CHAPTER 2

ROADS AS DISPERSAL CORRIDORS FOR ALIEN PLANTS IN PROTECTED AREAS OF SOUTH CENTRAL CHILE:

HOW ELEVATION, LANDUSE AND LANDSCAPE CONTEXT INFLUENCE INVASION PATTERNS.

ABSTRACT

Alien plant species are a growing concern for protected areas, yet little information is available on the role of roads as corridors for alien species and the effects of elevation, landuse 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. All alien species and their abundances were sampled along 21 km of roads inside parks and 22 km outside parks, using 500m roadside transects. We also sampled all plant species and abundance in 15 transects located perpendicular to forest-road edges in four forest types. Of the 66 total alien species encountered in roadsides, 61 were present outside parks and 39 inside parks. There was a significant negative correlation between elevation and alien species richness on roadsides ($R^2=0.56$, $p<0.001$). Elevation, landuse 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 a significantly higher number of alien species. We found no significant edge effect on native and alien species richness. Only few alien species percolate into forest interiors. We found no relationship between native and alien diversity in edge plots. Almost half of the alien species belong to 3 families and 85% originated in Eurasia. Our results suggest that alien species are moving into parks along road corridors and that elevation and landuse of the matrix influence these invasion processes. These findings corroborate the importance of early detection and control of invasive species in protected areas, and highlights the importance of considering surrounding matrix landuse in developing conservation strategies for reserves.

INTRODUCTION

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

Landuse, disturbance and climate are driving factors of alien plant invasion (Hobbs 2000, D'Antonio 1999; Lonsdale 1999). In temperate ecosystem, most alien species are invasive in human disturbed landscapes at low elevations mild climate (Hobbs 2000). However, accumulating evidence suggests that high elevation, pristine environments where most protected areas occur (Noss and Cooperrider 1994), can also be susceptible to invasion by alien plants (Stohlgren et al. 1999; Heckman 1999; DeFerrari and Naiman 1994).

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

Roads represent a priority for recognizing patterns of distribution of alien species along disturbed corridors and their potential for invasion into interior habitats (Trombulak and Frissell 2000). This is especially so in protected areas, which often are immersed in a human-disturbed landscape matrix and where ecological effects transgress administrative boundaries (Landres et al. 1998). Additionally, roadsides are useful sites to study the potential range of invaders at high levels of soil disturbance, where climatic conditions and propagule availability are the main constraints (Spellerberg 1998; Milton and Dean 1998; Wilson et al. 1992; Tyser and Worley 1992; D'Antonio et al. 2001).

The South Central Chile region 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 invasions (Armesto et al. 1998; Arroyo et al. 2000; Armesto et al. 2001). Chile has approximately 690 naturalized alien species (15% of total flora); 381 of them occur in humid-seasonal-rainforest of Chile (Arroyo et al. 2000). Protected areas in this region are mostly located at high elevations and therefore do not appear to be significantly threatened by alien plant invasions (Arroyo et al. 2000; Pauchard and Alaback 2002). However, due to the increasing human disturbance and dispersal, alien species are moving from agricultural landscapes to natural environments. At the same time, new sets of species are arriving from overseas, increasing the susceptibility to invasion of the biogeographically isolated temperate forests of Southern Chile (Arroyo et al. 2000).

To better understand the susceptibility to invasion of protected areas it is necessary to understand the role of elevation, landuse and the spatial arrangement of landuse (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 more pristine environments (Cadenasso and Pickett 2001). In this study, we evaluated the influence of elevation, landuse and landscape context on alien species abundance and distribution along roadsides in two representative protected areas in South-Central Chile and their adjacent matrices. We also explored alien species distribution and abundance in park forest-road edges.

Study Sites

The study sites are compromised of two national parks and surrounding matrices, located in the Chilean South-central Andes: Villarrica National Park and Huerquehue National Park.

Villarrica National Park (63,000 ha) is located south of the towns of Pucón and Villarrica and extends to Lanín National Park in Argentina (ca. 39˚W, 71˚S). Elevation ranges between 600 and 3747 m. Three volcanoes shape its geomorphology: Villarrica (2,847 m), one of the most active volcanos in the Southern Andes (Casertano 1963), Quetrupillán (2,382 m) and Lanín (3,747 m). Huerquehue National Park (12,500 ha) is located 30 km north of Villarrica National Park near Caburgua Lake (39˚W, 71˚). This park shares a similar environment and natural history with Villarrica National Park but has been less affected by recent volcanic disturbances.

The climate in these areas is temperate with dry summers and cool and moist winters. Average annual precipitation ranges from 2,500 to 3,500 mm at high elevations. 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). Soil development is less at higher elevations and areas closer to volcanic cones. In lower valleys, deep andisols or "trumaos" with high water retention and drainage represent a rich substrate for plant growth (Frank and Finckh 1997). However, low levels of plant available phosphates may be a constraint for growth in these volcanic soils (Frank and Finckh 1997).

Villarrica National Park and adjacent areas contain a strong elevational gradient of vegetation (Finckh 1996). In lower valleys natural vegetation consists of *Nothofagus dombeyi - Nothofagus obliqua* forests that have been extensively replaced by grazing pastures dominated by alien grasses and forbs. *Nothofagus dombeyi* forests, *Nothofagus alpina* forests, and isolated patches of evergreen rainforests occupy middle elevations (600-1200m). At higher elevations, *Nothofagus pumilio* and *Araucaria araucana* form forest and shrubland. The alpine zone starts around 1200 - 1500 m, and is frequently associated with 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. However, less productive and inaccessible land was not harvested and was set aside for protection in 1940 when Villarrica National Park was created (Finckh 1996). Secondary forests and low elevation pastures are the result of more recent fires (ca. 50 years) and continuous cattle grazing (Finckh and Thomas 1997). Currently, land clearing, firewood cutting, tourism and real estate development are affecting adjacent areas. However, aside from a popular ski development, the park maintains a relatively pristine status crossed only by a few dirt-gravel roads. Huerquehue National Park also covers an isolated area with rugged topography surrounded by private non-industrial agricultural land. There are no roads to the interior of the park, however intense recreation occurs on the park boundary and interior trails.

