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BIODIVERSITY REVIEW

Little evidence of invasion by alien conifers in Europe

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ABSTRACT

Aim Conifers are invasive species in many parts of the world, especially in the Southern Hemisphere. There are many introduced conifers in Europe, but their status as alien species is poorly documented. We conducted a comprehensive literature review to ascertain the extent to which alien conifers can be considered invasive.

Location Europe.

Methods We reviewed the historical record of alien conifer invasion in Europe (i.e. species with a native range outside the continental boundaries of Europe) by screening the DAISIE database and the ISI Web of Science.

Results According to DAISIE, there are 54 alien conifer species in Europe. *Pseudotsuga menziesii* is the species recorded as naturalized in the most countries (12) and the UK is the country with the most naturalized species (18). Thirty-seven of these conifers have been studied, to some extent, in a total of 131 papers (212 records). Nevertheless, only a few papers have investigated aspects related to biological invasions. In fact, the species are not referred to as alien by the authors in more than half of the papers (66%). Twenty-five per cent of the papers have investigated plant traits, 46% are about biotic and abiotic factors influencing tree performance and 29% deal with ecological and economic impacts. Most papers are related to entomology, dealing with natural enemies affecting the alien conifers.

Main conclusions Scientists have not yet perceived alien conifers in Europe as problematic species. Moreover, the low introduction effort, long lag-time since plantation and phylogenetic closeness between alien and native conifers are possible reasons for their low expansion in Europe to date. From a management point of view, careful observations of sites with alien conifers is necessary to watch for new invasions. From a scientific perspective, thorough analyses of the extent that introduction, rates of naturalization and biogeographical differences influence invasive spread between the two hemispheres will prove timely.

Keywords

Biological invasions, natural enemies, naturalization hypothesis, phylogenetic relatedness, propagule pressure, tree invasions.

INTRODUCTION

Many conifer species have been planted for forestry and ornamental purposes around the world, and some of these have escaped outside their area of plantation (Richardson, 1998). More than 30 species have been reported as invasive in at least one country (Richardson & Rejmánek, 2004). In recent decades, along with forests being attributed a more multifunctional value, there have been conservation concerns about the invasive spread of such conifers and the resulting economic and ecological impacts (Richardson *et al.*, 1994; Binimelis *et al.*, 2007). Introduced conifers can change vegetation life-form dominance, reduce structural diversity, increase ecosystem biomass, disrupt prevailing vegetation dynamics, modify nutrient cycling and alter hydrological regimes (Richardson *et al.*, 1994; Richardson & Higgins, 1998; Levine *et al.*, 2003).

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As with any introduced plant species, the invasion success of alien conifers depends on the intrinsic potential of the species to invade (i.e. invasiveness), the susceptibility of the recipient community to be invaded (i.e. invasibility) (Lonsdale, 1999), and the numbers of individuals introduced and of introduction attempts (i.e. propagule pressure) (Williamson, 1996; Richardson, 2006). These aspects have tended to be studied in isolation.

The most successful invasive conifer species are those with a short juvenile period, a short interval between large seed crops and a small seed mass (Rejmánek & Richardson, 1996; Richardson & Rejmánek, 2004). Such features are correlated with a fast relative growth rate (RGR) (Grotkopp *et al.*, 2002). Most concern regarding alien conifer invasions has been voiced in the Southern Hemisphere (Richardson & Higgins, 1998), especially South Africa, where at least eight species are recorded as invasive. Several pine species, notably *Pinus halepensis*, *Pinus pinaster* and *Pinus radiata* are highly invasive in the region of the country with Mediterranean-type climate. Fynbos, a shrubland vegetation type with a low representation of native trees is heavily invaded by pines. In South America, there is also evidence of significant invasion by conifers driven by a high demand for wood (Simberloff *et al.*, 2002, 2010; Pauchard *et al.*, 2004). Conifer invasions in South America have lagged behind those in Australia, New Zealand and South Africa, where many conifers were widely planted a century earlier or more, but are increasing rapidly (Richardson *et al.*, 2008).

