Relationship between fragmentation, degradation and native and exotic species richness in an Andean temperate forest of Chile

Relación entre fragmentación, degradación y riqueza de especies nativas y exóticas en un bosque templado andino de Chile

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ABSTRACT

Human impact such as forest fragmentation and degradation may have strong effects on native and exotic plant communities. In addition, these human-caused disturbances occur mostly in lowlands producing greater fragmentation and degradation there than in higher elevations. Plant invasion should be greater in more fragmented and degraded forests and hence lowlands should be more invaded than higher elevations. In turn, native species richness should be negatively related to fragmentation and degradation and hence greater in higher elevations within a forest type or elevation belt. We assessed these hypotheses in an Andean temperate forest of southern Chile, Araucanía Region. We recorded the vascular plant composition in twelve fragments of different size, perimeter/area, elevation level and evidence of human degradation (logging, fire, cattle faeces). Based on these variables we performed a fragmentation and a degradation index. Pearson correlations were used to analyze the relationship between all these variables. We found that fragmentation and degradation were positively correlated, and each of them decreased with altitude. Furthermore, fragmentation and degradation affected native and exotic species richness in different ways. Invasion was enhanced by both fragmentation and degradation, and as consequence of the altitudinal patterns of these human-caused disturbances, invasion seems to occur mainly in lowlands. In turn, native species richness decreased with fragmentation, and it was not related to degradation nor altitude.

KEYWORDS: Fragmentation, forest degradation, elevation gradient, invasion, plant diversity.

RESUMEN

Impactos humanos tales como la fragmentación y degradación de bosques pueden tener fuertes efectos en las comunidades de especies vegetales nativas y exóticas. Además, perturbaciones antrópicas ocurren principalmente en menores altitudes produciendo mayores grados de fragmentación y degradación que en mayores altitudes. La invasión de plantas exóticas debería ser mayor en bosques más fragmentados o degradados y, por lo tanto, en menores altitudes dentro de un tipo de bosque o piso altitudinal. En cambio, la riqueza de especies nativas debería ser negativamente afectada por la fragmentación y degradación, encontrándose mayor riqueza en mayores altitudes dentro de un tipo de bosque determinado. En este trabajo evaluamos estas hipótesis en un bosque templado andino de la Región de la Araucanía, Chile. Registramos la composición de plantas vasculares en doce fragmentos de diferente tamaño, razón perímetro/área, altitud y degradación antrópica (cortas, incendios, fecas de ganado). En base a estas variables construimos un índice de fragmentación y uno de degradación para estos fragmentos. Se analizaron las relaciones entre estas variables a través de correlaciones de Pearson. Nuestros resultados sugieren que la fragmentación y degradación están positivamente relacionadas y que ambos tipos de perturbación ocurren en altitudes más bajas del tipo de bosque estudiado. Además, la fragmentación y degradación están afectando en diferente forma a la riqueza de especies nativas y exóticas. La invasión se incrementó como consecuencia tanto de fragmentación como de degradación, y como consecuencia del patrón de distribución altitudinal de estas perturbaciones, la invasión aparentemente ocurre principalmente en zonas bajas. En cambio, la riqueza de especies nativas fue negativamente afectada sólo por la fragmentación, y no se relacionó con la degradación interna de los bosques ni con la altitud.

PALABRAS CLAVE: Fragmentación, degradación, gradiente altitudinal, invasión, diversidad vegetal.

INTRODUCTION

The temperate forests of southern South America are recognized as a global biodiversity hotspot because of their endemic and endangered biota (Myers *et al*. 2000). However, the processes of colonization for agriculture and cattle ranching have strongly degraded and fragmented these forests (Armesto *et al*. 1998). These processes of habitat degradation and fragmentation are amongst the top five current threats to biodiversity in Chile (Ceballos *et al*. 2009) as well as globally (Farhig 2003, Fischer & Lindenmayer 2007).

With fragmentation, habitat availability and the area available to native species of the original ecosystems are limited to smaller, often disconnected patches within a matrix of other new habitats (Wilcove *et al*. 1986, Saunders *et al*. 1991, Fischer & Lindenmayer 2007). On the other hand, habitat degradation implies both loss of quality and structural changes, which may be caused by human activities such as clearance, selective logging, cattle grazing, and fires (Lindenmayer & Fischer 2006). Though degradation may occur both in fragmented and continuous habitats, a relationship between fragmentation and degradation has previously been documented; fires, selective logging and cattle have been found more frequently in smaller fragments (Cochrane 2001, Hobbs 2001, Jaña *et al*. 2007).

