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**MODELLING THE MANAGEMENT OF FRAGMENTED  
FORESTS. IS IT POSSIBLE TO RECOVERY THE ORIGINAL  
TREE COMPOSITION? THE CASE OF THE MAULINO FOREST  
(CHILE)**

**Tesis**

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Ecología y Biología Evolutiva**

**Facultad de Ciencias**

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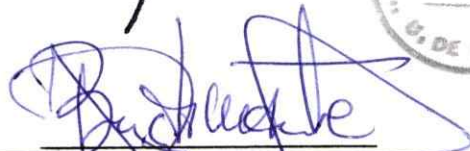
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*Dedicado a quienes  
no tienen voz para pedir  
por un mundo sano*



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**Modelling the management of fragmented forests. Is it possible to recover the original tree composition? The case of the Maulino forest (Chile)**

**Abstract**

In the fragmented Maulino forest (Chile), important differences in the relative frequencies of species that compose the forest, between seedlings and mature trees, are evidences of a changing replacement dynamics. Through iterations of a stationary Markov model, the long-term projection of this dynamics has demonstrated that future composition of Maulino forest fragments will be different in relation to continuous forest of the Reserva Nacional los Queules (RNLQ). In particular, we focused on the persistence probability, which is highest in *A. chilensis*, and too low in *N. glauca*, facts that somehow are related with the predictions at future, of dominance for the first species and almost extinction for the second one. To answer the question if just this species, the most affected by fragmentation, are the drivers of the general compositional dynamics, and therefore, if their management would be enough to avoid long-term changes in fragments and return the composition toward states more similar to the continuous forest, in this study we used the Markov matrix previously constructed, to calculate the future stable composition under management simulations: Reduction of *A. chilensis* recruitment, increase of *N. glauca* recruitment, and combined treatment.



Compositional future stages of fragments, with and without treatment, were compared with the expected composition for a continuous Maulino forest (RNLQ), to evaluate the management efficiency. A sensitivity analysis of the stable composition was developed to assess the intensity of changes in the future composition caused by the treatments, and determine to what extent the recruitment of other coexisting species contributes to the future frequencies of *A. chilensis* and *N. glauca*.

The management treatments reduced the predicted compositional divergence between fragments and continuous forest. The combined treatment achieved the highest effects, increasing the frequency of *N. glauca* and reducing the frequency of *A. chilensis*, but in no one case it was possible to avoid the long-term compositional change of fragments. Nevertheless, the only reduction of *A. chilensis* recruitment beneath its own mature tree was able to diminish in almost a third the compositional divergence, since this species showed the highest contributions to the general dynamics. Other species were identified as potential focus of conservation, either by their association with *N. glauca*, or by strong competition with *A. chilensis*.

**Key words:** Composition, Markov matrix, Persistence, Recruitment, Replacement dynamics.

## **Modelando el manejo de bosques fragmentados. ¿Es posible recuperar la composición arbórea original? El caso del bosque Maulino (Chile).**

### **Resumen**

En el bosque Maulino fragmentado (Chile), diferencias importantes entre plántulas y árboles adultos, en la frecuencia relativa de las especies que componen el bosque, son evidencias de una dinámica de reemplazos cambiante. A través de iteraciones de un modelo Markoviano estacionario, la proyección de esta dinámica a largo plazo ha demostrado que la composición futura de fragmentos de bosque Maulino será diferente en relación con el bosque continuo de la Reserva Nacional los Queules (RNLQ). En particular, nosotros nos enfocamos en la probabilidad de persistencia, máxima en *A. chilensis*, y muy baja en *N. glauca*, hechos que de algún modo están relacionados con las predicciones a futuro, de dominancia para la primera especie y casi extinción para la segunda. Para responder a la pregunta de si estas especies, justo las más afectadas por la fragmentación, son las que guían la dinámica general composicional, y por tanto, si su manejo pudiese ser suficiente para evitar los cambios a largo plazo en los fragmentos y retornar la composición hacia estados más parecidos a un bosque no disturbado, en este estudio nosotros usamos la matriz Markoviana previamente construida, para calcular la composición estable futura, bajo simulaciones de manejo: Reducción del reclutamiento de *A. chilensis*, incremento del reclutamiento de *N. glauca*, y tratamiento combinado.

Los estados futuros en fragmentos, con y sin tratamientos, fueron comparados con la composición esperada para un bosque no disturbado de Bosque Maulino (RNLQ), para evaluar la eficiencia de manejo. Un análisis de sensibilidad de la composición estable fue desarrollado para conocer la intensidad de cambio en la composición futura, provocado por los tratamientos, y determinar hasta qué punto el reclutamiento de otras especies coexistentes contribuye a las frecuencias futuras de *A. chilensis* y *N. glauca*.

Los tratamientos de manejo redujeron la divergencia composicional predicha entre fragmentos y bosque continuo. El tratamiento combinado logró los mayores efectos, incrementando la frecuencia de *N. glauca* y reduciendo la frecuencia de *A. chilensis*, pero en ningún caso fue posible evitar que los fragmentos cambiaran a largo plazo. Sin embargo, la sola reducción en el reclutamiento de *A. chilensis* bajo su propio árbol fue capaz de disminuir en casi un tercio la divergencia composicional, ya que esta especie tuvo los mayores aportes a la dinámica general. Otras especies fueron identificadas como focos potenciales de conservación, ya sea por su asociación con *N. glauca*, o por fuerte competencia con *A. chilensis*.

**Palabras clave:** Composición, Matriz Markoviana, Persistencia, Reclutamiento, Dinámica de reemplazos.

## **Modelling the management of fragmented forests. Is it possible to recover the original tree composition? The case of the Maulino forest (Chile)**

### **Introduction**

Land disturbances trigger a sequence of changes on forest structure and composition along time. Although natural disturbances are a persistent driver of tree compositional dynamics, currently anthropogenic disturbances are increasing at alarming rates, leading ecosystems toward a reduction in biodiversity (Novacek and Cleland, 2001). Among them, fragmentation is the most important process affecting forests, associated to extensive deforestation worldwide. During the 90's, over five millions of hectares of tropical forest were yearly deforested, and similar losses are expected for the southern temperate forest in the present century (Sala et al., 2000; Achard et al., 2002).

Fragmentation can induce long-term changes on forest composition through the richness reduction associated to habitat loss (Williams-Linera, et al, 1998; Fahrig, 2001; Hill and Curran, 2001; Simonetti et al., 2001), by the invasion of species from the vegetation matrix surrounding the fragments (Lovejoy, et al., 1986; Tabarelli et al., 1990; Fox et al., 1997; Honnay et al., 2002), or by differential recruitment along an edge-center environmental gradient (Chen et al., 1992; Laurance et al., 1998; Oosterhoorn and Kappelle, 2000; Harper et al., 2005). In this scenario, even if no further area reduction

occurs, successional changes could lead the composition toward a state different from the original forest (Turner et al., 1996; Oliveira-Filho et al., 1997).