Conifer invasions are far less conspicuous in the Northern Hemisphere (Richardson & Rejmánek, 2004). Although many conifers were introduced and widely planted in Europe in the past century, few species have become invasive. For example, Adamowski (2004) found no evidence of invasion by 49 alien conifer taxa planted in the Polish–Belarusian border. Similarly, of nine alien conifers widely planted in different parts of the USA, only two species are establishing in a few sites (Mortenson & Mack, 2006).

In this paper we review the scientific evidence of alien conifer invasion in Europe (i.e. we consider species with a native range entirely outside the continental boundaries of Europe). The main questions we address are: (1) What are the principal alien conifers in Europe? (2) Where have they been introduced and what is their invasion status? (3) Which aspects of these conifers have been studied? We discuss these results as they relate to the recognized problem of conifer invasion in the Southern Hemisphere and the limited evidence of the same in the Northern Hemisphere.

IDENTITY, DISTRIBUTION AND INVASION STATUS OF ALIEN CONIFERS IN EUROPE

A preliminary analysis was based on the database Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2009; http://www.europe-aliens.org), the largest database of alien species in the world. DAISIE was funded by the European Commission (2005–2008) to create an inventory of alien species that threaten European terrestrial, freshwater and marine environments in order to understand the environmental, economic, social and other factors involved in invasion. The DAISIE database has collated information for fungi, plants, vertebrates, invertebrates, marine and inland aquatic organisms from up to 63 countries/regions (including islands) and 39 coastal and marine areas, including regions adjacent to Europe. Presence of alien species was geographically assigned to NUTS as finer scale resolution (e.g. UTM) is not available for most species and countries.

According to DAISIE, 29 conifer species (35%) are alien in a part of Europe but native to another part, and 54 conifer species (65%) that are alien to Europe – i.e. have originated outside Europe (Lambdon *et al.*, 2008). We focused on the last group (alien conifers or alien to Europe, hereafter). Those conifers that are alien to Europe belong to six families and 24 genera. Pinaceae is the most represented family, with 30 species, followed by Cupressaceae, with 13 species (Fig. 1a). Most of these conifers are native to North America (56%) followed by temperate Asia (26%) (Fig. 1b).

On average (± SE), each alien conifer in Europe has been recorded in 4 ± 0.47 countries/regions, but most species have only been recorded in one country (Fig. 2). *Pseudotsuga menziesii* is the species with the widest geographical distribution (19 countries), followed by *Picea sitchensis*,

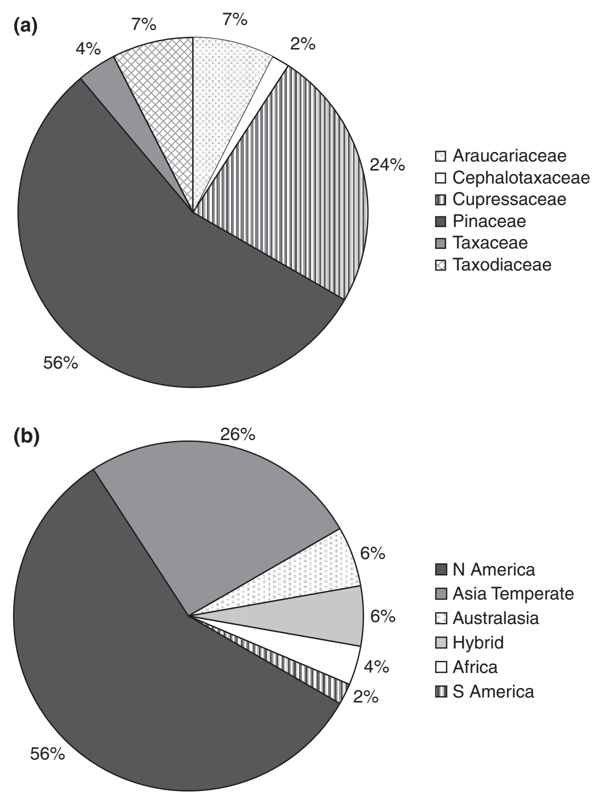

Figure 1 Percentage of alien conifers in Europe by family (a) and by origin (b) according to the DAISIE database (http://www.europe-aliens.org).

