Influence of Elevation, Land Use, and Landscape Context on Patterns of Alien Plant Invasions along Roadsides in Protected Areas of South-Central Chile

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Abstract: *Alien plant species are a growing concern in protected areas, yet little information is available on the role of roads as corridors for alien species and the effects of elevation, land use, and landscape context in these invasions. These concerns are of particular interest in temperate zones of South America, where protected areas have high concentrations of endemic species. We studied roadside alien plant communities and forest-road edges in Villarrica and Huerquehue national parks in the Andean portion of south-central Chile. We sampled alien species and their abundance along 21 km of roads inside parks and 22 km outside parks, using 500-m roadside transects. We also sampled plant species and recorded their abundance in 15 transects located perpendicular to forest-road edges in four forest types. Of the 66 alien species encountered along roadsides, 61 were present outside parks and 39 inside parks. Elevation and alien species richness along roadsides were significantly and negatively correlated ($R^2 = -0.56$, $p < 0.001$). Elevation, land use, and their interaction explained 74% of the variation in alien species richness along roadsides ($p < 0.001$). Transects located in pasture or disturbed secondary forests had significantly more alien species. We found no significant edge effect on native and alien species richness in any forest type. Few alien species have percolated into forest interiors. Native and alien diversity in edge plots were not related. Almost half the alien species belonged to three families and 85% were native to Eurasia. Our results suggest that alien species are moving into parks along road corridors and that elevation and land use of the matrix influence these invasion processes. Our findings corroborate the importance of early detection and control of invasive species in protected areas and highlight the importance of considering surrounding matrix land use in developing conservation strategies for reserves.*

Key Words: *Araucaria*, exotic species, forest edges, *Nothofagus*, protected areas, reserves, roads, southern Chile

Influencia de la Altitud, Uso de Suelo y Contexto del Paisaje sobre Invasiones de Plantas Exóticas

Resumen: *Las invasiones de especies de plantas exóticas son una preocupación creciente en áreas protegidas, sin embargo se dispone de escasa información sobre el papel de los caminos como corredores para especies exóticas y los efectos de la altitud, uso de suelo y contexto del paisaje en estas invasiones. Estas preocupaciones son de interés especial en las zonas templadas de Sudamérica, donde las áreas protegidas presentan altas concentraciones de especies endémicas. Estudiamos las comunidades de plantas exóticas en bordes de caminos y en bordes de caminos dentro de bosques en los parques nacionales de Villarrica y Huerquehue en la porción andina del centro-sur de Chile. Muestreamos especies exóticas y su abundancia a lo largo de 21 km de caminos dentro de los parques y 22 km fuera de los parques, utilizando transectos de 500 m. También muestreamos especies de plantas y registramos su abundancia a lo largo de 15 transectos localizados perpendicularmente a los bordes de los caminos dentro de bosques en cuatro tipos de bosque. De las 66 especies de plantas*

exóticas encontradas en los bordes de los caminos, 61 estuvieron presentes afuera de los parques y 39 dentro de los parques. La altitud y riqueza de especies exóticas en los bordes de caminos estuvieron significativa y negativamente correlacionados (R² = −0.56, p < 0.001). La altitud, uso de suelo y su interacción explicaron 74% de la variación en la riqueza de especies exóticas en los bordes de camino (p < 0.001). Los transectos localizados en pastizales o bosques secundarios perturbados tuvieron un número significativamente mayor de especies exóticas. No encontramos efecto de borde significativo sobre la riqueza de especies nativas y exóticas en ningún tipo de bosque. Pocas especies exóticas se han propagado al interior de los bosques. La diversidad nativa y exótica de parcelas en los bordes no estuvo relacionada. Casi la mitad de las especies exóticas pertenecía a tres familias y 85% fueron nativas de Europa. Nuestros resultados sugieren que las especies exóticas se están moviendo hacia los parques a lo largo de corredores – caminos y que la altitud y el uso del suelo en la matriz influyen en estos procesos de invasión. Nuestros hallazgos corroboran la importancia de la detección temprana y del control de especies invasoras en áreas protegidas y resaltan la importancia de considerar el uso del suelo en la matriz en el desarrollo de estrategias de conservación para reservas.

Palabras Clave: *Araucaria*, áreas protegidas, bordes de bosque, caminos, *Notophagus*, reservas, species exóticas, sur de Chile

Introduction

Alien plants (sensu Richardson et al. 2000) are recognized as a potential threat to the conservation of protected areas (e.g., MacDonald et al. 1989; Lonsdale 1999; Mack et al. 2000). These plant invasions may ultimately decrease the capacity of protected areas to conserve biodiversity because of detrimental effects on native species and ecosystem processes (Mack et al. 2000) and the difficulty in controlling them in natural environments (MacDonald et al. 1989).

Land use, disturbance, and climate are driving factors of alien plant invasion (Lonsdale 1999; Hobbs 2000). In temperate ecosystems, most alien species are invasive in human-disturbed landscapes at low elevations (Hobbs 2000). However, high-elevation, relatively undisturbed environments where most protected areas occur (Noss & Cooperrider 1994) can also be susceptible to invasion by alien plants (DeFerrari & Naiman 1994; Heckman 1999; Stohlgren et al. 1999; Pauchard et al. 2003).

