



The effect of small-scale land use on vegetation in the Valdivian Coastal Range (Chile)

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Abstract: Today, native vegetation in the Valdivian Coastal Range (VCR) is restricted to areas where small-scale land use dominates resulting in a vegetation mosaic. This study (1) provides a description of the vegetation types (VT) within the vegetation mosaic, (2) identifies land use drivers that lead to either degradation or recovery processes and, (3) attempts to provide an explanation for the vegetation mosaic with a conceptual model. In two regions of the VCR we sampled 102 plots for composition of vegetation and indicators of livestock browsing, timber cutting and coppice forestry. We classified the vegetation using a flexible beta method and Bray-Curtis distance. Diagnostic species were identified by an extended indicator species analysis. The clustering results were visualized in NMDS and recursive partitioning was used to explain variations in the VTs as a function of the land use variables. Differentiating effects were tested using PERMANOVA and a conceptual model for the vegetation dynamics was developed from the results. Four VTs such as (1) extensively grazed non-native grasslands (EGN); (2), closed and semi-closed grazed *Ugni* and *Berberis* shrublands; (3) severely impacted evergreen forests; and (4) sparsely disturbed evergreen forests were recognized. The browsing indicators were important for differentiating the VTs. The EGN grasslands were differentiated by having more than 0.075 dung piles/m². Areas with fewer dung piles but direct browsing effects had the greatest impact on vegetation. Forests were preserved when the mean browsing index was equal to or lower than 0.5. The cutting frequency was significant in determining overall floristic composition. We showed that shrublands and evergreen forests within the vegetation mosaic and the result of small-scale farming led to high native forest species richness. This makes the vegetation mosaic especially valuable in a landscape dominated by exotic tree monocultures.

Abbreviations: EGN – extensively grazed non-native grasslands, NMDS – non-parametric multidimensional scaling, PERMANOVA – permutational multivariate analysis of variance, SDF – sparsely disturbed evergreen forest, SIE – severely impacted evergreen forests, UBS – closed and semi closed grazed *Ugni* and *Berberis* shrublands, VCR – Valdivian Coastal Range, VT – vegetation type.

Nomenclature: The International Plant Names Index (2012).

Introduction

Human activities are a major cause of vegetation change in contemporary landscapes (Foster and Motzkin 1998, Hobbs et al. 2006, Armesto et al. 2010). Unfavorable socioeconomic conditions often lie behind the conversion of forests to pastures and the degradation of forests to shrublands. Conversely, improvements in socioeconomic conditions often lead to less intensive land use and the abandonment of farmland to which forest returns (Gutiérrez et al. 2012, 2013, Rojas et al. 2013). These changes in vegetation affect biodiversity and environmental services (Foley 2005).

Cultural landscapes characterized by traditional small-scale farming and livestock grazing support a wide range of more or less artificial to semi-natural vegetation types (VTs). The VTs, created and maintained by particular land use practices, often support high native species diversity

(Deutschewitz et al. 2003, Menzies 2007). There are various reasons why the vegetation mosaic created by small-scale land use activities is valuable for nature conservation. The vegetation mosaic (1) serves as a refuge for plant with animal species and connects large native forest areas and protected areas (Armesto 2002); (2) it supports the restoration of forest functions and services during succession (Guariguata and Ostertag 2001, Armesto 2002, Chazdon 2003); and (3) it represents a part of a heterogeneous cultural landscape with unique plant and animal communities which are especially valuable for species that depend on open and edge conditions (Foster and Motzkin 1998).

An understanding of the effects of land use on vegetation patterns and dynamics in areas where the vegetation has been altered by humans at a large-scale is valuable. It provides a scientific baseline for management and conservation of such ecosystems on a landscape scale. Land use modifies biotic

and abiotic conditions, thereby affecting species establishment, competition and growth, resulting in changes to the floristic composition. Changes in the composition that lead to a decrease in structural complexity and floristic diversity often result in a loss of ecosystem services (Thompson 2011). However, changes bring about an increase in structural complexity, usually called “succession”, as defined by Clements (1916), tends to increase the naturalness of the ecosystems and assist in the recovery of degraded ecosystems.

Cultural landscapes and the impacts of small-scale land use have been very well documented in many parts of the world and especially in Europe (e.g., Ellenberg and Leuschner 2010). However, little research has been done in south-central Chile even though it is a global biodiversity hotspot (Myers et al. 2000). It is home to the Valdivian evergreen rainforest, a threatened ecosystem with outstanding biodiversity and endemic species richness (Olson and Dinerstein 1998, Myers et al. 2000). In this region the highest rates of biodiversity and endemism occur on the eastern slopes of the Valdivian Coastal Range (VCR) below 600 m in altitude (Armesto 1998, Smith-Ramírez et al. 2006). In the 1970s, the conversion of the Valdivian rainforest into exotic tree plantations began (Armesto et al. 2001, 2010, Armesto 2002, Smith-Ramírez and Armesto 2002). Today's remaining rainforest ecosystem is insufficiently represented in the Chilean network of protected areas (SNASPE, Sistema Nacional de Áreas Silvestres Protegidas del Estado; Armesto 1998, Smith-Ramírez 2004, Pliscoff et al. 2005). This lack of protection in a landscape dominated by exotic tree plantations has limited most of the native taxa to extreme sites or to rural areas where disturbances by landowners are small-scale.

