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**RECLUTAMIENTO DENSO-DEPENDIENTE DE PLÁNTULAS EN UN
BOSQUE FRAGMENTADO**

Tesis
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Biológicas con mención en Ecología
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Facultad de Ciencias

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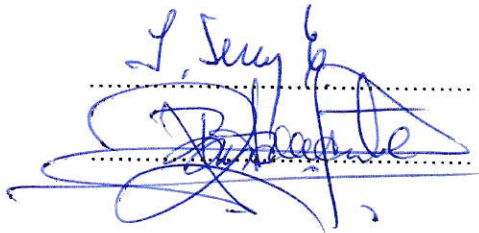


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DENSITY-DEPENDENT SEEDLING RECRUITMENT IN A FRAGMENTED
FOREST

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RESUMEN

El reclutamiento denso-dependiente negativo de plántulas mantiene la diversidad de árboles en bosques tropicales y templados, pues las especies más abundantes no excluyen las menos abundantes. Sin embargo, la fragmentación cambia las condiciones bióticas y abióticas de los fragmentos respecto del bosque continuo, lo cual puede alterar los procesos de reclutamiento y consecuentemente, la diversidad arbórea. Si la fragmentación desarticula el reclutamiento denso-dependiente negativo, esperaríamos una menor diversidad de plántulas en los fragmentos. Se analizó el proceso de reclutamiento, comparando un bosque continuo de 600 ha (R.N. Los Queules) y cuatro fragmentos de bosque nativo de 1 a 6 ha, determinando la abundancia de semillas y plántulas para estimar los efectos de la fragmentación del bosque sobre las transiciones semilla-plántula. En el bosque continuo, tres de las cuatro especies evaluadas presentaron reclutamiento denso-dependiente negativo, mientras que en los fragmentos de bosque ninguna de las tres especies evaluadas presentó reclutamiento denso-dependiente. Adicionalmente, la riqueza y diversidad de semillas fue mayor en el bosque continuo, mientras que la diversidad de plántulas no difirió entre ambos sitios. Por consiguiente, la fragmentación del bosque desarticula el reclutamiento denso-dependiente de plántulas, lo que sin embargo no se traduce en una disminución en la diversidad de plántulas.

ABSTRACT

Density dependence relationships between the abundance of seeds and seedlings of a tree assemblage was estimated in order to evaluate forest fragmentation effects on seed to seedling transitions. In continuous forest, three out of four species presented negative seedling recruitment related to seed abundance, whereas in forest fragments this relationship was uncoupled. In addition, seed richness was 1.5 times higher at the continuous forest, while seedling richness did not differ between these sites. In opposition, seed abundance did not differ between continuous forest and fragments, whereas seedling abundance was three times higher at the continuous forest. Consequently, seed diversity, assessed through Shannon-Wiener's index was two times higher at the continuous forest than fragments, while seedling diversity did not differ between these sites. In the same way, seed evenness, assessed through Pielou's index was 1.5 times higher at the continuous forest contrary to seedling evenness that was 1.3 times lower at the continuous forest. Thus, at the continuous forest seed diversity was around two times higher than seedling diversity, but not at the fragments where seed diversity did not differ respect to seedling diversity. Furthermore, at both continuous forest and fragments seed evenness was 1.3 and 2.5 times lower than seedling evenness respectively. Therefore, we conclude that forest fragmentation affects seedling recruitment uncoupling seed to seedling transitions, which nonetheless did not translate into a reduction in seedling diversity.

Key words: Forest fragmentation, density-dependent recruitment, diversity.

