



Revista Chilena de Historia Natural

ISSN: 0716-078X

info@biomedcentral.com

Sociedad de Biología de Chile

Chile

VALDIVIA, CARLOS E.; SIMONETTI, JAVIER A.

Denied density-dependent seedling recruitment in a fragmented forest does not decrease
seedling diversity

Revista Chilena de Historia Natural, vol. 84, núm. 2, 2011, pp. 279-287

Sociedad de Biología de Chile

Santiago, Chile

Available in: <http://www.redalyc.org/articulo.oa?id=369944298012>

- How to cite
- Complete issue
- More information about this article
- Journal's homepage in redalyc.org

redalyc.org

Scientific Information System

Network of Scientific Journals from Latin America, the Caribbean, Spain and Portugal

Non-profit academic project, developed under the open access initiative



RESEARCH ARTICLE

Denied density-dependent seedling recruitment in a fragmented forest does not decrease seedling diversity

El denegado reclutamiento denso-dependiente de plántulas en un bosque fragmentado no disminuye la diversidad de plántulas

CARLOS E. VALDIVIA^{1,*} & JAVIER A. SIMONETTI²

¹ Departamento de Ciencias Básicas, Universidad de Los Lagos, Casilla 933, Osorno, Chile

² Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

*Corresponding author: carlos.valdivia@ulagos.cl

ABSTRACT

Negative density-dependent relationships in plant communities are currently claimed as an important mechanism for the maintenance of plant diversity. However, anthropogenic perturbations such as forest fragmentation might modify such relationships. We evaluated density-dependent relationships between seed and seedling abundance of a tree assemblage in a fragmented forest for estimating seed-to-seedling transitions and their effects on seedling richness. In continuous forest, two out of four and one out of four species presented significant or a tendency to exhibit negative seedling recruitment which is in agreement with other temperate and tropical forests. In forest fragments (1-6 ha), however, this relationship was uncoupled. Seedling richness and diversity, assessed through Shannon-Wiener Index, did not differ between both types of sites. Therefore, forest fragmentation negatively affected seedling recruitment by uncoupling seed-to-seedling transitions, but not by diminishing seedling diversity. This leads to considering the role of density-dependent relationships for the maintenance of plant diversity in communities and claims for including forest fragments into conservation programmes.

Key words: density-dependent recruitment, diversity, forest fragmentation, seedlings, seeds.

RESUMEN

Las relaciones denso-dependientes negativas en las comunidades vegetales son actualmente señaladas como un importante mecanismo para la mantención de la diversidad de plantas. Sin embargo, las perturbaciones antropogénicas como la fragmentación del bosque podrían modificar este tipo de relaciones. Evaluamos las relaciones denso-dependientes entre las abundancias de semillas y plántulas en un ensamble de árboles en un bosque fragmentado para estimar las transiciones de semillas a plántulas y sus efectos sobre la riqueza de plántulas. En el bosque continuo tres de cuatro especies presentaron reclutamientos de plántulas negativos, lo cual se condice con otros bosques templados y tropicales. En los fragmentos de bosque (1-6 ha), no obstante, estas relaciones estuvieron desacopladas. La riqueza y diversidad de plántulas, evaluadas a través del Índice de Shannon-Wiener, no difirió entre ambos tipos de sitios. Por lo tanto, la fragmentación del bosque afectó negativamente el reclutamiento de plántulas modificando las transiciones de semilla a plántula, pero no disminuyendo la diversidad de plántulas. Este resultado nos conduce a considerar el rol de las relaciones denso-dependientes en la mantención de la diversidad de plántulas en las comunidades y aboga por incluir los fragmentos de bosque en los programas de conservación.

Palabras clave: diversidad, fragmentación del bosque, plántulas, reclutamiento denso-dependiente, semillas.

INTRODUCTION

Several mechanisms can account for the maintenance and coexistence of tree species in forests (Chesson 2000). Intra-specific relationships of density-dependence, positive or negative ones, are among the pivotal mechanisms (Wills et al. 1997, Wright 2002). Negative density-dependence occurs when conspecific neighbours reciprocally impair

their performance, albeit more intensively at higher abundances. Allelopathy, intraspecific competition, and pest facilitation may all contribute to modify the likelihood of survival of an individual seedling in dense stands, thereby affecting seedling diversity. Similarly, the density of heterospecific neighbours can modify survivorship or reproductive success of trees by facilitating or by inhibiting seedling recruitment among other causes (see Peters

2003). Negative density-dependence contributes to maintain seedling diversity (Harms et al. 2000) because it precludes that abundant species eliminate rare species by covering all available recruitment sites (Condit et al. 1994, Wills et al. 1997, Web & Peart 1999). This relationship has been claimed as an important mechanism for the maintenance of arboreal richness in a wide array of forests such as tropical forests of Central America and Asia as well as temperate forests in North America (Wills et al. 1997, Web & Peart 1999, Lambers et al. 2002).

