Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 255 (2008) 2236–2243
Forest Ecology and Management
www.elsevier.com/locate/foreco

Modelling the management of fragmented forests: Is it possible to recover the original tree composition?
The case of the Maulino forest in Central Chile

Carolina Ramos [a,*], Javier A. Simonetti [b], Jose D. Flores [c], Rodrigo Ramos-Jiliberto [d]

[a] *Laboratorio de Ecología Terrestre, Facultad de Ciencias, Universidad de Chile, Chile*
[b] *Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 635, Santiago, Chile*
[c] *Department of Mathematics, The University of South Dakota, 414 E. Clark Street, Vermillion, SD 57069, USA*
[d] *Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile*

Received 24 April 2007; received in revised form 5 December 2007; accepted 31 December 2007

Abstract

In the fragmented Maulino forest (in Central Chile), differences in the relative frequencies of species between seedlings and mature trees are strong indicators of a changing replacement dynamics in the community. Stationary Markov chain models predict that the future tree composition such Maulino forest fragments will differ from that of continuous, intact forest. We found that the persistence probability was highest for *Aristotelia chilensis* and lowest for *Nothofagus glauca*. These two tree species are the most affected by fragmentation, and changes in their abundances appear to be the main drivers of the long-term change in stand composition. The aim of our study was to test if the management of just these two species would be sufficient to avoid long-term changes in the composition of forest fragments or would recover their composition toward a state more similar to the continuous forest. For this purpose, we constructed a Markov matrix model from published information, and calculated the future stable stand composition under different management simulations: (1) reduction of *A. chilensis* recruitment, (2) increased recruitment of *N. glauca*, and (3) a combined treatment. To evaluate the effectiveness of management treatments, the future composition of fragments was compared with the composition expected for continuous (i.e., undisturbed) Maulino forest. We performed a sensitivity analysis of the stable composition in order to assess the intensity of changes in the future composition driven by the treatments, and to determine to what extend the recruitment of other coexisting species contributes to changes in relative frequencies of *A. chilensis* and *N. glauca*.

The simulated management treatments reduced the predicted compositional divergence between fragments and continuous forest. The combined treatment was the most effective, increasing the frequency of *N. glauca* and reducing the frequency of *A. chilensis*, but none of the management strategies totally prevented compositional change of fragments in the long term. Nevertheless, a single intervention to reduce recruitment of *A. chilensis* reduced by a third the compositional divergence, and was the most cost effective method to manage forest fragments. Other species were identified as potential focus for conservation management, either because of their positive impact on *N. glauca*, or negative impact on *A. chilensis*.

Keywords: Forest composition; Markov matrix; Persistence; Recruitment; Replacement dynamics; *Nothofagus glauca*; *Aristotelia chilensis*

1. Introduction

Land disturbances can trigger a sequence of changes in forest structure and composition through time, particularly changes in stem density, richness and species relative frequency (Chazdon et al., 2007; Makana and Thomas, 2006). Although natural disturbances are a persistent driver of tree compositional dynamics, anthropogenic disturbances are increasing at alarming rates, affecting the biodiversity (Novacek and Cleland, 2001). During the 1990s, over five million ha of tropical forest were yearly deforested worldwide and similar losses are expected for the southern temperate forest in the coming decades (Sala et al., 2000; Achard et al., 2002). As result of these disturbances, forest fragmentation has become a widespread phenomenon of terrestrial biomes.

---

* Corresponding author at: Subdirección Científica, Jardín Botánico José Celestino Mutis, Av. Calle 63 No. 68-95, Bogotá, Colombia.
E-mail addresses: charo.ramon@gmail.com (C. Ramos), jsimonet@abello.dic.uchile.cl (J.A. Simonetti), jflores@usd.edu (J.D. Flores), roramos@uchile.cl (R. Ramos-Jiliberto).

0378-1127/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2007.12.034

Fragmentation can induce long-term changes in forest composition through many processes such as the richness reduction that is frequently associated with habitat loss (Williams-Linera et al., 1998; Fahrig, 2001; Hill and Curran, 2001; Simonetti et al., 2001), the invasion of species from the vegetation matrix surrounding the fragments (Lovejoy et al., 1986; Tabarelli et al., 1999; Fox et al., 1997; Honnay et al., 2002), or 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 way, even if a fragment conserves its size, successional changes could result in a composition vastly different from the original forest (Turner et al., 1996; Oliveira-Filho et al., 1997).

Forest fragments are often the last reservoirs of threatened tree species, and are a potential focus for plant dispersion and recovery (Turner and Corlett, 1996; Chave et al., 2002; Köhler et al., 2003). Therefore, it is important to conserve them, developing management plans that will maintain their long-term composition. One such strategies consists of planting native tree species (Ashton et al., 2001), but it is difficult to determine directly the effectiveness of this approach, since monitoring would be required through decades and centuries. A useful solution to this problem is the employment of mathematical models that simulate the compositional dynamics of forest stands.

A modelling technique that is widely used 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 successional groups. The elements of a Markov matrix are the probabilities P_{ij} that one adult tree belonging to the jth species could be replaced in the future by a recruit of the ith species, at any single point in space. The product between the projection matrix and the initial composition vector gives the community 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 calculated analytically through the dominant right eigenvector of the Markov matrix (Baker, 1989; Caswell, 2001). The elements of a Markov matrix can be easily perturbed, in order to assess the effects of hypothetical disturbances or manipulations on the future stable composition (Ogden, 1983).