INTRODUCTION

Several mechanisms can account for the maintenance and coexistence of trees species in forests (Chesson 2000). Intra-specific relationships of density-dependence, positive or negative ones, are one of the most important mechanisms (Wills et al. 1997, Wright 2002). Negative density-dependence occurs when nearby conespecifics reciprocally impair their performance more intensively at higher abundances. Allelopathy, intraspecific competition, and pest facilitation may all contribute to modify the probability of individual seedling survival in dense stands affecting seedling diversity. Negative density-dependence contributes to maintain seedling diversity (Harms et al. 2000), as precludes abundant species of eliminating rare ones by covering all available recruitment sites (Condit et al. 1994, Wills et al. 1997, Web & Peart 1999). Similarly, the density of heterospecific neighbours can modify survivorship or reproductive success of trees by facilitating or avoiding seedlings' recruitment among other causes (see Peters 2003). This kind of relationship has been posited as a potentially important mechanism for the maintenance of the arboreal richness in a wide array 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). These factors and the results of its performance, might be modified by forest fragmentation. In fact, fragmentation significantly alters abiotic and biotic conditions of the remnant fragments (Saunders et al. 1991, Murcia 1995). Light and temperature increase, whereas air and soil moisture decrease in fragments compared to continuous forest (Kapos 1989, Murcia 1995). These new abiotic conditions should favour the establishment of shade-intolerant species in forest fragments and inhibit the recruitment of dominant shade-tolerant trees (Laurance et al. 1998). Moreover, biotic conditions such as herbivory, granivory and seed dispersion could be changed by fragmentation (e.g., Aizen & Feinsinger 1994), which can modify tree recruitment due to safe site modifications for seedlings' recruitment (Green 1983). Therefore, biotic and abiotic factors can modify composition and structure of the remaining forest fragments through direct effects on the seedling survivor, as well as indirect effects such as the uncoupling in negative density-dependency (Laurance et al. 1998, Rankin de Mérona & Hutchings 2001).

Currently, the northernmost region of the temperate rainforest of central Chile is severely fragmented and remnants are surrounded by plantations of the exotic pine *Pinus radiata* (Pinaceae). These plantations are acting as an anthropogenic matrix, embracing a large number of small and few large fragments of native forest, which can be regarded as continuous forests (Grez et al. 1997, Bustamante & Castor 1998). In the smaller fragments, soil moisture

and herbivory decrease significantly, while granivory increases (Henríquez 2002, Vega 2001, Donoso et al. 2004). These abiotic and biotic factors may modify the reproductive success of native species and consequently, can alter their regeneration dynamics. In fact, although the more abundant trees in continuous forests are also the more abundant trees in the remnant fragments (Bustamante et al. 2003), the pool of biotic and abiotic conditions in forest fragments has triggered a different regeneration pathway in fragments regarding the continuous forests (Bustamante et al. 2003). 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 (Bustamante et al. 2003). In addition, at the forest fragments there would be an increment of bird-dispersed trees by an active colonisation process (Bustamante et al. 2003). Therefore, in continuous forests, vegetation would be in a stabilizing regeneration dynamic, whereas in forest fragments, tree regeneration dynamic would be lead by non-stabilizing colonisation process, suggesting negative density-dependent seedling recruitment at the continuous forest but not at the forest fragments.

The main goal of this work is to evaluate seed to seedling transitions in a fragmented forest of central Chile. If the stabilizing regeneration dynamics in continuous forest tend to increase negative intraspecific interactions relative to negative interspecific interactions (see Chesson 2000: 343), we expect negative density-dependence relationship between seeds and seedlings' abundance in the continuous forest, while in forest fragments might be unrelated due to its

non-stabilizing regeneration dynamics. In addition, if forest fragmentation affects either abundance or richness of seeds and seedlings, in forest fragments we expect a higher seed diversity compared to seedlings' diversity due to future over-dominance of species such as shade-intolerant trees, whereas in continuous forest we expect a lower seed than seedlings' diversity. In order to reach this goal, seeds and seedlings' diversity were evaluated to assess if and how seedling recruitment in a fragmented forest change. Similarly, if seedling recruitment at the continuous forest is negative density-dependent, we do not expect relationships between seeds' richness or abundance with seedlings' richness or abundance respectively (Harms et al. 2000).

MATERIALS AND METHODS

Study site

The study 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 beeches *Nothofagus obliqua* and *N. glauca* among others (San Martín & Donoso 1996). Specifically, we worked at Los Queules National Reserve and four forest fragments neighbouring to the reserve. 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 between 1 to 6 ha, are surrounded by mature pine plantations of *P. radiata* (Grez et al. 1997, Bustamante & Castor 1998).