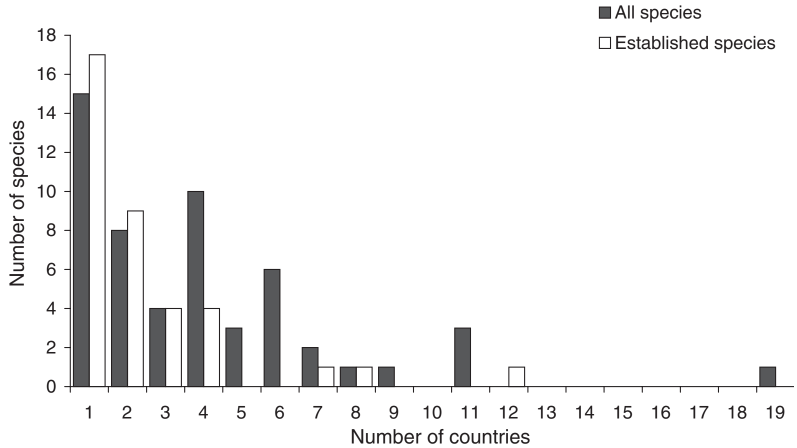

Figure 2 Frequency distribution of range sizes of alien conifers in Europe according to the DAISIE database (http://www.europe-aliens.org).

Pinus strobus and *Platycladus orientalis* (all found in 11 countries). The countries with the highest number of alien conifers are France (34), Sweden (25), Denmark (21) and UK (19).

DAISIE classifies invasion status as established (i.e. naturalized *sensu* Pyšek *et al.*, 2004), non-established and unknown. The status of alien conifers in Europe is unknown for half of the species, while only 31% of species are considered established, primarily in only one country (Fig. 2). The country with the largest number of established conifer species is the UK (18), and the species recorded most often as established is *P. menziesii* (12).

SCIENTIFIC LITERATURE ON CONIFER INVASION IN EUROPE

As a first step, we searched in the 'topic' function of the ISI Web of Science for published papers on each alien conifer in Europe that had been identified by DAISIE. Then, we used the following criteria in the search: (the scientific OR common name of the species) AND (conifer) AND (invasion OR exotic OR expansion) AND (Europe). We accessed the ISI Web from January to March 2009.

We also included some references listed by Richardson & Rejmánek (2004) who conducted a global survey of conifer invasion. A total of approximately 3500 papers were retrieved, but we selected only those studies conducted in Europe. Moreover, we did not consider publications on local or regional flora descriptions, which did not specify ecological information on particular alien conifers (e.g. Crawley *et al.*, 1996; Sádlo *et al.*, 2007; Lambdon, 2008; Lambdon *et al.*, 2008; Bucharova & van Kleunen, 2009). A total of 131 papers met our criteria (see Appendix S1 in Supporting Information). From each paper, the following information was gathered: study species, country of study, spatial scale of the study, pathway of introduction of the species and topic of the study (see specific subsection below) yielding a total of 212 records. We also screened the papers to determine whether the authors presented their study within a biological invasion context.

General overview of the alien conifers

Of the 54 conifer species mentioned in DAISIE as alien to Europe, 37 have been studied in Europe (Table 1). One hundred and nine papers (82%) focused on a single species, 11 (8%) on two and the remaining 11 papers on more than two species simultaneously. The species coverage was very uneven with five species accounting for more than half of the records (*P. sitchensis* – 63; *P. menziesii* – 25; *P. strobus* – 16; *P. radiata* – 15; and, *Larix kaempferi* and *Cedrus atlantica* – 11). Pinaceae was the family with the highest number of records analyzed (185). The species with the widest geographical distribution of studies was *P. menziesii* (11 countries) followed by *P. strobus* (8); *L. kaempferi*, *Abies grandis* and *C. atlantica* were studied in five different countries. Forty-seven per cent of the records were performed in the UK, followed by Spain (13%), the Czech Republic (8%) and Germany (5%) (Fig. 3). The spatial scales of the studies reviewed were grouped as local (i.e. plot), regional (i.e. administrative regions within a country), national (i.e. several areas within a country) or international (i.e. several countries). Most records had a local focus (55%), while 12% and 32% of the records were carried out at regional and national scales, respectively.

A large proportion of the reviewed literature (29%) did not specify the pathway of introduction of the conifer species. Of the remaining publications, the main introduction pathways were via silviculture (57%), as ornamentals (11%) or a combination of both purposes (3%).