One case of compositional changes driven by fragmentation has been described in the Chilean Maulino forest (Bustamante et al., 2005). This south temperate ecosystem is part of a biodiversity hotspot (Myers et al., 2000; Smith-Ramírez, 2004) and has been strongly affected by agricultural and forestry activities (Lara and Veblen, 1993; Echeverría et al., 2006). Using a stationary Markov model, significant changes in species frequencies at the fragments have been predicted, changing such fragments from a forest to an evergreen shrubland (Bustamante et al., 2005). In this study, we focused on the major changes predicted by Bustamante et al. (2005): the dominance of the pioneer species *Aristotelia chilensis* and the disappearance of *Nothofagus glauca*. These changes seem to derive from the high probability of recruitment of *A. chilensis* beneath adults of the same species, as well as beneath *Quillaja saponaria*, and the low self-replacement probability of *N. glauca*. These patterns suggest that some replacements are more important than others for the compositional forest dynamics. Therefore, assessing these specific factors could provide valuable information for the design of successful restoration plans for forest fragments.

In an attempt to prevent the loss of some species at the expense of the over-dominance of others, we simulated the impacts of management treatments aimed at the recruitment of the species most sensitive to forest fragmentation. Given that increase of *A. chilensis* and decrease in *N. glauca* are the main drivers of compositional divergence between fragments and continuous forest, we predict that composition changes can be avoided by management intended to (i) reduce *A. chilensis* recruitment beneath adult trees of the same species, (ii) reduce *A. chilensis* recruitment beneath *Q. saponaria*, and (iii) increase recruitment of *N. glauca* beneath adults of the same species.

2. Methods

2.1. Study site

The Maulino forest is located in the coastal range of Central Chile at elevations from 200 to 550 m, and its canopy is dominated by *N. glauca*, *Aextoxicon punctatum*, *Gevuina avellana* and *Cryptocarya alba* (San Martín and Sánchez, 2000; Bustamante et al., 2005). Forests in Central Chile harbor a fourth of the endemic genera in the temperate tip of South America (Arroyo et al., 1996). Data used in this study were taken from a transect-sampling of seedlings and adult trees in continuous Maulino forest at the Reserva Nacional Los Queules (RNLQ) (35°59′19″S, 72°41′15″W), and from four fragments of Maulino forest located near the Reserve but separated from it by *Pinus radiata* plantations (for details see Bustamante et al., 2005). Among the woody species in the study area, *N. glauca* has been classified as "vulnerable" by the IUCN (2006), and is considered as a highly persistent component that favors the establishment of late-successional species (Veblen et al., 1981; Fajardo and Alaback, 2005). On the other hand, *A. chilensis* is a short-cycle pioneer tree from Central Chile that is commonly found in association with introduced shrubs, and this species can impede or delay the natural recovery of native forest after disturbance (Armesto and Pickett, 1985; Dirnböck et al., 2003; Puccio, 2004).

2.2. Markov matrices and simulations

The matrices describing stand compositions of the Reserve and fragments were built with recruitment information of Bustamante et al. (2005) and then used in a Markov stationary model. Matrix elements are assumed to have constant values over time (Waggoner and Stephens, 1970). Values in the matrix are the probabilities P_{ij} that places already occupied by species j could be occupied in the future by species i. These values were calculated by dividing the number of ith species seedlings growing beneath jth species adult trees by the total of seedlings growing beneath *j*th species adult trees. Matrices included such information for 18 tree species.

For each matrix, we calculated the dominant right eigenvector (MATLAB 6.1, The MathWorks, Inc., 2001), or the future stable composition, according to Caswell (2001). To estimate the degree of long-term change, we compared these predicted compositions with the current state of the continuous forest (Reserve), through Spearman rank correlations (Statistica 6.0; StatSoft Inc., 2001). Significant Spearman correlations coefficients ($p < 0.05$) were considered as an indicator of high similarity to the original Maulino forest.

The simulated management tactics included both planting recruits of threatened species and reducing the recruitment of invasive species. These changes were implemented in the model by modifying 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 indicate the probability that one species recruits in a site already occupied by an adult of the same species (i.e., the persistence probability).

Since these *persistence probabilities* were high for *A. chilensis* and very low for *N. glauca* in the matrix for the fragments, we manipulated their values to reach a tree composition closer to the intact forest. In a first treatment we reduced the persistence of *A. chilensis* (P_{aa}), while a second treatment was to increase the persistence of *N. glauca* (P_{nn}). A third treatment was the reduction of the probability that *A. chilensis* would replace *Q. saponaria* (P_{aq}), species beneath which *A. chilensis* recruits at a high frequency. All treatments had four levels of intensity, which are presented in Table 1. A fourth treatment was the combination of the all three, applying their corresponding intensities in simultaneous way. In all cases, before determining the stable composition, a compensation of proportional type was employed to fulfill the condition that the sum of values in columns of a Markov matrix must be equal to one (Caswell, 2001). Through Spearman rank correlations, 16 future stable compositions resulting from modified matrices were compared with the continuous Maulino forest of the Reserve in the present state (which was considered the "expected" composition). Chi-square values testing the goodness of fit between the expected and "observed" fragment compositions were used to evaluate the effectiveness of the management treatments. Higher Chi-square values indicate higher levels of dissimilarity between compared compositions.

