esa

ECOSPHERE

The differential influences of human-induced disturbances on tree regeneration community: a landscape approach

CARLOS ZAMORANO-ELGUETA,[1,†] LUIS CAYUELA,[2] JOSÉ MARÍA REY-BENAYAS,[1] PABLO J. DONOSO,[3] DAVIDE GENELETTI,[4] AND RICHARD J. HOBBS[5]

[1]*Departamento de Ciencias de la Vida—UD Ecología, Edificio de Ciencias, Universidad de Alcalá, E-28871 Alcalá de Henares, Spain*
[2]*Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Universidad Rey Juan Carlos, c/ Tulipán s/n, E-28933 Móstoles (Madrid), Spain*
[3]*Instituto de Bosques y Sociedad, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, Casilla 567, Valdivia, Chile*
[4]*Department of Civil, Environmental and Mechanical Engineering, University of Trento, Via Mesiano 77, 38123 Trento, Italy*
[5]*School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009 Australia*

Citation: Zamorano-Elgueta, C., L. Cayuela, J. M. Rey-Benayas, P. J. Donoso, D. Geneletti, and R. J. Hobbs. 2014. The differential influences of human-induced disturbances on tree regeneration community: a landscape approach. Ecosphere 5(7):90. http://dx.doi.org/10.1890/ES14-00003.1

Abstract. Understanding the processes shaping biological communities under interacting disturbances is a core challenge in ecology. Although the impacts of human-induced disturbances on forest ecosystems have been extensively studied, less attention has been paid to understanding how tree regeneration at the community level responds to such disturbances. Moreover, these previous studies have not considered how these effects change according to major social and environmental factors that can influence forest use at a landscape scale. In this study, we investigate the effects of cattle grazing and selective logging on the composition of tree regeneration communities in relation to forest successional stage and land tenure regime in Chilean temperate forests, a global biodiversity hotspot. We recorded seedlings, saplings and basal area of stumps of tree species (as a surrogate for selective logging), and number of cattle dung pats (as a surrogate for cattle pressure) in 129 25 × 20 m plots in small (<200 ha) and large properties in different successional stages (old-growth, intermediate, secondary forests). The regeneration of the ten more abundant species as predicted by human disturbance, land tenure, forest successional stage, and number of parent trees was modelled using generalised linear models. Predictions for each individual model were made under different scenarios of human disturbance. The predicted regeneration results were assembled and subjected to ordination analyses and permutation multivariate analyses of variance to determine differences in regeneration composition under each scenario. In most cases, best-fit models contained at least one of the explanatory variables accounting for human disturbance. The effects of selective logging on tree regeneration varied depending on land tenure regime, but cattle grazing always exhibited a negative effect. Our results revealed that cattle have a more negative effect on forest regeneration than selective logging, especially in old-growth forests and small properties. Our analytical approach contributes to the understanding of the differential influence of human-induced disturbances on the tree regeneration community at a landscape scale. It can inform conservation policies and actions, which should focus on addressing the main disturbance factors and on developing strategies to conserve the most sensitive species to such disturbances.

Key words: cattle grazing; Chile; community composition; forest successional stages; land tenure; low-intensity disturbance; 'predict first, assemble later' modeling; selective logging; temperate forest.

Received 4 January 2014; revised 2 April 2014; accepted 13 May 2014; **published** 31 July 2014. Corresponding Editor: M. Anand.

Copyright: © 2014 Zamorano-Elgueta et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. http://creativecommons.org/licenses/by/3.0/

† **E-mail:** carlos.zamorano@edu.uah.es

Introduction

The impacts of human-induced disturbances on forest ecosystems have been extensively reported throughout the world (Belsky and Blumenthal 1997, Augustine and McNaughton 1998, Wisdom et al. 2006, Baraloto et al. 2012, Clark and Covey 2012). Forest degradation by both intense, episodic disturbances (e.g., extensive logging or forest conversion to other land uses) and low intensity, chronic disturbances (e.g., grazing, selective logging or invasion of exotic species and fires) have been studied in several forests (Belsky and Blumenthal 1997, Ramírez-Marcial et al. 2001, Stern et al. 2002, Timmins 2002, Fisher et al. 2009, Baraloto et al. 2012, Clark and Covey 2012). These disturbances, particularly cattle grazing and selective logging, change species diversity and composition, which may have a major influence on community and ecosystem functioning (Chapin et al. 1998, Cadotte et al. 2011, Baraloto et al. 2012). However, less attention has been paid to understanding how tree regeneration at the community level responds to such disturbances. Moreover, previous work has not considered how these effects change according to the major environmental and social factors that can influence use of forests at the landscape scale, namely forest successional stage and land tenure regime. For example, in South America, the few published studies have focused on analysing the impacts of introduced mammals on single forest species, such as *Nothofagus dombeyi* (Veblen et al. 1989, 1992), *Austrocedrus chilensis* (Veblen et al. 1992, Relva and Veblen 1998, Relva and Sancholuz 2000), and *Araucaria araucana* (Zamorano-Elgueta et al. 2012). Understanding the impacts of these disturbances on forest communities and how they vary according to forest successional stage and land tenure provides more comprehensive information to guide conservation efforts. Furthermore, Turner (2010) identified as research priorities the study of disturbances as catalysts of rapid ecological change, interactions among disturbances and relationships between land use and disturbance.

To evaluate the effects of human-induced disturbances on community composition, the study of regeneration of forest species can be particularly informative, as seedlings and saplings respond more rapidly to most low intensity and chronic human disturbances than long-lived adult trees do (Cayuela et al. 2006, Helm et al. 2006). Forest regeneration is the process that ensures successive generations of trees (Barnes et al. 1998), and is essential in maintaining the long-term ecological functions and values of forests (Donoso and Nyland 2005). Therefore, investigating the effects of human disturbance on tree regeneration can provide critical information about how these impacts will shape forest community composition and influence ecosystem functioning, as well as the resistance and resilience of these ecosystems to environmental change in the long term (Cadotte et al. 2011).

In this study we investigated (1) the influences of cattle grazing and selective logging on the composition of regeneration communities of a temperate forest ecosystem; and (2) whether these influences vary according to forest successional stage (old-growth, intermediate, and secondary forests) and land tenure regime (small and large properties). Taking into account the successional context is important because forest successional stage is one of the main factors that determine the baseline communities (Nyland 2002). Additionally, property size is also important because frequency and intensity of alterations are often related to this feature (Burschel et al. 2003, Zamorano-Elgueta et al. 2012). We investigated these effects in the Coastal Range of southern Chile, which is more exposed to human disturbance compared to the Andes. The Chilean temperate forests have been recognized as a global hotspot of biological diversity (Myers et al. 2000, Funk and Fa 2010) and were selected as a target for urgent conservation efforts by the World Wildlife Fund and the World Bank (Dinerstein et al. 1995).