Abiotic and biotic factors (e.g., nutrient availability, competition, predation) can determine density-dependence relationships (Wills et al. 1997) which, nonetheless, may be modified by forest fragmentation (Saunders et al. 1991, Murcia 1995). In fragments, light and temperature increase whereas air and soil moisture decrease as compared to continuous forest (Murcia 1995). These new abiotic conditions should favour the establishment of shade-intolerant species in forest fragments, therefore inhibiting the recruitment of dominant shade-tolerant trees (Laurance et al. 1998). Moreover, biotic conditions such as herbivory, granivory and seed dispersal could be changed by habitat fragmentation (Murcia 1995), which can also modify tree recruitment due to safe site modifications for seedling recruitment (Green 1983). Therefore, biotic and abiotic factors can modify composition and structure of the remaining forest fragments through direct effects on the seedling survival (Laurance et al. 1998), as well as indirect effects such as the uncoupling in negative density-dependency in seed-to-seedling transitions. In spite of their pivotal importance, however, human-mediated alterations of density-dependent relationships have not yet addressed.

Currently, the northernmost region of the temperate rainforest of central Chile is severely fragmented with numerous remnants surrounded by plantations of the exotic pine *Pinus radiata* L. (Pinaceae) (Grez et al. 1997). In the smaller fragments, soil moisture and herbivory decrease significantly while granivory increases (Vásquez 2004, Donoso et al. 2003). These abiotic and biotic factors may modify the reproductive success of native species. In fact, although the most abundant

trees in continuous forests are also the most abundant trees in the remaining fragments, changes in biotic and abiotic conditions in forest fragments have triggered a different regeneration pathway as compared to continuous forests (Bustamante et al. 2005). According to a Markovian model, in forest fragments there would be a higher dominance of shade-intolerant species, while in continuous forest, vegetation would maintain the dominance of their shade-tolerant species. In addition, at forest fragments there would be an increase of bird-dispersed trees by an active colonisation process (Bustamante et al. 2005). Therefore, vegetation in continuous forests would be in a stabilising regeneration dynamic, whereas in forest fragments, tree regeneration dynamic would be led by non-stabilising colonisation processes. This fact suggests negative density-dependent seedling recruitment at continuous forest, yet not at forest fragments.

Our goal is to evaluate seed-to-seedling transitions in a fragmented forest of central Chile. If the stabilising regeneration dynamics in continuous forest tend to increase negative intraspecific interactions relative to negative interspecific interactions (see Chesson 2000: 343), we expect a negative density-dependence relationship between seed and seedling abundance in the continuous forest, but not in forest fragments. In addition, if forest fragmentation affects either abundance or richness of seeds and seedlings, in forest fragments we expect a higher seed diversity of compared to seedling diversity due to future over-dominance of species such as shade-intolerant trees, whereas in continuous forest we expect a lower seed than seedling diversity. Similarly, if seedling recruitment at the continuous forest is negatively density-dependent, we do not expect relationships between seed richness or abundance with seedling richness or abundance respectively (Harms et al. 2000).

METHODS

Study site

Fieldwork was carried out from July 2001 to January 2003, in the northernmost zone of the South-American temperate rainforest (35°59' S, 72°41' W), the Maulino

forest (San Martín & Donoso 1996). This zone encompasses the richest zone in tree diversity with many endemic and endangered species such as the southern beeches *Nothofagus obliqua* (Mirb.) Bl and *N. glauca* (Phil.) Krasser among others (San Martín & Donoso 1996). Specifically, we worked at Los Queules National Reserve and four neighbouring forest fragments. Los Queules is a protected area of 145 ha of a native forest tract embedded in 600 ha of continuous forest, whereas fragments, whose surfaces range from 1 to 6 ha, are patches surrounded by mature pine plantations of *P. radiata*, located up to 3 km away from each other and from continuous forest (Grez et al. 1997). Currently, arboreal composition in continuous forest and fragments does not differ significantly, although they exhibit dissimilar regeneration patterns (Ramos et al. 2008). In fact, while in continuous forest arboreal composition will roughly remain constant throughout the time; in forest fragments the Maulino forest will be replaced by a sclerophyllous shrubland (see Ramos et al. 2008 for details).