Given that forest fragments can be considered as the last reservoirs of threatened tree species, and they are a potential focus of dispersion and recovery (Turner and Corlett, 1996; Chave et al., 2002; Köhler et al., 2003), it is necessary to conserve them, developing management plans to maintain their composition in the long term. One of such strategies is planting native tree species (Ashton et al., 2001), but it is difficult to determine the efficiency of this approach, as monitoring is required during decades and centuries. A solution to this problem is the employment of mathematical models that simulate the compositional dynamics.

A widely used modelling technique in successional studies is the Markov Chain (Orloci and Orloci, 1988; Acevedo et al., 1995; Logofet and Lesnaya, 2000; Yemshanov and Perera, 2002), which is based on the replacement dynamics among species or sucesional groups. A Markov matrix is built with the probabilities  $P_{ij}$  that one adult tree of  $j$ -th species could be replaced in the future by a recruit of the  $i$ -th species, at any single point in space. The product between the projection matrix and the vector of the initial composition, gives the composition predicted at time  $t+1$ . The stable, *climax* state toward which succession converges (Connell and Slatyer, 1977; Rees et al., 2001) can be numerically approached by multiple iterations of the model, or is calculated analytically through the dominant right eigenvector (Baker, 2989; Caswell, 2001). The components of a Markov matrix can be easily manipulated, simulating diverse hypothetical situations in the present, to assess their effects on the future stable composition (Ogden, 1983).

One case of compositional changes driven by fragmentation has been described in the Coastal Maulino forest (Chile). This south temperate ecosystem is part of a hotspot of biodiversity (Myers et al., 2000; Smith-Ramírez, 2004) and has been strongly affected by agricultural and forestry activities (Lara and Veblen, 1993; Echevarría et al., 2006). A stationary Markov model has predicted significant changes in species frequencies in the fragments, changing them from a forest to an evergreen shrubland (Bustamante et al., 2005). In this work we focused in the major changes predicted by Bustamante et al. (2005)(Appendix 1), as the dominance of the pioneer species *Aristotelia chilensis*, and the disappearance of *Nothofagus* species, which seems to be the result of extreme values in the data matrix from fragments, as a high probability of recruitment of *A. chilensis* beneath its own mature tree, and beneath *Quillaja saponaria*, and the low self-replacement probability of *Nothofagus glauca*. These patterns could suggest that some replacements are more important than others to lead the compositional forest dynamics, and therefore, identified them could be a key piece for the design of successful restoration plans.

To avoid the loss of some tree species to expenses of the over-dominance of others, we simulated management treatments on recruitment of the most affected species by fragmentation, expecting that fragments recover the floristic identity of a continuous, undisturbed Maulino forest. Thus, if the increase of *A. chilensis* and the reduction of *N. glauca* are the main drivers of the compositional divergence between fragments and continuous forest, we will avoid the long-term compositional changes in the fragments by (i) reduction of *A. chilensis* recruitment beneath adult trees of the same specie, (ii)

reduction of *A chilensis* recruitment beneath *Q. saponaria*, and (iii) increase of the recruitment of *N. glauca* beneath adults of the same specie.

## Methods

### *Study site*

Data used in this study arise from a sampling of seedlings and adult trees in the continuous forest at the Reserva Nacional Los Queules (RNLQ)(35°59'19''S, 72°41'15''W), and four forest fragments near the Reserve, isolated by *Pinus radiata* plantations (Bustamante et al., 2005). Among the species that compose the coastal Maulino forest, *N. glauca* has been classified as "vulnerable" by the IUCN (2006), considered as a highly persistent component that favors the establishment of late-successional species (Veblen et al., 1981; Fajardo and Alaback, 2005). On other side, *A. chilensis*, a short-cycle pioneer tree from central Chile, is known as an invasive species able to establish association with introduced species (Armesto and Pickett, 1985; Dirnböck et al., 2003).

### *Markov matrices and simulations*

Matrices of Reserve and fragments (Bustamante et al., 2005) were used in a Markov stationary model (the matrix elements are assumed as constant values along time; Waggoner and Stephens, 1970) to calculate the dominant right eigenvector and

determine the future stable composition at each place (Matlab 6.1, The MathWorks, Inc, 2001). To estimate the intensity of long-term change, we compared these predicted compositions with the current state of continuous forest (Reserve), through Spearman rank correlations (Statistica 6.0; StatSoft Inc, 2001); significant correlations will indicate high similarity with the original Maulino forest.

The simulation of management in fragments, considering both planting recruits of threatened species and reducing the recruitment of invasive species, involves the modification of one or more elements of the Markov matrix, where each element represents the probability  $P_{ij}$  that one species replaces itself or another species in a given site. Elements on the matrix diagonal are important for the compositional dynamics, because they indicate the probability that one species recruits in a site already occupied by an adult of the same specie; i.e. persistence probability.

Since these *persistence probabilities* were too high for *A. chilensis* and too low for *N. glauca* in the matrix of fragments, we modified their values: first, reducing the persistence of *A. chilensis* ( $P_{aa}$ ) and second, increasing the persistence of *N. glauca* ( $P_{nn}$ ). A third treatment was the reduction of the probability that *A. chilensis* replaces *Q. saponaria* ( $P_{aq}$ ), species beneath which *A. chilensis* recruits are at high frequency (Appendix 2). All treatments had four levels of intensity, changing the values at equal increments or decrements (Table 1). A fourth treatment was the simultaneous combination of the three first ones, at the same intensities. In all cases, the proportional form of compensation was employed to adjust the matrix elements, before to determine the stable compositions (Caswell, 2001).



Table 1. Treatments of change on  $P_{ij}$  values in the matrix from fragments. In parenthesis, the original values of these probabilities, according to Bustamante et al. (2005).

Species	Code	$P_{ij}$ to change	Treatment and intensity of change
<i>A. chilensis</i>	TR1	1. Probability of persistence $P_{aa}$ (0.54)	Reduction to 0.41, 0.28, 0.15 and 0.02
	TR2	2. Probability of replacing to <i>Quillaja saponaria</i> $P_{aq}$ (0.27)	Reduction to 0.21, 0.15, 0.09 and 0.03
<i>N. glauca</i>	TR3	3. Probability of persistence $P_{nn}$ (0.06)	Increase to 0.2, 0.34, 0.48 and 0.62
Both species	TR4	4. Simultaneous combination of changes on $P_{aa}$ , $P_{aq}$ , and $P_{nn}$	Example of the lowest change intensity: $\downarrow P_{aa}=0.41$ , $\downarrow P_{aq}=0.21$ and $\uparrow P_{nn}=0.2$

Through Spearman rank correlations, sixteen future stable compositions resulting from modified matrices were compared with the continuous Maulino forest of the Reserve, at the present. This last was considered as the “expected” composition, and Chi-square values testing the goodness of fit between the expected and “observed” (fragments) compositions were used to evaluate the efficiency of the management treatments. At higher Chi-square values, higher the dissimilarity between compared compositions.