There are only few rural areas left within the VCR where land use is still carried out on a small-scale. The smallholders mainly use their land for extensive livestock grazing and the selective cutting of trees for firewood. The purchase of land by large forest companies that convert it to exotic tree plantations is ongoing (Neira et al. 2002) and threatens the existence of the evergreen forest in the VCR (Armesto 1998, 2002, Smith-Ramírez 2004). Most Chilean ecosystem studies have been carried out from a forestry perspective, subsequently, the VCR forests were classified on the basis of the composition of the dominant tree species (e.g., Donoso 1981, Gajardo 1994) the same way that many temperate forests were classified. However, this approach is not suitable for obtaining an ecological understanding of the ways in which rural farming systems, with an agroforestry component, affect vegetation and biodiversity on a regional scale. In a pioneer work, Oberdorfer (1960) did a small-scale phytosociological study in which he set out a classification of plant communities. His proposal described a successional pathway from *Agrostis* pasture and *Rhaphithamno-Aristotelietum* shrubland to the *Laurietalia* climax forest. A more intensive survey and thorough description of shrubland communities followed (Hildebrand 1983, Hildebrand-Vogel 2002, Amigo et al. 2007). These studies highlighted the close floristic relationship that existed between various shrub and woodland communities, and suggested that they were the result of land use practices. However, this assumption was not further in-

vestigated or tested, e.g., by comparing the shrubland communities with other related formations on similar sites. Such a comparison was only done in a later study that analyzed the floristic similarity of different formations as an indicator of site degradation on a lee slope in the VCR (Ramírez et al. 1984). The study involved *Acaena-Agrostis* pastures, *Ulex* shrublands and *Aristotelia chilensis* shrublands, Dombeyo-Eucryphietum forests and *Pinus* spp. plantations. After the Dombeyo-Eucryphietum forests were cut, the area developed into a *Aristotelia chilensis* shrubland. It was assumed that the original forest would regenerate, although in the same study, no evidence was found for forest regeneration on *Acaena-Agrostis* pastures when sheep grazing was abandoned.

Based on the previous studies it can be assumed that the vegetation mosaic, in rural areas, can be classified into VTs. We hypothesized that these VTs were the result of, and maintained by land use activities and that furthermore, the VTs were indicators of either succession or degradation processes. In order to test our hypothesis and to increase the understanding of the disturbance and recovery processes, we selected the ‘Lomas del Sol’ and the ‘Caman’ regions on the eastern slopes of the VCR. These study areas were representative of the small-scale land use in this region. We collected extensive vegetation, environmental and land use indicator data with the following objectives in mind:

- to provide a description of the vegetation types within the vegetation mosaic in the study area;
- to identify the land use drivers responsible for recovery and degradation processes;
- and to develop and discuss a conceptual model, based on previous results, that attempts to explain the vegetation dynamics in the cultural landscape of the VCR.

Our results are expected to contribute to the current debate on the potential of traditional rural landscapes to integrate biodiversity conservation with sustainable land use.

Material and methods

Study site

Our study was conducted on the eastern slopes of the Valdivian Coastal Range (VCR), Chile. Two rural regions with similar climatic and soil characteristics were selected, ‘Caman’ (39° 58' S 73° 00' W) and ‘Lomas del Sol’ (39° 50' S 73° 07' W). The potential natural vegetation of these two regions is Valdivian evergreen forest (Ramírez and San Martín 2005). The climate is temperate, perhumid with an average annual rainfall of about 2,100 mm. Rainfall occurs throughout the year but peaks in winter (April–October). The average annual temperature is 12.2° C with a maximal monthly average of 23.3° C in January and a minimal average of 4.6° C in August (Fuenzalida 1965). Soils are well drained Ultisols of volcanic origin on metamorphic bedrock; soil texture varies from silty to sandy loam (CIREN 2001). All sites were located at altitudes between 250 and 500 m. The primary vegetation was Valdivian evergreen forest dominated by ‘Coihue’ (*Nothofagus dombeyi*) and ‘Ulmo’ (*Eucryphia cordifolia*);

(‘Bosque de Coihue-Ulmo’; Ramírez and San Martín 2005), which was described by Oberdorfer (1960) as the ‘Dombeyo-Eucryphietum’. This forest is especially rich in evergreen woody species (Myrtaceae and Proteaceae) but also in vines, lianas and epiphytes that exemplify its structural complexity. The tallest emergent trees in these forests, attaining a height of 45 m, are *N. dombeyi* and *E. cordifolia* (Oberdorfer 1960, Ramírez and San Martín 2005).

Around 1900, Chilean and European settlement began in Caman and Lomas del Sol. Settlement resulted in the exploitation and destruction of the native forests. Much of the forested land was converted to subsistence uses. In Caman a second massive conversion of state-owned forest, this time to exotic tree plantations, began in the 1970s. Additionally, more and more private farm land is being sold to large companies for plantations even though native forest in the Caman region is restricted to private properties. In the Lomas del Sol region a similar conversion of land to exotic tree plantations occurred, but the adjacent forest in the Llancahue watershed with some old-growth native forest survived because it was state-owned (Moorman et al. 2013b). However, in the 1990s neighboring farmers began to use this forest illegally for livestock grazing and tree cutting (Moorman et al. 2013a).

Vegetation and land use assessment

Stratified random sampling was conducted with three predefined strata based on vegetation height; 1) open pastures (vegetation height < 1 m, scarce presence of woody species); 2) shrublands (height 1 – 5 m, with greater than 20% shrub cover), and 3) forests (> 5 m tall). To handle the heterogeneity caused by the presence of different formations in the landscape, modified-Whittaker nested plots (Stohlgren et al. 1995) were established. The plot and subplot sizes were adapted to the tree heights in our study area. Within each tree plot (tree layer (> 5 m) 160 m²) a subplot for the shrub layer (1 – 5 m) 80 m² and for the herb layer (for the layer < 1 m) was 20 m² was established. The smaller subplots were centered in the middle of the larger plot to capture the influence of the layer above. To cope with the evergreen rainforests vertical complexity, the tree layer was subdivided into a lower tree layer (5 – 10 m) and an upper tree layer (> 10 m). Extreme sites like swamps and excessive slopes were excluded from sampling because they had not been harvested or grazed. Sampling points were randomly distributed according to the total cover proportional to the area of each stratum in all study regions (Table 1).