The amount of change that a treatment causes in the future composition depends on the contribution of each species to the forest replacement dynamics. Therefore, we performed a sensitivity analysis of the original matrix from fragments (i.e., the matrix without treatments), to determine the amount of change in the stable composition of fragments that would be caused by modifying the P_{ij} values. The sensitivity of the stable future composition results from the differentiation of the dominant right eigenvector respect to P_{ij} (Caswell, 2001):

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

where $\mathbf{w}_1$ is the dominant right eigenvector, $\mathbf{w}_m$ is the right eigenvector of the *m*th eigenvalue ($1 \ldots m$), $v_i^{(m)}$ is the *i*th component of the *m*th left eigenvector ($1 \ldots s$), λ_1 is the dominant eigenvalue, and λ_m is the *m*th eigenvalue. To obtain comparable and additive values, we employed the scaled and proportionally compensated form of sensitivity (Hill et al., 2004):

$$\frac{\mathrm{d}(\mathbf{w}_1/||\mathbf{w}_1||)}{\mathrm{d}p_{ij}} = \frac{\partial(\mathbf{w}_1/||\mathbf{w}_1||)}{\partial p_{ij}} + \sum_{m \neq i}^{s} \frac{\partial(\mathbf{w}_1/||\mathbf{w}_1||)}{\partial p_{mj}} \frac{\partial p_{mj}}{\partial p_{ij}} \tag{2}$$

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

$\frac{\partial \mathbf{w}_1}{\partial p_{\mathrm{nn}}}$: 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}).

$\frac{\partial \mathbf{w}_1}{\partial p_{\mathrm{aa}}}$: 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}).

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

$\sum_{j=1}^{s} \frac{\partial w_{\mathrm{Ach}}^{(1)}}{\partial P_{ij}}$: Changes in the frequency of *A. chilensis* within the future stable composition caused by changes in the recruitment of each *i* species ($1 \ldots s$).

3. Results

Model comparison between the present and future composition in the continuous forest of RNLQ showed a high level of similarity ($r_{\mathrm{S}} = 0.81$, $p < 0.01$). On the other hand, the fragments were dissimilar to the continuous forest ($r_{\mathrm{S}} = 0.31$,

Table 1
Changes of P_{ij} values (probability that species *i* replaces the species *j*) in the fragment matrices evaluated in models as management treatments

Species	Code	P_{ij} to change	Treatment and intensity of change
A. chilensis	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 *Quillaja saponaria* P_{aq} (0.27)	Reduction to 0.21, 0.15, 0.09, and 0.03
N. glauca	TR3	3. Probability of persistence P_{nn} (0.06)	Increasing 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: $P_{\mathrm{aa}} = 0.41$, $P_{\mathrm{aq}} = 0.21$ and $P_{\mathrm{nn}} = 0.2$

Starting values, according to Bustamante et al. (2005) are listed in parentheses.

Table 2
Spearman rank correlations between the expected composition for a continuous Maulino forest (RNLQ at the present) and the future stable composition of fragments with (FRTR) or without (FRF) management treatments

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
FRTR1: 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
FRTR2: Reduction of P_{aq}	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
FRTR3: 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
FRTR4: 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

Another correlations with the expected composition: continuous forest at future (CFF) and fragments at the present (FRP). Asterisks indicate a highly significant value.

$p = 0.19$), and this compositional divergence was predicted to increase 10-fold in the future (Table 2 and Fig. 1).

None of our management treatments led to the full recovery of composition by forest fragments. However, with use of these management treatments, the stable future composition of the studied fragments was predicted to be less divergent from the composition of intact forest than was otherwise predicted to occur (FRF; Fig. 1). In general, the highest intensities of treatment caused the lowest level of dissimilarity from the continuous forest, and in particular the combination of treatments was the most effective method in reducing the compositional divergence. On the other hand, the increase of P_{nn} and the reduction of P_{aq} were the least effective treatments. At maximum intensity, the reduction of P_{aa} was able to diminish by a third the predicted compositional divergence (dissimilarity reduction: 35.1%).

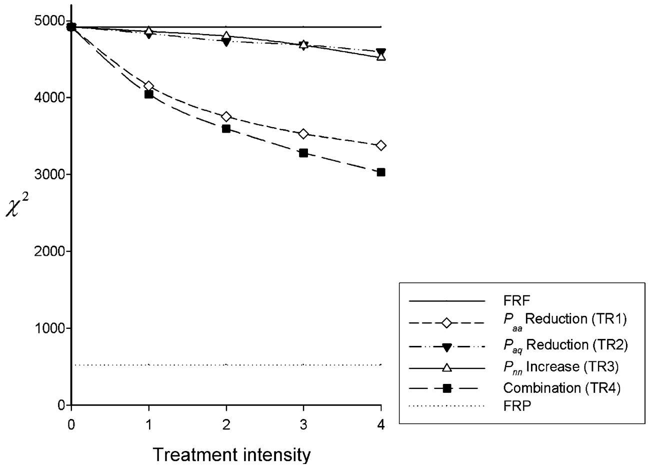

Fig. 1. Effectiveness of treatments in fragments, under the goodness-of-fit test (χ^2) between the observed (in legend) and the expected (RNLQ at the present) composition. The distance between present (FRP) and future (FRF) states of fragments without management estimates the long-term compositional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

At 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 increase of P_{nn} changed the frequency of *N. glauca* from 2.7 to 6.5%. The combined treatment at maximum intensity resulted in the greatest effect on the future frequencies of these species, with final percentages of 7.4% in both cases. The P_{aq} reduction had the lowest effectiveness (Fig. 2).