Roads represent the primary pathway for the introduction of alien plant species into protected areas, especially for generalist species with short life cycles and high reproductive rates (Spellerberg 1998; Parendes & Jones 2000; Trombulak & Frissell 2000). Fortunately, most alien species growing along roadsides are incapable of colonizing less disturbed natural environments. Roadsides, however, still may serve as starting points from which some species spread from the edges to the interiors of pristine or naturally disturbed environments (Murcia 1995; Cadenasso & Pickett 2001). Roadsides may also act as reservoirs of alien plant propagules that can be liberated in disturbance events (Parendes & Jones 2000).

Because of their role in plant invasions, roads are important places to examine patterns of distribution of alien species and their potential for invasion into interior habitats (Trombulak & Frissell 2000). Roads are particularly important vectors of alien plant invasions into protected areas because they often connect weed populations in the matrix with the interior of protected areas (Landres et al. 1998). Additionally, roadsides are useful for studying the influence of climatic factors and dispersal characteristics on alien species because the roads themselves provide a consistent disturbance environment across a wide elevational gradient (Tyser & Worley 1992; Wilson et al. 1992; Milton & Dean 1998; Spellerberg 1998; D'Antonio et al. 2001).

South-central Chile is of particular interest for studies of alien plant species because it contains a highly endemic and diverse flora that could be especially sensitive to invasion and has been little studied (Armesto et al. 1998, 2001; Arroyo et al. 2000). Chile has approximately 690 naturalized alien species (15% of total flora), 381 of which occur in its humid seasonal rainforest (Arroyo et al. 2000). Protected areas in this region are located mostly at high elevations and therefore do not appear to be significantly threatened by alien plant invasions (Arroyo et al. 2000; Pauchard & Alaback 2002). Because of increasing human disturbance and dispersal, however, alien species are moving from agricultural landscapes into natural environments. At the same time, increasing international trade is leading to greater rates of introductions to this biogeographically isolated temperate forest (Arroyo et al. 2000).

To better understand the susceptibility to invasion of protected areas, it is necessary to understand the role of elevation, land use, and the spatial arrangement of land use (landscape context) in patterns of distribution of alien species (D'Antonio et al. 2001). It is also important to assess the degree of percolation of alien species into undisturbed environments (Cadenasso & Pickett 2001). We evaluated the influence of elevation, land use, and landscape context on the abundance and distribution of alien species along roadsides in two representative protected areas in south-central Chile and their adjacent matrices. We also explored the distribution and abundance of

alien species in park forest-road edges to determine the extent of the spread of alien species into park interior habitats.

Study Sites

The study sites included two national parks and their surrounding matrixes, located in the Chilean south-central Andes (39°W, 71°S). Villarrica National Park (63,000 ha) is south of the towns of Pucón and Villarrica and extends to Lanín National Park in Argentina. Elevation ranges between 600 and 3747 m. Three volcanoes shape its geomorphology: Villarrica (2847 m), Quetrupillán (2382 m), and Lanín (3747 m) (Casertano 1963). Huerquehue National Park (12,500 ha) is 30 km north of Villarrica National Park near the Caburgua Lake. It has climatic and vegetational characteristics similar to those of Villarrica National Park but has been less affected by recent volcanic activity.

The climate in these areas is temperate, with dry summers and cool, moist winters. Average annual precipitation ranges from 2500 to 3500 mm. The mean annual temperature is 12°C, with accumulations of up to 2 m of snow in the winter (Finckh 1996; CONAF 2002). Soils have formed from andesitic volcanic ejecta, tuffs, and scoria over basaltic deposits (von Buch 1970). Soils are poorly developed at high elevations and in recent volcanic features. In lower valleys, deep andisols or "trumaos" with high water retention and good drainage represent a rich substrate for plant growth (Frank & Finckh 1997). However, low levels of phosphates may be a constraint on growth in these volcanic soils (Frank & Finckh 1997).

Our study sites contain a strong vegetation gradient with respect to elevation and soils (Finckh 1996). In lower valleys, natural vegetation consists of *Nothofagus dombeyi* (Mirb.) Blume–*Nothofagus obliqua* (Mirb.) Blume forests. *Nothofagus dombeyi* forests, *Nothofagus alpina* (Poepp. & Endl) Oerst. forests, and isolated patches of evergreen rainforests dominate the middle elevations (600–1200m). At higher elevations, *Nothofagus pumilio* (Poepp. & Endl) Krasser and *Araucaria araucana* (Mol.) K. Koch form forest and shrubland. Timberline is at 1200–1500 m and is frequently affected by volcanic deposits. Natural disturbances include frequent and catastrophic volcanic activity from the Villarrica Volcano, mudflows, and small-scale windthrows (Finckh 1996).

European settlers in the 1800s converted much of the forests in low-elevation valleys to grazing pastures. Less productive and inaccessible land was not logged and was set aside as Villarrica National Park in 1940 (Finckh 1996). Secondary forests and low-elevation pastures are the result of recent human-caused fires (approximately 50 years ago) and continuous cattle grazing (Finckh & Thomas 1997). Currently, land clearing, firewood cutting, tourism, and real estate development are affecting adjacent areas.

However, aside from a popular ski development and a few dirt and gravel roads, the park remains relatively undisturbed. Huerquehue National Park is also in an isolated area, with rugged topography surrounded by private agricultural and recreational land. There are no roads to the interior of the park, but intense recreation occurs on the park boundary and interior trails.