Scientific perception of alien conifers in Europe

Many papers cited the region of origin of the conifer species but did not explicitly mention the invasion status of the species in the introduced region (e.g. Day, 1984; Walsh *et al.*, 1999; Varbergen *et al.*, 2003; Barbagallo *et al.*, 2005; Straw *et al.*, 2005, 2006; Mason, 2007). We deemed that the context of biological invasions existed if the authors used the standard terminology of 'exotic', 'alien', 'non-native', 'introduced', 'aloctonous', 'invasive' or 'neophyte' to describe

Table 1 General information on alien conifers in Europe found from an analysis of papers listed in the ISI Web of Science (date of access up to March 2009). For references of data sources, see Appendix S1.

Genus	Species	Origin	Country*,†	Study topic (invasiveness/ invasibility/ impacts)	References†
Araucariaceae					
Araucaria	*araucana*	S America	SPA/UK	1/1/0	33, 73
Cupressaceae					
Chamaecyparis	*pisifera*	Asia temperate	UK	1/0/0	33
Cryptomerica	*japonica*	Asia temperate	UK	1/0/0	33
Cupressus	*arizonica*	N America	FRA/ITA/SPA	0/2/1	3, 4, 73
Cupressus	*lusitanica*	N America	SPA	0/1/0	73
Cupressus	*macrocarpa*	N America	POR/SPA/**UK**	1/3/1	5, **33**, 39, 41, 73
Juniperus	*chinensis*	Asia temperate	UK	1/0/0	33
Juniperus	*virginiana*	N America	SPA/UK	2/1/0	6, 33, 73
Platycladus	*orientalis*	Asia temperate	CZ/UK	2/0/0	33, 34
x Cuprocyparis	*leylandii*	N America	UK	1/0/0	6, 33
Pinaceae					
Abies	*balsamea*	N America	SK	0/0/1	88
Abies	*concolor*	N America	CZ/SE/SK/SWI	1/3/1	7, 8, 36, 88, 123
Abies	*grandis*	N America	CZ/FRA/GER/SK/**UK**	2/1/4	**33**, 51, 88, 107, 123
Abies	*lasiocarpa*	Asia temperate	UK	1/0/0	33
Abies	*procera*	N America	CZ/DEN/IR/**UK**	2/1/1	9, **33**, 35, 123
Cedrus	*atlantica*	Africa	FRA//ITA/SE/SPA/UK	1/8/2	8, 10, 11, 12, 33, 37, 73, 83, 88, 129, 130
Larix	*gmelinii*	Asia temperate	FIN/UK	1/1/0	33, 79
Larix	*kaempferi*	Asia temperate	FIN/GER/IR/SPA/**UK**	1/4/6	13, 14, 15, 16, **33**, 35, 56, 76, 78, 79, 106
Larix	*laricina*	Asia temperate	FIN/UK	1/1/0	33, 79
Larix	*x marschlinsii*	HYB	UK	1/1/0	33, 51
Picea	*engelmannii*	N America	CZ/UK	2/1/0	17, 33, 123
Picea	*mariana*	N America	CZ	1/0/0	123
Picea	*pungens*	N America	AUT/CZ/RUS/UK	2/1/1	33, 87, 88, 123
Picea	*sitchensis*	N America	DEN/FRA/IR/UK	0/33/30	17, 30, [45–72], 76, 86, 90, 91, 92, [94–120], 126, 127
Pinus	*banksiana*	N America	CZ/SPA/UK	2/1/0	33, 73, 123
Pinus	*ponderosa*	N America	SPA/UK	2/1/0	33, 73, 74
Pinus	*radiata*	N America	FRA/ITA/SPA/**UK**	3/6/6	[19–25], **33**, 37, 40, 41, 73, 75, 77, 89
Pinus	*rigida*	N America	SPA/UK	1/1/0	33, 73
Pinus	*strobus*	N America	**CZ‡**/GER/ITA/NET/POL/ POR/SPA/**UK**	5/10/1	27, **33**, **34‡**, 37, 38, 43, 44, 73, 75, 80, 93, 121‡, 123‡, 124‡, 125
Pinus	*wallichiana*	Asia temperate	UK	1/0/0	33
Pinus	*x rotundata*	HYB	CZ	0/1/0	26
Pseudotsuga	*menziesii*	N America	BGM/**CZ**/DEN/FIN/FRA/ GER/IR/POR/**SPA**/**SWI**/**UK**	7/9/9	**1**, 2, **18**, [28–**33**], **34**, 35, 42, 45, 51, 78, 81, 82, 85, 88, 96, 107, **123**, 125, 128, 131
Tsuga	*canadensis*	N America	GER/UK	1/1/0	33, 84
Taxaceae					
Sequoia	*sempervirens*	N America	SPA/UK	1/1/0	33, 73
Taxodiaceae					
Metasequoia	*glyptostroboides*	Asia temperate	UK	1/0/0	33
Sequoiadendron	*giganteum*	N America	SPA/UK	1/1/0	33, 73

