Running title: Impacts of forest fragmentation

Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile

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ABSTRACT

Aim Few studies have explicitly examined the influence of spatial attributes of forest fragments when examining the impacts of fragmentation on woody species. The aim of this study was to assess the diverse impacts of fragmentation on forest habitats by integrating landscape-level and species-level approaches.

Location The investigation was undertaken in temperate rain forests located in southern Chile. This ecosystem is characterized by high endemism and by intensive recent land use changes.

Method Measures of diversity, richness, species composition, forest structure and anthropogenic disturbances were related to landscape spatial attributes (size, shape, connectivity, isolation, and interior forest area) of forest fragments using generalized linear models. A total of 63 sampling plots distributed in 51 forest fragments with different spatial attributes were sampled.

Results Patch size was the most important attribute influencing different measures of species composition, stand structure and anthropogenic disturbances. The abundance of tree and shrub species associated with interior and edge habitats were significantly related to variation in patch size. Basal area, a measure of forest structure, significantly declined with decreasing patch size, suggesting that fragmentation is affecting successional processes in the remaining forests. Small patches also displayed a higher number of stumps, animal trails, and cow pats and lower values of canopy cover as a result of selective logging and livestock grazing in relatively accessible fragments. However, tree richness and β diversity of tree species were not significantly related to fragmentation.

Main conclusions This study demonstrates that the progressive fragmentation by logging and clearance is associated with dramatic changes in the structure and composition of the temperate forests in southern Chile. If this fragmentation process continues, the ability of the remnant forests to maintain their original biodiversity and ecological processes will be significantly reduced.

Keywords: broad-leaved evergreen forest, deforestation, human disturbances, landscape indices, richness.

INTRODUCTION

Habitat fragmentation is recognized as one of the main threats to biological diversity (CBD, 2005). Fragmentation is a dynamic process in which the habitat is progressively reduced into smaller patches that become more isolated and increasingly affected by edge effects (Forman & Godron, 1986; Reed *et al.*, 1996; Franklin, 2001; McGarigal, 2002). These alterations to spatial structure are well known to result in changes to community composition within the remnant patches (Saunders *et al.*, 1991; Laurance *et al.*, 1998; Drinnan, 2005) and to alter ecological processes such as nutrient cycling and predator-prey relationships (Bennett, 2003). However, the ecological consequences of forest fragmentation may depend on the spatial configuration of the fragments within the landscape and how the configuration changes both temporally and spatially (Forman and Godron, 1986; Drinnan, 2005). Recent studies reveal the importance of considering spatial configuration when assessing the impacts of fragmentation on herbaceous plants (Petit *et al.*, 2004), as well as on the richness and composition of bird species (Vergara & Simonetti, 2004; Castelletta *et al.*, 2005; Martinez-Morales, 2005; Uezu *et al.*, 2005), but few studies have explicitly considered the effect of spatial attributes when modeling the impacts of fragmentation on woody species (Metzger, 1997; Tabarelli *et al.*, 1999; Metzger, 2000). Moreover, all of these studies are based on relatively few replicates.

Three spatial attributes of fragmentation may be particularly important: core area, shape, and isolation of forest fragments (Franklin, 2001; Ochoa-Gaona *et al*., 2004; Echeverría *et al*., 2006; Cayuela *et al*., 2006). The core area of a fragment has a micro-environment similar to that of intact forest. It is well known that some species require these forest interior conditions and are sensitive to edges (Laurance *et al.*, 2000; Harper *et al*. 2005). At fragment edges, a range of physical and environmental transitions occur that have contrasting effects on different groups of organisms (Kapos *et al*., 1997; Bustamante *et al.*, 2003; Asbjornsen *et al.*, 2004; Tallmon & Mills, 2004; Aune *et al.*, 2005; Fletcher, 2005). The shape of a patch is characterised by the length of edges. Irregular shape of fragments as a result of forest fragmentation tends to increase the length of edges. Finally, isolation of forest fragments may reduce the possibility of movement of organisms between fragments (Bennett, 2003). Evidence shows that habitat fragmentation affects plants with specific dispersal modes (Tabarelli *et al.*, 1999; Kolb & Diekmann, 2005). Thus, some plant species that depend on biotic pollinators and dispersers are becoming rare as a result of forest loss and fragmentation (Bustamante & Castor, 1998).

In addition to these effects, fragments may be subject to change as a result of ongoing human exploitation, such as selective logging and pasturing of domestic stock. Such human disturbances may affect forest structure (Pollman, 2002; Hitimana *et al.,* 2004), tree diversity (Cannon *et al.,* 1998), and mammal communities (Lambert *et al.,* 2005). Some researchers suggest that human influences might play an important role in determining tree composition in tropical forest (Hill & Curran, 2001); however, the influence of human disturbance has not generally been the focus of study in fragmentation studies (Hobbs & Yates, 2003). In addition, little is known about whether relatively small forest fragments are particularly vulnerable to ongoing anthropogenic disturbances.

In comparison with the large numbers of studies undertaken in the lowland tropics, few researchers have explored the influences of fragmentation in temperate forests (Fukamachi *et al*., 1996; Gibson *et al*., 1988; Staus *et al*., 2002), and very little work has been done in southern hemisphere forests. Although some hypotheses have been stated on the processes influencing forest structure and composition in tropical forests (Hill & Curran, 2001; Laurance *et al*., 2006), little is known about the impacts of fragmentation on the floristic composition and stand structure of forest communities (Hobbs & Yates, 2003; Harper *et al*., 2005). In addition, most studies on spatial attributes have focussed on single species (Bustamante & Castor, 1998; Henríquez, 2004).

The overall objective of this study was to assess the impacts of forest fragmentation on temperate rain forests in southern Chile. We took measurements in 51 fragments spread over

500,000 hectares of Chile with the aim of assessing the correlation between fragmentation, as quantified by various of spatial attributes, and the composition and structure of forest stands. All of these fragments had been created sometime before 1976, and had remained in a similar state until 1999, as assessed by repeat satellite imagery. The strength of our approach is that long-term changes were measured, enhancing the chances of capturing the ecological impacts associated with fragmentation. Within each patch we also recorded signs of human disturbances, such as harvesting of trees, paths and livestock presence, enabling us to test whether smaller patches were particularly vulnerable to ongoing human alteration. Specifically, we hypothesized that (i) fragmentation of temperate forests is associated with substantial changes to tree and shrub species richness, and also to forest structure, (ii) woody species with different shade-tolerance will respond differently to forest fragmentation, and (iii) small fragments are most likely to be subjected to ongoing human disturbances, because of their relative accessibility.

