

Low vegetation recovery after short-term cattle exclusion on Robinson Crusoe Island

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Abstract

Livestock browsing and grazing are considered serious threats to the conservation of the Juan Fernández Islands' flora, Chile. Nowadays the elimination of grazing by cattle is very difficult. In order to prevent the entrance of cattle into the native forests, an 8.3 km-long fence was established on the main island (Robinson Crusoe). The response of the vegetation was evaluated during 27 months of exclusion. The changes in abundances and composition of species were monitored in 12 permanent plots, each of 25 m², located in ungrazed and grazed areas. We expected an increase in plant height and total ground cover in the ungrazed area, and also a directional compositional change towards forest species. We found five different patterns of variation or non-variation for the 22 species observed: (i) one species (*Acaena argentea*) diminished in abundance in the ungrazed area; (ii) another one (*Conium maculatum*) increased in the ungrazed area; (iii) one species (*Vulpia bromoides*) increased in the grazing area; and some species displayed no net variation, but they showed (iv) a nearly constant occurrence, or (v) they appeared and disappeared sporadically. Contrary to our hypothesis, the vegetation showed no net differences in cover on both sides of the fence. As expected, plant height increased in the ungrazed area. In this area, we detected no noteworthy changes in floristic composition towards forest species. On the contrary, four new pastureland species appeared outside of the exclusion area during the last year of evaluation. Other ungrazed sectors of the island showed qualitative differences from grazed sectors, such as major height and density of plants, and lower intensity of browsing, grazing, and trampling, attributable to a reduction of herbivorous pressure. The modest responses reported in this study could be related to the short lapse of time since the exclusion, soil compaction, overgrowth by a single species (*A. argentea*), great seasonal variations in different species' abundances, the reduction in the number of cattle grazing the area previous to the fence's installation, and persistent herbivory by rabbits (*Oryctolagus cuniculus* L.). We conclude that the effect of grazing by cattle is less than expected, and that there are other factors that delay the recovery of the Juan Fernández pasturelands.

Introduction

Livestock can change the composition, structure, and dynamics of entire communities through the inhibition of species recruitment, which strongly

affects the probability of survival of endangered taxa (Huntly 1991; Henríquez and Simonetti 2001). Furthermore, a long-term livestock grazing reduces plant genetic diversity (Aguar et al. 2001), produces changes in floristic richness and diversity

(Huntly 1991; Márquez et al. 2002; Nai-Bregaglio et al. 2002) and, moreover, decreases mycorrhizal colonization (Grigera et al. 2001). Other authors have also documented alterations in the species composition of the associated avifauna (Rey et al. 2001), as well as a reduction in the magnitude of some interspecific interactions (Cipriotti and Aguiar 2001). These effects are likely compounded by those produced by other herbivores, such as rabbits (Acevedo 1990).

The aforementioned phenomena are likely to be exacerbated on oceanic islands that have undergone the introduction of exotic domestic and wild animals, to whose negative effects plants are poorly adapted (Crawford et al. 1987; Sanders et al. 1987; Jaksic 1998). The native flora of oceanic islands is particularly remarkable, due to its long periods of evolution in the absence of negative biotic interactions, which results in flora with lower incidence of thorns (Sun et al. 1996) and stinging hairs (Stuessy 1992), in comparison to its continental relatives (Dirnböck et al. 2003). Examples of these issues are documented for the Galápagos Islands (Rodríguez 1993), New Zealand (Porteous 1993), and the Juan Fernández Islands (Skottsberg 1953). Even worse, the circumstances are more serious when the ecosystems contain unique biological resources, as is the case with these examples. For instance, since its discovery about four centuries ago, the Juan Fernández archipelago (Chile) has suffered the introduction of goats, pigs, dogs, cats, rabbits, coatimundis, and rats, among other mammals, as well as many exotic plant species (Cuevas and van Leersum 2001; Cuevas et al. 2004). In addition, a great portion of these islands' lowlands was transformed to pastures for raising livestock (cattle, sheep, and horses). Although ranching is not allowed inside Juan Fernández National Park, the two main islands (Robinson Crusoe and Alejandro Selkirk) support a population of cattle and horses close to 300 individuals. The livestock carrying capacity is largely exceeded on the Robinson Crusoe pasturelands (IREN-CORFO 1982). As a consequence of impacts by cattle and other herbivores, the grasslands have suffered a gradual impoverishment (illustrated by a reduction of total biomass and of palatable species), resulting in severe soil erosion (IREN-CORFO 1982) and deficient cattle quality. Most of this evidence is purely observational, but even so, the Park

authorities have insisted on the elimination of grazing by cattle (see Discussion). Given the unfeasibility of this solution, the Chilean Forest Service (Corporación Nacional Forestal -CONAF) established a fence (total length: 8286 m) along the lower boundary of Robinson Crusoe Island's forests in order to prevent entry by cattle and, consequently, the browsing of seedlings. This step is fully justified since the forests' vegetation consists of between 57 and 95% native or endemic plants, while anthropogenic pasturelands' vegetation consists of between 71 and 94% exotic plants, depending on the locality (Cuevas, unpublished data). Other exclusions, not included in this study, were established on Alejandro Selkirk Island.

The aim of this study is to assess whether plant communities exhibit successional changes in response to cattle exclusion. After the exclusion of cattle, several variables are expected to recover, for example, floristic richness, genetic and floristic diversity, biomass, nutrient cycles, etc. (Huntly 1991; Aguiar et al. 2001). We studied some simple variables as plant height and total vegetation cover, which we expected would increase in the ungrazed area. Moreover, we expected to observe a directional change in species composition towards species typical of the adjacent forest in the ungrazed area. In other words, we expected that there would be a reversal in the direction of the changes generated by the pressure of grazing by cattle. However, the rate of change can be foreseen to be delayed due to the particular traits of the islands' flora.

Finally, we attempt to collect new evidence in favor of, or against, the elimination of grazing by cattle and the establishment of fences for the exclusion of domestic animals. The present study links applied and basic science, with the aim of filling a gap in our scanty knowledge of the ecology of the Juan Fernández Islands.

Methods

Study area

The Juan Fernández Islands are widely recognized as one of the most important centers of plant endemism in the world (Hulm and Thorsell 1995), with 62.1% of their flora being endemic to the islands (Marticorena et al. 1998). The islands are

inhabited by 131 species, 12 genera, and one family endemic to the archipelago (Marticorena et al. 1998). The origin, mode of evolution and identity of these taxa are also very particular (Lammers et al. 1986; Sanders et al. 1987; Valdebenito et al. 1990).

The Juan Fernández archipelago consists of three islands located between 670 and 860 km from the Chilean coast, in the Southeast Pacific. The two main islands, Robinson Crusoe and Alejandro Selkirk (47.9 and 49.5 km², respectively), are inhabited by domestic animals. The study was carried out in the Puerto Inglés watershed, on Robinson Crusoe Island, at a site situated at 33° 37' 37.1" S-78° 51' 27.1" W and at 210 m a.s.l. The terrain exhibits a slope of approximately 9° (Figure 1).

The climate of the Juan Fernández archipelago, according to Köppen, is Csb, temperate-warm and humid, with a short and relatively dry summer (Marzol et al. 1996-1997). The maritime influence is intense. In San Juan Bautista village, 3 km from the study site, the mean annual temperature recorded at 30 m a.s.l. is 15.3 °C and the mean annual precipitation is around 1150 mm (di Castri and Hajek 1976). Almost half of the rainfall (44%)

occurs in winter (May to August), whereas 9% occurs in summer (November to February) (Marzol et al. 2001).

