EFECTO DEL HABITAT FISICO, COBERTURA VEGETAL Y HERBIVORIA SOBRE EL RECLUTAMIENTO DE PLANTULAS DE LOS ARBOLES EXOTICOS *PINUS RADIATA* Y *EUCALYPTUS GLOBULUS* EN CHILE CENTRAL

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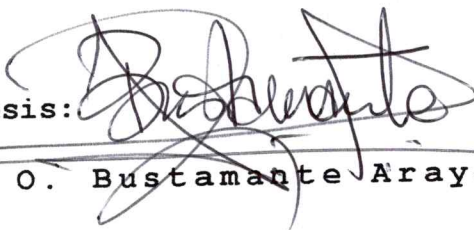
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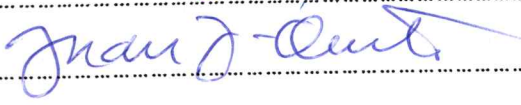
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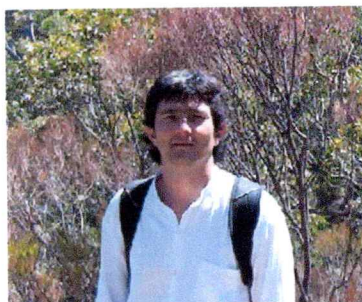Comisión de Evaluación de la Tesis

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Pablo Ignacio Becerra Osses es Ingeniero Forestal, de la Facultad de Ciencias Forestales de la Universidad de Chile. La tesis de grado fue desarrollada sobre patrones de diversidad florística y vegetacional de la Reserva Nacional Malalcahuello, IX región, Chile, guiada por el Dr. Gustavo Cruz. En 1997 ingresó al Magíster en Ciencias Biológicas, mención Ecología, de la Facultad de Ciencias, Universidad de Chile, obteniendo el grado en 2001. Su tesis de Magíster fue realizada sobre patrones geográficos de riqueza de especies de plantas leñosas en la zona Mediterránea de Chile. Sus tutores fueron la Dra. Mary Kalin Arroyo y el Dr. Italo Serey. El año 2002 ingresó al programa de doctorado en Ciencias, mención Ecología y Biología evolutiva, de la Facultad de Ciencias, Universidad de Chile. Durante el doctorado realizó una estadía en el Laboratory of Plant Ecology, Division of Biological Sciences, University of Montana, Missoula, Montana, USA, a cargo del Dr. Ragan Callaway.

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INDICE DE MATERIAS

RESUMEN

La invasión de especies exóticas es un fenómeno ecológico y un problema de conservación a escala global que ha recibido bastante atención en los últimos años. Entre los diferentes factores que tienen un rol en el proceso de invasión de plantas exóticas, aquellos citados como los más importantes son el hábitat físico, la presencia de plantas y los herbívoros residentes, tanto nativos como exóticos. Sin embargo, el proceso de invasión requiere además la existencia de una fuente de propágulos. En el caso de árboles exóticos, una de las fuentes más importantes son las plantaciones forestales de especies introducidas. En Chile, las especies forestales exóticas más importantes en términos de superficie plantada son *Pinus radiata* (originario de California, USA) y *Eucalyptus globulus* (originario de Victoria, Australia). Estas especies son además ampliamente plantadas en otros países del hemisferio sur y han llegado a ser invasoras en la mayoría de éstos. En Chile, ambas especies son plantadas principalmente en la región Mediterránea del país y su invasión en ambientes silvestres es aún incipiente y poco notoria pero ya existe evidencia de su ocurrencia. En esta tesis se evalúa cómo la variación de las condiciones físicas de hábitat dentro de la zona mediterránea de Chile (laderas de diferente exposición), la presencia de una especie arbórea nativa, *Lithrea caustica* (sitios bajo parches de esta especie vs. sitios abiertos) y la herbivoría por vertebrados (exclusiones vs. controles) influyen sobre el reclutamiento de plántulas (germinación y sobrevivencia de plántulas) de ambas especies forestales exóticas fuera de las plantaciones. Observamos que en sitios abiertos tanto la germinación como la

sobrevivencia de plántulas de ambas especies exóticas fue mayor en el hábitat mésico (ladera exposición sur) que en el xérico (ladera de exposición norte). La germinación de ambas especies en sitios bajo litre fue mayor que en sitios abiertos en el hábitat xérico, pero no hubo diferencias en el hábitat mésico. En contraste, la sobrevivencia de plántulas fue mayor en sitios abiertos que bajo parches de litre en el hábitat mésico y no hubo diferencias en el hábitat xérico. Finalmente, la herbivoría generó una reducción significativa de la sobrevivencia de plántulas en ambas especies exóticas, aunque fue más marcada en *P. radiata*. Además, el efecto de la herbivoría sobre la sobrevivencia de plántulas de *P. radiata* fue significativo bajo cualquier condición de vegetación o hábitat, pero en cambio, sobre *E. globulus* fue significativo sólo en sitios abiertos del hábitat mésico. En consecuencia, los tres factores analizados influyen en el proceso de invasión, sin embargo, existen interacciones entre ellos que determinan que la importancia de uno varíe en función de las condiciones de otro. Principalmente la combinación de hábitat mésico, sitio abierto y baja herbivoría podrían permitir un reclutamiento significativo de estas especies y por lo tanto aumentar su probabilidad de invasión dentro de la zona central de Chile.

ABSTRACT

Invasion of exotic species is an ecological phenomena and conservation issue which has received quite attention during the last years. Among the main factors documented as important for plant invasion processes are physical habitat conditions, resident vegetation cover and herbivores. However, for an invasion process take place, it also is necessary the existence of a propagule source of exotic species. Some of the most important sources of exotic trees are forestry plantations with introduced species. In Chile, the most important tree exotic species in terms of planted surface are *Pinus radiata* (original from California, USA) and *Eucalyptus globulus* (original from Victoria, Australia), distributed mainly through the Mediterranean region of the country. These species are also widely planted in other countries of the southern hemisphere, where they have become invasive. In Chile invasion of these species is still incipient and little notorious, but there already is evidence of its occurrence. In this thesis the role of variation of physical habitat within the Mediterranean region of Chile (comparing a xeric north-facing slope with a mesic south-facing slope), cover of a native tree species, *Lithrea caustica* (comparing sites under patches of this species with open sites without woody canopy), and vertebrate herbivory (comparing excluded with non-excluded sites) on the seedling recruitment of these exotic tree species are evaluated. It was observed that germination as well as seedling survival of the two exotic trees were higher in the mesic than in the xeric habitat, although mainly in open sites. Germination of these two species was higher under *Lithrea* patches than in open sites in the xeric habitat, but there

was no significant difference in the mesic habitat. In contrast, seedling survival was higher in open sites than under *Lithrea* patches in the mesic habitat with no difference in the xeric habitat. Finally, herbivory produced a significant reduction in seedling survival in the two exotic trees, although this was stronger in *P. radiata*. Furthermore, the effect of herbivory was significant on *P. radiata* regardless vegetation type or habitat condition. In turn on *E. globulus* it was significant only in open sites of the mesic habitat. In consequence, the three factors evaluated in this thesis should have an influence on the invasion processes of these exotic species; however, interactions among them which determine that the importance of anyone depends on other factors. Mainly, combination of a mesic habitat, open site and low or absence of herbivory may allow a significant recruitment of these species and therefore to increase their invasion probability within the Mediterranean region of Chile.

CAPÍTULO I: INTRODUCCIÓN GENERAL

Invasión de especies exóticas

Como consecuencia de diferentes actividades antrópicas, y en forma intencional o no, prácticamente en todos los países del mundo se han introducido especies provenientes de otras regiones biogeográficas (Elton 1958, Groves & Burdon 1986, Drake et al. 1989, Mooney & Hobbs 2000). Muchas de estas especies, denominadas exóticas o introducidas (sensu Richardson et al 2000a), han podido dispersarse hacia áreas silvestres y formar poblaciones sustentables, proceso que ha sido denominado invasión (Richardson et al 2000a). Además, numerosas especies exóticas invasoras han producido efectos negativos en los ecosistemas invadidos, constituyéndose así en una amenaza para la conservación de la biodiversidad (e.g. D'Antonio & Vitousek 1992, Richardson et al. 1996, Rodríguez 2001).

El éxito de los procesos de invasión de plantas exóticas depende del resultado de una serie de etapas tales como: lluvia de propágulos, establecimiento de plántulas, crecimiento individual, reproducción y dispersión de propágulos de los individuos invasores (Williamson & Fitter 1996, Richardson et al. 2000a). El éxito de cada una de estas etapas está determinado tanto por atributos biológicos de las especies exóticas (e.g. caracteres de historia de vida, requerimientos y tolerancias ecológicas), como por las condiciones físicas (e.g. clima, suelos, topografía) y bióticas (e.g. presencia de especies competidoras, facilitadoras, depredadores) de los ecosistemas invadidos (Lonsdale 1999, Shea & Chesson 2002, Myers & Bazely 2003).

abundancia plantas

En plantas, una de las etapas más críticas del ciclo de vida y fuertemente determinante de los patrones de distribución y abundancia poblacional es el reclutamiento de plántulas, en particular los procesos de germinación y posterior sobrevivencia de las plántulas (Harper 1977). Consistente con esto, el reclutamiento de plántulas también ha sido reconocido como una etapa clave en el éxito de los procesos de invasión de plantas exóticas (Johnstone 1986, Myers & Bazely 2003). Diferentes factores ambientales pueden afectar el reclutamiento de plántulas de especies invasoras (Lonsdale 1999, Shea & Chesson 2002, Myers & Bazely 2003). Los factores más ampliamente documentados ejerciendo un rol importante en el reclutamiento de plántulas de especies invasoras son: las restricciones ambientales físicas, el efecto de otras plantas residentes, y la herbivoría sobre plántulas (Shea & Chesson 2002, Myers & Bazely 2003, Sax et al. 2005).

El ambiente físico de los hábitats puede generar estrés fisiológico o restricción de la producción fotosintética (sensu Broker & Callaghan 1998) en semillas y plántulas de especies exóticas y así afectar su establecimiento en forma independiente de la presencia de otras especies de plantas o animales. En general, se ha observado un mejor reclutamiento de plántulas, así como mayor abundancia y número de especies exóticas en hábitats menos estresantes, especialmente más húmedos y menos fríos (Richardson & Bond 1991, Beerling 1993, Lonsdale 1999, Stohlgren et al. 2005, MacDougall et al. 2006).

Por otro lado, plantas ya presentes en los sitios invadidos (denominadas plantas residentes, Levine et al. 2004), las cuales podrían ser nativas o incluso otras exóticas, pueden modificar el microambiente donde crecen y así afectar la germinación y

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sobrevivencia de plántulas de especies exóticas (Davis et al. 2000, Shea & Chesson 2002, Levine et al. 2004, Bruno et al. 2005). Se ha observado que las plantas residentes pueden tener tanto efectos negativos (inhibición) como positivos (facilitación) sobre el reclutamiento e invasión de especies exóticas (Simberloff & Von Holle 1999, Bruno et al. 2005), lo cual a su vez puede depender del nivel de estrés generado por las condiciones físicas del hábitat (Bertness & Callaway 1994, Bruno et al. 2005). En ambientes poco estresantes, los efectos negativos (e.g. restricción de luminosidad, competencia por nutrientes, etc.) serían más importantes que los positivos (incremento de humedad del suelo y nutrientes, disminución del frío, etc), por lo que el efecto neto o total de una planta sobre otra podría ser negativo (Brooker & Callaghan 1998). En cambio, en ambientes comparativamente más estresantes los efectos positivos serían más importantes y así el efecto neto de una planta sobre otra podría ser positivo (Brooker & Callaghan 1998). Se han propuesto diversas formas mediante las cuales se podría producir esta modificación de los efectos a lo largo de gradientes de estrés (Callaway & Walker 1997). Una de las más documentadas es el cambio de los efectos generados por el sombreamiento que ejerce el dosel vegetal desde positivos a negativos en un gradiente de humedad (Holmgren et al. 1997, Kitzberger et al. 2000, Anderson et al. 2001, Hastwell & Facelli 2003, Lenz & Facelli 2003, Prider & Facelli 2004). Así, en hábitats xéricos (con estrés generado por restricciones de humedad del suelo, comunes en climas semiáridos y áridos) el sombreamiento puede producir un incremento de la humedad del suelo y así un efecto positivo, el cual sería más importante que el efecto negativo generado por la disminución de la luminosidad. Esto determinaría que el efecto neto de una especie sobre el reclutamiento de otra en hábitats xéricos sea positivo. En hábitats

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más mésicos, donde la humedad del suelo puede no ser limitante en sitíos sin cobertura vegetal, el sombreamiento ya no ejercería un efecto positivo. En cambio, éste aún produciría el efecto negativo de disminución de luminosidad, determinando un efecto neto negativo, expresado en que el reclutamiento bajo dosel sería similar ó menor que en sitios abiertos adyacentes (Holmgren et al. 1997).

Finalmente, si una especie exótica ha podido germinar y establecer sus plántulas bajo las condiciones físicas y vegetacionales del hábitat, el éxito del establecimiento de plántulas también puede ser afectado por herbívoros residentes depredadores de plántulas (especies herbívoras, nativas o exóticas que habitan las localidades de invasión) (e.g. D'Antonio 1993, Maron & Vilà 2001, Hobbs 2001, Chaneton et al. 2002, Bellingham & Coomes 2003, Levine et al. 2004, Kuijper et al. 2004, Colautti 2004, Bruno et al. 2005, Parker et al. 2006). El efecto directo de los herbívoros sobre una planta exótica es negativo como consecuencia de la depredación de las plántulas. Sin embargo, los herbívoros podrían también tener un efecto positivo indirecto, si depredan preferentemente sobre otras plantas competidoras (nativas o exóticas), liberando competitivamente a la planta exótica (Parker et al. 2006).

Especies exóticas de estudio

Una de las principales fuentes de plantas invasoras son las plantaciones forestales realizadas con especies exóticas (Richardson 1998). En Chile existen prácticamente sólo dos especies utilizadas masivamente en la industria forestal, *Pinus radiata* D. Don (Pinaceae) y *Eucalyptus globulus* Labill. (Myrtaceae). Entre ambas especies acumulan ya

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más de dos millones de hectáreas plantadas, especialmente dentro de la zona de clima mediterráneo del país (Donoso & Lara 1995). Estas especies son también plantadas frecuentemente en otros países y continentes del mundo (Richardson 1998, Etienne 2001), y en la mayoría de éstos ya han sido reconocidas como importantes invasoras, donde han alterado la composición de especies y estructura de la vegetación (Richardson et al. 1990, Groves & di Castri 1991, Boyd 1996, Higgins & Richardson 1998, Etienne 2001, Lindenmayer & McCarthy 2001, Rouget et al. 2002). En Chile ya existe alguna evidencia de invasión de ambas especies (Tabla 1) (Bustamante et al. 2003, Becerra 2006), aunque este proceso es aún reciente y poco evidente. No obstante, la gran superficie plantada de ambas especies conforma una importante fuente de propágulos disponible para dispersarse e invadir los ecosistemas naturales de Chile central (Figueroa et al. 2004). Debido a estos antecedentes, resulta importante estudiar la potencialidad de invasión de estas especies en la zona Mediterránea de Chile y los factores ambientales que la regulan, en particular aquellos ya documentados por ser los más relevantes para los procesos de invasión (hábitat físico, cobertura vegetal y herbivoría).

El conocimiento sobre el rol de estos factores en el desempeño de ambas especies exóticas es aún dispar y poco concluyente. Ambas especies son originarias de ecosistemas mediterráneos, *P. radiata* de California (USA) y *E. globulus* de Tasmania y Victoria (Australia). Si bien ambas especies se encuentran adaptadas a las sequías estacionales típicas de los climas Mediterráneos, en sus regiones de origen y rangos introducidos se distribuyen principalmente en los hábitats más mésicos, e incluso hidrófilos como en el caso de *Eucalyptus globulus* (Kaufmann 1977, Richardson & Brown 1986, Keeley & Zedler 1998, Boyd 1996, Becerra 2006). De hecho, existen

ensayos de laboratorio que indican que ambas especies mejoran su desempeño (germinación y tasa de crecimiento de plántulas) con mayor disponibilidad de agua del suelo (Correia et al. 1989, Kaufmann 1977, López et al. 2000). Sin embargo, no existen experimento de campo que demuestren el rol de la humedad del hábitat en el desempeño de ambas especies. Por otro lado, ambas especies son consideradas sombra-intolerantes (Richardson & Brown 1986, Correia et al. 1989, Keeley & Zedler 1998, Walcroft et al. 2002). Sin embargo, prácticamente no existen estudios experimentales sobre los requerimientos de luminosidad para el reclutamiento de estas especies. En *P. radiata* existen efectos negativos del sombreamiento sobre el crecimiento de individuos jóvenes (Walcroft et al. 2002), pero no sobre reclutamiento poblacional de plántulas. Otros estudios observacionales indican una mayor regeneración y densidad poblacional de ambas especies en sitios perturbados o con baja cobertura vegetal (Richardson & Brown 1986, Lindenmayer & McCarthy 2001, Becerra 2006). No obstante, también existe evidencia de que ambas especies son capaces de reclutar bajo un dosel arbóreo (Lindenmayer & McCarthy 2001, Close et al. 2002, Bustamante & Simonetti 2005, Williams & Wardle 2005, Becerra 2006). Por otra parte, las plántulas de ambas especies son depredadas por herbívoros vertebrados en sus ambientes nativos. Las plántulas de *Pinus radiata* son depredadas por cabras exóticas (Richardson & Bond 1991), mientras que plantas de *Eucalyptus globulus* son depredadas tanto por vertebrados nativos (O'Reilly-Wapstra et al. 2004; Moore & Foley 2005), como por exóticos (O'Reilly & McArthur 2000, McArthur & Appleton 2004). En cambio, no es conocido el rol de la herbivoría de vertebrados en el establecimiento de plántulas e invasión de estas especies en sus rangos introducidos, aunque existe evidencia de que ambas son fuertemente

depredadas por herbívoros vertebrados dentro de las plantaciones forestales de países o ecosistemas donde han sido introducidas (e.g. Ferriere et al. 1983, Muñoz & Murúa 1990, O'Reilly & McArthur 2000, McArthur & Appleton 2004). Sin embargo, los ambientes de las plantaciones de estas especies generalmente poseen escasa cobertura de plantas leñosas y herbáceas, son seleccionados por ser más productivos o son fertilizados, y la abundancia y distribución de las plántulas es mas espaciada y regular que en los ambientes naturales donde ocurre la invasión (Williams & Wardle 2005). En consecuencia, resulta importante evaluar experimentalmente bajo qué condiciones de hábitat, cobertura de vegetación y herbivoría, plántulas de ambas especies exóticas poseen una mayor probabilidad de establecerse, con lo cual conocer las condiciones bajo las cuales ellas tienen una mayor probabilidad de invadir.

Ecosistema y propuestas de estudio

Los ecosistemas mediterráneos poseen un clima semiárido, caracterizado por precipitaciones concentradas en invierno y veranos secos (Di Castri et al. 1981). Además, dentro de la mayoría de los ecosistemas mediterráneos la heterogeneidad topográfica genera diferentes condiciones ambientales físicas, marcadas por diferencias de humedad (Di Castri et al. 1981). En Chile central este contraste se produce entre laderas de exposición ecuatorial (xéricas) y polar (mésicas) (Armesto & Martínez 1978). Esta diferencia entre laderas determina en gran medida variación en composición de especies vegetales nativas y reclutamiento de especies arbóreas nativas (Armesto & Martínez 1978, Fuentes et al. 1986). Sin embargo, no es conocido si estas diferencias

abióticas determinan también diferencias en la probabilidad de invasión de plantas exóticas. Por ello, en esta tesis se propone evaluar el efecto de la exposición de la ladera sobre el reclutamiento de pinos y eucaliptos en la zona Mediterránea de Chile.

Por otro lado, la zona Mediterránea de Chile presenta una alta concentración de población humana, por lo que muchos ambientes han sido intensamente perturbados (Aschmann & Bahre 1977). La vegetación arbórea ha sido la más afectada, principalmente a través de incendios y tala masiva por lo que actualmente se presenta formando parches distribuidos alternadamente con parches herbáceos (Aschmann & Bahre 1977, Di Castri et al. 1981, Fuentes et al. 1984). Esta heterogeneidad vegetacional tiene un importante rol en la composición y abundancia de especies leñosas nativas y herbáceas y en la dinámica de regeneración (Jaksic & Fuentes 1980, Armesto & Pickett 1985, Fuentes et al. 1984, 1986, Holmgren et al. 2000a, 2000b). Además, ha sido documentado que la exposición del hábitat (ecuatorial vs. polar) puede modular las interacciones entre plantas leñosas nativas en Chile central (Fuentes et al. 1986, Holmgren et al. 2000b). Sin embargo, no se conoce la respuesta de especies arbóreas exóticas a esta heterogeneidad vegetacional, ni si esta respuesta es modulada por las condiciones ambientales físicas contrastantes entre laderas de diferente exposición solar. Una de las especies arbóreas nativas más abundantes en Chile central es el Litre (*Lithrea caustica* (Mol.) H. et A. (Anacardiaceae). Esta especie posee una amplia distribución geográfica y ecológica, y se presenta tanto en laderas de exposición ecuatorial como polar, generalmente formando parches de diversos tamaños (Fuentes et al. 1984). Por ello, en esta tesis se propone evaluar el efecto de la cobertura de especies arbóreas nativas sobre el reclutamiento de pinos y eucaliptos en hábitats de diferente exposición

solar, empleando al litre como especie nativa focal, lo cual a su vez permitirá realizar predicciones a escala regional.

