve) in old-growth forests in Bavaria and resulted in a total number of 429 detected fungi species out of 3,307 specimens. Pure Douglas fir stands exhibited the lowest total species richness of fungi compared to the other four stand types as well as the lowest number of endangered, rare and close-to-nature indicator fungi. The diversity and relative proportion of fungal guilds (mycorrhiza, saprotrophic fungi and others) matched most closely with that observed in Norway spruce. Saprotrophs together with mycorrhizal fungi were more abundant in conifer stands than wood decaying fungi, which dominated rather in deciduous tree stand types. The author concluded that pure

Douglas fir stands should be avoided in forestry whereas an admixture to a European beech-dominated stand type has less severe ecological impacts.

A similar picture was revealed by Buée et al. (2011) when they studied the fungal diversity within 1,000 m² large plantations of European beech, Oak (*Q. petraea*), Nordmann fir (*Abies nordmanniana* (Stev.) Spach), Norway spruce, Corsican pine (*Pinus nigra* J.F. Arnold) and Douglas fir. Over a study period of 7 years, they detected in total 331 fungal species, while Corsican pine and Douglas fir stands exhibited the lowest species numbers.

Jansen (1991) determined the fruit bodies of mycorrhiza in Douglas fir stands of three age classes (<20 years, 20–40 years, >40 years) over a large part of the Netherlands. She found decreasing species numbers and fruit body abundances of mycorrhizal fungi with increasing stand age, although no comparisons with other stand types were made. Such a pattern has already been observed in other regions on other tree species, e.g., in the study of Nordén and Paltto (2001) in hazel stands (*Corylus avellana* L.) in Sweden. As possible reasons, competitive exclusion or a more efficient recycling of nutrients of the tree were proposed. This result illustrates that temporal dynamics occur not only within or between years but also with proceeding succession over decades. Long-term studies or cross-sectional examinations to incorporate these dynamics are therefore necessary.

Co-introduced exotic fungi

As shown for arthropods in “Co-introduced exotic arthropods on Douglas fir in Europe” section, Douglas fir is not

only affecting forest ecosystems by direct interactions with other biota but also indirectly through the co-introduction of exotic species associated with Douglas fir. Seedlings of Douglas fir (and, more in general, of conifers) in tree nurseries are frequently inoculated with fungi to increase the fitness after the out-planting (Dickie et al. 2010; Brodribb et al. 2012; Parlade et al. 1995). The dissemination and persistence of the American strain of *Laccaria bicolor* S238N used as inoculant were studied 10 years after the establishment of a Douglas fir plantation in France (Selosse et al. 2002). Although no selfing or introgression with indigenous strains was detected, the strain was still present a decade after its introduction. The possibility of indirect long-term ecological impacts of exotic trees by introductions of biota from the native range exists therefore not only for plants or arthropods but for fungi as well (Slippers et al. 2005). In general, the knowledge of tree–fungus interactions of Douglas fir in Europe is rudimentary and demands further investigations.

This knowledge gap is particularly worrying in relation to (fungal) pathogens of Douglas fir. The host-specific needle parasites *Phaeocryptopus gäumannii* and *R. pseudotsugae* have already been introduced to Europe, South America and New Zealand (Watt et al. 2010; Morales et al. 2012). The increasing trade in plants for planting, bonsai, wood and other plant material poses a risk of inadvertent introduction of parasitic organisms currently unproblematic in the native range of Douglas fir (Ennos 2001; Augspurger 1984; Blaney and Kotanen 2001). Alternatively, but no less worryingly, globalization of trade could end up in introducing into Europe pathogens of Douglas fir originating from outside its native range, and thus potentially virulent due to the absence of co-evolution with the host (Fisher et al. 2012; Slippers et al. 2005; Loo 2009). For example, *Phytophthora ramorum* is an oomycete that has caused widespread tree (including Douglas fir) and shrub mortality in the west coast of the US, as well as in the British Isles, and which is likely to have been introduced to North America and Europe from Asia through the trade of ornamental plants for planting (Brasier and Webber 2010; Moslonka-Lefebvre et al. 2011; Moslonka-Lefebvre et al. 2009; Grünwald et al. 2012). Douglas fir is susceptible to this newly described pathogen (Garbelotto and Hayden 2012; Hansen et al. 2005; Davidson et al. 2002) and is thus at risk in Europe too, also given that *P. ramorum* has been frequently intercepted in the ornamental plant trade among EU countries (EFSA PLH 2011; Pautasso 2013; Prospero et al. 2013). Although introduced pathogens of Douglas fir may contribute in keeping this potentially invasive tree species under control and in producing deadwood, there is a risk that such pathogens may then jump to affect tree species native to Europe (Slippers et al. 2005). More research is needed on how to prevent the

introduction of such pathogens into semi-natural forests in the presence of exotic tree species and on how to respond to disease outbreaks once exotic tree pathogens have become established.