Census stations

In July 2001, forty seed traps were randomly distributed within the continuous forest, while other forty seed traps were placed in forest fragments (10 at each fragment). Each trap consisted of a 0.25 m², open-topped, 1 mm wire-mesh bag held 0.8 m above the ground on a PVC frame. All seeds falling into the traps were counted and identified to the species level each month from July 2001 to December 2002. It is worthwhile highlighting that seed rain registered by this method does not include the predation effect exerted by granivores. Furthermore, in September 2002, all woody plants less than 50 cm tall were tagged and identified to species in twenty plots of 2 m² at continuous forest and twenty plots at forest fragments. Seedlings at these randomly set stations were yearly tagged since 1998, therefore allowing the identification of recruits of each year. The plots were placed 1-2 m away from two seed traps. Survivors were re-measured and new recruits were tagged and identified in January 2003. Each pair of seed traps and its adjacent plot constitutes a census station (20 at continuous forest and 20 at forest fragments, 5 per forest fragment). Census stations were roughly linearly arranged at the core of each site, the average distance (± 1 SE) being 21.13 ± 2.14 m at the continuous forest, and 20.83 ± 3.14 m at forest fragments, which did not differ significantly (Mann-Whitney test: $U = 121$, $P = 0.305$). Additionally, surrounding each census station we registered the frequency of adult tree species (DBH > 10 cm) in plots of 100 m² ($n = 15$ at continuous forest, $n = 20$ at forest fragments). It is worthwhile highlighting that census stations were randomly set up at the core of each type of habitat (continuous forest and forest fragments) to avoid any edge effects (see Murcia 1995).

Regression analyses

To estimate the strength of density dependence on seedling recruitment, we examined the relationship $R = aS^b$ (equation 1) between seedling (R) and seed abundance (S), where a and b are constants. We assessed the seed-seedling relationship by using linear regression on log transformed values of $R + 1$ and $S + 1$ to normalise residuals. In these regressions, the fitted

constant b takes values of < 1 if the per seed probability of recruitment is inversely related to seed abundance, that is negative density-dependent seedling recruitment.

To evaluate the strength of conspecific density-dependence relationships, seedling abundance of each species was correlated to seed abundance of the same species, following the equation 1. Furthermore, to evaluate the strength of heterospecific density-dependence relationships, seedling abundance of each species was correlated to seed abundance of all other species as a whole, both including and excluding seed abundance of the focal species. Power tests were performed for each regression analysis using the Fisher z transformation for the critical value r and the sample r (Zar 1999).

Seeds and seedlings diversity

To evaluate the effect of forest fragmentation on seed and seedling diversity, we estimated the richness and abundance of seeds and seedlings at each census station. Richness and abundance of seedlings were correlated to richness and abundance of seeds, by using Spearman rank correlations, in order to determine if either seed richness or abundance is good indicators of seedling richness or abundance respectively. Then, we calculated the Shannon-Wiener Index of diversity (H) at each census station to jointly integrate analyses of richness and abundance. Seedling diversity and seed diversity were correlated in order to determine if seed diversity is a good indicator of seedling diversity. Similarly, to determine changes in dominance of each species we calculated the Pielou index of evenness (J) for seeds and seedlings at each census station.

RESULTS

Density-dependent seedling recruitment

We registered a total of twenty adult trees species (15 at the continuous forest and 19 at the fragments), of which 15 were shared between both types of sites (Table 1). Floristic similarity, assessed through Sorensen index was $S = 0.88$. In terms of regeneration niche, we registered a total of six shade-tolerant species, three generalist, and two shade-intolerant, as well as nine species with unknown characteristics (Table 1).

From July 2001 to January 2003, we registered a total of 11435 seeds (5879 at the continuous forest and 5556 at the forest fragments) and 171 seedlings (131 at the continuous forest and 40 at the forest fragments). The total number of species, i.e., adults, seeds, and seedlings, altogether combined, was 20 (Table 1). Floristic similarity, taking into account all species at all these stages was $S = 0.81$.

At the continuous forest, we found 16 species among adults, seeds and seedlings. As adults, we found 15 species, at the seedling stage we found six species, whereas at the seed stage 12 species (Table 1). Of these ones, 12 species were shared between adults and seeds with a floristic similarity of $S = 0.88$; whereas five species were shared between seeds and seedlings ($S = 0.77$), and five species were shared between adults and seedlings ($S = 0.48$).

