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Spread and impact of introduced conifers in South America: Lessons from other southern hemisphere regions

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Abstract The history of conifers introduced earlier elsewhere in the southern hemisphere suggests that recent invasions in Argentina, Brazil, Chile and Uruguay are likely to increase in number and size. In South Africa, New Zealand and Australia, early ornamental introductions and small forestry plantations did not lead to large-scale invasions, while subsequent large plantations were followed with a lag of about 20–30 years by troublesome invasions. Large-scale conifer plantation forestry in South America began about 50–80 years later than in South Africa, Australia and New Zealand, while reports of invasions in South America lagged behind those in the latter nations by a century. Impacts of invading non-native conifers outside South America are varied and include replacement of grassland and shrubland by conifer forest, alteration of fire and hydrological regimes, modification of soil nutrients, and changes in aboveground and belowground biotic communities. Several of these effects have already been detected in various parts of South America undergoing conifer invasion. The sheer amount of area planted in conifers is already very large in Chile and growing rapidly in Argentina and Brazil. This mass of reproductive trees, in turn, produces an enormous propagule pressure that may accelerate ongoing invasions and spark new ones at an increasing rate. Regulations to control conifer invasions, including measures to mitigate spread, were belatedly implemented in New Zealand and South Africa, as well as in certain Australian states, inspired by observations on invasions in those nations. Regulations in South America are weaker and piecemeal, but the existing research base on conifer invasions elsewhere could be useful in fashioning effective regulations in South America. Pressure from foreign customers in South Africa has led most companies there to seek certification through the Forestry Stewardship Council; a similar programme operates in Australia. Such an approach may be promising in South America.

Key words: Argentina, Brazil, Chile, conifer plantation, lag time, propagule pressure.

INTRODUCTION

Introduced woody plants are among the most consequential invaders, comprising 15 species in a compilation of 100 of the world's worst invasive species (Lowe *et al.* 2001). Woody invaders often transform formerly treeless communities such as grasslands, heaths and savannas; the very presence of such a new life form confers a different physical structure (Richardson *et al.* 1994). Forests, too, have been greatly affected by woody invaders (Daehler 2005; Knight *et al.* 2007). Impacts of woody invaders in various recipient communities have included modified hydrology (Le Maitre *et al.* 2000), nutrient regimes and cycles (Vitousek 1990; Jackson *et al.* 2002), fire characteristics (Brooks

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et al. 2004), ground cover and animal communities (Schmitz *et al.* 1997), litter and soil processes (Wardle 2002; Knight *et al.* 2007) and soil communities (Wardle 2002).

Invasions by conifers, especially pines, have received extensive attention from ecologists, biogeographers, conservationists and invasion biologists (e.g. Richardson *et al.* 1994; Rejmánek & Richardson 1996; Richardson & Higgins 1998). Most research has been on invasions in South Africa, Australia and New Zealand, where extensive conifer plantings occurred long ago. More recently, extensive conifer plantations and other plantings have been established in South America (Matthews & Brand 2005; Richardson *et al.* 2008). Richardson *et al.* (2008) raised the prospect that a major invasion by introduced conifers may be imminent there, lagging behind those documented in other southern hemisphere locations only because introduction and widespread planting of conifers occurred much later in South America. The wide distribution and extensive knowledge of conifer invasions in other regions should inform predictions and management decisions for regions where introduced conifers are not yet firmly established.

First we briefly review the history of conifer introduction elsewhere in the southern hemisphere, by region. Next we describe the history and current status of conifers in South America by nation, focusing on the nations containing the greatest area of planted conifers – Argentina, Brazil, Chile and Uruguay. Other nations (e.g. Colombia, Ecuador and Venezuela) have conifer plantations, but no substantive data exist on their extent and on invasions. We then consider what experiences with introduced conifers elsewhere may suggest about their future trajectory and impacts in South America. Finally, we discuss policies treating introduced conifers in other southern hemisphere nations and how they might inform an effective response to conifer invasions in South America.

It is important to clarify definitions. By 'introduced', we mean transported across a major biogeographical barrier by humans, as is the case for plantations of exotic conifers. By 'invasive', we refer not to environmental or economic impact but to the ability of a species to propagate itself in nature at some distance from the sites of introduction – Pyšek *et al.* (2004) suggest an approximate threshold of >100 m in <50 years for species spreading by seed.

OTHER SOUTHERN HEMISPHERE CONIFER INTRODUCTIONS

South Africa

In South Africa, *Pinus pinaster* and *P. pinea* were introduced to Cape Town about 1685, and both were widespread by 1810 (Shaughnessy 1986), while commercial *Pinus* plantations were established in Cape Province beginning in 1884 (Geldenhuys *et al.* 1986). In the Transvaal, thousands of seedlings of several *Pinus* species were distributed between 1904 and 1908 (Wells *et al.* 1986). By 1910, at least 79 species of *Pinus* had been planted (Le Maitre 1998; Richardson & Higgins 1998). In various parts of South Africa, afforestation increased quickly between 1910 and the early 1980s (Geldenhuys *et al.* 1986).

The earliest report of pines becoming invasive in South Africa was of *P. halepensis*, *P. pinaster* and *P. pinea* invading in the Caledon district in 1855 (Lister 1959), while *P. pinaster* was said to have been 'gradually taking possession . . . of the face of a mountain above Capetown' since the early 1890s (Sim 1927). These were the first records of substantial conifer invasion in the southern hemisphere (*cf.* Richardson & Higgins 1998). Concerns that invasive alien plants (including pines) could pose serious threats to natural vegetation in South Africa were raised as early as the 19th century by botanists, including Harry Bolus (in 1886), Peter MacOwan (in 1888) and Rudolf Marloth (in 1908) (references in Richardson & Higgins 1998).

Currently conifer plantations in South Africa cover just over 700 000 ha (mainly *P. radiata*, *P. patula*, *P. taeda* and *P. elliottii*). These have led to substantial invasions. Le Maitre *et al.* (2000) estimated the extent in two ways: a 'condensed area' of 77 000 ha that would be the equivalent amount of land with 100% pine cover, and a total invaded area of 2.95 million ha, which is the actual extent of land invaded (often sparsely) by pines.