All vascular plant species were identified and their cover was estimated using the Londo decimal scale (Londo 1976). Nomenclature follows the International Plant Names Project (2012). For every layer the cover of each plant species was estimated in each of the subplots. In the subplots, for the tree layers, the diameter at breast height (dbh) of all trees with a dbh > 5 cm and their heights were measured. Terrain variables (altitude, slope and aspect) were recorded and soil variables for the upper soil layer (bulk density, depth of Ah horizon, pH, and texture) were assessed using field methods (Arbeitskreis Standortkartierung 1996). Litter cover was es-

Table 1. Distribution of the plots for vegetation sampling among strata and study regions.

Stratum	Study region		Total
	Caman	Lomas del Sol	
Grassland	23	13	36
Shrubland	17	14	31
Forest	18	17	35
Total	58	44	102

timated in the 20 m² subplots (same plots where the herbs were measured) in three ordinal classes (1) none, (2) little and (3) thick). In the same subplots, the impacts of small-scale land use (livestock farming and cutting) were assessed. Cutting included the extraction of larger trees for timber and coppice for fire wood.

Livestock farming. The number of dung piles/m² has been used as a proxy for grazing intensity as herbivores defecate in the same area in which they feed (Relva and Veblen 1998). Therefore, dung piles were counted in the 20 m² subplots and expressed as dung piles/m². Browsing damage caused by livestock was assessed for the woody species in the herb and shrub layers. The mean browsing index (in the following “browse index”) was then calculated (Veblen et al. 1989). Dung piles and signs of browsing are variables that describe livestock damage on vegetation which can be readily measured and have been used frequently (Echeverría et al. 2007). As an indicator for trampling, the animal tracks, if present, were counted.

Cutting. Stumps were counted to assess the intensity and frequency of cutting. Deadwood age was estimated with a knife test (Rouvinen et al. 2002) done for each stump. Cutting intensity was then calculated as stumps/m² and cutting frequency as the number of different age classes present in a plot.

Data analysis

Description of the vegetation types. The floristic group structures in the vegetation data were examined using flexible beta agglomerative algorithm (Lance and Williams 1967) with $\beta = -0.25$ and Bray-Curtis distance measure, using the R package cluster (Maechler et al. 2013, R Core Team 2013). An appropriate cut level for the dendrogram was chosen by conducting an indicator species analysis (Dufrene and Legendre 1997) for each hierarchical group level. The group level that showed a high number of indicator species along with a low average p-value across all species was chosen for cutting the dendrogram (McCune et al. 2002). The significant floristic differences of the resulting vegetation types were then verified using a multi response permutation procedure from the R package vegan (Oksanen et al. 2013). For these and all subsequent analyses, plant cover values were transformed from the Londo ordinal scale (Londo 1976) to percentages of the class averages (Leyer and Wesche 2007). We combined the subplots representing the different layers within one plot. Species that occurred at frequencies lower than 5% were excluded

from further analyses. To characterize the vegetation types defined via diagnostic species, the extended indicator species analysis, proposed by De Cáceres et al. (2010) was applied (R package *indicspecies*; De Cáceres and Legendre 2009). This index identifies diagnostic species not only for each single vegetation type but also for combinations of vegetation types. Species that are diagnostic for more than one vegetation type may therefore indicate broader habitat conditions (De Cáceres et al. 2010) than those that indicate combinations of vegetation types because they are more restricted in their niche breadth to a certain habitat.

To visually explore the floristic gradient in our dataset non-parametric multidimensional scaling (NMDS) was performed on the Bray-Curtis dissimilarity matrix (R package *vegan*, Oksanen et al. 2013). Land use and environmental variables were fitted on the ordination and plotted on the ordination diagram. The NMDS results link the explorative analysis of the vegetation mosaic (first objective) to the second objective aiming at identifying the land use drivers for land recovery and degradation.

Identification of the land use drivers of degradation and recovery. Classification tree analysis was applied to determine which land use variables were influencing the categorical response variable vegetation type. We used recursive partitioning within a conditional inference framework to explain variation in the response variables as a function of the explanatory variables. This was accomplished with the non-parametric conditional inferences tree methods (function *ctree* in the R package *party*, Hothorn et al. 2006b). At each step of the analysis, one explanatory variable was selected from all the available variables, based on the best separation of two homogeneous groups using a permutation test; this point is determined by a numerical value (threshold) of the explanatory variable (Hothorn et al. 2006a,b, Hothorn and Zeileis 2008). The relationships between the response variable and explanatory variables are presented in a dichotomous tree

diagram with nodes that represent split points, branches that connect nodes, and leaves or terminal nodes that represent the final groups. To test the effect of all land use variables and their interactions on overall floristic patterns, permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was performed with the R package *vegan* (Oksanen et al. 2013) on the floristic dissimilarity matrix (Bray-Curtis distance measure) and the land use variables with 999 permutations. Additionally, we performed a PERMANOVA on pairs of vegetation types to investigate separating effects between groups.