On both sides of the exclusion fence, the flora is characterized by a deep accumulation of biomass, almost totally represented by *Acaena argentea* Ruiz et Pavón (Table 1, nomenclature after Marticorena et al. 1998). These pasturelands were created by direct and indirect human action, namely, logging, fires, cattle raising, and grazing by herbivores (Stuessy et al. 1998). The original forests extended to the seashores, 200-300 m below the present forest boundaries (Walter and Robins 1748).

The neighboring forest consists of arboreal endemic elements (*Myrceugenia fernandeziana* (Hook. et Arn.) Johow, *Boehmeria excelsa* (Bertero ex Steud.) Wedd., *Drimys confertifolia* Phil., *Fagara mayu* (Bertero ex Colla) Engler and *Rhaphithamnus venustus* (Phil.) B.L. Rob.), and alien species such as *Aristotelia chilensis*. This is the assemblage that we would expect to invade the non-grazed area. Most trees are endozoochorous, with the exception of *B. excelsa* (anemochorous) and *F. mayu* (barochorous) (Vargas 2004). There



Figure 1. Fence established for cattle exclusion at the beginning of year 2000, located in Puerto Inglés, Robinson Crusoe Island.

Table 1. Species composition of the study site on the Robinson Crusoe Island from March 2000 to June 2002.

Species	Family	Life cycle ^a
<i>Acaena argentea</i> Ruiz et Pavón	Rosaceae	P
<i>Anthoxanthum odoratum</i> L.	Poaceae	P
<i>Aristotelia chilensis</i> (Molina) Stuntz	Elaeocarpaceae	P
<i>Blechnum hastatum</i> Kaulf.	Blechnaceae	P
<i>Bromus stamineus</i> E. Desv.	Poaceae	P
<i>Conium maculatum</i> L.	Umbelliferae	AB
<i>Euphorbia peplus</i> L.	Euphorbiaceae	A
<i>Galium aparine</i> L.	Rubiaceae	A
<i>Geranium core-core</i> Steud.	Geraniaceae	P
<i>Juncus imbricatus</i> Laharpe	Juncaceae	P
<i>Oxalis corniculata</i> L.	Oxalidaceae	P
<i>Poa annua</i> L.	Poaceae	A
<i>Polypogon australis</i> Brongn.	Poaceae	P
<i>Rubus ulmifolius</i> Schott	Rosaceae	P
<i>Rumex acetosella</i> L.	Polygonaceae	P
<i>Rumex conglomeratus</i> Murray	Polygonaceae	P
<i>Silybum marianum</i> (L.) Gaertn.	Asteraceae	A
<i>Sonchus asper</i> (L.) J. Hill	Asteraceae	AB
<i>Ugni molinae</i> Turcz.	Myrtaceae	P
Unidentified dicot		
<i>Veronica persica</i> Poir.	Scrophulariaceae	A
<i>Vulpia bromoides</i> (L.) Gray	Poaceae	A

^a Symbology: P, perennial; A, annual; B, biennial (Matthei 1995; Marticorena et al. 1998).

are also endemic understory species (e.g., the ferns *Arthropteris altescandens* (Colla) J. Sm., *Rumohra berteroaana* (Colla) R.A. Rodr., and *Pteris berteroaana* J. Agardh), which are anemochorous. They would also be expected to be possible invaders, provided the canopy is relatively closed. Other endozoochorous species that are common in the area are *Rubus* and *Ugni*. In all, the only species that could have a limited potential for dispersal is *Fagara*, but the distance between forest and non-grazed plots is only 13 m (Figure 2).

Plot demarcation

The minimal sampling area was defined using the nested plot method (Mueller-Dombois and Ellenberg 1974). Most pastureland species were found to be contained in plots of only 4 m². However, to count with more sampling points, plots of 25 m² (5 m×5 m) were established. Cattle exclusion consisted of linear fences placed near the forest boundary. In some cases, the ungrazed side of the fence was merely forest, in other cases pasture-

lands were inside the ungrazed area, while the grazed side of the fence always corresponded to pasturelands (Figure 2). The plots were assigned to the following locations: three plots in the ungrazed area and three outside the fence (grazed area). These six plots were called “experimental plots”. Given that the expected differences in dynamics between these groups could be caused by factors independent from the fencing effect, it was necessary to demonstrate the absence of differences if both groups would be outside the fence. Therefore, we located two additional plot groups in the same way, but all in the grazing area (Figure 2). In other words, the vegetation changes would be interpreted to be attributable solely to the fencing effect if both reference plots, called “Near the fence” and “Far from the fence”, showed no differences.

Plot sampling

Each plot was subdivided into 100 squares of 50 cm × 50 cm, which generated 121 vertices. Every three months the species composition was checked at the same points, from March 2000 until June 2002. The sampling of reference plots started in June 2000. If two or more species overlapped at the same point, the total sum of sampled points was considered to be greater than 121. Additionally, plant cover height was measured in 10–15 randomly selected points in one ungrazed plot and one grazed plot.

Representativity of plots

The criteria for choosing this particular study area were, on one hand, the convenient distance between the fence and the forest (30 m), which allowed the location of plots in an ungrazed pastureland. On the other hand, next to this sector, the fence touches the forest edge, which permitted the establishment of reference plots in a manner very similar to the establishment of experimental plots. Other fence sectors were disregarded due to their long distance from the forest and due to severe soil erosion. Both factors may delay vegetation recovery. Therefore, in theory, the selected scenario was the best one for a study of plant succession.

In addition, we made qualitative observations to reinforce the quantitative study. This was done

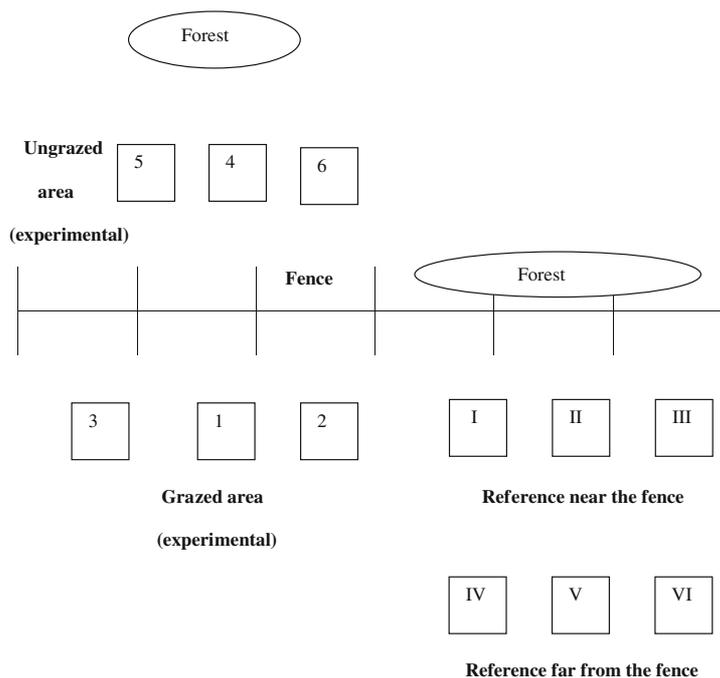


Figure 2. Simplified scheme of plot arrangement for the successional study. Distance between forest and nearest plots, as well as between the plots and the fence, was 13 m. The plots located “far from the fence” were 44 m from the fence and forest. Numbers inside the squares were only used for plot identification (see Appendix A).