Finalmente, los herbívoros de plántulas de especies arbóreas más comunes dentro de la zona central de Chile son principalmente vertebrados exóticos, tales como el conejo Europeo (*Oryctolagus cuniculus*), vacas (*Bos taurus*), caballos (*Equus caballus*) y cabras (*Capra hircus*) (Jaksic 1998, Henríquez & Simonetti 2001, Vázquez 2002). También se han documentado a algunos roedores nativos, tales como *Octodon degus*, *Octodon bridgesii* y *Abrocoma bennetti*, depredando plántulas de especies leñosas, aunque estos tendrían una menor abundancia en Chile central (Iriarte et al. 1989, Saavedra 2003) y menor importancia relativa en esta función respecto a los vertebrados exóticos (Fuentes et al. 1983). El efecto de herbívoros vertebrados sobre la sobrevivencia de árboles nativos, así como sobre la abundancia de hierbas nativas y exóticas ha sido ampliamente documentado (Jaksic & Fuentes 1980, Fuentes et al. 1983, 1986, Holmgren et al. 2000a, Holmgren 2002). Sin embargo, es escasamente conocido el efecto de estos herbívoros sobre la sobrevivencia de plántulas de árboles exóticos invasores. Por ello, en esta tesis también se propone evaluar el efecto de la herbivoría de vertebrados sobre la sobrevivencia de plántulas de pinos y eucaliptos en la zona Mediterránea de Chile.

Objetivos

Esta tesis tiene por objetivo general evaluar los efectos de las condiciones físicas del hábitat, cobertura de árboles nativos (en este caso litre) y ataque de herbívoros vertebrados residentes de la zona Mediterránea de Chile, sobre el establecimiento de plántulas de las especies exóticas *Pinus radiata* y *Eucalyptus globulus*. El efecto de las condiciones físicas del hábitat se evalúa comparando laderas de exposición ecuatorial (hábitat xérico) y de exposición polar (hábitat mésico). El efecto del litre se evalúa comparando sitios bajo y fuera de parches cubiertos por litre en laderas de exposición polar y ecuatorial. Además, se examina experimentalmente si este efecto es producido por el sombreamiento generado por el dosel de esta especie. Finalmente, el efecto de la herbivoría se evalúa examinando el nivel sobrevivencia en plántulas exóticas excluidas y no excluidas de herbívoros.

Hipótesis

Efecto del hábitat físico

Si laderas de exposición ecuatorial poseen menor humedad del suelo que laderas de exposición polar, entonces el reclutamiento experimental de plántulas de *Pinus* y *Eucalyptus* debiera ser mayor en una ladera de exposición polar.

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Efecto del litre bajo diferentes condiciones físicas

Si el sombreamiento generado por el dosel de parches de litre produce un incremento de la humedad del suelo respecto de sitios abiertos en hábitats xéricos, pero no en hábitats mésicos, entonces el reclutamiento de *Pinus* y *Eucalyptus* debiera ser mayor bajo parches de litre en hábitats xéricos y en sitios abiertos en hábitats mésicos.

Efecto de la herbivoría

Si existe depredación de plántulas de *Pinus* y *Eucalyptus* por vertebrados residentes, entonces la sobrevivencia de plántulas en sitios excluidos de herbívoros debiera ser mayor que en sitios sin exclusión.

Estas hipótesis son evaluadas y presentadas en dos manuscritos, el primero referido al efecto del hábitat físico (ladera ecuatorial vs. polar) y de la cobertura de litre, así como de la interacción entre ambos factores sobre la germinación y sobrevivencia de plántulas de ambas especies exóticas, y el segundo, respecto del efecto de herbívoros vertebrados sobre la sobrevivencia de plántulas de ambas especies exóticas.

Tabla 1. Densidad de individuos (mayores a 1 m de altura) de *Pinus radiata* y *Eucalyptus globulus* establecidos espontáneamente en ambientes naturales de diferentes localidades de la zona Mediterránea de Chile. También se indica la fuente de propágulos más probable (individuos plantados en forma ornamental o comercial). Fuente: Becerra, datos no publicados.

Localidad	*Pinus radiata*		*Eucalyptus globulus*	
	N° ind./ha	Posible fuente de propágulos	N° ind./ha	Posible fuente de propágulos
Quebrada San Ramón, Santiago (RM)	0.22	Plantación ornamental	5.55	Plantación ornamental
Cajón del Maipú, Santiago (RM)	1.56	Plantación ornamental	4.22	Plantación ornamental
Quebrada de Macul, Santiago (RM)	0.33	Plantación ornamental	160	Plantación ornamental
Rinconada de Maipú, Santiago (RM)	0.11	Plantación ornamental	0.22	Plantación ornamental
Parque Mahuida, Santiago (R.M)	0	Plantación ornamental	3.67	Plantación ornamental
Quebrada Alvarado, Olmué (V Región)	-	-	60	Plantación comercial
R.N. Los Queules (VII Región)	50	Plantación comercial	-	-
P.N. Laguna del Laja (VIII Región)	20	Plantación comercial	-	-

Bibliografía

Anderson, L. J., M. S. Brumbaugh & R. B. Jackson. 2001. Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. Ecology 82:33-49.

Armesto, J. J. & J. Martínez. 1978. Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. Journal of Ecology 66:881-889.

Armesto, J.J. & S.T.A. Pickett. 1985. A mechanistic approach to the study of succession in the Chilean matorral. Revista Chilena de Historia Natural 58:9-17.

Aschmann, H. & C. Bahre. 1977. Man's impact on the wild landscape. En: Mooney, H., ed. Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems. Dowden, Hutchinson and Ross, Stroudsburg.

Becerra, P. 2006. Invasión de árboles alóctonos en una cuenca de Chile central. Gayana Botanica, en prensa.

Beerling, D.J. 1993. The impact of temperature on the northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. Journal of Biogeography, 20: 45-53.

Bellingham, P.J. & D.A. Coomes. 2003. Grazing and community structure as determinants of invasion success by scoth broom in a New Zealand montane shrubland. Diversity and Distributions 9:19-28.

Bertness, M.D. & R. M. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191-193.

Boyd, D. 1996. Eucalyptus globulus: Bluegum Eucalyptus. Page 32 *in* J. M. Randall, and J. Marinelli, editors. Invasive plants: weeds of the global garden, Science

Press, New York.

Brooker, R.W. & T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos, 81:196-207.

Bruno, J. F., J. D. Fridley, K. D. Bromberg, and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. Pages 13-40 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Inc., USA.

Bustamante, R. O., I. A. Serey and S.T.A. Pickett. 2003. Forest fragmentation, plant regeneration and invasion processes across edges in central Chile. Pages 145-158 *in* G. A. Bradshaw and P. A. Marquet, editors. How Landscape Change. Springer-Verlag, Berlin.

Bustamante, R. O. & Simonetti, J. A. 2005. Is *Pinus radiata* invading the native vegetation in central Chile?, demographic responses in a fragmented forest. Biological Invasions 7: 243-249.

Callaway, R. M. & L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958-1965.

Chaneton, E.J., S.B. Perelman, M. Omacini & R. León. 2002. Grazing, environmental heterogeneity and alien plant invasions in temperate Pampa grasslands. Biological Invasions 4:7-24.

Close, D. C., Beadle, C. L., Holz, G. K. & Brown, P. H. 2002. Effect of shadecloth tree shelters on cold-induced photoinhibition, foliar anthocyanin and growth of *Eucalyptus globulus* and *E. nitens* seedlings during establishment. Australian

Journal of Botany 50:15-20.

Colautti, R.I., A. Ricciardi, I.A.Grigorovich, & J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis?. Ecology Letters 7:721-733.

Correia, M., F. Torres, and J. Pereira. 1989. Water and nutrients supply regimes and water relations of juvenile leaves of *Eucalyptus globulus*. Tree Physiology 5:459-471.

D'Antonio, C.M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology 74:83-95.

D'Antonio, C.M. & P.M. Vitousek. 1992. Biological Invasions by exotic grasses, the grass/fire cycle and global change. Annual Review of Ecology and Systematic 23:63-87.

Davis, M.A., J.P.Grime & K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology, 88:528-534.

Di Castri, F., D. Goodall & R. Specht. 1981. Mediterranean-Type Shrublands. Elsevier, Amsterdan.

Donoso, C. & A. Lara. 1995. Utilización de los bosques nativos en Chile: pasado, presente y futuro. En: Armesto, J.J., C. Villagrán & M.T.K. Arroyo (eds) Ecología de los bosques nativos de Chile. Editorial Universitaria, Santiago, Chile.

Drake, J., H.A. Mooney, F. Di Castri, R. Groves, F. Kruger, M. Rejmanek & M. Williamson. 1989. Biological Invasions: a global perspective. John Wiley, Chichester, UK.

Elton, C. 1958. The ecology of invasions by plants and animals. Methuen, London, UK.

Etienne, M. 2001. Pine trees - invaders or forerunners in mediterranean-type

ecosystems: a controversial point of view. Journal of Mediterranean Ecology 2:221-231.

Ferriere, G., Cerda, J. & Roach, R. 1983. El conejo silvestre en Chile. Boletín Técnico N°8, CONAF, Santiago, Chile.

Figueroa, J. A., S. A. Castro, P. A. Marquet, and F. M. Jaksic. 2004. Exotic plant invasion to the Mediterranean region of Chile: causes, history and impacts. Revista Chilena de Historia Natural 77:465-483.

Fuentes, E.R., F.M. Jaksic & J.A. Simonetti. 1983. European rabbits versus native rodents in Central Chile: effects on shrub seedlings. Oecologia 58:411-414.

Fuentes, E.R., R.D. Otaiza, M.C. Alliende, A.J. Hoffmann & A. Poiani. 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia 62:405-411.

Fuentes, E.R., A.J. Hoffmann, A. Poiani & M.C. Alliende. 1986. Vegetation change in large clearings: patterns in the Chilean matorral. Oecologia 68:358-366.

Groves, R. H. & J. Burdon. 1986. Ecology of biological invasions. Cambridge University Press, Cambridge, UK.

Groves, R. H. & F. di Castri. 1991. Biogeography of Mediterranean Invasions. Cambridge University Press, Cambridge, UK.

Harper, J.L. 1977. The Population Biology of Plants. Academic Press, London.

Hastwell, G. & J. M. Facelli. 2003. Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. Journal of Ecology 91:941-950.

Henríquez, C.A. & J.A. Simonetti. 2001. The effect of introduced herbivores upon an

endangered tree (Beilschmiedia miersii, Lauraceae). Biological Conservation, 98:69-76.

Higgins, S.I. & D.M. Richardson. 1998. Pine invasions in the southern hemisphere: modeling interactions between organism, environment and disturbance. Plant Ecology 135:79-93.

Hobbs, R. 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in Southwestern Australia. Conservation Biology 15:1522-1528.

Hobbs, R. & L. Huenneke. 1992. Disturbance, diversity, and invasions: implications for conservation. Conservation Biology 6:324-337.

Holmgren, M. 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternatives states. Biological Invasions, 4, 25-33.

Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966-1975.

Holmgren, M., Avilés, R., Sierralta, L., Segura, A.M. & Fuentes, E.R. 2000a. Why have European herbs so successfully invaded the chilean matorral? Effects of herbivory, soil nutrients and fire. Journal of Arid Environments, 44, 197-211.

Holmgren, M., Segura, A.M. & Fuentes, E.R. 2000b. Limiting mechanisms in the regeneration of the Chilean matorral. Plant Ecology, 147:49-57.

Iriarte, J.A., Contreras, L.C. & Jaksic, F.M. 1989. A long-term study of a small-mammal assemblage in the central Chilean matorral. Journal of Mammalogy, 70, 79-87.

Jaksic, F.M. 1998. Vertebrate invaders and their ecological impacts in Chile. Biodiversity and Conservation 7: 1427-1445.

Jaksic, F.M. & E.R. Fuentes. 1980. Why are native herbs in the Chilean matorral more

abundant beneath bushes: microclimate or grazing?. Journal of Ecology 68:665-669.

Johnstone, I.M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Review 61:369-394.

Kaufmann, M. 1977. Soil temperature and drought effects on growth of Monterey pine. Forest Science, 23:317-325.

Keeley, J.E. and P.H. Zedler. 1998. Evolution of life histories in *Pinus*. Pages 219- 250 *in* Ecology and Biogeography of *Pinus* D. M. Richardson editor. Cambridge University Press. Cambridge.

Kitzberger, T., D.F. Steinaker, and T.T. Veblen. 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology 81:1914-1924.

Kuijper, D.P., D.J. Nijhoff & J.P. Bakker. 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. Oecologia, 141:452-459.

Lenz, T. I., & J. M. Facelli. 2003. Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. Austral Ecology 28:480-490.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to alien plant invasions. Ecology Letters 7:975-989.

Lindenmayer, D.B., and M. A. McCarthy. 2001. The spatial distribution of non-native plant invaders in a pine-eucalypt landscape mosaic in south-eastern Australia. Biological Conservation 102:77-87.

Lonsdale, W. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology, 80:1522-1536.

López, M. J. Humara, A. Casares & J. Majada. 2000. The effect of temperature and

water stress on laboratory germination of *Eucalyptus globulus* Labill. seeds of different sizes. Annals of Forest Science, 57:245-250.

MacDougall, A.S., Boucher, J., Turkington, R. & Bradfield, G.E. 2006. Patterns of plant invasion along an environmental stress gradient. Journal of Vegetation Science 17: 47-56.

Maron, J.L. & M. Vilà. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. *Oikos*, 95:361-373.

McArthur, C. & Appleton, R. (2004) Effect of seedlings characteristics at planting on browsing of Eucalyptus globulus by rabbits. Australian Forestry 67: 25-39.

Mooney, H.A. & H.A. Hobbs. 2000. Invasive Species in a Changing World. Island Press, California.

Moore, B. D. & Foley, W. J. (2005) Tree use by koalas in a chemically complex landscape. Nature 435: 488-490.

Muñoz, A. & R. Murúa. 1990. Control of small mammals in a pine plantation (central Chile) by modification of the habitat of predators (Tyto alba, Strigiforme and Pseudolopex sp., Canidae). Acta Oecologica 11:251-261.

Myers, J.H. & Bazely, D.R. 2003. Ecology and control of introduced plants. Cambridge University Press.

O'Reilly-Wapstra, J.M., McArthur, C. & Potts, B.M. (2004) Linking plant genotype, plant defensive chemistry and mammal browsing in a *Eucalyptus* species. Functional Ecology 18:677-684.

O'Reilly, J. & McArthur, C. (2000) Damage to and intake of plantation seedlings by captive European rabbits (*Oryctolagus cuniculus*). Australian Forestry 63: 1-6.

Parker, J.D., Burkepile, D.E. & M.E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science*, 311, 1459-1461.

Prider, J. N. & J. M. Facelli. 2004. Interactive effects of drought and shade on three arid zone chenopod shrubs with contrasting distributions in relation to tree canopies. Functional Ecology 18:67-76.

Reyes, O. & M. Casal. 2001. The influence of seed age on germinative response to the effects of fire in *Pinus pinaster*, *Pinus radiata* and *Eucalyptus globulus*. Annals of Forest Science, 58:439-447.

Richardson, D.M. 1998. Forestry trees as invasive aliens. Conservation Biology 12:18-26.

Richardson, D.M. & P.J. Brown. 1986. Invasion of mesic mountain Fynbos by *Pinus radiata*. South African Journal of Botany, 52:529-536.

Richardson, D.M., R.M. Cowling & D.C. Le Maitre. 1990. Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos. Journal of Vegetation Science 1:629-642.

Richardson, D.M. & W.J. Bond. 1991. Determinants of plant distribution: evidence from pine invasions. American Naturalist, 137:639-668.

Richardson, D.M., B.W. van Wilgen, S.I. Higgins, T.H. Trinder-Smith, R.M. Cowling & D.H. McKell. 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. Biodiversity and Conservation 5:607-647.

Richardson, D.M., P. Pysek, M. Rejmanek, M.G. Barbour, F.D. Panetta & C.J. West. 2000a. Naturalization and invasion of Alien plants: concepts and definitions. Diversity and Distributions 6:93-107.

Richardson, D.M., N. Allsopp, C.M. D'Antonio, S.J. Milton & M Rejmánek. 2000b. Plant invasions - the role of mutualisms. Biological Review 75:65-93.

Rodriguez, J.P. 2001. Exotic species introductions into South America: an underestimated threat?. Biodiversity and Conservation 10:1983-1996.

Rouget, M., D. Richardson, S. Milton & D. Polakow. 2002. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecology 152:79-92.

Saavedra, B. 2003. Disminución en tamaño poblacional y asimetría fluctuante en *Octodon brïdgesi* (Rodentia), taxón especialista de hábitat. Thesis, Facultad de Ciencias, Universidad de Chile.

Sax, D.F, Stachowicz, J.J. & Gaines, S.D. 2005. Species invasions. Insights into ecology, evolution, and biogeography. Sinauer Associates, Inc.

Schierenbeck, K.A., R.N. Mack & R.R. Sharitz. 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology 75:1661-1672.

Shea, K. & P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17: 170-176.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown?. Biological Invasions 1:21-32.

Stohlgren, T.J., Barnett, D., Flather, C., Kartesz, J. & Peterjohn, B. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology 86:2298-2309.

Vásquez, D.P. 2002. Multiple effects of introduced mammalian herbivores in a

temperate forest. *Biological Invasions*, 4, 175-191.

Von Holle, B. & D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology, 86:3212-3218.

Walcroft, A. S., D. Whitehead, F. M. Kelliher, A. Arneth, and W. B. Silvester. 2002. The effects of long-term, partial shading on growth and photosynthesis in *Pinus radiata* D. Don trees. Forest Ecology and Management 163:151-163.

Williams, M.C. & Wardle, G.M. 2005. The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue mountains, New South Wales, Australia. Biological Conservation 125: 55-64.

Williamson, M. & Fitter, A. 1996. The varying success of invaders. Ecology 77: 1661-1666.

CAPÍTULO II

Effect of slope aspect and native tree cover on the recruitment of the exotic species *Pinus radiata* and *Eucalyptus globulus* in central Chile

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Summary

The importance of physical habitat conditions and resident vegetation cover for invasion processes of exotic tree species is investigated. Invasion has been documented to occur predominantly in less stressful habitats. On the other hand, the resident vegetation often affects plant invasion negatively, although positive effects have also been documented. However, habitat conditions under which resident vegetation produces negative and positive effects on invasion processes have been few assessed. The stress hypothesis states that negative interactions will be more important in less stressful habitats, while positive interactions will be more important in more stressful habitats. We evaluated the independent and interactive effects of contrasting physical habitat conditions and a native tree cover on the recruitment of two cosmopolitan invasive tree species, *Pinus radiata* and *Eucalyptus globulus*, in a Mediterranean-type ecosystem of central Chile. We also assessed whether native tree cover effects are due to shading. We evaluated the effect of physical conditions by comparing recruitment between a xeric habitat (north-facing slope) and a mesic habitat (south-facing slope). We also compared seedling recruitment of both exotic species under patches covered by the native tree *Lithrea caustica* (without other woody species) and in open sites, without *Lithrea*. Shading effects of *Lithrea* were evaluated by comparing open sites with sites where an artificial canopy (shade cloth) was installed. We evaluated two phases of recruitment processes: germination and seedling survival. Germination and seedling survival of both species was higher in the mesic habitat, although mainly in open sites. On the other hand, there was a positive effect of *Lithrea* and shading on germination of both exotic species in the xeric habitat. In the mesic habitat there was no significant *Lithrea* or shading effect on

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germination. Seedling survival of both species was negatively affected by *Lithrea* and artificial shading in the mesic habitat. In the xeric habitat there was no significant effect of *Lithrea* or artificial shading on seedling survival of either species. Our results suggest that differences in soil moisture between habitats and cover of *Lithrea caustica* are drivers of the invasion of these exotic species in the region. However, our results also suggest that the effect of *Lithrea* depends on habitat conditions and stage of the life cycle, and that the effect of physical habitat on invasion processes may depend on resident vegetation. In addition, for each recruitment phase separately (germination and seedling survival) our results were only partially consistent with the hypothesis on the relationship between plant-plant interaction and physical stress. However, if the whole recruitment process is considered our results are quite consistent with this hypothesis. Finally, our results also show how negative as well as positive interactions between native and exotic species may help to explain invasion processes.