The amount of change that a treatment causes in the future composition depends of the contribution of each species to the forest replacement dynamics. Therefore, we performed a sensitivity analysis of the original matrix from fragments (matrix without treatments), which determines the quantity of change in the stable composition of fragments, generated by modifications of  $P_{ij}$  values. The sensitivity of the stable future composition results from the differentiation of dominant right eigenvector of the matrix regarding  $P_{ij}$  (Caswell, 2001):

$$\frac{\partial \mathbf{w}_1}{\partial p_{ij}} = w_j^{(1)} \sum_{m=1}^s \frac{v_i^{(m)}}{\lambda_1 - \lambda_m} \mathbf{w}_m \quad (1)$$

Where:  $\mathbf{w}_1$  is the dominant right eigenvector,  $\mathbf{w}_m$  is the right eigenvector of the  $m$ -th eigenvalue ( $1 \dots m$ ),  $v_i^{(m)}$  is the  $i$ -th component from the  $m$ -th left eigenvector ( $1 \dots s$ ),  $\lambda_1$  is the dominant eigenvalue, and  $\lambda_m$  is the  $m$ -th eigenvalue. To obtain comparable and additive values of sensitivity, we employed the scaled and proportionally compensated form (Hill et al., 2004)(Appendix 3):

$$\frac{d \frac{\mathbf{w}_1}{\|\mathbf{w}_1\|}}{dp_{ij}} = \frac{\partial \frac{\mathbf{w}_1}{\|\mathbf{w}_1\|}}{\partial p_{ij}} + \sum_{m=1}^s \frac{\partial \frac{\mathbf{w}_1}{\|\mathbf{w}_1\|}}{\partial p_{mj}} \frac{\partial p_{mj}}{\partial p_{ij}} \quad (2)$$

From the sensitivity of the dominant right eigenvector, four important estimators were extracted for evaluating the contribution of *A. chilensis* and *N. glauca* to the general compositional dynamics:

$\frac{\partial \mathbf{w}_1}{\partial P_{nn}}$  Net changes in the relative abundance of each species within the stable composition, caused by changes in the persistence probability of *N. glauca* ( $P_{nn}$ ).

$\frac{\partial \mathbf{w}_1}{\partial P_{aa}}$  Net changes in the relative abundance of each species within the stable composition, caused by changes in the persistence probability of *A. chilensis* ( $P_{aa}$ ).

$\sum_{j=1}^s \frac{\partial w_{Ngl}^{(1)}}{\partial P_{ij}}$  Changes in the frequency of *N. glauca* within the future stable composition, caused by changes in the recruitment of each  $i$  species ( $1 \dots s$ ).

$$\sum_{j=1}^s \frac{\partial W_{Ach}^{(1)}}{\partial P_{ij}}$$

Changes in the frequency of *A. chilensis* within the future stable composition, caused by changes in the recruitment of each *i* species (1...s).

## Results

Comparison between present and future composition in the continuous forest of RNLQ showed a highly significant similarity ( $r_s=0.81$ ,  $P<0.01$ ). At the present, the fragments are dissimilar to the continuous forest ( $r_s=0.31$ ,  $P=0.19$ ), but this compositional divergence will be almost ten times wider in the future (Table 2, Figure 1).

With management treatments, the stable future composition of fragments was less divergent with the expected composition (currently composition of the continuous forest), than what originally was predicted (FRF) (Figure 1). The most drastic intensities of treatment caused the lowest dissimilarities with the continuous forest, and the combination of treatments was the most efficient method to reduce the compositional divergence, while the increase of the  $P_{nm}$  and the reduction of  $P_{aq}$  were the less effective treatments. In its maximum intensity, the reduction of  $P_{aa}$  value was able to diminish in a third the predicted compositional divergence (dissimilarity reduction: 35.1%). No one management treatment, however, was able to recover the current composition of fragments, or reach a state similar to the expected composition (Figure 1).

Table 2. Comparisons between the future stable composition of fragments with (TR) or without (FRF) management treatments, and the expected composition for a continuous Maulino forest (RNLQ at the present). Comparisons of reference with the expected composition: continuous forest at future (CFF) and fragments at the present (FRP).

Composition	$P_{ij}$ modified values	Intensity of treatment	$r_s$	P
CFF			0.807	***<0.001
FRP			0.311	0.195
FRF			0.098	0.689
TR1 Reduction of $P_{aa}$	0.41	1	0.125	0.610
	0.28	2	0.130	0.595
	0.15	3	0.130	0.595
	0.02	4	0.130	0.595
TR2 Reduction of $P_{aa}$	0.21	1	0.098	0.689
	0.15	2	0.098	0.689
	0.09	3	0.098	0.689
	0.03	4	0.101	0.681
TR3 Increasing of $P_{nn}$	0.20	1	0.121	0.623
	0.34	2	0.121	0.623
	0.48	3	0.128	0.600
	0.62	4	0.142	0.563
TR4 Combination of treatments	TR1+TR2+TR3 At the same intensities	1	0.147	0.548
		2	0.152	0.533
		3	0.160	0.512
		4	0.208	0.392

With the most intensive level, the  $P_{aa}$  reduction changed the frequency of *A. chilensis* within the future stable composition from 16.5% to 8.5%, whereas the  $P_{nn}$  increasing changed the frequency of *N. glauca* from 2.7% to 6.5%. The combined treatment at its maximum intensity, reached the highest effect on the future frequencies of this species,

with final percentages of 7.4% in both cases, whereas the  $P_{aq}$  reduction had the lowest effectiveness (Figure 2).

Figure 1. Effectiveness of treatments in fragments, under the goodness-of-fit test ( $\chi^2$ ) between the observed (in legend) and the expected (RNLQ at the present) composition. The distance between present (FRP) and future (FRF) states of fragments without management, estimates the long-term compositional divergence predicted by Bustamante et al. (2005).