Conclusion

Although relatively many studies have investigated the ecological effects of Douglas fir cultivation in Europe, several questions have not been answered yet or only insufficiently. For example, although it is clear that plantations of Douglas fir are susceptible to many root and butt rot fungi (Koch and Thomsen 2003; Ronnberg et al. 1999; Greig et al. 2001), little is known about the Douglas fir wood decay fungal community in Europe (Cornelissen et al. 2012; Deflorio et al. 2008). The available knowledge is sketchy, also because long-term experimental studies controlling for the many confounding factors in semi-natural and planted forests are rare (Rožen et al. 2010; Hobbie et al. 2006). The existing studies have been conducted in a small set of locations and may not be representative of the general situation in Europe. Only few studies compared silver fir with Douglas fir, although this native tree species is common in much of Central Europe and has abiotic demands similar to Douglas fir. Finally, the vast majority of the retrieved studies were conducted over 1 year, one growing season or across a single stand age only (Table 1). Such short-term studies fail to separate tree-related causes and relationships from temporal fluctuations, as the results of Jansen (1991), Budde (2006), and Goßner and Ammer (2006) show. Consequently, further investigations are necessary to confirm their results as well as the conjectures made in this review.

Despite the limitations of the available studies, what are the likely consequences of forest plantations of Douglas fir in Europe? The existing studies suggest that forest ecosystems in Central Europe are able to deal with the introduction of Douglas fir comparably well. Until now, no severe ecological or economic consequences have been detected, whereas large-scale attempts at eradicating Douglas fir from Europe would probably do more harm than good (Skurski et al. 2013). This is mainly because Douglas fir seems to shape the abiotic environment not that differently from native tree species. For example, species numbers of the ground-layer vegetation and of arthropod communities in soil, stem and crown were shown to be similar to those of Norway spruce (Budde 2006; Goßner et al. 2005; Leitl 2001; Ziesche and Roth 2008). But this is not always the case. When Douglas fir is able to invade native deciduous tree stands (in contrast to native conifers) or microclimatic conditions created by Douglas fir are considerably different in a specific time of the year,