METHODS

Road Transects

Roadside transects were used to evaluate the influence of elevation, landuse and landscape context on alien species distribution and abundance. We sampled 43 km of road habitat on 3 roads from Villarrica National Park and 1 road from Huerquehue National Park. Elevation of transects ranged from 280 m to 1290 m. All roads were approximately 10 m wide and consist of gravel and natural volcanic substrate. We located roadside transects (500 m in length) starting at each kilometer of road from the park core to the adjacent matrix. Twenty one transects were located inside parks and 22 in their surrounding matrices. Seventeen transects were located in the Pucón entrance of Villarrica National Park (Rucapillán); 14 in the main access road of Villarrica National Park (Chinay); 4 on the international road that crosses Villarrica National Park (Puesco); and 8 in the access road of Huerquehue National Park (Huerquehue). Transects were 5 m wide at each side of the road. In each transect, we recorded all alien species and their abundance on a qualitative scale: A: abundant (>25% of the transect length), C: common (10-25%), I: intermittent when more than one group of individuals was present (<10%), and R: rare when only one group of individuals was found. Alien plant species were considered as those non-native to Chile (sensu Richardson et al. 2000) and confirmed using Matthei (1995) for their taxonomic classification. We recorded for each transect the elevation and landuse in the surrounding matrix using four categories: pastures, secondary forests, primary forests and volcanic deposits. Elevation was recorded using an aneroid altimeter and a topographic map.

Edge transects

Forest-road edges in Villarrica National Park were studied to assess the degree to which alien plant species are percolating into interior habitat and explore the relationship between plant community attributes and the presence and abundance of alien species. A total of 15 edge-transects was established; 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=6), *N. dombeyi- N. obliqua* (n=3). Edge transects were composed of 4 plots of 2 x 20 m and were randomly established in representative forest-road edges. Plots were located at 0, 10, 20 and 40 m from the end of the road surface. Each plot was divided into 2 subplots of 2 x 10 m to increase cover estimation accuracy. In each subplot cover for native and alien species in the understory was recorded, using the Braun-Blanquet cover classes (Mueller-Dombois and Ellemberg 1974). Native taxonomy followed Marticorena and Quezada (1985). In each subplot, as indicators of forest structure, we visually estimated total canopy cover, recorded dominant tree height using a clinometer and counted total tree seedlings by species. Canopy cover was estimated by recording the percentage of the central plot axis that was intercepted by the canopy vertical projection.

Distributional patterns of alien species

To understand the general taxonomic and biogeographical patterns of alien species, a list of all alien species found in the 43 transects was compiled. Species biogeographic origin and life form group (annual, biennial, perennial herb or woody perennial) based on Matthei (1995) was established. Linear regression analysis was used to evaluate the correlation between alien species richness and elevation. The relative significance of elevation, landuse, and their interaction in explaining variation in alien species richness, was evaluated using multiple regression analysis (Ott and Longnecker 2001). The landuse and the interaction landuse-elevation factors were treated as sets of dummy variables (Ott and Longnecker 2001). To test for differences in the mean number of species by landuse type, the Kruskal-Wallis non-parametric test ($p \leq 0.01$) was used, for both the complete model and pairwise comparisons.

The elevational range for species present in at least two transects was determined. For each species, elevation of the lowest and highest transects where the species occurred was plotted. The influence of landscape context (location inside or outside the protected area) on alien species establishment was evaluated by calculating mean species richness for each transect inside and outside parks and testing for differences in abundance categories using the Kruskal-Wallis test ($p \leq 0.01$). To detect gradients in alien species assemblages we ran Detrended Correspondance Analysis (DCA) on transect species-abundance data using PC-ORD 4.0 (Hill and 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 % 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, the relationship of transect scores in DCA axis 1 with elevation and landuse was analyzed. We evaluated elevation with a simple linear regression analysis and included landuse categories as a set of dummy variables (Ott and Longnecker 2001).

Evaluation of alien species percolation into forest habitats

Percolation of alien species into forest interiors was studied by comparing mean native species richness and mean alien species richness at the four distances from the edge, using the non-parametric Kruskal-Wallis test ($p \leq 0.01$). Analyses were run for each of the four forest types. We averaged species abundance and canopy cover from the two subplots of 200 m^2 located at specific distances from the edge into one plot of 400 m^2 for all our edge transect data. Multiple regression models were used to determine which factors were most closely associated with native and alien species richness at the plot scale. Quantitative variables studied were distance from the edge, canopy cover (sum of all tree canopy cover), elevation, dominant forest height (the highest from the two subplots). Additionally, orientation (N, S, W, E) and forest type were included as set of dummy variables. Final models were selected using manual entry (all factors) and removing factors with $p>0.1$. The correlation between native and alien species richness at 200 and 400 m^2 plots was evaluated, considering both the complete set of sampling units and also stratified by distance from the edge. To determine gradients in community composition and their relationship with distance from the edge and forest type, we ran 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 and therefore its composition was affected by higher light availability. DCA diagrams with plots classified by distance from the edge and forest types were plotted to visualize any relationship of these variables with 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.

The effects of distance from the edge, elevation, canopy cover, forest dominant height, orientation and forest types in tree seedlings density were evaluated using multiple regression. We ran these models for total seedling density, and for *A. araucana*, *N. dombeyi*, and *N. alpina* seedling densities. All regression models and non-parametric statistics were performed using SPSS 10.0.