Methods

Study area

The study was carried out in the Coastal Range of the Región de los Ríos, southern Chile (39°28′ S, 73°16′ W; 40°20′ S, 73°18′ W). The area covers ca. 2,700 km^2 (Fig. 1) and elevation ranges from 4

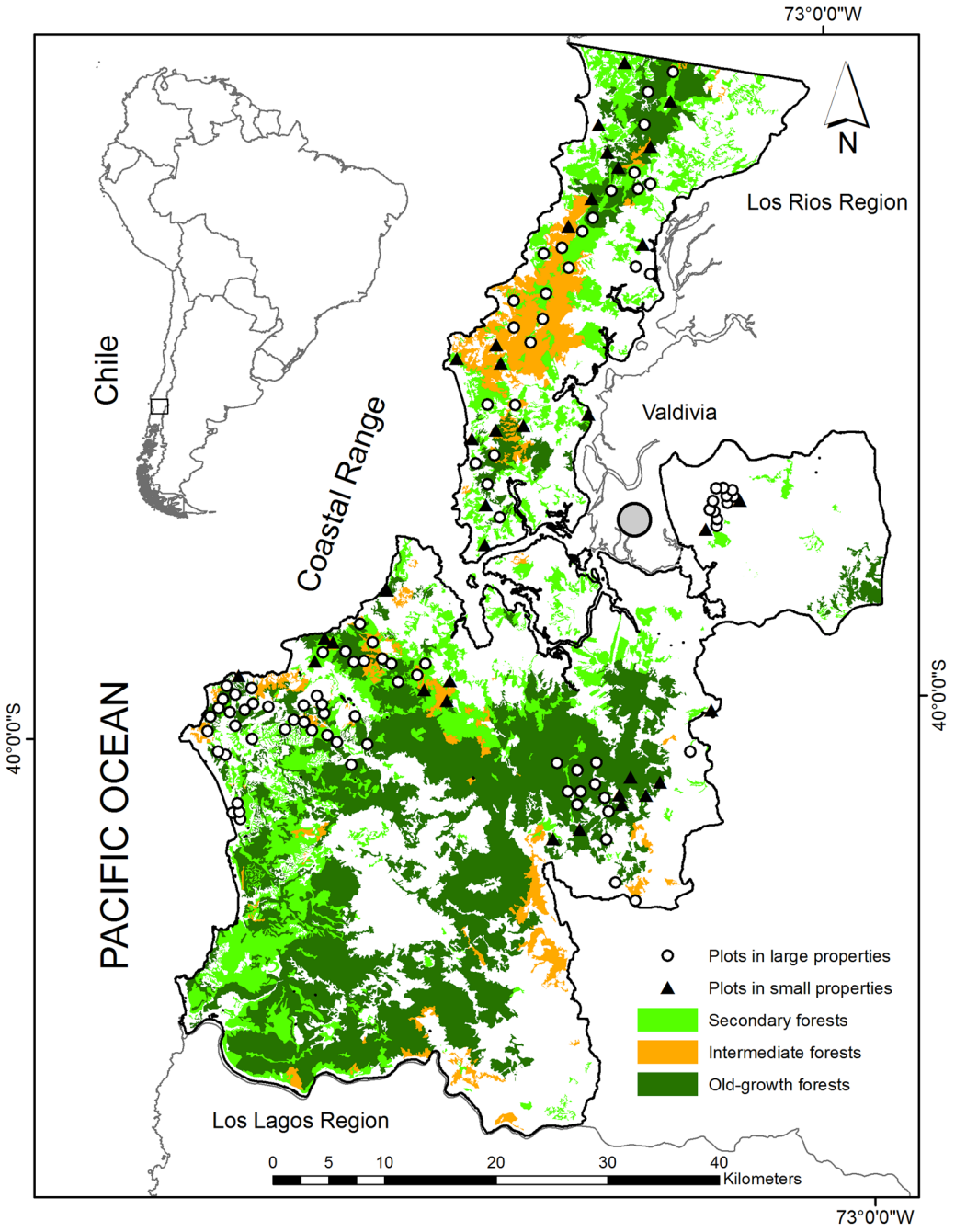

Fig. 1. Location of the study area and the 129 plots that were surveyed and information related to property size and forest successional stage within the Coastal Range, southern Chile.

to 684 m above sea level. The Coastal Range has abundant endemic flora and fauna, which probably reflects the location of vegetation refuges during the last glacial period (Armesto et al. 1995). Evergreen forests are the dominant vegetation type and occupy 79% of the total forest cover in the study area (CONAF et al. 1999). The predominant climate is temperate with Mediterranean influence. The average annual temperature and precipitation is 11.9°C and

2,500 mm, respectively (Di Castri and Hajek 1976). Soils derive from metamorphic material and granitic rocks, are thin to moderately deep (15–180 cm), have a loamy-clay to clay texture at depth, are very strongly to moderately acidic (pH = 4.6–5.7), and have moderate to high erodibility and low nutrient levels (IREN-CORFO 1964).

Land tenure in the study area is characterized by a mosaic of different land use types, productive activities and local actors, including indigenous communities, national protected areas, large private protected areas, and forest companies. The dominant types of land tenure correspond to small properties (67,656 ha, 25% of the study area) owned by "campesinos" (the Spanish name for rural people living in small-sized properties with a subsistence economy), and properties owned by forest companies (79,852 ha, 29%) that concentrate the area covered by exotic tree plantations. Although these plantations have increased during the last decades (CONAF-CONAMA 2008), a significant proportion of well-conserved old-growth forest (92,558 ha, 55%) still remains. High frequency and intensity of alterations are typically associated with small properties (i.e., <200 ha as defined by the Chilean laws) owned by peasants or campesinos due to the need to achieve levels of production to ensure family subsistence (Zamorano-Elgueta et al. 2012). In this study we used small (<200 ha) and large (≥200 ha) properties belonging to private landowners to evaluate logging and cattle grazing.

Three forest successional stages were defined according to the native forests cadastre, one of the most comprehensive cartographic studies of natural vegetation developed in Chile (CONAF et al. 1999): old-growth, old-growth/secondary and secondary forests. Old-growth forests correspond to uneven-aged stands dominated by broad-leaved evergreen tree species, with at least 50% canopy cover, high vertical heterogeneity, structural variability, higher tree species richness, and presence of large canopy emergents (>80 cm dbh, >25 m tall). Secondary forest corresponds to even-aged stands composed mainly of young trees, originating after large-scale disturbance, whether natural or anthropogenic. Old-growth/secondary forest corresponds to intermediate conditions of stand structure, and henceforth we will refer to these forests as 'intermediate forests.'

Sampling methods and forest species selection

A geographical information system (GIS) was used to randomly allocate plots across the study area using a sampling design stratified by land tenure and forest successional stage, and at a minimum distance of 1 km from each other. Once in the field, 129 25 × 20 m plots were established in evergreen forests, at a minimum distance of 200 m from forest edges. The average distance between pairs of plots was 1,600 m. Thirty-six plots were located in rural small properties (13 in old-growth forests, 8 in intermediate forest, 15 in secondary forest) and 93 plots in large properties owned by forest companies (31 in old-growth forest, 27 in intermediate forest, and 35 in secondary forest). These properties had an average area of 32 ha. In each plot, a 6 × 6 m subplot located at the plot centre was established, and all seedlings (<1.3 m tall) and saplings (>1.3 m tall and <5 cm in diameter at breast height [DBH]) were recorded. Overall, 60% of total regeneration corresponded to seedlings <0.3 m, which represented recently established regeneration and were ca. <5 years old (Vita 1977, Uteau 2003, Donoso et al. 2006*a*, *b*, *c*).

Within each plot, two human disturbance-related variables were measured, namely (1) number and basal area of stumps of each tree species without resprouts (a surrogate for selective logging) and (2) number of cattle dung pats (a surrogate for current cattle density and trampling pressure on tree regeneration). Henceforth we will refer to these variables as 'selective logging' and 'cattle intensity index' (CAI; sensu Zamorano-Elgueta et al. 2012), respectively. Fifty-seven percent of stumps were >10 years old based on qualitative information such as wood decomposition and the stump surface covered by lichens, mosses and fungi. Therefore, it was a reasonable assumption to consider that most of the logging activity pre-dated the establishment of the regeneration trees. In each plot, the number of parent trees of each species, defined as those individuals >5 cm in DBH, was also recorded to account for density-dependent effects. Based on the distribution of tree diameters, we estimated that 45% of the parent trees were >40 years old (Vita 1977, Uteau 2003, Donoso

and Escobar 2006, Donoso et al. 2006*a*, *b*, *c*).