Methods

Road Transects

We sampled the distribution and abundance of alien species along 43 km of road habitat on three roads from Villarrica National Park and one road from Huerquehue National Park from 280 to 1290 m in elevation. All roads were approximately 10 m wide and consisted of gravel and natural volcanic substrate. Five-hundred-meter transects started at each kilometer of road from the park core to the adjacent matrix. Transects were 5 m wide along each side of the road. Twenty-one transects were inside parks and 22 were in their surrounding matrices. Seventeen transects were located along the Pucón access road of Villarrica National Park (Rucapillán): 14 along a secondary road of Villarrica National Park (Chinay), 4 along the international road of Villarrica National Park (Puesco), and 8 along the access road of Huerquehue National Park (Huerquehue). In each transect, we recorded all alien species and their abundance on a qualitative scale: A, abundant (present in >25% of the transect length); C, common (10–25%); I, intermittent when more than one group of individuals was present but occupied <10% of the transect length; and R, rare when only one group of individuals was present. Alien plant species were those species not native to continental Chile (sensu Richardson et al. 2000), as confirmed by Matthei (1995) and the database of the Herbarium of the Botany Department, University of Concepción. Nomenclature for native species followed that of Marticorena and Quezada (1985). For each transect we recorded the elevation and land use in the surrounding matrix based on four categories: pastures, secondary forests, primary forests, and volcanic deposits. Elevation was determined with an aneroid altimeter and a topographic map.

Edge Transects

We studied forest-road edges in Villarrica National Park to assess the degree to which alien plant species are percolating into interior habitat, and we explored the relationship between plant-community attributes and the presence and abundance of alien species. We sampled 15 edge-transects, 10 in Chinay and 5 in Puesco. Transects were distributed in four forest types: *A. araucana*–*N. pumilio*

($n = 4$); *N. dombeyi, A. araucana* ($n = 2$); *N. alpina* ($n = 3$); and *N. dombeyi–N. obliqua* ($n = 3$). Edge transects were composed of four plots of 2 × 20 m and were randomly established in representative forest-road edges. We established plots at 0, 10, 20 and 40 m from the end of the road surface. Each plot was divided into two subplots of 10 × 2 m to increase the accuracy of cover estimation. We used Braun-Blanquet cover classes (Mueller-Dombois & Ellemberg 1974) in each subplot to record the cover of native and alien species in the understory. As indicators of forest structure, we visually estimated total canopy cover and recorded dominant tree height and tree seedlings by species in each subplot.

Analysis

DISTRIBUTIONAL PATTERNS OF ALIEN SPECIES

To understand general taxonomic and biogeographical patterns, we compiled a list of all alien species found in the 43 transects. We used Matthei (1995) to determine species' biogeographic origin and life-form group (annual, biennial, perennial herb, or woody perennial). We tested the correlation between alien species richness and elevation using linear-regression analysis. We used multiple-regression analysis (Ott & Longnecker 2001) to evaluate the relative significance of elevation, land use, and their interaction in explaining variation in alien species richness. Land use and the interaction of land use and elevation were treated as sets of dummy variables (Ott & Longnecker 2001). We used the Kruskal-Wallis nonparametric test ($p \leq 0.01$) to test for differences in the mean number of species by land use type for both the complete model and pairwise comparisons.

We determined the elevational range for species present in at least two transects. For each species, we plotted elevation of the lowest and highest transects where the species occurred. We evaluated the influence of landscape context on the establishment of alien species by calculating mean species richness for each transect inside and outside parks and by testing for differences in abundance categories with the Kruskal-Wallis test ($p \leq 0.01$). To detect gradients in alien species assemblages, we used detrended correspondence analysis (DCA) on transect species abundance (PC-ORD 4.0) (Hill & Gauch 1980). The ordination matrix contained 42 of the 43 transects (one lacked alien species) and all species present in more than one transect ($n = 45$). A subjective percent-cover value was assigned to each of the qualitative abundance classes: R = 1, I = 10, C = 25, and A = 50. Finally, to evaluate the role of physical variables in the compositional gradient, we analyzed the relationship of transect scores in DCA axis 1 with elevation and land use. We evaluated elevation with a simple linear-regression analysis and included land-use categories as a set of dummy variables (Ott & Longnecker 2001).

EVALUATION OF ALIEN SPECIES PERCOLATION INTO FOREST HABITATS

We studied percolation of alien species into forest interiors by comparing mean native species richness and mean alien species richness at the four distances from the edge. We tested for differences using the nonparametric Kruskal-Wallis test ($p \leq 0.01$) for each of the four forest types. We averaged species abundance and canopy cover from the two subplots of 200 m² located at specific distances from the edge into one plot of 400 m² for all our edge-transect data. We used multiple-regression models to determine which factors were most closely associated with native and alien species richness at the plot scale, including distance from the edge, canopy cover (sum of all tree-species canopy cover), elevation, and dominant forest height (the highest from the two subplots). Additionally, we included categorical variables of orientation (N, S, W, E) and forest type as sets of dummy variables. We selected final models through manual entry (all factors) and by removing factors with $p > 0.1$. We evaluated the correlation between native and alien species richness at 200- and 400-m² plots, first considering the complete set of sampling units and later stratifying by distance from the edge.