Census stations

In July 2001, eighty seed traps were erected within the continuous forest, while other eighty seed traps were placed in forest fragments (20 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. In September 2002, all woody plant less than 50 cm tall were tagged and identified to species in twenty plots of 2 m² at each station. Seedlings at these stations have been tagged from 1998, therefore it was possible to identify the recruits of each year. These plots were placed 1-2 m from the seed trap. Survivors were re-measured and new recruits were tagged and identified in January 2003. Each seed trap and their adjacent plots constitute a census station.

Additionally, surrounding each census station, we registered the frequency of adult trees species in plots of 100 m² (n = 15 at continuous forest, n = 20 at forest fragments).

Regression analyses

To estimate the strength of density dependence on seedling recruitment, we examined the relationship $R = aS^b$ between the abundance of seedlings (R) and the abundance of seeds (S). We assessed the seed-seedling relationship using linear regression of 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 related to seed abundance of the same species. Furthermore, to evaluate the strength of heterospecific density-dependence relationships, seedling abundance of each species was related to seed abundance of all other species as a whole, both including and excluding seed abundance of the focal species.

Power tests was 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 related to richness and

abundance of seeds in order to determine if either seed richness or abundance are good indicators of seedling richness or abundance respectively. Then, we calculated the Shannon-Wiener's Index of diversity (H) at each station to jointly integrate analyses of richness and abundance. Seedlings' diversity and seeds' diversity were related in order to determine if seed diversity is a good indicator of seedling diversity. In the same way, to determine changes in dominance of each species we calculated the Pielou's index of evenness (J) for seed 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 (Table 1). Floristic similarity, assessed through Sorensen's 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).

Since July 2001 to January 2003, we registered a total of 11,435 seeds (5,879 at the continuous forest and 5,556 at the forest fragments) and 171 seedlings (131 at the continuous forest and 40 at the forest fragments). The total

number of adults, seeds and seedlings' species 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 15 species among adults, seeds and seedlings. As adults, we found 15 species, at the seedling stage we found 6 species, whereas at the seed stage 20 species (Table 1). Of these, 20 species were shared between adults and seeds with a floristic similarity of $S = 0.88$; whereas 5 species were shared between seeds and seedlings ($S = 0.77$), and 5 species were shared between adults and seedlings ($S = 0.48$).

In the same way, 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 13 species while at the seed stage 9 species (Table 1). Of these, 8 species were shared between adults and seeds ($S = 0.59$), 3 species were shared between seeds and seedlings ($S = 0.32$), while 20 species were shared between adults and seedlings, with a floristic similarity of $S = 0.77$.

Seed and seedlings abundance of all species inhabiting both the continuous forest and the fragmented forests were unrelated ($R = -0.36$, $P = 0.12$ at continuous forest. $R = 0.24$, $P = 0.31$ at forest fragments. Table 1). However, regarding only those species that presented both seed and seedlings in trap and plots respectively, three out of four trees (75%) exhibited a significant or marginal significant negative density-dependence relation between seeds and seedlings' abundance at the continuous forest (Table 2). However, at the forest fragments seeds and seedlings' abundance of the three species assessed were unrelated (Table 2)

On the other hand, at both continuous and fragmented forests, seedlings' abundance of each species was unrelated to seeds' 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 1.5 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 4), despite the seedling abundance was 3.1 times higher at the continuous forest than 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).

Diversity and evenness of seeds and seedlings

Seed diversity (H) was 2 times higher at the continuous forest than 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 1.5 times higher at the continuous than forest fragments ($n = 20$, $U = 101$, $P = 0.01$. Table 3), contrary to seedling evenness, which was 1.3 times lower at the continuous forest 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 seedlings' diversity (Table 4).

Table 1. Regeneration niche, frequency of adults, and abundance of seeds and seedlings at the continuous forest and forest fragments (percentages are presented in parenthesis).