Results

Description of the vegetation types

Based on the floristic composition we identified four vegetation types (VTs) (Fig. 1): (1) extensively grazed non-native grasslands (EGN), (2) closed and semi closed *Ugni* and *Berberis* shrublands (UBS), severely impacted evergreen forest (SIE) and sparsely disturbed evergreen forest (SDE). The dendrogram shows that two VTs are aggregated in two formations respectively: (1) open and shrubby variants of *Agrostis capillaris* pastures and (2) variants of the impacted evergreen forests.

Open and shrubby Agrostis capillaris pastures. This formation has 11 diagnostic species (Appendix). All diagnostic species were herbs and non-native species except for *Leptostigma arnotianum*. The physiognomy comprised a transition from the EGN grasslands to the UBS shrublands. The EGN grasslands were indicated by two diagnostic species. The floristic composition was dominated by exotic herbaceous species which formed an herb layer covering 85% and rarely averaging more than 1 m in height. These plots in the EGN grasslands were located on flat terrain (average slope 4°).

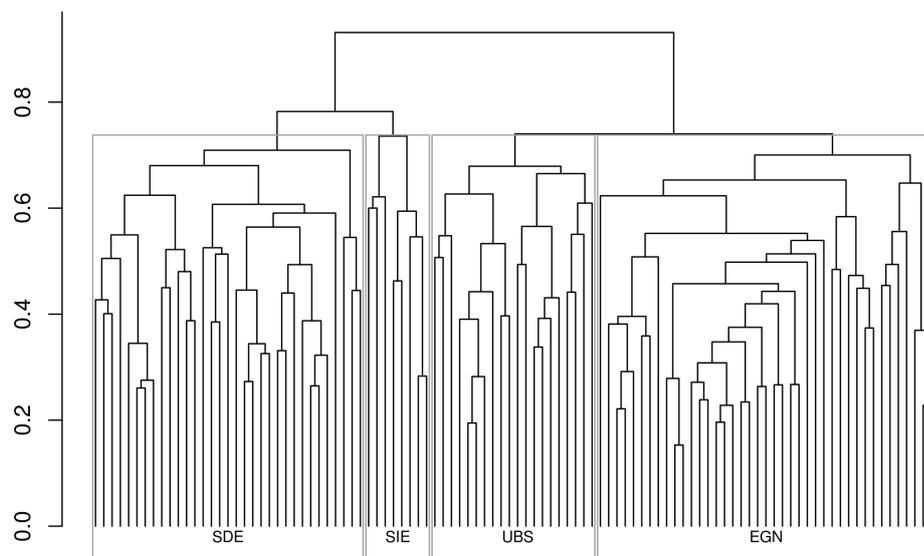


Figure 1. Dendrogram for the vegetation data (species and cover) in the study area. The dendrogram was generated with a flexible beta algorithm ($\beta = -0.25$). Boxes delimit the vegetation types (EGN = grazed non-native grasslands, SDE = sparsely disturbed evergreen forest, SIE = severely impacted evergreen forest, UBS = closed grazed *Ugni* and *Berberis* shrublands).

The *Ugni* and *Berberis* shrublands (UBS) had 7 diagnostic species representing different life forms: trees (*Embothrium coccineum*), shrubs (*Ugni molinae*, *Baccharis racemosa*, *Genista monspessulana*, *Berberis microphylla*), and herbs (*Vulpia bromoides*, and *Leucanthemum vulgare*). Trees with a dbh > 5 cm were rare. The average herb layer cover was 60% while the shrub layer averaged 65% with a maximum height of 5 m.

Impacted evergreen forests. The impacted evergreen forests were represented by plots situated in a stand with trees up to 100 years old. The formation was characterized by 21 diagnostic species (Appendix A) which are typical native tree, shrub, liana and herb species of the evergreen forest.

The severely impacted evergreen forest (SIE) had 6 diagnostic species: *Hypericum androsaemum*, *Blechnum hastatum*, *Aristolelia chilensis*, *Azara lanceolata*, *Ribes trilobum* and *Greigia sphacelata*. The basal area (6.8 m²/ha) and tree density (820 stems/ha) were still relatively low. The tree layer was simple or stratified with a maximum tree height of 7.3 m and a crown closure (11%) which was significantly lower than in the SDE forests.

The sparsely disturbed evergreen forest (SDE) had 5 diagnostic species. Study sites were often located on steeper slopes (12° on average). Basal area and tree densities were highest among the four VTs (basal area = 41 m²/ha, 2500 stems/ha). The tree layer could be stratified into a lower tree layer (5-10 m) and an upper tree layer (>10 m) up to 18.5 m in height with a 60% crown closure.

The vegetation types were ordered on a successional gradient along the first NMDS-axis (Fig. 2) from open and

shrubby *Agrostis* pastures to impacted evergreen forests. The little disturbed variant of the evergreen forest (SDE) was floristically most dissimilar to the extensively grazed *Agrostis* (EGN) pastures. Increasing stem density and litter amount as well as age, basal area and crown closure were mostly correlated with the impacted evergreen forest formations in the NMDS. However, the closeness of the arrows suggests a correlation between stem density, litter and age as well as basal area and crown closure. The variables that had the highest correlation with the floristic gradient in the NMDS (Fig. 2) were dung piles, a sign of open and shrubby *Agrostis capillaris* pastures, while cutting frequency pointed in the opposite direction on this axis, towards forests.