At the forest fragments we found 19 species among adults, seeds and seedlings. At the adult stage we found 19 species, at the seedling stage we found 12 species while at the seed stage eight species (Table 1). Of these ones, eight species were shared between

adults and seeds ($S = 0.59$), three species were shared between seeds and seedlings ($S = 0.32$), while 12 species were shared between adults and seedlings, with a floristic similarity of $S = 0.77$.

Seed and seedling abundance of all species inhabiting both the continuous forest and the fragmented forests were uncorrelated ($R = -0.36$, $P = 0.12$ at continuous forest. $R = 0.24$, $P = 0.31$ at forest fragments). However, regarding only those species that presented both seeds and seedlings in traps and plots respectively, two out of four (50 %) and one out of four (25 %) species exhibited a significant ($P < 0.05$) or a tendency ($0.05 < P < 0.10$) to face a negative density-dependence relation between seed and seedling

TABLE 1

Shade tolerance, frequency of adults, and abundance of seeds and seedlings at the continuous forest and forest fragments (percentages, with respect to the total number of plots or individuals at each stage and site, are presented in parenthesis).

Tolerancia a la sombra, frecuencia de adultos y abundancia de semillas y plántulas en el bosque continuo y fragmentos de bosque (los porcentajes, con respecto al número total de parcelas o individuos en cada estado y sitio, son presentados en paréntesis).

Tree	Shade tolerance	Continuous forest			Forest fragments		
		Total number of plots with adults	Total number of seeds	Total number of seedlings	Total number of plots with adults	Total number	Total number of seedlings
<i>Acrisione denticulada</i>	unknown	0 (0.0)	0 (0.0)	0 (0.0)	6 (30.0)	0 (0.0)	1 (2.5)
<i>Aextoxicon punctatum</i>	tolerant	15 (100.0)	27 (0.5)	23 (17.6)	13 (65.0)	0 (0.0)	2 (5.0)
<i>Aristotelia chilensis</i>	indifferent	7 (46.6)	59 (1.0)	0 (0.0)	16 (80.0)	363 (6.6)	2 (5.0)
<i>Azara integrifolia</i>	unknown	5 (33.3)	0 (0.0)	0 (0.0)	16 (80.0)	0 (0.0)	2 (5.0)
<i>Cryptocarya alba</i>	tolerant	14 (93.3)	35 (0.6)	92 (70.2)	18 (90)	0 (0.0)	19 (47.5)
<i>Gevuina avellana</i>	indifferent	13 (86.7)	9 (0.2)	3 (2.3)	20 (100.0)	68 (1.2)	5 (12.5)
<i>Kageneckia oblonga</i>	unknown	6 (40.0)	147 (2.5)	0 (0.0)	2 (10.0)	0 (0.0)	0 (0.0)
<i>Laurelia sempervirens</i>	unknown	2 (13.3)	825 (14.0)	0 (0.0)	4 (20.0)	38 (0.7)	0 (0.0)
<i>Lithrea caustica</i>	tolerant	0 (0.0)	0 (0.0)	0 (0.0)	16 (80.0)	0 (0.0)	1 (2.5)
<i>Lomatia dentata</i>	tolerant	11 (73.3)	61 (1.0)	0 (0.0)	7 (35.0)	0 (0.0)	0 (0.0)
<i>Lomatia hirsuta</i>	unknown	0 (0.0)	0 (0.0)	0 (0.0)	1 (5.0)	0 (0.0)	1 (2.5)
<i>Luma apiculata</i>	tolerant	2 (13.3)	0 (0.0)	0 (0.0)	16 (80.0)	0 (0.0)	2 (5.0)
<i>Nothofagus glauca</i>	unknown	12 (80.0)	1963 (33.4)	0 (0.0)	12 (60.0)	300 (5.4)	0 (0.0)
<i>Nothofagus obliqua</i>	tolerant	4 (26.7)	2743 (46.7)	0 (0.0)	20 (100.0)	4498 (81.2)	0 (0.0)
<i>Persea lingue</i>	indifferent	14 (93.3)	5 (0.1)	8 (6.1)	14 (70.0)	0 (0.0)	1 (2.5)
<i>Peumus boldus</i>	tolerant	1 (6.7)	4 (0.1)	0 (0.0)	8 (40.0)	17 (0.3)	2 (5.0)
<i>Pinus radiata</i>	tolerant	0 (0.0)	0 (0.0)	0 (0.0)	5 (25.0)	252 (4.5)	0 (0.0)
<i>Raphitamnus spinosus</i>	unknown	3 (20.0)	0 (0.0)	0 (0.0)	8 (40.0)	5 (0.1)	0 (0.0)
<i>Senna stipulacea</i>	unknown	8 (53.3)	1 (0.02)	2 (1.5)	3 (15.0)	0 (0.0)	2 (5.0)
<i>Sophora macrocarpa</i>	unknown	0 (0.0)	0 (0.0)	3 (2.3)	0 (0.0)	0 (0.0)	0 (0.0)
Total	-	15 (100.0)	5879 (100.0)	131 (100.0)	20 (100.0)	5541 (100.0)	40 (100.0)