METHODOLOGY

Study area

The study was carried out in an area located between 41° 30’S, 73°W and 42° 20’S, 74°W in the Lake Region in southern Chile (Fig. 1). The prevailing climate is wet-temperate with strong oceanic influences (Di Castri & Hajek, 1976). Rainfall occurs throughout the year, with a mean annual precipitation of 2,090 mm. Two different types of soil occur in the area: a) acidic, shallow, poorly drained soil referred to as Ñadi (< 50 cm depth), derived from glacio-fluvial deposits which are classified as Gleysols; b) deep well-drained soil derived from volcanic ash deposits (FAO-UNESCO, 1971; INIA, 1985). The landscape is dominated by a mosaic of mixed broad-leaved evergreen forests within a matrix of pasture and agricultural lands. Since the early 1800s, intense logging and human-set fires for clearance have shaped the landscape (Willson &

Armesto, 1996; Donoso & Lara, 1995; Lara *et al.*, 2003). In Chiloé Island (Fig. 1), the process of deforestation by logging and cultivation started mainly in recent decades, due to its isolation from the mainland. At present, clearance for agricultural expansion and logging for fuelwood are still the most important causes of forest destruction and degradation in the study area (Lara *et al.*, 2002; Reyes, 2000). Chiloé Island is considerably less populated than the neighboring mainland where highways, industrial areas, towns and ports have expanded rapidly associated with the recent growth of the capital city of the region, Puerto Montt.

Floristically, the native forests are characterized by the presence of several broad-leaved evergreen tree species such as *Amomyrtus luma, Amomyrtus meli* (both Myrtaceae), *Drimys winteri* (Winteraceae), *Eucryphia cordifolia* (Eucryphiaceae), *Laurelia philippiana* (Moniniaceae), *Nothofagus dombeyi* (Nothofagaceae), accompanied by a dense understory composed mainly of Chilean bamboos (*Chusquea quila* and *Chusquea* spp., Gramineae) and ferns. In some sites, the long-lived conifers *Fitzroya cupressoides* and *Pilgerodendron uvifera* (both Cupressaceae) can also be found. Anthropogenic actions have led to the dominance by early successional stages, which are characterized by a high abundance of *D. winteri* and *N. nitida*. In such sites, it is common to find shrub species such as *Berberis* spp (Berberidaceae), *Baccharis* spp. (Asteraceae), and *Gaultheria* spp. (Ericaceae).

We obtained forest cover data using a set of three Landsat satellite scenes acquired at different time intervals and from different sensors: 1976 (Multi Spectral Scanner, MSS) 1985 (Thematic Mapper, TM), and 1999 (Enhanced Thematic Mapper, ETM+) (C.E., unpublished data). Each image was geometrically, atmospherically and topographically corrected and then classified using field control points and a set of thematic land cover maps developed by one of the most comprehensive cartographic studies of natural vegetation in Chile known as Catastro (CONAF *et al.*, 1999). The following land cover types were distinguished in the satellite images: urban areas, pasture and agricultural lands, shrubland, arboreus shrubland, secondary forest, old-growth forest, bare ground, water, and wetlands. These categories were based on the land cover types defined by Catastro (CONAF *et al.*, 1999). For the present study, maps of native forest were derived using the land cover types secondary and old-growth forests. Forest fragments were defined as those fragments dominated by tree species greater than 2 m height and of at least 50% of forest cover (CONAF *et al.,* 1999). Each land cover map was validated using ground-based data. Overall agreement of classification was 88.8% for the 1976 MSS, 89.6% for 1985 TM image, and 91.9% for the 1999 ETM+ image.

Selection of fragments for field sampling

From the classified images, we used the following indices to characterize the spatial attributes of the native forest fragments: a) patch size (ha), b) total edge length (km), c) total interior forest area (core area remaining after removing a edge depth of 100, 300, and 500 m, in hectares), d) proximity index (ratio between the size and proximity of all patches whose edges are within 1 km-search radius of the focal patch), e) radius of gyration (mean distance between each cell in the patch and the patch centroid, in meters) (Franklin, 2001; Echeverria et al., 2006; Cayuela et al., 2006). These attributes were estimated in ARC VIEW 3.2 using the Spatial Analyst 2.0 extension (©ESRI, 1999). We then constructed a correlation matrix for these attributes and discarded some which were closely correlated with others (i.e. if $r > 0.6$). By this approach we identified mean proximity index, patch size and radius of gyration as attributes to be used for fragment selection (Table 1). For each of these attributes, patches were divided into five bins, the boundaries of which were chosen so that each bin contained the same number of patches. For instance, in the case of patch size for the 1976 forest map the classes were 0.45-0.72; 0.73-1.08; 1.09-2.16; 2.17-6.03; 6.04 -132,972 and each class contained 1,144 patches. The mean of the three attributes was then calculated and it was used to place each patch into one of five fragmentation categories: 1= 0.66-1.33; 2 = 1.66-2.33; 3 = 2.66-3.0; 4 = 3.33-4.0; 5 = 4.33-5.0. This classification was conducted for patches in the 1976, 1985 and 1999 forest maps.

Next, we discarded all patches for which the fragmentation category had changed over the study period (1976 - 1999). To ensure that we sampled patches which had been fragmented to more-or-less the same extent for at least 23 year. From the remainder, a total of 10 patches within each of the five fragmentation categories was then selected at random (Table 1) with the constraint that about half were located in the Ñadi soil type and half in the volcanic ash soil type (the total number of patches selected was 51).

Field sampling

We established a total of 63 sampling plots within the 51 fragments selected across the study area (Table 2). Owing to the different size of the fragments, the number of sampling plots per fragment depended on patch size (Table 2). Owing to the low number of large fragments in the landscape, we sampled all the fragments greater than 10,000 ha (n=4). Using Arc View to obtain coordinates, sampling plots of 20 x 25 m were located in the central area of each fragment. The plot was divided into 20 contiguous 5 x 5m subplots, in each of these subplots, shrub and tree species were identified and counted to estimate the number of individuals per species. Diameter at 1.3 m height was measured for each tree (≥ 5 cm diameter and > 1.3 m height) in the plot. The number of saplings (< 5 cm diameter and ≥ 1.3 m height) and seedlings (< 1.3 m height) was recorded in a 2x2 m subplot located in the south-west corner of each 5x5m subplot.

Data analyses

Measures of richness and species composition

The diversity of fragments (β diversity) was estimated in R-statistical software, using Bray-Curtis' method (Faith *et al.*, 1987). This method evaluates differences in species composition amongst fragments using measures of similarity. We also estimated the following measures of richness: a) total richness (shrub and tree species), b) tree species richness, c) shrub species richness, d) interior tree species richness, e) interior tree and shrub species richness, f) edge tree species richness, and g) edge tree and shrub species richness. Tree richness was estimated by counting the number of tree species (including sapling and seedling) recorded in each sampling plot. For those large fragments with more than one sampling plot, the mean number of species per plot was calculated. Species were classified to interior and edge functional groups based on relative shade-tolerance and habitat usage characteristics described by previous studies (Donoso *et al.*, 1999; Lusk, 2002; Donoso & Nyland, 2005).

To assess the influence of the spatial attributes on individual species, several Generalized Linear Models (GLMs, Crawley, 2005) were fitted using abundance of each tree and shrub species as response variables and proximity index, patch size and radius of gyration as the explanatory variables. The β slope coefficients resulting from the models were ranked in a list to assess the sensitivity of tree and shrub species to forest fragmentation. Those species with high absolute values of coefficient correspond to species that react more strongly to changes in patch size.

Measures of forest structure

The total basal area (m^2 ha^{-1}) of tree species and the mean quadratic diameter (diameter of the tree of mean basal area) were determined for each fragment. Similarly, the density (N ha^{-1}) of trees, saplings, seedlings, and shrub was estimated for each species. The influence of the spatial attributes on these variables was conducted using also GLMs.