Table 1 (Continued).

Genus	Species	Origin	Country*,†	Study topic (invasiveness/invasibility/impacts)	References†
Taxodium	*distichum*	N America	SE	0/1/0	122

*Country – AU, Austria; BGM, Belgium; CZ, Czech Republic; DEN, Denmark; FIN, Finland, FRA, France, GER, Germany; IR, Republic of Ireland; ITA, Italy; NET, the Netherlands; POL, Poland; POR, Portugal; RUS, Russia; SE, Serbia; SK, Slovakia; SPA, Spain; SWI, Switzerland; UK, United Kingdom.

†In bold: the species is considered naturalized.

‡*Pinus strobus* is considered invasive in the Czech Republic.

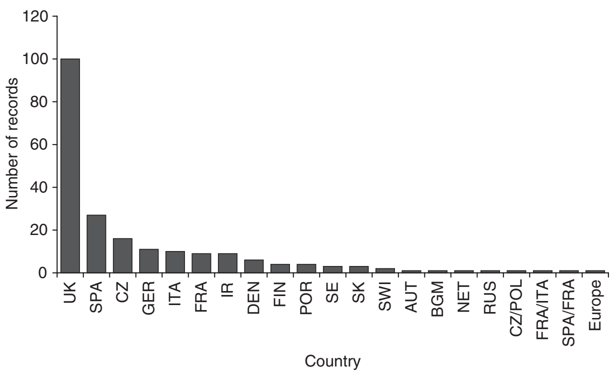

Figure 3 Geographical distribution of records (n = 212) for studies of alien conifers in Europe found at the ISI Web of Science from 1971 up to March 2009. See Table 1 for country identification.

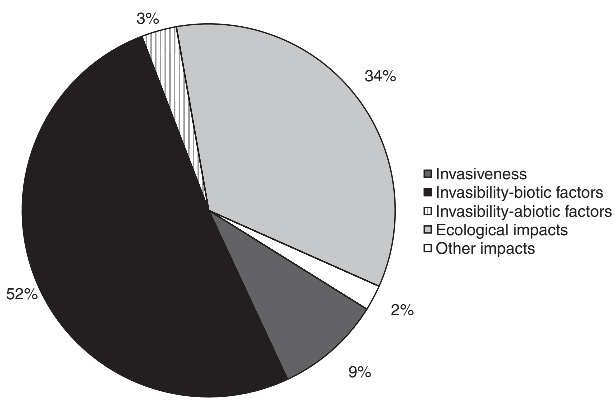

Figure 4 Percentage of papers (n = 131) for studies of alien conifers in Europe found at the ISI Web of Science from 1971 up to March 2009 classified by the topic of study.

the species. We also recorded if the authors mentioned other terminology common in the field of biological invasion, e.g. invasiveness, invasibility, range expansion or species spread. Only a third of the papers (34%) considered the species to be alien or studied an aspect related to invasion biology.

Since the biological invasion literature has increased exponentially in the last decade in Europe (Pyšek *et al.*, 2008), we related whether the perception (yes or no) of alien conifers in the studies has increased though time by a binary logistic regression with publication year as the explanatory variable. We did not find a significant relationship between perception trend and publication year (χ^2 = 9.384; r^2 = 0.07; $P < 0.005$; n = 131). This suggests that alien conifers in Europe have not yet started to interest ecologists working on biological invasions.