Degradation and fragmentation have been frequently related to different changes in plant communities, in particular, declining native species diversity (e.g. Saunders *et al*. 1991, Soulé *et al*. 1992, Gilliam *et al*. 1995, Laurance *et al*. 1998, Tabarelli *et al*. 1999, Hersperger & Forman 2003, Lindenmayer & Fischer 2006, Echeverría *et al*. 2007, Schmitt *et al*. 2010), as well as increases in exotic species diversity and abundance (Brothers & Spingarn 1992, Hobbs & Huennecke 1992, Wilson *et al*. 1992, D'Antonio 1993, Mooney & Hobbs 2000, Hobbs 2001, Rouget *et al*. 2002, Pauchard & Alaback 2004, Sax *et al*. 2005). These fragmentation effects may be related to micro-environmental changes in the new edges, such as increase of light, higher temperatures and the potential release of other resources (Saunders *et al*. 1991, Brothers & Spingarn 1992, Chen *et al*. 1995, Hobbs 2001). In addition, Brothers & Spingarn (1992) proposed that decrease in native species in fragmented ecosystems may reduce biotic resistance against further invasion. However, this is clearly not always the case, and there are studies where no invasion has been observed in remnant patches of habitat that keep their internal structure (Teo *et al*. 2003). Similarly, habitat degradation has also been documented as a facilitator of exotic invasion. For example, events causing canopy and soil openings may create micro-environmental conditions that stimulate germination and establishment of invasive species (Sakai *et al*. 2001). This may also adversely affect native species, especially as exotic species can be more competitive than native species under disturbed conditions, thus further favouring invasion (Brothers & Spingarn 1992, Hester & Hobbs 1992, Hobbs & Huennecke 1992, Sakai *et al*. 2001, Teo *et al*. 2003). Furthermore, large herbivores (cows, horses, swine, etc.) can also be significant seed vectors of exotic species, and cause large scale modifications in understory vegetation, adversely affecting native species and favouring invasion (Hobbs 2001, Vázquez 2002).

On the other hand, human activity tends to concentrate in sites that are environmentally more benign and easier to access, having for instance better weather, deeper and more fertile soils, generally located in lower altitudes. This may produce a non-random distribution pattern of fragmentation, degradation, native diversity and plant invasion (Hobbs 2001, Lindenmayer & Fischer 2006, Alexander *et al*. 2011). Lower altitude sites, where more productive habitats are found, have customarily been used for farming, logging and urban development, resulting in smaller remnant fragments that are more degraded and invaded by alien species than those in higher elevations (Pauchard & Alaback 2004, Schmitt *et al*. 2010, Alexander *et al*. 2011).

In different Chilean temperate forests, previous studies have documented several negative impacts of forest fragmentation and degradation on native biodiversity (Bustamante *et al*. 2005, Grez *et al*. 2006, Echeverría *et al*. 2007). However, little is known about the effects of these human-caused disturbances on plant invasion. Some studies performed in Chile have assessed the impact of fragmentation (Bustamante & Simonetti 2005, Bustamante *et al*. 2003) and forest degradation (e.g. Pauchard & Alaback 2004, Becerra 2006, Fuentes-Ramírez *et al*. 2010) on plant invasion. Also, some biogeographical studies have correlated exotic species richness with human settlement documenting greater plant invasion where mostly forest fragmentation and degradation has occurred –mainly in the centre-south region (Arroyo *et al*. 2000, Castro *et al*. 2005). However, in Chile no study has assessed the relationship between fragmentation, degradation and altitude and their effects on plant invasion. In this paper we examined how exotic and native species richness are correlated with fragmentation and degradation along an altitudinal gradient in an andean temperate forest. We expect that fragmentation and degradation will affect positively the exotic species and negatively the native species richness. We also expect that fragmentation and degradation will be greater in lower altitudinal levels and hence that exotic species richness should be negatively and native richness positively related to altitude. As consequence of these trends, we also expect that native and exotic species richness will be negatively related.

METHODS

STUDY AREA

We selected 12 forest fragments (Table I) on private land estates in the pre-Andean zone of the Araucanía Region, specifically in Cautín, Pucón and Curarrehue districts (39º S, 72º W) (Fig. 1). The mean altitude of these fragments (average between the higher and lower level of each fragment) varied between 300 and 1020 m a.s.l. (Table I). The area has deep andisoils or fine volcanic soils with good water-retention capacity and is well-drained (Pauchard & Alaback 2004). The climate in this area is temperate-humid, with a short dry season (less than 4 months) and 2,000 mm annual average rainfall, predominantly in winter (Di Castri & Hajek 1976). Maximum and minimum mean temperatures for the warmest month (January) are 25.3º and 10.4ºC respectively, while in the coldest month (July), maximum and minimum mean temperatures range from 12.1ºC to 4.2ºC (Di Castri & Hajek 1976).

The natural vegetation of the study area is comprised mostly by one type of forest corresponding to a mix of deciduous species such as *Nothofagus alpina* (Poepp. & Endl.) Oerst., *Nothofagus obliqua* (Mirb.) Oerst., and evergreen species such as *Persea lingue* (Miers ex Bertero) Nees, *Aextoxicon punctatum* Ruiz & Pav., *Laurelia sempervirens* (Ruiz & Pav.) Tul., *Nothofagus dombeyi* (Mirb.) Oerst., *Laureliopsis philippiana* (Looser) Schodde, and *Saxegothaea conspicua* Lindl. (Gajardo 1993). The matrix surrounding fragmented patches is composed by grasslands for cattle farming, croplands, and scrub and forest plantations in almost all fragments.