In addition to the field based study of fragmentation, we examined the relationship between forest stand structure and patch size. To quantify the amount of secondary and old-growth forests by patch size, the native forest cover map for 1999 was overlaid on a set of digital forest cover maps of the Catastro database (CONAF *et al.*, 1999). Old-growth forest corresponded to uneven-aged stands of broad-leaved evergreen tree species, with at least 50% of canopy cover. Secondary forest corresponds to even-aged stands composed mainly of young trees (CONAF *et al.,* 1999). These two categories are widely distributed over the landscape and represent 38% and 62% respectively of the total forest area in the study area.

Measures of anthropogenic disturbance

We assessed anthropogenic disturbances along four transects of 40 m length and 2 m width oriented in each cardinal direction from the central point of the sampling plot. We measured the following variables: a) canopy cover (%), b) number of stumps, c) number of animal trails, d) number of fire scars, and e) number of cow pats. Canopy cover (%) is defined as the fraction of ground covered by the vertically projected crown envelopes (Rautiainen *et al.,* 2005). Canopy cover of undisturbed forests normally ranges from 75 to 100% in the study area (CONAF *et al.*, 1999). Selective logging (highgrading) can produce a reduction of the canopy cover which can be used as an indicator of human disturbances. The relationship between all these variables and the spatial attributes of fragmentation was assessed using GLMs.

RESULTS

GLM analyses

Our best GLM model fits were obtained when patch size was the single spatial attribute used to assess the impacts of forest fragmentation (Table 3). Proximity index and radius of gyration did not have significant effect on any of the response variables when it was added after patch size in the GLMs.

Species richness

A total of 46 woody species were identified from all sampled fragments. Twenty-four of these species were native trees, one was an exotic tree (*Acer* sp.), 19 were native shrubs, and two were exotic shrubs (*Rubus constrictus* and *Ulex europaeus*).

Neither tree species richness ($\chi_1^2 = 0.24,\ P = 0.62, n = 51$), beta diversity ($F_{1,49} = 1.22,\ P = 0.28$), nor total richness ($\chi_1^2 = 1.84,\ P = 0.18$) was significantly related to patch size (Table 3). However, within functional groups there were some significant relationships between patch size and richness: richness of interior trees alone ($\chi_1^2 = 4.71,\ P < 0.05$) and of interior tree and shrub species ($\chi_1^2 = 8.60,\ P < 0.01$) was higher in large fragments. On the other hand, small fragments contained higher combined richness of edge tree and shrub species ($\chi_1^2 = 32.58,\ P < 0.001$) and of edge tree species ($\chi_1^2 = 4.39,\ P < 0.05$). Similarly, richness of shrub species decreased significantly as patch size increased ($\chi_1^2 = 7.81,\ P < 0.01$, Table 3, Fig. 2a).

Forest structure

Total basal area was the variable most strongly related to patch size ($F_{1,49} = 20.41,\ P < 0.001$, Table 3, Fig. 2b). Quadratic mean diameter was also positively related to patch size ($F_{1,49} = 4.11,\ P < 0.05$), while the other measures of forest structure were not (Table 3). The distribution of old-growth and secondary forests was closely related to the size of forest fragments (Fig. 3). Almost 70% of the forest stands that were classified as secondary forests were found in patches < 250 ha. A decreasing proportion of secondary forest was found in patches increasing in size from 500 to 1,000 ha, while forest fragments greater than 5,000 ha contained little secondary forests (Fig. 3).

Effects of fragmentation on species composition

The abundance of some tree species increased with patch size, while others decreased (Table 4). In particular, there was a significant decline in the abundance of *Persea lingue, N. dombeyi,* and *Embothrium coccineum* as patch size increased. In contrast, the abundance of *N. nitida, Amomyrtus meli, Laurelia philippiana, Weinmannia trichosperma,* and *Saxegothaea conspicua* significantly increased as patch size increased. A set of 15 tree species showed no significant change, including *Drimys winteri*, *Gevuina avellana*, and *Caldcluvia paniculata.*

A relatively similar order of the species was observed by ranking the b coefficients obtained using basal area as response variable in the GLMs in ascending order (Table 5). Patch size was negatively associated with the basal areas of *P. lingue* and *E. coccineum*. On the other hand, patch size was positively related to the basal areas of *A. meli*, *W. trichosperma* and *S. conspicua*. Similar to the trend observed for abundance, the basal areas recorded for *G. avellana* and *D. winteri* with β coefficients close to zero were not significantly related to patch size (Table 5).

Shrub species were also grouped in terms of abundance across patch sizes (Table 6). The abundances of *Ugni molinae, Rubus constrictus, Ribes magellanica*, *Azara integrifolia*, and *Aristotelia chilensis* significantly decreased as patch size increased. Conversely, the abundance of *Pseudopanax laetevirens* and *Crinodendron hookerianum* were positively significantly associated with patch size. Some species such as *Myrceugenia parvifolia* recorded a β coefficient near zero and were not significantly affected by changes in patch size (Table 6).

Human disturbance

Significant relationships were found between patch size and most of the variables associated with human disturbances. Thus, number of animal trails ($F_{1,49} = 27.66,\ P < 0.001$), number of cow pats ($\chi_1^2 = 25.52,\ P < 0.001$), and number of stumps ($F_{1,49} = 5.65,\ P < 0.05$) per plot decreased with increasing patch size (Table 3). Conversely, the percentage of canopy cover significantly increased as the patch size increased ($\chi_1^2 = 17.62,\ P < 0.001$).

DISCUSSION

Patch size as an index of forest fragmentation

Our results suggest that patch size was more important than proximity index and radius of gyration in terms of explaining richness of shrub species, richness of functional groups for tree and shrub species, forest structure, human disturbances, and abundance and basal area at the species level. However, patch size was not significantly related to richness of tree species in the present study. Similar results were found for tree communities in Atlantic tropical forest in Brazil (Metzger, 1997), in which tree richness of the forest fragments appeared to be similar among patches of different sizes. Similarly, tree species richness in the Highlands of Chiapas Mexico, is not related to patch size and to any other spatial attribute (Ochoa-Gaona *et al.*, 2004). However, it is important to mention that in our research the lowest richness of tree species (between one and three tree species per 500m^2 plot) was recorded in the smallest fragments. In the Atlantic tropical forests, forest connectivity and the complexity of the matrix may be more important than fragment area and isolation in explaining variation in tree species richness (Metzger, 1997) and functional group richness (Metzger, 2000). However, patch size appears to have a significant relationship with shade-tolerant species in tropical forests (Metzger, 2000). Conversely, a previous study conducted in the montane Atlantic forests of southeastern Brazil, fragment size was found to be the major determinant of changes in woody plant composition and guild structure (Tabarelli *et al.,* 1999).

Effects on functional groups and species composition

In the present study, as forest fragments increased in size, the richness of interior tree and shrub species (mostly shade-tolerant) increased whereas richness of edge tree and shrub species (mostly shade-intolerant) declined. A similar pattern was found in five fragments studied in the Atlantic forests, where the smallest fragment had more shade-intolerant species than the largest one (Tabarelli *et al.,* 1999). In tropical tree communities, shade-tolerant tree species appear to be more sensitive to forest fragmentation than shade-intolerant species (Metzger, 2000).