abundance at the continuous forest (Table 2). However, at the forest fragments seed and seedling abundance of the three species herein assessed were unrelated (Table 2).

Moreover, at both continuous and fragmented forests, seedling abundance of each species was unrelated to seed abundance of other species as a whole, including and excluding the focal species (Table 2).

Richness and abundance of seeds and seedlings

Seed richness was 1.4 times higher at the continuous forest than fragments ($n = 20$, $U = 39$, $P < 0.001$; Table 3), whereas seedling

richness did not differ between continuous forest and fragments ($n = 20$, $U = 135.5$, $P = 0.08$; Table 3). Moreover, seed abundance did not differ between continuous and forest fragments ($n = 20$, $U = 194$, $P = 0.87$; Table 3), despite the seedling abundance was 3.1 times higher at the continuous forest than at fragments ($n = 20$, $U = 52.5$, $P < 0.001$; Table 3).

Seedling richness was unrelated to seed richness at both continuous and fragmented forest (Table 4). Seedling abundance presented a significant negative relationship with seed abundance at the continuous forest but not at the fragments (Table 4).

TABLE 2

Conspecific and heterospecific effects of seed abundance on seedling recruitment including (In) and excluding (Ex) seed abundance of the focal species (b = exponent, see equation 1; r = regression coefficient; n = sample size).

Efectos de la abundancia de las semillas de conespecíficos y heteroespecíficos sobre el reclutamiento de plántulas incluyendo (In) y excluyendo (Ex) la abundancia de semillas de la especie focal (b = exponente, véase ecuación 1; r = coeficiente de regresión; n = tamaño de la muestra).

Regression	Continuous forest					Forest fragments				
	b	r	n	P	Power	b	R	n	P	Power
<i>Aextoxicon punctatum</i>										
Conspecific	0.49	0.48	13	0.10	0.66	-	-	-	-	-
Heterospecific (In)	-0.67	0.25	20	0.28	0.95	-	-	-	-	-
Heterospecific (Ex)	-0.79	0.28	20	0.23	0.93	-	-	-	-	-
<i>Aristolelia chilensis</i>										
Conspecific	-	-	-	-	-	-0.58	0.16	20	0.50	0.98
Heterospecific (In)	-	-	-	-	-	1.33	0.28	20	0.23	0.94
Heterospecific (Ex)	-	-	-	-	-	0.66	0.10	20	0.72	0.97
<i>Cryptocarya alba</i>										
Conspecific	0.72	0.48	19	0.04	0.70	-	-	-	-	-
Heterospecific (In)	-0.29	0.11	20	0.66	0.99	-	-	-	-	-
Heterospecific (Ex)	-0.50	0.17	20	0.48	0.98	-	-	-	-	-
<i>Gevuina avellana</i>										
Conspecific	-1.39	0.77	6	0.07	0.74	1.18	0.36	7	0.43	0.71
Heterospecific (In)	0.69	0.10	20	0.67	0.99	0.51	0.17	20	0.47	0.98
Heterospecific (Ex)	0.62	0.09	20	0.71	0.99	0.15	0.05	20	0.82	0.99
<i>Persea lingue</i>										
Conspecific	-1.04	0.71	10	0.02	0.73	-	-	-	-	-
Heterospecific (In)	0.77	0.15	20	0.52	0.98	-	-	-	-	-
Heterospecific (Ex)	0.84	0.16	20	0.49	0.98	-	-	-	-	-
<i>Peumus boldus</i>										
Conspecific						-0.27	0.22	9	0.57	0.86
Heterospecific (In)	-	-	-	-	-	-1.06	0.26	20	0.27	0.95
Heterospecific (Ex)	-	-	-	-	-	-1.16	0.28	20	0.23	0.94

Diversity and evenness of seeds and seedlings

Seed diversity (H) was 2 times higher at the continuous forest than at fragments ($n = 20$, $U = 65$, $P < 0.001$; Table 3), whereas seedling diversity did not differ between continuous and forest fragments ($n = 20$, $U = 169$, $P = 0.40$; Table 3). Furthermore, at the continuous forest seed diversity was 1.9 times higher than seedling diversity ($U = 1.00$, $P < 0.001$; Table 3), while at the forest fragments seed diversity did not differ respect to seedling diversity ($U = 161$, $P = 0.29$; Table 3).