Among the tested manipulations, the future stable composition was most sensitive to changes in P_{aa}. Changes in the frequency of *A. chilensis* caused by modification of P_{aa} values overcame in more of one order of magnitude the changes that modifications of P_{nn} could cause to the frequency of *N. glauca*. Effects of P_{aa} and P_{nn} manipulations on the future frequencies of any other species were much lower than those on the target species (Fig. 3).

When evaluating the contributions per species, we found that increases in *A. punctatum* (Apu), *Laurelia sempervirens* (Lse), *Peumus boldus* (Pbo), *Q. saponaria* (Qsa), and even the exotic *P. radiata* (Pra), led to increases in *N. glauca* in the future stable forest composition (Fig. 4). Nevertheless, with the exception of *A. punctatum*, all these species will be rare (relative frequencies below of 5%) in the stable composition of fragments without treatments. Also, the recruitment of *A. chilensis* (Ach) has a negative effect on the future stable frequency of *N. glauca*.

The frequency of *A. chilensis* in the future forest composition is favored by *Q. saponaria* recruitment, but the

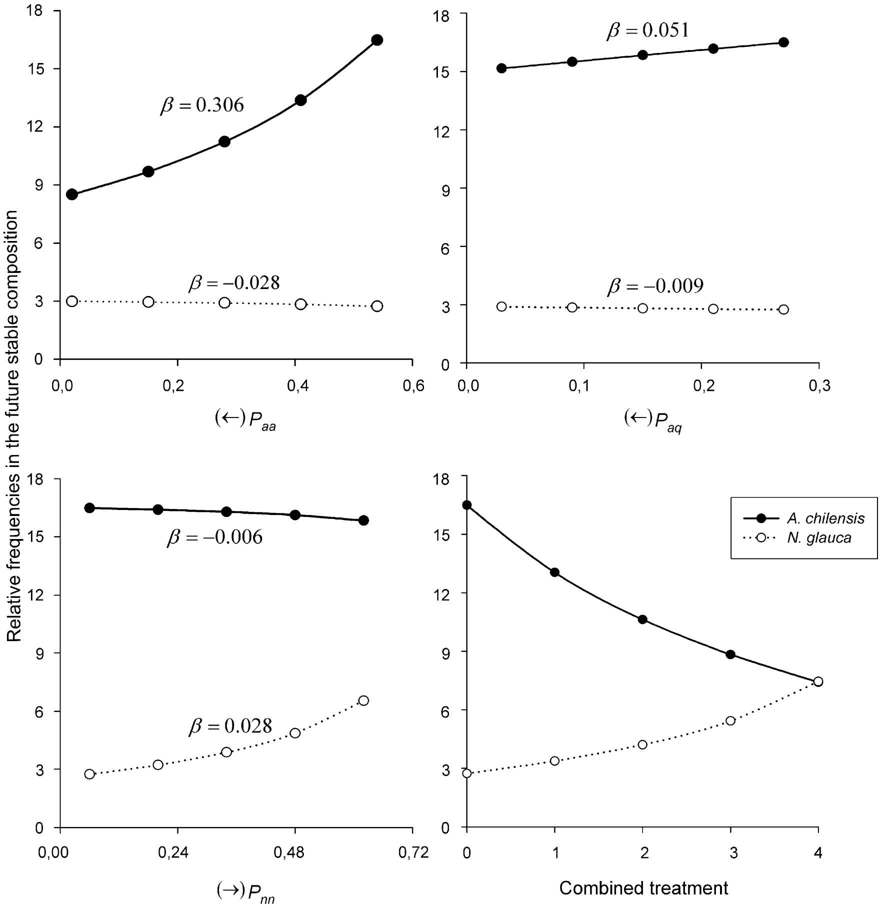

Fig. 2. Changes in the frequency of *A. chilensis* and *N. glauca* within the projected stable composition driven by management treatments. The *X*-axis in the combined treatment shows the intensity of change in P_{ij} values. Beta values (regression model $Y = \alpha + \beta X$) approach the sensitivity calculated for this species within the stable composition (Fig. 3).