RESULTS

Roadside transects

A total of 66 alien species was found in roadsides, 39 in park transects and 61 outside parks (Table 1). Only five species were restricted to roadsides inside parks. The other 34 alien species present in the park were a subset of the species found in adjacent areas. The 66 species belonged to 26 families. The most 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*, *Agrostis capillaris*, *Rumex acetosella.* and *Lotus uliginosus* (Table 1). Only five species were classified as abundant in 10 or more transects: *Agrostis capillaris* (19), *Lotus uliginosus* (14), *Hypochaeris* radicata (11), *Holcus lanatus* (11), and *Rubus constrictus* (10). Of the 66 species, 57 (86%) were native from Eurasia, 4 from North America and 2 from Australia (Table 1). Perennial herbs were the most abundant life form with 23 species (34.8%). Annuals and woody perennials follow with 18 species each (27.2%) and 4 biennials account for only 6.0%.

Alien species richness was negatively correlated to 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 ($p>0.1$). Multiple regression showed that elevation, landuse and their interaction are significantly correlated to alien species richness for all transects, explaining 71% of the variation (Table 2). Mean alien species richness for road transects differed significantly with landuse. Pastures and secondary forests had the most diverse alien flora (Fig. 2). Roads inside parks had a significant lower mean number of alien species per transect (ca. 9) than roads in the adjacent matrix (ca. 18) (Fig. 3). This trend also applied to the number of alien species by abundance classes (abundant, common and intermediate) (Fig. 2). The only abundance class that did not show a significant difference based on landscape context was “rare”.

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; and for 8 species it occurred over 1000m (Table 1; Fig. 4). Agricultural weeds such as *Lotus uliginosus* and *Dactylis glomerata* tended to colonize low to mid 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=0.268), was closely correlated with elevation (R^2=0.64, p<0.001). DCA axis 2 was not significantly correlated with either elevation or landuse. In the ordination diagram, transects appear weakly clumped by landuse (Fig. 5)

Forest-road edge transects

Mean native species richness was not significantly different at the four distances from the forest-road edge in any of the forest types. However, for all plots, elevation and distance were negatively correlated with native species richness. The final model including type, elevation and distance only explained 36% of the variation (Table 3). All other factors were not significant in explaining residual variation. All 17 alien species found in edge transects were already recorded in roadsides transects (Table 1). Alien species did not appear in forest interiors in both subalpine forest types (*A. araucaria - N. pumilio* and *N. dombeyi – A. araucaria* forests) and only one species occurred in 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 (p>0.1). Elevation, canopy cover and forest type explained 47% of the variation in alien species richness (Table 2) and all variables were negatively correlated. No significant correlation was found between alien and native species richness in the 200 or 400m^2 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 (Fig 6a), while DCA axis 2 (EIG=0.384) was weakly associated with distance from the edge (R^2=0.05, p<0.1) (Fig.

6b). *Araucaria araucaria - N. pumilio* forests appeared clustered showing little variation in composition. On the other hand, low elevation forest 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 axis 2 value, especially those located at the edge (Fig. 6b).

No significant effect of distance from the edge in total tree seedling density was detected ($p>0.1$). *Araucaria araucana* seedling density was positively correlated with elevation (Table 3). *Nothogagus dombeyi* seedling density was correlated with type and positively correlated with height (Table 3). *Nothofagus alpina* seedling density was correlated with forest type and orientation (Table 3). Overall, total seedling density was weakly correlated with type (Table 3).

DISCUSSION

Elevation as a constraint for alien species

Elevation is assumed to be a key factor influencing invasion success worldwide, yet few studies have documented this relationship or tested its generality. Elevation is an important indicator of microclimatic variations, which may physiologically constrain alien plant invasion (Forcella and Harvey 1983; Wilson et al. 1992). For example, Chong et al. (2001) found that elevation is the second most important variable, after location, to explain variability in the number of alien species in Rocky Mountain National Park. Similarly, Stohlgren et al. (2002) found that low elevation areas were more invaded than higher ones in North-central United States.

In Southern Chile, most alien species have originally evolved in agricultural systems in Eurasia (Arroyo et al. 2000); therefore, they are adapted to moderate climatic conditions and may lose their competitive advantage at high elevations (Sax and Brown 2000). High elevation environments also present unpredictable and stressful conditions that may constrain R-strategy species (Grime 1977). These factors may explain, at least partially, the reduction of species richness and abundance with increase in elevation in our study site. However, elevation may also be acting as a physical barrier for alien species dispersal, restraining propagule flow to higher elevations. In our study site, the few alien species found over 1,000 m were “rare”. This suggests that even when climatic conditions are sufficient for the establishment of alien plants, few propagules get dispersed to these higher roadsides or only a small portion of the propagules are successful.

The negative correlation between elevation and alien species richness in our study site supports the hypothesis that elevation is an important constraint to invasion and that alien species tend to concentrate in milder, low elevation environments (Forcella and Harvey 1983). However, the correlation ($R^2=0.492$, $p<0.001$) between elevation and landuse complicates the independent role of each variable. In our study sites, anthropogenic landuses of the matrix tend to be clumped at low elevations. Thus, elevation not only is an indicator of microclimate, but also indirectly represents the gradient of landuse from intense pasture use at low elevations to pristine forests at high elevations. This relationship between elevation and landuse occurs worlwide, especially around protected areas, making it difficult to isolate the effect of elevation as a climatic constraint.

Landuse and landscape processes

Landuse is one of the most influential variables in determining the distribution of alien species worldwide (Hobbs 2000; Sax and Brown 2000). Landuse directly affects the invasion processes by modifying disturbance regimes and environmental conditions. However, it can also influence the invasion process by indirectly creating sources of propagules in the landscape. Areas with higher human intervention, such as agricultural or urban landscapes, serve as sources for invasions into more pristine environments (Hobbs 2000; Parendes and Jones 2000; Tyser and Worley 1992). Propagule pressure from these sources appears as the most influential mechanism by which landuse affects abundance and distribution of alien species in roadsides of our study sites. Consequently, alien species invasions may be responding to the spatial arrangement of landuse. Landscape context explains why park interiors, are less invaded than those located in the human disturbed matrix (Fig. 3).