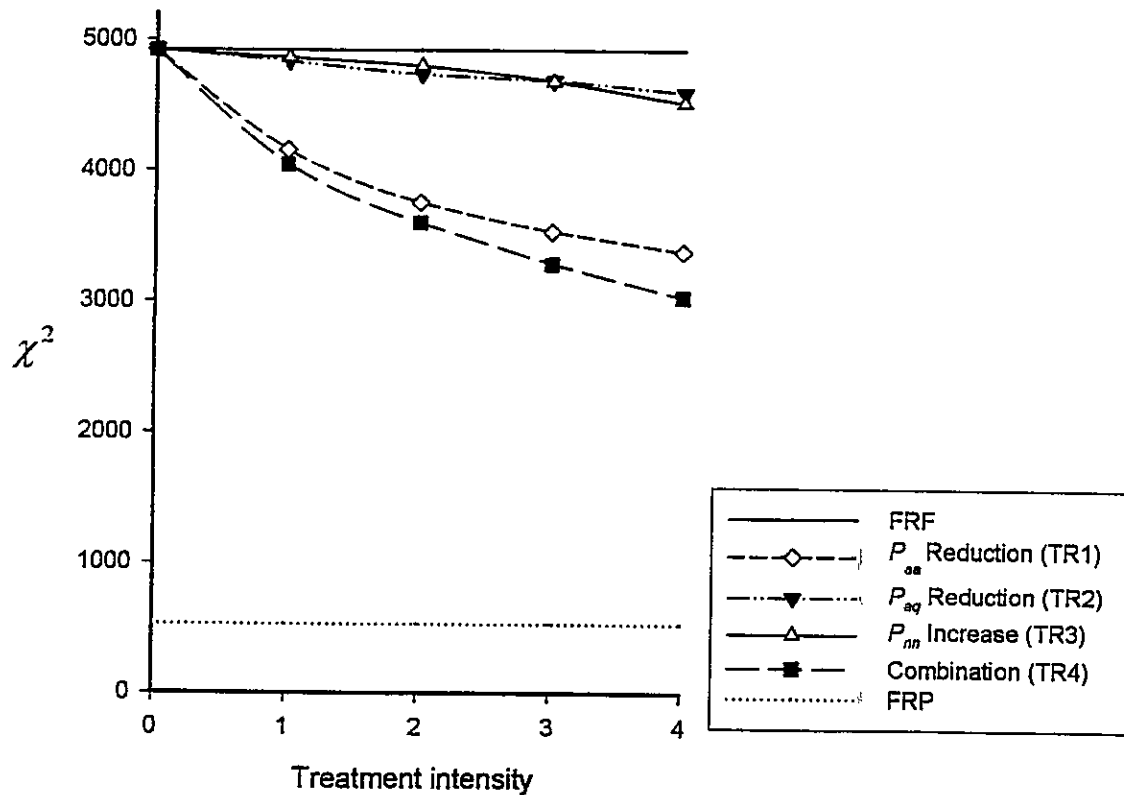


Figure 2. Changes in the frequency of *A. chilensis* and *N. glauca* within the projected stable composition, caused by management treatments. X-axis in the combined treatment shows the intensity of change in  $P_{ij}$  values. Beta values are near to the sensitivity calculated for this species, within the stable composition (Figure 3).

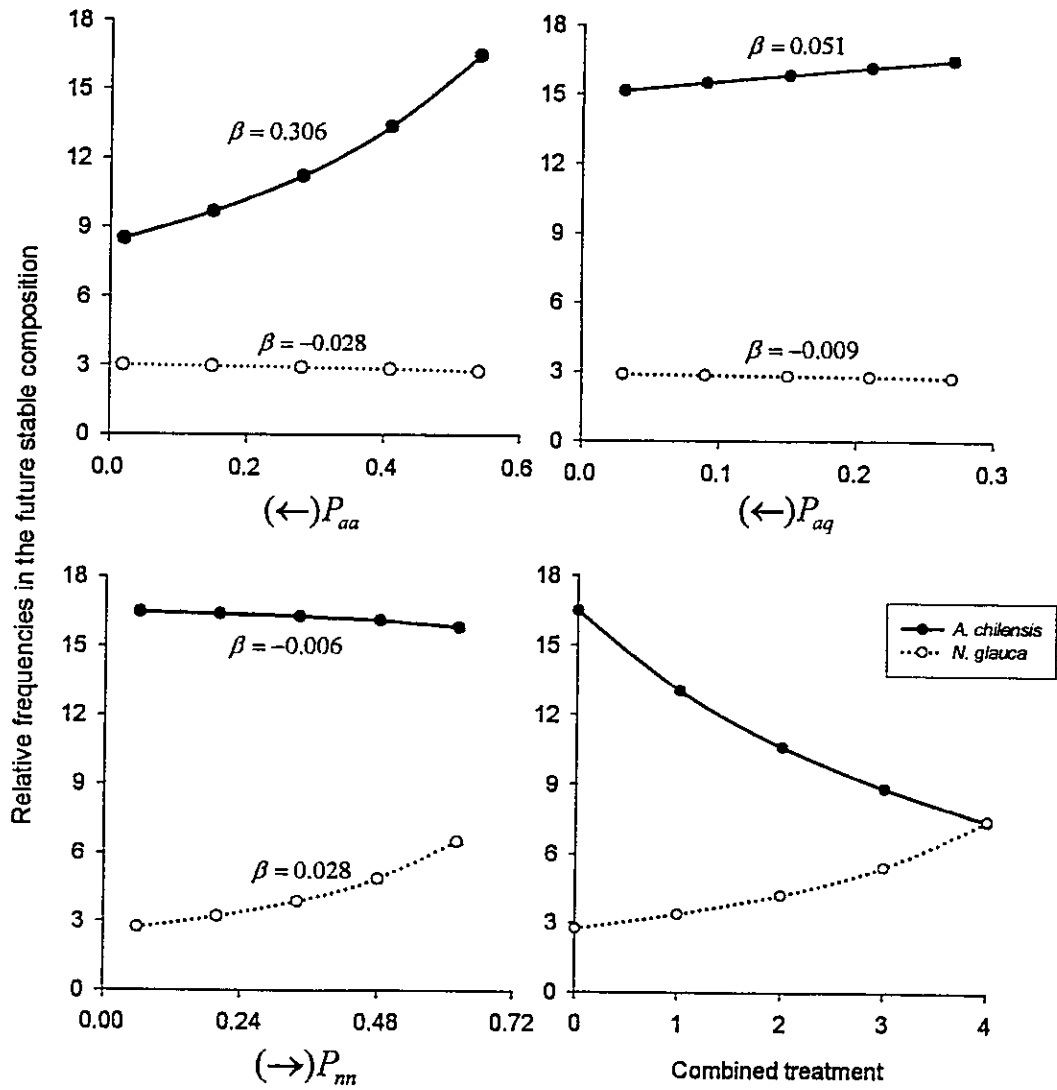


Figure 3. Net changes in the frequency of each species within the stable future composition (sensitivity of  $w_1$ ), caused by changes in the persistence probabilities of *A. chilensis* ( $P_{aa}$ ) and *N. glauca* ( $P_{nn}$ ).