VEGETATION SURVEY

In the summer of 2008, all patches were sampled to gather information on floristic plant composition and anthropic indicators. Fragmentation level was evaluated by the patch size and perimeter/area ratio. Both variables were determined from orthorectified aerial photographs (2007) using the software Arc-View 3.2. Two 140 m-long linear transects were sampled in each patch 100 m apart. Transects were located in an altitudinal range between 300 and 900 m a.s.l. (including all patches) (Table I), as close as possible to the centre of the patches. In each transect, eight 25-m^2 (5 x 5 m) plots were located every 15 m along both lines. The number and composition of vascular plants (excluding epiphyte species) was recorded for each plot, determining the biogeographical origin (native or exotic) and life form of each species. Nomenclature follows The International Plant Names Index (http://www.ipni.org/index.html). Stumps from logging, livestock faeces and fire-signs were also counted in each 5 x 5 m plot. First, we added values of each variable among all plots and transects per fragment to obtain one value per fragment. Then, separately by variable, stump, faeces and fire-sign numbers were indexed from 0 to 1 through the division of their counts per transect by the maximum number recorded among all fragments. These rates were used to build a degradation index by adding values of these three factors. Degradation indexes therefore vary from 0 to 3, where 0 indicates no degradation and 3 is the maximum degradation shown by the assessed variables. In the same way, the patch size and the perimeter/area ratio (one value per fragment) were indexed from 0 to 1 separately through the division of their counts per fragment
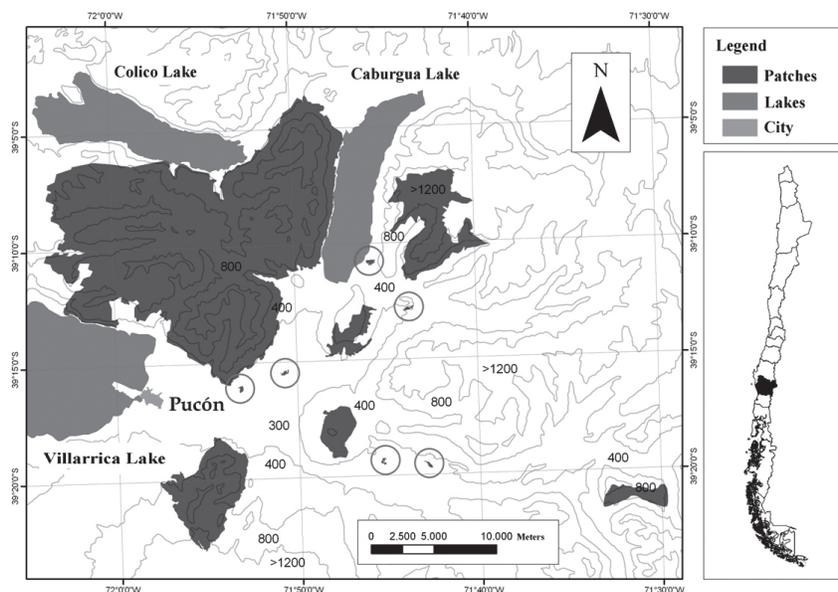

FIGURE 1. Study Area. Location in Chile and studied fragments are shown. Circles show smaller fragments.

FIGURA 1. Area de estudio. Se muestra la ubicación en Chile y los fragmentos estudiados. Círculos muestran los fragmentos más pequeños.

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TABLE I. Fragments included in the study. Altitudinal range, altitude of transects in each fragment and area of fragments. Smaller patches are enumerated from P 1 to P 6.

TABLA I. Fragmentos incluidos en el estudio. Rango altitudinal, altitud de transectos muestreados en cada fragmento y área de fragmentos. Fragmentos más pequeños son enumerados como P1 a P6.

FRAGMENT NAME	ALTITUDE RANGE (m a.s.l.)	TRANSECT ALTITUDE	AREA (ha)
Kawelluco	447-1207	768	3,242
Namuncai	661-1276	760	29,642
La Barda	517-1160	700	729
Río Nevado	630-1400	690	3,253
Curarrehue	560-1260	860	598
Huelemolle	610-843	775	805
P 1	562-711	640	21
P 2	404-442	430	16
P 3	370-378	375	12
P 4	300-352	315	14
P 5	269-333	320	13.5
P 6	384-411	395	13

by the maximum number recorded among fragments. These rates were used to build a fragmentation index by adding values of these two factors. Fragmentation indexes can vary between 0 and 2, being 0 the minimal fragmentation and 2 the maximal fragmentation.

An overall number of native and exotic species per fragment was derived from combining the total observed species lists from all 5 x 5 m plots and both transects per fragment.

STATISTICAL ANALYSES

We first assessed normality distribution of data (Shapiro Wilk's test: Degradation Index, W=0.91, P=0.21; Fragmentation Index, W= 0.90, P = 0.17; Native Richness, W= 0.98, P = 0.98; Exotic Richness, W = 0.93, P = 0.44). Because all data showed normal distribution, statistical analyses were conducted by Pearson correlation analyses using the software *Statistica 6.0*. The relationships between native and exotic species richness, fragmentation index, degradation index and altitude were assessed using the altitude where transects were sampled (Table I). The relationships between degradation index, fragmentation index and altitude were assessed using the mean altitude of fragments (average between the higher and lower altitude value per fragment) (Table I).

RESULTS

PLANT SPECIES COMPOSITION

The species composition found in the study area comprised 110 species, from 95 genera and 64 families of vascular plants (Table II). Among these species, 32.7% (36) are herbaceous, 28% (31) trees, 18% (20) bushes, 11% (12) climbers, 8% (9) ferns and 1% (2) parasitic.