To determine gradients in community composition and their relationship with distance from the edge and forest type, we performed a DCA ordination of all plots ($n = 60$) and all species present in more than one plot ($n = 60$). One outlier plot was removed in the final DCA model ($n = 59$) because it was located in a forest gap. We plotted the DCA diagrams with plots classified by distance from the edge and forest type to visualize relationships of these variables to axis 1 and axis 2. Using linear-regression models, we tested for correlations between DCA axis 1 and axis 2 and elevation and distance from the edge.

We used multiple regression to evaluate the effects of distance from the edge, elevation, canopy cover, forest dominant height, orientation, and forest type on tree seedlings. We ran these models for total seedling density and for *A. araucana*, *N. dombeyi*, and *N. alpina* seedling densities. We performed regression models and nonparametric statistics using SPSS 10.0.

Results

Roadside Transects

We found 66 alien species in roadsides: 39 were in park transects and 61 were outside parks. Only 5 species were restricted to roadsides inside parks; the other 34 alien species present in the park were a subset of the species in adjacent areas. The 66 species belonged to 26 families. The best-represented families were Poaceae (14), Asteraceae (10), Fabaceae (7), and Scrophulariaceae (4). The most common species, measured by constancy in road transects, were *Hypochaeris radicata* L., *Agrostis*
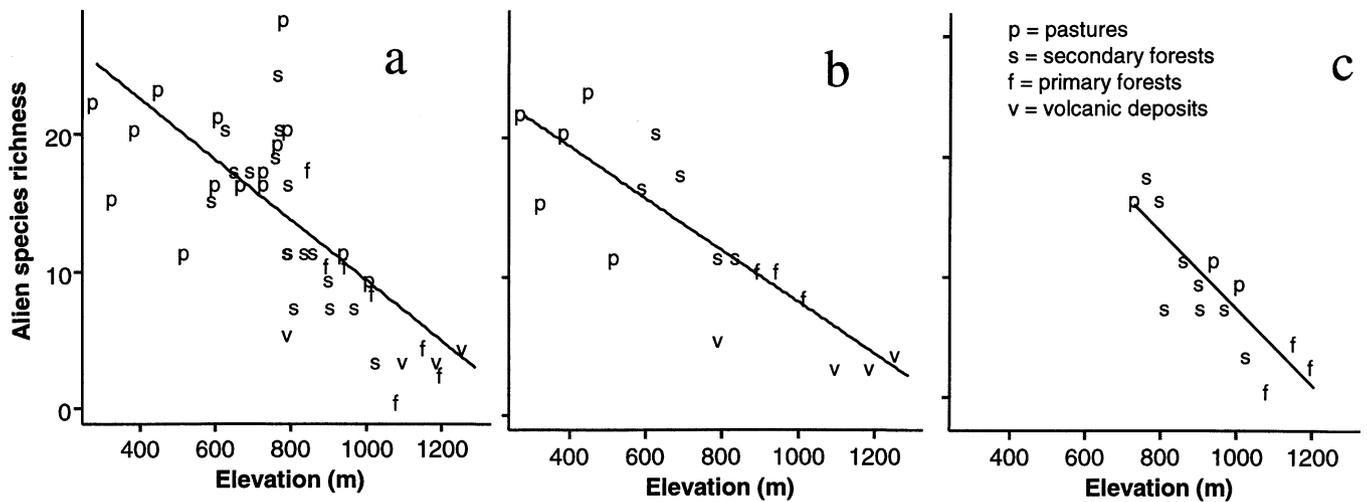
Figure 1. Linear regression of number of alien plant species per roadside transect on elevation: (a) all transects samples (n = 43, r² = 0.539, p < 0.001, constant = 31.46, slope = −0.0221), (b) Rucapillan road (n = 17, r² = 0.716, p < 0.001, constant = 26.88, slope = −0.0187), (c) Chinay road (n = 14, r² = 0.721, p < 0.001, constant = 38.76, slope = −0.0320). Letters indicate land use along roadside.

capillaris L., *Rumex acetosella* L., and *Lotus uliginosus* Schkur. Only five species were classified as abundant in 10 or more transects: *Agrostis capillaris* (19), *Lotus uliginosus* (14), *Hypochaeris radicata* (11), *Holcus lanatus* L. (11), and *Rubus constrictus* Lef & Muell. (10). Of the 66 species, 57 (86%) were native to Eurasia, 4 to North America, and 2 to Australia. Perennial herbs were the most abundant life form, with 23 species (35%). Annuals and woody perennials followed with 18 species each (27%), and 4 biennials accounted for only 6%.