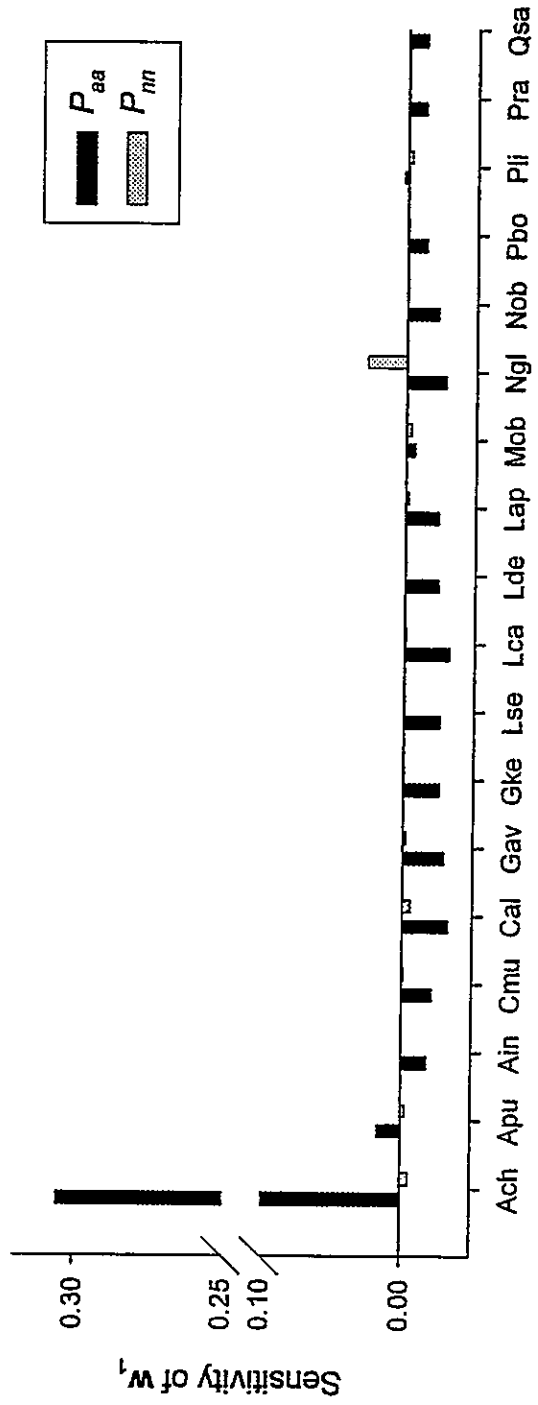


Figure 4. Changes in the stable future frequency of *N. glauca*, associated to recruitment of each species that composes the Maulino forest. In line and secondary Y-axis, the expected frequencies at future.

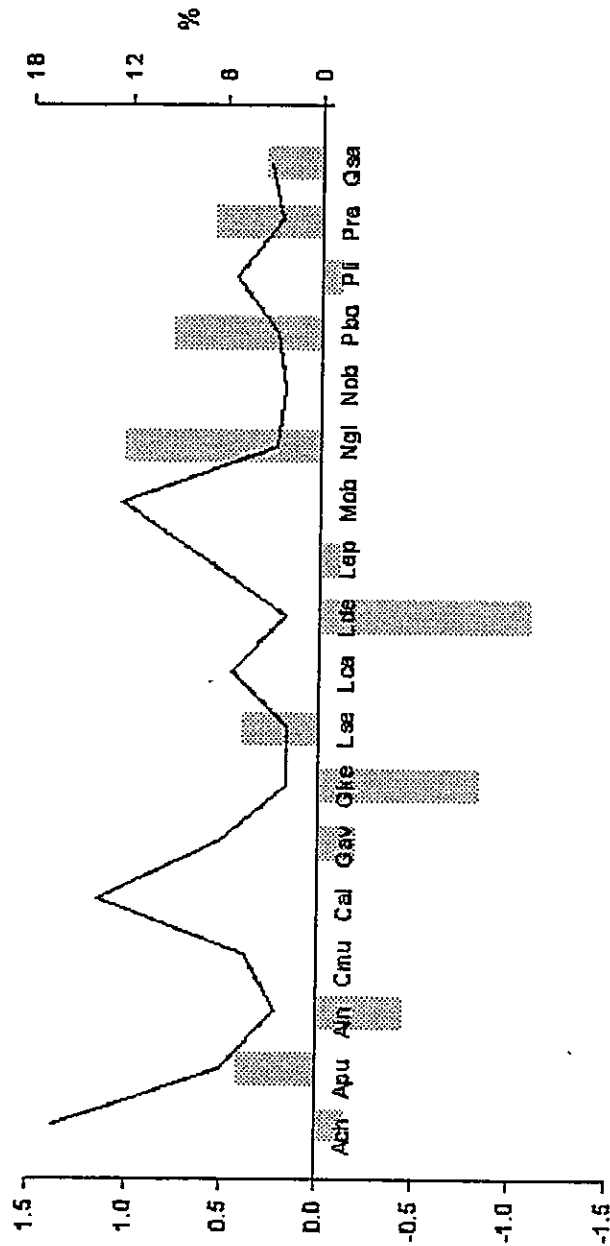
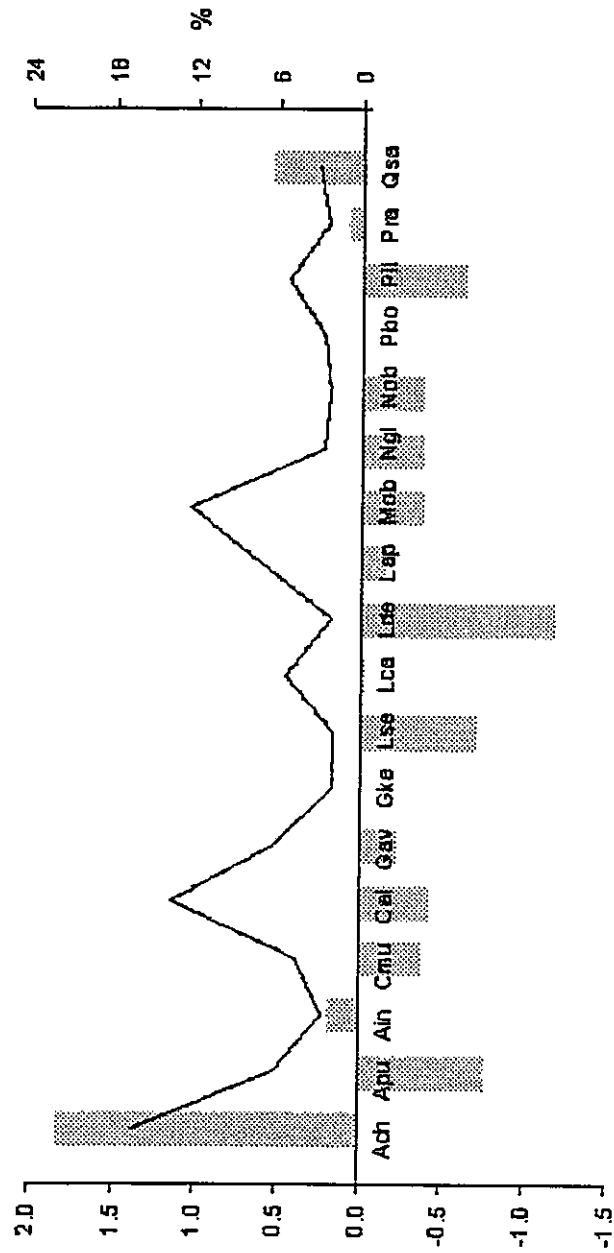