Table 1 Retrieved studies on the ecological impacts of Douglas fir in Europe

Authors	Type	Topic	Land	Region	Tree species	Stand ages (years)	Stratum	Study period (years)
Burmeister et al. (2007)	Field study	Arthropods	Germany	South-west Bavaria	Aa, Ld, Pa, Pm, Ps		Crown	1
Engel (2001)	Field study	Arthropods	Germany	South-west Bavaria	Fs, Pa-Fs, Pa, Pm-Pa, Pm		Forest floor	1
Finch and Szumelda (2007)	Field study	Arthropods	Germany	North-west	Qp, Pm	~30	Soil surface	1
Gößner (2004)	Dissertation	Arthropods	Germany	South-west Bavaria	Fs, Pa, Pm	>100	Stem, Crown	3
Gößner and Simon (2002)	Field study	Arthropods	Germany	South-west Bavaria	Pa, Pm	~100	Crown	2
Gößner and Ammer (2006)	Field study	Arthropods	Germany	South-west Bavaria	Fs, Pa, Pm	>100	Stem, Crown	3
Roques et al. (2006)	Review	Arthropods	Europe					
Gößner et al. (2005)	Field study	Arthropods—aphidoph. insects	Germany	South-west Bavaria	Fs, Pa, Pm	>100	Crown	1
Bertheau et al. (2009)	Field study	Arthropods—bark beetles	France	Jura, Limousin	Aa, Ag, Pa, Pm, Ps, Psit, Pstr, Tp		Trunk, Bark	2
Bringmann (2001)	Review	Arthropods—bark beetles	Germany		Pm			
Wainhouse and Beech-Garwood (1994)	Lab study	Arthropods—bark beetles	France		Pa, Pm, Ag, Lk, Po		Bark	1 generation
Füldner and Spork (2003)	Lab study	Arthropods— <i>Dendrolimus pini</i>	Germany	Brandenburg	Pa, Pm, Ps		Needle	
Gruppe and Gößner (2006)	Lab study	Arthropods—lepidoptera larvae	Germany		Pa, Pm		Needle	1 generation
Auger-Rozenberg and Roques (2012)	Field study	Arthropods—seed chalcid	France	South-west	Pm		Seed	27
Blick and Gößner (2006)	Field study	Arthropods—spiders	Germany	South-west Bavaria	Pa, Pm	>100	Crown	1
Ziesche and Roth (2008)	Field study	Arthropods—spiders	Germany	South-west Bavaria	Pa, Pm, Fs-Pa, Qt-Fs	15–112	Soil	1
Utschik (2006)	Field study	Birds	Germany	South-west Bavaria	Pm, Qp-Fs, Fs-Pa, Fs-Qp, Fs, Pa, Pa-Pm		Crown, Stem	1
Haarstick (1979)	Breeding	Birds— <i>Tetrao urogallus</i>	Germany	Harz	Aa, Pa, Pm, Ps,		Needle	
Buée et al. (2011)	Field study	Fungi	France	East (Morvan)	Pa, Pn, Pm, Pn	37	Soil	7
Jansen (1991)	Field study	Fungi	Netherlands	East	Pm	>20, 40<	Soil	3
Kubartová et al. (2009)	Field study	Fungi	France	East (Morvan)	Fs, Qp, Pa, Pm	37	Forest floor	1
Parlade et al. (1995)	Lab study	Fungi	Spain	North	Pa, Pc, Pr, Pm, Pn, Ppin		Seedlings	1

Table 1 continued

Authors	Type	Topic	Land	Region	Tree species	Stand ages (years)	Stratum	Study period (years)
Selosse et al. (2002)	Field study	Fungi	France	East (Morvan)	Pm	10	Soil	3
Utschik (2001)	Field study	Fungi	Germany	South-west Bavaria	Pa, Pm, Pa-Fs,		Soil	2
Wang et al. (2013)	Field study	Needle chemistry	Denmark, Finland, Netherland		Fs, Pm, Ps	46, 90	Needle	2 (3 Pm)
Augusto et al. (2003)	Field study	Plants	France	North	Aa, Fs, Qp, Qr, Pa, Pm, Ps	20–190	Forest floor	1
Budde (2006)	Dissertation	Plants	Germany	North-west	Fs, Pa, Pm-Pi, Pm-Fs, Pm-Pa,		Forest floor	1
Leitl (2001)	Field study	Plants	Germany	South-west Bavaria	Pa, Pm, Fs-Pa, Fs, Qr-Fs		Forest floor	
Voloscuk (2012)	Field study	Plants	Slovakia	South-central	Aa, Fs, Ld, Pa, Pm, Pn, Ps, Qr, Rb	80–100	Forest floor	2
Knoerzer (1999)	Dissertation	Plants—natural regeneration	Germany	Black Forest	Pm		Forest floor	3
Broncano et al. (2005)	Field study	Plants—natural regeneration	Spain	North-east	Pm	10–54	Forest floor	1
Carrillo-Gavilán et al. (2012)	Field study	Plants—natural regeneration	Spain	North-east	Aa, Pm		Forest floor	1
Jonášová et al. (2006)	Field study	Plants—natural regeneration	Netherland	North-east	Pa, Pm, Psit	80–90	Forest floor	1
Calvaruso et al. (2011)	Field study	Rhizosphere	France	East (Morvan)	Fs-Qp, Qp, Pm, Pa,	150, 35	Rhizosphere	1
Hendriks and Bianchi (1995)	Field study	Rhizosphere	Netherland	Central	Bp, Pm	40, 70	Rhizosphere	1
Turpault et al. (2005)	Field study	Rhizosphere	France	East	Pm	48	Soil	1
Turpault et al. (2007)	Field study	Rhizosphere	France	East	Pm	45	Soil	1
Lei et al. (2012)	Field study	Root competition	Germany	Thuringia	Fs, Pa, Pm, Qp	Seedl./sapl.	Soil	
Reyer et al. (2010)	Modelling	Root competition	Germany, Netherland	Gelderland, Brandenburg	Fs-Pm		Soil	
Augusto et al. (2002)	Review	Soil chemistry			Ap, Bsp, Cb, Fs, Pa, Pm, Ps, Qssp		Soil	
Malchair and Carnol (2009)	Field study	Soil chemistry	Belgium, Luxembourg		Fs, Pa, Pm, Qp		Soil	1
Mareschal et al. (2010)	Field study	Soil chemistry	France	East (Morvan)	Fs-Qp, Qp, Pm, Pa,	150, 35	Rhizosphere	
Mareschal et al. (2013)	Field study	Soil chemistry	France	East (Morvan)	Fs, Pa, Pm, Pn, Qp	37	Soil	1
Prietzl and Bachmann (2012)	Field study	Soil chemistry	Germany	Bavaria	Fs, Pa, Pm, Ps	32–150	Soil	1
Van Nevel et al. (2013)	Field study	Soil chemistry	Belgium	North-east	Bp, Ps, Pt, Pm, Qp, Qr, Rp	12	Soil	1