Key-words: Plant invasion, facilitation, biotic resistance, plant establishment, alien species, plant-plant interactions, shading effects.

Introduction

Biological invasions have long been recognised as an important ecological phenomenon occurring in natural communities (Elton 1958; Drake *et al.* 1989; Sax *et al.* 2005). More recently invasions have received considerable attention due to their detrimental effect on biodiversity (Mooney & Hobbs 2000), motivating ecologists to understand the factors and mechanisms influencing invasion processes.

Once propagules of exotic species have arrived into a new site, physical conditions of habitats and resident plants may critically determine whether the recruitment of the exotic species will occur or not (Lonsdale 1999; Davis *et al.* 2000; Shea & Cheeson 2002; Levine *et al.* 2004; Mitchell *et al.* 2006). In general, it has been documented a higher invasion of exotic species in habitats with lower physical stress, mainly moister and warmer, or where productivity is higher (Richardson & Bond 1991; Beerling 1993; Lonsdale 1999; Stohlgren *et al.* 2005; MacDougall *et al.* 2006). In contrast, the effects of resident plants on exotic plants are less obvious as both negative and positive effects have been documented (Bruno *et al.* 2005). According to the stress hypothesis proposed for plant-plant interactions (Bertness & Callaway 1994; Brooker & Callaghan 1998), the effect of resident plants on plant invasion may depend on physical stress produced by habitats. In less stressful environments, negative interactions may be more important than positive interactions resulting in a negative effect on recruitment of an exotic species. Under high stress, positive interactions may become more dominant determining the effect of a plant on an exotic species is positive. Different ways have

been suggested by which this change of interactions along physical stress gradients may occur (Callaway & Walker 1997). One of the most documented ways is the change from negative to positive effects with increasing drought (Holzapfel & Mahall 1999; Kitzberger *et al.* 2000; Anderson *et al.* 2001; Hastwell & Facelli 2003; Lenz & Facelli 2003; Prider & Facelli 2004). Thus, in xeric habitats, where stress is imposed by soil moisture constraints, increases in soil moisture due to shading may be more important than the negative effect generated by light reduction. This may then cause the final (or net) effect of one species on the recruitment of another in xeric habitats to be positive. In mesic habitats, where soil moisture is not limiting in areas with no plant cover, shading may not produce a positive effect by increasing in soil moisture, but it would still be having a negative influence via a reduction in luminosity. Under these circumstances recruitment under a canopy would be often similar or lower than in open sites (Holmgren *et al.* 1997). Few studies have evaluated environmental conditions, in particular soil moisture, under which plant invasion is facilitated or inhibited by resident species (e.g. Williamson & Harrison 2002; Lenz & Facelli 2003; Von Holle 2005), despite the acknowledgment that physical conditions of habitats have a large influence on plant-plant interactions (Goldberg *et al.* 1999; Lortie & Callaway 2006).

Some of the main sources of exotic plants from which invasion process originate are forestry plantations (Richardson 1998; Mooney & Hobbs 2000). In Chile, forestry plantations are predominantly composed of *Pinus radiata* D. Don (Pinaceae) or *Eucalyptus globulus* Labill. (Myrtaceae). Both of these exotic species have widely been planted through the Mediterranean region of Chile, thus generating an enormous propagule source available for a potential invasion of these trees in this region (Figueroa

et al. 2004). In fact, the invasion process by these species is already beginning to occur in several Mediterranean ecosystems of the country (Bustamante *et al.* 2003; Becerra 2006). Both species are also widely used as forestry trees in other parts of the world, and have become recognised aggressive invaders with detrimental effects on biodiversity in most of places where they have been planted (Richardson *et al.* 1990; Groves & Di Castri 1991; Boyd 1996; Higgins & Richardson 1998; Lindenmayer & McCarthy 2001; Rouget *et al.* 2002, Williams & Wardle 2005).

The Mediterranean region of Chile, like other Mediterranean ecosystems, has a semiarid climate, with precipitation concentrated in winter and dry summers. Furthermore, within this region exists an important topographic heterogeneity which determines contrasting physical conditions, mainly respect to soil moisture, between north-facing (more xeric) and south-facing (more mesic) slopes (Armesto & Martínez 1978). On the other hand, within the Mediterranean region of Chile is present the most part of the human population of the country and hence has been intensively disturbed (Aschmann & Bahre 1977). Tree vegetation has been the most affected, determining that currently is distributed as isolated patches surrounded by shrubby and herbaceous patches (Aschmann & Bahre 1977; Fuentes *et al.* 1984). One of the most widely distributed and abundant native tree species in this region is *Lithrea caustica* (Mol.) H. *et* A. (Anacardiaceae). This species is distributed in xeric as well as mesic habitats and is common in different vegetation-types of this region. In this paper we evaluated the effect of the physical condition of habitats, the presence of *Lithrea* patches, and the interaction of both factors on the recruitment of *Pinus radiata* and *Eucalyptus globulus*. Additionally, we examined whether the effect of *Lithrea* is produced by shading effects.

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Both exotic species studied originated from Mediterranean ecosystems, *P. radiata* from California (USA) and *E. globulus* from Tasmania and Victoria (Australia). Although these species are adapted to seasonal droughts typical of Mediterranean climates, they tend to be distributed in moister habitats in their native country as well as in their introduced ranges (Kaufmann 1977; Richardson & Brown 1986; Correia *et al.* 1989; Boyd 1996; Keeley & Zedler 1998; Becerra 2006). In addition, experimental evidence indicates that both species improve their performance (germination and growth rate of seedlings) with increasing soil moisture (Correia *et al.* 1989; Kaufmann 1977; López *et al.* 2000; Humara *et al.* 2002). Therefore, we expect that the germination and seedling survival of both species is higher in moister habitats within the Mediterranean region of Chile (polar-facing slopes). On the other hand, both species are considered shade-intolerant (Correia *et al.* 1989; Keeley & Zedler 1998; Walcroft *et al.* 2002). However, no previous experimental studies have experimentally evaluated this statement. Only, it has been showed negative effects of shading on growth of *Pinus radiata* saplings (but not in seedlings) (Walcroft *et al.* 2002) and a positive effect of shading on seedling growth (but not germination and seedling survival) of *Eucalyptus globulus* (Close *et al.* 2002). Other studies indicate that both species regenerate better in naturally open and/or disturbed sites with low vegetation cover (Richardson & Brown 1986; Higgins & Richardson 1998; Lindenmayer & McCarthy 2001; Becerra 2006), although both species are able to recruit under a plant canopy (Lindenmayer & McCarthy 2001; Close *et al.* 2002; Bustamante & Simonetti 2005; Becerra 2006). We expect that the germination and seedling survival of these species is negatively affected by shading of *Lithrea* when soil moisture is not limiting as in mesic habitats of the

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Chilean Mediterranean region, and enhanced by cover when soil moisture is limiting, such as in xeric habitats.

Methods

STUDY SITE

The study was carried out in a watershed immediately adjacent to the East border of Santiago city (33°30' S, 70°30' W), central Chile, specifically in the "San Ramón River" watershed. Climate is semiarid Mediterranean-type, with 5-6 dry months and precipitation concentrated during winter, reaching an annual average of 330 mm and an annual mean temperature of 15°C (Di Castri & Hajek 1976). The topography of the study site is dominated by a north-facing slope and a south-facing slope. The study site has not been disturbed during the last 10 years (extensive fires, domestic livestock, and logging of trees) and currently is protected by the Chilean Forest Service (CONAF).

The vegetation is spatially heterogeneous, composed of herbaceous, shrub and arboreal patches. Woody (tree and shrub patches) are composed almost exclusively of native species (*Lithrea caustica* and *Retanilla trinervia*) while herbaceous patches are composed of native plants including *Bromus berteroanus* and *Pasithea coerulea* as well as exotic herbs such as *Conium maculatum*, *Centaurea melitensis* and *Fumaria* spp. Tree patches of the watershed reach approximately 30% cover (70% of shrub and herb patches) and are dominated by *Lithrea caustica*. This spatial heterogeneity of vegetation is important for the recruitment of native tree species in central Chile, because seedling recruitment tends to be concentrated under woody patches in xeric habitats but not in

mesic habitats (Fuentes *et al.* 1984, 1986; Holmgren *et al.* 2000).

EXPERIMENTAL DESIGN

In order to evaluate the effect of physical conditions on the recruitment of *Pinus radiata* and *Eucalyptus globulus* we compared two habitat-types: a xeric habitat located in an equatorial-facing slope and a mesic habitat located in a polar-facing slope. Within each habitat we evaluated the effect of *Lithrea* patch on the recruitment of both exotic species. The total or net effect of *Lithrea* on recruitment was evaluated comparing open sites (without woody plant cover) with recruitment under *Lithrea* patches. This comparison assumed that recruitment differences (if they exist) may be produced by the canopy, the litter, the roots, microorganisms associated to *Lithrea*, and herb composition (but not herb cover, see results). In order to isolate the shading effect, we compared "artificial" canopies with open sites. Artificial canopies consisted of a 4 x 4 m piece of black nylon shade-cloth, suspended 1.5 m above the ground from iron posts, located in originally open sites, thus simulating the reduction of light, protection of soil moisture and lower temperature (see results) measured under patches of *Lithrea*. In total, we used three canopy treatments: open sites (without woody canopy), *Lithrea* covered patches and artificial canopies. In order to evaluate the hypothesis on the effect of physical habitat conditions, we compared recruitment between contrasting habitats, pooling all canopy treatments per habitat. However, comparison between habitats was also performed per each canopy treatment separately. To evaluate the effect of *Lithrea* and shading under contrasting habitat conditions, we compared recruitment among canopy treatments within each habitat.

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Each canopy treatment was replicated ten times, giving a total of 30 replicates per habitat-type (polar vs. equatorial slope) and 60 replicates in total. Replicates were located at least 10 m apart, separated by other patch types in order to maximise statistical independence among them. In each replicate we installed a 1 x 1.5 m plot, fenced on the sides and the top by a wire mesh in order to exclude mammals and birds. Each plot was separated into two contiguous sections: one 1 x 0.5 m section and a 1 x 1 m section. The smaller section was used to evaluate seedling survival and the larger one to evaluate seed germination. At the beginning of winter (20-25 June 2004) we planted three seedlings of each exotic species in each replicate, separated by 20 cm between them and 30 cm from the fence. Seedlings of each species were ten months old at time of planting. Seedling heights at time of planting were 19.7 cm ± 0.15 and 22.9 cm ± 0.19 (mean ± 1 SE) for *Pinus* and *Eucalyptus* respectively. In the larger section of the plot we sowed 50 seeds of each species at a depth of no more than 1 cm in order to simulate the depth at which seeds are located after a natural seed rain. Seeds of each species were sowed in alternating rows with 8 cm separating each row (20-25 June, 2004), thus using a 72 x 72 cm space for seeds in the centre of the larger section of the plot. Seedlings and seeds were obtained from the greenhouse of the University of Chile, Santiago. Seeds have certified viability of 95% and were collected from plantations located in the Mediterranean zone of Chile. Seedlings were produced from the same seed types.

MICROENVIRONMENTAL MEASUREMENTS

We measured photosynthetic active radiation (PAR), soil water content (SWC), soil nutrient concentration (N, P, K), soil pH, air temperature and herb cover. PAR was

measured at the soil level and at 30 cm from soil (in order to differentiate light on the top of seedlings and light affected by herbs). PAR was quantified in each replicate once in spring (October, 2004) using a quantum sensor (LI-190) during one clear sunny day, registering one value of light per height per replicate per treatment between 12:00 PM and 13:00 PM of the same day. SWC was evaluated using the gravimetric method and was measured once in each season for each experimental replicate. Statistical analysis of SWC (ANOVA) was conducted with the average values obtained for each replicate during the four seasons in order to obtain a global value of SWC per treatment. Air temperature was measured once in summer (January, 2005) by an air thermo-hygrometer (Deltatrak 13307, resolution: 0.1°C), thus registering one value per replicate during a clear sunny day between 12:00 PM and 13:00 PM. Soil nutrients and pH were evaluated once by sampling the soil (10 cm of soil without leaf litter) on a summer day in January, 2005. Soil samples for nutrient analyses were collected in three randomly selected replicates per treatment. In order to account for the large variability in the height of herbs, herb cover was evaluated at two heights in each replicate using the intercept point method. Cover was recorded at soil level and at 30 cm above soil level. We used 10 points per stratum and thus a total of 20 points per replicate.

PLANT RECRUITMENT ASSESSMENT

We evaluated germination and seedling survival in each plot. Germination Probability (GP) was evaluated by the percentage of seeds that germinated from the 50 seeds initially sown in each replicate. Because seed germination occurred very synchronically since two months after seeds were buried (pers. obs.), we considered GP as the

percentage of emerged seedlings four months after sowing. No recently germinated seedling died before four months and no seed germinated after four months. All analyses for the germination experiment were performed with ANOVA (habitat and canopy as factors). Seedling survival (SS) was monitored each two months during one year since planting (June 2004-June 2005). As the percentage of living seedlings per replicate at the end of the experiment did not satisfy the normality assumption for parametric statistical tests, we randomly selected one from the three originally planted seedlings with which we performed survival analyses?. Thus, the comparisons of SS among treatments were performed by comparing seedling survival curves using the log-rank procedure and Holm-Sidak method for post-hoc tests.

In order to quantitatively evaluate spatial independence among replicates we performed spatial autocorrelation tests (Mantel test) within each canopy and habitat treatment. For germination we evaluated spatial autocorrelation of germination probability (GP). For seedling survival we quantified the seedling survival probability by the percentage of living seedlings at the end of the experiment from the three originally planted.

Results

MICROENVIRONMENTAL MEASUREMENTS

PAR at the soil level as well as at 30 cm above ground differed significantly among shaded and open treatments but not between habitats (Table 1). Also, no statistical interaction was detected among habitat and canopy treatments for both measures of light

(Table 1). In both habitats PAR was significantly higher in open sites than under *Lithrea* patches and artificial canopies, and no difference was observed in light conditions between *Lithrea* and artificial canopies (Fig. 1). Absence of differences between *Lithrea* patches and artificial canopy sites indicates that in terms of light intensity artificial canopies simulated efficiently shading effects of *Lithrea* canopy.

Soil Water Content differed significantly between habitats (Table 1), being higher in the mesic than in the xeric habitat (Fig. 2). Within each canopy treatment, mesic sites (polar-facing slope) had higher SWC than xeric sites (Fig. 2). On the other hand, SWC showed significant differences among canopy treatments, and a significant interaction between habitat and canopy type (Table 1). In the xeric habitat, open sites had a significantly lower SWC than *Lithrea* patches and artificial canopy sites, with no difference between these treatments (Fig. 2). Instead, in the mesic habitat there were no significant differences among canopy treatments (Fig. 2). Absence of differences between *Lithrea* patches and artificial cover in terms of SWC showed that this treatment simulated efficiently shading effects of *Lithrea* canopy.

Herbaceous cover did not differ among patches, although there was a marginally significant difference given by the tall herbaceous cover in the mesic habitat under artificial cover relative to open and *Lithrea* patches (Table 1, Fig. 3). There was no significant difference in herbaceous cover between habitats and the statistical interaction was not significant (Table 1, Fig. 3).

Air temperature varied significantly between canopy treatments and habitats (Table 1, Fig. 4). The interaction between habitat and patch type was not significant (Table 1). Globally, air temperature in the xeric habitat (equatorial-facing slope) was

higher than in mesic habitat (Fig. 4). However, within each canopy treatment, air temperature did not differ between habitats (Fig. 4). On the other hand, in both habitats, air temperature was significantly higher in open sites than under *Lithrea* patches and under artificial shading with no difference between the last two canopy treatments (Fig. 4). This indicates that artificial shading accurately simulated air temperature effects of *Lithrea* cover.

There were no statistical differences in soil pH and nutrient levels between shading treatments within each habitat (Table 2). However, in the xeric habitat soil pH was significantly higher than in the mesic habitat and phosphorous was significantly lower in the xeric than in mesic habitat (Table 2). The absence of differences is as expected in order to simulate shading conditions under similar soil nutrient conditions.

SEED GERMINATION

The germination probability (GP) of *Pinus radiata* seeds differed significantly between habitats and canopy treatments and the statistical interaction between these factors was marginally significant (Table 3). GP in the xeric habitat was significantly lower than in the mesic habitat under any canopy condition (Fig. 5). On the other hand, GP differed between canopy treatments only in the xeric habitat. GP was significantly lower in open sites than under *Lithrea* patches and artificial shading with no difference between the latter two canopy treatments (Fig. 5). Instead, in the mesic habitat, GP of *Pinus* showed the same pattern as in xeric habitat, but no significant difference between canopy treatments was observed (Fig. 5).

In the case of *Eucalyptus*, GP differed between habitats, canopy treatments and

the statistical interaction was also significant (Table 3). GP in the xeric habitat was significantly lower than in the mesic habitat but only in open sites. In other canopy treatments there was no difference between habitats (Fig. 5). GP differed between canopy treatments only in the xeric habitat. GP in open sites was significantly lower than in either *Lithrea* patches or under artificial shading, with no difference between these shading treatments (Fig. 5).

There was no spatial autocorrelation among replicates for germination probability of each species within each canopy treatment per habitat, or within each habitat in general (Table 5). This indicates that replicates within each canopy and habitat treatment were spatially independent.

SEEDLING SURVIVAL

In *Pinus*, there were significant differences among survival curves for each combination of canopy and habitat treatment (Chi ^{2} = 35.69; d.f. = 5; P < 0.001). Seedling survival of *P. radiata* was significantly higher in mesic than in xeric habitat but only in open sites (Table 4; Fig. 6). On the other hand, in the xeric habitat we observed significant differences in SS only between artificial shading and *Lithrea* patches (Table 4), being SS higher under artificial shading (Fig. 6). In the mesic habitat SS in open sites was significantly higher than under artificial shading, which was in turn higher that under *Lithrea* patches (Table 4, Fig. 6).

In *Eucalyptus* survival curves obtained for each combination of canopy and habitat treatment differed significantly (Chi ^{2} = 25.39; d.f. = 5; P < 0.001). There was a significantly higher SS in the mesic habitat than in the xeric habitat but only in open

sites (Table 4, Fig. 6). In the xeric habitat we observed no difference between canopy treatments (Table 4, Fig. 6). Instead, in the mesic habitat SS in open sites was significantly higher than under *Lithrea* patches and artificial shading, with no difference between these last two treatments (Table 4, Fig. 6).

We observed no spatial autocorrelation among replicates for seedling survival probability of each species in any canopy or habitat treatment (Table 6). This indicates that in terms of SS replicates were spatially independent in both species.

Discussion

EFFECT OF PHYSICAL HABITAT ON INVASION

We confirmed that polar-facing habitat is moister, colder and thus more mesic than the equatorial-facing-slope habitat. Both invasive species had a higher germination and seedling survival in open sites of the mesic habitat than in open sites of the xeric habitat. In addition, GP of *Pinus* was higher in the mesic than in the xeric habitat under *Lithrea* and artificial canopies as well. Both species respond positively to experimental increases of soil moisture (Correia *et al.* 1989; Kaufmann 1977; López *et al.* 2000). Hence, our results suggest that differences in soil moisture between habitats may have produced significant differences in recruitment probabilities and that soil moisture may be determinant in the distribution mostly on moister habitats in both species either in their native or introduced ranges (Kaufmann 1977; Richardson & Brown 1986; Correia *et al.* 1989; Boyd 1996; Keeley & Zedler 1998; Becerra 2006). These results are consistent with previous studies which suggest that invasion probability would be higher in less

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stressful habitats, in this case polar-facing slopes, as long as shading is low (Richardson & Bond 1991; Beerling 1993; Lonsdale 1999; Stohlgren *et al.* 2005; MacDougall *et al.* 2006). However, these inferences should be made with caution as there were differences in soil pH and phosphorous between habitats, which may also have a role in recruitment success between habitats.

EFFECT OF *LITHREA* COVER ON INVASION

In general, *Lithrea* cover had a similar effect on the recruitment process of *Pinus* and *Eucalyptus*. The effect of *Lithrea* on the germination probability was positive in the xeric habitat and null in the mesic habitat for both species. Because seed germination was higher under artificial shading than in open sites in the xeric habitat, the positive effect of *Lithrea* was largely due to shading. Instead, in the mesic habitat possibly the absence of difference in soil moisture between canopy treatments determined no difference in germination. Thus, light exposure does not seem to affect the germination of these species as under similar conditions of soil moisture, the higher light level in open sites did not increase seed germination of these species.