Statistical analyses

The sum of all seedlings and saplings of each species found at each subplot was the response variable in the regeneration models. Not all species were equally present in all plots. In order to fit reliable statistical models, only the most abundant species (i.e., those present in at least 60 plots either in adult or juvenile form) were analyzed in this study. Given the low rate of occurrence of many species, we could only fit statistical models for 10 out of the 33 species recorded in this study. The list of forest species recorded and their occurrence is given in Appendix A.

We followed a 'predict first, assemble later' modelling approach (Ferrier et al. 2002) to study the effects of human-induced disturbances on tree regeneration. Regeneration of the 10 selected individual species were modelled one at a time as a function of human disturbances, land tenure, forest successional stage, and number of parent trees. Predictions for each individual model were made under four different scenarios of human disturbance namely, (1) undisturbed, (2) high cattle grazing pressure, (3) high selective logging pressure, and (4) both high cattle grazing and selective logging pressures, which were defined based on the range of the observed data. The resulting array of predicted abundances of seedling and saplings (i.e., regeneration) was then assembled and subjected to ordination analyses (non metric multidimensional scaling, NMDS) and permutation multivariate analyses of variance using distance matrices (PERMANOVA), to determine differential effects of human disturbance on regeneration composition in each land tenure regime and forest successional stage.

For the individual species, we used generalised linear models (GLM) with a log-log link function to linearize the observed exponential relationship between the response and the explanatory variables, and a negative binomial error distribution to account for overdispersion. The use of a negative binomial error distribution required estimating an additional parameter, delta, to determine the scaling of the variance to the mean. We used maximum likelihood methods and model selection as an alternative to traditional hypothesis testing (Johnson and Omland 2004). We estimated model parameters that maximized the likelihood of the regeneration measured in the field, given a suite of alternative models. For each species, we examined 85 different nested models including the effects of CAI, selective logging, land tenure regime, successional stage, and number of parent trees, as well as some particular interactions between the explanatory variables. The most complex model takes the form:

$$\begin{aligned}\log(Y_i) = {} & \mathrm{NT}_i + \log(\mathrm{CAI}_i) \times \mathrm{LT}_i \times \mathrm{FS}_i \\ & + \log(\mathrm{SL}_i) \times \mathrm{LT}_i \times \mathrm{FS}_i \\ & + \log(\mathrm{CAI}_i) \times \log(\mathrm{SL}_i)\end{aligned}$$

where Y_i is the number of seedlings and saplings per hectare in plot i; NT_i is the number of parent trees; CAI_i is the cattle intensity index; LT_i is the land tenure regime; FS_i is the forest successional stage; and SL_i refers to selective logging pressure. Interactions among covariates and between covariates and factors would indicate that the effect of a covariate in the response variable changes, depending on the value of the other covariate or factor level.

Alternative models were compared using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). Delta AICc (ΔAICc) was calculated as the difference in AICc between each model and the best model in the set. Models with AICc differences < 2 have substantial support (Burnham and Anderson 2002). Therefore, models with $\Delta\mathrm{AICc} > 2$ were excluded from further calculations. Akaike weights (w_i) were calculated for the confidence set of models ($\Delta\mathrm{AICc} < 2$) to determine the weight of evidence in favor of each model and to estimate the relative importance of each individual parameter in the set of candidate models (w_i). If no single model is clearly superior to the others in a set of models (model with $w_i < 0.9$), a (weighted) model averaging approach should be used (Burnham and Anderson 2002). Hence, we used the entire set of plausible models ($\Delta\mathrm{AICc} < 2$) to calculate model-averaged estimates for variables included in the confidence set of models and their unconditional standard errors (SE). This approach reduces model selection bias effects on regression coefficient estimates in all selected subsets (Burnham and Anderson 2002).

Residual plots were explored to assess model assumptions. In addition, spatial correlograms

based on Moran's Index were used to explore the autocorrelation of the best-fit model's residuals at different geographical distances (Diniz-Filho et al. 2003). If spatial autocorrelation was detected in a distance class, then one could assume that there were spatially patterned variables not included in the model that contributed to explaining patterns of regeneration for that particular species.

To make model predictions, values for each human-induced variable were set to either zero (no disturbance) or to a value close to the maximum value observed in the field (high disturbance). To account for the stochastic component in each individual model, we added a random error from a negative binomial error distribution using the 'delta' parameter estimated by each individual model. In addition, when there were a set of plausible models for a particular species, we made predictions using only one of the best fit models at a time. This model was randomly selected from the set of best fit models using probabilities proportional to model weights (w_i). Thus, for a single set of values for the explanatory variables, different predictions were possible depending on the random error and the model selected. To account for these sources of variability, we made 250 predictions for the regeneration of each species under each of the four disturbance scenarios in each land tenure regime and forest successional stage.

Next, the resulting array of predicted abundances of regeneration was assembled and subjected to NMDS. Data were square-root transformed and then submitted to Wisconsin double standardization (Legendre and Gallagher 2001). We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix among assembled communities. Finally, differences in regeneration composition of the assembled communities as a function of the two human-induced disturbance variables in each land tenure and forest successional stage were statistically determined by means of PERMANOVA (Anderson 2001). We used the Bray-Curtis distance and 999 permutations for these analyses (permutations of residuals under the reduced model; Anderson and Ter Braak 2003).

All analyses were performed using R (R Development Core Team 2010), including the 'MASS' (Venables and Ripley 2002), 'vegan' (Oksanen et al. 2010) and 'MuMIn' (Barton 2013) packages.

Results

Human-induced disturbances on individual species regeneration

The response of forest regeneration to cattle and selective logging was heterogeneous. In seven out of the 10 modeled species there was no single best-fit model (Table 1). Model assumptions were fulfilled in all cases. Based on the correlograms of model residuals, we only detected significant spatial autocorrelation at some intermediate distance lags for some species, yet the degree of autocorrelation was in general low and followed no particular pattern (detailed results not shown). All species except *Aextoxicon punctatum* and *Amomyrtus meli* were affected by at least one of the two human disturbance-related variables (Table 1). In some cases, these two variables interacted significantly, further exacerbating (i.e., negative interaction such as for *Gevuina avellana*) or ameliorating (i.e., positive interaction such as *Drimys winteri* and *Laureliopsis philippiana*) the individual effects of these disturbances on species regeneration. Details of parameters for the best fitted models are given in Appendix B.

The variable number of parent trees was not included in any of the best-fit models for *Amomyrtus luma* and *L. philippiana* (Table 1), and had little weight in model-averaged estimates for *D. winteri* and *G. avellana*. For the remaining species, the overall effect of parent trees on regeneration was negative, except for *A. meli* where there was a positive density-dependent effect. As for the effect of land tenure, large properties registered, on average, more regeneration of *A. punctatum*, *D. winteri*, *Eucryphia cordifolia*, *L. philippiana* and *Podocarpus nubigena*, whereas small properties had more regeneration of *A. meli*, *G. avellana* and *Myrceugenia planipes*. Secondary and intermediate forests exhibited low regeneration of *A. meli*, *E. cordifolia* and *M. planipes* as compared to old-growth forests; on the contrary, they exhibited relatively high regeneration of *L. philippiana* (maximum regeneration attained in secondary forests) and *Saxegothaea conspicua* (maximum regeneration

Table 1. Ranking of the generalized linear models of individual species following an AIC-based model selection procedure. ΔAIC and w_i correspond to AIC differences and Akaike weights, respectively. Abbreviation of the model parameters are: NT, the number of parent trees; CAI, the cattle intensity index; LT, the land tenure regime; FS, the forest successional stages; and SL, selective logging pressure. Coefficients in bold indicate the best-fit models for each forest species.