Alien species richness was negatively correlated with elevation along roadsides ($p < 0.001$, $R^2 = -0.552$) (Fig. 1). Two roads in Villarrica National Park (Chinay and Rucapillán) showed a highly significant negative relationship between elevation and alien species richness ($p <$

0.001); the other two roads studied showed no significant trend. Multiple regression showed that elevation, land use, and their interaction were significantly correlated with alien species richness for all transects, explaining 71% of the variation (Table 1). Mean alien species richness for road transects differed significantly with land use. The mean number of species in roadside transects along volcanic deposits (3.75, SE = 0.48) and primary forests (7.29, SE = 2.19) was significantly lower than in pastures (13.24, SE = 1.40) and secondary forests (17.6, SE = 1.30). Roads inside parks had a significantly lower mean number of alien species per transect (approximately 9) than roads in the adjacent matrix (approximately 18) (Fig. 2). This trend also applied to the number of alien species by abundance classes (abundant, common, and intermittent)

Table 1. Regression models for native and alien plant diversity in plots along roadside and road-forest edge transects.*

Dependent variables/factors of variation	R²	Relation	df (no. of variables)	p for the factor	p for the model
Alien spp. richness in roadside transects (*n* = 43)	0.714		35		0.0000
elevation		+		0.1269	
land use		na	(3)	0.0099	
interaction		na	(3)	0.0058	
intercept			(1)	<0.0001	
Native spp. richness in edge plots (*n* = 60)	0.360		54		0.0002
elevation		−		0.0002	
forest type		na	(3)	0.0196	
distance		−	(1)	0.0244	
intercept			(1)	<0.0001	
Alien spp. richness in edge plots (*n* = 60)	0.477		54		0.0000
forest type		na	(3)	0.0159	
canopy cover (%)		−	(1)	0.0025	
elevation		−	(1)	0.0247	
intercept			(1)	0.0032	

Abbreviation: na, relation for a set of dummy variables is not applicable.
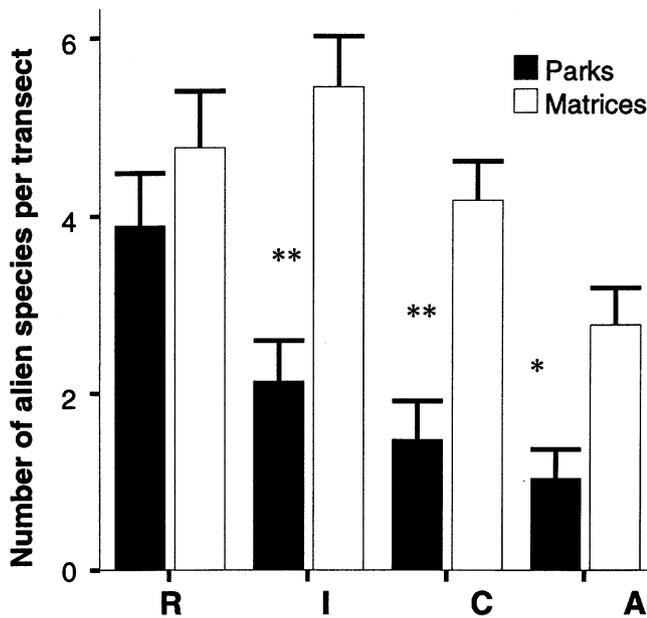
Figure 2. Mean (±SE) number of alien species in transects classified by abundance classes (A, abundant; C, common; I, intermittent; R, rare) and by location (inside parks or matrices). Levels of significant differences based on Kruska-Wallis: *p < 0.05; **p < 0.001. Mean numbers of alien species are 8.52 for parks and 17.09 for matrixes (p < 0.001). Mean elevation for parks is 996 m and for matrixes is 690 m.

Figure 3. Range of elevation for some common alien species on the roadside. Sampling ranged from 284 to 1290 m.

(Fig. 2). The "rare" abundance class was the only one that did not show a significant difference based on landscape context.

Elevational ranges of 45 alien species indicated that the upper limit was restricted to low elevations (<700 m) for only 3 species. For 35 species it occurred between 700 and 1000 m, and for 8 species it occurred at over 1000 m (Fig. 3). Agricultural weeds such as *Lotus uliginosus* and *Dactylis glomerata* L. tended to colonize low to middle elevations. However, species associated with grazing reached higher elevations (e.g., *Hypochaeris radicata* and *Rumex acetosella*). The principal gradient for alien species assemblages, DCA axis 1 (EIG[eigen value] = 0.268), was closely correlated with elevation (R^2 = 0.64, p < 0.001). The DCA axis 2 was not significantly correlated with either elevation or land use. In the ordination diagram, transects appeared weakly clumped by land use (Fig. 4)