Results from tropical forest studies have demonstrated that some bird species show distinct responses to habitat fragmentation (Uezu *et al.,* 2005). Similarly, some of the tree species considered here benefited from fragmentation while others were highly sensitive to habitat loss. In particular, *E. coccineum* and *A. chilensis* are two very shade-intolerant species that are restricted to forest edge or open areas (Romero *et al.,* 1987; Donoso *et al.,* 1999; Lusk, 2002). The greater abundance and basal area of *E. coccineum* in small fragments recorded here may be related to a greater density of seedings as forest patches become smaller and more irregular (Rovere *et al.,* 2004). Similarly, *A. chilensis* readily colonizes open areas or small fragments as a result of its high production of seeds that are dispersed by birds (Donoso, 1993). Patch size was highly negatively correlated to edge length, so a reduction of fragment size also leads to an increase of edge areas which, in turn, leads to the creation of suitable sites for establishment of *E. coccineum* and *A. chilensis*.

As a result of the division of forest fragments, microclimatic changes near the edges have favored the establishment of alien species such as *Rubus constrictus*, extending into the center of some of the smallest fragments. In addition to such changes in microclimate, edge effects have been found to alter patterns of species colonization, growth, mortality and survival, as well as other ecological processes (Laurance *et al.*, 2000), and may have negative consequences on the survival of interior tree species (Laurance *et al.,* 1998). The increased density of fast-growing, invasive species such as *R. constrictus* may cause a decline in the abundance of some native plants, particularly in highly fragmented forests (Gigord *et al.,* 1999). In central Chile, the decline of *N. alessandrii*, a critically endangered tree, has been associated with the expansion of industrial plantations of *Pinus radiata* (Bustamante & Castor, 1998), because *P. radiata* has been able to invade the small neighboring patches dominated by *N. alessandrii* (Bustamante *et al.,* 2003).

However, *S. conspicua*, *L. philippiana*, and *A. meli* recorded higher abundances and basal areas in larger forest fragments. The site conditions in the interior of these fragments facilitated the establishment and growth of these shade-tolerant tree species, which normally require a certain degree of canopy protection during the first stages of growth. Larger fragments contained larger areas of interior forest habitats, which are characterized by a great abundance of shade-tolerant trees. The GLM analyses showed that the understory species *Pseudopanax laetevirens* and *Crinodendron hookerianum* were also significantly associated with relatively large forest fragments dominated by shade-tolerant species. These two species have also been described in old-growth and late-successional forest, where *P. laetevirens* may grow on branches of giant, emergent individuals of *S. conspicua* and *W. trichosperma* (Aravena *et al.,* 2002).

The ranking of the species should be interpreted with caution, as some species appear to be reacting to other attributes other than shading. For instance, *P. lingue* is a shade-tolerant tree (Donoso *et al.*, 1999) that was grouped with those species that benefited from fragmentation. This species is distributed in lowlands in the northern part of the study area, which is characterized mainly by small fragments of native forests. Owing to this, the abundance and basal area of *P. lingue* was significantly related to small patches. Conversely, results showed that *W. trichosperma*, a shade-intolerant tree, was more associated with large fragments, both in terms of abundance and basal area. After colonizing open areas, the great longevity of *W. trichosperma* trees has enabled them to persist in late-successional forests, which correspond to large forest fragments that occur in the landscape (Veblen *et al.*, 1981; Donoso, 1989; Lusk, 1999). This persistence of early colonizers of disturbed areas has also been described in New Zealand for some long-lived conifers such as *Libocedrus bidwillii* and *Podocarpus hallii*, and angiosperm species such as *Weinmannia racemosa* (Wells *et al.*, 2001).

Some studies have demonstrated that plant species with long-distance dispersal have the potential to migrate rapidly through fragmented landscapes (Pearson & Dawson, 2005). In the tropical forest of south-east Brazil, the high degree of connectivity among fragments was positively related to tree species diversity because many species had high dispersal capabilities and used structures such as habitat corridors and ‘stepping stones’ for their dispersal through the landscape (Metzger, 1997). In Central Chile, concern has been expressed about several shade-tolerant tree species of the Maulino forest that depend on biotic pollinators and dispersers that are becoming rare as a result of forest loss and fragmentation (Bustamante & Castor, 1998). In the present study, zoochorous species such as *A. meli* and *A. luma* and anemochorous species such as *N. dombeyi* and *D. diacanthoides* (Donoso, 1989) have higher capacity to colonize sites along the forest margin (Armesto *et al.*, 2001). This suggests that a progressive division and isolation of the forested habitats might seriously affect shade-tolerant species such as *S. conspicua* and *P. nubigena* that are dispersed by gravity.

Changes in forest structure

A reduction of patch size by fragmentation was related to a decline in the basal area of the fragments. The highest values of basal areas were found in large fragments of old-growth forest, where large trees of shade-tolerant species occur. Similar to this result, high basal areas are also associated with old-growth forests in Western Ghats, India (Bhat *et al.*, 2000) and with larger fragments in south-eastern Madagascar (Ingram *et al.*, 2005). A reduction of basal area in the study landscape represented a modification of the forest structure in which the forest returned to an earlier successional stage. This has also been described for the forests in Klamath-Siskiyou, Pacific North-west USA (Staus *et al.*, 2002), where the forest stands have become younger and more fragmented in response to logging of the larger (and older) trees. The current analysis of forest structure distribution by patch size revealed that most of the mid-successional forests or secondary forests were concentrated in the smallest classes of fragment size. These forests contain the lowest basal areas recorded, as a result of a simpler forest structure characterized by a high abundance of saplings and young trees. These changes in forest structure may have negative consequences on some species dependent on particular characteristics of forest structure (Pardini *et al.,* 2005). For example, in the study area, the density of bird species associated with old-growth forests may be reduced due to changes in availability of canopy emergent trees, snags, logs and understory bamboo cover (Diaz *et al.,* 2005). Our results suggest that the landscape is increasingly becoming dominated by early successional forest fragments with low basal areas. This simplification of the evergreen forest may lead to a decline in regional bird species richness and abundance (Diaz *et al.,* 2005). In Amazonian forests the accelerated dynamics due to fragmentation are likely to exacerbate changes in forest structure, floristic composition and microclimate of the forests, which could help drive the local extinctions of disturbance-sensitive species (Laurance *et al.,* 1998; Laurance *et al*., 2006). While such processes may be occurring in the present study area (Aravena *et al.,* 2002), the current analyses indicate that remaining forest fragments are also being affected by recurrent human disturbances.