We note that Swaziland had about 80 000 ha of pine plantations between 1988 and 1999 (R. Hassan & P. Ngwenya, unpubl. data 2006), while Zimbabwe had approximately the same amount between 1995 and 2001 (Mabugu & Chitiga 2002). We have found no reports of invasion.

New Zealand

Pinus pinaster was probably the first conifer introduced to New Zealand, shortly before 1830 (Richardson & Higgins 1998). *Pinus radiata*, *P. sylvestris* and *Cupressus macrocarpa* arrived in the 1860s, and in 1871 the government passed the Forest Trees Encouragement Act promoting plantations (Roche 1990; Roche & Le Heron 1993). The government became more heavily involved in fostering plantations with the establishment in 1897 of a Forestry Branch of the Department of Lands and Surveys (Roche 1990; Roche & Le Heron 1993). The first substantial successful plantation was established in 1896 (Le Maitre 1998), and pines and other species were extensively planted by the early 20th century (Williams & Cameron 2006), with

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15 000 ha of state forests planted by 1920 (Roche 1990; Roche & Le Heron 1993). The main areas of plantation forestry were established in the late 1920s and early 1930s (Roche 1990; Roche & Le Heron 1993; Richardson & Higgins 1998).

Invasion by conifers in New Zealand was first reported in the late 1890s. By 1903, *P. pinaster* was described as invasive, often spreading great distances, and similar reports for *P. radiata* date from as early as 1913 (Thomson 1922). Rapid increases in invasions occurred in the first two decades of the 20th century and especially after the late 1940s (Richardson & Higgins 1998). Conifer invasions are now believed to affect over 600 000 ha on the eastern side of the South Island alone. The lag between species establishment and invasion varied from 20 to 65 years (Richardson & Higgins 1998). Ledgard (2004) summarized the history and research associated with the spread of introduced conifers in New Zealand.

Australia

In Australia, *P. radiata*, *P. nigra*, *P. pinaster* and *P. pinea* were all established at least by the 1850s (Richardson & Higgins 1998), and the first commercial pine plantations in the southern hemisphere were established in South Australia in 1875 (Le Maitre 1998). However, substantial cultivation began only shortly before 1900, with *P. halepensis* and *P. radiata* (Richardson & Higgins 1998), and large-scale planting of *P. radiata* began in the late 1800s in South Australia (Virtue & Melland 2003). By 1987 there were 793 000 ha of northern hemisphere pines (*P. radiata*, *P. elliottii*, *P. pinaster*, *P. caribaea*), of which 78% were *P. radiata* (McDonald 1993).

No conifer invasions were reported in Australia before the 20th century, and a comprehensive list of complaints by conservationists and others about conifer plantations in 1979 did not include invasions (Carron 1979). The earliest documented invasions by conifers were in the 1950s (Richardson & Higgins 1998). Invasion by *P. elliottii* in Queensland followed introduction by about 30 years (Richardson & Higgins 1998), and pine invasions in the Australian Capital Territory and Western Australia also followed major plantation establishment by several decades.

New Caledonia

Thirteen species of introduced conifers (including 11 pines) have been planted in New Caledonia beginning in 1959 (Crémière & Ehrhart 1990). One of these, *P. caribaea*, introduced about 1968, was quickly observed self-sowing seeds within and at the edges of plantations. By 1990, there were about 6000 ha of *P. caribaea* plantations (Crémière & Ehrhart 1990), and this species was recognized as invasive by 1996 (Gargominy *et al.* 1996; Le Mire Pécheux 1996; Meyer *et al.* 2006).

INTRODUCED CONIFERS IN SOUTH AMERICA

Argentina

The first records of Old World conifers introduced to Argentina were reported in 1813 by Perez Castellano (1968). The species cannot be determined, and the introductions were for ornamental uses. In Argentina, conifers were first experimentally introduced for forestry purposes to Isla Victoria, in the Patagonian Andes, in 1910. A *P. ponderosa* plantation initiated there in 1927 is one of the first conifer plantations in Latin America (Cozzo 1987). Plantations on this island served as a government nursery for the rest of Argentina through the 1960s (references in Simberloff *et al.* 2002), and plantation forestry in Patagonia increased rapidly in the 1970s (Schlichter & Laclau 1998).

Today, there are substantial plantings of 10 species (*P. halepensis, P. radiata, P. pinaster, P. pinea, P. elliottii, P. taeda, P. caribaea, P. ponderosa, P. contorta* and *Pseudotsuga menziesii*) and lesser plantings of two others (*P. roxburghii* and *P. patula*) in six regions (Table 1a). In the humid pampas, plantations were established between 1930 and 1960, while in the Patagonian steppe and Valdivian temperate forest, the first plantings were in the mid-1960s and most occurred beginning in the mid-1970s. Pine plantations were also numerous by the 1950s in the mountains of central Argentina, where they now cover more than 36 000 ha (Plevich *et al.* 2002). For other regions dates of plantings are not recorded. The total area planted in conifers in Argentina exceeds 500 000 ha (the majority consisting of *P. elliottii* and *P. ponderosa*), and this area does not include the humid pampas, for which data are unavailable. Most of the area in commercial conifer plantations is in northeastern Argentina, where the total coverage in 1998 was 287 000 ha (SAGPyA 2001). The Argentinean government estimated that an additional 20 million hectares of grasslands and scrub are suitable for forestry plantations because they have favourable growing conditions and would not entail direct competition with agriculture or native forests (SAGPyA 2001).