The effect of *Lithrea* cover on the survival of seedlings was similar but not equal for the two exotic species. In the mesic habitat, *Lithrea* had a negative effect on SS of *Pinus* and *Eucalyptus*. In both cases this was produced by negative shading effects as SS was higher in open sites than under artificial canopies. In the xeric habitat, *Lithrea* had no significant effect on SS of *Pinus* or *Eucalyptus*. Either there was no shading effect in the xeric habitat. However, SS of *Pinus* (but not *Eucalyptus*) in artificial canopy sites was significantly higher than in *Lithrea* patches in both habitats. These two types of

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canopy treatments had very similar light intensity, soil moisture, air temperature and even herb cover. Thus, differences between artificial canopy sites and *Lithrea* patches may be mainly related to soil conditions such as litter, soil microorganisms, nutrients (below 10 cm soil deep as soil of the superficial stratum did not differ between artificial canopies and *Lithrea* patches in nutrients and soil pH), etc. This suggests that soil of *Lithrea* patches had a significant negative effect on SS of *Pinus*, but this effect was not enough to produce a negative total effect of *Lithrea* in the xeric habitat. Instead, in the mesic habitat this negative soil effect of *Lithrea* may have contributed to produce the negative total effect of *Lithrea* on SS of *Pinus*. Other studies have used the comparison between artificial canopies and natural patches of plants (thus contrasting two sites with equal shading and different soil) to evaluate soil effects globally (e.g. Holzapfel & Mahall 1999; Gómez-Aparicio *et al.* 2005), observing in some cases stronger soil effects than shading effects (e.g. Belsky 1994; Holzapfel & Mahall 1999; Ganade & Brown 2002; Gómez-Aparicio *et al.* 2005), similarly to our results in the xeric habitat.

Our results suggest that the effects of native *Lithrea* cover may change with the physical conditions of habitats and life-cycle stage of the invasive tree. In the xeric habitat we found only positive effects of *Lithrea* (on germination) produced by shading and in the mesic habitat only negative effects (on seedling survival) also produced by shading. Thus, considering the whole recruitment process, the result would be a positive effect of *Lithrea* on the recruitment in the xeric habitat and a negative effect in the mesic habitat. These results agree with Bertness & Callaway (1994), Brooker & Callaghan (1998) and Lortie & Callaway (2006) who suggest that plant-plant interactions are driven by physical conditions of habitats, and to Holmgren *et al.* (1997) who specifically

suggest that soil moisture of habitats and shading effects of plants are main drivers of the outcome of plant-plant interactions in semiarid and arid regions. However, these hypotheses are only partially corroborated if we consider each life-cycle stage separately. Other studies have also documented dependency of this hypothesis on life-cycle stage and performance variable of plants (Berkowitz *et al.* 1995; Goldberg *et al.* 1999; Holzapfel & Mahall 1999; Hastwell & Facelli 2003; Siemann & Rogers 2003; Maestre *et al.* 2005). This could be due to shifts in ecological requirements with age. Our species of *Pinus* and *Eucalyptus* are considered shade-intolerant (Correia *et al.* 1989; Walcroft *et al.* 2002). However, this ecological attribute seems to be valid only for more advanced life cycle stages than seed as we found no negative shading effect on germination, and even they turned positives in the xeric habitat. Probably other factor such as soil moisture is more important for germination. Instead, for seedlings we observed mainly negative shading effects, although only in the mesic habitat. Thus, we observed that under mesic habitat conditions the effect of *Lithrea* changed from a null effect on germination to negative effects on seedling survival in both species, and under xeric habitat conditions the effect of *Lithrea* changed from positives to nulls. Bustamante & Simonetti (2005) also documented a good germination of *Pinus radiata* but subsequent high mortality of seedlings within a more humid Mediterranean forest of Chile. These ontogenetic changes of plant-plant interactions have been documented previously (Shupp 1995; Callaway & Walker 1997; Miriti 2006). Therefore, in order to understand and predict the whole invasion process of a particular exotic species, the entire plant life cycle should be taken in account. Then, the effect of *Lithrea* on the later developmental stages may be different than the results reported here.

Finally, it has recently been highlighted that both negative and positive interactions between native and exotic species may play a role in invasion processes (Richardson *et al.* 2000; Bruno *et al.* 2005). In particular, positive effects of natives on exotic species have recently been documented (e.g. Lenz & Facelli 2003; Siemann & Rogers 2003; Von Holle 2005; Cavieres *et al.* 2005). Our results corroborate that negative but also positive interactions may help to explain invasion processes in the case of Pinus and Eucalyptus in central Chile.

Conclusions

Pinus radiata and *Eucalyptus globulus* are widely planted in central Chile and other parts of the world. These plantations are logged every 15 years. Because both species can reproduce since they are seven years old approximately, plantations are an important propagule source for invasion. Moreover, *Pinus* seed rain has been documented in natural ecosystems of central Chile outside plantations (Bustamante & Simonetti 2005). Therefore, propagule availability does not seem to be limiting invasion of these species at least closed to plantations. Hence knowledge of the effect of physical habitats and native trees, such as *Lithrea caustica* and eventually other native plants, on recruitment of these two exotic species is needed to determine their invasion probabilities in this region. From our results we can predict that the probability of invasion is the highest, in open sites of mesic habitats. In these habitats, *Lithrea* patches (and possibly other trees and shrubs) tend to slow the invasion process. In contrast, in xeric habitats, *Lithrea* patches may facilitate invasion, although this will depend on shade tolerance under

Lithrea canopies during more advanced stages of the life cycle of these exotic trees. Finally, invasion into open sites in xeric habitats should be unlikely.

Acknowledgements

References

Anderson, L.J., Brumbaugh, M.S. & Jackson, R.B. (2001) Water and tree-understory interactions: a natural experiment in a savanna with oak wilt. Ecology, 82, 33-49.

Armesto, J.J. & Martínez, J. (1978) Relations between vegetation structure and slope aspect in the Mediterranean region of Chile. Journal of Ecology, 66, 881-889.

Aschmann, H. & Bahre, C. (1977) Man's impact on the wild landscape. *Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems* (ed H. Mooney), pp. 73-84. Dowden, Hutchinson and Ross, Stroudsburg.

Becerra, P. (2006) Invasión de árboles alóctonos en una cuenca de Chile central. Gayana Botanica, en prensa.

Beerling, D.J. (1993) The impact of temperature on the northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. Journal of Biogeography, 20, 45-53.

Belsky, A. J. (1994) Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology, 75, 922-932.

Berkowitz, A.R., Caham, C.D. & Kelly, V.R. (1995) Competition vs. Facilitation of tree seedling growth and survival in early successional communities. Ecology, 76, 1156-1168.

Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. Trends in Ecology and Evolution, 9, 191-193.

Boyd, D. (1996) Eucalyptus globulus: Bluegum Eucalyptus. *Invasive plants: weeds of the global garden* (eds J.M. Randall & J. Marinelli), pp. 32. Science Press, New York.

Brooker, R.W. & Callaghan, T.V. (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos, 81, 196-207.

Bruno, J.F., Fridley, J.D., Bromberg, K.D. & Bertness, M.D. (2005) Insights into biotic interactions from studies of species invasions. *Species Invasions: insights into ecology, evolution and biogeograph.* (eds D.F. Sax, J.J. Stachowicz & S.D. Gaines), pp. 13-40. Sinauer Associates, Inc., USA.

Bustamante, R.O., Serey, I.A. & Pickett, S.T.A. (2003) Forest fragmentation, plant regeneration and invasion processes across edges in central Chile. *How Landscape Change* (eds G.A. Bradshaw & P.A. Marquet), pp. 145-158. Springer-

Verlag, Berlin.

Bustamante, R.O. & Simonetti, J.A. (2005) Is *Pinus radiata* invading the native vegetation in central Chile?, demographic responses in a fragmented forest. Biological Invasions, 7, 243-249.

Callaway, R. M., & Walker, L. R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology, 78, 1958-1965.

Cavieres, L.A., Quiroz, C.L., Molina-Montenegro, M.A., Muñoz, A.A. & Pauchard, A. (2005) Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. Perspectives in Plant Ecology, Evolution and Systematics, 7, 217-226.

Close, D. C., Beadle, C. L., Holz, G. K. & Brown, P. H. (2002) Effect of shadecloth tree shelters on cold-induced photoinhibition, foliar anthocyanin and growth of *Eucalyptus globulus* and *E. nitens* seedlings during establishment. Australian Journal of Botany, 50, 15-20.

Correia, M., Torres, F. & Pereira, J. (1989) Water and nutrients supply regimes and water relations of juvenile leaves of *Eucalyptus globulus*. Tree Physiology 5:459-471.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology, 88, 528-534.

Di Castri, F., & Hajek, E. (1976) Bioclimatología de Chile. Universidad Católica de Chile, Chile.

Drake, J., Mooney, H.A., Di Castri, F., Groves, R., Kruger, F., Rejmanek, M. & Williamson, M. (1989) *Biological Invasions: a global perspective*. John Wiley,

Chichester, UK.

Elton, C. (1958) *The ecology of invasions by plants and animals*. Methuen, London, UK.

Figueroa, J.A., Castro, S.A., Marquet, P.A. & Jaksic, F.M. (2004) Exotic plant invasion to the Mediterranean region of Chile: causes, history and impacts. Revista Chilena de Historia Natural, 77, 465-483.

Fuentes, E.R., Otaiza, R.D., Alliende, M.C., Hoffmann, A.J. & Poiani, A. (1984) Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia, 62, 405-411.

Fuentes, E.R., Hoffmann, A.J., Poiani. A. & Alliende M.C. (1986) Vegetation change in large clearings: patterns in the Chilean matorral. Oecologia, 68, 358-366.

Ganade, G. & Brown, V.K. (2002) Succession in old pastures of central Amazonia: role of soil fertility and plant litter. Ecology, 83, 743-754.

Goldberg, D., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. Ecology, 80, 1118-1131.

Gómez-Aparicio, L., Gomez, J.M., Zamora, R. & Boettinger, J.L. (2005) Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. Journal of Vegetation Science, 16, 191-198.

Groves, R.H. & Di Castri, F. (1991) *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge, UK.

Hastwell, G. & Facelli, J.M. (2003) Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. Journal of Ecology, 91, 941-950.

Higgins, S.I. & Richardson, D.M. (1998) Pine invasions in the southern hemisphere: modeling interactions between organism, environment and disturbance. Plant Ecology, 135, 79-93.

Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. Ecology, 78, 1966-1975.

Holmgren, M., Segura, A.M. & Fuentes, E.R. (2000) Limiting mechanisms in the regeneration of the Chilean matorral. Plant Ecology, 147, 49-57.

Holzapfel, C. & Mahall, B.E. (1999) Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. Ecology, 80, 1747-1761.

Humara, J.M., Casares, A. & Majada J. (2002) Effect of seed size and growing media water availability on early seedling growth in *Eucalyptus globulus*. Forest Ecology and Management, 167, 1-11.

Kaufmann, M. (1977) Soil temperature and drought effects on growth of Monterey pine. Forest Science, 23, 317-325.

Keeley, J.E. & Zedler, P.H. (1998) Evolution of life histories in *Pinus. Ecology and Biogeography of* Pinus (ed D.M. Richardson), pp. 219- 250. Cambridge University Press. Cambridge.

Kitzberger, T., Steinaker, D.F. & Veblen, T.T. (2000) Effects of climatic variability on facilitation of tree establishment in northern Patagonia. Ecology, 81, 1914-1924.

Lenz, T. I. & Facelli, J.M. (2003) Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. Austral Ecology, 28, 480-490.

Levine, J. M., Adler, P. B. & Yelenik, S. G. (2004) A meta-analysis of biotic resistance to alien plant invasions. Ecology Letters, 7, 975-989.

Lindenmayer, D.B. & McCarthy M.A. (2001) The spatial distribution of non-native plant invaders in a pine-eucalypt landscape mosaic in south-eastern Australia. Biological Conservation, 102, 77-87.

Lonsdale, W. (1999) Global patterns of plant invasions and the concept of invasibility. Ecology, 80, 1522-1536.

López, M., Humara, J.M., Casares, A. & Majada, J. (2000) The effect of temperature and water stress on laboratory germination of *Eucalyptus globulus* Labill. seeds of different sizes. Annals of Forest Science, 57, 245-250.

Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. Journal of Ecology, 94, 7-16.

MacDougall, A.S., Boucher, J., Turkington, R. & Bradfield, G.E. (2006) Patterns of plant invasion along an environmental stress gradient. Journal of Vegetation Science, 17, 47-56.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant-plant interactions with abiotic stress predicatble? A meta-analysis of field results in arid environments. Journal of Ecology, 93, 748-757.

Miriti, M.N. (2006) Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology, 94, 973-979.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Huafbauer, R.A., Kironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloon, E.W., Torchin, M.E. & Vasquez, D.P. (2006) Biotic interactions and plant invasions. Ecology Letters, 9, 1-15.

Mooney, H.A. & Hobbs, H.A. (2000) *Invasive Species in a Changing World.* Island

Press, California.

Prider, J. N. & Facelli, J.M. (2004) Interactive effects of drought and shade on three arid

zone chenopod shrubs with contrasting distributions in relation to tree canopies.

Functional Ecology, 18, 67-76.

Richardson, D.M. (1998) Forestry trees as invasive aliens. Conservation Biology, 12,

18-26.

Richardson, D.M. & Brown, P.J. (1986) Invasion of mesic mountain Fynbos by *Pinus*

radiata. South African Journal of Botany, 52, 529-536.

Richardson, D.M. & Bond W.J. (1991) Determinants of plant distribution: evidence

from pine invasions. American Naturalist, 137, 639-668.

Richardson, D.M., Cowling, R.M. & Le Maitre, D.C. (1990) Assessing the risk of

invasive success in *Pinus* and *Banksia* in South African mountain fynbos. Journal

of Vegetation Science, 1, 629-642.

Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmánek, M. (2000)

Plant invasions - the role of mutualisms. Biological Review, 75, 65-93.

Rouget, M., Richardson, D.M., Milton, S. & Polakow, D. (2002) Predicting invasion

dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland

in South Africa. Plant Ecology, 152, 79-92.

Sax, D.F., Stachowicz, J.J. & Gaines, S.D. (2005) Species Invasions. Insights into

ecology, evolution and biogeography. Sinauer Associates, Inc. USA.

Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant

recruitment. American Journal of Botany, 82, 399-409.

Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological

invasions. Trends in Ecology and Evolution, 17, 170-176.

Siemann, E. & Rogers, W.E. (2003) Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. Journal of Ecology, 91, 923-931.

Stohlgren, T.J., Barnett, D., Flather, C., Kartesz, J. & Peterjohn, B. (2005) Plant species invasions along the latitudinal gradient in the United States. Ecology, 86, 2298-2309.

Von Holle, B. (2005) Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. Journal of Ecology, 93, 16-26.

Walcroft, A.S., Whitehead, D., Kelliher, F.M., Arneth, A. & Silvester, W.B. (2002) The effects of long-term, partial shading on growth and photosynthesis in *Pinus radiata* D. Don trees. Forest Ecology and Management, 163, 151-163.

Williams, M.C. & Wardle, G.M. (2005) The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue mountains, New South Wales, Australia. Biological Conservation, 125, 55-64.

Williamson, J. & Harrison, S. (2002) Biotic and abiotic limits to spread of alien revegetation species. Ecological Applications, 12, 40-51.

Table 1 Statistical results of the effect of canopy treatment and habitat on environmental variables (ANOVA). Categories of variables are Canopy treatment: Open, *Lithrea* and Artificial canopy; Habitat: Xeric and Mesic.

Variable	Patch			Habitat			Patch x Habitat		
	d.f.	F	*P*	d.f.	F	*P*	d.f.	F	*P*
Light at soil level	2,54	30.99	**<0.001**	1,54	3.39	0.071	2,54	0.98	0.381
Light at 30 cm level	2,54	93.49	**<0.001**	1,54	0.01	0.939	2,54	0.53	0.591
Soil water content	2,54	12.65	**<0.001**	1,54	73.73	**<0.001**	2,54	4.36	**0.018**
Temperature	2,18	57.49	**<0.001**	1,18	12.45	**0.002**	2,18	0.02	0.983
Herb cover	2,54	2.97	0.06	1,54	2.97	0.091	2,54	0.76	0.475

Table 2 Nutrient and soil pH values (mean ± 1 S.E.) per treatment (N = 3 for all treatments) (different letters indicate significant differences with $P < 0.05$ between patches and habitats, ANOVA).

Habitat	Canopy treatment	pH	N (ppm)	P (ppm)	K (ppm)
Mesic	Artificial	$6.13^a \pm 0.12$	$50.0^a \pm 11.5$	$45.7^{a.c} \pm 4.1$	$452.3^a \pm 80.8$
Mesic	Open	$6.33^a \pm 0.12$	$39.3^a \pm 11.6$	$59.0^a \pm 10.2$	$608.0^a \pm 153.4$
Mesic	Lithrea	$6.20^a \pm 0.21$	$26.0^a \pm 4.0$	$70.3^a \pm 2.7$	$587.3^a \pm 127.3$
Xeric	Artificial	$6.70^b \pm 0.15$	$27.7^a \pm 4.4$	$24.0^{b.c} \pm 7.2$	$280.0^a \pm 42.6$
Xeric	Open	$6.67^b \pm 0.32$	$20.3^a \pm 2.9$	$21.7^{b.c} \pm 4.8$	$259.3^a \pm 14.2$
Xeric	Lithrea	$6.73^b \pm 0.23$	$21.0^a \pm 1.5$	$15.3^b \pm 6.3$	$305.0^a \pm 21.4$

Table 3 Statistical results of germination probability (ANOVA). Categories of variables are Canopy: Open, Lithrea and Artificial; Habitat: Xeric and Mesic. Germination probability of *Pinus* was Arc-sen transformed.

Effect	*Eucalyptus*			*Pinus*		
	d.f.	F	P	d.f.	F	P
Canopy	2	11.21	< 0.0001	2	15.00	< 0.0001
Habitat	1	5.92	0.018	1	47.28	< 0.0001
Canopy x Habitat	2	3.66	0.032	2	3.07	0.054

Table 4 Statistical comparison between survival curves of experimental seedlings by Holm Sidak post-hoc tests. Comparison are shown between pairs of canopy treatments (L: *Lithrea*, O: Open, A: Artificial) per habitat (Xeric, Mesic) and between habitats per canopy treatment type. Significant differences are in bold ($P < P$critical).

Comparisons		*Pinus*			*Eucalyptus*		
		Chi^2	*P* value	*Pc*	Chi^2	*P* value	*Pc*
	L vs O	4.54	0.0331	0.0085	1.20	0.2720	0.0085
Xeric	O vs A	0.19	0.6650	0.0500	0.28	0.5920	0.0170
	A vs L	**7.52**	**0.0061**	**0.0064**	3.03	0.0819	0.0064
	L vs O	**19.11**	**<0.0001**	**0.0037**	**18.23**	**<0.0001**	**0.0034**
Mesic	O vs A	**7.93**	**0.0049**	**0.0057**	**8.29**	**0.0039**	**0.0047**
	A vs L	**8.72**	**0.0032**	**0.0051**	5.73	0.0167	0.0051
	L	1.88	0.1700	0.0102	012	0.7340	0.0500
Mesic vs Xeric	O	**10.96**	**0.0009**	**0.0043**	**9.69**	**0.0019**	**0.0039**
	A	0.41	0.5240	0.0253	0.28	0.5950	0.0253

Table 5 Results from mantel test for spatial autocorrelation for germination of each species within each canopy (Open sites, Artificial canopies, *Lithrea* patches) and habitat (Mesic and Xeric) treatment. Level of autocorrelation is indicated by the coefficient of correlation (R).

Species	Habitat	Canopy	R (Mantel)	*P* value
Pinus	Mesic	Open	-0.092	0.541
		Artificial	-0.223	0.142
		Lithrea	0.060	0.711
		Total	-0.201	0.161
	Xeric	Open	-0.880	0.625
		Artificial	-0.115	0.552
		Lithrea	-0.024	0.911
		Total	-0.079	0.667
Eucalyptus	Mesic	Open	-0.289	0.054
		Artificial	-0.173	0.250
		Lithrea	-0.132	0.393
		Total	-0.151	0.317
	Xeric	Open	0.181	0.223
		Artificial	-0.152	0.281
		Lithrea	-0.210	0.153
		Total	-0.093	0.596

Table 6 Results from mantel test for spatial autocorrelation for seedling survival of each species within each canopy (Open sites, Artificial canopies, *Lithrea* patches) and habitat (Mesic and Xeric) treatment. Level of autocorrelation is indicated by the coefficient of correlation (R).