Tree	Regeneration Niche	Continuous forest			Forest fragments		
		Adults	Seeds	Seedlings	Adults	Seeds	Seedlings
<i>Acrisione denticulata</i>	?	0 (0.0)	0 (0.0)	0 (0.0)	6 (2.8)	0 (0.0)	1 (2.5)
<i>Aetoxicon punctatum</i>	shade-tolerant	15 (12.5)	27 (0.5)	23 (17.6)	13 (6.0)	0 (0.0)	2 (5.0)
<i>Aristolelia chilensis</i>	generalist	7 (5.8)	59 (1.0)	0 (0.0)	16 (7.3)	363 (6.6)	2 (5.0)
<i>Azara integrifolia</i>	?	5 (4.2)	0 (0.0)	0 (0.0)	16 (7.3)	0 (0.0)	2 (5.0)
<i>Cryptocarya alba</i>	shade-tolerant	14 (11.7)	35 (0.6)	92 (70.2)	18 (8.3)	0 (0.0)	19 (47.5)
<i>Gevuina avellana</i>	generalist	13 (10.8)	9 (0.2)	3 (2.3)	20 (9.2)	68 (1.2)	5 (12.5)
<i>Kageneckia oblonga</i>	?	6 (5.0)	147 (2.5)	0 (0.0)	2 (0.9)	0 (0.0)	0 (0.0)
<i>Laurelia sempervirens</i>	?	2 (1.7)	825 (14.0)	0 (0.0)	4 (1.8)	38 (0.7)	0 (0.0)
<i>Lithrea caustica</i>	shade-tolerant	0 (0.0)	0 (0.0)	0 (0.0)	16 (7.3)	0 (0.0)	1 (2.5)
<i>Lomatia dentata</i>	shade-tolerant	11 (9.2)	61 (1.0)	0 (0.0)	7 (3.2)	0 (0.0)	0 (0.0)
<i>Lomatia hirsuta</i>	?	0 (0.0)	0 (0.0)	0 (0.0)	1 (0.5)	0 (0.0)	1 (2.5)
<i>Luma apiculata</i>	shade-tolerant	2 (1.7)	0 (0.0)	0 (0.0)	16 (7.3)	0 (0.0)	2 (5.0)
<i>Nothofagus glauca</i>	?	12 (10)	1,963 (33.4)	0 (0.0)	12 (5.5)	300 (5.4)	0 (0.0)
<i>Nothofagus obliqua</i>	shade-tolerant	4 (3.3)	2,743 (46.7)	0 (0.0)	20 (9.2)	4,498 (81.2)	0 (0.0)
<i>Persea lingue</i>	generalist	14 (11.7)	5 (0.1)	8 (6.1)	14 (6.4)	0 (0.0)	1 (2.5)
<i>Peumus boldus</i>	shade-tolerant	1 (0.8)	4 (0.1)	0 (0.0)	8 (3.7)	17 (0.3)	2 (5.0)
<i>Pinus radiata</i>	shade-tolerant	0 (0.0)	0 (0.0)	0 (0.0)	5 (2.3)	252 (4.5)	0 (0.0)
<i>Raphitamnus spinosus</i>	?	3 (2.5)	0 (0.0)	0 (0.0)	8 (3.7)	5 (0.1)	0 (0.0)
<i>Senna closiana</i>	?	8 (6.7)	1 (0.02)	2 (1.5)	3 (1.4)	0 (0.0)	2 (5.0)
<i>Sophora macrocarpa</i>	?	0 (0.0)	0 (0.0)	3 (2.3)	0 (0.0)	0 (0.0)	0 (0.0)
Total			5,879	131		5,541	40

Table 2. Conspecific and heterospecific effects of seeds' abundance on seedlings' recruitment including (In) and excluding (Ex) seeds' abundance of the focal species (b = slope, r = regression coefficient, n = sample size. Significant and marginal significant relations are presented in bold).

Regression	Continuous forest					Forest fragments				
	b	r	n	P	Power	b	r	n	P	Power
<i>Aetoxicon 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>Aristotelia 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

Table 3. Richness, abundance, diversity (Shannon-Wiener's index) and evenness (Pielou's index) of seed and seedlings at the continuous forest and forest fragments (mean \pm se).