Forest species	Model parameters	AIC	ΔAIC_c	w_i
Aextoxicon punctatum	NT × LT	...	**0.00**	**1.00**
Amomyrtus luma	CAI	...	**0.00**	**1.00**
Amomyrtus meli	NT × LT × FS	...	**0.00**	**1.00**
Drimys winteri	SL × CAI + SL × LT	**840.04**	**0.00**	**0.53**
	NT + SL × CAI + SL × LT	841.44	1.40	0.26
	SL × LT	841.96	1.92	0.20
Eucryphia cordifolia	NT	**336.75**	**0.00**	**0.32**
	NT × LT	**336.75**	**0.00**	**0.32**
	NT × FS	337.28	0.53	0.24
	NT + CAI	338.72	1.97	0.12
Gevuina avellana	SL	**425.73**	**0.00**	**0.27**
	SL + CAI	425.82	0.09	0.26
	CAI + SL × LT	427.10	1.38	0.14
	SL × LT	427.32	1.59	0.12
	SL × CAI	427.41	1.68	0.12
	NT + SL	427.65	1.92	0.10
Laurelia philippiana	FS × CAI + SL × CAI	**638.46**	**0.00**	**0.32**
	SL × CAI	638.83	0.37	0.26
	FS × SL + SL × CAI	640.01	1.56	0.15
	FS × SL + FS × CAI + SL × CAI	640.08	1.63	0.14
	FS × CAI + SL × CAI + SL × LT	640.21	1.75	0.13
Myrceugenia planipes	SL × LT	**450.72**	**0.00**	**0.38**
	NT + SL × LT	451.64	0.92	0.24
	NT × FS	451.76	1.03	0.23
	NT	452.57	1.84	0.15
Podocarpus nubigena	NT + SL	**409.41**	**0.00**	**0.37**
	NT + SL + CAI	410.36	0.96	0.23
	NT + CAI	410.47	1.07	0.22
	NT × LT	410.89	1.48	0.18
Saxegothaea conspicua	NT + FS × CAI	**408.59**	**0.00**	**0.64**

attained in intermediate forests).

In some species, the response of regeneration to human disturbance-related variables varied depending on land tenure regime and forest successional stages (Fig. 2). Such changes occasionally reversed the sign of the effect, from positive to negative or vice-versa. Thus, cattle grazing, on one hand, had a negative effect on the regeneration of *D. winteri*, *G. avellana*, *L. philippiana*, *P. nubigena*, and *S. conspicua* in old-growth and secondary forests; and a positive effect on *A. luma* and *E. cordifolia* except in intermediate forests of large properties, and *S. conspicua* in intermediate forests in both small and large properties. Selective logging, on the other hand, had a negative effect on regeneration of *D. winteri*, *P. nubigena*, *G. avellana*, and *M. planipes* in small properties regardless of the forest successional stage. Similar effects were registered for *L. philippiana*, *D. winteri* and *P. nubigena* in large properties. Selective logging had a positive effect on *G. avellana* and *M. planipes* in large properties, and on *L. philippiana* in small properties in intermediate and old-growth forests. Finally, the effect of selective logging on *S. conspicua* was positive in old-growth and secondary forests in both small and large properties.

Changes in regeneration composition of the assembled communities

The regeneration assemblages inferred from individual species model predictions depicted clear patterns in relation to the four disturbance scenarios analyzed, land tenure regimes and forest successional stages (Fig. 3). The overall variability in predicted species abundances explained by human-induced disturbances ranged from 10.7% to 21.7% (Table 2). The cattle intensity index explained most of the variability in community composition in all cases, followed by selective logging and the interaction between

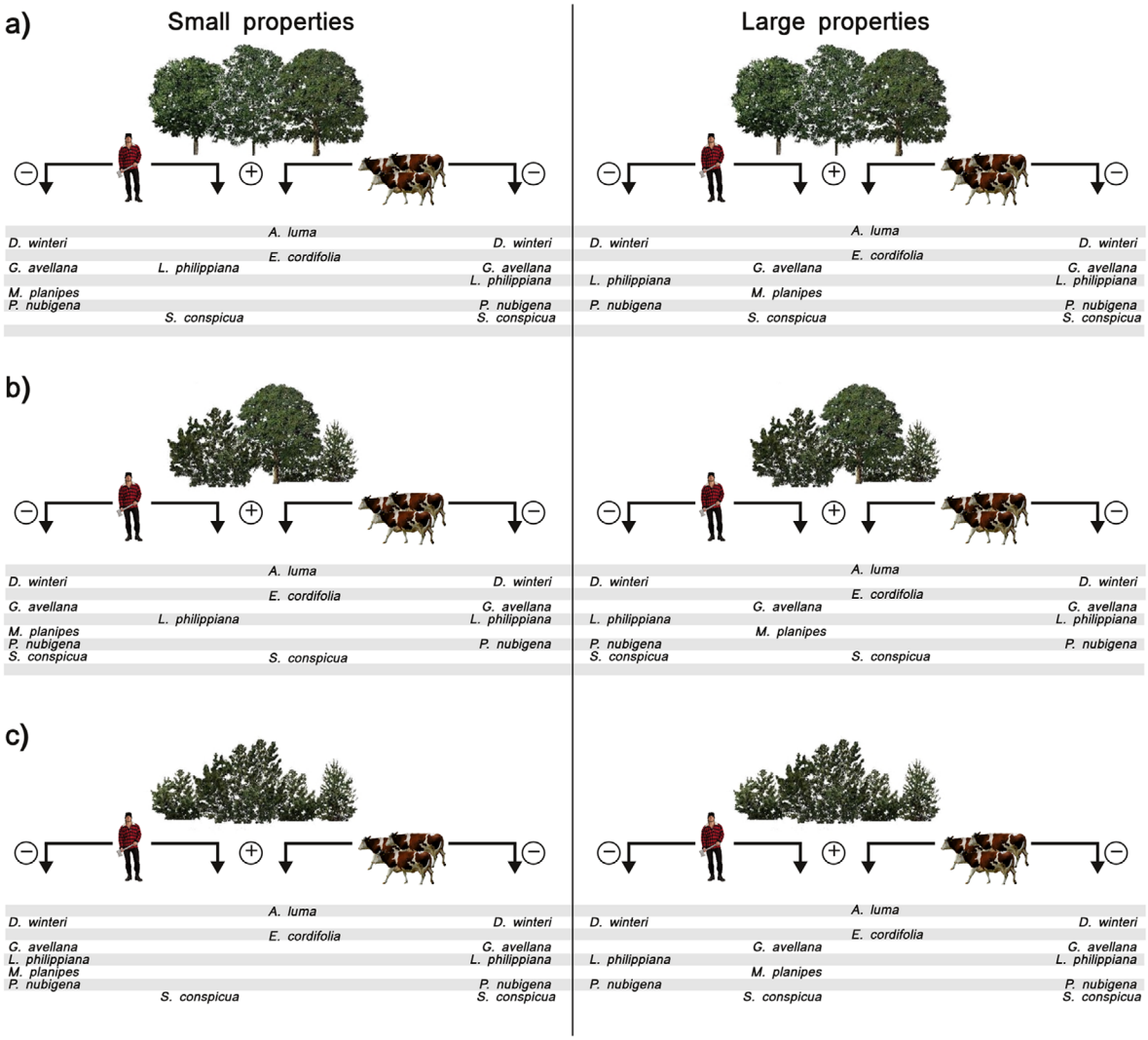

Fig. 2. Summary of the Cattle Intensity Index and selective logging effects on forest regeneration predicted by land tenure in (a) old-growth forests, (b) intermediate forests, and (c) secondary forests. Symbols represent positive (+) or negative (−) effects on forest species, respectively.

these two variables (Table 2). Indeed, there was a clear separation in the ordination diagrams between assemblages with and without cattle disturbance (Fig. 3). This separation was most clear in old-growth forests and less in secondary forests.