Forest-Road Edge Transects

Mean native species richness was not significantly different at four distances from the forest-road edge in any of the forest types. For all plots, however, elevation and distance were negatively correlated with native species richness. The final model including forest type, elevation, and dis-
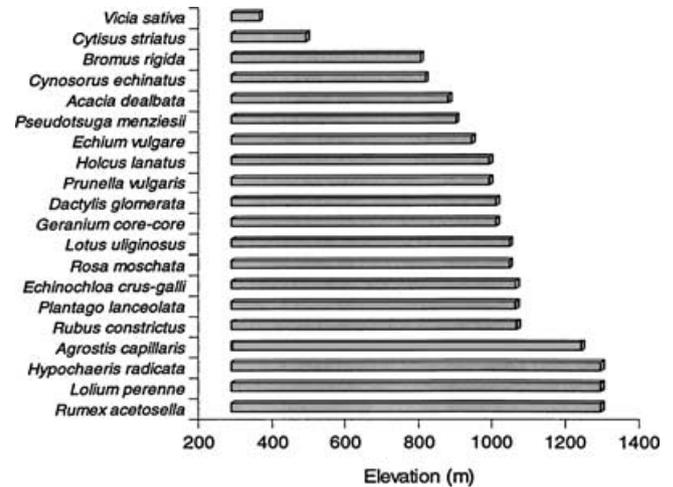
tance explained only 36% of the variation (Table 1). All other variables did not significantly explain residual variation. All 17 alien species found in edge transects were already recorded in roadsides transects. Alien species did not appear in forest interiors in subalpine forest types (*A. araucaria-N. pumilio* and *N. dombeyi-A. araucaria*), and only 1 species occurred at their edges. In the case of *N. alpina* forests, a significantly higher number of alien species occurred in edges than in interiors (p < 0.005). However, there was no significant difference between edges and interiors of *N. dombeyi-N. obliqua* forests. Elevation, canopy cover, and forest type explained 47% of the
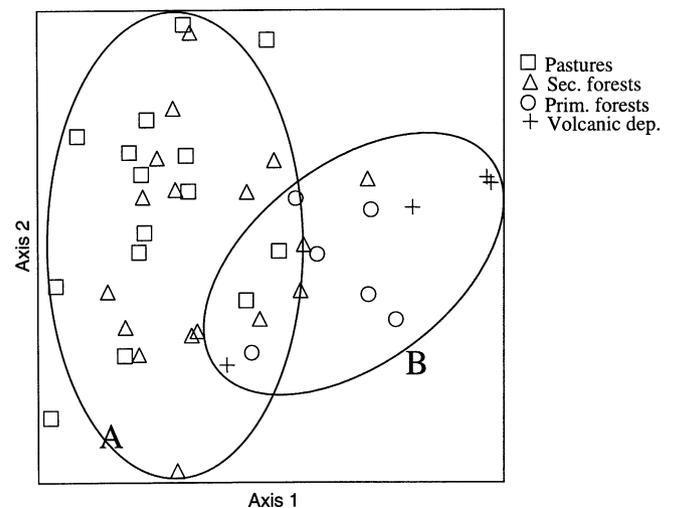

Figure 4. Detrended correspondence analysis (DCA) diagram for roadside transects. Transects are classified by land use. Ellipses show two groups: A, pastures and secondary forests; B, primary forests and volcanic deposits.
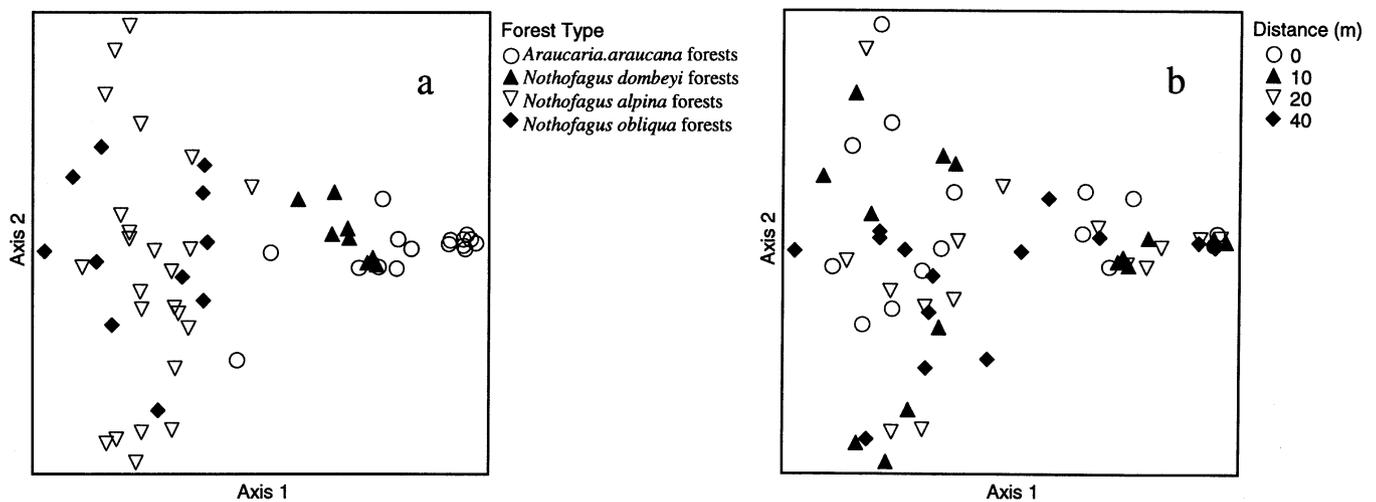
Figure 5. Detrended correspondence analysis (DCA) diagram of forest-road edge plots. Plots classified by (a) forest type and (b) distance from the edge. Axis 1 represents a gradient (a) from low elevation (left) to high elevation (right). Plots near edges tend to occur in the upper section of the diagram (b).

variation in alien species richness (Table 1), and all variables were negatively correlated. We found no significant correlation between alien and native species richness in the 200- or 400-m² plots.

The most significant compositional gradient (DCA axis 1, EIG = 0.884) in forest-road edges was associated with elevation ($R^2 = 0.815$, $p < 0.001$) and forest type, whereas DCA axis 2 (EIG = 0.384) was insignificantly related to environmental factors (Fig. 5). *Araucaria araucaria-N. pumilio* forests appeared clustered, showing little variation in composition. On the other hand, low-elevation forests dominated by *N. dombeyi* or *N. alpina* showed a higher level of variation in their composition. Overall, plots closer to the edge had a higher score in axis 2, especially those located at the edge (Fig. 5). Density of tree

seedlings was not related to distance from edge but was generally associated with forest type (Table 2).