Table 1 continued

Authors	Type	Topic	Land	Region	Tree species	Stand ages (years)	Stratum	Study period (years)
Zeller et al. (2007)	Field study	Soil chemistry (Nflux)	France	East (Morvan)	Fs, Pa, Pm, Qp, Pl	150 (Fs), 25 (others)	Soil	1
Augusto et al. (2003)	Field study	Soil chemistry/plants	France	Northern part	Aa, Fs, Pa, Pm, Ps, Qr, Qp		Soil	1

In many studies, there was no information on stand age and previous stand composition. A qualitative positive or negative effect as a separate column was not included because the definition of a positive ecological impact is not clear and many positive effects on biodiversity arise because of the forest management rather than because of Douglas fir itself
Aa, *Abies alba*; Ag, *Abies grandis*; Ap, *Acer platanoides*; Bp, *Betula pendula*; Bsp, *Betula sp.*; Cb, *Carpinus betulus*; Fs, *Fagus sylvatica*; Lk, *Larix kaempferi*; Pa, *Picea abies*; Pm, *Pseudotsuga menziesii*; Po, *Picea omorika*; Pc, *Pinus contorta*; Pl, *Pinus laricio*; Pn, *Pinus nigra*; Pp, *Pinus ponderosa*; Ppin, *Pinus pinaster*; Ps, *Pinus sylvestris*; Pst, *Picea sitchensis*; Pstr, *Pinus strobus*; Pt, *Pinus radiata*; Pp, *Populus tremula*; Qr, *Quercus robur*; Qp, *Quercus petraea*; Rp, *Robinia pseudoacacia*; Tc, *Tilia cordata*; Tp, *Thuja plicata*

negative consequences for plants, arthropod and bird communities have been observed (Knoerzer 1999; Goßner and Utschik 2002). Similar negative effects are reported from a comparison of the vegetation and soil properties in Douglas fir plantations versus native *Nothofagus* forests in southern Chile (Frank and Finckh 1997). Larger differences to native tree species seem to exist at the molecular level in the chemical composition of plant tissues. This is supported by the observation that Douglas fir has not been victim of larger pest outbreaks in Europe so far (Roques et al. 2006). Moreover, Douglas fir hosts a low diversity of phytophagous arthropods (Roques et al. 2006) and fungi (Utschik 2001). Nonetheless, species numbers are not a sufficient biological indicator for the ecological impacts of exotic species (Magee et al. 2010). In the studies of Utschik (2001), Leitel (2001), and Roques et al. (2006), organisms in association with Douglas fir were shown to be almost exclusively generalist and common species, which is of concern from the conservational point of view.

On the whole, the ecological consequences of Douglas fir seem to be minor. But negative consequences for single groups of organisms have been detected and are relevant for nature conservation. Although no severe impacts have been detected in the 150 years since the introduction to Europe, Douglas fir still poses a risk as a source of problems in the future. Some niches are not or only poorly occupied (Goßner et al. 2005; Auger-Rozenberg and Roques 2012; Roques et al. 2006) and accidentally introduced exotic herbivores or native insect species performing a host jump could therefore exploit such vacant niches (Roques et al. 2006) within a short time scale. Together with unexpected emerging fungal pathogens, such host jumps could cause sudden changes in the Douglas fir system with unknown ecological and economic outcomes.

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