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 \pm 0.23	2.20 \pm 0.24	4.40 \pm 0.23	1.50 \pm 0.28
Abundance	293.95 \pm 74.02	6.55 \pm 0.88	277.80 \pm 96.22	2.10 \pm 0.38
Diversity (H)	1.03 \pm 0.09	0.54 \pm 0.09	0.52 \pm 0.07	0.42 \pm 0.09
Evenness (J)	0.57 \pm 0.05	0.75 \pm 0.05	0.36 \pm 0.05	0.89 \pm 0.05

Table 4. Relationship 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. Significant relations are presented in bold).

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)

DISCUSSION

Trees thriving in fragmented Maulino forest are facing an uncoupling in density-dependence relationships in the seed-to-seedling transition. Changes in density-dependence relations and consequently in diversity at the early stage of the tree

life cycles may in turn lead to a community drift and therefore to modify the composition and structure of the remaining tree assemblage into the fragments.

In the same way of tropical, sub-tropical and temperate forests around the world, at the Maulino continuous forest the more frequent species exhibit a negative density-dependence relationship in seed to seedling transitions (see Wills et al. 1997, Web & Peart 1999, Harms et al. 2002). Therefore, as we expected, in fragments the negative density dependent seedling recruitment was uncoupled, which could be lead the different regeneration dynamic (Bustamante et al. 2003). Tree species assessed in our study are the dominant ones. At the continuous forest, they account for 46.7% of the adult trees, 1.4% of the seeds, and 96.2% of the seedling abundance, while at the forest fragments they account for 20.2% of the adult frequency, 6.9% of the seeds, and 57.5% of the seedling abundance. Furthermore, the incidence of the negative density-dependent seedling recruitment at the continuous forest (75%) is similar to other temperate forest in North America (~80%, Lambers et al. 2002). Moreover, the ability of heterospecific neighbours to affect the seedling recruitment through density-dependent mechanisms, it seems to be not important neither at the continuous nor fragmented forest.

The altered density-dependent seedling recruitment at the forest fragments is in accordance with the theoretical Markovian model (Bustamante et al. 2003), which pointed out to the uncoupling in seed to seedling transitions as a potentially important factor that might be triggering a change in the

regeneration dynamic, and consequently modifying the coexistence of trees species (Bustamante et al. 2003).

Even though at the forest fragments grow 1.3 times more adult tree species compared to continuous forest, at both continuous and fragmented forest seed rain is the same in terms of the abundance, but in the fragments arrive a lower number of species compared to continuous forest. This finding differs from Bustamante et al. (2003), who registered only twelve adult tree species compared to the nineteen species reported here. Furthermore, seed diversity equally than evenness is higher at the continuous forest. Nevertheless, this pattern does not translate into a similar seedling pattern. In fact, seedling richness is equal between fragments and continuous forest but abundance is lower in the first one. Therefore, the lower number of seedlings observed at the fragments can be a response of the lower seedling herbivory together with the higher seed granivory, but not due to seed germination because it does not differ at the fragments compared to continuous forest (Vega 2001, Donoso et al. 2004, Guerrero 2003). The higher seed granivory is probably due to a higher rodents' abundance thriving into the fragments (Bustamante et al. 2003). Thus, despite at the continuous forest and fragments there are equal seedling diversity, at the continuous forest evenness was significantly lower indicating an over-dominance by a few species. Accordingly, *Cryptocarya alba*, a shade-tolerant tree, increases their seedling abundance at the continuous forest because presents a massive seed productions which germinate in the same

reproductive season, rendering a great seedling bank onto the forest floor, which is accumulated throughout the time (Bustamante et al. 2003).

Although at the continuous forest the abundant species present a negative density-dependent seedling recruitment, it does not translate into a higher seedling diversity, and contrary to our expectations, the negative density-dependence does not enhance seedling diversity. For this reason, despite the uncoupling of density dependent relations in seed to seedling transitions, the pool of biotic and abiotic changes could be responsible of the higher evenness observed into the fragments respect to continuous forest (Bustamante et al. 2002).