Seed evenness (J) was 1.6 times higher at the continuous than at forest fragments ($n = 20$, $U = 101$, $P = 0.01$; Table 3), while seedling evenness was 1.2 times lower at the continuous forest with respect to the

fragments ($n = 15$, $U = 41$, $P = 0.03$; Table 3). In addition, at both continuous forest and forest fragments seed evenness was 1.3 and 2.5 times lower than seedling evenness, respectively ($U = 79$, $P = 0.02$ at the continuous forest, and $U = 5$, $P = 0.001$ at the forest fragments; Table 3).

At the continuous forest, seedling diversity was unrelated to seed diversity (Table 4), while in forest fragments there was a significant negative relation between seed and seedling diversity (Table 4).

DISCUSSION

Trees thriving in the fragmented Maulino forest are facing an uncoupling of density-dependence relationships in seed-to-seedling

TABLE 3

Richness, abundance, diversity (Shannon-Wiener index) and evenness (Pielou index) of seeds and seedlings at the continuous forest and forest fragments (mean \pm SE). Dissimilar letter depict significant differences ($P < 0.05$) following Mann-Whitney Tests when comparisons are made between sites (continuous forest and forest fragments), but within the same stage (seed or seedling)

Riqueza, abundancia, diversidad (Índice de Shannon-Wiener) y equidad (Índice de Pielou) de semillas y plántulas en el bosque continuo y los fragmentos de bosque (media \pm EE). Letras disímiles significan diferencias significativas ($P < 0.05$) realizando Pruebas de Mann-Whitney cuando las comparaciones son hechas entre sitios (bosque continuo y fragmentos), pero dentro del mismo estado (semilla o plántula).

Parameter	Continuous forest		Forest fragments	
	Seeds ($n\ 0.5\ m^{-2}$)	Seedlings ($n\ 2\ m^{-2}$)	Seeds ($n\ 0.5\ m^{-2}$)	Seedlings ($n\ 2\ m^{-2}$)
Richness	6.30 ± 0.23^a	2.20 ± 0.24^b	4.40 ± 0.23^b	1.50 ± 0.28^b
Abundance	293.95 ± 74.02^a	6.55 ± 0.88^a	277.80 ± 96.22^a	2.10 ± 0.38^b
Diversity (H)	1.03 ± 0.09^a	0.54 ± 0.09^a	0.52 ± 0.07^b	0.42 ± 0.09^a
Evenness (J)	0.57 ± 0.05^a	0.75 ± 0.05^a	0.36 ± 0.05^b	0.89 ± 0.05^b

TABLE 4

Relationships of richness, abundance, and diversity between seeds and seedlings at the continuous forest and forest fragments (r_s = Spearman rank correlation coefficient, n = sample size).

Relaciones de riqueza, abundancia y diversidad entre semillas y plántulas en el bosque continuo y los fragmentos de bosque (r_s = coeficiente de correlación de Spearman, n = tamaño de la muestra).

Regression	Continuous forest			Forest fragments		
	r_s	P	Power (n)	r_s	P	Power (n)
Seedling richness / seed richness	-0.06	0.81	0.99 (20)	-0.19	0.44	0.99 (20)
Seedling abundance / seed abundance	-0.48	0.03	0.98 (20)	0.25	0.30	0.95 (20)
Seedling diversity / seed diversity	-0.03	0.89	0.99 (20)	-0.69	< 0.01	0.99 (20)

transitions, a change that may lead to a different regeneration dynamic and, consequently, to modifications in composition and structure of the remaining tree assemblage of fragments (Bustamante et al. 2005).

At the Maulino continuous forest the incidence of the negative density-dependent recruitment is roughly the same (75 %) as that of other temperate forests in North America (~80 %, Lambers et al. 2002). Similarly, as in tropical, sub-tropical and temperate forests around the world, the most frequent species exhibit a negative density-dependence relationship in seed to seedling transitions (Harms et al. 2002). Tree species herein assessed are the dominant ones. At the continuous forest, they account for the abundance of 46.7 % of adult trees, 1.4 % of seeds, and 96.2 % of seedlings, while at fragments they account for 20.2 % of the adults, 6.9 % of seeds, and 57.5 % of seedlings. In these species, density-dependent recruitment depends upon the abundance of its own species as heterospecific neighbours do not affect seedling recruitment neither at the continuous nor fragmented forest. This pattern suggests no competitive or allelopathic effects among species, even though this fact must be carefully clarified in further studies (see Willis 2007 for a broader discussion).