because the total length of the exclusion fence was 8.3 km, distributed over different sectors of the island. The fence’s total length greatly exceeds the segment of 100 m considered in the quantitative study. During June–July of the year 2002, almost the entire length of the fence was inspected to verify whether the vegetation showed differences between both sides of the exclusion. A pattern was recognized as consistent for a given species only if the greater density, height, or browsing were always found on the same side of the fence. If the pattern showed a reversal, we assumed that this was not attributable to the presence or absence of cattle. Moreover, if the vegetation on both sides of the fence displayed no differences, this did not invalidate the distinctions found at other sites, because the effect of browsing could be less marked or absent in some local sites. This methodology is only an approximation, and it is only used because the same inspection was not performed before construction of the fence. Nevertheless, it is possible to verify if there were rough, coherent patterns between ungrazed and grazed areas and between sites and species, which are consistent or not with the expected results.

Analyses of the results

The plots (12) were analyzed as separate groups: ungrazed area, grazed area, near the fence and far from the fence, although the last three groups were outside the exclusion. For each group, the average \pm the standard error of the percentage occurrence for each species was calculated, out of a total of 121 (or more) sampled points. To assess if richness and abundance of species (summarized as diversity) displayed changes as a consequence of browsing, the Shannon–Wiener–Weaver index was calculated following the equation:

$$H' = -\sum p_i \cdot \log_2 p_i$$

where p_i means the relative proportion of occurrence of the i th species in each analyzed plot and where \log_2 is the logarithm with base 2; p_i was recalculated starting from the percentages showed in the figures, disregarding the proportion of bare ground, and dividing by 100.

The comparisons of occurrence, richness and diversity between sampling dates were carried out through Repeated Measures ANOVAs, because

the same plots were checked at different dates. An assumption of these tests is that the plot factor does not interact with the time factor (Sokal and Rohlf 1995). Even if this were the case, the analysis would not be invalidated, because Sokal and Rohlf (1995, p. 345) pointed out that in mixed models only the fixed factor (date) can be tested, not the random factor (plot). As our focus lies on the former, the results of interaction between variables (time \times plot) were not presented.

The comparisons of plant height as a function of time were achieved through one-way ANOVA, because different plants were sampled at each date. For all the analyzed variables, we used Tukey, T' , Tukey-Kramer, or GT2 *a posteriori* tests. In a few cases, the non-parametric Kruskal-Wallis test and Fisher's LSD *a posteriori* test were also used (Conover 1980), when the parametric *post hoc* methods did not detect any differences between pairs of dates.

Results

Species composition

We registered the presence of 22 plant species in the pastureland (Table 1). Most species are herbs, with the exception of *Rubus* and *Ugni*, which are shrubs, and *Aristotelia*, which is a tree. All taxa are adventitious in Juan Fernández, except for *Blechnum* and *Juncus*. We do not know the origin of the unidentified dicot. Most species are perennials.

Temporal changes in species abundance

Dynamics of the 22 species analyzed can be summarized in five patterns of variation or absence of variation (Figures 3–7). In Appendix A, we present the complete database, as well as the results of the statistical tests. This will allow the reanalysis of data when more time has passed since establishment of the exclusion.

(1) *Acaena argentea* showed a slight decrease in abundance in the ungrazed area (Figure 3). It was the most abundant species in the pasturelands, with a mean occurrence often above 60%. There were seasonal variations in abundance, but these differences were only significant in the grazed area. Even so, the *post hoc* Tukey test did not detect any difference between March 2000 and March or June 2002 ($p > 0.05$), that is, no net changes in abundance occurred. On the other hand, although the decrease of this species in the ungrazed area in June 2002 was not significant, it is interesting for two reasons: (i) neither the grazed area nor the reference plots showed a parallel response (Figure 3); (ii) it did not occur in the usual month for this species (March). Additional sampling is required in the future to determine whether this diminution is a long-term phenomenon.

Regarding the reference plots, they showed a very similar dynamics, therefore they were good references for comparison with the ungrazed and grazed areas.

(2) *Conium maculatum* showed a slight increase in the ungrazed area (Figure 4). It was only

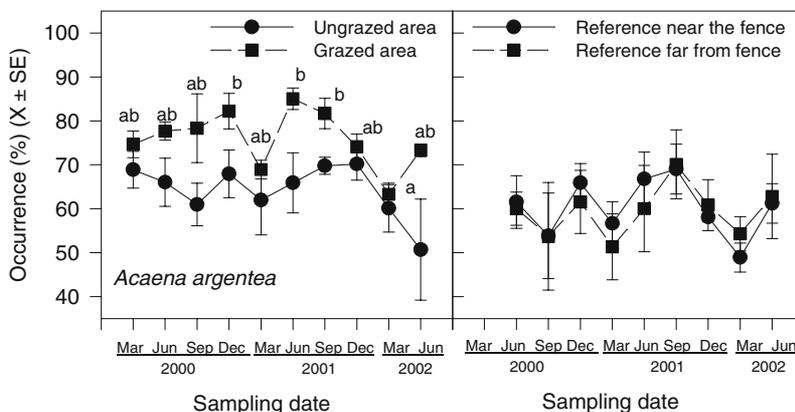


Figure 3. Species that decreased in abundance in the ungrazed area. Different superscripts (a, b) indicate significant differences ($p \leq 0.05$, Tukey test).

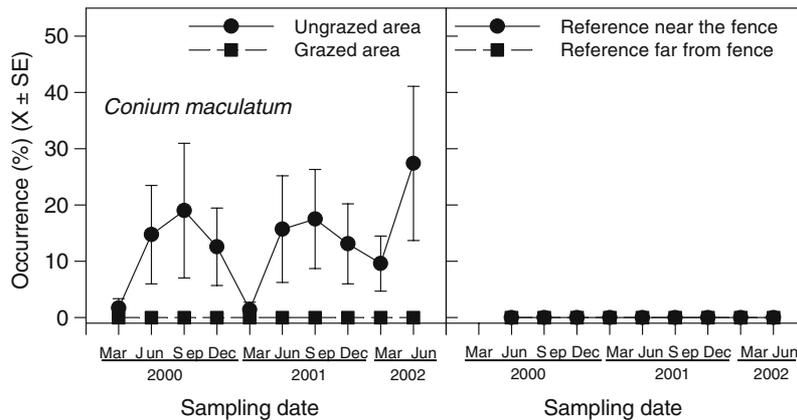


Figure 4. Species that increased in abundance in the ungrazed area.