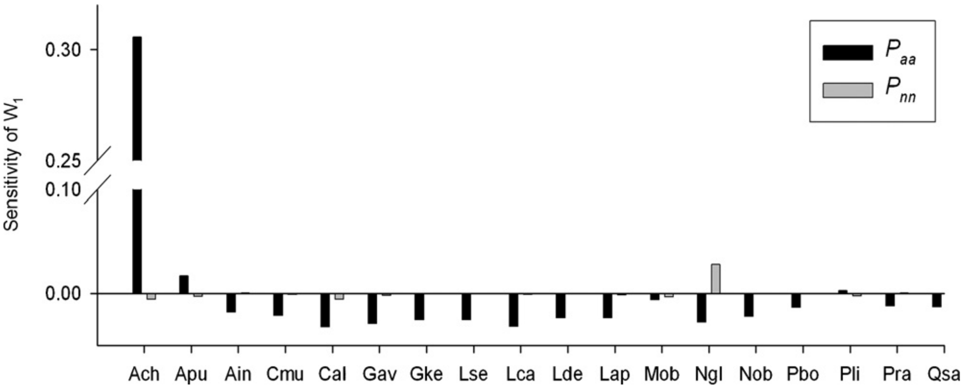

Fig. 3. Net changes in the species frequencies within the stable future composition (sensitivity of $\mathbf{w}_1$) caused by changes in the persistence probabilities of *A. chilensis* (P_{aa}) and *N. glauca* (P_{nn}). Ach: *Aristotelia chilensis*. Apu: *Aextoxicon punctatum*. Ain: *Azara integrifolia*. Cmu: *Citronella mucronata*. Cal: *Cryptocarya alba*. Gav: *Gevuina avellana*. Gke: *Gomortega keule*. Lse: *Laurelia sempervirens*. Lca: *Litraea caustica*. Lde: *Lomatia dentata*. Lap: *Luma apiculata*. Mob: *Myrceugenia oblonga*. Ngl: *Nothofagus glauca*. Nob: *Nothofagus obliqua*. Pbo: *Peumus boldus*. Pli: *Persea lingue*. Pra: *Pinus radiata*. Qsa: *Quillaja saponaria*.

model predicts that *Q. saponaria* will only be present in low percentages (3.2%) (Fig. 5). Among the species negatively affecting *A. chilensis*, *C. alba* (Cal) and *Myrceugenia obtusa* (Mob) will be abundant in the future forest (13.8 and 12.5%, respectively). *A. punctatum* and *Persea lingue* (Pli) will have an even more negative effect, despite their predicted lower levels of frequency (around 6%).

4. Discussion

Currently, the composition of Maulino forest fragments differs from that of the continuous forest composition, with *N. glauca* as a very abundant species in the fragments (relative frequency: 24.5% in fragments, 9% in the continuous forest). Nevertheless, our Markov model predicted that that fragments

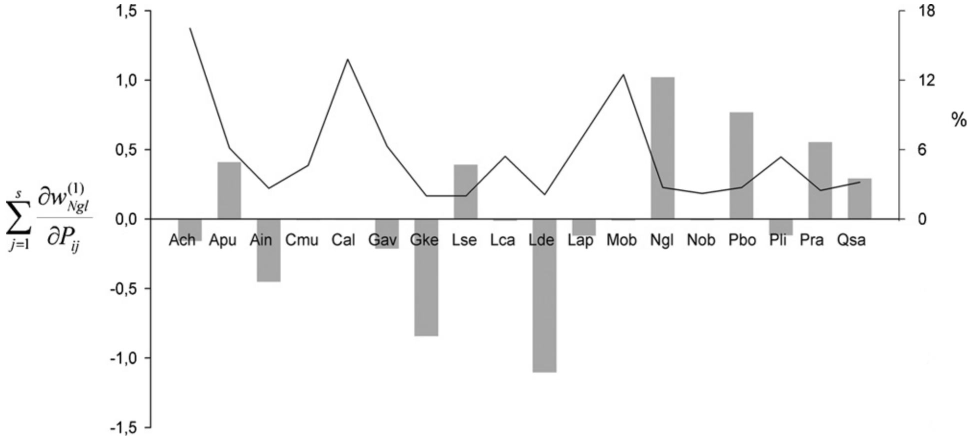

Fig. 4. Changes in the stable future frequency of *N. glauca* associated with the recruitment of each species that composes the Maulino forest. The solid line and secondary *Y*-axis represent the expected future frequencies.

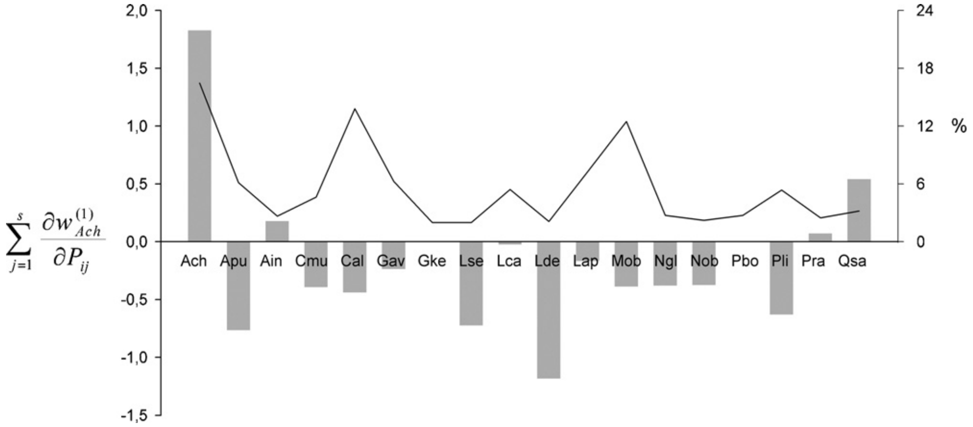

Fig. 5. Changes in the stable future frequency of *A. chilensis* associated with the recruitment of each species that composes the Maulino forest. The solid line and secondary *Y*-axis represent the expected future frequencies.

will change enough to deepen this compositional divergence by almost 10-fold, and these changes will lead to a stable state where *N. glauca* will comprise only 3% of the fragments' canopy.