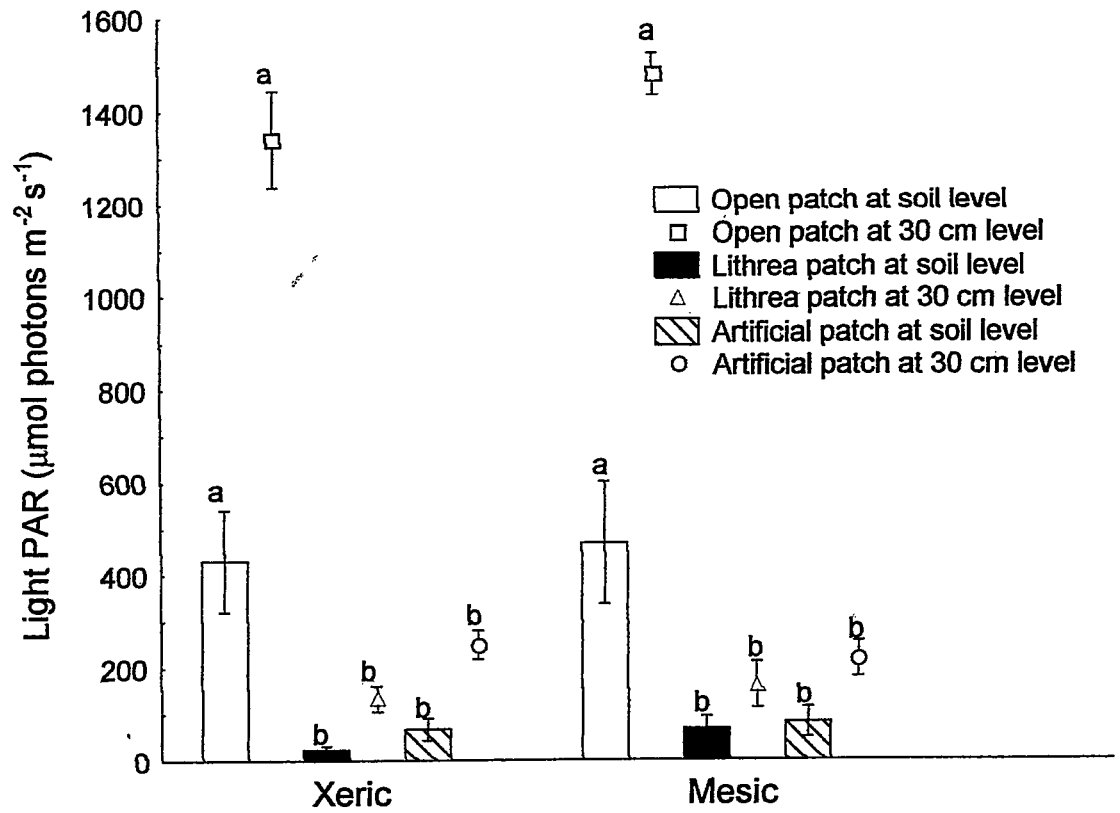| Species	Habitat	Canopy	R (Mantel)	P value
Pinus	Mesic	Open	-0.118	0.549
		Artificial	-0.282	0.061
		Lithrea	0.189	0.219
		Total	-0.139	0.387
	Xeric	Open	-0.218	0.154
		Artificial	-0.088	0.549
		Lithrea	-0.148	0.291
		Total	-0.113	0.578
Eucalyptus	Mesic	Open	0.076	0.701
		Artificial	-0.856	0.645
		Lithrea	-0.041	0.891
		Total	-0.078	0.669
	Xeric	Open	-0.171	0.253
		Artificial	-0.205	0.158
		Lithrea	-0.223	0.143
		Total	-0.152	0.315

Fig. 1 Midday light levels at 30 cm and at soil level in each type of experimental patch (Open, *Lithrea*, Artificial) (mean ± 1 SE). *N* for each bar and symbol = 10. Measurements were made in October, 2004. Different letters indicate significant statistical differences (*P*< 0.05) within each habitat (Mesic and Xeric) and within each height level of measure. There were no significant differences between habitats (ANOVA, HSD Tukey post-hoc tests) for any type of patch or height of measure.
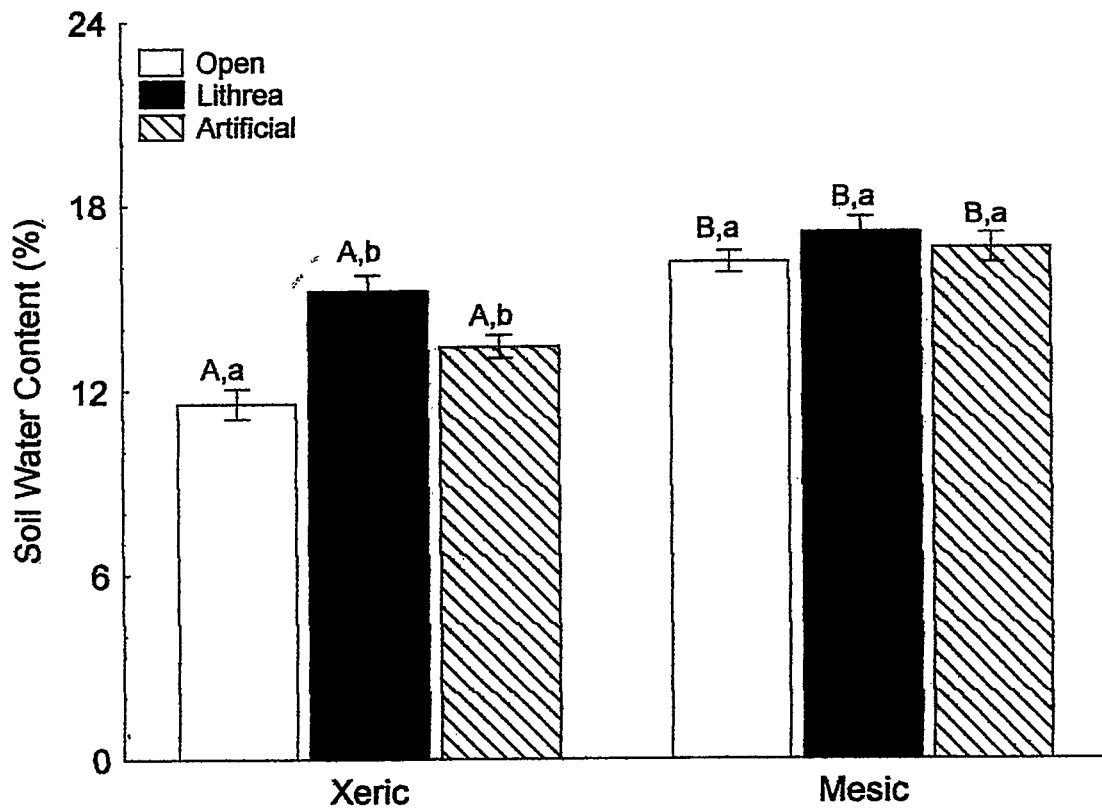
Fig. 2 Soil water content (SWC) (percentage of water weight in a volume of soil) in the top 10 cm in each type of canopy treatment (Open, *Lithrea*, Artificial) per habitat (Mesic and Xeric) (mean ± 1 SE). N for each bar = 10. Measurements correspond to the average of four records, each taken in a different season between June, 2004 and June, 2005. Different uppercase letters indicate significant statistical differences ($P < 0.05$) between habitats for a single canopy treatment and different lowercase letters indicate significant statistical differences ($P < 0.05$) among canopy treatments for a single habitat (ANOVA, HSD Tukey post-hoc tests).
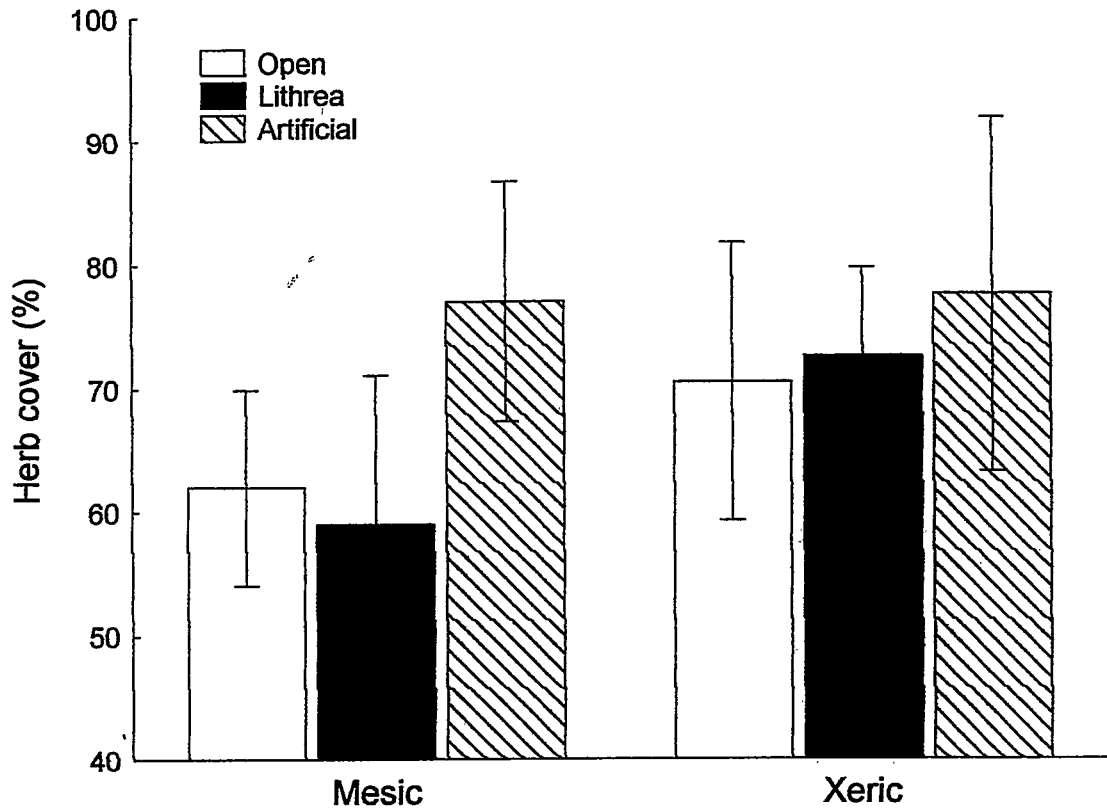
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Fig. 3 Herbaceous cover (evaluated by the intercept point method) under each canopy treatment (Open, *Lithrea*, Artificial) in two contrasting habitats (Mesic and xeric) (mean ± 2 SE). *N* for each bar = 10. Measurements made in spring, 2004 during the potential maximum herbaceous cover in this region. There were no statistically significant differences ($P > 0.05$) among canopy treatments within or between habitats (ANOVA, HSD Tukey post-hoc tests).
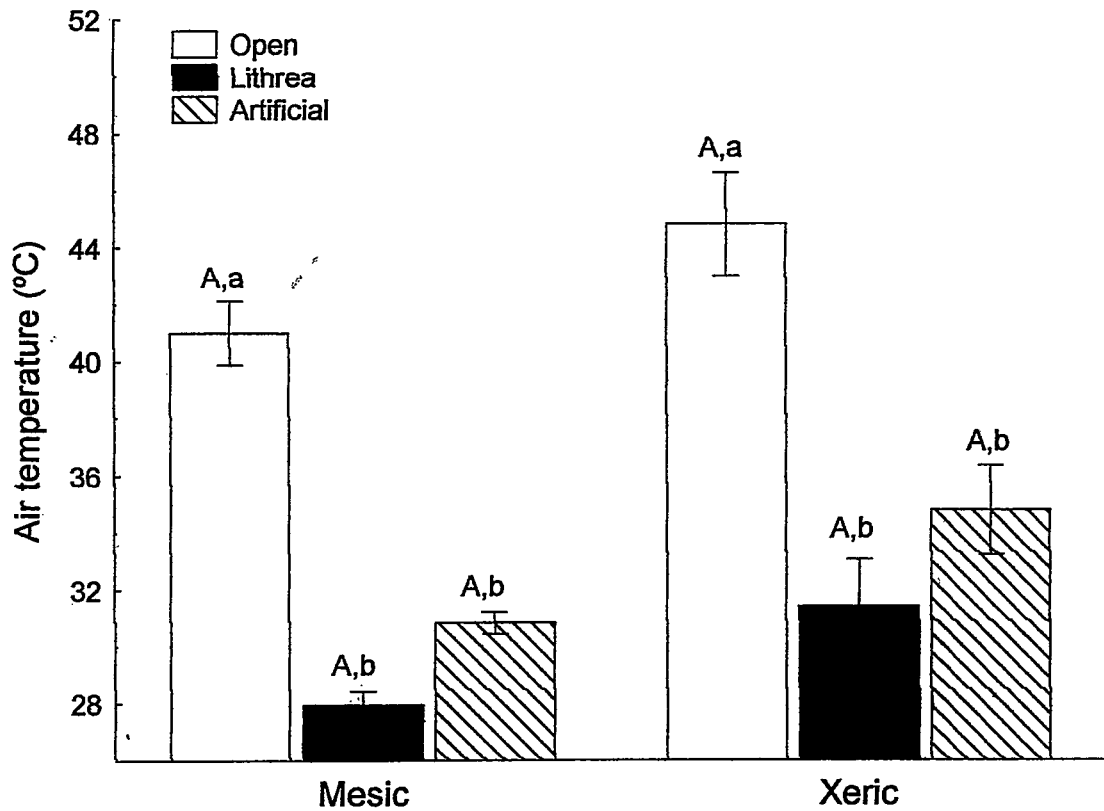
Fig. 4 Midday air temperature (°C) at a height of 1 m in each canopy treatment (Open, *Lithrea*, Artificial) and in two contrasting habitats (Mesic and Xeric) (mean ± 1 SE). N for each bar = 4. Measurements were taken in January (summer), 2005. Different uppercase letters indicate significant statistical differences ($P<0.05$) between habitats for a single canopy treatment and different lowercase letters indicate significant statistical differences among patches for a single habitat (ANOVA, HSD Tukey post-hoc tests).

Fig. 5 Germination probability of *Pinus* and *Eucalyptus* in each type of canpy treatment (Open, *Lithrea*, Artificial) and habitat (Mesic and Xeric) (mean ± 1 SE). *N* for each bar = 10. Measurements were made four months after seeds were buried and two months after seeds began to germinate. Different uppercase letters indicate significant statistical differences ($P < 0.05$) between habitats for a single canopy treatment and different lowercase letters indicate significant statistical differences among patches for a single habitat (ANOVA, HSD Tukey post-hoc tests).
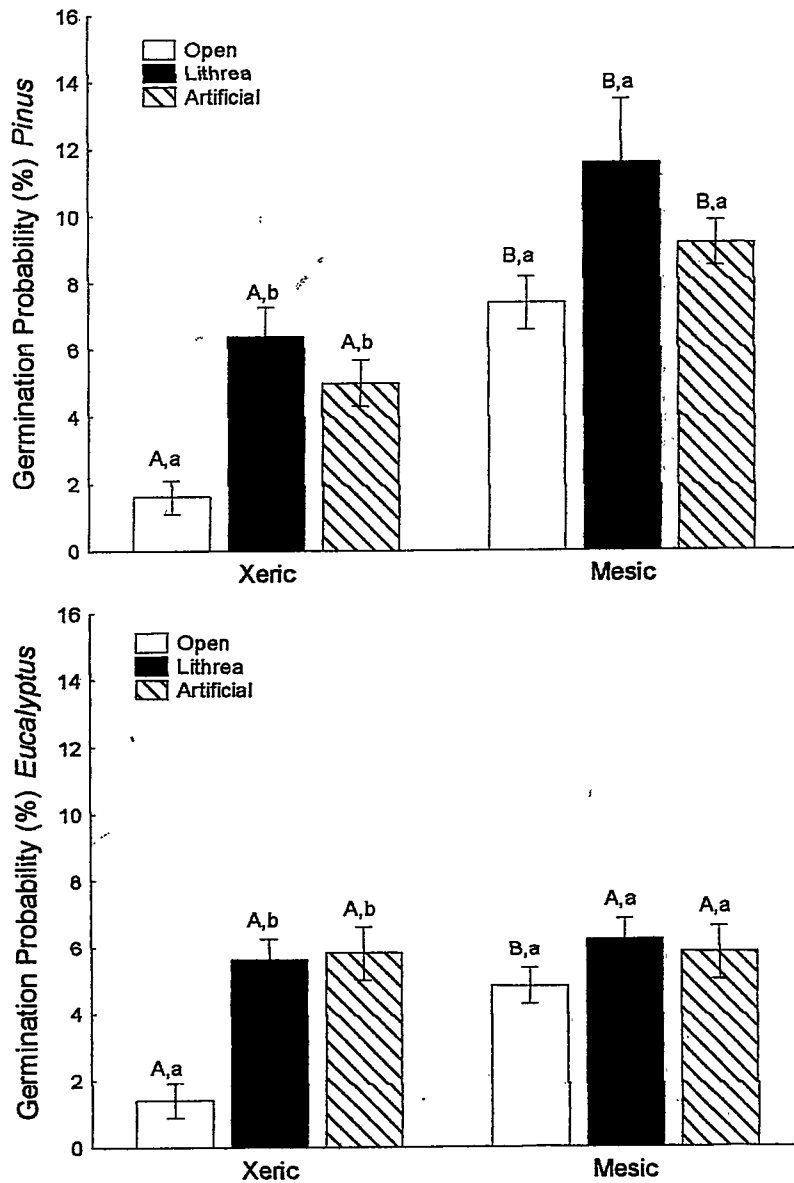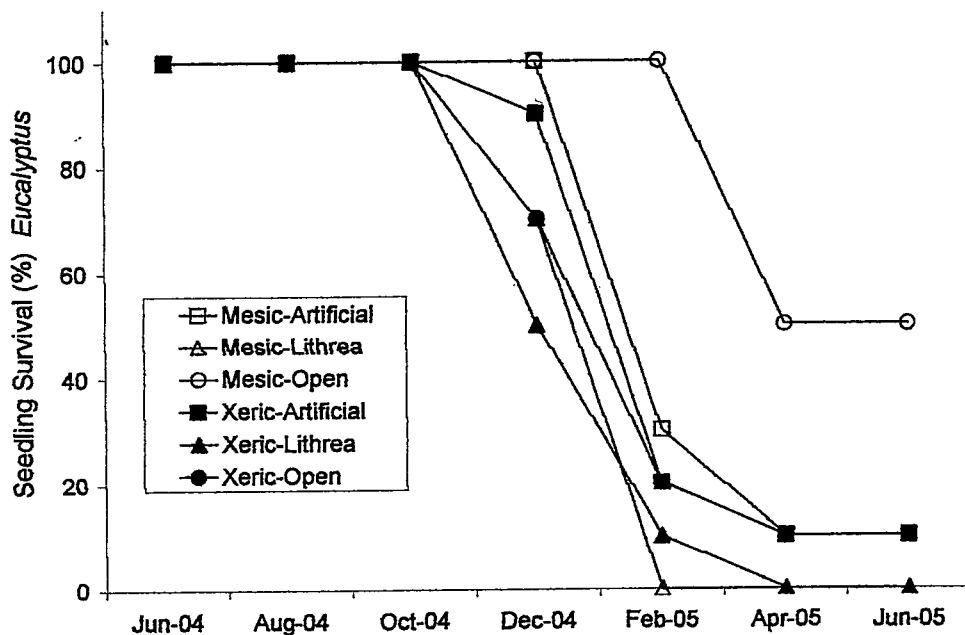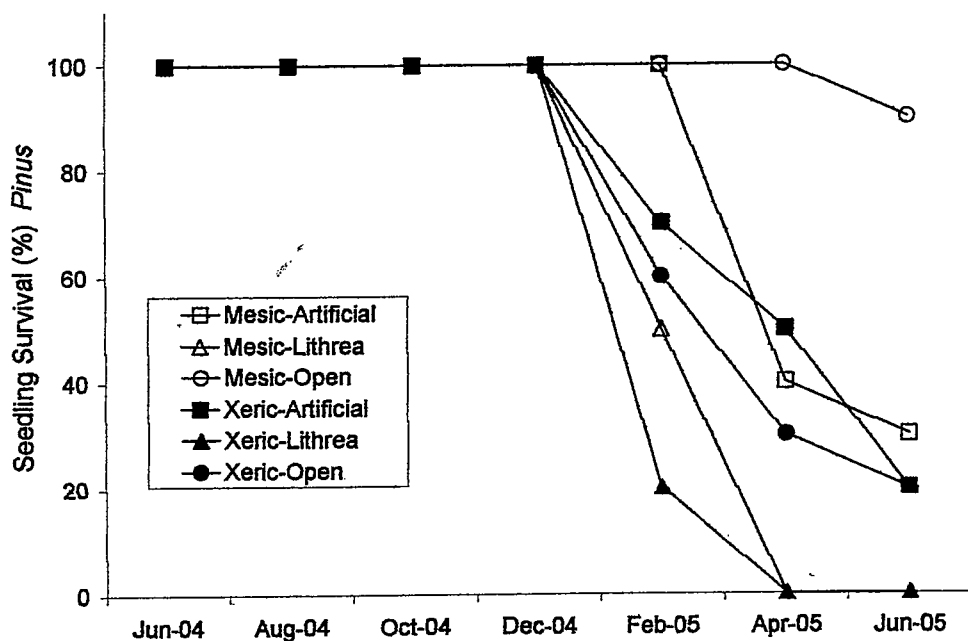
Fig. 6 Survival curves of experimental seedlings of *Pinus* and *Eucalyptus* in each type of experimental canopy treatment (Open, *Lithrea*, Artificial) and habitat (Mesic and Xeric). Values correspond to percentage of surviving seedlings per treatment ($N = 10$ for each curve).