A. luma was always associated with assemblages disturbed by cattle, whereas *L. philippiana* and *D. winteri* were typically associated with undisturbed forests by cattle in all land tenure regimes and forest successional stages. Other species were associated with either disturbed or undisturbed assemblages by cattle depending on the forest successional stage. Such was the case for *S. conspicua*, which was associated with assemblages disturbed by cattle in intermediate forests and undisturbed ones in old-growth forests (Fig. 3). Associations between specific species and selective logging were not consistent in the different land tenure regimes and forest successional stages, and more difficult to visualise in the ordination diagrams (Fig. 3).

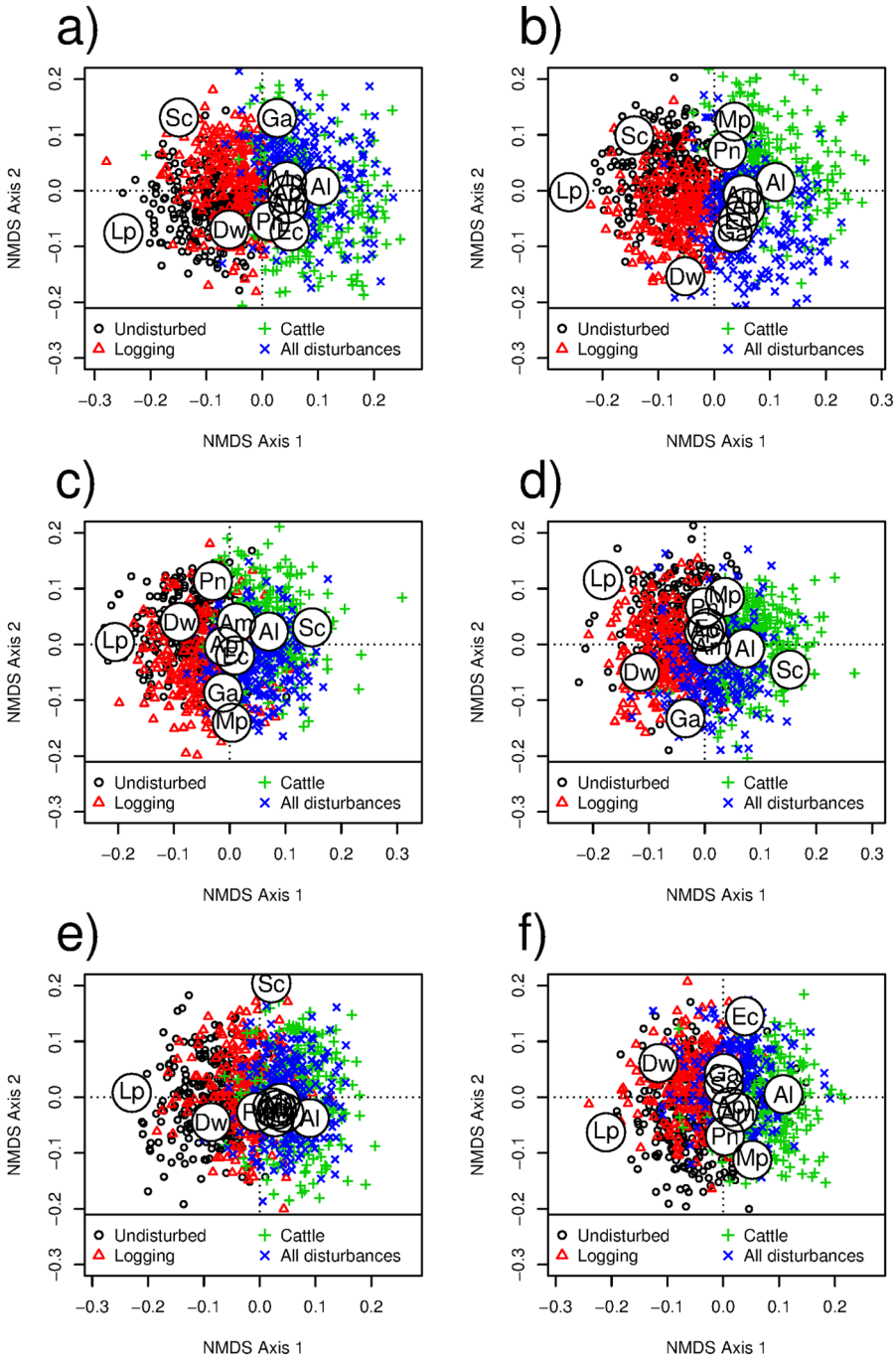

Fig. 3. Ordination analyses (NMDS) of forest regeneration communities predicted under several scenarios of joint effects of low-intensity disturbances, land tenure and forest successional stage. (a) Old-growth forests in large properties; (b) old-growth forests in small properties; (c) intermediate forest in large properties; (d) intermediate forest in small properties; (e) secondary forest in large properties and (f) secondary forest in small properties. Species abbreviations are the following: Am, *A. Meli*; Al, *A. Luma*; Ap, *A. punctatum*; Dw, *D. Winteri*; Ec, *E. Cordifolia*; Ga, *G. avellana*; Lp, *L. philippiana*; Mp, *M. Planipes*; Pn, *P. nubigena*; Sc, *S. conspicua*. Symbols represent regeneration assemblages in relation to the four disturbance scenarios analysed and main forest species involved.

Table 2. Summary of the PERMANOVA to test the effects of the cattle intensity index (CAI), selective logging (SL), and their combined effect (CAI × SL) on the regeneration composition of the assembled communities in each land tenure (property size) and forest successional stage: (a) old-growth forests in large properties; (b) old-growth forests in small properties; (c) intermediate forest in large properties, (d) intermediate forest in small properties, (e) secondary forest in large properties, (f) secondary forest in small properties. Abbreviations are: df, degrees of freedom; SS, sum of squares; MS, mean squares; F = F statistic; R^2 = explained variance.

Parameter	df	SS	MS	F	R^2	P
a) Old-growth forest in large properties						
CAI	1	6.714	6.714	168.218	0.139	0.001***
SL	1	1.011	1.011	25.341	0.021	0.001***
CAI × SL	1	0.872	0.872	21.852	0.018	0.001***
Residuals	996	39.754	0.040		0.822	
Total	999	48.352			1.000	
b) Old-growth forest in small properties						
CAI	1	7.396	7.396	166.961	0.138	0.001***
SL	1	1.583	1.583	35.860	0.030	0.001***
CAI × SL	1	0.354	0.354	8.017	0.006	0.001***
Residuals	996	43.961	0.044		0.825	
Total	999	53.267			1.000	
c) Intermediate forest in large properties						
CAI	1	4.513	4.513	108.875	0.095	0.001***
SL	1	1.111	1.111	26.812	0.023	0.001***
CAI × SL	1	0.703	0.703	16.967	0.015	0.001***
Residuals	996	41.281	0.041		0.867	
Total	999	47.608			1.000	
d) Intermediate forest in small properties						
CAI	1	3.394	3.394	82.732	0.074	0.001***
SL	1	1.265	1.265	30.834	0.028	0.001***
CAI × SL	1	0.215	0.215	5.239	0.005	0.001***
Residuals	996	40.863	0.041		0.893	
Total	999	45.737			1.000	
e) Secondary forest in large properties						
CAI	1	9.364	9.364	208.257	0.164	0.001***
SL	1	1.473	1.473	32.751	0.026	0.001***
CAI × SL	1	1.591	1.591	35.394	0.028	0.001***
Residuals	996	44.782	0.045		0.783	
Total	999	57.210			1.000	
f) Secondary forest in small properties						
CAI	1	8.469	8.469	175.188	0.142	0.001***
SL	1	2.448	2.448	50.631	0.041	0.001***
CAI × SL	1	0.668	0.668	13.818	0.011	0.001***
Residuals	996	48.150	0.048		0.806	
Total	999	59.735			1.000	

Discussion

Our study reveals that cattle grazing and selective logging have contrasting effects on the regeneration of different tree species, which ultimately shapes the composition of future communities. These effects were conditioned by land tenure regime and forest successional stages. By adding a random error to our simulated communities under a variety of disturbance scenarios, we predicted a diverse array of future forest composition.