Figure 5. Changes in the stable future frequency of *A. chilensis*, associated to recruitment of each species that composes the Maulino forest. In line and secondary Y-axis, the expected frequencies at future.



Among the manipulations,  $P_{aa}$  induced the highest sensitivity to change in the stable composition. Changes in the future stable frequency of *A. chilensis*, caused by modification of  $P_{aa}$  values, exceed in one order of magnitude the changes that modifications in the  $P_{mn}$  can achieve on the future stable frequency of *N. glauca*. For all other species, any effect on the frequencies caused by  $P_{aa}$  and  $P_{mn}$  manipulations, were much lower than those of the target species (Figure 3).

Evaluation of recruitment contributions per species indicated that besides itself, *A. punctatum* (Apu), *L. sempervirens* (Lse), *P. boldus* (Pbo), *Q. saponaria* (Qsa), and even the exotic *Pinus radiata* (Pra), favor with their recruitment positive changes of *N. glauca* in the future stable composition (Figure 4). Except *A. punctatum*, all these species will be scarce (relative frequencies below of 5%) according with the original future composition predicted for fragments. Also, the recruitment of *A. chilensis* (Ach) has negative effects on the future stable frequency of *N. glauca*.

On the other hand, only *Q. saponaria* and itself favor positive changes of *A. chilensis* frequency in the future composition. However, *Q. saponaria* is expect to be present in low percentages at future (3.2%) (Figure 5). Among species affecting negatively *A. chilensis*, two will be abundant in the future: *Cryptocarya alba* (Cal) (13.8%) and *Myrceugenia obtusa* (Mob) (12.5%), and two have a highly negative effect, despite their moderate presence predicted at future (around 6%): *A. punctatum* and *Persea lingue* (Pli).

## Discussion

The fragmentation of Maulino forest threatens the persistence of *N. glauca* and favors the expansion of *A. chilensis*. This dynamics of change has been synthesized in a replacement Markov matrix, and we have used it to simulate management treatments on recruitment of *A. chilensis* and *N. glauca*, to explore the level of compositional recovery that is possible to reach at future in the fragments.

Currently, there is a compositional divergence between the fragments and the continuous forest, although *N. glauca* is even more abundant in the fragments (relative frequency: 24.5% in fragments, 9% in the continuous forest). Markov model predict that fragments will change as to deepen this compositional divergence almost ten times. Under management treatments, however, the fragments could be less dissimilar to the expected composition. (Table 2, Figure 1).

The simultaneous control of *A. chilensis* recruitment and planting of *N. glauca* was the most effective method to reduce the long-term changes predicted for fragments (Figures 1 and 2). However, our results indicate that the best compositional recovery was obtained with the highest intensity of change on  $P_{ij}$  values, which represent unrealistic management options in the field. For example, to reduce the persistence probability of *A. chilensis* from 0.56 to 0.02 is equivalent to eradicate all recruits of this species beneath their own mature trees, during the mean generational time required for the compositional stabilization. Moreover, no treatment achieved a composition similar to the current one at fragments.

To increase the recruitment of *N. glauca* was the less efficient treatment, which can be explained by the sensitivity analysis. The contributions of  $P_{nn}$  to long term changes in the stable composition were lower than the contributions of *A. chilensis* persistence, in more of one order of magnitude (Figure 3), and this low capacity of *N. glauca* to affect the natural replacement dynamics, is caused by the low recruitment reported by Bustamante et al. (2005). Since high intensities of treatment are required to maintain *N. glauca* at future abundances up to 4% (Figure 2), it would be necessary to manage other species to avoid its extinction. Many species are positively associated to the dynamics of *N. glauca* (Figure 4), but some of them, *L. sempevirens*, *P. boldus* and *Q. saponaria* will be few frequent to future (<5%). We can deduce that planting of *N. glauca* recruits is not sufficient, and the conservation of this species would require conserving its associated species too. *A. chilensis* recruitment affect negatively the future frequency of *N. glauca*, and its predicted high abundance is the principal reason to perform simultaneous strategies of management for both species (Figure 4). An interesting result was the contribution of *Pinus radiata* to the future frequency of *N. glauca*, which coincides with other studies that have found high recruitment and biodiversity of native tree species on understory of pine plantations (Keenan, 1997; Kanowski et al., 2005; Arrieta and Suárez, 2006).

On the other hand, *A. chilensis* success in the fragments, both as frequent species and as agent of long term changes on the stable composition, is associated with the fact that the contribution of this species to its own persistence was the highest of all sensitivity values (Figure 3, Figure 5). *A. chilensis* has only one important associated species, *Q. saponaria*, its most effective “nurse”, but the reduction of  $P_{aq}$  had low effect on the

stable composition and *A. chilensis* frequency (Figure 1, Figure 2). Through sensitivity analysis were possible to identify strong competitors of *A. chilensis*, as *M. obtusa* and *C. alba*, since they are at high frequency within the stable composition, and their recruitment has a negative effect on the  $P_{aa}$  value. Other two potential competitors of *A. chilensis* are *A. punctatum* and *P. lingue*, which contribute with the highest negative effect, and to future are expected at moderate frequencies (around 6%).

In sum, our results suggest that although the management of the most affected species by fragmentation reduces the long-term changes in their frequencies, this is not enough to avoid the predicted compositional divergence between fragments and the continuous Maulino forest of the Reserve. Previous experiences indicate that the forest natural regeneration and the plantation of many native species have better results for the diversity restoration (Murcia, 1997; Kaewkrom et al., 2005), and modelling approaches support the idea that the abundance of individual populations must not be used to evaluate the level of recuperation or disturbance of a whole community (Anand and Desrochers, 2004). Nevertheless, we found that an intensive reduction of *A. chilensis* recruitment beneath its own mature tree is able to reduce near a third of the compositional divergence (Figure 1, Appendix 4). Moreover, this treatment is three times less expensive than the combined treatment, and its cost/effectiveness is almost six times higher than the increasing of *N. glauca* recruitment (Appendix 4). The sensitivity analysis allowed us to demonstrate that effectively, some species are more important than others for the forest restoration. After of similar approaches in marine ecosystems (Tanner et al., 1996; Hill et al., 2004), this is the first work, to our knowledge, that uses sensitivity analysis in Markov models to test options of forest restoration.