Exotic and native species accounted for 15% (16) and 85% (89) of 105 species with known origen (Table II). The best represented families of exotic species were: Poaceae with 27.7% (5 species), Asteraceae with 22.2% (4 species), Rosaceae with 16.6% (3 species) and Fabaceae with 16.6% (3 species). Exotic species included 72% (13) herbaceous species, 17% (3) shrubs and 11% (2) trees.

The most frequent native species were *Aristotelia chilensis* Stuntz, *Blechnum hastatum* Kaulf., *Luzuriaga radicans* Ruiz & Pav., *Rhaphithamnus spinosus* (Juss.) Moldenke, *Nothofagus dombeyi* and *Aextoxicon punctatum*, all present in more than 80% of fragments (Table II). The most frequent exotic species were *Rubus constrictus* Lefèvre & P.J.Müll., *Rosa rubiginosa* L., *Taraxacum officinale* F.H.Wigg and *Prunella vulgaris* L., all present in more than 50% of fragments (Table II).

RELATIONSHIPS BETWEEN ALTITUDE, FRAGMENTATION AND DEGRADATION

Patch sizes ranged from 12 to 29,642 hectares. Perimeters varied between 1,779 m and 127,065 m and the perimeter/area ratio between 4.29 and 228.51. The lowest fragmentation index was 0.012 and the highest 1.997. All fragments showed a degradation index above cero. The lowest degradation index was 0.57 and the highest 1.75. The degradation index was significantly negatively related to mean altitude of fragments (Pearson, r = -0.64, P = 0.02, N = 12) (Fig. 2), and a positive relationship between degradation and fragmentation indexes was observed (Pearson, r = 0.75, P = 0.004, N = 12) (Fig. 2). Finally, fragments with lower mean altitude showed significantly greater fragmentation index (Pearson, r = -0.86, P < 0.001, N = 12) (Fig. 2).

SPECIES RICHNESS PATTERNS

Total species richness varied from 30 species in the poorest fragment to 57 in the richest. Richness of native species ranged from 27 to 48 species per fragment, while exotic species richness from 0 to12 species per fragment. We found no significant relationship between richness of exotic and native species (Pearson, r = -0.11, P = 0.72, N = 12). Exotic species richness was significantly positively related to the degradation index (Pearson, r = 0.61, P = 0.03, N = 12) (Fig. 3) as well as with the fragmentation index (Pearson, r = 0.66, P = 0.02, N = 12) (Fig. 4). In particular, a significant positive relationship was found between exotic species richness and the density of domestic livestock faeces (Pearson, r = 0.73; P = 0.01, N =12). Furthermore, exotic species richness was only marginally negatively related to altitude (Pearson, r = -0.52, P = 0.08, N = 12) (Fig. 5). In turn, native species richness was not significantly related to degradation index (Pearson, r = -0.19; P = 0.54, N = 12) (Fig. 3) nor altitude (Pearson, r = 0.41; P = 0.18, N =12) (Fig. 5), but it was marginally negatively related to the fragmentation index (Pearson, r = -0.54; P = 0.06, N = 12) (Fig. 4).
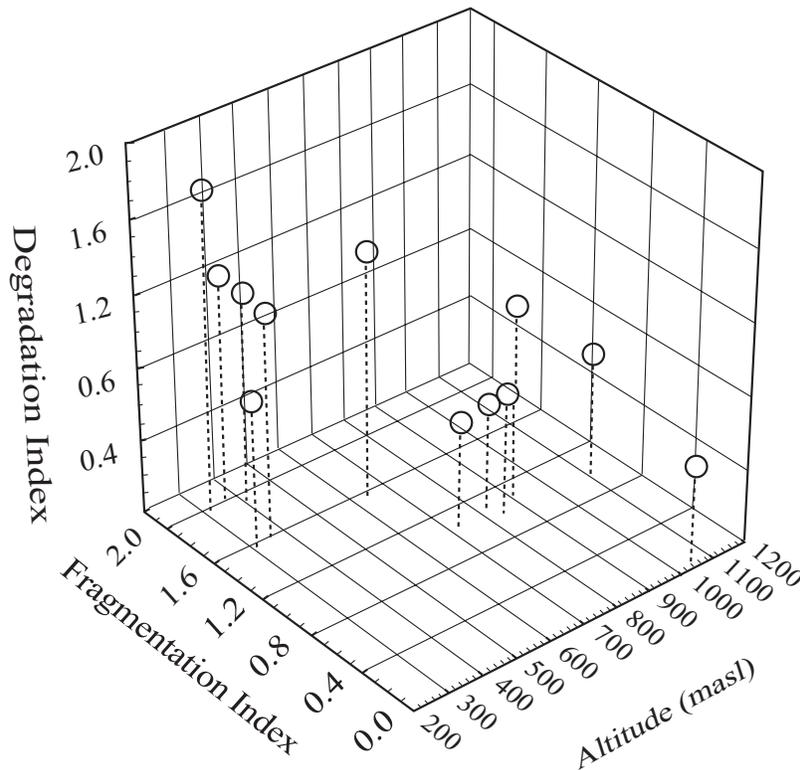

FIGURE 2. Relationship between fragmentation index, degradation index and mean altitude of fragments (average between the higher and lower levels of each fragment).