Effects of cattle and selective logging on regeneration communities

Our study suggests that cattle grazing and, to a lesser extent, selective logging, have a major impact on the composition of regeneration communities, and that these impacts are more severe in small than in large properties and in old-growth than in intermediate or secondary forests. Overall, our results suggest negative effects of cattle and selective logging on the regeneration of most of the species studied. Selective logging had a negative influence on more species in small properties. This could be explained by the intensity of tree harvesting necessary to ensure family subsistence among

campesinos, mainly through firewood and charcoal production (Burschel et al. 2003). On the other hand, cattle grazing had similar negative effects regardless of the land tenure regime and forest successional stage. Cattle raising in the forests studied is mainly by campesinos in small properties. However, in large properties, especially in public properties and protected areas, forests are commonly used by neighbouring farmers as a source of fodder and refuge for their cattle, without any control over livestock density or logging intensity, and for firewood production—a pattern followed elsewhere in protected areas (Moorman et al. 2013). Similar conclusions were reported by Zamorano-Elgueta et al. (2012) in temperate forests dominated by the monkey puzzle tree *Araucaria araucana*. These results confirmed that cattle grazing can diminish, damage or prevent the recruitment of tree species by browsing and trampling, which can in turn induce changes in species composition (Hobbs 2001, Baraloto et al. 2012, Zamorano-Elgueta et al. 2012). Selective logging, on the other hand, can cause negative impacts on seedling richness (Farwig et al. 2008), tree species diversity (Polyakov et al. 2007, Ramírez-Marcial et al. 2001), and functional composition of forest communities (Baraloto et al. 2012).

Regeneration of shade-tolerant species such as *S. conspicua* and *L. philippiana* was differentially affected by selective logging according to forest successional stage and land tenure. The models showed that selective logging was less intense and the establishment of seedlings was favored in old-growth forests. Seedlings of these species require some shelter to have high survival and growth rates (Donoso et al. 2006*a*). In secondary forests of small and large properties and intermediate forests in large properties, regeneration of *L. philippiana* was negatively associated with selective logging, which could be due to higher intensity of logging and cattle grazing. A high proportion of seedlings and saplings of *E. cordifolia* showed damage by grazing (C. Zamorano-Elgueta, *unpublished data*). However, while this is a highly palatable species, its regeneration appears to be positively associated with cattle for all situations evaluated.

Changing microclimatic conditions inside forests might have caused the negative response observed for the pioneer species *D. winteri* in our study area. This species requires permanent soil moisture and abundant organic matter to regenerate (Donoso et al. 2007 and references therein). As pointed out by other studies (Farwig et al. 2008), disturbed habitat conditions might likewise influence the establishment of late successional species such as *S. conspicua*, *P. nubigena* or *L. philippiana*. In contrast, *A. luma*, a forest species with wider tolerance to several altered conditions, showed a positive response to human-induced disturbances, due mostly to its capacity to reproduce asexually (Donoso and Escobar 2006); this might be one of the reasons why *A. luma* is one of the most common species in temperate evergreen forests of the region (Veblen et al. 1981). The competitive ability of this species may be greater under a scenario of permanent human-induced disturbances.

Cattle had a greater influence than selective logging on forest regeneration, especially in old-growth forests, which appear to be more sensitive to human-induced disturbances. Thus, cattle grazing could influence habitat conditions in this forest type, changing their future composition dramatically. Undisturbed old-growth forests or forests associated only with selective logging would be dominated by late-successional species like *S. conspicua*, *A. punctatum* and *L. philippiana*. Instead, the persistent occurrence of either cattle or cattle and selective logging could prevent the establishment of these shade-tolerant and shade-semitolerant species and favor a composition dominated by *A. luma*, *A. meli* and *G. avellana*.

Implications for forest conservation

Understanding the processes shaping biological communities under interacting disturbances is a core challenge in ecology (Mouillot et al. 2012). If forests are permanently disturbed by low-intensity disturbances such as cattle grazing and selective logging, their composition will be profoundly altered by loss of biodiversity and changes in the dominance of different species. Effects of altered habitat conditions on forest regeneration could lead to less phenotypic diversity in characteristics such as fruit type, seed mass by area unit and flowering period (Fisher et al. 2009). These changes could generate unknown impacts on functional ecosystem properties and on the ecosystem's response to disturbance (Fisher et al. 2009). In this context,

there is an urgent need to quantify and predict the effects of disturbance on biodiversity patterns to guide conservation efforts and the management of ecological resources (Mouillot et al. 2012).

Our analytical approach contributes to the understanding of the differential influences of human-induced disturbances on the tree regeneration community at the landscape scale, with variable land tenure regimes and forest successional stages. Furthermore, it may strongly support conservation policies and actions, which should first focus on addressing the main disturbance factors and on developing strategies to conserve the most sensitive species to such disturbances.

Acknowledgments

C. Zamorano-Elgueta was supported by a CONICYT pre-doctoral fellowship (Government of Chile), the European Comission (Project contract DCI-ENV/2010/222-412), the Chilean NGO Forest Engineers for Native Forest (Forestales por el Bosque Nativo, www.bosquenativo.cl) and project REMEDINAL-2 (Comunidad de Madrid, S2009/AMB-1783). L. Cayuela was supported by project REMEDINAL-2. This work is part of the objectives of projects CGL2010-18312 (CICYT, Ministerio de Economía y Competividad de España). The authors acknowledge the valuable support of Verónica Píriz, Cony Becerra, Rodrigo Gangas, Óscar Concha, Eduardo Neira and staff from the Valdivian Coastal Reserve, as well as the National Forest Service of Chile (Corporación Nacional Forestal).

Literature Cited

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, M. J. and C. F. J. Ter Braak. 2003. Permutation tests for multi-factorial analysis of variance. Journal of Statistical Computing Simulation 73:85–113.

Armesto, J. J., J. C. Aravena, C. Villagrán, C. Pérez, and G. Parker. 1995. Bosques templados de la Cordillera de la Costa. Pages 199–213 *in* J. J. Armesto, C. Villagrán, and M. Arroyo, editors. Ecología de los bosques nativos de Chile. Editorial Universitaria, Santiago, Chile.

Augustine, D. J. and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of wildlife management 62:1165–1183.

Baraloto, C., B. Hérault, C. E. Paine, H. Massot, L. Blanc, D. Bonal, J. F. Molino, E. Nicolini, and D. Sabatier. 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. Journal of Applied Ecology 49:861–870.

Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. 1998. Forest ecology. Fourth edition. John Wiley and Sons, New York, New York, USA.

Barton, K. 2013. Multi-model inference. R package version 1.9.5. http://CRAN.R-project.org/package=MuMIn

Belsky, A. J. and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. Conservation Biology 11:315–327.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Burschel, H., A. Hernández, and M. Lobos. 2003. Leña: Una fuente energética renovable para Chile. Editorial Universitaria, Santiago, Chile.