We found that using the management treatments it would significantly reduce the predicted divergence of fragment composition from that of the intact forest. The simultaneous reduction of *A. chilensis* recruitment and planting of *N. glauca* was the most effective method to reduce the long-term changes predicted for fragments. However, our results indicate that the best compositional recovery was achieved with the highest intensity of change in P_{ij} values, which represent unrealistic levels of management in the field. For example, decreasing 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, none of the treatments was sufficiently effective to maintain the current composition of fragments over the long term.

Increasing the recruitment of *N. glauca* was the least effective treatment, as shown by the sensitivity analysis. The contribution of P_{nn} to long-term changes in the stable composition was lower that the contribution of *A. chilensis* persistence, by more than one order of magnitude (Fig. 3). This low capacity of *N. glauca* to affect the natural *replacement* dynamics is a result of its low recruitment reported by Bustamante et al. (2005). Since high intensities of treatment are required to conserve *N. glauca* at future abundances of 4% (Fig. 2), we conclude that to maintain *N. glauca*, it will be necessary to manage other species.

Recruitment of many other species can favor positive changes in the future frequency of *N. glauca* (Fig. 4), even though some of them, like *L. sempevirens* and *P. boldus*, will tend to be uncommon (<5%). Also, *A. chilensis* recruitment negatively affects the future frequency of *N. glauca*. The expectation that its abundance will increase, suggests that simultaneous management of both this species and *N. glauca* will be required (Fig. 4). An interesting result was the contribution of the exotic *P. radiata* to the future frequency of *N. glauca*, which agrees with other studies that have found high recruitment and biodiversity of native tree species in the understory of pine plantations (Keenan et al., 1997; Kanowski et al., 2005; Arrieta and Suárez, 2006). This finding suggests that is possible that the conservation of *N. glauca* in forest

Table 3
Estimated cost of treatments per hectare and calculations of cost/effectiveness, in Maulino forest fragments

Treatment	Dissimilarity reduction (%)	Cost (CH$/ha)	Unitary price reduction (CH$/1%)
TR1	35.08	200,000	5,700
TR2	7.32	200,000	27,322
TR3	9.10	295,500	31,376
TR4	42.98	695,500	15,949

These amounts consider costs of *A. chilensis* cutting, *N. glauca* sapling planting, and government subsidies, but do not consider associated costs of personnel transportation and lodging. The information was extracted from diverse interviews with Corporación Nacional Forestal (CONAF), Forestal Masisa S.A., and the Forestal Service of Universidad de Chile and Universidad de Concepción (for more details, see Ramos, 2006).

fragments can be influenced by the proximity of pine plantations.

The success of *A. chilensis* in fragments, both as an abundant species and as an agent of change in the stable composition, is related to the contribution of this species to its own persistence, the highest of all sensitivity values. *A. chilensis* has only one important associated species, *Q. saponaria*, which is its most effective ‘‘nurse’’ species. Nevertheless, the reduction of P_{aq} had a low effect on both the stable composition and the frequency of *A. chilensis* (Figs. 1 and 2). Through sensitivity analysis, it was possible to identify *M. obtusa* and *C. alba* as strong competitors of *A. chilensis*, since they occur at high frequencies within the stable composition, and their recruitment has a negative effect on P_{aa}. Two other potential competitors of *A. chilensis* are *A. punctatum* and *P. lingue*, which have highly negative effects of *A. chilensis*, and are expected to reach moderate future frequencies (around 6%). In general, *C. alba*, *P. lingue*, *A. punctatum* and the genus *Laurelia* are associated with the genus *Nothofagus* in Central and South of Chile, and the canopy of these forests can be dense enough to limit the quantity of light on the understory, and to avoid the recruitment of the shade-intolerant species *A. chilensis* (González et al., 2002; Lusk et al., 2006).

In summary, our results suggest that although the management of the species most affected by fragmentation reduces the long-term changes of their frequencies, this is not enough to avoid the predicted compositional divergence between fragments and the continuous Maulino forest. Previous experience indicates that natural forest regeneration and planting of native species can help restore forest diversity (Murcia, 1997; Kaewkrom et al., 2005). Nevertheless, we found that an intensive reduction of *A. chilensis* recruitment beneath mature trees of the same species is able to reduce by almost a third the compositional divergence otherwise expected over time in fragments (Fig. 1). Moreover, this treatment is three times less expensive than the combined treatment, and its cost/effectiveness is almost six times higher than that of increasing *N. glauca* recruitment (Table 3). The sensitivity analysis allowed us to demonstrate that contributions of different species to successional dynamics are not equal and therefore the management of some few species can achieve the most important effects on restoration. Besides 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 for restoration management.