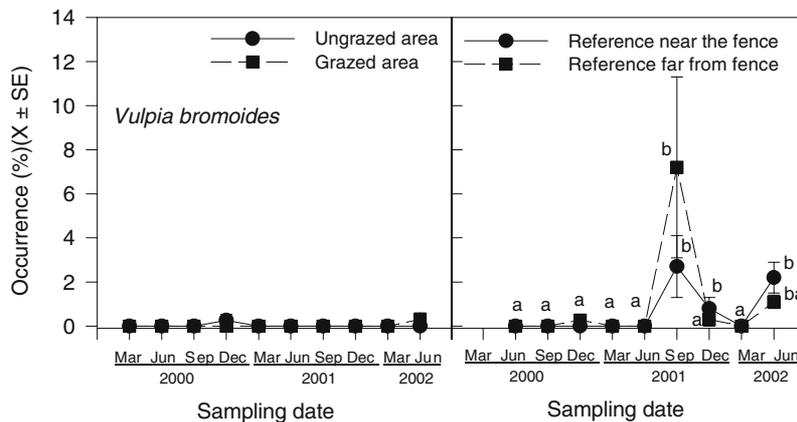


Figure 5. Species that increased in abundance in the grazed area (reference plots near the fence). Different superscripts (a, b) indicate significant differences ($p \leq 0.05$, Fisher's LSD test for plots near the fence; Tukey test for plots far from the fence).

present in the ungrazed area, where it showed a cyclic pattern of change in abundance, which was marginally significant (Repeated Measures ANOVA, $F_{9,18} = 2.37$, $p = 0.057$). During June 2002, its occurrence increased compared with June of the previous years, filling the space released by *Acaena* (Figure 3). Possibly, the great variation between plots made the detection of significant effects more difficult.

(3) *Vulpia bromoides* increased in the plots near the fence (Figure 5). Although it was detected for the first time in December 2000, during the last year of observation it appeared frequently in the reference plots. There were significant variations in these plots, but the difference was only significant between the beginning and the end of the study,

for the plots near the fence (non-parametrical Fisher's LSD test, $p < 0.01$). This significance produces a divergence in *Vulpia* abundance when comparing it with the ungrazed area.

(4) *Blechnum*, *Geranium*, *Juncus*, *Rubus*, *Rumex acetosella*, *Sonchus*, *Ugni* and *Anthoxanthum-Bromus* were species with no net variation between the beginning and the end of the study, but they were often present. *Anthoxanthum-Bromus* were considered as one, due to the lack of flowers during most of the year, which makes their identification difficult. We only show the graphs for the four most abundant species within this category (Figure 6). *Blechnum*, a small fern, showed some seasonal variation, being significant only in the plots that were far from the fence.

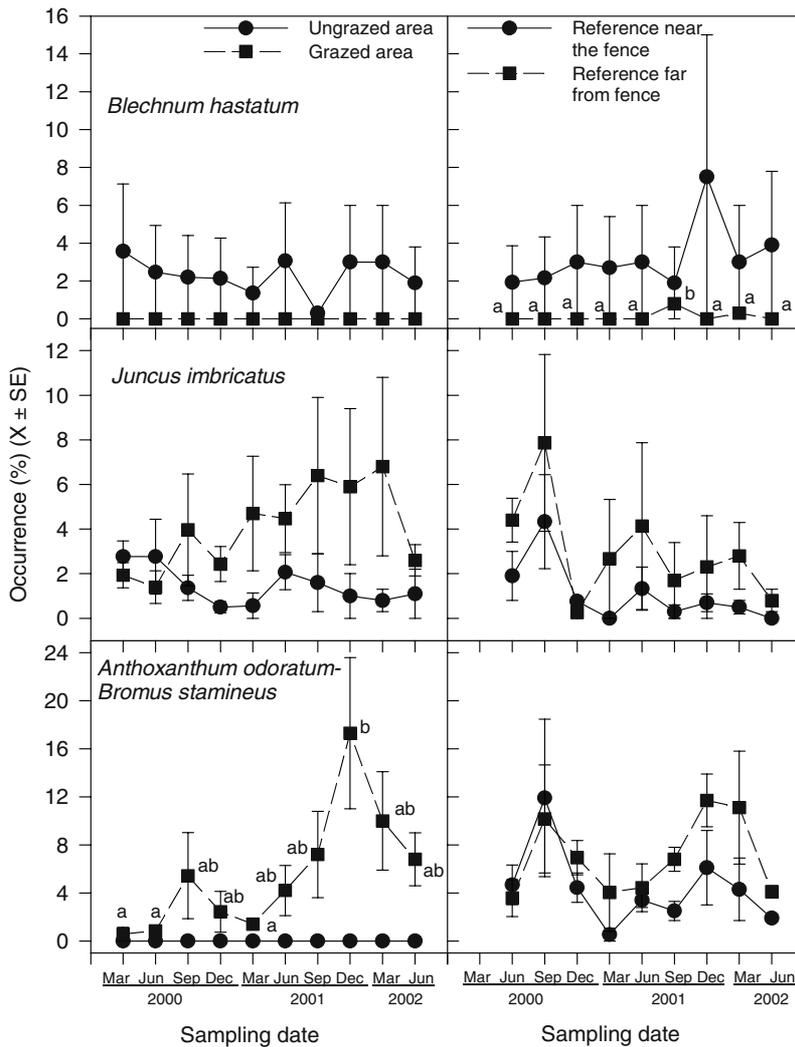


Figure 6. Species without variations in net abundance between the beginning and the end of the study, with nearly constant occurrences. Different superscripts (a, b) indicate significant differences ($p \leq 0.05$, Tukey test).

Juncus showed greater, but not significant, variations, with large differences between plots. Lastly, the variation of *Anthoxanthum-Bromus* in the grazed area was generally significant (Figure 6), but not between March 2000 and June 2002 (Tukey test, $p > 0.05$). When plots near the fence and far from the fence are compared, the trends for the last three species showed similar behaviors.

(5) *Aristotelia*, *Euphorbia*, *Galium*, *Oxalis*, *Poa*, *Polypogon*, *Rumex conglomeratus*, *Silybum*, *Veronica* and the unidentified dicot were species with no net variation between the beginning and

of the study, but they appeared and disappeared sporadically, with low abundances. We show the examples for *Oxalis*, *Silybum* and *Poa* (Figure 7). At least half of the species in this category are annual herbs, which can be detected only in certain seasons of the year. Consequently, the observed changes are seasonal and not successional.

Bare ground

The experimental plots showed significant temporal changes. The proportion of bare ground