Cadotte, M., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087.

Cayuela, L., D. J. Golicher, J. M. Rey Benayas, M. González-Espinosa, and N. Ramírez-Marcial. 2006. Fragmentation, disturbance and tree diversity conservation in tropical montane forests. Journal of Applied Ecology 43:1172–1181.

Chapin, III, F. S., O. E. Sala, I. C. Burke, J. P. Grime, D. U. Hooper, W. K. Lauenroth, A. Lombard, H. A. Mooney, A. R. Mosier, S. Naeem, S. W. Pacala, J. Roy, W. L. Steffen, and D. Tilman. 1998. Ecosystem consequences of changing biodiversity. BioScience 48:45–52.

Clark, J. A. and K. R. Covey. 2012. Tree species richness and the logging of natural forests: A meta-analysis. Forest Ecology and Management 276:146–153.

CONAF-CONAMA. 2008. Catastro de uso del suelo y vegetación: Monitoreo y actualización Región de Los Ríos. Gobierno de Chile, Ministerio de Agricultura.

Di Castri, F. and E. R. Hajek. 1976. Bioclimatología de Chile. First edition. Editorial Universidad Católica de Chile, Santiago.

Dinerstein, E., D. M. Olsen, D. J. Graham, A. L. Webster, S. A. Primm, M. P. Bookbinder, and G. Ledec. 1995. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. The World Bank, Washington, D.C., USA.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in

geographical ecology. Global Ecology and Biogeography 12:53–64.

Donoso, C., D. Alarcón, P. Donoso, B. Escobar, and A. Zúñiga. 2006*a*. *Laurelia* (=*Laureliopsis*) *philippiana* Looser. Tepa, Huahuan, Laurela. Familia: *Monimiaceae*. Pages 302–313 *in* C. Donoso, editor. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología, Marisa Cuneo ediciones, Valdivia, Chile.

Donoso, C., and B. Escobar. 2006. *Amomyrtus luma* (Mol.) Legr. Et Kausel. Luma, Reloncaví (=en los valles), Lang-llang (=bien sumergido), Familia: *Myrtaceae*. Pages 148–157 *in* C. Donoso, editor. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología, Marisa Cuneo ediciones, Valdivia, Chile.

Donoso, C., B. Escobar, P. Donoso, and F. Utreras. 2006*b*. *Drimys winteri* J.R. et G. Forster. Canelo, Foique. Familia: *Winteraceae*. Pages 220–232 *in* C. Donoso, editor. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología, Marisa Cuneo ediciones, Valdivia, Chile.

Donoso, C., M. Núñez, P. Donoso, and B. Escobar. 2006*c*. *Aextoxicon punctatum* R. et Pav. Olivillo, Tique, Palo muerto. Familia: *Aextoxicaceae*. Pages 135–147 *in* C. Donoso, editor. Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología, Marisa Cuneo ediciones, Valdivia, Chile.

Donoso, P. J. and R. D. Nyland. 2005. Seedling density according to structure, dominance and understory cover in old-growth forest stands of the evergreen forest type in the Coastal Range of Chile. Revista Chilena de Historia Natural 78:51–63.

Donoso, P. J., D. P. Soto, and R. A. Bertín. 2007. Size–density relationships in *Drimys winteri* secondary forests of the Chiloe Island, Chile: Effects of physiography and species composition. Forest Ecology and Management 239:120–127.

Farwig, N., N. Sajita, G. Schaab, and K. Böhning-Gaese. 2008. Human impact diminishes species richness in Kakamega Forest, Kenya. Basic and Applied Ecology 9:383–391.

Ferrier, S., M. Drielsma, G. Manion, and G. Watson. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in north-east New South Wales. II. Community-level modelling. Biodiversity and Conservation 11:2309–2338.

Fisher, J. L., W. A. Loneragan, K. Dixon, J. Delaney, and E. J. Veneklaas. 2009. Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. Biological Conservation 142:2270–2281.

Funk, S. M. and J. E. Fa. 2010. Ecoregion prioritization suggests an armoury not a silver bullet for conservation planning. PLoS ONE 5:e8923.

Helm, A., I. Hanski, and M. Pärtel. 2006. Slow response of plant species richness to habitat loss and fragmentation. Ecology Letters 9:72–77.

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

IREN-CORFO. 1964. Informaciones Meteorólogicas y Climáticas para la determinación de la Capacidad de Uso de la Tierra. First edition. Santiago, Chile.

Johnson, J. B. and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Legendre, P. and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Moorman, M. C., N. Peterson, S. E. Moore, and P. J. Donoso. 2013. Stakeholders perspective on prospects for co-management of an old-growth forest watershed near Valdivia, Chile. Society & Natural Resources: An International Journal 0:1–15.

Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2012. A functional approach reveals community responses to disturbances. Trends in Ecology and Evolution 28:167–177.

Myers, N., R. A. Mittermeler, C. G. Mittermeler, G. A. B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Nyland, R. D. 2002. Silviculture: concepts and applications. Second edition. McGraw-Hill, New York, New York, USA.

Oksanen, J., G. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. B. O'Hara, G. Simpson, P. Solymos, M. H. Stevens, and H. Wagner. 2010. Vegan: community ecology package. R package version 2.0-8. http://CRAN.R-project.org/package=vegan

Polyakov, M., I. Majumdar, and L. Teeter. 2007. Spatial and temporal analysis of the anthropogenic effects on local diversity of forest trees. Forest Ecology and Management 255:1379–1387.

Ramírez-Marcial, N., M. González-Espinosa, and G. Williams-Linera. 2001. Anthropogenic disturbance and tree diversity in Montane Rain Forests in Chiapas, Mexico. Forest Ecology and Management 154:311–326.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Relva, M. A. and L. A. Sancholuz. 2000. Effects of simulated browsing on the growth of *Austrocedrus chilensis*. Plant Ecology 151:121–127.

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

Stern, M., M. Quesada, and K. E. Stoner. 2002. Changes

in composition and structure of a tropical dry forest following intermittent cattle grazing. Revista de Biología Tropical 50:1021–1034.

Timmins, S. M. 2002. Impact of cattle on conservation land licensed for grazing in South Westland, New Zealand. New Zealand Journal of Ecology 26:107–120.

Turner, M. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Uteau, D. 2003. Desarrollo inicial de Laurel (*Laurelia semperviens*) y Ulmo (*Eucryphia cordifolia*) en plantaciones mixtas con especies nativas. Undergraduate Thesis. Universidad Austral de Chile, Valdivia, Chile.

Veblen, T. T., C. Donoso, F. M. Schlegel, and B. Escobar. 1981. Forest dynamics in South-Central Chile. Journal of Biogeography 8:211–247.

Veblen, T. T., M. Mermoz, C. Martín, and T. Kitzberger. 1992. Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. Conservation Biology 6:71–83.

Veblen, T. T., M. Mermoz, C. Martín, and E. Ramilo. 1989. Effects of exotic deer on forest regeneration and composition in northern Patagonia. Journal of Applied Ecology 26:711–724.

Venables, W. N. and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA.

Vita, A. 1977. Crecimiento de algunas especies forestales nativas y exóticas en el Arboretum del Centro Experimental Forestal Frutillar, X Región. Boletín Técnico. 47. Depto. Silvicultura. Universidad de Chile.

Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Journal of Wildlife Management 34:283–292.

Zamorano-Elgueta, C., L. Cayuela, M. González-Espinosa, A. Lara, and M. R. Parra-Vázquez. 2012. Impacts of cattle on the South American temperate forests: challenges for the conservation of the endangered monkey puzzle tree (*Araucaria araucana*) in Chile. Biological Conservation 152:110–118.