Effects of ongoing anthropogenic disturbances

In the present study, the fragmentation of temperate rain forests was related with an increase of ongoing human disturbances such as forest logging and animal grazing. In particular, smaller remnant fragments were highly vulnerable to ongoing disturbances as they were accessible for logging and clearance (Echeverría, 2005). Logging and clearance may be partly responsible for the decline in the basal areas within small fragments. In Madagascar, the spatial pattern analysis of forest structure showed that levels of basal area were associated with accessibility to the fragments (Ingram *et al.,* 2005). In the present study, the significant decrease of forest canopy cover and increase of stumps in small fragments confirm that these small fragments are being seriously disturbed by logging. In particular, logging for fuelwood has caused a severe deterioration of the remnant forest, especially of those forests situated near urban centers (Reyes, 2000). On the other hand, the significant increase in the number of animal trails and cow pats show that the smaller fragments are utilized by livestock. Small forest patches surrounded by pasture lands are frequently used as shelter for domestic animals that may disturb the dynamics of the forests by browsing, grazing, and trampling of tree seedlings. In Mediterranean ecosystems of southern Spain, grazing has caused an alteration of the spatial organization of browse-sensitive species and a decline in the richness of some plants, particularly in the most heavily browsed sites (Alados *et al.,* 2004). Such results suggest that animal disturbances may have negative consequences on the dynamics of the species that occur in the forest studied. This may become even more severe as the forest is also being altered by edge effects and gap formations by logging and other ongoing human disturbances.

CONCLUSIONS

We found that patch size is closely correlated with other measures of habitat fragmentation such as variation in area of interior habitat, patch shape and connectivity. Patch size may be therefore used as an indicator of the integrity of forest ecosystems in this study and to monitor forest fragmentation over time and space.

We observed that the responses to forest fragmentation are species-specific. The abundance and basal area of some species was strongly related to changes in fragment size while others did not exhibit significant changes. The long-term survival of species sensitive to forest fragmentation such as shade tolerant species depends on whether remaining forest patches are large enough to provide the suitable condition for the establishment and growth of these species.

This study demonstrates that the progressive fragmentation is associated with dramatic changes in the structure and composition of the temperate forests in southern Chile. Our results also reveal that the fragmentation of temperate rainforests is significantly related to ongoing human disturbances such forest logging and grazing. Therefore, if the fragmentation process is maintained, the ability of the remnant forests to maintain their original biodiversity and ecological processes may be reduced.

Some limitations of the present work should be considered. The sampling in the center did not include edge habitats in large fragments, which may contain different tree and shrub species from those that occur in the interior areas. Additionally, the lack of repeated field sampling over time constrains the relationship between fragmentation and ecological impacts. Even though the number of fragments in this study was much higher than that used in other fragmentation studies (Metzger, 1997; Gigord *et al.,* 1999; Tabaralli *et al.,* 1999; Metzger, 2000; Cadotte *et al.,* 2002; Murakami *et al.,* 2005), further analyses should consider a larger number of fragments owing to the degree of variation in landscape characteristics. Further insights could also be provided by adopting an experimental approach to fragmentation, rather than the essentially correlative approach adopted here.

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Table 1. Range of values assigned to each category of mean proximity index, patch size, and radius of gyration. Forest fragmentation decreases gradually from category 1 to 5. Values were used to stratify the selection of forest fragments in the field.

Category	Mean Proximity Index	Patch size (ha)	Radius of Gyration (m)
1	0 - 4.37	0.45 - 0.72	24 - 32.84
2	4.38 - 14.49	0.73 - 1.08	32.85 - 41.71
3	14.50 - 52.50	1.09- 2.16	41.72 - 58.61
4	52.51 - 467.59	2.17 – 6.03	58.62 - 99.40
5	467.60 - 369,603.5	6.03 – 132,972	99.41 - 17,007.7

Table 2. Number of fragments sampled in each size class.

Fragment size class (ha)	Number of selected fragments	Number of sampling plots assigned per fragment
0,1-25	21	1
25-100	12	1
100-1,000	10	1
1,000-10,000	4	2
>10,000	4	3
Total	51	63

Table 3. Regression relationships between patch attributes (grouped into attributes associated with diversity, species richness, forest structure, and human disturbances) and patch area, *A* (in hectares). The relationship $y = a + b \log_{10}(A)$ was fitted for each attribute using generalised linear modelling, and estimates of parameters *a* and *b* (± 1 SEM) are provided, and its statistical significance is shown. The extent of attribute variation in the field is illustrated in the final three columns, which provide means for different ranges of patch size.

Attribute of patch	a ± S.E.	b ± S.E.	*P*-value	Mean values when patch area is		
				< 50 ha	50-250 ha	> 250 ha
Diversity						
β diversity	-0.344 ± 0.05	-0.025 ± 0.02	n.s.	0.70	0.56	0.65
Richness[a]						
Total richness (trees + shrubs)	2.671 ± 0.06	-0.040 ± 0.03	n.s.	14	13	13
Shrub spp richness	1.620 ± 0.11	-0.158 ± 0.06	**	5	3	3
Interior tree spp richness	0.846 ± 0.14	0.132 ± 0.06	*	3	6	5
Interior tree & shrub spp richness	1.195 ± 0.12	0.148 ± 0.05	**	4	6	5
Edge tree spp richness	0.599 ± 0.19	-0.208 ± 0.10	*	3	1	1
Edge tree & shrub spp richness	1.690 ± 0.12	-0.394 ± 0.08	***	4	3	2
Forest Structure						
Total basal area ($m^2\ ha^{-1}$)	3.375 ± 0.14	0.237 ± 0.05	***	37	50	63
Mean Quadratic Diameter (cm)	2.701 ± 0.09	0.076 ± 0.04	*	17	16	19
Tree density ($N\ ha^{-1}$)	7.545 ± 0.11	0.086 ± 0.05	n.s.	1,960	2,680	2,498
Sapling density ($N\ ha^{-1}$)	7.507 ± 0.12	0.089 ± 0.05	n.s.	1,786	2,675	2,597
Seedling density ($N\ ha^{-1}$)	8.514 ± 0.16	0.082 ± 0.07	n.s.	5,168	6,643	6,450
Shrub density ($N\ ha^{-1}$)	7.910 ± 0.26	-0.126 ± 0.13	n.s.	2,605	1,355	1,878
Human Disturbances						
Canopy cover (%)[a]	4.214 ± 0.03	0.052 ± 0.01	***	70	75	80
Number of stumps	2.818 ± 0.21	-0.265 ± 0.12	*	14	9	7
Number of animal trails	1.985 ± 0.13	-0.427 ± 0.08	***	6	3	2
Number of fire scars [a]	-1.264 ± 0.50	-0.315 ± 0.29	n.s.	1	0	0
Number of cow pats	2.011 ± 0.35	-1.095 ± 0.38	***	4	1	0

[a] The residual errors were assumed to be Poisson distributed, and significance was assessed using χ^2 tests. For all other analyses, the residual errors were treated as quasipoisson distributed and significance was assessed using F tests. There were 49 residual degrees of freedom.

* $p<0.05$
** $p<0.01$
*** $p<0.001$
n.s.: not significant

Table 4. Regression relationships between the abundance of tree species and patch area, *A* (in hectares). The relationship $y = a + b \log_{10}(A)$ was fitted for each species using generalised linear modelling, and estimates of parameters *a* and *b* (± 1 SE) are provided, and its statistical significance is shown[a]. The variation in abundance of tree species in the field is illustrated in the final three columns, which provide means for different ranges of patch size.