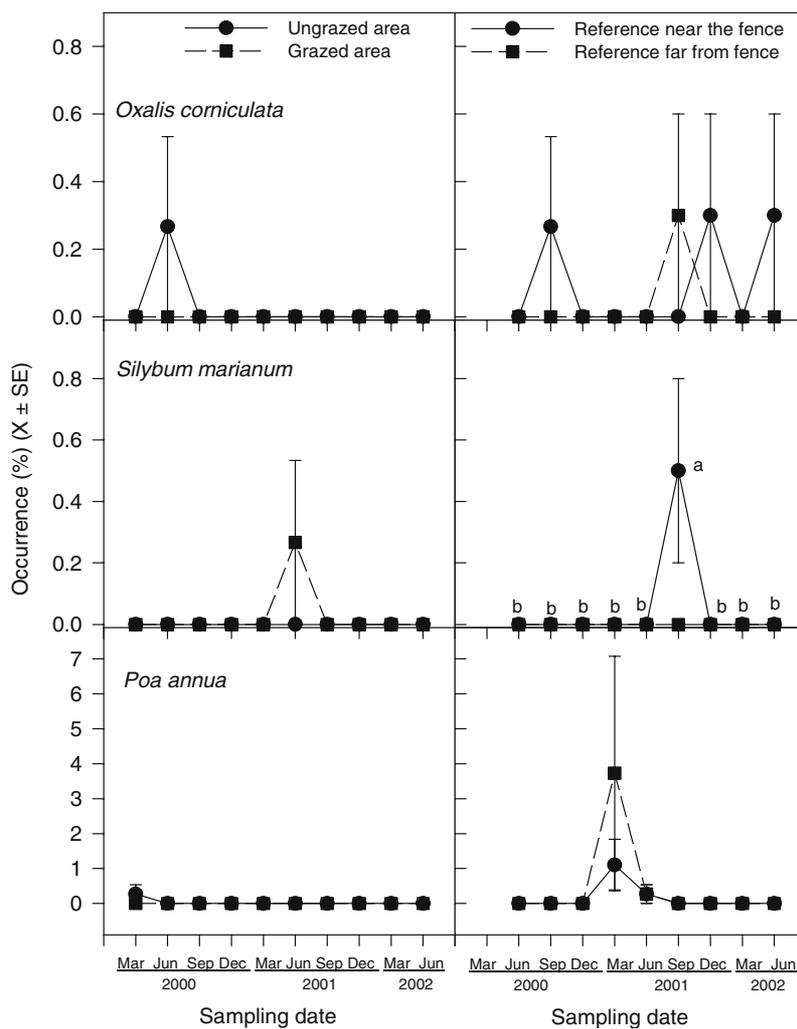


Figure 7. Species without variations in net abundances between the beginning and the end of the study, but they appeared and disappeared sporadically. Different superscripts (a, b) indicate significant differences ($p \leq 0.05$, Tukey test).

reached a maximum during March of each year (Figure 8), most likely due to the low summer precipitation. However, there were no net differences between the beginning and the end of the study (Tukey test, $p > 0.05$). These results do not support the hypothesis that predicts an increase in plant cover in the ungrazed area.

Species richness

In Table 2, we detail the presence or absence of species as a function of time in the experimental plots, facilitating the interspecific comparisons. In the ungrazed area, some species were always present, such as *Acaena*, *Blechnum*, *Conium*, *Juncus* and

Rumex acetosella. *Geranium*, *Oxalis*, *Galium*, *Poa*, *Veronica*, and *Vulpia* appeared sporadically. The last four species have annual life cycles, which can explain their sporadic occurrence. During the last year of observation, only two new species appeared in this area: *Galium* and *Aristotelia*. The last species was the only seedling found of a tree typical of the adjacent forest. Regarding species richness, if we consider all the ungrazed-area plots, we did not find major changes: six species were observed in March 2000 and in June 2002. The species composition was virtually the same. There was only a marginally significant variation in richness (Repeated Measures ANOVA: $F_{9,18} = 2.35$, $p = 0.059$).

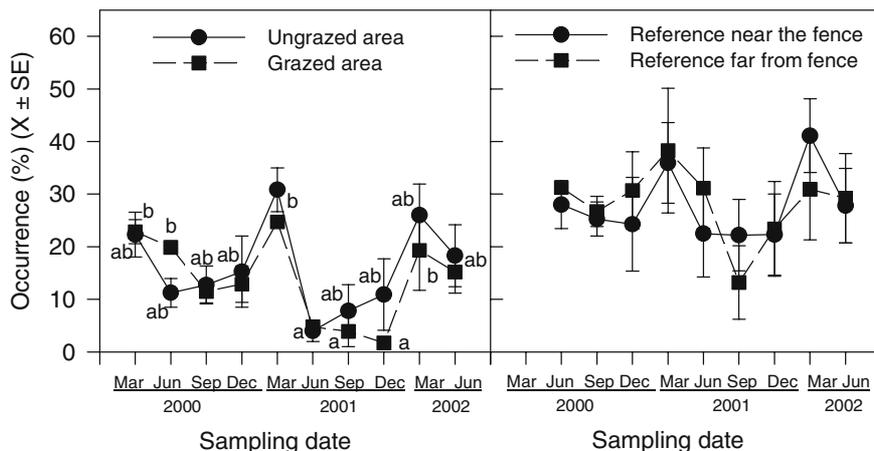


Figure 8. Changes in occurrence of bare ground cover. Different superscripts (a, b) indicate significant differences ($p \leq 0.05$, Tukey test).

In the grazed area, other taxa with constant presence were the *Anthoxanthum-Bromus* complex (Table 2). Five species appeared during the last

year (*Polypogon*, *Rumex conglomeratus*, *Silybum*, *Sonchus* and *Vulpia*). In June 2002, we detected three additional species compared with March

Table 2. Species occurrence (+) in the experimental plots of the ungrazed or grazed areas ($N = 3$ in both cases).

	Mar 2000	Jun 2000	Sept 2000	Dec 2000	Mar 2001	Jun 2001	Sept 2001	Dec 2001	Mar 2002	Jun 2002
Ungrazed area										
<i>Acaena argentea</i>	+	+	+	+	+	+	+	+	+	+
<i>Aristotelia chilensis</i>										+
<i>Blechnum hastatum</i>	+	+	+	+	+	+	+	+	+	+
<i>Conium maculatum</i>	+	+	+	+	+	+	+	+	+	+
<i>Galium aparine</i>							+			
<i>Geranium core-core</i>		+	+			+	+			
<i>Juncus imbricatus</i>	+	+	+	+	+	+	+	+	+	+
<i>Oxalis corniculata</i>		+								
<i>Poa annua</i>	+									
<i>Rumex acetosella</i>	+	+	+	+	+	+	+	+	+	+
Unidentified dicot			+							
<i>Veronica persica</i>		+	+							
<i>Vulpia bromoides</i>				+						
Number of species	6	8	8	6	5	6	7	5	5	6
Grazed area										
<i>Acaena argentea</i>	+	+	+	+	+	+	+	+	+	+
<i>Anthoxanthum odoratum-Bromus stamineus</i>	+	+	+	+	+	+	+	+	+	+
<i>Juncus imbricatus</i>	+	+	+	+	+	+	+	+	+	+
<i>Polypogon australis</i>									+	
<i>Rumex acetosella</i>		+	+		+	+	+	+	+	+
<i>Rumex conglomeratus</i>						+				
<i>Silybum marianum</i>						+				
<i>Sonchus asper</i>										+
Unidentified dicot			+							
<i>Vulpia bromoides</i>										+
Number of species	4	5	6	4	5	7	5	5	6	7

2000. However, there were no significant differences between sampling dates (Repeated Measures ANOVA: $F_{9,18}=1.96$, $p = 0.11$).

Regarding reference plots (Table 3), *Euphorbia*, *Silybum* and *Vulpia* only appeared during the last year of observation in the plots near the fence. In the case of the plots that were far from the fence, the new species were *Blechnum*, *Euphorbia*, *Oxalis*, *Rubus*, and *Rumex acetosella*. In general, outside the fence we found four other species during the last year of observation (*Euphorbia*, *Polypogon*, *Rumex conglomeratus*, *Silybum*), which were not previously detected in the sampling plots, vs. only two new species that were found in the ungrazed area.

There was an increasing trend in species richness in the plots near the fence. The number of species increased from eight to 10 between the beginning and the end of the study. In the plots that were

far from the fence, the species increased from five to nine during the same period (Table 3). However, in both cases the variation was not significant (Repeated Measures ANOVA; near the fence: $F_{8,16}=2.1$, $p = 0.098$; far from the fence: $F_{8,16}=1.37$, $p = 0.28$).