It was only possible to identify the invasion status for 72 of the 212 records. Fifty-seven records (27%) corresponded to non-established conifers, 11 (5%) to established and four (2%) to invasive. All records on invasive conifers referred to *P. strobus* in the Czech Republic (Hanzélyová, 1998; Pyšek *et al.*, 2002; Křivánek *et al.*, 2006; Hadincová *et al.*, 2008). Most cases of establishment were found in the UK and referred to *A. grandis*, *Abies procera*, *Cupressus macrocarpa*, *L. kaempferi*, *P. radiata*, *P. strobus* and *P. menziesii* (Crook, 1997). *P. menziesii* is also considered established in the Czech Republic (Pyšek *et al.*, 2002; Křivánek *et al.*, 2006), Spain (Broncano *et al.*, 2005) and Switzerland (Wittenberg, 2005) (Table 1).

Topics of study involving alien conifers in Europe

Although most papers did not explicitly focus on topics related to biological invasions, we attempted to classify all papers with regard to the following aspects of invasion biology: (1) invasiveness: examination of plant performance and demography without any specific association to site characteristics; (2) invasibility: exploration of the biotic and abiotic factors in the study site that determine the success or performance of the species; and (3) impacts: analysis of ecological patterns (e.g. species richness) or processes (e.g. nutrient cycling) between areas where the species occurs or not, or between species. Any mention of health or economic impacts was also recorded (Fig. 4).

Invasiveness of alien conifers

Only 12 papers (9%), constituting 52 records, examined plant performance. These records were conducted in five countries (UK – 32; Czech Republic – 13; Spain – 4; Germany – 2; and, Switzerland – 1). All papers were published in the last decade and the study species were always considered as alien species by authors. They examined, for example, tree growth rates (Mason, 2007; Willoughby *et al.*, 2007) and seed production (Křivánek *et al.*, 2006). A few papers have classified the conifers' invasion status according to their population growth and rate of spread (Crook, 1997; Lavery & Mead, 1998; Pyšek *et al.*, 2002; Chytrý *et al.*, 2008). The majority of these studies focused on *P. menziesii* (e.g. Crook, 1997; Kowarik, 2005), *P. strobus* (e.g. Křivánek *et al.*, 2006; Hadincová *et al.*, 2008) and *P. radiata* (e.g. Lavery & Mead, 1998; Lombardero *et al.*, 2008).

Invasibility to alien conifers

The biotic and abiotic characteristics of the study site where conifers were introduced have been the main area of interest (Fig. 4) with 71 papers (54%) accounting for 96 records. Most papers focused on conifer species as the host tree of natural enemies (94%). Curiously, a large proportion of these studies described the entomology of their natural enemies (e.g. Parry, 1979; Evans, 1985; Masutti & Battisti, 1990; Wilson & Day, 1995; Alonso-Zarazaga & Goldarazena, 2005; Bajo *et al.*, 2008) rather than focusing on the damage they inflicted on the conifers (e.g. Nichols, 1987; Pulkkinen, 1989; Watt *et al.*, 1992; Day *et al.*, 1999; Fabre *et al.*, 2004). A remarkable number of publications deal with the life cycle of insects, mainly Diptera, Hymenoptera and Coleoptera. The insects most studied were those which cause major damage to economically important alien conifers (Battisti, 2006), such as *Elatobium abietinum* and *Thaumetopoea pytiocampa* (12 and 4 papers, respectively), and *P. sitchensis* was the most studied host conifer (32 records). The majority of studies were carried out in the UK (35 records).

Alternatively, the other 6% of papers about abiotic factors focused mainly on the influence of soil properties (e.g. Pedersen & Bille-Handsen, 1995; Hanzélyová, 1998) and climatic conditions (e.g. Parry, 1980; Cuadros & Francia, 1999) on tree performance.

Impacts of alien conifers

Forty-eight papers (37%) with 64 records were classified as studies on impacts. *P. sitchensis* and *P. menziesii* were the most studied species (30 and 9 records, respectively), and the UK and the Republic of Ireland were the countries with the most records (32 and 9, respectively).