FIGURA 2. Relación entre índice de fragmentación, índice de degradación y altitud media de los fragmentos (promedio entre el nivel altitudinal máximo y mínimo).
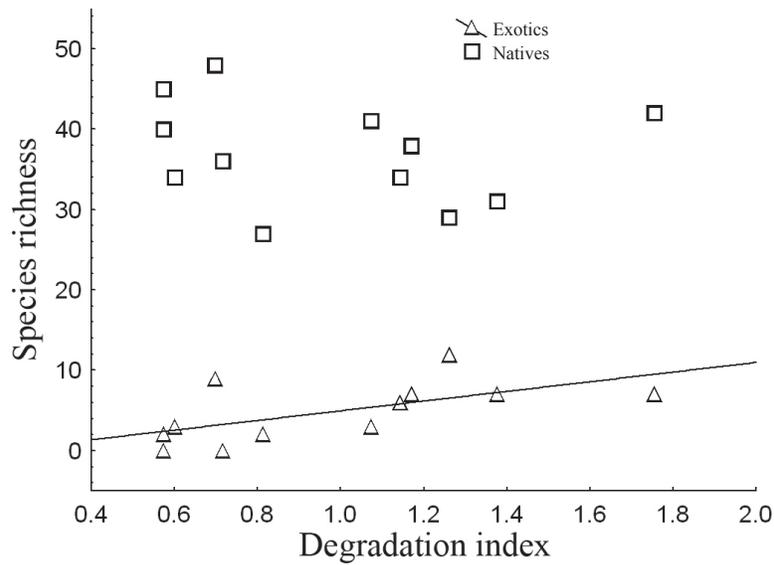
FIGURE 3. Relationship between degradation index and native and exotic species richness. Only significant (P< 0.05) or marginally significant (P<0.1) relationships have a trend line (see text for results).

FIGURA 3. Relación entre índice de degradación y riqueza de especies exóticas y nativas. Sólo las relaciones significativas (P<0,05) o marginalmente significativas (P<0,1) tienen línea de tendencia (ver texto para resultados).
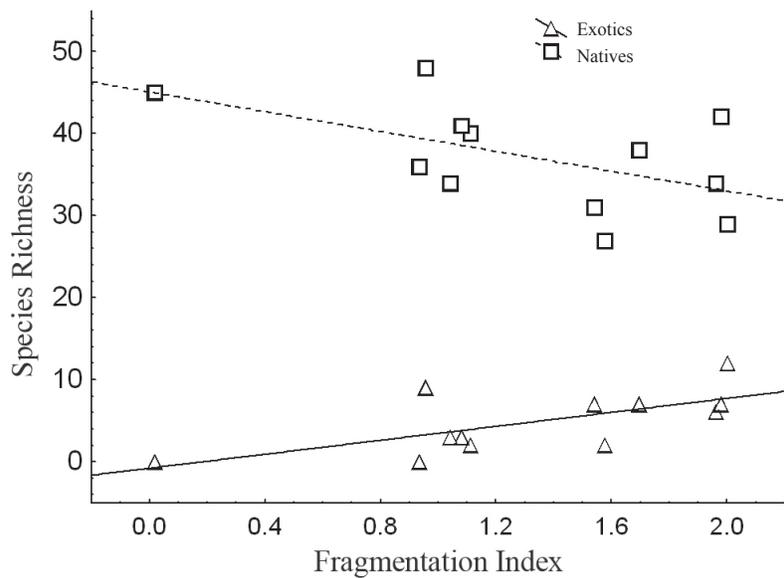

FIGURE 4. Relationship between fragmentation index and native and exotic species richness. Only significant (P< 0.05) or marginally significant (P<0.1) relationships have a trend line (see text for results).

FIGURA 4. Relación entre índice de fragmentación y riqueza de especies exóticas y nativas. Sólo las relaciones significativas (P<0,05) o marginalmente significativas (P<0,1) tienen línea de tendencia (ver texto para resultados).
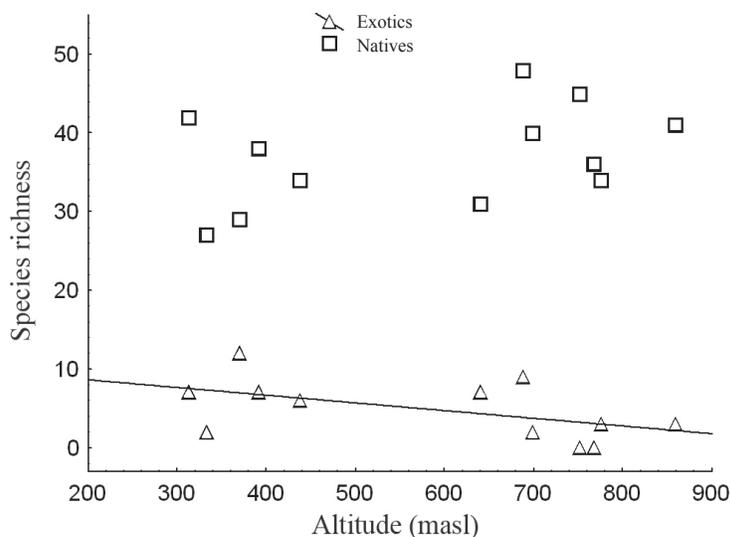
FIGURE 5. Relationship between altitude and native and exotic species richness. Only significant (P< 0.05) or marginally significant (P<0.1) relationships have a trend line (see text for results).