In summary, the ungrazed area and the grazed area (including the six reference plots and the three experimental ones), diverged in composition, but not due to noticeable changes in the ungrazed area; instead, the changes mainly occurred outside of the fence.

Species diversity

We found seasonal variations, but these were only significant in the grazed plots of the experimental area (Figure 9). However, the Tukey test did not detect differences between any pair of dates (the

Table 3. Species occurrence (+) in the reference plots near to and far from the fence ($N = 3$ in both cases), sampled since June 2000.

	Mar 2000	Jun 2000	Sept 2000	Dec 2000	Mar 2001	Jun 2001	Sept 2001	Dec 2001	Mar 2002	Jun 2002
Near the fence										
<i>Acaena argentea</i>		+	+	+	+	+	+	+	+	+
<i>Anthoxanthum odoratum-Bromus stamineus</i>		+	+	+	+	+	+	+	+	+
<i>Aristotelia chilensis</i>							+			
<i>Blechnum hastatum</i>		+	+	+	+	+	+	+	+	+
<i>Euphorbia pepus</i>						+				
<i>Geranium core-core</i>		+	+			+		+		+
<i>Juncus imbricatus</i>		+	+	+		+	+	+	+	
<i>Oxalis corniculata</i>			+					+		+
<i>Poa annua</i>					+	+				
<i>Rubus ulmifolius</i>		+	+	+	+	+		+	+	+
<i>Rumex acetosella</i>				+	+	+			+	+
<i>Silybum marianum</i>							+			
<i>Sonchus asper</i>			+	+		+		+		
<i>Ugni molinae</i>		+	+	+	+	+	+	+	+	+
<i>Vulpia bromoides</i>							+	+		+
Number of species		8	10	10	8	12	8	11	8	10
Far from the fence										
<i>Acaena argentea</i>		+	+	+	+	+	+	+	+	+
<i>Anthoxanthum odoratum-Bromus stamineus</i>		+	+	+	+	+	+	+	+	+
<i>Blechnum hastatum</i>							+		+	
<i>Euphorbia pepus</i>									+	+
<i>Geranium core-core</i>		+	+							+
<i>Juncus imbricatus</i>		+	+	+	+	+	+	+	+	+
<i>Oxalis corniculata</i>							+			
<i>Poa annua</i>					+	+				
<i>Rubus ulmifolius</i>									+	
<i>Rumex acetosella</i>								+		+
<i>Sonchus asper</i>			+	+				+		+
<i>Vulpia bromoides</i>				+			+	+		+
Number of species		5	6	6	5	5	7	7	7	9

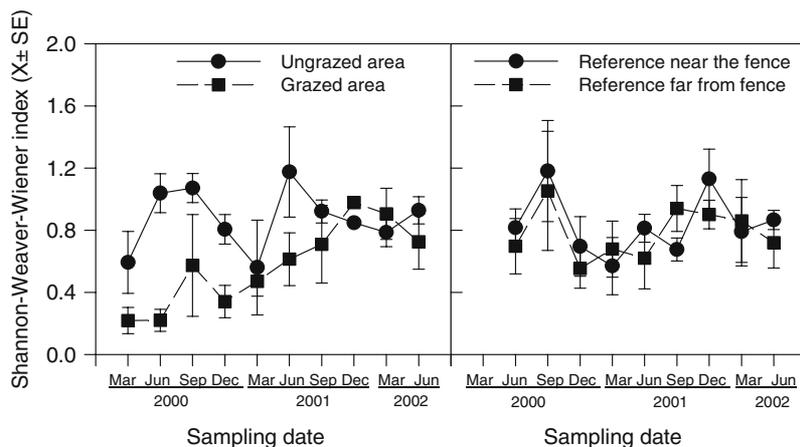


Figure 9. Species diversity as a function of time: ungrazed area ($F_{9,18} = 1.56$, $p = 0.20$), grazed area ($F_{9,18} = 2.89$, $p = 0.026$), near the fence ($F_{8,16} = 1.39$, $p = 0.27$), far from the fence ($F_{8,16} = 0.62$, $p = 0.75$).

same is true when we used the non-parametric Kruskal-Wallis test). In all, new temporal evaluations are required to verify whether this rise in diversity in the grazed plots is a long-term phenomenon.

Height of the plant cover

Figure 10 does not show significant temporal variations in plant height in the grazed area. Regarding the ungrazed area, we found two patterns: (i) if we consider *Conium* in December, its inflorescences reach up to 170 cm in height, very tall when compared to the habitual average. Thereafter, the inflorescences dieback and the mean height of the plant cover decreases to about 30 cm. Therefore, the height variation is clearly significant and is only the consequence of the height maxima in December ($p < 0.05$, T' -test); (ii) when we exclude the *Conium* inflorescences, the variation remains significant, but much lower than it originally was. As the GT2 and Tukey-Kramer *a posteriori* tests did not detect when the height differences occurred, we reanalyzed these data using the non-parametric Kruskal-Wallis and Fisher's LSD tests. We found that the vegetation was higher in June 2002 than in June 2000 ($p < 0.05$), supporting our expectations.

Representativity of plots

Applying the consistency criterion detailed in Methods, we detected some consistent patterns

between sites, species, fence sides, and with the hypotheses of this study (Table 4). Although throughout the island there were not many changes between both sides of the fence, in some sites

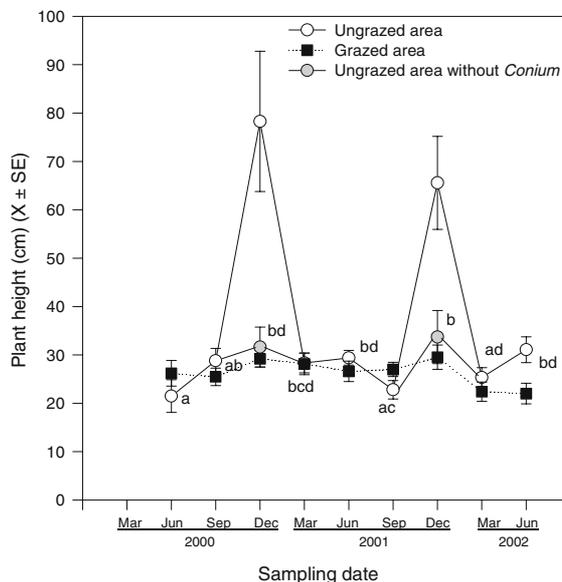


Figure 10. Plant height on both sides of the cattle exclusion fence. Different superscripts (a-d) indicate significant differences ($p \leq 0.05$, Fisher's LSD test; Kruskal-Wallis test: $H = 18.1$, $p = 0.020$, d.f. = 8, for the ungrazed area without *Conium*). The two *Conium* height peaks were not significantly different; however, they were significantly different from the plant heights that occurred during the other seasons ($F_{8,120} = 10.6$, $p = 0$; T' test: $p \leq 0.05$). Grazed area: $F_{8,121} = 1.74$, $p = 0.096$.

Table 4. Floral observations on both sides along 8.3 km of the cattle exclusion fence, on Robinson Crusoe Island.