The first conifer invasion records in Argentina that we have found were of burned and grazed sites by *P. radiata* and of open *Austrocedrus* forest by *Ps. menziesii*, both in 1988 (Chauchard *et al.* 1988; Richardson *et al.* 1994). Of the substantially planted species,

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Table 1. Pinaceae species planted, invasive status, purpose of original plantations and area planted in different ecoregions of South America. Question mark signifies unknown

Ecoregion	Species	Established outside plantations?	Invasive?	Purpose of planting	Area planted (×1000 ha)	Source of data
a. Ecoregions of Argentina and Uruguay						
Humid pampas	*Pinus halepensis*	Yes	Yes	Commercial plantations, by-road afforestation, sand dune stabilization, ornamental, shade	N/A	Long, M.A.1997
	Pinus radiata	Yes	Yes			Zalba, S.M. & Villamil, C.B. 2002
	Pinus pinaster	Yes	Yes			Zalba, S.M., Cuevas Y.A. & Boó R. 2008
	Pinus pinea	No	No			Cozzo, D. 1994
	Pinus elliottii	Yes	Yes			Cozzo, D. & Tuset R. 1996
	Pinus taeda	Yes	?			
Espinal	*Pinus elliottii*	Yes	Yes	Commercial plantations, by-road afforestation, commercial plantations	200	CIDEIBER, Argentina, Actividades del sector primario, Sector forestal. http://www.cideiber.com/infopaises/Argentina/Argentina-04-02.html
	Pinus taeda	Yes	?			InBiAr – Base de Datos sobre Invasionbes Biológicas en Argentina, www.inbiar.org.ar
	Pinus halepensis, P. elliottiii, P. taeda, P. insigne	?	No		36	Plevich *et al.* (2002)
Southern cone mesopotamian savanna	*Pinus elliottii*	Yes	?	Commercial plantations	200	CIDEIBER, Argentina, Actividades del sector primario, Sector forestal. http://www.cideiber.com/infopaises/Argentina/Argentina-04-02.html
	Pinus taeda	Yes	?			
	Pinus caribea var. *hondurensis*	?	?			
	Pinus caribea var. *caribea*	?	?			
Uruguayan savanna	*Pinus elliottii*	Yes	?	Commercial plantations, sand dune stabilization, ornamental	174.2	Cozzo, D. & Tuset R. 1996
	P. patula	?	Yes			Petraglia, C. & Dell'Acqua M. 2006
	Pinus pinaster	Yes	Yes			Silvana Masciadri. Base de Datos de Invasiones Biológicas en el Uruguay
	Pinus roxburghii	?	?			
	Pinus radiata	?	?			
	Pinus taeda	Yes	?			
	Pinus elliottii	?	?			

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Table 1. *Continued*

Ecoregion	Species	Established outside plantations?	Invasive?	Purpose of planting	Area planted (×1000 ha)	Source of data
Dry chaco	*Pinus ponderosa*	Yes	No	Commercial plantations	30	CIDEIBER, Centro de Información y Documentación Empresarial sobre Iberoamérica. Argentina, Actividades del sector primario, Sector forestal. http://www.cideiber.com/infopaises/Argentina/Argentina-04-02.html
Patagonian steppe	*Pinus contorta*	Yes	Yes	Commercial plantations	49.2	Sarasola *et al.* (2006)
	Pinus insigne	?	No			Luis Tejera (pers. comm. 2008)
	Pseudotsuga menziesii	Yes	No			
	Pinus ponderosa	Yes	No			
Valdivian temperate forest	*Pinus contorta*	Yes	No		14.1	Chauchard *et al.* (1988); Sarasola *et al.* (2006)
	Pinus insigne	Yes	?			
	Pseudotsuga menziesii	Yes	Yes			
b. Ecoregions of Chile						
Chilean matorral	*Pinus radiata*	Yes	Yes	Commercial plantations	1304.0	CONAF-CONAMA 2005
	Pseudotsuga menziesii	?	?			Boletín estadístico 74 (INFOR 1999)
Valdivian temperate forest	*Pinus radiata*	?	Yes	Commercial plantations	641.0	CONAF-CONAMA 2005
	Pseudotsuga menziesii	Yes	Yes			Boletín estadístico 74 (INFOR 1999)
Magellanic subpolar forest	*Pinus radiata*	?	?	Commercial plantations	35.5	Alberto Avila 2007 (pers. comm.)
	Pseudotsuga menziesii	?	?	Experimental (control erosion)		Gascón 2005
	Pinus contorta	Yes	Yes			
	Pinus ponderosa	?	?			
	Pinus sylvestris	Yes	Yes			
c. Ecoregions of Brazil						
Alto Paraná Atlantic forest	*Pinus taeda*	Yes	Yes	Commercial plantations	166	Brazilian Association of Forest Plantation Producers
	Pinus elliottii	Yes	Yes	Ornamental		Leonardo von Linsingen (pers. comm. 2007)
	Pinus caribaea	No	No			
	Pinus caribaea var. *bahamensis*	No	No			
	Pinus caribaea var. *hondurensis*	No	No			
	Pinus maximinoi	No	No			
	Pinus oocarpa	No	No			
	Pinus chiapensis	No	No			
	Pinus tecunumanii	No	No			
	Pinus patula	No	No			