Although at forest fragments there is 1.3 times more adult tree species as compared to continuous forest, there is a lower number of species at the seed stage. Furthermore, seed diversity and evenness are higher at the continuous forest, but these patterns do not occur at the seedling level. In fact, seedling richness is similar between fragments and continuous forest but abundance is lower in fragments. The scarcity of seedlings at forest fragments can be a response to higher seed granivory, due to increased consumer abundance in the fragments (Donoso et al. 2003). Putative germination differences can be ruled out because seed germination is similar at the fragments and the continuous forest (Guerrero 2005). Additional factors such as increased mortality may also contribute to this pattern. Despite similar seedling diversities, evenness was significantly lower at the continuous forest indicating over-dominance by a few species. For instance, the abundance

of *Cryptocarya alba* (Mol.) Looser seedlings, a shade-tolerant tree, increases at the continuous forest because presents a massive seed production which germinates in the same reproductive season, thus rendering a great seedling bank (Bustamante et al. 2005). Contrary to our expectations, the lack of density-dependence at forest fragments did not decrease seedling diversity. This fact calls into considering the real importance of negative density dependence relationships for the maintenance of plant diversity in the Maulino forest. In this regard, new research programs should be performed for disentangling these patterns and the confusing relationships between seeds and seedling at the richness, abundance and diversity levels.

Recruitment limitations may involve more than one life stage, and their relative importance might vary in time and space, depending on climate fluctuation and the appearance of canopy gaps, and nurse logs among other factors (Clark et al. 1999). Thus, density-dependence relationships might act at the early life stage by enhancing seedling diversity and by regulating adult tree mortality at later stages as well (Harms et al. 2002, Peters 2003). Thus, since at the Maulino forest fragments seedling diversity does not differ with respect to continuous forest, and evenness is higher in the fragments, anthropogenic disturbances as the forest fragmentation does not translate into a reduction in diversity as we expected, suggesting that niche differences associated with micro-topography as well as the differences associated with a trade-off between survivorship and growth could be enhancing seedling diversity into the fragments (Chesson 2000, Wright 2002). Likewise, the Maulino forest fragments seem to be part of a source-sink system where forest diversity is enhanced by an active colonisation process by bird-dispersed trees, which would maintain a richer tree assemblage with respect to continuous forest (Bustamante et al. 2005, Loreau & Mouquet 1999). In fact, twelve tree species thrive at forest fragments at the seedling stage, none of them presenting any seed yet; of these species, six (*Aextoxicon punctatum* R. et P., *Azara integrifolia* R. et P., *C. alba* (Mol.) Looser, *Lithrea caustic* (Mol.) H. et A., *Luma apiculata* (DC) Burret, and *Persea lingue* (R. et

P.) Nees ex Kopp) present bird-dispersed fleshy-fruits suggesting a colonisation process mediated by birds. Forest fragmentation in fact, does not negatively affect the abundance of the frugivorous birds, which might move seeds across the landscape with no restrictions (Vergara & Simonetti 2004). Additionally, early as well as late successional species coexist at forest fragments, which would contribute to increase tree diversity. However, we cannot test the hypothesis about the future overdominance of shade-intolerant species in fragments, because we registered seed-to-seedling transitions in only few species.

In short, two main conclusions can be obtained from the present report. First, forest fragmentation can significantly modify patterns of seedling recruitment which might have far-reaching consequences upon the biodiversity of plant communities. Nevertheless, in spite of traditional mechanisms invoked as of great importance for the maintenance of plant diversity in forests are not necessarily related to species diversity as previously claimed, the present report highlights the importance of conserving and managing (see Ramos et al. 2008) the Maulino forest fragments because it currently harbours a significant proportion of tree diversity of this forest. Certainly, further studies in other forests and including several years would be desirable.

ACKNOWLEDGEMENTS: We are indebted to the Chilean Forest Service (CONAF) and Forestal Millalemu for kindly allowing us to work in their lands. This research was funded by FONDECYT 1010852 to J.A. Simonetti, and corresponds to M.Sc. Thesis by C.E. Valdivia. This manuscript was improved with comments of two anonymous reviewers.