Sector	Ungrazed area	Grazed area
Puerto Inglés	– Taller <i>Acaena argentea</i>	– Lower height
	– <i>Dipsacus sativus</i> (L.) Honck. present	– Absent
	– <i>Silybum marianum</i> present	– Absent
Piedra Agujereada	– Denser and taller <i>A. argentea</i>	– Lower density and height
	– <i>Haloragis masatierrana</i> Skottsbo. present	– Absent
	– Less grazed <i>Juncus imbricatus</i> and <i>Nassella laevissima</i> (Phil.) Barkworth	– More grazed
Tres Puntas	– Denser and taller <i>N. laevissima</i>	– Lower density and height
	– Less grazed <i>J. imbricatus</i>	– More grazed
	– Denser and taller <i>H. masatierrana</i>	– Trampled <i>Erigeron fernandezianus</i> (Colla) Solbrig
Between Tres Puntas and Villagra	– Higher density and lower browsing of <i>H. masatierrana</i>	– Lower density and height
	– Less grazed <i>J. imbricatus</i>	– Lower density and higher browsing
Villagra shelter	– Denser <i>A. argentea</i> and <i>Conium maculatum</i>	– More grazed
		– Lower density

we detected ungrazed areas with higher and denser plants, with a lower degree of browsing, grazing, or trampling than in the grazed areas (these factors still persist in the ‘ungrazed’ areas due to the pressure of grazing by rabbits; see Discussion). In other cases, species that are palatable to cattle were only present in the ungrazed area (e.g., *Silybum marianum*). A very noticeable case was found in a site between Tres Puntas and Villagra, where the endemic shrub *Haloragis masatierrana* only occurred in the ungrazed area, forming a very sharp border adjacent to the fence. It is very unlikely that the establishment of the fence in a straight line left all shrubs on the same side. Therefore, we discard the possibility of a pattern that existed previous to the exclusion of cattle. These qualitative observations enable us to conclude that, although few changes in vegetation were observed in our main study site, they are slowly developing throughout the island.

Discussion

Species composition

From Table 1, only *Sonchus asper* is not cited in the most recent Juan Fernández plant species checklist (Marticorena et al. 1998), but it is mentioned by Cuevas et al. (2004). A superficial inspection of this table reveals that most species are weeds *sensu* Matthei (1995), that is, plants that compete with cultivated species, as well as those

that are noxious to man and other animals. They can also be adapted to disturbed habitats and may be ecologically aggressive (Swenson et al. 1997). We can also characterize this flora using the ecological indicator values of Ellenberg (1974), slightly corrected by Ramírez et al. (1991) for mainland Chile. We found that the mean ecological behavior of 18 out of 22 species (82%) is typical of intermediate to full light conditions, intermediate to warm temperatures, neutral to weakly acidic soils, intermediate to rich levels of soil nitrogen, and fresh soil moisture (i.e., intermediate). We do not have information about the behavior of these plants on the Juan Fernández Islands, therefore, this characterization is only an approximation.

IREN-CORFO (1982) also characterized the pastureland species of the Juan Fernández archipelago according to an index of forage quality (Is), which varies between 0 and 5, where the highest value indicates the highest quality. Some of the most abundant species of the present study have an Is = 0 (*Acaena*, *Conium*, *Geranium*). *Anthoxanthum*, *Juncus* and *Oxalis* have an Is = 1; *Poa* and *Rumex acetosella* have an Is = 2. No species has greater values of quality. Several species are even considered toxic for animal consumption; these are *Conium* (Roth et al. 1988), *Euphorbia* (Matthei 1995), *Oxalis* (Forsyth 1980) and *R. acetosella* (Roth et al. 1988). Even so, the Puerto Inglés sector had one of the best forage potentials on Robinson Crusoe Island at the beginning of the 1980s (IREN-CORFO 1982).

These antecedents perfectly describe the degraded condition of the pastures, with the consequence of badly fed cattle and, therefore, poor livestock quality. During starvation periods, the animals must eat plants of very low forage quality, sometimes even plants that are poisonous, which can cause death.

Floristic richness and diversity

Disregarding the grazed area, which showed an increase in diversity, these two variables did not change in all groups of analyzed plots. This is in contrast with published evidence, which shows that in some cases both variables increase in ungrazed areas (Cesa and Paruelo 2001), while in other cases the diversity decreases and the richness does not vary (Márquez et al. 2002), or both variables decrease (Nai-Bregaglio et al. 2002). Both patterns of change are possible, because cattle can either decrease or increase the heterogeneity of the pastureland, depending on their feeding preferences, the dispersal of propagules from other areas, the removal of reproductive structures of the vegetation already extant, the creation of new regeneration niches, the mitigation of competitive exclusion processes, and also on the original condition of the pastureland (Huntly 1991; Hulme 1996; Olf and Ritchie 1998; Nai-Bregaglio et al. 2002). For instance, herbivores that disproportionately damage the more common species in a patch or community tend to increase plant diversity; those that disproportionately damage rare species will have the opposite effect (Huntly 1991). For Robinson Crusoe Island, the most probable scenario, supported by some empirical evidence, is the enrichment of the pastured sites (Tables 2 and 3; Figure 9). Abiotically- or cattle-dispersed flora may also contribute to this enrichment (Olf and Ritchie 1998). This increasing diversity is typical of sites with a long history of pasturage (Milchunas et al. 1988; Noy-Meir et al. 1989; Nai-Bregaglio et al. 2002), such as the Juan Fernández Islands. Also large grazing mammals, natural or domesticated, have been reported to increase floristic diversity at low stocking rates (Olf and Ritchie 1998), this being the case, once again, for the animal density that occurred at the studied area (see Section Other factors involved in vegetational inertia).

Changes in vegetation

Generally, the net changes in the vegetation were low. Some species increased and one decreased in abundance; plant height also increased in the ungrazed area, coherent with other studies (e.g., Nai-Bregaglio et al. 2002). However, as we did not sample the height in the reference plots, we cannot be sure that the fence produced this effect. In general, the successional variation is less than that expected after cattle exclusion. For instance, Porteous (1993) showed dramatic changes in the herbaceous vegetation in an ungrazed area in New Zealand, forming a very sharp border between the grasslands inside and outside of the fence.

According to Mueller-Dombois and Ellenberg (1974), the colonization of a denuded area depends on a complex of factors, namely, the assemblage of neighbor species, accessibility to the habitat (neighborhood of the involved area, dispersal mechanisms, etc.), the chances of establishment upon germination (ecological plant properties), the habitat (soil, climate, topography), and the elapsed time. Applying these concepts to our study, we could expect that the following factors would not be limiting for pastureland recovery: (i) the assemblage of neighbor species, because the native forest is adjacent to the ungrazed plots (see Methods: Study area); (ii) although diaspore production is cyclical, the forest species produce seeds or spores (Cuevas 2002); (iii) the distance between forest and the ungrazed area is only 13 m, and (iv) most forest species are epizoochorous or anemochorous.