CAPÍTULO III

The effect of herbivory on seedling survival of the invasive exotic trees *Pinus radiata* and *Eucalyptus globulus* in a Mediterranean ecosystem of Central Chile

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Abstract

Herbivory may become an important factor controlling plant invasion. In this paper we evaluated this hypothesis in a Mediterranean-type ecosystem of central Chile, by examining the effect of vertebrate herbivores on seedling survival of two global commercially planted and invasive tree species, *Pinus radiata* and *Eucalyptus globulus*. An important role of herbivory on seedling survival of these two species in their introduced ranges has previously been documented. However, this has only been evaluated in forestry plantations in which habitat and vegetation conditions differ from wild habitat where invasion occurs. We established excluded and non-excluded seedlings under different habitat conditions (a mesic polar-facing slope and a xeric equatorial-facing slope) and vegetation physiognomies (open sites and tree patches). We found that regardless of vegetation and habitat condition, herbivory, in our case due mainly to exotic vertebrates, significantly affected seedling survival of both species. Furthermore, the effect of herbivory on *P. radiata* was significant in any vegetation and habitat condition, but only in the open sites of the mesic habitat for *E. globulus*. These results suggest that, as observed in forestry plantations, vertebrate herbivory may diminish important seedling establishment of these two exotic trees and therefore play an important role in the resistance against them, and possibly other exotic tree species, invasion. However, the relevance of herbivores may vary depending on the vegetation and habitat conditions in some species, as is the case for *Eucalyptus globulus*.

Key-words: Alien plants, alien herbivores, biological invasions, biotic resistance.

1. Introduction

Invasion of alien species is considered an important ecological phenomenon and conservation issue (Drake et al., 1989; Mooney and Hobbs, 2000). Many factors and hypotheses have been proposed in order to explain why exotic species can become successful invaders (Shea and Chesson, 2002; Bruno et al., 2005). Herbivory is a major factor commonly used to explain the success or failure of the invasion process of exotic species (Maron and Vilà, 2001; Keane and Crawley, 2002; Levine et al., 2004; Parker et al., 2006). Invasion of a plant species may be hindered by herbivory due to direct consumption, or facilitated by it, if resident herbivores preferentially consume competitive resident plants (Maron and Vila, 2001; Colautti et al., 2004; Joshi and Vrieling, 2005; Parker et al., 2006).

Forestry plantations of exotic trees are one of the main sources of invasive species (Richardson, 1998). In Chile the most common tree species used in the forestry industry are *Pinus radiata* D. Don (Pinaceae), originally from Monterey (USA), and *Eucalyptus globulus* Labill. (Myrtaceae), originally from Tasmania and Victoria (Australia). The extent of these plantations has grown rapidly during the last decades, covering more than two million hectares, especially in the Mediterranean region of Chile. Both species are also widely planted throughout the world and have been recognised as important invaders in different countries where they have been planted (Richardson and Brown, 1986; Richardson and Bond, 1991; Boyd, 1996; Rouget et al., 2002; Williams and Wardle, 2005). In Chile, invasion by these species is still incipient but it is already beginning to occur in several localities of the country (Bustamante et al.,

2003; Becerra, 2006).

A number of environmental factors such as climate, and vegetation cover and type, are known to be related to invasion of these species (e.g. Richardson and Brown, 1986; Boyd, 1996; Higgins and Richardson, 1998; Rouget et al., 2002; Williams & Wardle 2005; Becerra, 2006). In contrast, the role of herbivory on their invasive capabilities has as yet not been assessed. Currently, evidence exists for an important role of seedling predation on the survival of these trees within their exotic ranges, but only in the context of forestry plantations (Ferriere et al., 1983; Muñoz and Murúa, 1990; Richardson and Bond, 1991; O'Reilly and McArthur, 2000; McArthur and Appleton, 2004). This is important because inside forestry plantations, natural vegetation has generally been logged or eliminated and habitat conditions selected or altered to improve productivity, hence, environmental conditions in plantations are very different to environmental conditions where invasion occurs. Furthermore, seedling abundance and distribution of these exotic trees under invasion conditions are generally low and clumped (e.g. Williams and Wardle, 2007). In contrast, inside forestry plantations there are generally a high density of seedlings that are regularly spaced. Therefore, the behaviour of herbivores and hence the extent of herbivory on exotic species may differ between natural habitats and plantations.

In central Chile, exotic vertebrates such as rabbits (*Oryctolagus cuniculus*), cows (*Bos taurus*), horses (*Equus caballus*) and goats (*Capra hircus*), are the main potential seedling vertebrate predators of exotic and native woody seedlings (Fuentes et al., 1983; Jaksic, 1998; Henríquez and Simonetti, 2001; Vázquez, 2002). Nonetheless, some native rodents such as *Octodon degus*, *Octodon bridgesii* and *Abrocoma bennetti* have also

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been documented to predate seedlings of tree species (Fuentes et al., 1983; Muñoz and Murúa, 1990). Of these predators, at least rabbits are known to predate on seedlings of both *P. radiata* and *E. globulus* in forestry plantations in Chile (Ferriere et al., 1983). In this paper we experimentally assessed the role of vertebrate herbivory on seedling survival of *P. radiata* and *E. globulus* under natural vegetation and habitat conditions in a Mediterranean ecosystem of central Chile. We predict that high predation by vertebrate herbivores in this environment may significantly diminish seedling survival of these exotic trees and therefore hinder their invasion.

2. Methods

2.1. The study area

The study was carried out in the San Ramón watershed, located at the East border of the city of Santiago (33°30' S, 70°30' W), central Chile. The climate is semiarid and Mediterranean-like, with 5-6 dry months and precipitation concentrated during winter, reaching an annual average of 330 mm. The annual mean temperature is 15°C (Di Castri and Hajek, 1976). In the watershed two main habitat types occur: a north-facing slope and a south-facing slope, which generally differ significantly in moisture conditions in the Mediterranean region of Chile (Armesto and Martínez, 1978). In all these habitats vegetation is composed of tree, shrub and herbaceous patches. Tree patches are dominated by the native tree species *Lithrea caustica*, shrub patches by native species such as *Colliguaya odorifera* and *Retanilla trinervia*, and herbaceous patches are

composed of native species including *Pasithea coerulea* and *Bromus berteroanus*, as well as exotic herb species including *Fumaria* spp., *Centaurea melitensis* and *Conium maculatum*.

The watershed has been protected (from logging, cattle and fires) for the last 10 years by the national forest service. Large exotic herbivores (cows and goats) have been completely excluded from the study site by forest service management, although on rare occasions, horses are freed into the watershed. Evidence of their presence in the study area is presented in Table 1. On the other hand, the presence of other potential herbivores, such as the diurnal caviomorph *Octodon degus*, can be established either directly by visual observation, or indirectly by burrows, faeces and bare zones produced by their activities (Fuentes et al. 1983). In order to evaluate the presence of *O. degus* we established 20 transects 200 x 2 m each (10 in a north-facing and 10 in a south-facing slope) to record some of these indicators. We observed no evidence of any of these indicators of *O. degus* in the study site, hence we are confident that they are not present in the study area or at least their abundance is very low. In addition, this rodent has been documented to be a less important seedling consumer of native trees than rabbits in central Chile (Fuentes et al. 1983). Other species of the *Octodon* genus are not present in this locality (Saavedra 2003). Finally, another potential seedling predator, the rodent *Abrocoma bennetti*, seems to be scarce in central Chile (Iriarte et al. 1989), especially in the pre-Andean zone of Santiago and its influence (if any) as a seedling predator may be negligible (Fuentes et al. 1983). Thus, the main herbivore tree seedling predator in the study area is the European rabbit (*Oryctolagus cuniculus*), although horses may also play a minor role.

2.2. Experimental design

To evaluate seedling predation and the effect of this herbivory on seedling survival of *P. radiata* and *E. globulus*, we established sampling stations in the field containing protected (excluded from herbivores) and unprotected (non-excluded from herbivores) seedlings of these trees. Due to natural environmental conditions of vegetation and habitat in the study area include a mosaic of woody and herbaceous patches and at least two main physical habitats (slopes), we distributed these stations in herbaceous (open patches) and tree patches (dominated mainly by the native tree *Lithrea caustica*), in a xeric (north-facing slope) and mesic (south-facing slope) habitat. Exclusions consisted of 1.0 x 1.5 m plots, fenced on the sides and the top by a wire mesh to exclude mammals and birds. In each station, excluded and non-excluded seedlings were located adjacently. We planted three seedlings per species (each separated by 20 cm from each other) outside the exclusions and three seedlings per species inside them. We used clumps of three seedlings to partially simulate the clumping of seedlings during the invasion process, as has been documented for *P. radiata* (Williams and Wardle, 2007). However, in order to avoid pseudoreplication we selected only one excluded and one non-excluded seedling from each station to perform statistical analyses. In total we used 10 stations in open sites and 10 in tree patches (*Lithrea* patches) in each habitat. Thus, we established 20 stations in each habitat and 40 in total. Within each habitat, the patches that were selected in which stations were to be located were distributed at least 10 m apart and separated by a different vegetation patch type. This minimized spatial dependence among stations. Preliminary observations confirmed the efficacy of fences as we observed no excluded seedlings with signs of browsing.

Planting was carried out during winter (20-25 June, 2004). Seedling height at time of planting was 19.7 cm ± 0.15 and 22.9 cm ± 0.19 (mean ± 1 SE) for *P. radiata* and *E. globulus* respectively. Seedlings were obtained from the greenhouse of the Faculty of Forest Sciences, University of Chile. These seedlings are produced from seeds collected from plantations located in the Mediterranean region of Chile.

2.3. Herbivory assessments and analyses

Seedlings were monitored every two months, from June 30, 2004 until June 30, 2005. Thus, we obtained six records for each seedling across this period. We performed two analyses: i) seedling predation and ii) effect of herbivory on seedling survival. Seedling predation assessment considered only non-excluded seedlings and measured the proportion of predated seedlings at the end of the experiment (one year long), from 10 seedlings of each species randomly selected for this analyses per combination of vegetation patch and habitat. Predation was recognized by the absence of the original seedling. We observed no browsed living seedlings, thus, all browsed seedlings were completely killed. In order to evaluate differences between vegetation patch-types and habitats in seedling predation we performed logistic regressions (GLZ procedure, logit function) considering each one of 10 selected seedlings per treatment as a replicate and assigning 0 if the seedling was alive and 1 if it was browsed at the end of the experiment.

To evaluate the effect of herbivory on seedling survival we compared excluded and non-excluded seedlings per species. Here we performed two evaluations: one general per species (pooling data of different vegetation and habitat condition) in which

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we compared all excluded seedlings (40) with all non-excluded seedlings (40). The second analysis was also performed separately for each species, comparing excluded with non-excluded seedlings per vegetation patch-type and habitat, and using 10 seedlings of each species as replicates in each comparison. All comparisons of seedling survival were performed by Log-rank survival curve tests and Holm-Sidak post-hoc tests.

To evaluate the spatial dependence among stations we performed a spatial autocorrelation analysis (Mantel test) for the proportion of non-excluded predated seedlings at the end of the experiment, quantified by the quotient between the number of browsed seedlings and the three original seedlings planted per species in each station. The analysis was performed for each vegetation patch-type per habitat in order to detect spatial autocorrelation for a particular vegetation patch-type in each habitat (ten replicates per combination of species, vegetation patch-type and habitat), and general per habitat in order to detect spatial autocorrelation among stations within each habitat (no differentiating vegetation patch-types) (20 replicates per combination of species and habitat).

3. Results

3.1. Seedling predation

By the end of the experiment, predation reached 92.5 % and 57.5 % for *P. radiata* and *E. globulus* seedlings respectively. Considering different vegetation patches and habitats, predation on *P. radiata* was 100 % in both vegetation patch-types in the

mesic habitat and 90% and 80% in open sites and *Lithrea* patches respectively in the xeric habitat (Fig. 1). Predation on *E. globulus* showed a different pattern, reaching 90% in both vegetation patch-types of the mesic habitat and only 40 % and 10 % in open and *Lithrea* patches respectively in the xeric habitat (Fig. 1). In *P. radiata* as well as in *E. globulus* we observed significant differences between habitats in seedling predation (Table 2). Overall, predation on both species was significantly higher in the mesic than in the xeric habitat (Fig. 1). In turn, we observed no significant difference in seedling predation on both species between vegetation patch-types (Table 2). Also, no significant statistical interaction between habitat and vegetation patch-type was detected in either species (Table 2).

We observed no spatial autocorrelation for seedling predation either in *Pinus* or *Eucalyptus* under any vegetation and habitat condition (Table 4). This indicates that stations used to evaluate seedling predation were independent among them.

3.2. Effect of herbivory on seedling survival

Considering the two pooled habitats and vegetation patch-types, survival of excluded seedlings was significantly higher than non-excluded seedlings in both *E. globulus* (Log-rank test: Chi ^{2} = 19.73; d.f. = 1; $P < 0.001$) and *P. radiata* (Log-rank test: Chi ^{2} = 58.31; d.f. = 1; $P < 0.001$), (Fig. 2). In *E. globulus*, excluded seedlings had a survival probability of 15 % while only 2.5 % of non-excluded seedlings were present at the end of the experiment. In *P. radiata*, survival of excluded seedlings was 27.5 % while no non-excluded seedling survived by the end of the experiment (Fig. 2).

Regarding the comparison between excluded and non-excluded seedlings for

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each species, per habitat and vegetation patch-type separately, we observed that in *P. radiata* the effect of herbivory was significant and negative in all types of habitats and vegetation patch-types (Table 3, Fig. 3). In *E. globulus*, herbivory significantly reduced seedling survival only in open sites of the mesic habitat (Table 3, Fig. 3).

4. Discussion

We observed significant negative effects of vertebrate herbivory on seedling survival of both *P. radiata* and *E. globulus*. This effect was stronger on *P. radiata* than on *E. globulus* as differences between survival curves of excluded and non-excluded seedlings during all monitoring time were greater in *P. radiata* than in *E. globulus*. This result was most likely due to observed higher predation levels on *P. radiata* than on *E. globulus*. A high importance of vertebrate herbivory on seedling establishment of these species has already been documented in forestry plantations (Ferriere et al., 1983; Muñoz and Murúa, 1990; Richardson and Bond, 1991; O'Reilly and McArthur, 2000; McArthur and Appleton, 2004). However, our results suggest that under natural conditions of vegetation (higher cover of woody species than in plantations) and different habitats (mesic and xeric), vertebrate herbivores may strongly reduce the chances of seedling establishment and thus play an important role in the community resistance to invasion of these exotic species.

In addition to these general findings, we also documented some species-specific differences with respect to the role of herbivory on seedling survival. For example, while

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the effect of herbivory on seedling survival of *P. radiata* was significant throughout the different vegetation and habitat conditions, the role of herbivory on *E. globulus* survival differed depending on the vegetation patch-type and habitat. Herbivory on *E. globulus* was significant only in open sites of the mesic habitat. The high importance of herbivory on *P. radiata* across both vegetation and habitat types corresponds to the high seedling predation on this species under any environmental condition. Likewise, the high importance of herbivory on *E. globulus* in open sites of the mesic habitat is consistent to the high seedling predation under these conditions. Also, the low importance of herbivory on *E. globulus* in both vegetation types of the xeric habitat is consistent to the low seedling predation on this species in this habitat. In contrast, in spite of the high seedling predation on *E. globulus* in *Lithrea* patches of the mesic habitat, herbivory did not have a significant effect on seedling survival. Under those vegetation and habitat conditions, mortality by desiccation (for example due to lower light availability (Becerra and Bustamante unpublished data)) overrides herbivory effects. This pattern has been observed in many other studies which have documented an important role of habitat, plant productivity and vegetation physiognomy in modulating the effect of herbivory on performance of native and exotic plants (Fuentes et al., 1986; Hobbs, 2001; Fowler, 2002; DeWalt et al., 2004; Kuijper et al., 2004).

Our observations indicate that the main seedling predator in our study site is the European rabbit. The higher seedling predation level in the mesic habitat in both species contrasts with a previous study which documented higher browsing on native trees by this herbivore in xeric habitats (Fuentes et al., 1983). We can not infer differences in rabbit abundance between habitats or vegetation patch-types based on faeces frequency

due to possible differences in faeces decay rates between them (Simonetti, 1989). Thus, causes for different predation may be related to higher rabbit abundance in the mesic habitat, but also to a lower availability of some of their most important food sources (some herbs) in this habitat, which might have forced rabbits to prefer these exotic species there. Other studies have found that rabbits have preferences for certain plants (Crawley, 1990).

Despite the great number of studies assessing the effect of herbivory on plant invasion (D'Antonio 1993; Holmgren et al. 2000; Maron and Vilà 2001; Bellingham and Coomes 2003; Levine et al. 2004; Parker et al. 2006), the role of exotic vertebrate herbivores in the invasion of exotic plant species has been poorly studied (Parker et al. 2006). The effect of exotic herbivores on exotic plants has been observed to be mainly positive, determined indirectly by higher predation on native plants relative to exotic plants, thus reducing competition on exotics (Parker et al. 2006). The main herbivores in our study site (the European rabbit and secondarily horses) were exotics, although the possibility of minor predation by native vertebrates (such as *Abrocoma bennetti* and much less probably *Octodon degus*) can not be discarded. In contrast to most previous studies, we found that the effect of herbivory, when significant, was negative despite the presence of herbs (natives and exotics) which also are consumed by rabbits, horses and native rodents. Thus, there was no important indirect positive effect of exotic herbivores on *P. radiata* and *E. globulus* through their predation upon herbs. This result contrasts to findings in central Chile, in which the same herbivores were found to indirectly facilitate exotic herb survival by preferentially predating native herbs (Holmgren et al. 2000, Holmgren 2002). However, our results are consistent with other studies where negative

effects of exotic herbivores on exotic plants were more important than any possible positive indirect effect (e.g. Chaneton et al. 2002; Fowler 2002; Valone et al. 2002; DeWalt et al. 2004). Thus, our results contrast to the meltdown hypothesis that exotic species facilitate invasion of other exotic species (Simberloff and Von Holle 1999).

The importance of native herbivores as resistance agents against plant invasion has recently been highlighted (Maron and Vilà 2001; Levine et al. 2004; Parker et al. 2006). Likewise, the role of exotic herbivores on native plants is also a relevant ecological and conservation issue (Jaksic and Fuentes 1980; Relva and Veblen 1998; Cabin et al. 2000; Holmgren et al. 2000; Vásquez 2002; Parker et al. 2006). In the latter case, a logical conservation action would be to eradicate exotic herbivores if these negatively affect native plant species. However, if exotic herbivores also have a negative effect on exotic plants, their exclusion may have undesirable consequences, for example, an increase of plant invasion (e.g. Cabin et al. 2000). Therefore, control strategies of exotic species must be performed with caution, for example controlling exotic plants as well as exotic herbivores.

Overall, our results suggest that, as observed in forestry plantations, vertebrate herbivory may diminish seedling establishment of these two exotic trees and may therefore play an important role in the resistance against invasion in wild habitats. However, this importance may depend on the vegetation and habitat conditions in some species such as in *Eucalyptus globulus*.

Acknowledgements

References

Armesto, J.J., Martínez, J., 1978. Relations between vegetation structure and slope aspect in the mediterranean region of Chile. Journal of Ecology 66, 881-889.

Becerra, P.I., 2006. Invasión de árboles alóctonos en una cuenca pre-andina de Chile central. Gayana Botanica, in press.

Bellingham, P.J., Coomes, D.A., 2003. Grazing and community structure as determinants of invasion success by scoth broom in a New Zealand montane shrubland. Diversity and Distributions 9, 19-28.

Boyd, D., 1996. *Eucalyptus globulus*: Bluegum Eucalyptus, in: Randall, J. M., Marinelli, J. (Eds), Invasive plants: weeds of the global garden, Science Press, New York, pp. 32.