LITERATURE CITED

- BUSTAMANTE RO, JA SIMONETTI, AA GREZ & J SAN MARTÍN (2005) Fragmentación y dinámica de regeneración del bosque Maulino: Diagnóstico actual y perspectivas futuras. In: Smith-Ramírez C, JJ Armesto & C Valdovinos (eds) Historia, biodiversidad y ecología de los bosques costeros de Chile: 555-564. Editorial Universitaria, Santiago.
- CHESSON P (2000) Mechanisms of maintenance of species diversity. *Annual Reviews of Ecology and Systematics* 31: 343-366.
- CLARK JS, B BECKAGE, P CAMILL, B CLEVELAND, J HILLERISLAMBERS et al. (1999) Interpreting recruitment limitation in forests. *American Journal of Botany* 86: 1-16.
- CONDIT R, SP HUBBELL & RB FOSTER (1994) Density dependence in two understory tree species in a Neotropical forest. *Ecology* 75: 671-680.
- DONOSO D, A GREZ & JA SIMONETTI (2003) Effects of forest fragmentation on the granivory of differently sized seeds. *Biological Conservation* 115: 63-70.
- GREEN DS (1983) The efficacy of dispersal in relation to safe site density. *Oecologia* 56: 356-358.
- GREZ AA, RO BUSTAMANTE, JA SIMONETTI & L FAHRIG (1997) Landscape ecology, deforestation and forest fragmentation: The case of the rui forest. In: Chávez E & J Middleton (eds) Landscape ecology as a tool for sustainable development in Latinamerica. URL: <http://www.conservacion.cl/Quienes/JAS/084.pdf>.
- GUERRERO PC (2005) Procesos de regeneración en un bosque templado fragmentado. M.Sc. Thesis, Facultad de Ciencias, Universidad de Chile, Santiago.
- HARMS KE, SJ WRIGHT, O CALDERÓN, A HERNÁNDEZ & EA HERRE (2000) Pervasive density-dependent recruitment enhanced seedling diversity in a tropical forest. *Nature* 404: 493-495.
- LAMBERS JHR, JS CLARK & B BECKAGE (2002) Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417: 732-735.
- LAURANCE WF, LV FERREIRA, JM RANKIN DE MERONA & SG LAURANCE (1998) Rain forest fragmentation and the dynamics of the Amazonian tree communities. *Ecology* 79: 2032-2040.
- LOREAU M & N MOUQUET (1999) Immigration and the maintenance of local species diversity. *American Naturalist* 154: 427-440.
- MURCIA C (1995) Edge effects in fragmented forests: Implication for conservation. *Trends in Ecology and Evolution* 10: 58-62.
- PETERS HA (2003) Neighbour-regulated mortality: The influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6: 757-765.
- RAMOS C, JA SIMONETTI, JD FLORES & R RAMOS-JILIBERTO (2008) Modelling the management of fragmented forests: Is it possible to recover the original tree composition? The case of the Maulino forest in Central Chile. *Forest Ecology and Management* 255: 2236-2243.
- SAN MARTÍN J & C DONOSO (1996) Estructura florística e impacto antrópico en el bosque maulino de Chile. In: Armesto JJ, C Villagrán & MK Arroyo (eds) Ecología de los bosques nativos chilenos: 153-168. Editorial Universitaria, Santiago.
- SAUNDERS DA, RJ HOBBS & CR MARGULES (1991) Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5: 18-32.
- VÁSQUEZ PA (2004) Efecto de la fragmentación del bosque maulino sobre la herbivoría, sobrevivencia foliar, crecimiento de ramas y fauna de insectos herbívoros asociados a *Aristotelia chilensis* (maqui). B.Sc. Thesis, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago.
- VERGARA PM & JA SIMONETTI (2004) Avian

- response to forest fragmentation in central Chile. *Oryx* 38: 383-388.
- WEBB C & D PEART (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80: 2006-2017.
- WILLIS RJ (2007) The history of allelopathy. Springer. Dordrecht, The Netherlands.
- WILLS C, R CONDIT, RB FOSTER & SP HUBBELL (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a Neotropical forest. *Proceedings of the National Academy of Sciences USA* 94: 1252-1257.
- WRIGHT SJ (2002) Plant diversity in tropical forest: A review of mechanisms of species coexistence. *Oecologia* 130: 1-14.
- ZAR JH (1999) Biostatistical analysis. Prentice Hall, New Jersey.

Associate Editor: Rodrigo Ramos-Jiliberto

Received January 13, 2011; accepted May 9, 2011