Recovery and degradation: land use drivers

The importance of the land use variables for differentiating the vegetation types was reflected in the results shown by the classification tree (Figure 3). The number of dung piles per m² and the browse index were the two most important splitting variables. At the first split, the number of dung piles was selected from the variables. A value higher than 0.075/m² for dung piles explained 100% of the EGN grassland plots. When the number of dung piles was less than or equal to 0.075/m², the number of dung piles were again selected for the second split. If the number of dung piles was higher than 0.006/m² at the second split, about 55% of the plots belonged to the UBS shrublands. If the number of dung piles was equal to or lower than 0.006/m² the third splitting variable was browse index. Values higher than 0.5 for the browse index explained 60% of

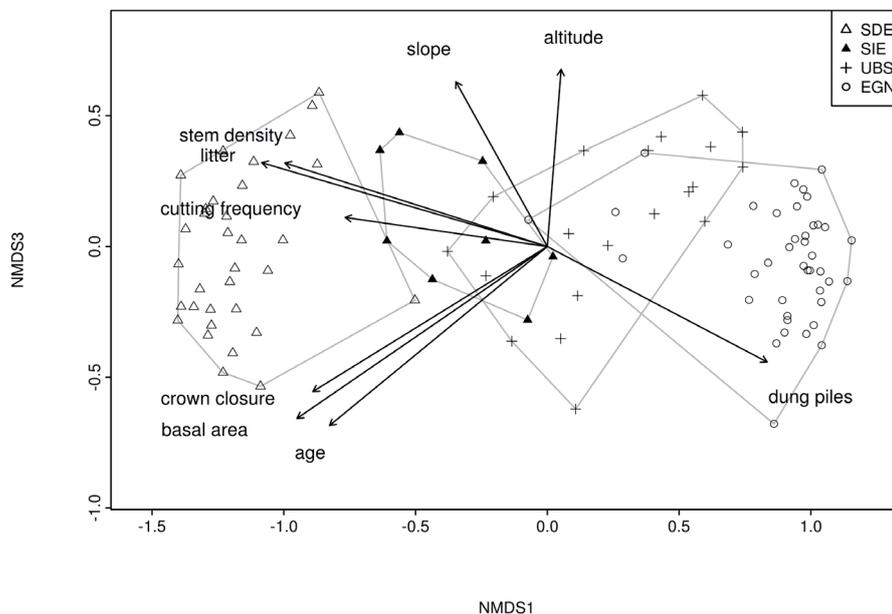


Figure 2. Ordination diagram from non-metric multidimensional scaling (NMDS). The composition dataset was based on cover values per plot by species. Bray-Curtis distance was used for the ordination (30 maximum random starts, iteration for 3 dimensions, stress: 0.084). We choose axes 1 and 3 for the presentation of the results. Symbols represent individual plots coded by vegetation type that are further delimited with polygons. The arrows represent the explanatory variables fitted onto the ordination (age: age of the trees in the plot). Polygons delimit the vegetation types (EGN = grazed non-native grasslands, SDE = sparsely disturbed evergreen forest, SIE = severely impacted evergreen forest, UBS = closed grazed *Ugni* and *Berberis* shrublands).

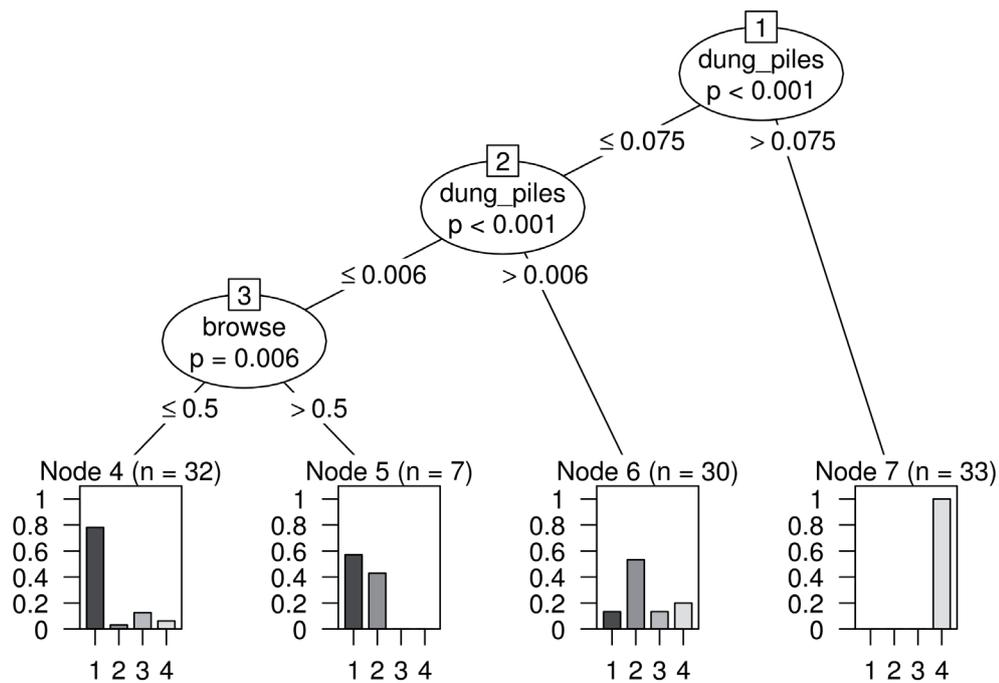


Figure 3. Classification tree to predict the vegetation type based on the conditional inference tree (cTree) model. The encircled explanatory variables are those showing the strongest association to the response variable. Values on lines connecting explanatory variables indicate splitting criteria; for example, the first split separated plots of the EGN grasslands (right split) from those in the other three vegetation types (left side of the split). Numbers in boxes above the explanatory variable indicate the node number. The p-values listed at each node represent the test of independence between the listed independent variable and the response variable. “n =” next to terminal nodes indicates the number of plots classified in that node. Bar graphs illustrate the proportion of plots in a vegetation type within that node. 1 = sparsely disturbed evergreen forest (SDE), 2 = closed grazed *Ugni* and *Berberis* shrublands (UBS), 3 = severely impacted evergreen forest (SIE) and 4 = grazed non-native grasslands (EGN).

the SDE forests and 40% of the UBS shrublands. When the browse index was lower than or equal to 0.5, 80% of the plots belonged to the SDE forests.