Many studies explored the effects of the conifers on biodiversity, focusing on, for example, the avifauna (e.g. Tellería, 1983; Carrascal & Tellería, 1990), rodents (Fernandez *et al.*, 1994), spiders (Oxbrough *et al.*, 2006), weevils (Parry *et al.*, 1990), squirrels (Gurnell *et al.*, 2004), deer (Staines *et al.*, 1985) and wild boar (Irizar *et al.*, 2004). Other studies examined the effect of reforestation on the edaphic collembola community composition (Arbea & Jordana, 1988); the niche relationships among four sympatric bark beetles with respect to conifer species (*P. radiata*) and swarming time (Amezaga & Rodríguez, 1998); or the sustainability of Monterrey pine for the pine shoot beetle (*Tomicus piniperda* L.; Amezaga, 1996). Overall, despite major efforts in studying insects attacking alien conifers, this research does not provide support for the natural enemy hypothesis which states that alien species in the introduced range are less damaged by pathogens and herbivores than in the native range (Maron & Vilà, 2001).

A few studies have focused on ecosystem processes affected by alien conifers. For example, Harriman & Morrison (1982) studied the combined and individual effects of acid precipitation and coniferous afforestation on stream ecology.

In summary, although we classified these studies as dealing with 'impacts', the conifers were not of invasion concern in most cases (only 27%), and the study simply documented differences in ecological patterns and processes between conifer species or between forested stands. Only two papers dealt with economic impacts: the effect of bark stripping on timber production (Welch & Scott, 1998) and the effect of forest management practices on the age structure and composition of forests (Mason, 2007). Finally, one paper analyzed the allergenic impact of cypress pollen on human health (Charpin *et al.*, 2005).

DISCUSSION

Despite the fact that there are many studies on alien conifers in Europe, few ecological aspects related to biological invasions have been investigated. The invasion status of these alien conifers is not mentioned in most cases suggesting either that (1) scientists have not perceived them to be of conservation concern, despite evidence that many of these species are invasive in the Southern Hemisphere (Richardson & Higgins, 1998), or (2) such conifers are not expanding as notably as in other parts of the world (Mortenson & Mack, 2006; Simberloff *et al.*, 2010).

Studies have concentrated on species of greater economic relevance such as *P. sitchensis* and *P. menziesii*. Additionally, the lack of terminology related to biological invasions is partly due to the fact that the main conservation interest has been alien conifers as hosts of harmful insects rather than the conifer itself (Pyšek *et al.*, 2004). Moreover, the published information is likely biased to those countries with a longer tradition in the study of forestry species (e.g. the UK), and possibly substantially more evidence could be found in the grey literature not listed in the ISI Web of Science. We only found information for 37 of the 54 alien conifers in Europe listed in DAISIE. Among them, ISI papers only mention seven species as naturalized and one species (*P. strobus* in the Czech Republic) as invasive. In contrast, Richardson & Rejmánek (2004), whose review also considered other scientific papers, the grey literature and unpublished sources, listed 18 species as naturalized and nine as invasive. For example, naturalization of *P. strobus* has also been documented in Poland and Austria according to non-ISI papers (Adamowski, 2004; Essl, 2007).

There are several explanations for the reducer invasion status of alien conifers in Europe as compared to the Southern Hemisphere. These explanations could be classified first based on the historical and socioeconomic features which have determined its introduction and second, the ecologically-based causes which have limited their establishment and spread.

First, one well-grounded generalization is that the probability of invasion increases with introduction effort (i.e. propagule pressure) and time since introduction (Rejmánek, 2000). In trees, the probability of becoming invasive is primarily determined by the introduction history of the species, such as time since introduction and the spatial scale of the plantations (Pyšek & Jarošik, 2005; Bucharova & van Kleunen, 2009; Simberloff *et al.*, 2010). The majority of alien conifers in Europe were introduced during the last century. The earliest record in Europe seems to be from 1800 for *P. strobus* in the Czech Republic (Hanzélyová, 1998; Pyšek *et al.*, 2002; Křivánek *et al.*, 2006; Hadincová *et al.*, 2008). In contrast, pine introduction in the Southern Hemisphere started during the 17th century (Richardson & Higgins, 1998) and the scale of these introductions has increased dramatically in the last century, particularly in South America (Pauchard *et al.*, 2004; Richardson *et al.*, 2008). Time lags are important determinants of the invasions process (Crook, 2005). In a recent review of alien conifers introduced in the Southern Hemisphere, Simberloff *et al.* (2010) suggested that the later introduction of large conifer plantations in South America, compared to other regions of the Hemisphere such as South Africa, might lead to an increase of invasions into the region in the near future. Kowarik (1995) determined the lag-time for 184 woody species and has suggested that approximately 150 years elapsed before species began to escape from cultivation. Both time since introduction and introduction effort are probably smaller in Europe compared to the Southern Hemisphere regions. As an example, 970,000 and 18,500 ha of alien conifers have been planted in the UK (Forestry Commission, 2003) and in the Czech Republic (Křivánek *et al.*, 2006) in the last century, respectively. For the same time period, 2.05 and 1.5 million ha of alien conifers have been planted in Chile and in Brazil, respectively (Simberloff *et al.*, 2010).

