

Introduced ungulates and their effects on plant-animal interactions in the temperate forest of the southern Andes

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Introduction

Biological invasions are one of the most serious threats to biodiversity. They are the main cause of recent extinctions (i.e., since the year 1600), and one of the main causes of current endangerment of species, second only to habitat destruction (Brown and Lomolino 1998; Vitousek et al. 1997). Many invasions have led to drastic and fundamental changes in species composition, habitat structure, and ecosystem processes (Elton 1958; Simberloff 1991; Williamson 1996). Many introduced mammalian herbivores generate the latter effect (de Vos et al. 1956; Ebenhard 1988).

Introduced mammalian herbivores affect ecosystems in several ways. Through browsing, grazing, and trampling, they cause the population decline of individual plant species by decreasing survival, growth, or fitness (Crawley 1986; Ebenhard 1988). Some such effects are quite dramatic. For example, goats introduced to Santa Catalina Island off the coast of California drove the local population of *Artemisia californica* to extinction (Coblentz 1978). Of course, effects on multiple plant species can also lead to drastic changes in the diversity and species composition of the entire plant community. For example, intense herbivory on competitively dominant plant species can result in increased abundance of less palatable, competitively inferior species (Huntly 1991). In English chalk grasslands, rabbit grazing maintains plant diversity and prevents colonization by a few dominant woody species (Hope-Simpson 1940; Tansley and Adamson 1925). In many forest ecosystems, high densities of introduced mammalian herbivores can sometimes impair forest regeneration, modifying the entire forest habitat (Ebenhard 1988; Gill 1992). Furthermore, altered community structure resulting from introduced mammalian herbivores is in some cases accompanied by increased richness of exotic plant species (Chaneton et al. 2002; Hobbs 2001; Hobbs and Huenneke 1992; Mack 1989).

Besides the effects on the plant community, introduced herbivores sometimes directly or indirectly affect other components of the ecosystem. Introduced herbivores can affect native herbivores through competition. For example, the introduced North American grey squirrel (*Sciurus carolinensis*) is believed to outcompete the native red squirrel (*S. vulgaris*) in England (Williamson 1996), and the North American beaver (*Castor canadensis*) is believed to displace the native European beaver (*C. fiber*) in Finland (Nummi 1996). Other animal species that use plants as resources can also be affected, such as pollinators and frugivores. Sheep grazing in California is believed to affect native pollinators of *Astragalus monoensis* through food removal (Sugden 1985).

In this case study I discuss results of recent studies aimed at understanding the effect of introduced ungulates in the temperate forest of the southern Andes (TFSA). In particular, I will present result of studies addressing two questions: (1) can introduced affect the network of interactions of plants and pollinators in the resident community?; and (2) can introduced ungulates affect plants not only directly (through browsing and trampling) but also indirectly by affecting their interactions with pollinators? Results presented here are based on previously published research (Vázquez 2002a; Vázquez 2002b; Vázquez and Simberloff 2002; Vázquez and Simberloff 2003; Vázquez and Simberloff 2004), and readers are encouraged to consult these sources for further information.

Study system

Natural history of plant-pollinator interactions in the temperate forest of the southern Andes

The temperate forest of the southern Andes (TFSA) lies on the southwestern fringe of South America, between 39° and 55° S (Fig. 2.1). The biota of the TFSA evolved under a warm climate in the former Gondwanaland—a continental land mass formed by South America, Antarctica, and Australia until the early Tertiary (Arroyo et al. 1996). The many shared taxa between southern South America and Oceania are a legacy of that former connection. For example, Arroyo et al. (1996) estimate that 21 woody genera presently found in the TFSA can be traced to the former Gondwanaland. Charismatic examples of shared plant genera include the tree families Nothofagaceae and Araucariaceae (Kershaw and Wagstaff 2001; Veblen et al. 1996). To these Gondwanean elements, many taxa of Neotropical origin can be added, such as the bamboo *Chusquea* and the woody genus *Schinus*. The separation from Antarctica that began in the early Tertiary, the rise of the Andes, and the resulting rearrangement of the regional wind circulation patterns led to the development of the arid climates to the east and north, isolating the southern Andean forest from other moist forest regions (Aizen and Ezcurra 1998; Arroyo et al. 1996).