	Abundance (n ha^{-1})			Mean values when patch area is		
Species	a ± S.E.	b ± S.E.	*P*-value	< 50 ha	50-250 ha	> 250 ha
Nothofagus obliqua	-2.154 ± 1.09	-1.958 ± 1.60	n.s.	2	0	0
Persea lingue	-1.284 ± 0.46	-1.565 ± 0.83	**	3	0	0
Nothofagus dombeyi	1.049 ± 0.17	-1.049 ± 0.21	***	27	0	2
Embothrium coccineum	1.058 ± 0.85	-0.785 ± 0.22	**	73	25	22
Lomatia hirsuta	1.809 ± 0.57	-0.377 ± 0.37	n.s.	131	0	33
Blepharocalyx cruckhankii	2.302 ± 0.75	-0.328 ± 0.47	n.s.	170	0	157
Myrceugenia exsucca	0.891 ± 0.74	-0.033 ± 0.35	n.s.	44	0	46
Eucryphia cordifolia	2.090 ± 0.33	-0.033 ± 0.16	n.s.	234	95	121
Drimys winteri	2.992 ± 0.24	-0.000 ± 0.11	n.s.	456	925	312
Caldcluvia paniculata	0.360 ± 0.82	0.030 ± 0.37	n.s.	36	0	22
Luma apiculata	1.839 ± 0.47	0.033 ± 0.21	n.s.	130	145	132
Gevuina avellana	1.846 ± 0.48	0.060 ± 0.21	n.s.	129	325	132
Amomyrtus luma	2.752 ± 0.31	0.231 ± 0.12	n.s.	355	315	669
Tepualia stipularis	0.784 ± 1.10	0.265 ± 0.42	n.s.	33	0	82
Lomatia ferruginea	-1.209 ± 0.91	0.279 ± 0.35	n.s.	5	15	12
Podocarpus nubigena	-0.573 ± 0.74	0.322 ± 0.28	n.s.	15	0	8
Myrceugenia planipes	0.669 ± 0.71	0.335 ± 0.25	n.s.	55	153	50
Aextoxicon punctatum	-1.847 ± 1.69	0.369 ± 0.59	n.s.	1	107	0
Amomyrtus meli	-0.731 ± 0.59	0.616 ± 0.19	***	82	345	246
Nothofagus nitida	-0.653 ± 0.71	0.658 ± 0.22	**	44	320	57
Laurelia philippiana	0.605 ± 0.54	0.730 ± 0.18	**	101	265	220
Weinmannia trichosperma	-4.858 ± 1.85	1.388 ± 0.48	***	2	2	20
Saxegothaea conspicua	-5.382 ± 1.45	1.559 ± 0.37	***	0	20	35

[a]:List of tree species ranked according to the values of slope coefficients (b) obtained in the GLMs. A F test was applied using a quasipoisson family distribution and log link function. Df=1, number of fragments= 51.

S.E.: Standard error.
* p<0.05
** p<0.01
*** p<0.001
n.s.: not significant

Table 5. Regression relationships between the basal area of tree species and patch area, A (in hectares). The relationship $y = a + b \log_{10} (A)$ was fitted for each species using generalised linear modelling, and estimates of parameters a and b (± 1 S.E.) are provided, and its statistical significance is shown[a]. The variation in basal area in the field is illustrated in the final three columns, which provide means for different ranges of patch size.

	Basal area (m^2 ha^{-1})			Mean values when patch area is		
Species	a ± S.E.	b ± S.E.	*P*-value	< 50 ha	50-250 ha	> 250 ha
Nothofagus obliqua	-1.961 ± 1.09	-1.957 ± 1.39	n.s.	0.33	0	0
Persea lingue	-1.092 ± 0.78	-1.274 ± 0.80	***	0.41	0	0
Embothrium coccineum	-0.697 ± 0.82	-0.866 ± 0.36	**	0.87	0	0.21
Caldcluvia paniculata	0.111 ± 0.84	-0.719 ± 0.69	n.s.	0.80	0	0.35
Lomatia hirsuta	1.271 ± 0.58	-0.542 ± 0.43	n.s.	3.66	0	0.31
Nothofagus dombeyi	0.729 ± 0.44	-0.503 ± 0.32	*	1.67	0	0.29
Drimys winteri	2.374 ± 0.20	-0.065 ± 0.10	n.s.	10.13	19.70	8.30
Gevuina avellana	0.730 ± 0.38	-0.033 ± 0.18	n.s.	2.03	3.04	1.77
Blepharocalyx cruckhankii	0.212 ± 0.81	0.141 ± 0.34	n.s.	1.15	0	2.67
Amomyrtus luma	0.945 ± 0.44	0.199 ± 0.18	n.s.	2.28	2.31	5.73
Lomatia ferruginea	-3.194 ± 0.85	0.206 ± 0.34	n.s.	0.05	0	0.06
Aextoxicon punctatum	-2.924 ± 1.53	0.350 ± 0.56	n.s.	0.05	1.22	0
Myrceugenia exsucca	-0.102 ± 1.40	0.360 ± 0.51	n.s.	0.53	0	2.88
Podocarpus nubigena	-1.319 ± 0.76	0.452 ± 0.26	*	0.47	0.00	0.98
Eucryphia cordifolia	1.483 ± 0.52	0.460 ± 0.17	**	7.60	20.13	21.68
Laurelia philippiana	0.605 ± 0.54	0.475 ± 0.18	**	3.00	9.78	9.54
Tepualia stipularis	-2.062 ± 1.28	0.477 ± 0.41	n.s.	0.11	0.0	1.51
Luma apiculata	-0.735 ± 0.55	0.495 ± 0.19	**	0.81	0.83	3.42
Myrceugenia planipes	-1.881 ± 0.87	0.584 ± 0.28	**	0.23	0.86	2,54
Amomyrtus meli	-0.731 ± 0.59	0.616 ± 0.19	***	0.62	0.57	4.42
Nothofagus nitida	-0.654 ± 0.70	0.658 ± 0.22	***	0.79	5.7	6.12
Saxegothaea conspicua	-5.382 ± 1.45	0.977 ± 0.34	***	0.00	4.98	7.16
Weinmannia trichosperma	-4.978 ± 2.22	1.427 ± 0.58	***	0.12	0.20	1.37

[a]:List of tree species ranked according to the values of slope coefficients (b) obtained in the GLMs. A F test was applied using a quasipoisson family distribution and log link function. Df=1, number of fragments= 51.

S.E.: Standard error.
* p<0.05
** p<0.01
*** p<0.001
n.s.: not significant

Table 6. Regression relationships between the abundance of shrub species and patch area, *A* (in hectares). The relationship y = *a* + *b* $\log_{10}$ (*A*) was fitted for each species using generalised linear modelling, and estimates of parameters *a* and *b* (± 1 S.E.) are provided, and its statistical significance is shown[a]. The variation in abundance of shrub species in the field is illustrated in the final three columns, which provide means for different ranges of patch size.