In southern Chile, pastures are dominated by alien plant species because few native species tolerate grazing by cattle, serving as the main source for invasions (Scherer and Deil 1997; Finckh and Thomas 1997). We found that the species that are more frequent and more abundant in roadsides were reported as dominant in pastures of Villarrica National Park and its surroundings (Finckh and Thomas 1997). This included *Trifolium repens*, *Plantago lanceolata*, *Dactylis glomerata*, *Taraxacum officinale*, *Holcus lanatus*, *Rumex acetosella*, *Hypochaeris radicata*, *Agrostis capillaris* and *Poa pratensis*. Finckh and Thomas (1997) found these species in most pastures in the area of Villarrica National Park, but their abundance was proportional to the degree of grazing. In our study sites, cows and horses are probably the main vectors for seed dispersal, bringing alien species propagules from pastured lands in adjacent matrices to park interiors (Personal observation; Arroyo et al. 2000). Dispersal via cattle dung is predominant for many grasses and herbs with small seeds (e.g. *Agrostis* spp. *Bromus* spp., *Rumex acetosella*, *Trifolium* spp.) including exozoochorous species like *Lotus uliginosus*, and anemochorous species like *Cirsium vulgare*, *Hypochaeris radicata* and *Taraxacum officinale* (Malo and Suarez 1995, Matthei 1995, Finckh and Thommas 1997).

Our results suggest that roadsides in secondary forests and agricultural areas have higher alien species due to the higher propagule flow from surrounding areas, frequent grazing, milder climate associated with lower elevations, and higher sunlight due to open canopies (Milton and Dean 1998, Finckh and Thommas 1997, Wilson et al. 1992, Parendes and Jones 2000). In addition, secondary forests occur in areas that previously have been clearcut and used as pastures. Thus, some species may still remain in the seedbank and are establishing themselves given the adequate soil disturbance and light levels (Finckh and Thomas 1997, Holmes et al. 1997). These low elevation areas are heavily grazed, incorporating new alien species brought in livestock food supplies (Park rangers personal communication; Tyser and Worley 1992). Low levels of alien species on roadsides in primary forests may be caused by lower light availability due to a closer canopy and because these forest are now restricted only to higher elevations (Parendes and Jones 2000; Finckh 1996). Soils in primary forests have a low nitrogen mineralization rate due to shady-cool conditions, which may be an additional constraint for the establishment of agricultural weeds adapted to high nutrient levels (Scherer-Lorenzen et al. 2000). Finally, a thick litter layer and a low proportion of bare soil may limit the establishment of invasive species (Mazia et al. 2001, Myster 1994). 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 close to pastures. Our results indicate that landuse may overcompensate for the effects of elevation gradients in alien species richness. For example, Huerquehue National Park is located in a lower elevation site surrounded by agricultural fields, which translates into an increasing number of alien species in higher elevations outside the park.

Edge effects

The inconsistency of edge effects on native plant diversity and seedling density in the four forest types studied is similar to other edge studies reported in the literature (Murcia 1995). Our results may be explained by the high structural diversity of the forests studied. *Araucaria araucana - N. pumilio* forest are usually open with narrow roads, which may explain the lack of an edge-effect (Finckh 1996). *Nothofagus dombeyi - A. araucana* are closed forests (over 80% canopy cover) and secondary roads only partially disrupt the canopy; therefore, edge effects are due to changes in soil disturbance but not in light availability. In lower elevations, *N. alpina* forms closed forests that are affected by wider and more “heavily used” roads, showing significant edge effects. Finally, *N. dombeyi- N. obliqua* forests are open communities under intense pressure for grazing and firewood, which makes it difficult to isolate the causal variable of species richness spatial patterns.

While roadsides represent a continuously disturbed environment ideal for alien plant colonization, the conditions in interior forested habitats represent a much higher challenge (Cadenasso and Pickett 2001; Honnay et al. 2002). Nonetheless, our results for Villarrica National Park showed that elevation, type and canopy cover explain the distribution of alien species more precisely than distance from the edge**.** As found for roadsides, the strong elevational and landuse gradients appeared as the driving factors for alien species richness in forest-road edges (Table 2). The presence of alien species in the interior of secondary forests may be explained as a combination of the following factors: 1) these forest have reclaimed open areas affected by fire and clearcuts, therefore while most alien species quickly disappear as the canopy closed, some still remain mainly in sterile forms (Finckh and Thomas 1997), 2) dispersion by cattle still occurs in these areas, bringing propagules from outside sources, and 3) higher light and bare soil in these younger and more disturbed forests favors alien plant establishment (Parendes and 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 documented in this study suggest a significant alien flora for the park. Villarrica National Park has approximately 310 species of native plants (Finckh 1996). Our results suggest an alien/total species ratio of 11.2%, considering both alien species in roadsides of Villarrica and Huerquehue National Parks. The estimation is conservative because even though most alien species tend to appear first in roadsides, additional alien species could be established in grasslands or forests in boundary areas of the park. For Villarrica National Park and surrounding pastures, Finckh and Thomas (1997) estimated an alien/total species proportion that varied from 75% in low elevation pastures in the matrix, around 30% in regenerating shrublands to 7% in forests outside the park and 0% in forests in the park. Pauchard et al. (2000) found an alien/total species ratio of 18% in the main recreational area of Conguillio National Park, located 100 km north from Villarrica. Muñoz-Schick (1980 in Arroyo et al. 2000) found 12 percent of alien species for Puyehue National Park, which is 200 km south of our study area. However in the highly urban and agricultural central valley, 150 km northwest from Villarrica National Park, alien species account for 45% of the total flora of an small 60 ha reserve (Hauenstein et al. 1988). Arroyo et al. (2000) predicted a growth in the ratio of alien species in Chilean protected areas with increasing visitors and horse trekking.