The smaller scale of alien conifer plantations might be due to some non-exclusive reasons. In the last few decades, Europe has changed forest management policies towards a more conservative approach that emphasizes awareness of the use of native species for planting (Quine *et al.*, 2004). European foresters have long had native fast growing tree species, most of them conifers, for fibre production and restoration services while, for example, foresters in South America needed to introduce alien conifer species due to the lack of commercial native trees for planting. In South America, plantations of alien conifers have probably been exacerbated by foreign forestry investment and the potential of wood exports to the Northern Hemisphere (Nuñez & Pauchard, 2009). Moreover, the area of Europe is much less than that of South America and the scale of plantations has therefore likely been proportional.

Second, invasion differences might also depend on similarities between native and alien species. Empty niches prone for conifer exploitation are probably less common in the Northern Hemisphere than in the Southern Hemisphere. For example, South African fynbos has no native tree species and therefore is prone to invasion by alien fire-adapted trees like pines (Richardson & Brown, 1986).

Increased attention is being paid to the effects of phylogenetic relationships between the alien and native flora on invasion success. The naturalization hypothesis proposes that novel genera with native representatives should be less successful than genera lacking them in the native flora (Strauss *et al.*, 2006). Phylogenetic proximity between alien and native trees can result in higher colonization rates of natural enemies on alien trees (Goßner *et al.*, 2009). Most alien conifers in Europe have a temperate North American and Asian origin and have European congeners (e.g. the genus *Pinus*). Thus, once introduced, these conifers might recruit pathogens and phytophages from closely related species which in turn would decrease their capacity to spread in the new range. For example, Adamowski (2004) already suggested that the failure of invasions by alien conifers in Central Europe might be, among other reasons, due to the presence of pathogens in the introduced range because of the presence of native conifer congeners. The same argument was put forth by Mortenson & Mack (2006) who observed that some alien conifers planted in large extensions in North America are heavily attacked by pathogens in the introduced areas where they coexist with native conifers. Our review showed that a high proportion of published papers focused on the natural enemies associated to the alien conifers. This suggests that, in Europe, alien conifers might be strongly controlled by phytophages and pathogens, and this may be one reason why invasion events are less common in Europe.

Nevertheless, recent research has noted the importance of mycorrhizal symbiosis in explaining invasion success in conifers (Pringle *et al.*, 2009). It may be easier for alien conifers to get soil mutualists in areas where there are native Pinaceae (Collier & Bidartondo, 2009; Nuñez *et al.*, 2009), which might be beneficial for their establishment. All else being equal, the success of invasion might depend on the balance between the role of natural enemies and mutualists. These two opposing biotic forces, in general, have been explored in isolation and deserve further exploration.

CONCLUSIONS

Our review illustrates a gap in the understanding of alien conifer invasion in Europe. From the management point of view, we recommend the careful observation of sites where alien conifers are present to watch for new invasions (Richardson & Rejmánek, 2004). From the scientific perspective, research on alien conifers should have a biogeographical focus. For example, a global analysis about the extent of introduction, rates of naturalization and regional differences influencing invasive spread between the two hemispheres is needed. Experimentally, parallel experiments following standard protocols on the biotic and environmental mechanisms controlling seed and seedling performance in different regions and ecosystems would shed light onto differences in ecosystem resistance to alien conifers.

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SUPPORTING INFORMATION

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Appendix S1 List of references for data sources used in Table 1.

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