Discussion

Elevation as a Constraint for Alien Species

Elevation is an important indicator of microclimatic variation, which may physiologically constrain alien plant invasion (Forcella & Harvey 1983; Wilson et al. 1992). For example, elevation is the second most important variable, after location, explaining variability in the number of alien species in Rocky Mountain National Park (Chong et al. 2001). Similarly, low-elevation areas are more invaded

Table 2. Regression models for seedling density in edge-transect plots.

Dependent variables/factors of variation	R²	Relation*	df (no. of variables)	p for factor	p for the model
Total seedling density in edge transects (*n* = 60)	0.132		56		0.0462
type		na	(3)	0.0452	
intercept			(1)	0.2606	
Araucaria araucana seedling density in edge transects (*n* = 60)	0.403		56		<0.0001
type		na	(3)	<0.0001	
intercept			(1)	1.0000	
Nothofagus dombeyi seedling density in edge transects (*n* = 60)	0.435		55		<0.0001
type		na	(3)	<0.0001	
dominant height		+	(1)	0.0189	
intercept			(1)	0.0104	
Nothofagus alpina seedling density in edge transects (*n* = 60)	0.372		53		0.0040
type		na	(3)	0.1000	
orientation		na	(3)	0.0221	
intercept			(1)	<0.0001	

*Abbreviation: na, relation for a set of dummy variables is not applicable.

than higher ones in the north-central United States (Stohlgren et al. 2002). In southern Chile, most alien species originated in agricultural systems of Eurasia (Arroyo et al. 2000); therefore, they are adapted to moderate climatic conditions and may lose their competitive advantage at high elevations (Sax & Brown 2000). At higher elevations, energetic limitations may constrain r-strategist species (Grime 1977). In our study, these factors may partially explain the reduction in the richness and abundance of alien species with an increase in elevation. High-elevation areas are the most isolated and distant from weed population centers and have the least vehicular traffic, and thus the lowest propagule pressure.

Anthropogenic land uses of the matrix were clumped at low elevations. Thus, elevation was not only an indicator of microclimate but also indirectly represented the gradient of land use from grazing pastures at low elevations to pristine forests at high elevations. This relationship between elevation and land use occurs worldwide, especially around protected areas, making it difficult to isolate the effect of elevation as a climatic constraint.

Land Use and Landscape Processes

Land use is one of the most influential factors that determine the distribution of alien species (Hobbs 2000; Sax & Brown 2000). Land use directly affects the invasion process because it modifies disturbance regimes and environmental conditions. It can also affect the invasion process by creating sources of propagules in the landscape. Areas with high human intervention, such as agricultural or urban landscapes, serve as sources for invasions into more pristine environments (Tyser & Worley 1992; Hobbs 2000; Parendes & Jones 2000). Propagule pressure from these sources appears the most influential mechanism by which land use affects the abundance and distribution of alien species in our roadsides.

In southern Chile, pastures are a major source of invasions because they are dominated by alien plant species that out-compete native species, which cannot tolerate grazing by cattle (Finckh & Thomas 1997; Scherer & Deil 1997). The species that were more frequent and more abundant in roadsides are reported as dominant in grazed pastures of Villarrica National Park and its surroundings (e.g., *Trifolium repens* L., *Plantago lanceolata* L., *Dactylis glomerata*, *Taraxacum officinale* G.H. Weber ex Wiggers, *Holcus lanatus*, *Rumex acetosella*, *Hypochaeris radicata*, *Agrostis capillaries*, *Poa pratensis* L.) (Finckh & Thomas 1997). In our study sites, cows and horses were probably the main vectors for seed dispersal, bringing alien species propagules to park interiors (personal observation; Malo & Suarez 1995; Matthei 1995; Finckh & Thommas 1997; Arroyo et al. 2000).

Our results suggest that roadsides in secondary forests and agricultural areas have more alien species because of higher propagule flow from surrounding areas, frequent grazing, milder climate associated with lower elevations, and higher sunlight due to open canopies (Wilson et al. 1992; Finckh & Thommas 1997; Milton & Dean 1998; Parendes & Jones 2000). These areas of low elevation are heavily grazed, incorporating new alien species brought in livestock food supplies (Tyser & Worley 1992; Villarrica National Park rangers, personal communication). Low levels of alien species on roadsides in primary forests may be caused by (1) higher elevations, (2) lower light availability due to a closer canopy, (3) low nitrogen mineralization rate due to shady and cool conditions, and (4) a thick litter layer and a low proportion of bare soil, which limit the establishment of invasive species (Myster 1994; Finckh 1996; Parendes & Jones 2000; Mazia et al. 2001). Low soil development and nutrient content may explain the extremely low susceptibility to invasion of roadsides in volcanic deposits, which are barely colonized even at low elevation and areas near pastures. Land use may overcompensate for the effects of elevational gradients on alien species richness. For example, Huerquehue National Park is lower in elevation than the surrounding agricultural fields; therefore, an increasing number of alien species are found at higher elevations outside the park.