The families Poaceae (21%), Asteraceae (15%), Fabaceae (11%) accounted for 47% of the alien species. Pysek (1998) found that these families are the most represented in alien floras worldwide. 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%) is higher but consistent with the ratio for Chile (71.2%) and for the central region (74.4%) (Arroyo et al. 2000). However, this is much higher than the worldwide average of 59% (Pysek 1998). Most species in our sites are natives to European grasslands and probably were introduced to Chile before the 1900s (Finckh and Thomas 1997). For example, 11 Eurasian species are common both in our study sites and in roads and streams of the Cascade Range in Oregon, USA (Parendes and Jones 2000). Certainly this trend toward a high proportion of Eurasian species may change with increasing global dispersion and new “exotic” introductions of ornamentals (Swenson et al. 1998). We also found a higher proportion of woody perennials compared to the 14.1% for the Chilean alien flora (Arroyo et al. 2000). The high rainfall of the area may favor woody species over annuals. Additionally, the shorter growing season may also provide an advantage for those perennial alien species (34.8%) over annuals (27.2%), differing from the overall Chilean pattern where annuals account for 50.9% and perennial for 37.5% (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; Trombulak and Frissell 2000; Parendes and Jones 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 their potential ranges of invasion (Spellerberg 1998; Trombulak and Frissell 2000; Parendes and Jones 2000, Tyser and Worley 1992, Forman and Alexander 1998).

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

If regional patterns applied to a smaller scale, the increasing changes in landuse and increasing road density may increase the number and the impact of alien species in reserves of Southern Chile (Arroyo et al. 2000). At present, few species are aggressively invading. 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* and *Pinus contorta* has been reported as invading native forest understory in protected areas of the region (Peña and Pauchard 2002). *Citisus scoparius* and *Ulex europaeus*, 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 management recommendations for protected areas in southern Chile should include 1) the complete elimination of cattle grazing in park interiors and boundaries (Finckh and Thomas 1997), 2) impact assessment of road construction and increasing traffic in the dispersion of alien species propagules (Spellerberg 1998, Tyser and Worley 1992), 3) control of invasive species in the surroundings of the parks before their dispersion (Chapters 4 and 6) 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 and Worley 1992).

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Table 1. Alien species for the study areas. LF: life form (W: woody, P: perennial herb, B: Biannual, A: annual). * Species occurring in roadside transects inside parks (P) or forest-road edge transects (E). Constancy indicates the number of roadside transects were the species was found. Habitat: 1) low elevation, 2) low-middle elevation, 3) high elevation. Continental origin, AU: Australia, E: Eurasia, NA: North America.

Species	Family	LF	P	E	Constancy	Habitat	Origin
Acacia dealbata	Fabaceae	W	*		4	2	AU
Acer platanoides	Aceraceae	W			1		E
Achillea millefolium	Asteraceae	P	*		5	3	E
Agrostis capillaris	Poaceae	P	*	*	38	3	E
Anagallis arvensis	Primulaceae	A			1		E
Arrhenatherum elatius ssp. bulbosus	Poaceae	P			5	2	E
Asteracea	Asteraceae		*		1		-
Asteracea	Asteraceae				1		-
Asteracea	Asteraceae				1		-
Briza minor	Poaceae	A			4	1	E
Bromus hordeaceus	Poaceae	A	*	*	20	2	E
Bromus rigida	Poaceae	A			7	2	E
Castanea sativa	Castanaceae	W			1		E
Cerastium arvensis	Cerastaceae	P	*		5	3	E
Cirsium vulgare	Asteraceae	A	*	*	22	2	E
Crepis capillaris	Asteraceae	A	*		8	2	E
Cupressus macrocarpa	Cupressaceae	W			1		E
Cynosorus echinatus	Poaceae	A			6	2	E
Cytisus striatus	Fabaceae	W			3	1	E
Dactylis glomerata	Poaceae	P	*	*	18	2	E
Daucus carota	Apiaceae	A			1		E
Dichondra sericea	Convulvalaceae	P	*		6	2	E
Digitalis purpurea	Scrophulariaceae	B	*		10	2	E
Echinochloa crus-galli	Poaceae	A	*		8	2	E
Echium vulgare	Boraginaceae	B	*		10	2	E
Eucalyptus nitens	Myrtaceae	W			1		AU
Festuca arundinacea	Poaceae	P		*	1		E
Foenicum vulgare	Apiaceae	P			1		E
Geranium core-core	Geraniaceae	P	*	*	11	2	E
Hedera helix	Araliaceae	W			1		E
Holcus lanatus	Poaceae	A	*	*	24	2	E
Hypericum perforatum	Hypericaceae	W	*	*	10	2	E
Hypochaeris radicata	Asteraceae	P	*		39	3	E
Leucanthemum vulgare	Asteraceae	P	*		1		E
Lolium perenne	Poaceae	P	*		3	3	E
Lotus uliginosus	Fabaceae	A	*	*	33	2	E
Melissa officinalis	Lamiaceae	P	*		2	2	E
Mentha pulegium	Lamiaceae	P			1		E
Myosotis arvensis	Boraginaceae	B			1		E
Panicum capillare	Poaceae	A	*		3	2	NA
Parentucellia viscosa	Scrophulariaceae	A	*		1		E
Pinus radiata	Pinaceae	W			1		NA
Plantago lanceolata	Plantiginaceae	P	*		26	2	E
Plantago major	Plantiginaceae	P			2	2	E
Polygonum persicaria	Polygonaceae	A	*		2	2	E
Polypogon monspeliensis	Poaceae	A	*		5	2	E