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Table 1. *Continued*

Ecoregion	Species	Established outside plantations?	Invasive?	Purpose of planting	Area planted (×1000 ha)	Source of data
Araucaria moist forests	*Pinus taeda*	Yes	Yes	Commercial plantations	1190	Brazilian Association of Forest Plantation Producers
	Pinus elliotii	Yes	Yes	Ornamental		Leonardo von Linsingen (pers. comm. 2007)
	Pinus oocarpa	Yes	Yes			
	Pinus caribaea var. *bahamensis*	No	No			
	Pinus caribaea var. *hondurensis*	No	No			
	Pinus chiapensis	No	No			
	Pinus radiata	No	No			
	Pinus patula	No	No			
	Pinus maximinoi	Yes	Yes			
	Pinus serotina	?	Don't know			
	Pinus tecunumanii	Yes	Yes			
Cerrado	*Pinus taeda*	Yes	Yes	Commercial plantations	74	Brazilian Association of Forest Plantation Producers
	Pinus oocarpa	Yes	Yes	Ornamental		Leonardo von Linsingen (pers. comm. 2007)
	Pinus elliottii	Yes	Yes			
	Pinus tecunumanii	Yes	Yes			
	Pinus maximinoi	No	No			
	Pinus patula	No	No			
	Pinus kesiya	No	No			
	Pinus pseudo-strobus	No	No			
	Pinus chiapensis	No	No			
	Pinus caribaea	No	No			
	Pinus caribaea var. *bahamensis*	No	No			
	Pinus caribaea var. *hondurensis*	No	No			
Serra do Mar coastal forests	*Pinus maximinoi*	Yes	Yes	Commercial plantations, ornamental	N/A	Leonardo von Linsingen (pers. comm. 2007)
	Pinus elliottii	Yes	Yes			
	Pinus taeda	Yes	Yes			
	Pinus caribaea var. *bahamensis*	Yes	Yes			
	Pinus caribaea var. *hondurensis*	Yes	Yes			
Uruguayan savanna	*Pinus taeda*	Yes	Yes	Commercial plantations	N/A	Leonardo von Linsingen (pers. comm. 2007)
	Pinus elliottii	Yes	Yes			
Bahia interior forest	*Pinus caribaea* var. *bahamensis*	No	No	Commercial plantations	N/A	Leonardo von Linsingen (pers. comm. 2007)
	Pinus caribaea var. *hondurensis*	No	No			
	Pinus oocarpa	No	No			
Guianan savanna	*Pinus* sp.	?		Commercial plantations	28	Brazilian Society of Silviculture

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all save *P. pinea* and *P. caribaea* are established outside plantations, with *P. radiata*, *P. ponderosa*, *P. contorta* and *Ps. menziesii* all heavily established in at least some regions. Six species (*P. halepensis*, *P. radiata*, *P. pinaster*, *P. elliottii*, *P. contorta* and *Ps. menziesii*) are considered invasive in certain locations, while *P. ponderosa* may be invasive in some regions, but in smaller areas than the above species. In particular, in Patagonia, *P. contorta* is already invading steppe vegetation and *Ps. menziesii* is invading forest dominated by *Austrocedrus chilensis* (Sarasola *et al.* 2006).

Chile

In Chile, non-native conifers were first introduced by Spaniards and other Europeans in the 17th century, initially as ornamentals and later to control erosion and stabilize dunes. In the late 19th century, monospecific plantations began where native forests had been destroyed (e.g. by mining). The species currently most abundant, *P. radiata*, was introduced unintentionally in 1885 and subsequently planted with other North American conifers as an ornamental species (see Lara & Veblen 1993). Starting in the late 1960s, *P. radiata* was widely planted in afforestation projects, heavily subsidized by the Chilean government since 1974 as the species was found to be especially suitable for the timber and pulp industries (Espinosa *et al.* 1990; Le Maitre 1998). The Forestry Institute (Instituto Forestal) developed a species introduction programme in the early 1960s, establishing trial plots in more than 100 areas located between the semi-arid and temperate regions, including protected areas such as parks and reserves (Loewe & Murillo 2001). Much of the plantation expansion was at the expense of native forests, with up to 18% of native forests of the coastal range in the Río Maule region converted to plantations between 1978 and 1987 (Lara & Veblen 1993).

Today, plantations of *P. radiata* total nearly 2000 000 ha, and plantations of *P. contorta*, *P. ponderosa*, *P. sylvestris* and *Pseudotsuga menziesii* account for another 50 000 ha (Table 1b). Peña and Pauchard (2001) warned that introduced conifers were becoming invasive in certain settings. All species have been shown to be able to establish outside plantations, and *P. contorta* and *Ps. menziesii* are considered invasive in particular types of ecosystems (Peña *et al.* 2007). *Pinus radiata* from plantations is invading coastal maulino forest, following deforestation and fragmentation (Bustamante & Castor 1998; Bustamante *et al.* 2003).

Brazil

Shimizu (2006) has recently described the history of pine introductions and forestry in Brazil. Although immigrants may have brought unrecorded plant species in the previous two centuries, the first recorded pine was *P. canariensis* in 1880, planted as an ornamental in Rio Grande do Sul. The first experiments using pines for silviculture started around 1936, but the chosen species, all European, did not thrive. In 1948, North American species known as 'yellow pines' were introduced for silvicultural experiments near São Paulo: *P. palustris, P. echinata, P. elliottii* and *P. taeda*, of which the latter two appeared particularly promising (Baldanzi *et al.* 1974). Subsequently, many species were introduced for similar experiments throughout Brazil, but primarily in the south and southeast. Today, 12 species (*P. taeda, P. elliottii, P. caribaea, P. patula, P. oocarpa, P. tecunumanii, P. chiapensis, P. maximinoi, P. radiata, P. serotina, P. kesiya, P. pseudostrobus*) are grown in plantations totalling nearly 1.5 million ha in seven regions, mostly in the moist *Araucaria* forest ecoregion (Table 1c).

The first reported invasions by conifers in Brazil were by *P. taeda, P. elliottii* and *P. caribaea* in southern grasslands in the early 1990s (Ziller 2000; Liesenfeld & Pellegrim 2003; Zenni 2005; Zanchetta & Diniz 2006). Other species may have become invasive before then without being recorded, as there was little concern about this sort of problem until the 1990s and we have found no previous records. By 2008, *P. oocarpa* and *P. patula* were also reported as established outside plantations and invasive (I3N-Brasil 2008).

Uruguay

The first conifers recorded as introduced to Uruguay were reported in 1813 by Perez Castellano (1968), as for Argentina, but these did not lead to successful plantations; the Old World species cannot be determined. *Pinus radiata* was introduced in 1871 and was planted widely in the 1940s and 1950s, but the plantations were soon abandoned. Substantial plantations probably started in the 1890s using *P. pinaster* for dune stabilization on the coast, near Maldonado (Villegas Suárez 1941). *Pinus elliottii* and *P. taeda* were introduced about 1960. López and Cussac (1943) reported thousands of hectares of *P. pinaster* plantations, less than 30 years old, in the coastal dunes, plantations of *P. pinea* in the mountains, and isolated *P. halepensis* trees planted in small farms. A great increase in plantation forestry began in the mid-1990s.