FIGURA 5. Relación entre altitud y riqueza de especies exóticas y nativas. Sólo las relaciones significativas (P<0,05) o marginalmente significativas (P<0,1) tienen línea de tendencia (ver texto para resultados).

TABLE II. Floristic composition of the study area. Scientific name, origin (native: N, exotic: E), family, and frequency (percentage of fragments with presence) of the species are shown.

TABLA II. Composición florística del área de estudio con nombres científicos, origen geográfico de las especies (nativo: N, exótico: E), familia y frecuencia (porcentaje de fragmentos con presencia).

SCIENTIFIC NAME	ORIGIN	FAMILY	FREQUENCY (%)
Acaena ovalifolia Ruiz & Pav.	N	Rosaceae	50.0
Acer pseudoplatanus L.	E	Aceraceae	16.7
Acrisione denticulata (Hook. & Arn.) B. Nord.	N	Asteraceae	16.7
Adenocaulon chilense Less.	N	Asteraceae	33.3
Adiantum chilense Kaulf. var. *chilense*	N	Adiantaceae	50.0
Aextoxicon punctatum Ruiz & Pav.	N	Aextoxicaceae	83.3
Agrostis capillaris L.	E	Poaceae	16.7
Alstroemeria aurea Graham	N	Alstroemeriaceae	33.3
Amomyrtus luma (Molina) D.Legrand & Kausel	N	Myrtaceae	58.3
Aristotelia chilensis Stuntz	N	Elaeocarpaceae	100.0
Asteraceae	-	Asteraceae	8.3
Azara integrifolia Ruiz & Pav.	N	Flacourtiaceae	16.7
Azara lanceolata Hook.f.	N	Flacourtiaceae	66.7
Azara microphylla Hook.f.	N	Flacourtiaceae	41.7
Baccharis sphaerocephala Hook. & Arn.	N	Asteraceae	16.7
Berberis darwinii Hook. var. *darwinii*	N	Berberidaceae	66.7
Blechnum mochaenum Kunkel	N	Blechnaceae	75.0

Scientific name	Origin	Family	Frequency (%)
Blechnum hastatum Kaulf.	N	Blechnaceae	83.3
Blechnum magellanicum (Desv.) Mett.	N	Blechnaceae	41.7
Blechnum penna-marina (Poir.) Kuhn	N	Blechnaceae	8.3
Boquila trifoliata Decne.	N	Lardizabalaceae	75.0
Caldcluvia paniculata D.Don.	N	Cunoniaceae	58.3
Campsidium valdivianum (Phil.) Skottsb.	N	Bignoniaceae	33.3
Cardamine aff. *cordata* Barnéoud	N	Brassicaceae	16.7
Carex inconspicua Steud.	N	Cyperaceae	8.3
Chusquea culeou E.Desv.	N	Poaceae	50.0
Chusquea quila Kunth	N	Poaceae	50.0
Cissus striata Ruiz & Pav.	N	Vitaceae	58.3
Codonorchis lessonii Lindl.	N	Orchidaceae	16.7
Dactylis glomerata L.	E	Poaceae	33.3
Dasyphyllum diacanthoides (Less.) Cabrera	N	Asteraceae	66.7
Desfontainia fulgens D.Don	N	Desfontainiaceae	8.3
Dioscorea brachybotrya Poepp.	N	Dioscoreaceae	58.3
Diplolepis menziesii Schult.	N	Asclepiadaceae	16.7
Drimys winteri J.R.Forst & G. Forst.	N	Winteraceae	25.0
Dysopsis glechomoides Müll.Arg.	N	Euphorbiaceae	33.3
Elytropus chilensis Müll.Arg.	N	Apocynaceae	16.7
Embothrium coccineum J.R.Forst. & G.Forst.	N	Proteaceae	33.3
Escallonia rosea Griseb.	N	Escalloniaceae	8.3
Eucryphia cordifolia Cav.	N	Eucryphiaceae	33.3
Fascicularia bicolor (Ruiz & Pav.) Mez	N	Bromeliaceae	16.7
Francoa appendiculata Cav.	N	Francoaceae	8.3
Fuchsia magellanica Lam.	N	Onagraceae	75.0
Galium hypocarpium Endl.ex Griseb.	N	Rubiaceae	25.0
Gaultheria mucronata Phil.	N	Ericaceae	33.3
Geranium sp.	-	Geraniaceae	25.0
Gevuina avellana Molina	N	Proteaceae	41.7
Hydrangea serratifolia F. Phil.	N	Hydrangeaceae	66.7
Hydrocotyle poeppigii DC.	N	Apiaceae	33.3
Hypochaeris radicata L.	E	Asteraceae	25.0
Hypolepis poeppigii (Kunze) R.A.Rodr.	N	Dennstaedtiaceae	41.7
Lapageria rosea Ruiz & Pav.	N	Philesiaceae	41.7
Lapsana communis L.	E	Asteraceae	16.7
Laurelia sempervirens (Ruiz & Pav.) Tul.	N	Monimiaceae	41.7
Laureliopsis philippiana (Looser) Schodde	N	Monimiaceae	75.0
Lepidoceras chilense (Molina) Kuijt	N	Loranthaceae	8.3
Loasa acanthifolia Lam.	N	Loasaceae	41.7