When all species of all vegetation types were included in the PERMANOVA, there was a significant differentiation based on the land use variables (number of dung piles $F = 10.698$, $p = 0.012$, cutting frequency $F = 5.07$, $p = 0.002$). There was also an interaction between cutting frequency and browse index ($F = 1.873$, $p = 0.004$). Furthermore, the results proved that cutting frequency ($F = 2.289$, $p = 0.003$) and the number of dung piles ($F = 4.816$, $p = 0.025$) significantly differentiated the UBS shrublands from the extensively grazed non-native grasslands. For the differentiation of UBS shrublands from SDE forests, cutting frequency ($F = 2.380$, $p = 0.035$) and the number of dung piles ($F = 5.203$, $p = 0.022$) were the most significant single variables. Furthermore, interactions between cutting frequency, mean browsing index, cutting intensity and tracks were also significant (cutting frequency and browse index ($F = 1.506$, $p = 0.004$), cutting intensity and browse index ($F = 3.193$, $p = 0.017$); tracks, cutting frequency and browse index ($F = 1.254$, $p = 0.043$); tracks, cutting intensity and browse index ($F = 1.308$, $p = 0.033$)). For the separation of SIE forests from the SDE forests the following individual and interactions between land use variables were significant: the number of dung piles ($F = 1.998$, $p = 0.014$); tracks and number of dung piles ($F = 2.556$, $p = 0.005$); tracks,

cutting frequency and browse index ($F = 1.633$, $p = 0.021$); cutting frequency and browse index ($F = 1.424$, $p = 0.018$)).

A conceptual model for the vegetation dynamics in the cultural landscape in the VCR

Based on the results described above we developed a conceptual model (Fig. 4) that links the identified VTs along a successional gradient through regeneration and diverting degradation gradients driven by land use activities and the associated disturbances.

Discussion

Vegetation types comprising the vegetation mosaic

The identified floristic gradient (Fig. 2) is a structural gradient from grassland to forest. Along the first NMDS axis the diagnostic species change from open land species, mostly non-native annuals, to native forest species. Extensively grazed non-native grasslands (EGN) contain a low number of diagnostic species. This reflects the high variability in floristic composition due to the variety of microsite conditions or different disturbances which have a strong influence on the floristic composition of grasslands. The presence of the two diagnostic species indicates that disturbances had either low

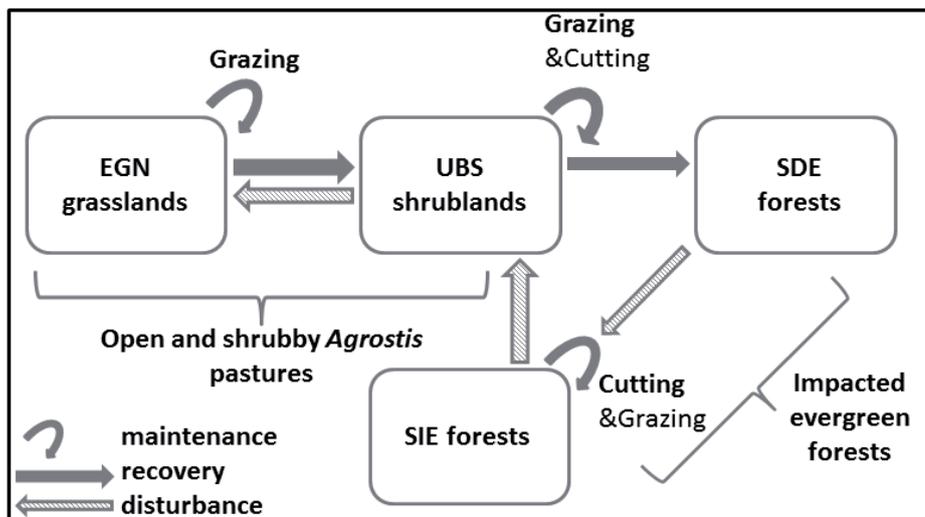


Figure 4. Conceptual model showing the dynamic relationships, disturbances and recovery processes between the vegetation types in the traditional rural landscape of the Valdivian Coastal Range (EGN = grazed non-native grasslands, SDE = sparsely disturbed evergreen forest, SIE = severely impacted evergreen forest, UBS = closed grazed *Ugni* and *Berberis* shrublands). Arrow size approximates the probability of recovery from disturbance or maintenance under the recent scenario.

or extremely high impact in this vegetation type. *Trifolium repens* (Fabaceae) is known to be common in anthropogenic grasslands in the Valdivian Coastal Range (VCR; Ramírez et al. 1992) indicating low disturbance because it disappears when soils become degraded due to soil compaction (Ramírez et al. 1992). On the other hand, *Chevreulia sarmen-tosa* (Asteraceae) indicates sites that are degraded and dry due to soil compaction (Ramírez et al. 1992).