Bruno, J.F., Fridley, J.D., Bromberg, K.D., Bertness, M.D., 2005. Insights into biotic interactions from studies of species invasions, in: Sax, D.F., Stachowicz, J.J., Gaines, S.D. (Eds.), Species Invasions: insights into ecology, evolution and biogeography, Sinauer Associates, Inc., USA., pp. 13 - 40

Bustamante, R. O., Serey, I. A., Pickett., S.T.A., 2003. Forest fragmentation, plant regeneration and invasion processes across edges in central Chile, in: Bradshaw, G.A., Marquet, P.A. (Eds.), How Landscape Change. Springer-Verlag, Berlin, pp. 145-158

Cabin, R.J., Weller, S.G., Lorence, D.H., Flynn, T.W., Sakai, A.K., Sandquist, D. Hadway, L.J., 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. Conservation Biology 14, 439-453.

Chaneton, E.J., Perelman, S.B., Omacini, M., León, R., 2002. Grazing, environmental heterogeneity and alien plant invasions in temperate Pampa grasslands. Biological Invasions 4, 7-24.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac., J., 2004. Is invasion success explained by the enemy release hypothesis?. Ecology Letters 7, 721-733.

Crawley, M.J., 1990. Rabbit grazing, plant competition, and seedling recruitment in acid grassland. Journal of Applied Ecology 27, 803-820.

D'Antonio, C.M., 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology 74, 83-95.

DeWalt, S.J., Denslow, J.S., Ickes, K., 2004. Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. Ecology 85, 471-483.

Di Castri, F., Hajek, E., 1976. Bioclimatología de Chile. Universidad Católica de Chile, Chile.

Drake, J., Mooney, H.A., Di Castri, F., Groves, R., Kruger, F., Rejmanek, M., Williamson, M., 1989. Biological Invasions: a global perspective. John Wiley, Chichester, UK.

Ferriere, G., Cerda, J., Roach, R., 1983. El conejo silvestre en Chile. Boletín Técnico N°8, CONAF, Santiago, Chile.

Fowler, N.L., 2002. The joint effects of grazing, competition and topographic position of six savanna grasses. Ecology 73, 2477-2488.

Fuentes, E.R., Jaksic, F.M., Simonetti, J.A., 1983. European rabbits versus native rodents in Central Chile: effects on shrub seedlings. Oecologia 58, 411-414.

Fuentes, E.R., Hoffmann, A.J., Poiani, A., Alliende, M.C., 1986. Vegetation change in large clearings: patterns in the Chilean matorral. Oecologia 68, 358-366.

Henríquez, C.A., Simonetti, J.A., 2001. The effect of introduced herbívores upon an endangered tree (*Beilschmiedia miersii*, Lauraceae). Biological Conservation 98, 69-76.

Higgins, S. I., Richardson, D. M., 1998. Pine invasions in the southern hemisphere: modeling interactions between organism, environment and disturbance. Plant Ecology 135, 79-93.

Hobbs, R., 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in Southwestern Australia. Conservation Biology 15, 1522-1528.

Holmgren, M., 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternatives states. Biological Invasions 4, 25-33.

Holmgren, M., Avilés, R., Sierralta, L., Segura, A.M., Fuentes, E.R., 2000. Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients and fire. Journal of Arid Environments 44, 197-211.

Iriarte, J.A., Contreras, L.C., Jaksic, F.M., 1989. A long-term study of a small-mammal assemblage in the central Chilean matorral. Journal of Mammalogy 70, 79-87.

Jaksic, F.M., 1998. Vertebrate invaders and their ecological impacts in Chile. Biodiversity and Conservation 7, 1427-1445.

Jaksic, F.M., Fuentes, E.R., 1980. Why are native herbs in the Chilean matorral more abundant beneath bushes: microclimate or grazing?. Journal of Ecology 68, 665-669.

Joshi, J., Vrieling, K., 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters 8, 704-714.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17, 164-169.

Kuijper, D.P.J., Nijhoff, D.J., Bakker, J.P., 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. Oecologia 141, 452-459.

Levine, J.M., Adler, P.B., Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7, 975-989.

Maron, J.L., Vilà, M., 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. Oikos 95, 361-373.

McArthur, C., Appleton, R., 2004. Effect of seedlings characteristics at planting on browsing of *Eucalyptus globulus* by rabbits. Australian Forestry 67, 25-39.

Mooney, H.A., Hobbs, H.A., 2000. *Invasive Species in a Changing World*. Island Press, California.

Muñoz, A., Murúa, R., 1990. Control of small mammals in a pine plantation (central Chile) by modification of the habitat of predators (Tyto alba, Strigiforme and Pseudolopex sp., Canidae). Acta Oecologica 11, 251-261.

O'Reilly, J., McArthur, C., 2000. Damage to and intake of plantation seedlings by captive European rabbits (*Oryctolagus cuniculus*). Australian Forestry 63, 1-6.

Parker, J.D., Burkepile, D.E., Hay, M.E., 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 311, 1459-1461.

Relva, M.A., Veblen, T.T., 1998. Impacts of introduced large herbivores on *Austrocedrus chilensis* forests in northern Patagonia, Argentina. Forest Ecology and Management 108, 27-40.

Richardson, D.M., 1998. Forestry trees as invasive aliens. Conservation Biology 12, 18-26.

Richardson, D.M., Brown, P.J., 1986. Invasion of mesic mountain Fynbos by *Pinus radiata*. South African Journal of Botany 52, 529-536.

Richardson, D.M., Bond, W.J., 1991. Determinants of plant distribution: evidence from pine invasions. American Naturalist 137, 639-668.

Rouget, M., Richardson, D.M., Milton, S., Polakow, D., 2002. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecology 152, 79-92.

Saavedra, B., 2003. Disminución en tamaño poblacional y asimetría fluctuante en *Octodon bridgesi* (Rodentia), taxón especialista de hábitat. Thesis, Facultad de

Ciencias, Universidad de Chile.

Shea, K., Chesson, P., 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17, 170-176.

Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown?. Biological Invasions 1, 21-32.

Simonetti, J.A., Fuentes, E.R., 1982. Microsite use by European rabbits (*Oryctolagus cuniculus*) in central Chile: are adult and juvenile patterns the same?. Oecologia 54, 55-57.

Simonetti, J.A., 1989. Microhabitat use by *Oryctolagus cuniculus* in central Chile: a reassessment. Mammalia 53, 363-368.

Valone, T.J., Meyer, M., Brown, J.H., Chew, R.M., 2002. Timescale of perennial grass recovery in desertified arid grasslands following livestock removal. Conservation Biology 16, 995-1002.

Vásquez, D.P., 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. Biological Invasions 4, 175-191.

Williams, M.C., Wardle, G.M., 2005. The invasion of two native Eucalypt forests by *Pinus radiata* in the Blue mountains, New South Wales, Australia. Biological Conservation 125, 55-64.

Williams, M.C., Wardle, G.M., 2007. The spatial pattern of invading *Pinus radiata*. Proceeding of the Linnean Society of New South Wales (in press).

Williams, M.C., Wardle, G.M., 2005. The influence of vegetation structure and composition on invasibility by Pinus radiata in the Blue Mountains, NSW. Cunninghamia 9, 285-294.

Table 1 Frequencies (%) of rabbit and horse faeces in each type of habitat and vegetation patch. Values correspond to percentage of ten 10 x 10 cm plots with presence of faeces. Plots per 4.5 m long transects were separated by 0.5 m (N = 10 transects per type of vegetation patch in each habitat).

Habitat-Vegetation Patch	Rabbits	Horses
	Mean (%) ± 1 S.E.	Mean (%) ± 1 S.E.
Mesic-Lithrea	28 ± 6.79	2 ± 1.33
Mesic-Open	63 ± 6.33	3 ± 1.53
Xeric-Lithrea	50 ± 5.96	5 ± 2.24
Xeric-Open	75 ± 3.73	11 ± 3.14

Table 2 Statistical results of logistic regression for a comparison of seedling predation of each exotic species between vegetation patches (Lithrea vs Open) and habitats (xeric vs mesic).

Effect	*Eucalyptus globulus*			*Pinus radiata*		
	d.f.	Chi-squared	P	d.f.	Chi-squared	P
Vegetation patch	1	0.93	0.336	1	0.37	0.545
Habitat	1	19.79	<0.0001	1	4.43	0.035
Vegetation patch x Habitat	1	0.86	0.352	1	0.001	0.999

Table 3 Effect of herbivory on seedling survival (excluded vs non-excluded seedlings) per species, habitat and vegetation patch-type. Results correspond to Holm-Sidak post-hoc tests from a Log-rank test of survival curves. Significant differences between excluded and non-excluded seedlings are in bold.

Species	Habitat	Patch	Chi-squared	P	P critical
P. radiata	Xeric	Lithrea	**8.56**	**0.0034**	**0.0051**
		Open	**17.75**	**<0.0001**	**0.0023**
	Mesic	Lithrea	**11.11**	**0.0009**	**0.0037**
		Open	**21.19**	**<0.0001**	**0.0021**
E. globulus	Xeric	Lithrea	1.88	0.17	0.0057
		Open	0.32	0.5720	0.0170
	Mesic	Lithrea	4.36	0.0367	0.0037
		Open	**21.19**	**<0.0001**	**0.0019**

Table 4 Results of the Mantel test to detect spatial autocorrelation among replicates (stations, see text for explanation) for seedling predation of *Pinus radiata* and *Eucalyptus globulus* for each habitat and vegetation condition. Also, spatial autocorrelation within each habitat no differentiating between vegetation patch-types (total) is shown. The level of spatial autocorrelation is indicated by the R (Mantel) value and its statistical significance by the *P* value.

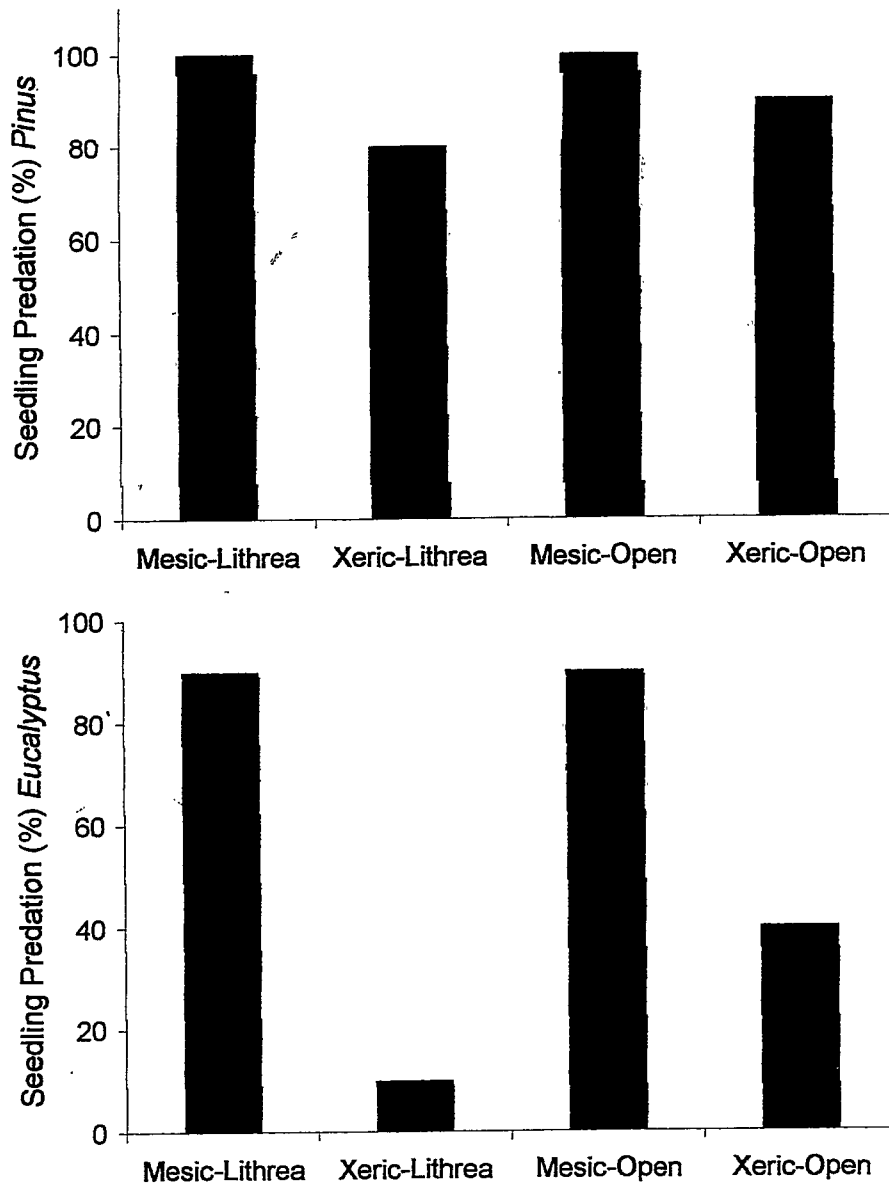| Species	Habitat	Vegetation	R (Mantel)	*P* value
Pinus	Mesic	Open	-0.279	0.069
		Lithrea	-0.176	0.248
		Total	-0.171	0.253
	Xeric	Open	-0.229	0.139
		Lithrea	-0.071	0.702
		Total	-0.220	0.145
Eucalyptus	Mesic	Open	-0.133	0.391
		Lithrea	-0.180	0.241
		Total	-0.115	0.453
	Xeric	Open	0.060	0.711
		Lithrea	-0.138	0.385
		Total	0.095	0.535

Fig. 1. Seedling predation percentage of *Pinus radiata* and *Eucalyptus globulus* in open and *Lithrea* patches of a mesic and a xeric habitat. Each value corresponds to the proportion of predated seedlings from the 10 originally non-excluded seedlings at the end of the experiment (June, 2005).
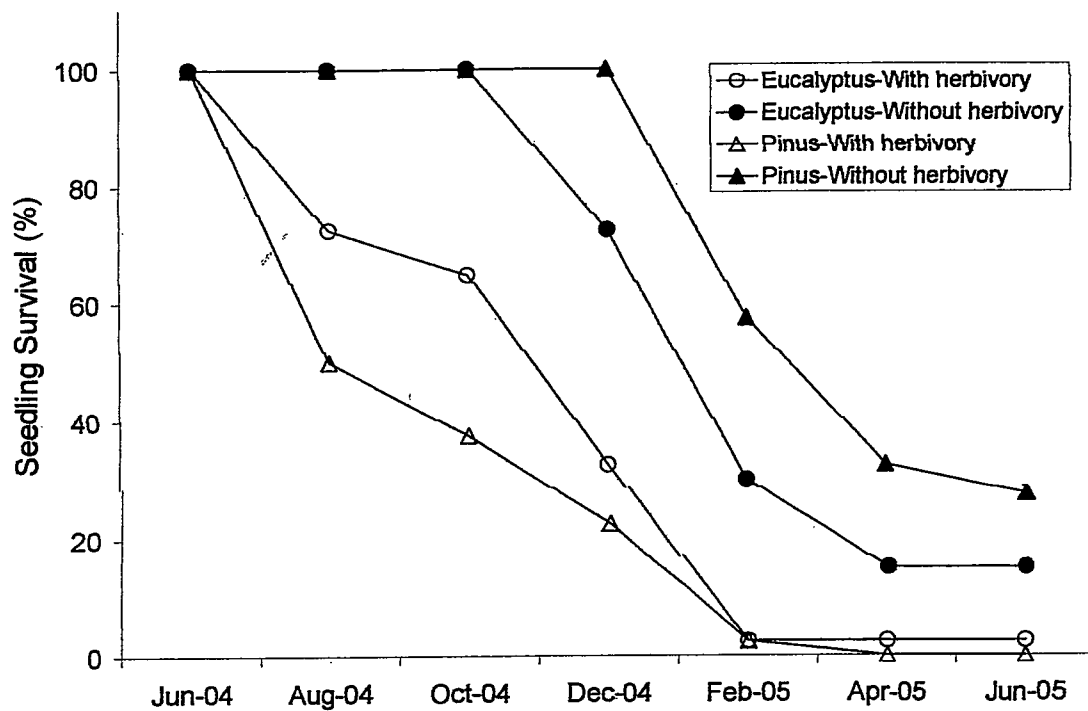
Fig. 2. Seedling survival curves of excluded (without herbivory) and non-excluded (with herbivory) seedlings of *Pinus radiata* and *Eucalyptus globulus*. Each point corresponds to the percentage of living seedlings from a total of 40 originally disposed per species and herbivory treatment.
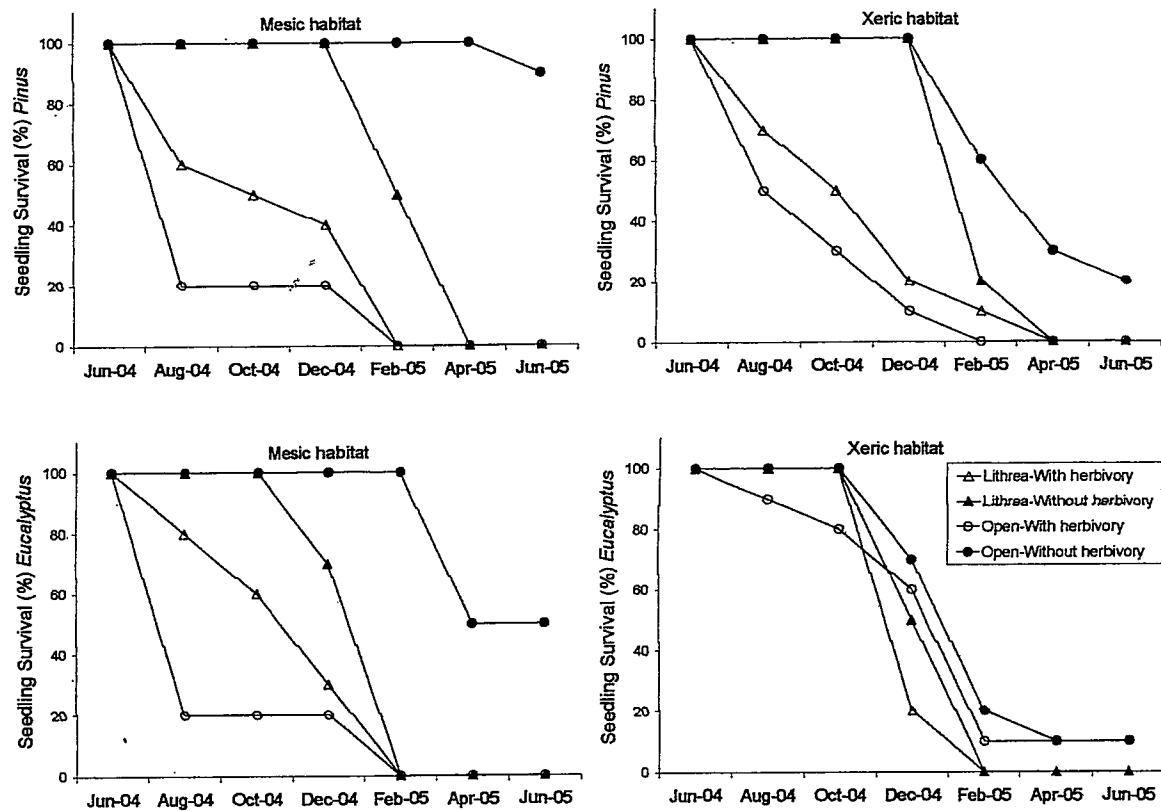
Fig. 3. Survival curves of excluded (without-herbivory) and non-excluded (with-herbivory) seedlings for each species (*Pinus radiata* and *Eucalyptus globulus*), habitat and vegetation patch. Each point corresponds to the percentage of living seedlings from a total of 10 originally disposed per species, herbivory, habitat and vegetation patch treatment.