Scientific name	Origin	Family	Frequency (%)
Lomatia dentata R. Br.	N	Proteaceae	66.7
Lomatia ferruginea (Cav.) R. Br.	N	Proteaceae	33.3
Lomatia hirsuta (Lam.) Diels. ex J.F.Macbr.	N	Proteaceae	58.3
Lophosoria quadripinnata (J.F.Gmel.) C.Chr.	N	Dicksoniaceae	41.7
Lotus uliginosus Schkuhr	E	Fabaceae	33.3
Luma apiculata (DC.) Burret	N	Myrtaceae	75.0
Luzuriaga radicans Ruiz & Pav.	N	Philesiaceae	83.3
Lysimachia sertulata Baudo	N	Primulaceae	8.3
Maytenus boaria Molina	N	Celastraceae	25.0
Maytenus magellanica Hook.f.	N	Celastraceae	41.7
Mitraria coccinea Cav.	N	Gesneriaceae	66.7
Muehlenbeckia hastulata (Sm.) I.M.Johnst.	N	Polygonaceae	41.7
Myoschilos oblongum Ruiz & Pav.	N	Santalaceae	25.0
Myrceugenia planipes O.Berg	N	Myrtaceae	25.0
Nertera granadensis Druce	N	Rubiaceae	75.0
Nothofagus alpina (Poepp. & Endl.) Oerst.	N	Nothofagaceae	16.7
Nothofagus dombeyi (Mirb.) Oerst.	N	Nothofagaceae	91.7
Nothofagus obliqua (Mirb.) Oerst.	N	Nothofagaceae	75.0
Osmorhiza chilensis Hook. & Arn.	N	Apiaceae	75.0
Ourisia ruelloides (L.f.) Kuntze	N	Scrophulariaceae	33.3
Oxalis sp.	-	Oxalidaceae	8.3
Oxalis valdiviensis Barnéoud	N	Oxalidaceae	16.7
Persea lingue (Miers ex Bertero) Nees	N	Lauraceae	41.7
Peumus boldus Molina	N	Monimiaceae	8.3
Plantago lanceolata L.	E	Plantaginaceae	16.7
Polystichum sp.	N	Dryopteridaceae	41.7
Prunella vulgaris L.	E	Labiatae	66.7
Prunus sp.	E	Rosaceae	33.3
Pteris semiadnata Phil.	N	Pteridaceae	8.3
Raukaua laetevirens (Gay) Frodin	N	Araliaceae	33.3
Rhamnus diffusus Clos	N	Rhamnaceae	25.0
Rhaphithamnus spinosus (Juss.) Moldenke	N	Verbenaceae	83.3
Ribes valdivianum Phil.	N	Saxifragaceae	66.7
Rosa rubiginosa L.	E	Rosaceae	50.0
Rubus constrictus Lefèvre & P.J.Müll.	E	Rosaceae	58.3
Rumex acetosella L.	E	Polygonaceae	8.3
Saxegothaea conspicua Lindl.	N	Podocapaceae	41.7
Solanum crispum Ruiz & Pav.	N	Solanaceae	8.3
Solanum cyrtopodium Dunal	N	Solanaceae	41.7
Solanum nigrum L.	E	Solanaceae	8.3

Scientific name	Origin	Family	Frequency (%)
Sophora cassioides (Phil.) Sparre	N	Fabaceae	16.7
Taraxacum officinale G.Weber ex F.H.Wigg.	E	Asteraceae	50.0
Trifolium pratense L.	E	Fabaceae	16.7
Trifolium repens L.	E	Fabaceae	8.3
Tristerix corymbosus (L.) Kuijt	N	Loranthaceae	8.3
Tropaeolum speciosum Poepp. & Endl.	N	Tropaeolaceae	8.3
Ugni molinae Turcz.	N	Myrtaceae	41.7
Uncinia erinacea Pers.	N	Cyperaceae	50.0
Urtica magellanica Juss. ex. Poir.	N	Urticaceae	16.7
Vicia sp.	-	Fabaceae	8.3
Viola reichei Skottsb. ex Macloskie	N	Violaceae	41.7
Weinmannia trichosperma Cav.	N	Cunoniaceae	50.0
Poaceae	-	Poaceae	16.7

DISCUSSION

All the studied forest fragments, regardless the size and shape, revealed signs of some anthropic disturbance, such as selective logging, cattle and fires. Thus, the forest landscape in this locality is both fragmented and internally degraded. However, as expected, patches were not evenly degraded, with higher degradation levels observed in fragments with greater fragmentation index. In other Chilean temperate forests, more frequent fire events, cattle presence and logging have also been observed in smaller fragments (Jaña *et al*. 2007). Similarly, Cochrane (2001) observed a greater number of fire events in smaller fragments of tropical forests, and Hobbs (2001) more cattle presence in smaller fragments of Australian forests. Thus, the positive relationship between fragmentation and degradation seems to be a common pattern. In addition, our results suggest that human impact has mainly occurred in lowlands, which is a pattern frequently documented in fragmentation studies (Lindenmayer & Fischer 2006).