Plantations in Uruguay today total about 275 000 ha and consist of six species (primarily *P. elliottii*, *P. pinaster* and *P. taeda*, but also including *P. radiata*, *P. roxburghii* and *P. patula*), of which at least the first three are established outside plantations (DGF 2007; Table 1a). *Pinus elliottii* and *P. pinaster,* which were also planted to stabilize sand dunes and as urban amenities, are considered invasive at certain sites (I3N-Uruguay 2008).

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IMPACTS OF SOUTHERN HEMISPHERE CONIFER INVASIONS

We focus on impacts not of introduced conifer plantations themselves, which can be considerable, but of invasions by self-sown conifers outside the plantations. Invasive introduced conifers at various locations in the southern hemisphere have several documented impacts, although these have not been studied in detail at many sites. Additionally, some observations from plantations can also suggest impacts that might reasonably be expected from self-sown conifers (Richardson *et al.* 1994). Such inferences are credible because invading conifers often produce monospecific stands that resemble plantations, but the ecological similarities, including impacts, between plantations and forests that establish outside plantations, merit much more research. A major difference is that plantations are generally preceded by clearing, and it is often difficult to separate the effects caused by the clearing operations from those caused by the presence of the conifers.

Observed impacts outside South America

Foremost among impacts are overtopping and replacing native treeless vegetation with dense thickets (Richardson *et al.* 1994; Richardson & Higgins 1998). For instance, in the Cape floristic region of South Africa, invasive pines (especially *P. pinaster* and *P. radiata*) have converted large areas of native fynbos shrubland to pine forests, with the local disappearance of many native plants (Richardson *et al.* 1994, and references therein). Similarly, in New Zealand, *P. contorta* grows 200 m above the treeline established by native species, thus invading shrubland (Wardle 1985a,b). Also in New Zealand, introduced conifers invade tussocklands and herbaceous communities, overgrowing and suppressing native vegetation (Richardson *et al.* 1994, and references therein; Ledgard 2001). In some instances, they threaten to convert entire shrubland and grassland communities to conifer forests, with several native species in danger of at least local extirpation (Harding 2001). *Pseudotsuga menziesii* also invades shrublands in New Zealand (Anon. 1997; Ledgard 2002).

Introduced conifers have also invaded forests. Examples in New Zealand of conifers that invade seasonally or permanently open native forest include *P. contorta* in open forests at treeline in New Zealand (Wardle 1985a, b) and *Pseudotsuga menziesii* in canopy gaps in native *Nothofagus* forest (Maclaren 1996; Ralston 1997; Harding 2001, and references therein; Ledgard 2002). The invasion into gaps may threaten to replace native dominant trees (Harding 2001; Ledgard 2002). *Pinus radiata* has slowly invaded intact, native eucalypt dry sclerophyll forest in the Australian Capital Territory (Burdon & Chilvers 1994), New South Wales (Williams & Wardle 2005) and South Australia (van der Sommen 1978).

Pine plantations and pine invasions have also altered fire regimes so that fires can spread into native vegetation that may not be fire-adapted. In South Africa, the greatly increased fuel load associated with invasive pines as well as plantations increases the intensity of fires in the fire-prone fynbos and grassland vegetation, leading to severe erosion as well as decreased local plant species diversity (Richardson *et al.* 1994; Richardson & Higgins 1998, and references therein). In New Caledonia, pine plantations have contributed to an increase in the number of fires in the native vegetation; this problem is exacerbated by a form of invasional meltdown (Simberloff & Von Holle 1999), with the native fern *Pteridium aquilinum* (L.) Kuhn replacing indigenous and endemic plants beneath the pines and augmenting the initiation of fires (Le Mire Pécheux 1996; Jaffré *et al.* 1998). Although the New Caledonian research pertains to plantations, there is no reason to think that self-sown conifer stands could not behave similarly.

The impact of invasive conifers on hydrology can be enormous, particularly where they replace non-forest vegetation. Given the great hydrological consequences documented for tree plantations (Jackson *et al.* 2005), this impact might have been expected. In South Africa, invasive introduced pines were estimated to use 232 million m^3 of water per year, about 7% of water use by all invasive plants and about 17% as much as all commercial forestry (Le Maitre *et al.* 2000). Run-off in heavily invaded catchments declines by 30–70% (Van Wyk 1987). In New Zealand, conifer plantations can yield dramatically lower mean water flows and lower minimum flows than either native forest or pasture (Harding 2001, and references therein), but the changes vary greatly depending on the precise nature of the conversion, stand management and harvesting regimes (Fahey 1994). However, the hydrological impact of invasive, self-sown conifers is unquantified in New Zealand.

Conifer invasions can affect soils and nutrients. In New Zealand tussocklands, conifers take up and hold more nutrients than the species they replace (Harding 2001, and references therein), although, in plantations, these may be returned to the soil when the trees are cut. There is concern that, wherever they are introduced, conifers will accelerate acidification and podzolization, processes often associated with pine afforestation globally but that depend on the exact nature of the original vegetation and soil (Scholes & Nowicki 1998).

Extensive studies in New Zealand and Australia of impacts of converting grasslands or shrublands to pine plantations on soil nutrient pools and fluxes showed

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substantial changes, often depending on age of the plantation and rainfall regime (Scholes & Nowicki 1998). For instance, on the South Island of New Zealand, mineralizable nitrogen concentrations were increased under young plantations in wet areas and decreased in older pine stands in dry areas. Decreases in organic carbon concentration were associated with the increased N-mineralization, while plant-available phosphorus concentrations were consistently higher in older plantations. Scholes and Nowicki (1998) suggested that generally pine introduction depletes nutrients from upper mineral soil layers and accumulates them in the overlying organic layers, and that nitrogen mineralization and nitrification are generally decreased because of increased acidity. These soil and nutrient changes, in turn, lead to great changes in the soil organism community (Scholes & Nowicki 1998).