Edge Effects

The unpredictability of edge effects on native diversity and seedling density in the four forest types is consistent with the literature (Murcia 1995). Our results may be explained by the high structural diversity of the forests studied. *Araucaria araucana–N. pumilio* forests are usually open and have narrow roads, which may limit edge effects (Finckh 1996). *Nothofagus dombeyi–A. araucana* forests are closed (over 80% canopy cover), and secondary roads only partially disrupt the canopy. Therefore, edge effects are mainly produced by soil disturbance. In lower elevations, *N. alpina* forms closed forests that are affected by wider and more "heavily used" roads, showing significant edge effects. *N. dombeyi–N. obliqua* forests are open communities under intense pressure from grazing and firewood collection, which makes it difficult to isolate the causal variable of species-richness spatial patterns.

The presence of alien species in the interior only of secondary forests may be explained as a combination of the following factors: (1) these forests have colonized areas affected by fire, logging, and grazing, where alien species were abundant but have disappeared as the canopy closed, remaining mostly in sterile forms (Finckh & Thomas 1997); (2) cattle bring propagules from outside sources; and (3) higher light and bare soil exposure favors alien plant establishment (Parendes & Jones 2000).

General Taxonomic and Biogeographical Patterns of Invasion

Even though Villarrica National Park is a moderate- to high-elevation temperate park and has low levels of human disturbance, the number of alien species we

documented suggests a significant alien flora for the park. Considering that Villarrica National Park has approximately 310 native species (Finckh 1996), our results suggest that alien species represent 11.2% of all species (including alien species in roadsides of both Villarrica and Huerquehue national parks). This estimation is conservative because new alien species established in grasslands or forests in boundary areas of the park may have been missed. For Villarrica National Park and surrounding pastures, Finckh and Thomas (1997) estimated that alien species varied from 75% of all species in low-elevation pastures in the matrix to 30% in regenerating shrublands, 7% in forests outside the park, and 0% in forests in the park. In the main recreational area of Conguillio National Park, 100 km north of Villarrica, alien species represent 18% of the flora (Pauchard et al. 2000). Puyehue National Park, 200 km south of our study area, has 12% alien species (Muñoz-Schick 1980, cited in Arroyo et al. 2000). In the highly urban and agricultural central valley, however, 150 km northwest of the study area, alien species account for 45% of the flora of a 60-ha reserve (Hauenstein et al. 1988). A growth in this ratio has been predicted for Chilean protected areas with increasing visitation and horse trekking (Arroyo et al. 2000).

The families Poaceae (21%), Asteraceae (15%), and Fabaceae (11%) comprised 47% of the alien species and are those best represented in alien floras worldwide (Pysek 1998). Surprisingly, Brassicaceae, the fourth most abundant family in global alien floras (Pysek 1998) was not represented. The percentage of Eurasian species in our study sites (85%) was higher but consistent with the ratio for Chile (71.2%) and its central region (74.4%) (Arroyo et al. 2000). This trend toward a high proportion of Eurasian species may change with increasing global dispersion and new introductions of ornamentals (Swenson et al. 1997). We also found a higher proportion of perennials than for Chile overall, perhaps due to the cool, wet climate (Grime 1977; Arroyo et al. 2000).

Management Recommendations

Our results confirm the importance of roads as corridors of plant invasions from disturbed landscape matrices into protected areas in temperate forest regions (Spellerberg 1998; Parendes & Jones 2000; Trombulak & Frissell 2000). Although elevational gradients produce climatic constraints for alien species, sufficient propagule availability allows some species to establish in harsh environmental conditions. Our results also support evidence that roadsides are the first landscape elements to be colonized by alien species and therefore may indicate potential ranges of invasion (Tyser & Worley 1992; Forman & Alexander 1998; Spellerberg 1998; Parendes & Jones 2000; Trombulak & Frissell 2000).

Because propagules disperse from source populations abundant in specific land-use conditions, management of invasive species in protected areas should include both reserve corridors and adjacent matrixes to limit the rate of invasion and new introductions (Tyser & Worley 1992; Parendes & Jones 2000; Pauchard et al. 2003). The increasing rate of development of matrices adjacent to protected areas makes early detection and control of invasive species a priority for conservation both inside and outside parks (Pauchard et al. 2003).

If regional patterns found by Arroyo et al. (2000) apply to a smaller scale, changes in land use and increasing road density may increase the number and impact of alien species in reserves of southern Chile. At present, few species seem to be invading aggressively. However, the increasing rate of introductions and genetic adaptation could change this scenario (Arroyo et al. 2000; Mack et al. 2000). Two groups of concern are conifers and Fabaceae shrubs. *Pseudotsuga mensiezii* (Mirb.) Franco and *Pinus contorta* Dougl. ex Land. have invaded native forest understory in protected areas of the region (Peña & Pauchard 2001). *Citisus scoparius* L. Link and *Ulex europaeus* L., both recognized invaders of temperate climates (Matthei 1995; Bossard et al. 2000), are abundant in low-elevation areas, and populations are establishing around Villarrica National Park.

Specific recommendations for the management of alien species in protected areas of southern Chile should include (1) the complete elimination of cattle grazing in park interiors and boundaries (Finckh & Thomas 1997), (2) impact assessment of road construction and increasing traffic in the dispersion of alien-species propagules (Tyser & Worley 1992; Spellerberg 1998), (3) control of invasive species in the surroundings of the parks before their dispersion (Pauchard et al. 2003), and (4) establishing monitoring plans for alien species to prioritize the control of species with negative effects over those that have no significant impact (Byers et al. 2002; Tyser & Worley 1992).

Acknowledgments

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