Fragmentation has been observed to affect species richness both negatively and positively, depending on the biogeographical origin of species (Saunders *et al*. 1991, Tabarelli *et al*. 1999, Fahrig 2003, Teo *et al*. 2003, Lindenmayer & Fischer 2006). Our findings support the hypothesis that fragmentation causes an increase in exotic plant invasion as we found a positive significant relationship between the fragmentation index and exotic richness. Thus, our results are consistent with many other studies about the effect of fragmentation on invasion which have generally shown a increase of exotic invasion within fragments relative to continuous or larger fragments (e.g. Harrison 1999, Hobbs 2001, Rouget *et al*. 2002, With 2002), and a positive edge effect (e.g. Brothers & Spingarn 1992, Meiners & Pickett 1999, Hobbs 2001, Bustamante *et al*. 2003). It is probable that increase of light in smaller fragments (Chen *et al*. 1995) may be enhancing exotic invasion (Saunders *et al*. 1991, Murcia 1995). Also, in smaller fragments interior sites (where sampling was performed) are closer to edges than the interior of larger fragments. Hence, the interior of smaller fragments is closer to the propagule source of exotic species growing in the matrix and dispersal of seeds of exotic species is more probable (e.g. Cadenasso & Pickett 2001).

On the other hand, despite we observed only a marginally significant relationship between native species richness and fragmentation, the trend was clearly negative, similar to our hypothesis. It is probable that the low number of fragments has limited the statistical power to get a significant negative relationship. Then, this result is concordant to other studies documenting negative effects of fragmentation on native biodiversity (e.g. Saunders *et al*. 1991, Soulé *et al*. 1992, Gilliam *et al*. 1995, Laurance *et al*. 1998, Tabarelli *et al*. 1999, Hersperger & Forman 2003, Lindenmayer & Fischer 2006, Echeverría *et al*. 2007, Schmitt *et al*. 2010). As with exotic species, environmental changes produced by fragmentation (Chen *et al*. 1995, Murcia *et al*. 1995) may be detrimental for some forest-specialist native species. Therefore, our results suggest that fragmentation affects inversely to native and exotic species in this region.

Forest degradation has strong implications for habitat quality of wildlife as well as for plant species themselves (Hobbs & Huenneke 1992, Gilliam *et al*. 1995, Dzwonko

& Loster 1997). However, we did not find a significant relationship between native species richness and degradation. It is probable that human disturbances in studied forests have produced similar environmental changes than natural disturbances commonly observed in these forest-types (e.g. small-gap dynamic) (Saldaña & Lusk 2003, Gutiérrez *et al*. 2004), and hence native species are not being negatively affected by this forest degradation. By contrast, it was clear that exotic species were positively correlated with degradation, suggesting that exotic species may react faster than native ones to anthropic disturbances (e.g. Hobbs 2001, Burns 2004). The positive correlation between number of livestock faeces and exotic species richness suggests that cattle plays a role in both degrading the sites and aiding arrival/colonization of exotic species (Hobbs 2001, Brothers & Spingarn 1992, D'Antonio 1993). Thus, herbivores may well be important facilitators of invasion in this region. Therefore, these results suggest that degradation affects in different way but not inversely to native and exotic species.

Our results suggest that the elevation range (300 to 800 masl) covered by transects had no influence on the number of native species despite we observed reduced fragmentation and degradation at higher sites. In contrast, we observed a slight although non-significant negative relationship between altitude and exotic species richness (P=0.08). Thus, these results may be consistent to other studies documenting a decreasing invasion with altitude mediated by a increase in fragmentation and degradation levels (e.g. Wilson *et al*. 1992, Schmitt *et al*. 2010, Alexander *et al*. 2011). The absence of a statistically significant correlation suggests that this may be a developing pattern while the invasion process occurs. It is unlikely that this slight trend has been produced by climatic effects of this altitudinal gradient as all fragments corresponded to the same forest type along this altitudinal gradient (Gajardo 1993). Consistent with this, we observed no significant relationship between native species richness and altitude.

Currently there is much debate about the relationship between native and exotic species (Bruno *et al*. 2004, Davies *et al*. 2005). Recent studies have demonstrated dependence on the geographic scale of this relationship (Davies *et al*. 2005). Generally, local scale studies have found a negative relationship between native and exotic species richness (Hobbs 2001, Davies *et al*. 2005), which could be explained by competition processes that are not applicable at larger scales (Hester & Hobbs 1992, Huston 1999). However, other studies at local scale have not found significant relationships, and in some others, the relationships have been positive (Bruno *et al*. 2004, Chown *et al*. 2005). As in several other locally-based studies (e.g. Bruno *et al*. 2004, Chown *et al*. 2005), we found no significant relationship between the richness of exotic and native species. Probably, different but not inverse effects of forest degradation on exotic and native species richness contributed to this result.

In conclusion, our results suggest that the human impact in forests of this region has affected plant communities. However, specific human-caused disturbances such as fragmentation and degradation affect differently to native and exotic species, being exotics facilitated by both degradation and fragmentation and natives only negatively affected by forest fragmentation. This suggests that management of exotic species should be focused on reducing internal degradation of remnant forests as well as fragmentation and probably edge effects. In turn, in order to conserve native species management should be focused on reducing fragmentation and edge effects.

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