Changes in the aboveground animal and plant communities documented in conifer plantations are numerous and may be expected as well in extensive self-sown stands. Pine plantations in Australia are less useful as habitat for various wildlife species than native eucalypt forests (Richardson *et al.* 1994, and references therein). In the fynbos of South Africa, pine invasions threaten endemic plants with extinction (Richardson *et al.* 1996), and the unusual ability of *P. caribaea* to invade ultramafic soils of New Caledonia threatens the highly endemic ultramafic maquis vegetation (Morat *et al.* 1999). Even relatively small areal percentages under afforestation (by eucalypts as well as pines) in Mpumalanga Province, South Africa, negatively affect grassland bird communities (Allan *et al.* 1997).

Observed impacts of South American conifer introductions

By the sheer size of the area planted to conifers in parts of South America, invasion may occur simply because of the staggering density of the seed rain by a sort of 'mass effect' (Richardson & Cowling 1992), even in areas that might have been considered quite resistant (e.g. protected areas and/or forests). In fact, such invasion has been suggested as underway in Chile (Bustamante *et al.* 2003; Bustamante & Simonetti 2005). Similarly, in Argentinean Patagonia *Ps. menziesii* is invading normal evergreen native forest dominated by *N. dombeyi* and *Austrocedrus chilensis*, but only slowly and, so far, not far from exotic plantations (Simberloff *et al.* 2002; Nuñez *et al.* 2008). Likewise, in south-central Chile, *Ps. menziesii* is establishing more than 120 m from the edge of 30-year-old plantations, in densities that depend on the nature of the vegetation and levels of disturbance (A. Pauchard *et al.*, unpubl. data 2007). *Pinus contorta* has also been documented invading native vegetation, including forests, from trial plots at a nature reserve in south-central Chile that produce large numbers of propagules (even at early ages), some of which disperse great distances (Peña *et al.* 2008). Sarasola *et al.* (2006) found *Pseudotsuga menziesii* invading native forests dominated by *Austrocedrus chilensis* in the Argentian Patagonian Andes.

Several impacts previously observed in other regions where conifers were introduced earlier have been documented recently in South America. As in other regions, introduced conifers have begun to invade and overgrow treeless vegetation and seasonally open forest. *Pseudotsuga menziesii* invades abandoned fields (Simberloff *et al.* 2002) and scrub vegetation (Sarasola *et al.* 2006) in Argentinean Patagonia. *Pinus radiata* invades deciduous *N. alessandri* forest in Chile (Bustamante & Castor 1998) and grasslands in Buenos Aires province, where *P. halepensis* also is spreading over relictual areas of native grassland (Zalba & Villamil 2002; Zalba *et al.* 2008). In Brazil, *P. taeda* and *P. elliottii* invade natural grasslands, wetlands and degraded forest (Ziller & Galvão 2002; Zanchetta & Diniz 2006).

As in South Africa and New Caledonia, introduced conifer plantations in Argentinean Patagonia have increased fire frequency and/or severity. For example, plantations of *P. ponderosa* and *P. sylvestris* have produced major fires, at least some initiated by lightning (Anon. 1999, 2000). Also, exotic trees have been planted in areas that were formerly steppe or open woodland, where lack of fuel continuity was a major limitation to spread of fire (Nuñez & Raffaele 2007). Today, however, large areas of these exotic conifers have burned and others create the potential for extensive crown fires in habitats previously characterized by surface fires and lower fuel volumes (Veblen *et al.* 2003). Burned plantations interfere with post-fire succession to the original matorral vegetation (Nuñez & Raffaele 2007; Cuevas & Zalba 2009). Invasive pines in native pampas grasslands have also been associated with high intensity fires that, in turn, promote the dispersal of these same pine species (Zalba *et al.* 2008)

A few South American studies have shown impacts of introduced conifers on biodiversity, in either plantations or invaded areas. In small mixed plantations of *Pseudotsuga menziesii*, *P. radiata* and *P. sylvestris* embedded in forests dominated by *N. dombeyi* in northwest Patagonia, Paritsis and Aizen (2008) found decreased species richness of understory vascular plants, epigeal beetles and birds, with a loss of rare and specialist species and an increase in introduced plant species aside from these three conifers. Corley *et al.* (2006), in northwest Patagonia, found fewer ants in introduced pine plantations than in native steppe vegetation and fewer ant species in dense plantations. In the Argentinean pampas, exotic pines invading local grasslands reduced the diversity of native plants, displacing a number of endemic species and promoting invasion by

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Table 2. Earliest conifer introductions, plantations and invasions in the southern hemisphere. Question mark signifies suspected by unconfirmed date

Nation	First conifer planting	Earliest major plantation	Earliest report of invasion
South Africa	ca. 1685	1884	Early 1890s
New Zealand	<1830	1896	Late 1890s
Australia	By 1850s	1875	1950s
New Caledonia	1959	1962	1996
Argentina	1813	1970s?	1988?
Chile	1885	1970s?	Early 1990s
Brazil	1880	1948?	Early 1990s
Uruguay	1813	1990s	Unknown

other exotics (Zalba & Villamil 2002; Cuevas & Zalba 2009). Pine invasion in Argentinean pampas is also associated with changes in bird communities, including decline of obligate grassland birds and colonization by species that are less habitat-specific and colonize from forested regions (Zalba 2000).

PROSPECTS FOR SOUTH AMERICA

The history of conifer introductions and plantation forestry in South Africa, New Zealand, Australia, and more recently, New Caledonia (Table 2) suggests that, although introductions and the earliest plantations preceded substantial plantation establishment, the first reports of worrisome invasion occurred 20–30 years after substantial planting. Large-scale plantation forestry of conifers in Chile and Argentina began in the 1970s, somewhat earlier in Brazil, and in the mid-1990s in Uruguay. It is therefore not surprising that conifer invasions have recently been reported in Brazil (Ziller 2000; Liesenfeld & Pellegrim 2003; Zenni 2005; Zanchetta & Diniz 2006), Argentina (e.g. Simberloff *et al.* 2002; Sarasola *et al.* 2006) and Chile (e.g. Bustamante & Castor 1998; Peña *et al.* 2008), again with a time lag of 20–30 years. Because major conifer plantation forestry began 50–80 years later in South America than in South Africa, Australia and New Zealand, it is also unsurprising that invasions in South America were first reported about a century after the first reports outside of South America. Conifer invasions in South America are not nearly as widespread as outside South America, and concern about the phenomenon and research on it are relatively meager in South America. Nevertheless, the entire history of conifer invasions in the rest of the southern hemisphere plus the scope and severity of potential effects warrant increased vigilance as well as planning to ameliorate impacts (Richardson *et al.* 2008).