As the community that is experiencing recovery (i.e., the pastureland) is already established, we must also consider the traits of this community. For instance, the overexploitation of pastureland resources, where palatable species are generally annuals, may have strongly decreased the size of the seed bank, hampering the regeneration of the pasture species. Some evidence from the literature supports this hypothesis (Bertiller 1992; Ortega et al. 1997), while in other cases grazing did not have any effect on seed bank size (Milberg and Hansson 1993; Márquez et al. 2002). On the other hand, the habitat and the time passed since the beginning of livestock exclusion would also be limiting for pastureland recovery. Regarding biotic habitat, there is only one dominant species in the pastureland (*Acaena*), which makes the growth of

other species difficult (Greimler et al. 2002b), due to its vigorous clonal and sexual reproduction (Greimler et al. 2002a). Although seeds could germinate in the dense *Acaena* carpet, soil compaction and drying winds (abiotic habitat factors typical of these pastures) would impose severe site conditions for the potential seedlings (personal observations). These negative effects can be expressed by hampered or delayed recruitment of seedlings. The thick carpets formed by this species – up to 60 cm in depth – can also deeply shade recruiting seedlings of other plant species. Although *Acaena* likely makes the recruitment of forest species difficult, it would die shortly after it is surmounted by growing trees, as *Acaena* is a very shade-intolerant species (personal observation). Finally, *Acaena* also produces a great amount of “vegetation noise” that obscures the contributions of other species when we try to detect a signal expressed as successional changes in low abundance species.

Regarding the temporal scale, probably not enough time has passed to observe successional changes. In fact, Rodríguez et al. (2001) demonstrated noticeable changes in the vegetation after 9 years of study in Uruguay. Márquez et al. (2002), on the other hand, demonstrated differences in the seed bank with or without the presence of cattle, in a 10-year-study in Córdoba, Argentina. It is worthwhile to mention the case of a complete watershed on Robinson Crusoe Island (Vaquería), in which livestock grazing was discontinued in 1985. In open sites, the herbaceous vegetation has recovered noticeably. On the contrary, Montaldo (1977, 1990, 1999) observed vegetation changes after 2 years of livestock exclusion, in his outstanding 34-year-study in the Valdivia province of Chile. As Mueller-Dombois and Ellenberg (1974) pointed out, the time factor also includes the rate of change, which in our study has been slow, probably due to the long-lasting, intense history of perturbation by cattle (more than 100 years, Skottsberg 1920–1956).

In spite of the limitations for pastureland recovery mentioned above, some very invasive exotic species have already been observed in our plots: *Rubus*, *Aristotelia* and *Ugni*, all of which are bird-dispersed. The only tree species that appeared as a seedling in the ungrazed area was *Aristotelia*. From the perspective of biological conservation, this is not a positive aspect, as *Aristotelia* is an

invader that has been excluding the native forest since about 140 years ago (Greimler et al. 2002a; Dirnböck et al. 2003). Therefore, if no management measures are taken, the pasturelands could be transformed into a shrubland or woodland dominated by exotic elements, rather than by the native flora (Dirnböck et al. 2003).

Other factors involved in vegetational inertia

On one hand, the seasonal changes are noticeable, which obscures the expected successional changes. On the other hand, the Puerto Inglés zone is presently exposed to much less grazing from cattle than it was in the past: during the year 2000, we counted only 11 animals in a 132 ha-valley (IREN-CORFO 1982), compared with 26 animals in the same valley in 1999. This is a low stocking rate compared with those found in other studies (Márquez et al. 2002; Nai-Bregaglio et al. 2002). Therefore, with such low grazing pressure, great differences between ungrazed and grazed areas would not be expected.

Finally, other herbivores, such as the rabbit (*Oryctolagus cuniculus* L.), may be causing a successional lag. Its population density has been estimated at between 9 and 12 rabbits/ha in Puerto Inglés (Sáiz and Ojeda 2000). At least one of the plant species found in the present study (*Juncus imbricatus*) exhibited clear signs of rabbit herbivory in several sites on the island, regardless of whether cattle were excluded or not (personal observations). The effects of herbivory by rabbits were assessed in small-scale exclusions without cattle and rabbits. The vegetation showed a huge recovery in plots from which rabbits and cattle were excluded, compared with the low variation in vegetation that was found when only cattle were excluded. Obviously, recovery is impossible without the exclusion of herbivores. On the other hand, forest regeneration has not shown the same pattern mentioned above for the grasslands of Vaquería; the presence of tree seedlings is very ephemeral (Cuevas 2002). Acevedo (1990) determined that the limiting factor was, once again, the grazing pressure exerted by rabbits, although summer drought could also be involved (Cuevas 2002). These precedents call into question the role of the cattle as one of the main factors that impede the recovery of the Juan Fernández

pasturelands. Instead, they highlight the influence of the rabbits.

A visual inspection of the studied plots five years after the initiation of livestock exclusion revealed that vegetational changes are still slight; however, in other areas not covered by *Acaena* (i.e., Puerto Francés) the differences between grazed and non-grazed areas were much more visible (H. González and P. Novoa, personal communications). Therefore, the findings of our 27-month-study are consistent with longer-term evaluations but, of course, it will be necessary to reassess the changes in vegetation over the long term (10 years or more).

Social aspects

From this study, the evidence is too weak to convince stockbreeders of the necessity of the elimination of cattle or of their exclusion from forested areas. However, the following phenomena had previously been used as arguments for cattle eradication: pastureland impoverishment, severe soil erosion, deficient cattle quality and periods of starvation, mostly occurring in winter. Even so, stockowners have repeatedly refused to reduce their herds. Neither the offer of exorbitant prices for cattle, nor a forced strategy of animal removal have met with success, due to the pressures exerted by islanders and also because political decisions have favored human activities over the conservation of local flora. The stockbreeders argue that they need to sustain a supply of meat and milk. Nevertheless, only a small number of domestic animals is sacrificed per year, since at present a high-quality supply of both products is provided regularly from the mainland. The true reason for cattle raising lies in the maintenance of the islanders' own traditions. In fact, a livestock herd is a kind of self-sufficient saving account that does not require any special care. Overall, an issue that initially seemed easy to solve, in comparison to other pests like rabbits or rats, has become a huge problem.

Implications for forest restoration

The low level of natural vegetational recovery documented in this study implicates that a better

strategy for forest restoration could involve the search of those plant associations that facilitate the colonization of endemic species at the forest edge. The alien *Aristotelia* could probably serve as a nursery species for plant recruitment. We can suggest the opening of strips, both along the edge and inside of *Aristotelia* woodlands, followed by the planting of native species in these opened sites. Given that *Aristotelia* has significant vegetative growth, it should be constantly thinned to prevent excessive shading that would preclude the development of new seedlings. In addition, seedlings should be protected against rabbits. We expect that on a medium to long time scale, the interior side of the fence could constitute a colonization front. If this took place, the forest border would migrate downwards and, accordingly, the fence should be displaced to lower elevations.

Conclusions

Considering our hypotheses, after 27 months of study we found an increase in plant height only in the ungrazed area, which was consistent with our expectations. However, we did not find a noticeable directional change in floristic composition towards forest species, nor did the total vegetation cover increase in the ungrazed area. These two last results are not consistent with our expectations. Notwithstanding, there were small net changes in the abundances of some species (*Acaena*, *Conium*, *Vulpia*), and some new species appeared in the grazed areas (e.g., *Euphorbia*, *Polypogon*). This last phenomenon produces a divergence in floristic composition in the plant communities found on either side of the fence. A qualitative evaluation of the fenced areas of Robinson Crusoe Island also showed some recovery of the vegetation cover. Generally, the ecosystem shows a low capacity of recovery, over the short term, upon the termination of one of the causes of disturbance that gave rise to the community as it now exists (i.e., the domestic cattle). As a summary, the evidence is too weak to convince stockbreeders of the necessity of the elimination of cattle or of their exclusion from forested areas.

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