Supplemental Material

Appendix A

Table A1. List of forest species registered and their occurrence (number of plots where the species was present) for adult, regeneration and all individuals (total occurrence).

Family	Forest species	Occurrence		
		Adults	Regeneration	Total
Myrtaceae	*Amomyrtus meli* (Phil.) D. Legrand & Kausel.	87	112	119
Winteraceae	*Drimys winteri* J.R. Forst & G. Forst.	105	101	116
Monimiaceae	*Laureliopsis philippiana* (Looser) Schodde.	101	91	113
Myrtaceae	*Amomyrtus luma* (Molina) D. Legrand & Kausel.	102	94	110
Proteaceae	*Gevuina avellana* Molina.	86	80	97
Eucryphiaceae	*Eucryphia cordifolia* Cav.	66	51	78
Myrtaceae	*Myrceugenia planipes* O. Berg.	45	70	78
Podocarpaceae	*Saxegothaea conspicua* Lindl.	72	62	78
Aextoxicaceae	*Aextoxicon punctatum* Ruiz. & Pav.	56	69	74
Podocarpaceae	*Podocarpus nubigena* Lindl.	54	62	74
Asteraceae	*Dasyphyllum diacanthoides* (Less.) Cabrera.	41	35	49
Myrtaceae	*Myrceugenia ovata* O. Berg.	41	27	45
Myrtaceae	*Luma apiculata* (DC.) Burret.	33	16	35
Verbenaceae	*Rhaphithamnus spinosus* (Juss.) Moldenke.	21	27	35
Araliaceae	*Pseudopanax laetevirens* (Gay) Franch.	12	18	28
Laureaceae	*Persea lingue* Nees.	19	19	27
Podocarpaceae	*Podocarpus salignus* D. Don.	13	21	24
Fagaceae	*Nothofagus nitida* Krasser.	23	5	23
Cunoniaceae	*Weinmannia trichosperma* Cav.		9	23
Thymelaeaceae	*Ovidia pillo-pillo* Hohen. Ex Meisn.	17	11	21
Myrtaceae	*Myrceugenia parvifolia* (DC.) Kausel.	7	18	20
Cunoniaceae	*Caldcluvia paniculata* D. Don.	10	11	17
Proteaceae	*Lomatia dentata* R. Br.	7	12	14
Fagaceae	*Nothofagus dombeyi* (Mirb.) Oerst.	11	4	11
Proteaceae	*Embothrium coccineum* J.R. & G. Forst.	8	6	10
Proteaceae	*Lomatia hirsuta* (Lam.) Diels. Ex J.F. Macbr.	2	4	5
Monimiaceae	*Laurelia sempervirens* (Ruiz et Pav.) Tul.	4	2	4
Myrtaceae	*Tepualia stipularis* Griseb.	4	1	4
Elaeocarpaceae	*Aristotelia chilensis* Stuntz.	1	2	3
Fagaceae	*Nothofagus alpina* (Poepp. & Endl.) Oerst.	1	0	1
Fagaceae	*Nothofagus obliqua* (Mirb.) Oerst.	1	0	1

APPENDIX B

Table B1. Model-averaged estimates, standard errors and relative importance (w_i), for selected variables in the best fitted models of the regeneration of individual tree species. Generalised linear models were used with a log-log link function and a negative binomial error distribution. Estimated coefficients therefore refer to the response variable on a log scale. Abbreviation of the model parameters are: CAI, cattle intensity index; SL, selective logging; NT, number of parent trees. Forest corresponds to old-growth, intermediate and secondary forest. Type of property was defined as large (>200 ha) and small (<200 ha) properties.

Model parameters	Estimate	SE	Relative variable importance (w_i)
Aextoxicon punctatum			
(Intercept)	3.252	0.175	...
NT	−0.335	0.111	1.00
Small properties	−0.684	0.308	1.00
NT × Small properties	0.314	0.112	1.00
Amomyrtus luma			
(Intercept)	2.135	0.163	...
CAI	0.186	0.074	1.00
Amomyrtus meli			
(Intercept)	3.053	0.173	...
NT	0.350	0.223	1.00
Small properties	0.191	0.346	1.00
Intermediate forests	−0.184	0.263	1.00
Secondary forests	−0.086	0.239	1.00
NT × Small properties	−0.366	0.223	1.00
NT × Intermediate forests	0.039	0.015	1.00
NT × Secondary forests	−0.359	0.223	1.00
Small properties × Intermediate forests	0.321	0.505	1.00
Small properties × Secondary forests	0.038	0.481	1.00
NT × Small properties × Intermediate forests	NA	NA	NA
NT × Small properties × Secondary forests	NA	NA	NA
Drimys winteri			
(Intercept)	3.624	0.233	...
CAI	−0.402	0.154	0.80
SL	−0.234	0.111	1.00
Small properties	−2.463	0.616	1.00
SL × Small properties	0.540	0.228	1.00
SL × CAI	0.151	0.054	0.80
NT	0.005	0.005	0.26
Eucryphia cordifolia			
(Intercept)	2.382	0.264	...
NT	−0.030	0.010	1.00
Small properties	−0.634	0.361	0.32
NT × Small properties	−0.053	0.064	0.32
Intermediate forests	−0.737	0.407	0.24
Secondary forests	−0.629	0.371	0.24
NT × Intermediate forests	NA	NA	NA
NT × Secondary forests	−0.063	0.061	0.24
CAI	0.046	0.077	0.12
Gevuina avellana			
(Intercept)	1.041	0.217	...
SL	0.207	0.091	1.00
CAI	−0.063	0.112	0.51
Small properties	0.518	0.485	0.26
SL × Small properties	−0.297	0.174	0.26
SL × CAI	−0.043	0.056	0.12
NT	−0.002	0.004	0.10

Table B1. Continued.

Model parameters	Estimate	SE	Relative variable importance (w_i)
Laurelia philippiana			
(Intercept)	2.966	0.317	...
CAI	−1.221	0.426	1.00
Intermediate forests	−0.818	0.454	0.74
Secondary forests	0.329	0.492	0.74
SL	−0.207	0.128	1.00
Intermediate forests × CAI	0.610	0.265	0.59
Secondary forests × CAI	0.485	0.277	0.59
SL × CAI	0.230	0.096	1.00
Intermediate forests × SL	0.001	0.238	0.29
Secondary forests × SL	−0.351	0.226	0.29
Small properties	−1.330	0.645	0.13
SL × Small properties	0.413	0.244	0.13
Myrceugenia planipes			
(Intercept)	1.943	0.392	...
SL	0.256	0.125	0.62
Small properties	0.777	0.578	0.62
SL × Small properties	−0.553	0.225	0.62
NT	−0.039	0.033	0.62
Intermediate forests	−0.738	0.386	0.23
Secondary forests	−0.333	0.332	0.23
NT × Intermediate forests	NA	NA	NA
NT × Secondary forests	0.070	0.035	0.23
Podocarpus nubigena			
(Intercept)	2.467	0.194	...
NT	−0.054	0.017	1.00
SL	−0.182	0.095	0.60
CAI	−0.155	0.100	0.45
Small properties	−0.616	0.332	0.18
NT × Small properties	NA	NA	NA
Saxegothaea conspicua			
(Intercept)	1.595	0.298	...
NT	−0.159	0.104	1.00
CAI	−0.203	0.212	1.00
Intermediate forests	0.927	0.450	1.00
Secondary forests	0.358	0.470	1.00
Intermediate forests × CAI	0.556	0.283	1.00
Secondary forests × CAI	0.149	0.247	1.00
SL	0.032	0.146	0.36
Intermediate forests × SL	−0.331	0.215	0.36
Secondary forests × SL	0.279	0.206	0.36