In conclusion, our hypothesis, which proposes the floristic preservation of fragments, or their compositional recovery toward states more similar to the continuous Maulino forest, cannot be accepted, although two management strategies avoided the loss of *N. glauca* and achieved the reduction of *A. chilensis* abundance. However, if the principal problems derived from the changing compositional dynamics can be solved with this plans or any other option that has arisen from this work, their implementation will be an important contribution for the diversity conservation.

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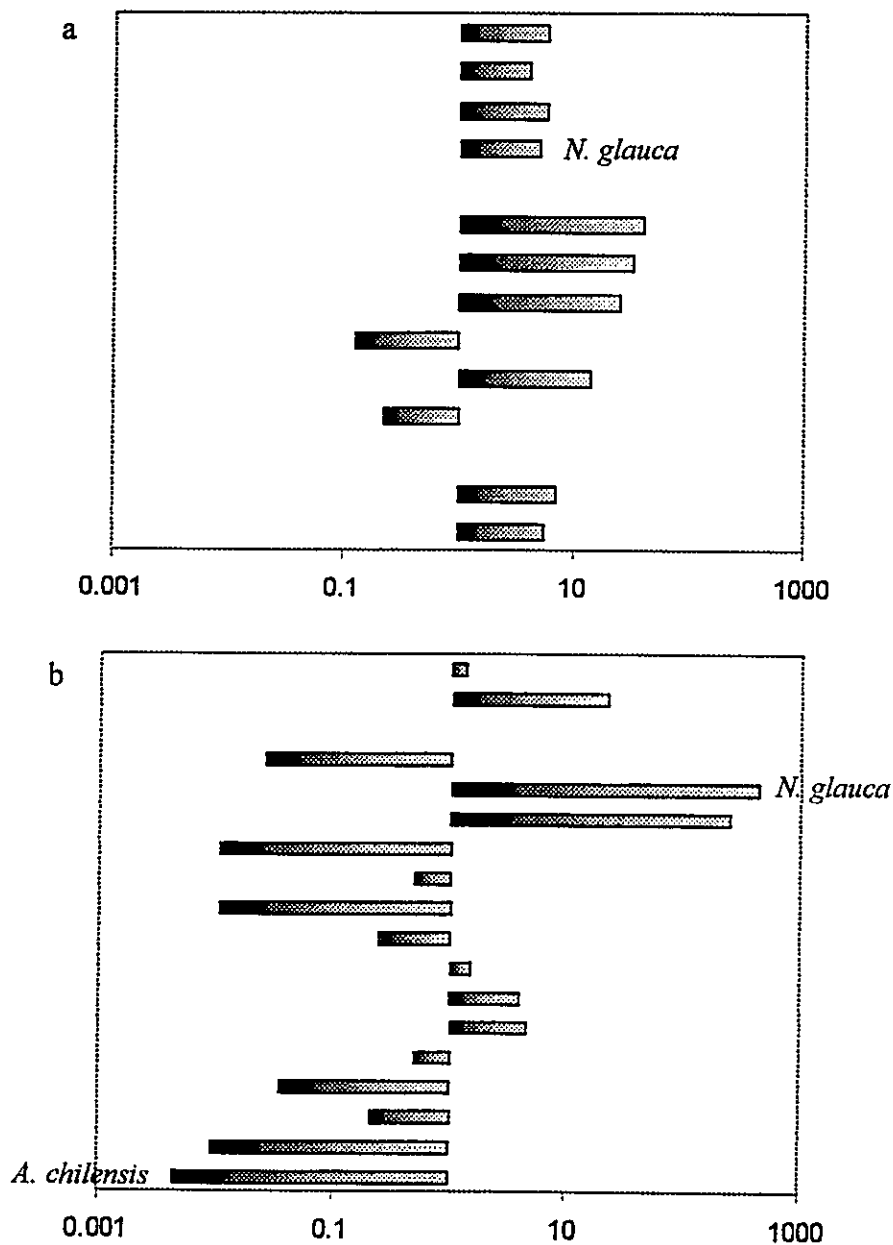
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## APPENDIX 1

Changes in the relative frequencies in Maulino forest, predicted by Bustamante et al. (2005). Bars measure the relation current frequency / future frequency, at continuous forest (a), and fragments (b).



## APPENDIX 2

Original Markov matrix from fragments. Marked  $P_{ij}$  values were employed for management simulations.

	Ach	Apu	Ain	Cmu	Cal	Gav	Gke	Lse	Lca	Lde	Lap	Mob	Ngl	Nob	Pbo	Pli	Pra	Osa
<i>Aristotelia chilensis</i>	0.54	0.00	0.00	0.06	0.06	0.25	0.00	0.00	0.25	0.08	0.17	0.06	0.06	0.06	0.00	0.00	0.20	0.27
<i>Aetoxicum punctatum</i>	0.08	0.00	0.11	0.06	0.06	0.08	0.00	0.00	0.25	0.00	0.04	0.06	0.06	0.06	0.14	0.00	0.00	0.00
<i>Azara integrifolia</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.06	0.04	0.06	0.06	0.06	0.00	0.00	0.00	0.08
<i>Citronella mucronata</i>	0.08	0.00	0.11	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.20	0.00	0.00
<i>Cryptocarya alba</i>	0.15	0.00	0.00	0.06	0.06	0.25	0.33	0.50	0.25	0.33	0.29	0.06	0.06	0.06	0.29	0.20	0.00	0.00
<i>Gevuina avellana</i>	0.00	0.00	0.22	0.06	0.06	0.00	0.33	0.00	0.00	0.11	0.13	0.06	0.06	0.06	0.07	0.20	0.20	0.04
<i>Gomortega keule</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.00	0.00	0.00
<i>Laurelia sempervirens</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.00	0.00	0.00
<i>Lithraea caustica</i>	0.08	0.00	0.33	0.06	0.06	0.00	0.33	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.00	0.00	0.19
<i>Lomatia dentata</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.06	0.00	0.06	0.06	0.06	0.00	0.00	0.00	0.00
<i>Luma apiculata</i>	0.08	0.00	0.00	0.06	0.06	0.17	0.00	0.00	0.00	0.00	0.21	0.06	0.06	0.06	0.14	0.20	0.00	0.00
<i>Myrceugenia obtusa</i>	0.00	1.00	0.22	0.06	0.06	0.08	0.00	0.50	0.00	0.11	0.00	0.06	0.06	0.06	0.29	0.00	0.40	0.08
<i>Nothofagus glauca</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.00	0.20	0.08
<i>Nothofagus obliqua</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.11	0.00	0.06	0.06	0.06	0.00	0.00	0.00	0.00
<i>Peumus boldo</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.11	0.04	0.06	0.06	0.06	0.07	0.00	0.00	0.00
<i>Persea lingue</i>	0.00	0.00	0.00	0.06	0.06	0.17	0.00	0.00	0.25	0.06	0.08	0.06	0.06	0.06	0.00	0.00	0.00	0.08
<i>Pinus radiata</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.00	0.00	0.15
<i>Quillaja saponaria</i>	0.00	0.00	0.00	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.06	0.00	0.20	0.00	0.04