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Species	Family	LF	P	E	Constancy	Habitat	Origin
Populus alba	Populaceae	W			1		E
Prumnus avium	Prumnaceae	W	*	*	4	2	E
Prunella vulgaris	Lamiaceae	P	*	*	28	2	E
Pseudotsuga menziesii	Pinaceae	W	*		5	2	NA
Rosa moschata	Rosaceae	W	*	*	23	2	E
Rosa vulgaris	Rosaceae	W			1		E
Rubus constrictus	Rubiacea	W	*	*	25	2	E
Rubus radicans	Rubiacea	W			2	2	E
Rumex acetosella	Rumeaceae	P	*	*	34	3	E
Rumex crispus	Rumeaceae	P			2	2	E
Sonchus asper	Asteraceae	A	*		5	2	E
Symphorocarpus albus	Caprifoliaceae	W			1		NA
Taraxacum officinale	Asteraceae	P	*	*	20	2	E
Trifolium pratensis	Fabaceae	P	*		15	2	E
Trifolium repens	Fabaceae	P	*	*	18	2	E
Triticum aestivum	Poaceae	A	*	*	2	2	E
Ulex europaeus	Fabaceae	W			2	2	E
Verbascum thapsus	Scrophulariaceae	B	*		8	2	E
Veronica cf. anagallis-aquatica	Scrophulariaceae	P	*		1		E
Vicia sativa	Fabaceae	A			2	1	E

Table 2. Regression models for native and alien diversity in plots along roadside and road-forest edge transects in Villarrica National Park. Relation for a set of dummy variables is non-applicable (NA).

Dependent variables/ Factors of variation	R^2	Relation +/-	df/ (variables)	p for the factor	p
a) 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	
b) Native spp richness in edge plots (n=60)	0.360		54		0.0002
Elevation		-		0.0002	
Type		NA	(3)	0.0196	
Distance		-	(1)	0.0244	
Intercept			(1)	<0.0001	
c) Alien spp. richness in edge plots (n=60)	0.477		54		0.0000
Type		NA	(3)	0.0159	
% Canopy cover		-	(1)	0.0025	
Elevation		-	(1)	0.0247	
Intercept			(1)	0.0032	

Table 3. Regression models for seedling density in edge-transect plots. Relation for a set of dummy variables is non-applicable (NA).

Dependent variables/ Factors of variation	R^2	Relation +/-	df/ variables	P for the factor	P for the model
a) Total seedling density in edge transects (n=60)	0.132		56		0.0462
Type		NA	(3)	0.0452	
Intercept			(1)	0.2606	
b) *Araucaria araucana* seedling density in edge transects (n=60)	0.403		56		<0.0001
Type		NA	(3)	<0.0001	
Intercept			(1)	1.0000	
c) *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	
d) *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	

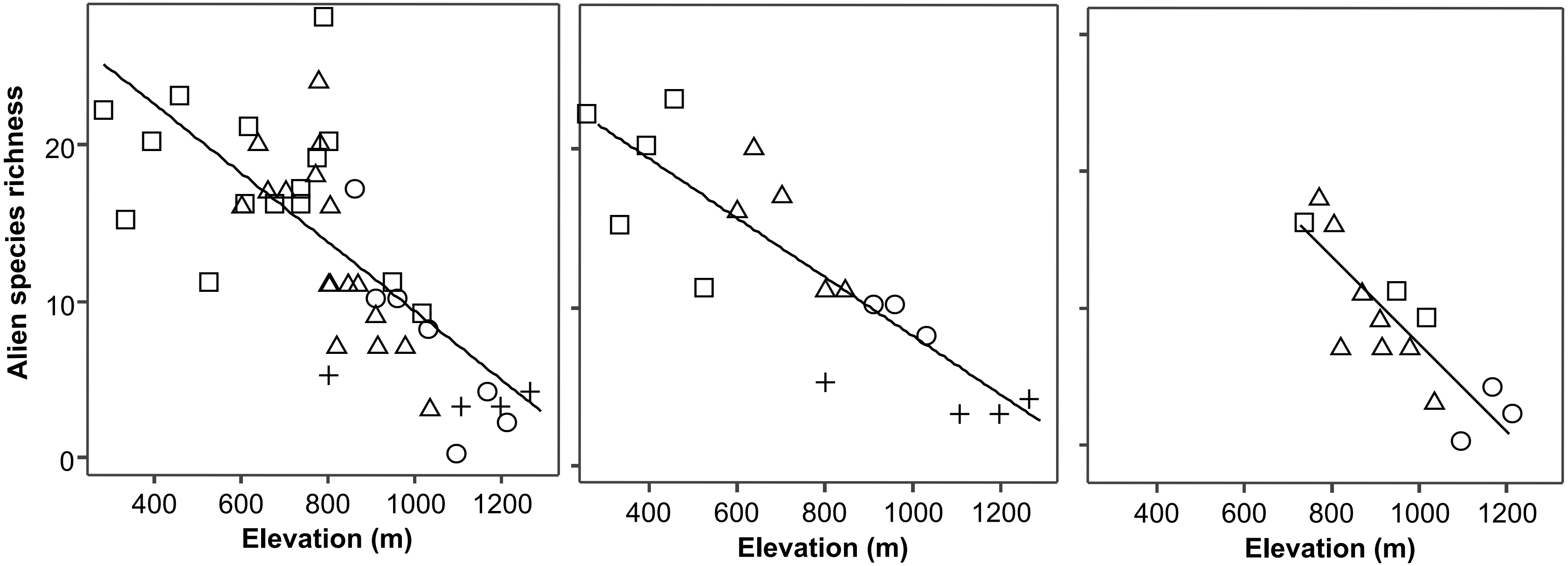

Fig. 1. Linear regression of number of alien species per roadside transect on elevation. A) All transects sampled (n=43, r2=0.539, p<0.001, constant=31.46, slope=-0.0221), B) Rucapillan road (n=17, r2=0.716, p<0.001, constant=26.88, slope=-0.0187), C) Chinay road (n=14, r2=0.721, p<0.001, constant=38.76, slope=-0.0320). Symbols indicate land-use of the surrounding matrix. Land-use: +=Volcanic deposits, o=primary forests, △ =secondary forests and □ =pastures.