Recruitment limitation may involve more than one life stage, and relative importance might vary in time and space, depending on climate fluctuation and the appearances of canopy gaps, and nurse logs among other factors (Clark et al. 1999). Thus, density-dependence relationships that act at the early life stage enhancing seedlings' diversity, and it regulates adult tree mortality at later stages as well (Harms et al. 2002, Peters 2003). Nevertheless, there are other mechanisms that also may enhance the species diversity, which are mutually compatible among them (Wright 2002). For instance, niche differences are evident from non-random spatial distributions along microtopographic gradients and from a survivorship-growth trade-off during regeneration. Host-specific pests, which can be regarded as a particular case of negative density-dependence, reduce recruitment near reproductive conspecific adults (i.e., the Janzen-Connell effect). These mechanisms together with the negative density-

dependence as such, have received strong support to explain the tree diversity in forests (Chesson 2000, Wright 2002).

Thus, since at the Maulino forest fragments seedling diversity does not differ respect to continuous forest, and evenness is higher in the fragments, anthropogenic perturbations 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 trade-off between survivorship and growth could be enhancing seedlings' diversity into the fragments (Wright 2002). On the other hand, 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 further the spatial heterogeneity would maintain a richest tree assemblage respect to continuous forest (Bustamante et al. 2003, Loreau & Mouquet 1999). In fact, twelve tree species thrives at forest fragments at the seedling stage, of which nine does not present any seed; of these species, six (*Aetoxicon punctatum*, *Azara integrifolia*, *Cryptocarya alba*, *Lithrea caustica*, *Luma apiculata* and *Persea lingue*) present bird-dispersed fleshy-fruits suggesting a colonisation process mediated by birds. It is worth noting that forest fragmentation does not negatively affect the abundance of the frugivorous birds, which might move the seeds across the fragments with no restrictions (Simonetti & Vergara 2003).

In addition, inside the fragments it is possible to find several species of early as well as later succession stages, which would contribute to increase tree

diversity into the fragments. However, we are unable of accepting or rejecting our hypothesis about the future over-dominance of shade-intolerant species inside the fragments, because we registered the seed to seedling transition only in few species respect to the total species growing in the fragments and continuous forest.

Different recruitment rates of woody species in forest fragments compared to continuous forests might lead to long-term modifications in composition and structure of the flora (Bustamante et al. 2003). Consequently, altered seedling recruitment as expressed in forest fragments might have far reaching consequences upon the biodiversity of the Maulino forest.

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REFERENCES

AIZEN, M.A. & FEINSINGER, P. 1994. Forest fragmentation, pollination and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75: 330-351.

- BECKER, P., LEE, L.W., ROTHMAN, E.D., & HAMILTON, D.W. 1985. Seed predation and the coexistence of tree species: Hubbell's models revisited. *Oikos* 44: 382-390.
- BUSTAMANTE, R.O. & CASTOR, C. 1998. The decline of an endangered temperate ecosystem: the ruii (*Nothofagus alessandrii*) forest in central Chile. *Biodiversity and Conservation* 7: 1607-1626.
- BUSTAMANTE, R.O., SIMONETTI, J.A., GREZ, A.A. & SAN MARTÍN, J. 2003. La fragmentación del bosque Maulino y su dinámica regeneracional: diagnóstico actual y perspectivas futuras. In: Smith-Ramírez, C.S., Armesto, J.J. & Valdovinos, C. (eds.). Historia, biodiversidad y conservación de los bosques de la Cordillera de la Costa, Chile. Editorial Universitaria, Santiago: en prensa.
- CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Reviews of Ecology and Systematic* 31: 343-366.
- CLARK, J.S., BECKAGE, B., CAMILL, P., CLEVELAND, B., HILLERISLAMBERS, J., LICHTER, J., MACLACHLAN, J., MOHAN, J. & WYCKOFF, P. 1999. Interpreting recruitment limitation in forests. *American Journal of Botany* 86: 1-16.
- CONDIT, R., HUBBELL, S.P. & FOSTER, R.B. 1994. Density dependence in two understory tree species in a Neotropical forest. *Ecology* 75: 671-680.
- DEBINSKY, D.M. & HOLT, R.D. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342-355.