	Abundance (n ha^{-1})			Mean values when patch area is		
Species	Intercept ± S.E.	Slope ± S.E.	*p*-value	< 50 ha	50-250 ha	> 250 ha
Ugni molinae	-2.591 ± 0.88	-9.471 ± 3.11	***	16	0	0
Rubus constrictus	0.089 ± 0.36	-2.959 ± 1.13	***	23	0	0
Ribes magellanica	-1.736 ± 0.36	-2.499 ± 0.99	***	19	0	0
Azara integrifolia	-1.521 ± 0.49	-0.802 ± 0.48	**	11	0	0
Aristotelia chilensis	1.236 ± 0.30	-0.774 ± 0.28	***	312	53	5
Chusquea uliginosa	1.260 ± 0.42	-0.548 ± 0.32	n.s.	818	705	44
Ovidia pillo-pillo	-1.406 ± 0.47	-0.476 ± 0.34	n.s.	19	0	0
Myoschilos oblonga	-0.145 ± 0.55	-0.463 ± 0.39	n.s.	55	0	16
Berberis darwini	0.562 ± 0.53	-0.392 ± 0.34	n.s.	130	24	44
Fuchsia magellanica	-0.924 ± 0.67	-0.299 ± 0.41	n.s.	13	20	0
Myrceugenia parvifolia	0.345 ± 0.40	-0.213 ± 0.22	n.s.	97	12	57
Rhaphithamnus spinosus	1.942 ± 0.22	-0.136 ± 0.11	n.s.	381	395	144
Berberis buxifolia	-3.607 ± 1.54	-0.127 ± 0.84	n.s.	2	0	0
Gaultheria mucronata	-1.340 ± 0.79	-0.112 ± 0.40	n.s.	27	0	9
Chusquea quila	1.043 ± 0.36	0.211 ± 0.14	n.s.	583	1852	833
Azara lanceolata	-2.976 ± 1.15	0.238 ± 0.45	n.s.	2	12	9
Gaultheria insana	-1.104 ± 0.71	0.262 ± 0.28	n.s.	50	40	44
Pseudopanax laetevirens	-0.490 ± 0.56	0.459 ± 0.19	**	72	120	210
Crinodendron hookerianum	-1.317 ± 0.65	0.482 ± 0.22	**	7	125	59
Azara serrata	-3.910 ± 2.02	0.608 ± 0.65	n.s.	0	0	60

[a] Species have been ranked according to the values of slope coefficients (b) obtained in the GLMs. A F test was applied using a quasipoisson family distribution and log link function. Df=1, number of fragments= 51.

S.E.: Standard error.
* p<0.05
** p<0.01
*** p<0.001
n.s.: not significant

Figure 1. Distribution of native forest fragments (in black) and other land cover types (in grey) in the study area in southern Chile.

Figure 2. Relationships between $\log_{10}$ (patch size +1, in hectares) and some of the most statistically significant response variables. Measures of richness, forest structure and canopy were obtained at the plot level. Number of animal trails was measured along four transects of 40 m length and 2 m width oriented in each cardinal direction from the central point of the sampling plot.

Figure 3. Proportion of old-growth and secondary forests in different patch size classes.

The graph was generated by overlaying the position of all the forest fragments onto a thematic map of forest subtypes developed by national inventory and mapping known as Catastro (CONAF *et al.*,, 1999).

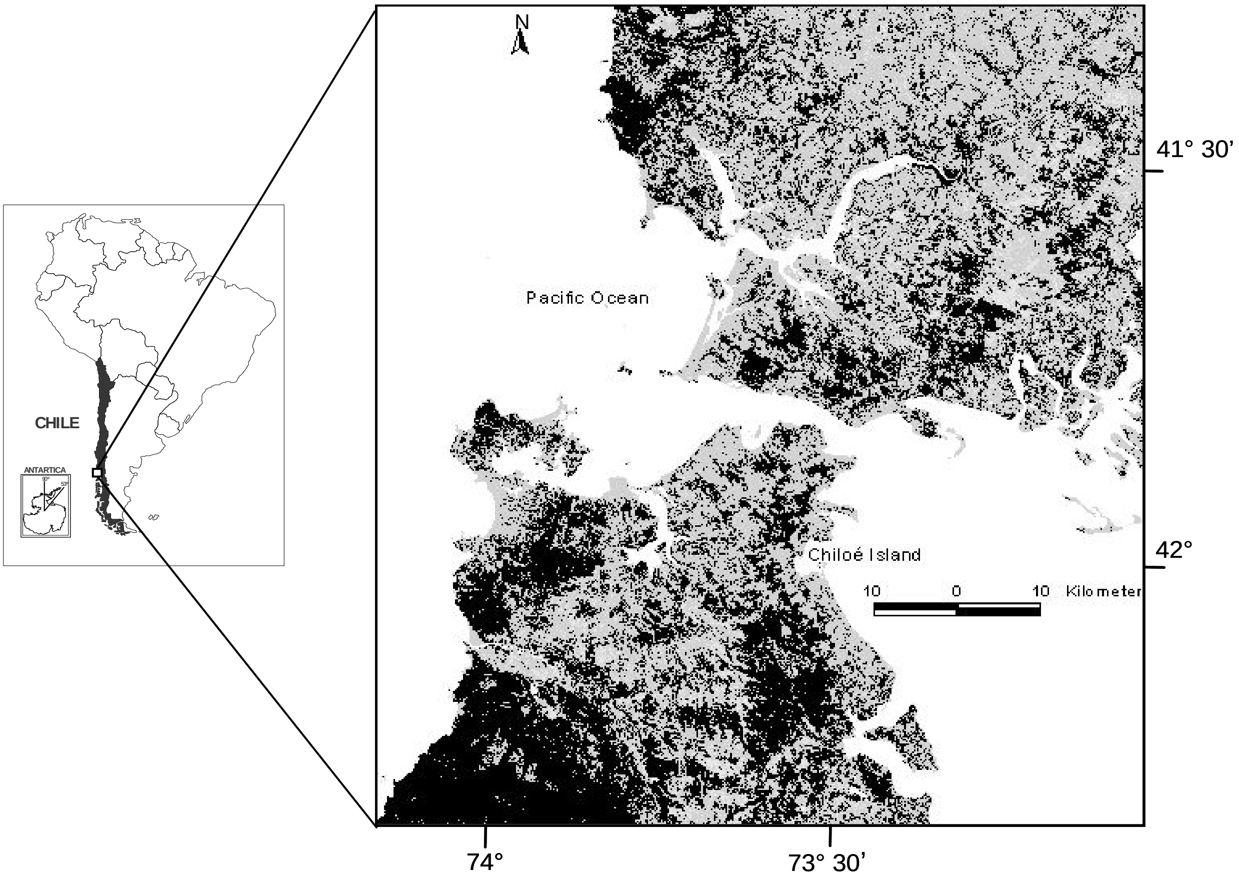
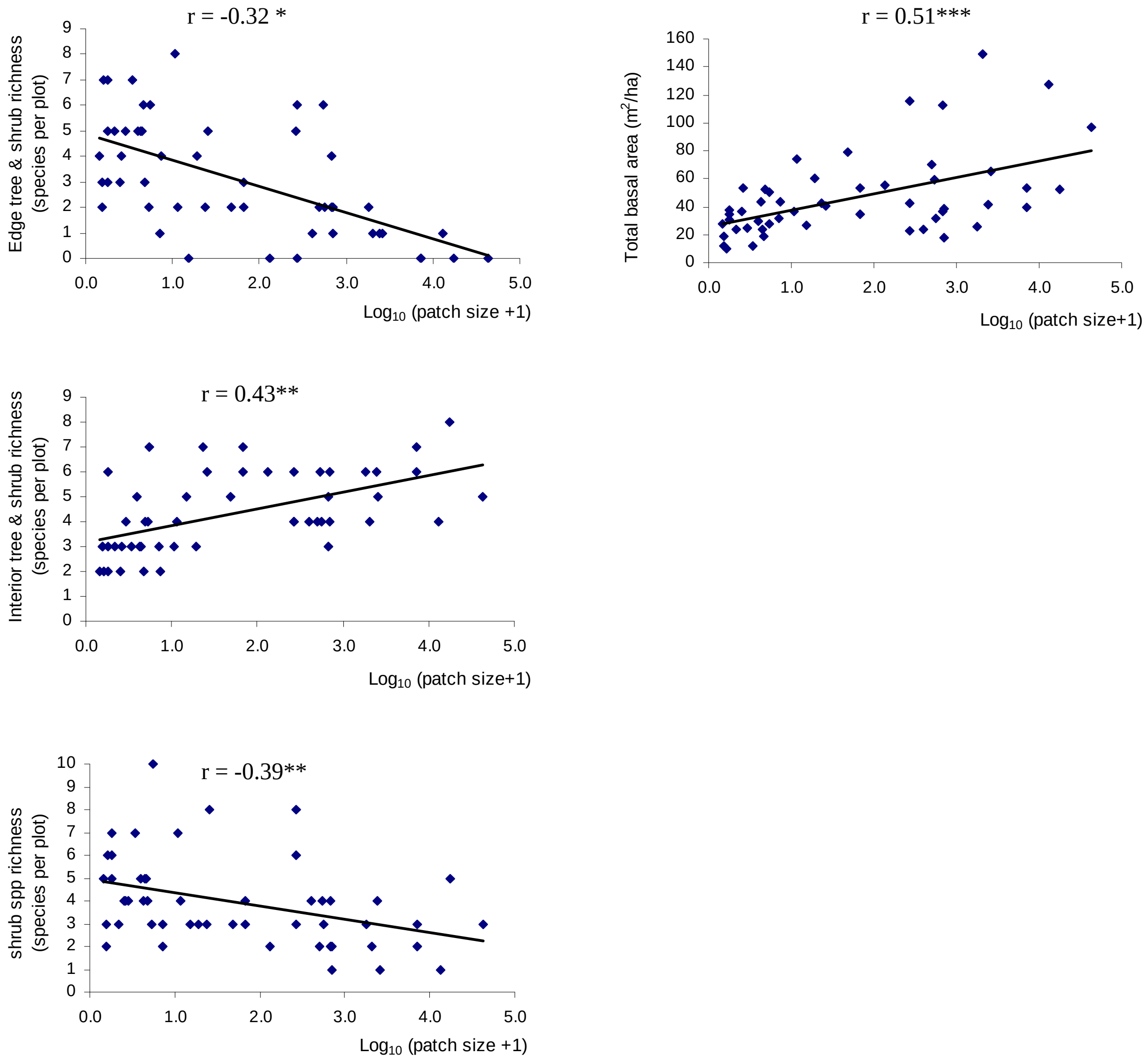