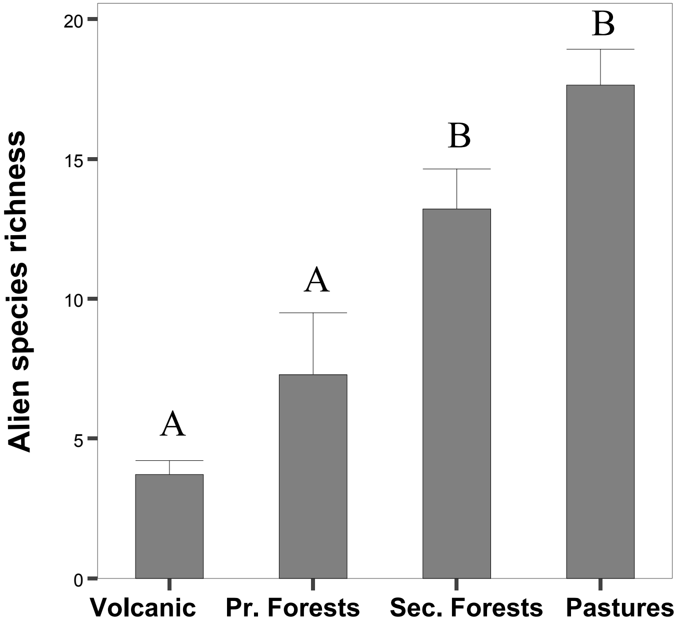

Fig. 2. Mean (+SE) of alien species in transects classified by land use and ordered by mean number of species. Groups with different letters are significantly different using Kruskal-Wallis ($p<0.05$). Overall model has a $p<0.001$.

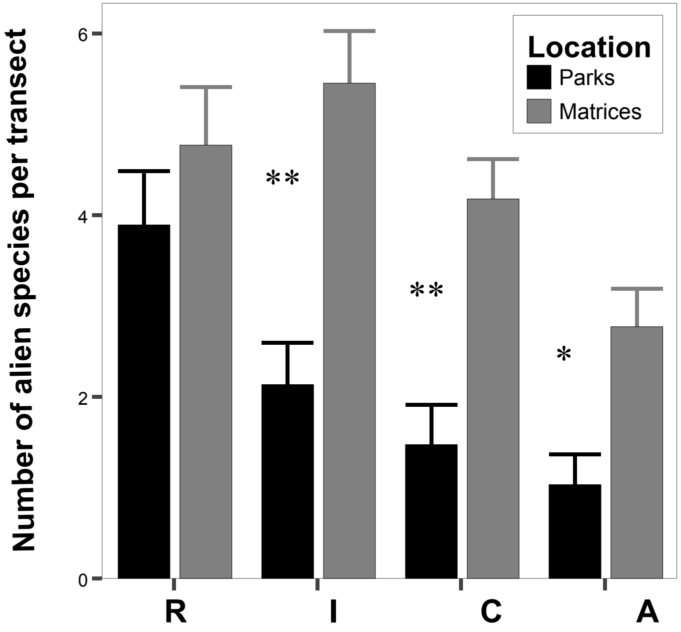

Fig. 3. Mean (+SE) number of alien species in transects classified by abundance classes (A: Abundant, C: Common, I: Intermediate, R: Rare) and by location (inside parks or matrixes). Levels of significant differences using Kruskal-Wallis: *=$p<0.05$, **=$p<0.001$, #=not significant. Symbols indicate differences due to location for each abundance class. Totals are 8.52 for parks and 17.09 for matrixes ($p<0.001$). Mean elevation for parks is 996 m and for matrixes 690 m.

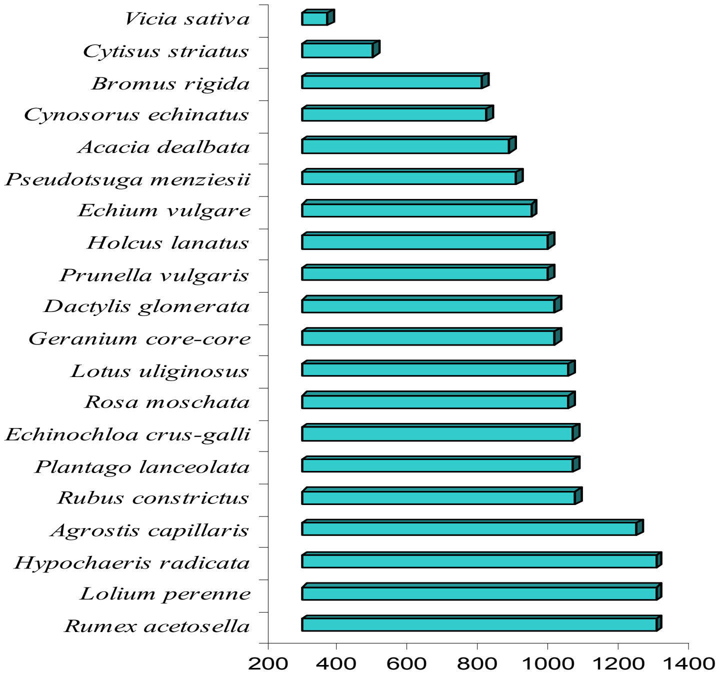

Fig. 4. Range of elevation for some common alien species on roadsides. Sampling ranges from 284 m to 1290 m.