The closed and semi-closed grazed *Ugni* and *Berberis* shrublands (UBS) were the VTs floristically most similar to the EGN grasslands. UBS shrublands were mainly characterized by the shrub species (*Ugni molinae*, *Berberis microphylla*, *Genista monspessulana*, and *Baccharis racemosa*). *U. molinae* and *B. microphylla* are rapid colonizing thermophilous shrub species. Within one to three years they can form a closed shrub layer (Hildebrand 1983). These two shrub species often begin colonizing from forest fringes (Amigo et al. 2007). The presence of *Embothrium coccineum* indicates that succession is occurring in the UBS shrublands. This suggests that shrub establishment, in turn, facilitates the regeneration and establishment of trees. This could be because some spiny (e.g., *B. microphylla*), or unpalatable shrubs (*G. monspessulana* (Hildebrand 1983)) prevent browsing (Cornelissen et al. 2003), or because a dense shrub layer acts as a barrier to livestock. The herbs *Vulpia bromoides* and *Leucanthemum vulgare* indicate disturbance. They grew in places where there was no shrub layer, such as on livestock tracks between shrub patches. The closed sward in these places is typical for open land species like those diagnostic for *Agrostis capillaris* pastures (Appendix A). Some of them are known to be especially trample-resistant species (e.g., *Plantago lanceolata*) which lends support to the thesis that *Agrostis capillaris* pastures are strongly affected by disturbance.

Severely impacted evergreen forests (SIE) comprise the transition from open shrubby *Agrostis* pastures to the impacted evergreen forests (Fig. 2). The shared diagnostic species of the UBS shrublands and the SIE forests are, with one exception (*Centaurium littorale*), characteristic species of *Aristotelia chilensis* shrublands (*sensu* Hildebrand (1983)). In this study, *A. chilensis* was also a diagnostic species for the SIE forests. However, it showed a higher floristic similarity to the SDE forests than to the UBS shrublands. This indicates that SIE forests represent an advanced state of succession towards closed forest. The species diagnostic for the SIE forests only indicate open conditions in forests and forest fringes, i.e., of openings created by cutting. Therefore, species diagnostic for the SIE forests appear to be less resistant to grazing and trampling. This includes species such as *Blechnum hastatum* (Godoy et al. 1981, Hildebrand-Vogel 2002, Saldaña et al. 2005, Amigo et al. 2007), *A. chilensis* and *Azara lanceolata* (Veblen and Schlegel 1982, Hildebrand, R 1983, Hildebrand-Vogel 2002, Amigo et al. 2007). The diagnostic species *Hypericum androsaemum*, an exotic species in Chile native to temperate regions of Europe and Western Asia, has escaped from gardens and fields and become naturalized in Chile (Robson 1985). Local landowners recognized that *Greigia sphacelata* frequently occurs on burned sites (personal communication by Belarmino Roller (landowner) December 01, 2010) and can be considered a ruderal species indicating disturbed sites.

Diagnostic species of the sparsely disturbed evergreen forest (SDE) reveal less disturbed conditions compared to the SIE forest. Among others, the tree species, *Aextoxicon punctatum* and *Drimys winteri* are typical for the evergreen temperate rainforest (Oberdorfer 1960, Donoso 1981, Veblen and Schlegel 1982). The fact that the epiphyte *Fascicularia bicolor* was a diagnostic species emphasizes that the structural complexity of the SDE forests is comparatively high.

F. bicolor is the dominant epiphyte of temperate rainforests in Chile (Díaz et al. 2010). It was present in 24% of the SDE forest plots and may indicate less disturbed conditions. Since vascular epiphytes are slow growing (Zotz 1995, 1998, Hietz et al. 2002) they are susceptible to anthropogenic disturbances that alter their habitat (tree crowns) and changes in microclimatic conditions on which epiphytes depend (Freiberg 1997). In contrast, the tall fern *Lophosoria quadripinnata* is associated with the typical hyperhumid conditions of Valdivian woodlands occurring on steep slopes (Oberdorfer 1960). Previously it was also associated with disturbances and clearings in the forest (Amigo et al. 2007). Therefore, it may indicate disturbed sites in the VT.

Remarkable was the total absence of *Notofagus dombeyi* in the impacted evergreen forests. The site conditions there suggest good growing conditions for this species characteristic of the 'Coihue-Ulmo' forests. There are many plausible reasons for its absence including past selective cutting of *Nothofagus* (Ramírez and San Martín 2005), a lack of large-scale disturbances in the coastal range (Smith-Ramírez 2004), an absence of fire, a deficit of seed trees and the grazing of livestock on *N. dombeyi* (Coihue) seedlings.

E. cordifolia (Ulmo), although present in our dataset, could not be verified as an indicator species for either the impacted evergreen forests or one of its variants. This is because the species was not restricted to forests in our dataset. *E. cordifolia* is no longer the typical emergent once found in Coihue-Ulmo forests because of the past and present exploitation of *E. cordifolia* (Ramírez and San Martín 2005).

Land use drivers that influence recovery and degradation processes

The number of dung piles and cutting frequency correlated best with overall floristic composition. Dung piles and browse index were the most significant variables for differentiating the discrete vegetation types. However, the browse index interacted strongly with other land use variables. High intensity, frequent land use leads to degradation, but when the land use declines or stops, the process of succession ensues. Land use activities therefore drive the recovery and degradation processes that lead to changes in floristic composition and turnover in vegetation types.

Forest recovery through succession requires that grazing and cutting be significantly reduced. The forests existing today have developed despite extensive land use activities in the past. On smallholders land, this development has taken place on small patches. Fragmented forests in Chile are often simplified in structure because older trees have been harvested. Succession is reset to an earlier forest stage with low basal area and a high abundance of saplings and young trees (Echeverría et al. 2007). This phenomenon has also been reported from Amazonian forests where the vegetation dynamics were accelerated due to fragmentation which is likely to exacerbate changes in forest structure, floristic composition and forest microclimate which could in turn cause the extinction of disturbance-sensitive species locally (Laurance et al.