- DONOSO, D., GREZ, A. & SIMONETTI, J.A. 2004. Effects of forest fragmentation on the granivory of differently sized seeds. *Biological Conservation* 115: 63-70.
- GUERRERO, P. 2003. Efectos de la fragmentación del bosque Maulino costero sobre la germinación y reclutamiento de *Cryptocarya alba* (Lauraceae). Seminario de título, Biología Ambiental. Facultad de Ciencias, Universidad de Chile. Santiago.
- GREEN, D.S. 1983. The efficacy of dispersal in relation to safe site density. *Oecologia* 56: 356-358.
- GREZ, A.A., BUSTAMANTE, R.O., SIMONETTI, J.A. & FAHRIG, L. 1997. Landscape ecology, deforestation and forest fragmentation: the case of the rui forest. En: Chávez, E. & Middleton, J. (eds.). *Landscape ecology as a tool for sustainable development in Latinoamerica*. www.brocku.ca/epi/lebk/grez.html.
- HARMS, K.E., WRIGHT, S.J., CALDERÓN, O., HERNÁNDEZ, A. & HERRE, E.A. 2000. Pervasive density-dependent recruitment enhanced seedling diversity in a tropical forest. *Nature* 404: 493-495.
- HENRÍQUEZ, C.A. 2002. El dilema de *Lapageria rosea* en bosques fragmentados: ¿Calidad o cantidad de la progenie?. Tesis de Doctorado, Facultad de Ciencias, Universidad de Chile. Santiago.
- HUBBELL, S.P. & FOSTER, R.B. 1986. Commonness and rarity in a Neotropical forest: implications for tropical tree conservation. In: Soulé,

- M.E. (ed.). Conservation Biology: the science of scarcity and diversity. Sinauer, Sunderland: 205-231.
- KAPOS, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazons. *Journal of Tropical Ecology* 5: 173-185.
- LAMBERS, J.H.R., CLARK, J.S. & BECKAGE, B. 2002. Density-dependent mortality and the latitudinal gradient in species diversity. *Nature* 417: 732-735.
- LAURANCE, W.F., FERREIRA, L.V., RANKIN DE MERONA, J.M. & LAURANCE, S.G. 1998. Rain forest fragmentation and the dynamics of the Amazonian tree communities. *Ecology* 79: 2032-2040.
- LOREAU, M. & MOUQUET, N. 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, H.A. 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.
- RANKIN DE MÉRONA, J.M. & HUTCHINGS, R.W. 2001. Deforestation effects at the edge of an Amazonian forest fragment. In: Bierregard, R.O., Gascon, C., Lovejoy, T.E. & Mesquita, R. (eds.). *Lesson from Amazonia. The ecology and conservation of a fragmented forest.* Yale University Press, London.

- SAN MARTÍN, J. & DONOSO, C. 1996. Estructura florística e impacto antrópico en el bosque maulino de Chile. In: Armesto, J.J., Villagrán, C. & Arroyo, M.K. (eds.). Ecología de los bosques nativos chilenos. Editorial Universitaria, Santiago: 153-168.
- SAUNDERS, D.A., HOBBS, R.J. & MARGULES, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.
- SIMONETTI, J.A. & VERGARA, P. 2003. Avian response to fragmentation of the maulino forest in central Chile. *Oryx* (in revision).
- VEGA, M.I. 2001. Efecto de la fragmentación del bosque maulino sobre la herbivoría de plántulas de *Cryptocarya alba* (peumo). Memoria de Título, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile. Santiago.
- WEBB, C. & PEART, D. 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80: 2006-2017.
- WILLS, C., CONDIT, R. FOSTER, R.B. & HUBBELL, S.P. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a Neotropical forest. *Proceedings of National Academy of Science, USA* 94: 1252-1257.
- WRIGHT, S.J. 2002. Plant diversity in tropical forest: a review of mechanisms of species coexistence. *Oecologia* 130: 1-14.
- ZAR, J.H. 1999. *Biostatistical Análisis*. Prentice Hall. New Jersey.