CAPÍTULO IV: DISCUSIÓN GENERAL

Efecto del hábitat físico, cobertura arbórea y herbivoría sobre el reclutamiento de *Pinus* y *Eucalyptus*: respuestas a las hipótesis propuestas

La hipótesis sobre el efecto del hábitat físico indica que el reclutamiento de *Pinus radiata* y *Eucalyptus globulus* sería mayor en el hábitat mésico que en el xérico. En esta tesis se observó que en general tanto *Pinus* como *Eucalyptus* germinaron en mayor proporción en el hábitat más mésico tal como lo propuesto en la hipótesis. Sin embargo, al examinar las diferencias de germinación por tipo de parche de vegetación, esta tendencia se observó sólo para *Pinus* en ambos tipos de parche. En cambio, *Eucalyptus* presentó esta tendencia sólo en sitios abiertos. Similarmente, ambas especies presentaron mayor sobrevivencia de plántulas en el hábitat más mésico, aunque esta tendencia fue sólo observada en sitios abiertos. En consecuencia, en sitios abiertos las dos especies presentarían un mayor reclutamiento general en el hábitat más mésico. Además, en *Pinus* el reclutamiento también sería mayor en hábitats más mésicos bajo los parches de Litre como producto del proceso de germinación. En cambio, el reclutamiento de *Eucalyptus* no sería mayor en hábitats mésicos bajo parches de Litre ya que ni la germinación ni la sobrevivencia de plántulas presentaron diferencias entre hábitats bajo este tipo de parche. No obstante, estos resultados son consistentes con otros estudios que documentan que la invasión se produciría mayormente en hábitats menos estresantes para las plantas como son los hábitats de laderas de exposición sur de Chile Central (Richardson & Bond 1991, Beerling 1993, Lonsdale 1999, Stohlgren et al. 2005,

MacDougall et al. 2006). Por otro lado, la hipótesis propuesta en esta tesis sobre el efecto de la cobertura de Litre plantea que este árbol nativo tendría un efecto positivo en hábitats xéricos y negativo en hábitats mésicos sobre el reclutamiento de ambos árboles exóticos como consecuencia del sombreamiento generado por el dosel. En esta tesis se observó que cada etapa del proceso de reclutamiento por separado (germinación y sobrevivencia de plántulas) se ajusta sólo parcialmente a lo predicho en la hipótesis. Tal como era esperado, el efecto de la cobertura de Litre a través del sombreamiento generado por su dosel, fue positivo sobre la germinación de ambas especies en el hábitat xérico, pero, contrario a lo esperado, no tuvo efectos negativos en el hábitat mésico, e incluso la tendencia fue también positiva. Además, tal como se esperaba, la cobertura de Litre tuvo un efecto negativo sobre la sobrevivencia de plántulas en ambas especies en el hábitat mésico. En cambio, y contrario a lo esperado, la cobertura de Litre no tuvo efectos positivos significativos sobre la sobrevivencia de plántulas de ambas especies en el hábitat xérico. Al conjugar las dos etapas del reclutamiento analizadas (germinación y sobrevivencia de plántulas), en el hábitat xérico habría un efecto positivo del Litre sobre el reclutamiento de ambas especies, determinado principalmente porque la germinación se ve incrementada. En cambio, en el hábitat mésico habría un efecto negativo del Litre sobre el reclutamiento de ambas especies, generado por el patrón de mortalidad de plántulas. Así, en forma global, la hipótesis general sobre el cambio de efectos desde negativos a positivos a medida que se incrementa el estrés de humedad del suelo desde un hábitat mésico a un hábitat xérico (Bertness & Callaway 1994, Holmgren et al. 1997), es corroborada. Además, estos resultados sustentan la hipótesis de que interacciones negativas y también positivas entre especies nativas y exóticas podrían permitir explicar

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los procesos de invasión (Richardson et al. 2000, Bruno et al. 2005).

Finalmente, la hipótesis del efecto de la herbivoría indica que ésta ejercería un efecto negativo en la sobrevivencia de plántulas, la es corroborada por los datos. En esta tesis se observó que las plántulas de ambas especies son depredadas por herbívoros vertebrados de esta zona. En términos generales la herbivoría tuvo un efecto negativo sobre la sobrevivencia de plántulas de ambas especies exóticas. Si embargo, sólo sobre *Pinus* el efecto de la herbivoría fue significativo bajo todas las condiciones de hábitat y vegetación estudiadas. En cambio, sobre *Eucalyptus*, esto dependió del hábitat y parche de vegetación. En ambos parches de vegetación del hábitat xérico la depredación sobre *Eucalyptus* fue lo suficientemente baja como para no producir efectos significativos sobre la sobrevivencia de plántulas. En cambio en parches de Litre del hábitat mésico, a pesar de haber una alta depredación, el efecto de la herbivoría no fue significativo, probablemente debido a una alta mortalidad producida por desecación de las plántulas. Finalmente, en sitios abiertos del hábitat mésico hubo una alta depredación y baja desecación que generaron un efecto significativo de la herbivoría sobre *Eucalyptus*. De acuerdo a estos resultados, la herbivoría, en este caso principalmente generada por vertebrados exóticos (conejo Europeo), afectaría negativamente la invasión de estos árboles exóticos. Esto contradice la hipótesis del "invasion meltdown" de Simberloff & Von Holle (1999) de que especies exóticas facilitarían la invasión de otras especies exóticas, y más bien apunta a que la herbivoría generada por vertebrados generalistas produciría una resistencia a la invasión (Levine et al. 2004, Joshi & Vrieling 2005).

En consecuencia, los tres factores analizados tendrían influencia en el proceso de invasión de ambas especies, sin embargo, existen interacciones entre ellos que

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determinan que la importancia de uno de ellos en los procesos de invasión de ambas especies dependa de las condiciones de otro.

En función de estos resultados, y en base al conocimiento existente respecto de la ecología de estas especies arbóreas exóticas, es posible plantear diferentes predicciones sobre la potencialidad de invasión de ellas en Chile central.

Potencial de invasión de *Pinus radiata* y *Eucalyptus globulus* en Chile central

Los procesos de invasión dependen en primera instancia de que exista una fuente de propágulos y de que éstos se dispersen hacia áreas naturales (Lonsdale 1999). Las plantaciones forestales (tanto comerciales como con fines ornamentales) de *Pinus radiata* y *Eucalyptus globulus* en Chile central conforman una importante fuente de propágulos disponibles para dispersarse hacia áreas más naturales (Figueroa et al. 2004). De hecho, existe evidencia de lluvia de semillas de *Pinus radiata* en ambientes naturales aledaños a plantaciones (Bustamante & Simonetti 2005). Esto se ve confirmado por la presencia de individuos de *Pinus* regenerados espontáneamente en ambientes naturales (Capítulo I esta tesis, Bustamante et al. 2003, Becerra 2006). Similarmente, si bien no existen estudios sobre lluvia de semillas de *Eucalyptus* en ambientes naturales, la presencia de individuos regenerados naturalmente en diversas localidades de Chile central (Capítulo I) sugiere que semillas de esta especie pueden dispersarse desde plantaciones hacia ambientes naturales. En consecuencia, en ambas especies existiría disponibilidad de semillas en ambientes naturales cercanos a plantaciones, y así este proceso no sería restrictivo para la invasión de ambas especies, al menos en zonas cercanas a las fuentes de propágulos.

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Posteriormente, el éxito de la invasión de una especie puede depender de que las semillas sobrevivan a la depredación durante el tiempo que se encuentran en el suelo previo a la germinación (revisión en Maron & Vilà 2001). Hasta la fecha no existe algún trabajo que haya evaluado la importancia de la depredación de semillas de *Pinus radiata* y *Eucalyptus globulus* en sus ambientes nativos o introducidos.

Posterior a la dispersión de semillas y su período de permanencia en el suelo, el éxito del proceso de invasión también puede depender de si las especies exóticas reclutan bajo las condiciones físicas y vegetacionales de los sitios donde se dispersan las semillas (Lonsdale 1999, Levine et al. 2004, Bruno et al. 2005). Un primer paso crítico en el reclutamiento es la germinación de semillas (Harper 1977). De acuerdo a los resultados observados en esta tesis (Capítulo II), ambas especies presentan probabilidades de germinación superior a cero en situaciones de hábitat tanto xérico como mésico y en sitios con o sin parches de Litre aunque con variación entre ellos. La mayor germinación es en parches de Litre del hábitat mésico y la menor en sitios abiertos del hábitat xérico en ambas especies. Esto sugiere que la germinación no es una etapa fuertemente restrictiva para la invasión de estas especies, aunque las probabilidades de germinación son en general bajas, menores al 12% (Capítulo II). Posterior a la germinación, la sobrevivencia de plántulas puede ser una etapa decisiva del éxito del reclutamiento e incluso presentar patrones diferentes a los de germinación (Harper 1977, Schupp 1995). De acuerdo a los resultados de esta tesis (Capítulo III) la sobrevivencia de plántulas es mayor en sitios abiertos de hábitats más mésicos y menor en parches de Litre de hábitats xéricos. Además, en sitios abiertos de hábitats mésicos la probabilidad de sobrevivencia de plántulas al cabo de un año es bastante alta (50% en

Eucalyptus y 90% en *Pinus*). Similarmente, en sitios abiertos de hábitats xéricos la probabilidad de sobrevivencia de plántulas es superior a cero. Luego, dada la alta frecuencia y cobertura de sitios abiertos en Chile central en ambos tipos de hábitats, la sobrevivencia de plántulas no sería una etapa fuertemente restrictiva para el establecimiento de poblaciones invasoras de estas especies, aunque sí variable en función del hábitat y cobertura vegetal. Por otra parte, tanto la germinación como la sobrevivencia de plántulas fueron mayores en *Pinus* que en *Eucalyptus* (Capítulo II), lo cual sugiere que al menos en función de las condiciones físicas del hábitat y de vegetación estudiadas en esta tesis, *Pinus* tiene una mayor probabilidad de invasión que *Eucalyptus*.

Posteriormente, si la germinación y sobrevivencia de plántulas son posibles en función de las características físicas y vegetacionales de un ecosistema, el establecimiento final de plántulas y con ello el posible éxito de los procesos de invasión también puede depender del nivel de herbivoría que sufran las plántulas (Lonsdale 1999, Maron & Vilà 2001, Shea & Cheeson 2002). De acuerdo a los resultados de esta tesis (Capítulo III), ya sea en *Pinus* como en *Eucalyptus*, bajo ninguna situación de hábitat físico y vegetación estudiada la depredación alcanzó al 100 % de las plántulas después de un año de observaciones aunque la sobrevivencia de plántulas resultante tanto del efecto de la herbivoría como de la desecación fue nula en sitios bajo Litre. Sin embargo, dado el bajo número de plántulas utilizadas como réplicas (10 plántulas por combinación de hábitat y tipo de parche de vegetación) es posible que con un mayor número de plantas disponibles, por ejemplo generado por una mayor lluvia de semillas, e incluso con los mismos porcentajes de germinación y sobrevivencia de plántulas resultantes del

efecto del hábitat físico y vegetación, más de alguna (un porcentaje mayor a cero) pueda sobrevivir. Por otro lado, especialmente en *Eucalyptus*, existe una importante variabilidad del efecto de la herbivoría tanto entre hábitats como parches de vegetación (Capítulo III). Finalmente, si bien *Pinus radiata* tiene una mayor probabilidad de reclutar que *Eucalyptus globulus* bajo las condiciones físicas y vegetacionales imperantes de Chile central, las plántulas de *Pinus* son mayormente depredadas que las de *Eucalyptus*. Así, las probabilidades de invasión en función de los factores de reclutamiento estudiados en esta tesis podrían equipararse entre estas especies.

Los resultados de esta tesis, los cuales corresponden exclusivamente a la etapa de reclutamiento de plántulas, podrían ser generalizables a la región mediterránea de Chile. En cuanto al efecto del hábitat físico, es posible que en cualquier localidad de esta región del país ambas especies exóticas tengan una mayor probabilidad de reclutar en laderas de exposición sur que en laderas de exposición norte. Además, sería posible predecir que ambas especies tendrían una mayor probabilidad de reclutamiento en la zona más meridional de esta región. Por otra parte, dada la amplia distribución del Litre (Rodríguez et al. 1983) y la alta frecuencia de sitios abiertos dentro de la región Mediterránea de Chile (Fuentes et al. 1984, 1986), el rol de los parches de litre y de los sitios abiertos podría ser generalizable a toda la región mediterránea de Chile. El efecto del litre podría depender de la exposición de las laderas tal como fue observado en esta tesis, pero también de la latitud. Si consideramos que el área de estudios se encuentra en una localidad más bien nortina dentro de la zona de plantaciones de ambas especies (comerciales y ornamentales), el mayor reclutamiento en sitios abiertos que en parches de Litre observado en esta tesis en la ladera de exposición sur, debiera mantenerse

prácticamente en todas las laderas de exposición sur de la región mediterránea de Chile. Más aún, este efecto negativo del Litre podría comenzar a generarse también en laderas de exposición norte en latitudes intermedias y más sureñas en la medida que éstas lleguen a presentar humedades del suelo similares a las observadas en la ladera de exposición sur del área de estudio de esta tesis. Así, el mayor reclutamiento en parches de litre que en sitios abiertos quedaría restringido a las laderas de exposición ecuatorial de la zona más nortina de la región Mediterránea de Chile. Finalmente, con respecto al efecto de la herbivoría de vertebrados, es posible que el patrón observado se repita a lo largo de toda la región mediterránea debido a la amplia distribución del conejo europeo, así como del ganado y otros herbivoros nativos (Jaksic 1998).

Independiente de la generalidad de los resultados de esta tesis dentro de la región mediterránea de Chile, el reclutamiento también podría verse afectado por factores no estudiados, como por ejemplo, otras plantas, tales como hierbas, arbustos, y otras especies arbóreas, así como por herbivoría de insectos, patógenos foliares y microorganismos edáficos (Maron & Vilà 2001, Shea & Cheeson 2002, Bruno et al. 2005). Dado que el litre genera menor luminosidad bajo su dosel que especies arbustivas y herbáceas (Del Pozo et al. 1989), es posible que su efecto negativo sea mayor que el efecto generado por hierbas y arbustos. De la misma manera, es posible que su efecto positivo en hábitats xéricos también sea superior al generado por especies de plantas de otras formas de vida. Sin embargo, según lo observado en esta tesis el suelo de los parches de litre parece tener un efecto negativo (Capítulo II), y no se sabe si otras especies lo producen. Luego, no sería posible generalizar los efectos del litre a otras especies de plantas, incluso arbóreas. No obstante, el hecho de que ambas especies

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exóticas tengan un alto reclutamiento en sitios abiertos con presencia de hierbas, especialmente en el hábitat más mésico (Capítulo II), sugiere que las hierbas no generan una fuerte resistencia al reclutamiento de estas especies. Por otra parte, es conocida la influencia de diversos insectos y microorganismos sobre plántulas de ambas especies aunque éstos pocas veces generan alta mortalidad en poblaciones de estas especies exóticas arbóreas (Cogollor 1992, Baldini & Pancel 2000).

Posterior a la etapa de reclutamiento, diversos factores, entre ellos los estudiados en esta tesis, podrían afectar la probabilidad de sobrevivencia y reproducción de individuos adultos de estos árboles exóticos. Por un lado, el efecto positivo de la humedad del hábitat observado sobre el reclutamiento de ambas especies probablemente no cambie fuertemente con la edad de los individuos. Así, la proporción de individuos de mayor edad que mueren en cada tipo de hábitat debiera ser superior en hábitats más xéricos, especialmente durante eventos de sequía. Similarmente, la reproducción de individuos creciendo en hábitats más húmedos podría ser mayor que la de individuos presentes en hábitats más xéricos. En cambio, el efecto del litre podría cambiar fuertemente sobre individuos de mayor edad respecto de lo observado en la etapa de reclutamiento, tal como se ha documentado en otras especies (e.g. Schupp 1995, Miriti 2006). Por ejemplo, individuos adultos de *Pinus* y *Eucalyptus* podrían requerir mayor luminosidad o nutrientes y por lo tanto incrementar la competencia con el Litre. Luego, el resultado final de la interacción entre ambos árboles exóticos y el Litre puede depender del momento en que éstos sobrepasen el dosel del Litre o sus raíces alcancen sitios no ocupados previamente por las raíces del Litre. En este caso, debido a la mayor tasa de crecimiento de *Eucalyptus* que *Pinus*, el efecto negativo del sombreamiento

tendría menor duración en *Eucalyptus* por lo cual esta especie podría verse menos afectada que *Pinus*. Por su parte, es probable que la importancia de la herbivoría generada por vertebrados, especialmente de conejos, disminuya en individuos de mayor edad debido a que los tallos más anchos y las hojas a mayor altura podrían permitirles resistir la depredación (e.g. Ferriere et al. 1983, O'Reilly & McArthur 2000, McArthur & Appleton 2004). Finalmente, otros factores podrían tener efectos sobre individuos de mayor edad de ambos árboles exóticos, especialmente la herbivoría de insectos y patógenos, la cual si bien pocas veces genera mortalidad en forma masiva (Cogollor 1992, Baldini & Pancel 2000), podría afectar el éxito reproductivo y así afectar significativamente la tasa de invasión de estas especies (Lockwood et al. 2005).

En conclusión, dado que i) semillas de ambas especies exóticas se están dispersando hacia ambientes naturales cercanos a las plantaciones, ii) ambas especies pueden reclutar especialmente en sitios abiertos de hábitats mésicos pero también de xéricos, iii) existe una alta frecuencia de sitios abiertos dentro de la región Mediterránea de Chile (Fuentes et al. 1984, 1986), iv) sus plántulas no son completamente depredadas por herbívoros vertebrados (aunque se debe evaluar la intensidad de depredación por herbívoros vertebrados diferentes a los involucrados en esta tesis), y v) la herbivoría de insectos y patógenos no genera alta mortalidad de plántulas e individuos adultos, es posible predecir que ambas especies poseen una real potencialidad de invasión en la zona mediterránea de Chile, aunque con variabilidad espacial, especialmente generada por las condiciones físicas del hábitat, vegetación, y composición y abundancia de herbívoros.

Bibliografía

Baldini, A. & Pancel, L. 2000. Agentes de daño en el bosque nativo. Editorial Universitaria.

Becerra, P. 2006. Invasión de árboles alóctonos en una cuenca de Chile central. Gayana Botanica, en prensa.

Beerling, D.J. 1993. The impact of temperature on the northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. Journal of Biogeography, 20: 45-53.

Bertness, M.D. & R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191-193.

Bruno, J. F., J. D. Fridley, K. D. Bromberg, and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. Pages 13-40 *in* D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. Species Invasions: insights into ecology, evolution and biogeography. Sinauer Associates, Inc., USA.

Bustamante, R. O. & Simonetti, J. A. 2005. Is *Pinus radiata* invading the native vegetation in central Chile?, demographic responses in a fragmented forest. Biological Invasions 7: 243-249.

Bustamante, R. O., I. A. Serey and S.T.A. Pickett. 2003. Forest fragmentation, plant regeneration and invasion processes across edges in central Chile. Pages 145-158 *in* G. A. Bradshaw and P. A. Marquet, editors. How Landscape Change. Springer-Verlag, Berlin.

Cogollor, G. 1992. Vulnerabilidad biológica de las plantaciones. XIV Jornadas Forestales, Colegio de Ingenieros Forestales de Chile, Temuco, Chile.

Del Pozo, A.H., E.R. Fuentes, E.R. Hajek & J.D. Molina. 1989. Zonación microclimática por efecto de los manchones de arbustos en el matorral de Chile central. Revista Chilena de Historia Natural 62:85-94.

Ferriere, G., Cerda, J. & Roach, R. 1983. El conejo silvestre en Chile. Boletín Técnico N°8, CONAF, Santiago, Chile.

Figueroa, J. A., S. A. Castro, P. A. Marquet, and F. M. Jaksic. 2004. Exotic plant invasion to the Mediterranean region of Chile: causes, history and impacts. Revista Chilena de Historia Natural 77:465-483.

Fuentes, E.R., R.D. Otaiza, M.C. Alliende, A.J. Hoffmann & A. Poiani. 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. Oecologia 62:405-411.

Fuentes, E.R., A.J. Hoffmann, A. Poiani & M.C. Alliende. 1986. Vegetation change in large clearings: patterns in the Chilean matorral. Oecologia 68:358-366.

Harper, J. L. 1977. Population Biology of Plants. London, Academic Press.

Holmgren, M., M. Scheffer & M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966-1975.

Jaksic, F.M. 1998. Vertebrate invaders and their ecological impacts in Chile. Biodiversity and Conservation 7: 1427-1445.

Joshi, J. & Vrieling, K. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters, 8:704-714.

Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to alien plant invasions. Ecology Letters 7:975-989.

Lockwood, J.L., P. Cassey & T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution, 20:223-228.

Lonsdale, W. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology, 80:1522-1536.

MacDougall, A.S., Boucher, J., Turkington, R. & Bradfield, G.E. 2006. Patterns of plant invasion along an environmental stress gradient. Journal of Vegetation Science 17: 47-56.

Maron, J.L. & M. Vilà. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypothesis. *Oikos*, 95:361-373.

McArthur, C. & Appleton, R. (2004) Effect of seedlings characteristics at planting on browsing of Eucalyptus globulus by rabbits. Australian Forestry 67: 25-39.

Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology, 94:973-979.

O'Reilly, J. & McArthur, C. (2000) Damage to and intake of plantation seedlings by captive European rabbits (*Oryctolagus cuniculus*). Australian Forestry 63: 1-6.

Richardson, D.M. & W.J. Bond. 1991. Determinants of plant distribution: evidence from pine invasions. American Naturalist, 137:639-668.

Richardson, D.M., N. Allsopp, C.M. D'Antonio, S.J. Milton & M Rejmánek. 2000. Plant invasions - the role of mutualisms. Biological Review 75:65-93.

Rodríguez, R., O. Matthei, & M. Quezada. 1983. Flora arbórea de Chile. Edit. Universitaria de Concepción.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82:399-409.

Shea, K. & P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17: 170-176.

Simberloff, D., & B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown?. Biological Invasions 1:21-32.

Stohlgren, T.J., Barnett, D., Flather, C., Kartesz, J. & Peterjohn, B. 2005. Plant species invasions along the latitudinal gradient in the United States. Ecology 86:2298-2309.