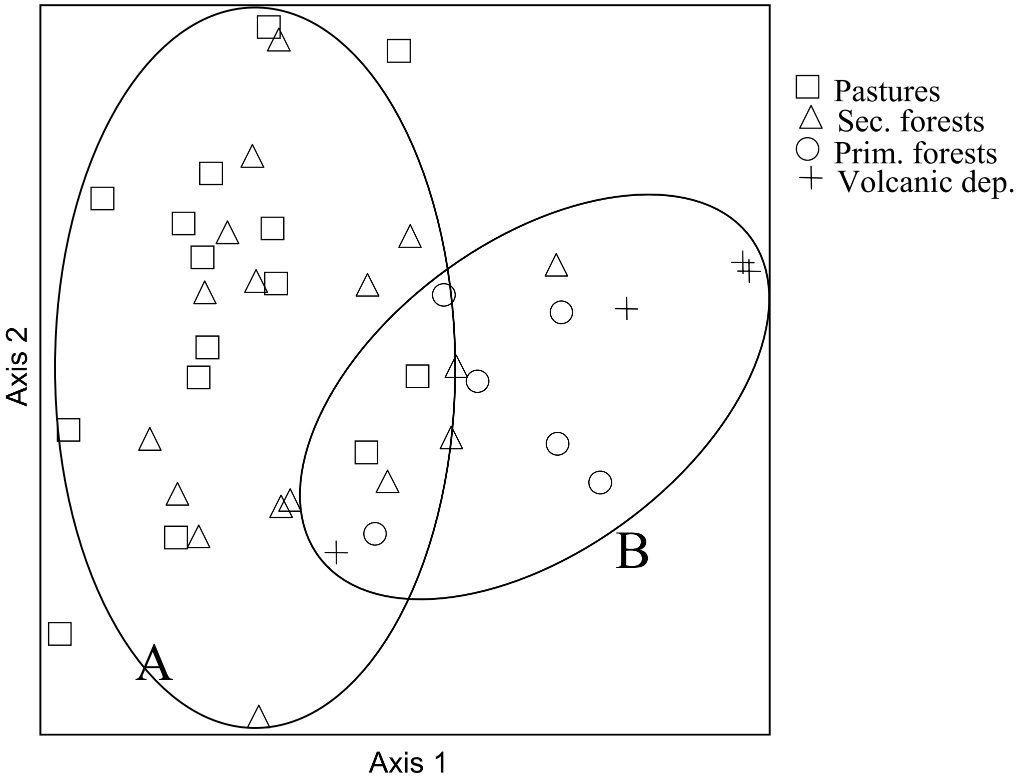

Fig. 5. DCA diagram for roadside transects. Transects are classified by landuse. Ellipses show two groups A: pastures and secondary forests, and B: primary forests and volcanic deposits.

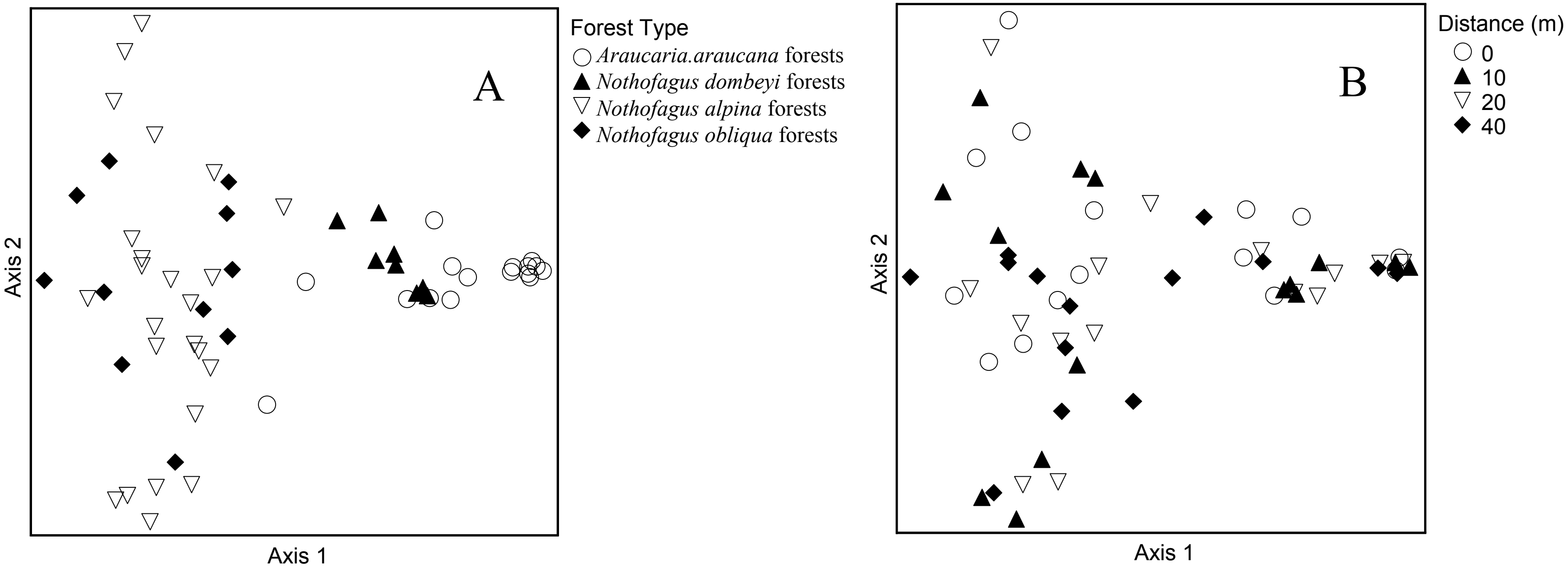

Fig. 6. DCA diagram of forest-road edge plots. Plots classified by A) forest type and B) distance from the edge. Axis 1 represents a gradient from low (left) to high (right) elevation (A). Plots near edges tend to occur in the upper section of the diagram (B).