In conclusion, although we rejected our initial hypothesis of complete preservation of the fragments, or their compositional convergence with the continuous forest, we were able to demonstrate that the recruitment management of a few species can have a great impact on the Maulino forest composition. These strategies can reduce the long-term effects of fragmentation. Markov modelling is a useful tool to study the forest replacement dynamics, and to evaluate the contribution of possible management strategies to the restoration.

Acknowledgements

This work has been supported by Fondecyt 1050745. We are grateful to Conaf and Forestal Masisa S.A. for granting permits to work in their stands. We also thank to Ramiro Bustamante, who helped with valuable comments and suggestions.

References

Acevedo, M.E., Urban, D.L., Alban, M., 1995. Transition and gap models of forest dynamics. Ecol. Appl. 5, 1040–1055.

Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.P., 2002. Determination of deforestation rates of the World’s humid tropical forests. Science 297, 999–1002.

Armesto, J.J., Pickett, S.T.A., 1985. A mechanistic approach to the study of succession in the Chilean matorral. Rev. Chil. Hist. Nat. 58, 9–17.

Arrieta, S., Suárez, F., 2006. Scots pine (*Pinus sylvestris* L.) plantations contribute to the regeneration of holly (*Ilex aquifolium* L.) in mediterranean Central Spain. Eur. J. Forest Res. 125, 271–279.

Arroyo, M.T.K., Riveros, M., Peñaloza, A., Caviares, L., Faggi, A.M., 1996. Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of southern South America. In: Lawford, R.G., Alaback, P.B., Fuentes, E. (Eds.), High-Latitude Rainforests and Associated Ecosystems of the West Coasts of the Americas: Climate, Hydrology, Ecology and Conservation. Springer Verlag, New York, pp. 134–172.

Ashton, M.S., Gunatilleke, C.V.S., Singhakumara, B.M.P., Gunatilleke, I.A.U.N., 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. For. Ecol. Manage. 154, 409–430.

Baker, W.L., 1989. A review of models of landscape change. Lanscape Ecol. 2, 111–133.

Bustamante, R.O., Grez, A.A., Simonetti, J.A., San Martín, J., 2005. La fragmentación del bosque Maulino y su dinámica regeneracional: diagnóstico actual y perspectivas futuras. In: Smith, C., Armesto, J.J., Valdovinos, C. (Eds.), Historia, Biodiversidad y Ecología de los Bosques de la Cordillera de la Costa. Editorial Universitaria, Santiago, pp. 529–539.

Caswell, H., 2001. Matrix Population Models. Sinauer Associates, Sunderland, 722 pp.

Chave, J., Wiegand, K., Levin, S., 2002. Spatial and biological aspects of reserve design. Environ. Model. Assess. 7, 115–122.

Chazdon, R.L., Letcher, S.G., Van Breugel, M., Martínez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary neotropical forest following major disturbances. Philos. Trans. R. Soc. B 362, 273–289.

Chen, J., Franklin, J.F., Spies, T.A., 1992. Vegetation responses to edge environments in old-growth Douglas-fir forest. Ecol. Appl. 2, 387–396.

Connell, J.H., Slatyer, R.O., 1977. Mechanism of successions in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.

Dirnböck, T., Greimler, J., Lopez, P., Stuessy, T.E., 2003. Predicting future threats to the native vegetation of Robinson Crusoe Island, Juan Fernandez Archipelago, Chile. Conserv. Biol. 17, 1650–1659.

Echeverría, C., Coomes, D., Salas, J., Rey-Benayas, J.M., Lara, A., Newton, A., 2006. Rapid deforestation and fragmentation of Chilean temperate forests. Biol. Conserv. 130, 481–494.

Fahrig, L., 2001. How much habitat is enough? Biol. Conserv. 100, 65–74.

Fajardo, A., Alaback, P., 2005. Effects of natural and human disturbances on the dynamics and spatial structure of *Nothofagus glauca* in south-Central Chile. J. Biogeogr. 32, 1811–1825.

Fox, B.J., Taylor, J., Fox, M.D., Williams, C., 1997. Vegetation changes across edges or rainforest remnants. Biol. Conserv. 82, 1–13.

González, M., Veblen, T.T., Donoso, C., Valeria, L., 2002. Tree regeneration responses in a lowland *Nothofagus*-dominated forest after bamboo dieback in South-Central Chile. Plant Ecol. 161, 59–73.

Harper, K.A., MacDonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Eukirchen, E., Roberts, D., Jaiteh, M.S., Essen, P.A., 2005. Edges influence on forest structure and composition in fragmented landscapes. Conserv. Biol. 19, 768–782.

Hill, J.L., Curran, P.J., 2001. Species composition in fragmented forest: conservation implications of changing forest area. Appl. Geogr. 21, 157–174.

Hill, M.F., Witman, J.D., Caswell, H., 2004. Markov chain analysis of succession in rocky subtidal communities. Am. Nat. 164, E46–E61.

Honnay, O., Verheyen, K., Hermy, M., 2002. Permeability of ancient forest edges for weedy plant species invasion. For. Ecol. Manage. 161, 109–202.

IUCN, 2006. IUCN Red List of Threatened Species. Available at http://www.iucnredlist.org.

Kaewkrom, P., Gajaseni, J., Jordan, C.F., Gajaseni, N., 2005. Floristic regeneration in five types of teak plantations in Thailand. For. Ecol. Manage. 210, 351–361.