1998, 2006). An example of such changes in structure and composition can be seen in the severely impacted evergreen forests (SIE). SIE forests are often the only wood-producing vegetation types on small farmsteads and are therefore harvested. In contrast, a large number of plots placed in the sparsely disturbed evergreen forest (SDE) were a part of the Llancahue watershed adjacent to the Lomas del Sol where interventions after initial heavy cutting took place in the early 1900s, were reduced for a long time but have increased since the 1990s (Moorman et al. 2013a). In Caman, SDE forests were found on steeper slopes or in remote locations and were therefore less attractive to smallholders. Thus, forest recovery through natural succession here depends largely on socioeconomic circumstances. A similar scenario resulted after the abandonment of farmsteads allowed forests to recover in the Concepción metropolitan area (Rojas et al. 2013). On the other hand, if the current economic model of the farmsteads continues, the SDE forests will also face degradation.

The SDE forests that developed after land use activities declined still have a significant portion of the original native flora and have a complex structure, although they do not have the emergent *Eucryphia* and *Nothofagus* trees. This challenges Ramírez et al. (1984) framework for describing forest degradation and the forest succession model proposed by Oberdorfer (1960) which assumes a recovery to previous "climax" conditions in a foreseeable time frame. But it supports Guariguata and Ostertag (2001) who suggest that tropical forest functions and services may recover long before floristic composition does. This is especially important when considering that these little impacted evergreen forests have many native species of the Valdivian evergreen forest that provide timber and non-timber products for smallholders.

A conceptual model for the vegetation dynamics in the traditional rural landscape in the VCR

Grazed non-native grasslands (EGN) are maintained by extensive grazing. Dung piles distinguished the two variants of open and shrubby *Agrostis capillaris* pastures. When grazing is abandoned, floristic composition changes towards the closed and semi-closed grazed *Ugni* and *Berberis* shrublands (UBS). However, abandonment in our study area did not occur as a deterministic process, like that presumed in the study of Ramírez et al. (1984). Instead it occurred gradually, depending on the level of avoidance of the sites by browsers (Baudry 1991). However this fast-growing shrub layer will recede if grazing is intensified and floristic composition will revert to EGN. UBS shrublands and SIE forests did not differ significantly in terms of impacts from land use. This may be due to the origin of SIE forests which were a product of degradation of SDE forests rather than a regeneration of the UBS shrublands. Cutting and grazing impede the forest recovery on EGN grasslands and GNU shrublands. Recovery is indicated by their transitional status. Apart from the recovery, we observed landowners clearing shrubs from pastures. This suggests that under the present scenario, succession is interrupted at an early stage. The disturbance regime in SIE forest is not created by a single land use activity, but by the

interaction of cutting and grazing. This may be because even though livestock generally avoid the forest due to its inaccessibility, wood cutting makes it more accessible which results in browsing, grazing and trampling of tree seedlings. This activity might be more intense in winter when grasslands are unproductive leaving only evergreen trees and shrubs to provide forage (personal communication with landowners, who mentioned specifically the species *D. diacanthoides* as being very palatable). Although SDE forests are not impacted as much, they are still browsed and cut. The absence of floristic indicators for these impacts may be due to a high resilience of these forest ecosystems to disturbance.

Our findings generally fit the pathways proposed by Oberdorfer (1960) and Ramírez et al. (1984). However, for the first time, the intensity of anthropogenic impacts caused by grazing and cutting are reported in a study using measurable variables directly related to vegetation composition and species turnover. Our data confirm Oberdorfer's (1960) theory of a "diversity of human influence" on floristic composition. The complex factor 'human influence' can promote either succession or degradation, depending on the intensity and interactions resulting from land use activities.

General conclusions

The occurrence of the different vegetation types (VTs; 1) grazed non-native grasslands (EGN), (2) closed and semi-closed grazed *Ugni* and *Berberis* shrublands (UBS) belonging to the formation of 'open and shrubby *Agrostis capillaris* pastures', (3) severely impacted evergreen forests (SIE) and (4) sparsely disturbed evergreen forest (SDE) grouped with the 'impacted evergreen forest' formation in small-scale rural landscapes in the VCR depends on land use type, intensity and interactions between land use impacts. Livestock farming in this case, is especially significant. This was highlighted by the importance of dung piles for group differentiation of EGN grassland, UBS shrubland and the little impacted evergreen forest in the classification tree. When the value for dung piles was low (< 0.001 dung piles/m²) cutting frequency becomes important in differentiating between the forest vegetation types. Furthermore, cutting frequency was significant in determining overall floristic composition. The present land use regime indicates that the vegetation dynamics are being affected by disturbance rather than recovery processes. A lack of fencing has led to degradation due to interactions involving livestock and cutting, particularly in SIE forests. The indicator species found there indicated forest degradation. For the other VTs, succession or degradation determined floristic composition. We therefore recommend the use of our study as a baseline for research beyond the species level (e.g., functional traits) and to study regeneration processes for tree species on a landscape scale to understand which forest structures and functions will result from these VTs and on which time scale. We found high native species richness in shrublands and forests. This makes these UBS shrublands, SIE forests and SDE forests valuable landscape elements in rural areas with small-scale activities dominated by monoculture exotic tree plantations. We therefore recommend an intensification

of research on other taxa that may be associated with the three VTs, such as birds, and to integrate these or future elements of rural landscapes in conservation planning for the future.

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Appendix

Indicator species. The file may be downloaded from www.akademaii.com.