### APPENDIX 3

**Matlab routine employed to calculate the scaled right eigenvector.**

```
Function dYdp=ntd(P,i,j)
n=size(P);
n=n(1);
saw = sum(abs(w));
for k=1:n
nw(:,k)= w(:,k)/saw(k);
end
w=nw;
v=inv(conj(w));
lambda=diag(lambda);
[lambda, index]=sort(lambda);
lambda=flipud(lambda);
index=flipud(index);
w=w(:,index);
v=v(index,:);
v=v.';
e=ones(n-1,1);
d=e-lambda(2:n);
dd=e./d;
for k=1:n
colv = v(k,2:n).'*dd;
temp = w(:,2:n)*colv;
dYdpkj = w(j,1)*temp;
dydp = dYdpkj -w(:,1)*sum(dYdpkj); dYdp(:,k)= dydp;
end
Pj= (-1/(1-P(i,j)))*P(:,j);
Pj(i)=1.0;
dYdp = real(dYdp*Pj);
end
```



## APPENDIX 4

### Estimated costs of management plans in forest fragments.

The treatments 1 and 2 consist on reducing the recruitment of *Aristotelia chilensis* beneath the canopy of *A. chilensis* and *Q. saponaria*, respectively. This treatment implies cutting recruits and logging saplings of *A. chilensis*, a practice used for the maintenance of service roads in forest plantations. Clearing *A. chilensis* has an average cost of CH\$ 50.000 / ha, according to the amount paid by Forestal Masisa S.A. in Tregualemu (M. Manríquez, Supervisor of Forest Protection, Forestal Masisa, personal communication). We arbitrarily set a time framework of 20 years to carry out these treatments, applying them four times, once every five years, assuming this time span is long enough to ensure the recruitment of seedling of species other than *A. chilensis* under its canopy.

Preliminary estimates (N. Lagos, personal communication) report densities of 1.040 individuals / ha of *A. chilensis* in forest fragments. To remove seedlings and saplings of *A. chilensis* growing under the canopy of *Q. saponaria* involves 40 times less individuals to cut, as there are only 25 individuals /ha of *Q. saponaria*. However, as more time might be involved in detecting all *Q. saponaria* individuals, we assume a cutting cost equivalent in treatment 1 and 2, reaching CH\$ 200.000 (Table 3).

Treatment 3 consists on increasing the recruitment of *N. glauca* beneath its own canopy. This management practice implies planting saplings > 1m height, at a density similar to the density achieved by adults' *N. glauca* in forest fragments. Planting saplings of *N. glauca* might be considered equivalent to afforestation of exotic trees in order to estimate the costs associated to this treatment. Hence, the cost of planting as an average cost of CH\$ 35.000 / ha according to the amount paid by Forestal Masisa S.A. in Tregualemu to plant 1.000 seedlings per hectare (M Manríquez, Supervisor of Forest Protection, Forestal Masisa, personal communication). The costs of saplings should be added to the costs. Each sapling has a commercial value of CH\$ 1.500, as priced by Universidad Austral and Universidad de Chile. Considering there are 190 individuals / ha of *N. glauca*, saplings costs amount to \$ 285.000 /ha. Assuming half the individuals

might die and should be replaced during a 20 years periods, saplings costs adds to CH\$427.500. Treatment 3 amounts then to CH\$ 497.500 / ha.

Corporación Nacional Forestal (CONAF) subsidizes forestry plantations under Decree Law 701, including reforestation of native species. According to budgeted values for 2007, CONAF will reimburse CH\$106.000 per every 100 individuals on any native tree species in the Maule Region. Considering this treatment involves almost 200 individuals, incentives adds to CH\$ 202.000 / ha. This figure is then discounted from the planting costs, rendering the final cost per ha of treatment 3 (Table 3). Comparatively, to manage forest fragments reforesting with *N. glauca* is 1,5 times more expensive than cutting *A. chilensis*.

Finally, treatment 4 consists on carrying out simultaneously all three treatments. Adding costs per treatment, this options is 3,5 time more expensive than treatments 1 and 2 and, 2,3 time more costly than treatment 3 (Table 3).

Table 3. Estimated cost of treatments per hectare of fragment. These amounts do not consider associated costs of personnel transportation and lodging, considered constants in treatments 1 to 3. Treatment 4, which involves several activities simultaneously, it might require more personnel. Excluding such costs from our calculation render the estimated cost of treatment 4 a conservative one.

Treatment	Description	Cost CH \$/ha
TR1	Reduction of <i>A. chilensis</i> recruitment beneath its own mature tree	\$ 200.000
TR2	Reduction of <i>A. chilensis</i> recruitment beneath <i>Q. saponaria</i>	\$ 200.000
TR3	Increasing of <i>N. glauca</i> recruitment beneath its own mature tree	\$ 295.500
TR4	Simultaneous management of <i>A. chilensis</i> and <i>N. glauca</i>	\$ 695.500

To calculate cost/effectiveness, we assess the economic value of achieving a 1% reduction in compositional dissimilarity by a given treatment. To do so, we divided the cost /ha (Table 3) by the percentage of dissimilarity reduced by each treatment (Figure 1). In these terms, the most cost/effective way to manage forest fragments in order to reduce the predicted compositional divergence between them and continuous Maulino forest, is to cut and log recruits of *A. chilensis*. This treatment is the least expensive one, achieving 82% of the maximum reduction in composition dissimilarity reached by the combined treatment 4. Treatment 4 reduces 1,2 times more the compositional dissimilarity but costs 2,8 times more to achieve it (Table 4).

Table 4. Cost/effectiveness of treatments to reduce the compositional divergence between fragments and continuous Maulino forest.

Treatment	Dissimilarity reduction (%)	Cost (CH\$/ha)	Unitary price reduction (%) (CH\$ / 1%)
TR1	35,08	200.000	5,70
TR2	7,32	200.000	27,39
TR3	9,10	295.500	32,47
TR4	42,98	695.500	16,18

Therefore, to conserve the composition of the fragmented Maulino forest, the management of one species is an option better than the simultaneous management of two species.