It is noteworthy that both outside and inside South America, lone conifers planted as ornamentals seldom lead to invasions, although in the Paraná and Argentinean grasslands small stands or even single trees planted as ornamentals or for shade have occasionally been seen to initiate local invasions. However, the first reports of invasion generally followed and were associated with plantation forestry (cf. Richardson & Brown 1986). This fact suggests that propagule pressure is a key determinant of conifer invasion, a conclusion that accords with much recent research on many sorts of invasions showing that the importance of propagule pressure has been underestimated (see Lockwood *et al.* 2007). In light of the enormous and growing areas of South America devoted to conifer plantations, propagule pressure must be a staggering, ongoing factor increasing the probability of invasion.

Most of the invasive conifers discussed above can begin producing seed at age 5–6 years (Simberloff *et al.* 2002, and references therein; cf. Richardson *et al.* 1990; Harding 2001), although many conifers produce more abundant seeds much later than their earliest age of reproduction (e.g. Barnhart *et al.* 1996). Ledgard and Langer (1999) found that significant coning does not occur until at least twice that age. *Pseudotsuga menziesii* matures much later than the pines, at 10–15 years in New Zealand (Miller & Knowles 1994) and at 20 years in North America (Hermann & Lavender 1990). Thus, some fraction of the lag between first introduction and the beginning of invasion is due simply to the growth of the original immigrants. Often an infrequent disturbance event, such as a fire (Richardson *et al.* 1994) or a storm (Belton & Ledgard 1991), is required for successful recruitment. In Argentina, the policy of preventing wildfires in remnant native grasslands may also partially explain the delay in conifer expansion and rapidity of spread once fire does occur (Zalba *et al.* 2008). Dispersal of most of these conifers is by wind, and, though distances of 100 m or less are normal, some small fraction of seeds disperse much further (Richardson *et al.* 1994). Once reproductive individuals are established on sites such as ridgetops or hilltops, long-distance dispersal may be far more frequent (Ledgard 1988). Even small amounts of long-distance dispersal greatly increase the predicted rate of spread; Higgins and Richardson (1999) showed by simulation that a tiny fraction (0.001) of seeds moving long distances (1–10 km) can lead to an order of magnitude increase in spread rate.

Many plant invasions reflect a stepwise pattern of spread, in which an initial population (e.g. a plantation) spreads rather slowly at its border, but eventually long-distance dispersal establishes a number of satellite foci, each of which becomes the centre of a local invasion and can, in turn, spawn further long-distance dispersers and satellite foci (Ledgard 1988, 2001;

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Moody & Mack 1988; Richardson *et al.* 1994; Richardson & Higgins 1998). Satellite foci and the original infestation enlarge and may eventually coalesce. If an invasion is occurring into forest, particularly of long-lived trees (as in *Nothofagus*-dominated forests of Patagonia), an invasion may be greatly retarded by a sort of inertia imposed on the process simply by the longevity of the existing plants, even though these will ultimately be replaced (Von Holle *et al.* 2003). For conifers in New Zealand grasslands, the steps appear usually to be 20–30 years apart (Ledgard 1988); these figures accord well with data available for Argentinean grasslands, where drought (Zalba *et al.* 2008) and competition with native grasses (de Villalobos & Zalba, in review 2009) appear responsible for temporal variation in pine recruitment.

Because these introduced conifers are ectomycorrhizal, and these fungi are generally highly host-specific (Molina *et al.* 1992), it has often been suggested that plantations of these species that have failed did so because of absence of suitable fungal species (e.g. Mikola 1990; Read 1998). Richardson *et al.* (1994) dismissed this factor as a potential hindrance to current invasion in the southern hemisphere on the grounds that appropriate mycorrhizal symbionts are now ubiquitous there. However, Nuñez *et al.* (2009) have shown that failure of introduced pines to spread beyond the plantations on Isla Victoria is likely due to absence of suitable mycorrhizae beyond the plantations. For these conifers, the mycorrhizae are present in the plantations but do not produce a sufficient number of aerial spores to permit conifer colonization far from plantations, so they spread very slowly, mostly by mycelial growth. Thus, even though reproductively mature trees may disperse seeds far into the forest to suitable microsites, the requisite fungus is generally absent there, so absence of appropriate mycorrhizae certainly delays invasion. By contrast, in southern Argentinean mountain grasslands, *P. halepensis* and *P. radiata* can colonize areas more than 1000 m from plantations, and no site seems immune to pine invasion (Zalba 1995).

The time lag and step-like pattern of conifer invasion suggest that the early stages of invasion are the most amenable to cost-effective management, as is generally true for invasions (Wittenberg & Cock 2001) and that attention to isolated individuals or small groups of them can be crucial in preventing or at least greatly delaying widespread invasion. Early control has also resulted in good recovery of the structure and species composition of grassland communities in experimental plots in Argentinean grasslands (Cuevas & Zalba 2009). Detailed models of the interaction between characteristics of the particular species of concern, the local environment and the precise spatial arrangement of reproductive individuals (e.g. Higgins & Richardson 1998; Higgins *et al.* 2000; Rouget *et al.* 2001) may be able to pinpoint sites that warrant particular ongoing attention.