Kanowski, J., Catterall, C.P., Wardell-Johnson, G.W., 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. For. Ecol. Manage. 208, 359–372.

Keenan, R.J., Lamb, D., Woldring, O., Irvine, A., Jensen, R., 1997. Restoration and plant biodiversity beneath tropical tree plantations in Northern Australia. For. Ecol. Manage. 99, 117–131.

Köhler, P., Chave, J., Riéra, B., Huth, A., 2003. Simulating the long-term response of tropical wet forest to fragmentation. Ecosystems 6, 114–128.

Lara, A., Veblen, T.T., 1993. Forest plantations in Chile: a successful model. In: Mather, A. (Ed.), Afforestation Policies, Planning and Progress. Belhaven Press, London, pp. 118–139.

Laurance, W.F., Ferreira, L.V.M., Rankin-De Merona, J., Laurance, S.G., Hutchings, R.W., Lovejoy, T.E., 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conserv. Biol. 12, 460–464.

Logofet, D.O., Lesnaya, E.V., 2000. The mathematics of Markov models: what Markov chains can really predict in forest successions. Ecol. Model. 126, 285–298.

Lovejoy, T.E., Bierregaard Jr., R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown Jr., K.S., Powell, A.H., Powell, G.V.N., Schubart, H.O., Hays, M.B., 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soule, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, pp. 257–285.

Lusk, C.H., Chazdon, R.L., Hoffman, G., 2006. A bounded null model explains juvenile tree community structure along light availability gradients in a temperate rain forest. Oikos 112, 131–137.

Makana, J.R., Thomas, S.C., 2006. Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. Biodivers. Conserv. 15, 1375–1397.

Murcia, C., 1997. Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. For. Ecol. Manage. 99, 163–170.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Novacek, M.J., Cleland, E.E., 2001. The current biodiversity extinction events: scenarios for mitigation and recovery. Proc. Natl. Acad. Sci. U.S.A. 98, 5466–5470.

Ogden, J., 1983. Community matrix model predictions of future composition at Russell state forest. N. Z. J. Ecol. 6, 71–77.

Oliveira-Filho, A.T., De Melo, J.M., Scolforo, J.R., 1997. Effects of past disturbance and edges on tree community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987–1992). Plant Ecol. 131, 45–66.

Oosterhoorn, M., Kappelle, M., 2000. Vegetation structure and composition along an interior-edge-exterior gradient in a Costa Rica montane cloud forest. For. Ecol. Manage. 126, 291–307.

Orloci, L., Orloci, M., 1988. On recovery, Markov chains, and canonical analysis. Ecology 69, 1260–1265.

Puccio, C.B., 2004. Evaluación del efecto ecológico del fuego sobre la vegetación arbórea del Cerro Andecul, IX región, Chile. Lineamientos para su restauración ecológica. Thesis. Facultad de Ciencias, Universidad Católica de Temuco, Temuco, Chile, 127 pp.

Ramos, C., 2006. Modelling the management of fragmented forest: it is possible to recovery the tree composition? The case of the Maulino forest, Chile. Thesis. Facultad de Ciencias, Universidad de Chile, Santiago, Chile, 43 pp.

Rees, M., Condit, R., Crawley, M., Pacala, S., Tilman, D., 2001. Long term studies of vegetation dynamics. Science 293, 650–655.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwarld, E., Huenneke, L.E., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Stikes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

San Martín, J., Sánchez, A., 2000. Las comunidades relictas de *Gomortega keule* (Geomoryegaceae, Magnoliopsida) en Chile Central. Ann. Jard. Bot. Madrid 57, 317–326.

Simonetti, J.A., Moraes, M., Bustamante, R.O., Grez, A.A., 2001. Regeneración de bosques tropicales fragmentados del Beni, Bolivia. In: Mostacedo, B., Fredericksen, T.S. (Eds.), Regeneración y Silvicultura de Bosques Tropicales en Bolivia. Bolfor, Santa Cruz, pp. 139–155.

Smith-Ramírez, C., 2004. The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforest. Biodivers. Conserv. 13, 373–393.

Tabarelli, M., Mantovani, W., Peres, C.A., 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeast of Brazil. Biol. Conserv. 91, 119–127.

Tanner, J.E., Hughes, T.P., Connell, J.H., 1996. The role of history in community dynamics: a modelling approach. Ecology 77, 108–117.

Turner, I.M., Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol. Evol. 11, 330–333.

Turner, I.M., Chua, K.S., Ong, J.S.Y., Soong, B.C., Tan, H.T.W., 1996. A century of plant species loss from an isolated fragment of lowland tropical rain forest. Conserv. Biol. 10, 1229–1244.

Veblen, T.T., Donoso, C., Schlegel, F.M., Escobar, B., 1981. Forest dynamics in South-Central Chile. J. Biogeogr. 8, 211–247.

Waggoner, P.E., Stephens, G.R., 1970. Transition probabilities for a forest. Nature 225, 1160–1161.

Williams-Linera, G., Dominguez-Gastelú, V., García-Zurita, M.E., 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. Conserv. Biol. 12, 1091–1102.

Yemshanov, D., Perera, A.H., 2002. A spatially explicit stochastic model to simulate boreal forest cover transitions: general structure and properties. Ecol. Model. 150, 189–209.