N
Pacific Ocean
Chiloé Island
10 0 10 Kilometer
41° 30’
42°
74°
73° 30’
CHILE
ANTARTICA

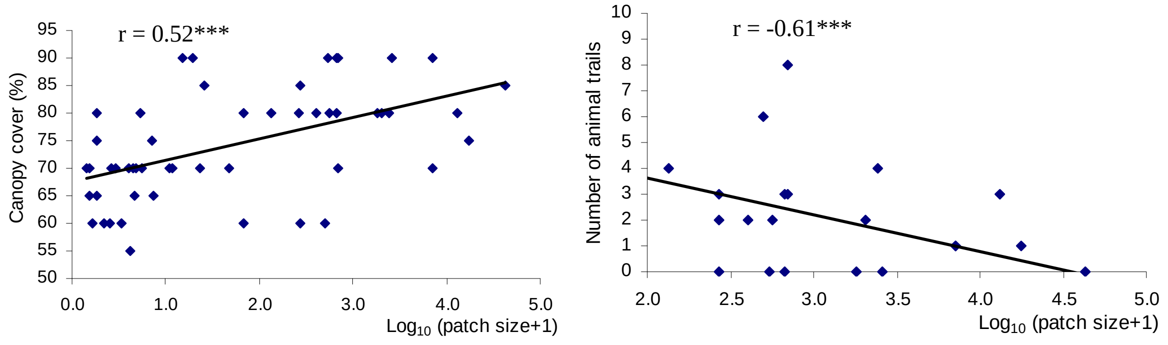
Figure 1.

a) Richness

b) Forest structure



c) Anthropogenic disturbances



* p<0.05, ** p<0.01, *** p<0.001

Figure 2.

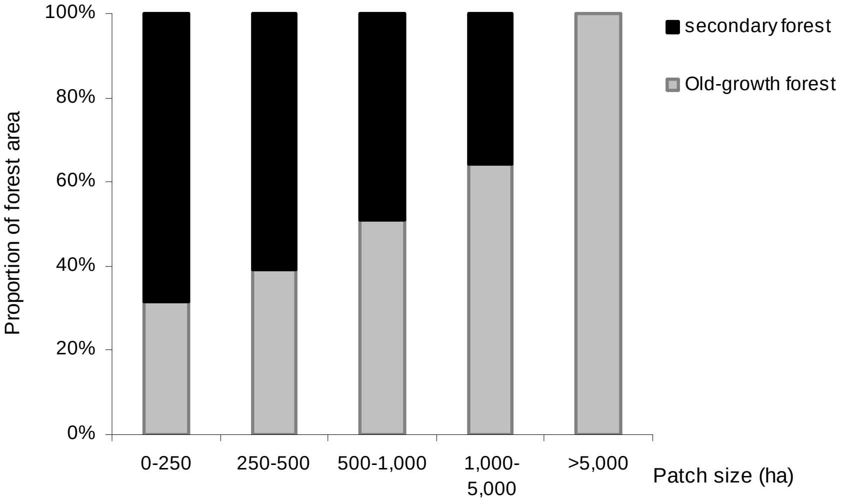

100%
80%
60%
40%
20%
0%
Proportion of forest area
0-250
250-500
500-1,000
1,000-5,000
>5,000
Patch size (ha)
secondary forest
Old-growth forest

Figure 3.

Appendix 1. Matrix of Spearman correlation coefficients[1] of landscape spatial attributes for the sampled forest fragments. Core forest area is defined by distance to the edge of 100, 300, and 500 m.

Index	Core area - 100	Core area - 300	Core area - 500	Radius of gyration	Patch size	Proximity index	Edge length
Core area (100 m)	1.00						
Core area (300 m)	0.80***	1.00					
Core area (500 m)	0.96***	0.70***	1.00				
Radius of gyration (m)	0.80***	0.44**	0.37**	1.00			
Patch size (ha)	0.90***	0.68***	0.58***	0.86***	1.00		
Proximity index	0.49**	0.50***	0.45**	0.54**	0.51**	1.00	
Edge length (km)	0.91***	0.69***	0.55**	0.92***	0.95***	0.72***	1.00

** p<0.01, *** p<0.001

[1]: The test of normality one-sample Kolmogorov-Smirnov revealed that each spatial attribute significantly differs from a normal distribution. Therefore, a Spearman correlation test (non-parametric relations) was used.