A variety of methods are possible both to minimize the likelihood of spread (e.g. by planting pattern and location with respect to local topographic features) and to manage invasions once these are detected, depending strongly on the species involved and aspects of the local geography, vegetation and socioeconomic factors (e.g. Ledgard 2001). National-scale planning can also identify areas where alien conifers can be grown with the lowest risk of invasion and also areas where special measures are needed to manage spread from plantations (Rouget *et al.* 2002). The extent of existing plantations will limit the potential for selecting appropriate sites, particularly in Chile; however, all South American nations still contain vast areas that could probably be converted to conifer plantations (the Argentinian government identifies about 20 million ha (SAGPyA 2001)), so choices are possible that would minimize invasions. When invasions nevertheless occur, the important point is to recognize the potential problems early enough and to act on them before effective management becomes logistically and economically impossible. For example, a South African public works programme, Working for Water, has been effective in stemming and redressing tree invasions and has generated additional social and economic benefits (McQueen *et al.* 2000; van Wilgen *et al.* 2000); there is no analogue yet in South America. Biological control may be a feasible approach to limiting spread of certain conifer species, particularly if seed- and cone-feeding insects can be found and the risk of spreading pathogens such as pitch canker can be minimized (Moran *et al.* 2000). However, given the economic value of plantation trees, the risk of escape of such detrimental organisms may deter acceptance of such biological control projects.

REGULATORY AND VOLUNTARY APPROACHES

In New Zealand, regulations to prevent the spread of introduced trees were first implemented in 1983, when the government declared *P. contorta* a Class B noxious weed (Ledgard 2002). Many local New Zealand governments have subsequently addressed the risk of invasion by introduced trees under requirements of the Resource Management Act of 1991 and the Biosecurity Act of 1993 (Bowman 2004), primarily by requiring tree planters to obtain consent from territorial authorities before planting trees in spread-susceptible areas. Consent requires plans showing how invasion risk will be avoided, remedied, or mitigated. Invasion from older plantations is currently unregulated.

Australia is a federation of states each with its own regulations on weeds and their management. Conifers

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appear on only three state weed lists (http://www.weeds.org.au/noxious.htm, accessed 28 September 2008). In South Australia, *P. halepensis* must be controlled except for trees that have been planted for commercial or domestic use (that is, plantations or ornamentals). In the Australian Capital Territory, *P. radiata* is listed as a pest plant that must be 'contained', as suppression or destruction is viewed as impractical. In Western Australia, neither species is introduced, but, if they were to be proposed for importation, they would have to undergo a risk assessment because they are listed in other states. The Australian Forestry Standard, a non-profit public company that promotes sustainable forest management and manages the Australian Forest Certification Scheme, mandates limiting the spread into adjacent native vegetation of introduced species used in plantations. However, this mandate has proven difficult to enforce, and control rarely occurs outside plantation owners' lands (M. Williams 2009, pers. comm.).

Between 1972 and 1995, South Africa required forestry permits for plantings over 10 ha, but these were issued on the basis of the predicted direct impact on water resources, not on likelihood of subsequent invasion (van der Zel 1995; Richardson *et al.* 2003). South Africa's water law of 1996 overhauled the permitting system, recognizing planting trees for forestry purposes as a 'streamflow reduction activity.' Estimates of water use by such planting from observation and modelling (Gush *et al.* 2002) led to a controversial figure for annual water use by plantations that is now the basis of permitting decisions. Legislation was further broadened in 1996 to include control of conifers invading outside of plantations (Richardson & Petit 2005). Six species of *Pinus* have been declared as 'category 2' weeds (commercially valuable but invasive species). These species may be grown under permit, but permit holders must take steps to control spread. This requirement has proved difficult to enforce. Responsible landowners, especially those who seek certification of their products by the Forestry Stewardship Council (which in turn is required for the sale of forest products into certain markets), do carry out control operations, but these almost never go beyond the boundaries of their own lands.

Regulations in South America for preventing conifer invasions are piecemeal and weak. In Brazil, a national biodiversity policy includes several recommendations for prevention and control of introduced species, but specific regulations implementing the policy have not yet been issued. The federal law instituting the National Protected Area System forbids the introduction of non-native species, while the state of Paraná restricts nurseries of municipalities and public agencies from producing certain plant species and encourages plantation owners to take preventive measures. Other South American nations lack analogous federal laws. Requiring proactive weed risk assessment, as in New Zealand and Western Australia, and mitigation plans, as in New Zealand, would be the strongest measures but may be politically unachievable in the near future, when action is most needed.

Certification through the Forestry Stewardship Council (FSC) may be a promising means of reducing the threat of conifer invasions in South America. For instance, pressure from foreign customers asking South African forestry companies to show compliance with various environmental standards has encouraged most companies to obtain FSC certification (Richardson *et al.* 2003). The FSC-certification criteria permit the use of introduced species, although with stipulations that minimize damage from invasions (Strauss *et al.* 2001; Richardson & Petit 2005). However, a potential drawback is that absence of legal enforcement powers may greatly limit adherence to environmental standards, as has happened in Australia. A further problem is that the FSC explicitly forbids the use of any genetically modified species, and this prohibition prevents the use of modifications that could lower the risk of invasion from plantations, such as reduced seed set or sterility (Richardson & Petit 2005).

CONCLUSIONS

In sum, nothing unique about South America makes conifer invasion there more or less likely than elsewhere, or suggests impacts in South America will differ from those elsewhere. However, the lessons that can be garnered from elsewhere about the trajectories of such invasions and about how to manage them should be important aids in developing programmes and legislation to mitigate such invasions in South America. The accumulated research on introduced conifers also contributes to a general understanding of the ecology of invasions. Such research has been particularly important in understanding the potential scope and mechanisms of ecosystem-wide impacts through modified hydrology and fire regimes, while the detailed information on the chronology of conifer invasions informs discussion and understanding of the widespread phenomenon of time lags in invasions (Crooks 2005). Also, research on conifer invasions has elucidated the complexity of the invasion process and demonstrated that a diversity of factors operates in different invasions. Some are well known, such as propagule pressure and disturbance, while others, such as belowground mutualisms, have been studied much less frequently. Finally, research from South America and elsewhere on the ecology and management of forestry trees motivates the hope that it is not too late to forestall massive conifer invasions in South America.

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