This unique biogeographical history has resulted in a species-rich biota with many tropical elements and high endemism. For example, 34% of the woody plant genera and three complete plant families are endemic to the TFSA (Arroyo et al. 1996). High endemism is also found in many other groups, such as bees (Michener 1979), weevils (Morrone and Roig-Juñent 1995), amphibians (Duellman 1999) and birds (Stattersfield et al. 1998). This relatively high species richness and endemism is accompanied by an unusually diverse life-form spectrum, with an abundance of life forms more commonly seen in warmer forest types (Arroyo et al. 1996).

The TFSA has one of the highest incidences of animal pollination and seed-dispersal recorded for any temperate biome (Aizen et al. 2002). For example, in Chile more than 90% of woody plants have animal-pollination syndromes (Smith-Ramírez and Armesto 1994), and more than 70% have animal seed-dispersal syndromes (Armesto and Rozzi 1989). Another salient characteristic of this biome is the high ratio of number of bird-pollinated plants to number of bird-pollinators: about 20% of the woody genera in the TFSA that produce tubular flowers are visited by the single hummingbird species present in the area, *Sebania* (Armesto et al. 1996; Fraga et al. 1997; Smith-Ramírez 1993). A similar pattern is observed for animal-seed dispersal (Armesto et al. 1996; Willson 1991).

Introduced mammalian herbivores in the TFSA

Introduced vertebrate herbivores are a main source of anthropogenic forest alteration in this temperate forest. Cattle have been present for about two centuries (Vázquez 2002b; Veblen and Alaback 1996). In Nahuel Huapi National Park, cattle are found today in 56% of the total area of the park suitable for them (Lauria Sorge and Romero 1999). Red deer (*Cervus elaphus*) were introduced in the Nahuel Huapi area in the early twentieth century (Jaksic et al. 2002; Veblen et al. 1992); they are currently the most widespread exotic deer in the region, ranging from Neuquén to Chubut provinces in Argentina (Bonino 1995) and between regions VII and XI in Chile (Jaksic 1998). Two other species of deer (fallow, *Dama dama*, and axis, *Axis axis*) were introduced in the 1930s in Nahuel Huapi National Park but are not present in the study sites (Bonino 1995; Navas 1987). Cattle and deer have important effects on the native biota (Vázquez 2002b).

Study sites

The study was conducted in Nahuel Huapi National Park and surrounding areas, Río Negro, Argentina. This park lies in the eastern range of the TFSA, limited by the Patagonian steppe in the east; it encompasses a striking gradient of decreasing humidity from west to east (Cabrera and Willink 1973; Dimitri 1962).

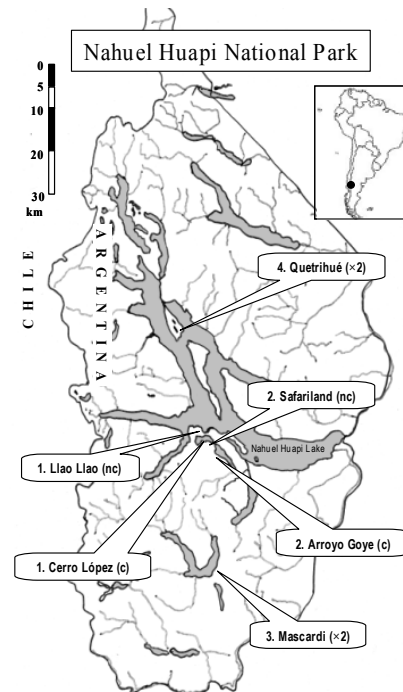


Figure 2.2. Four pairs of sites included in the study: (1) Llao Llao (without cattle = nc) - Cerro López (with cattle = c); (2) Safariland (nc) - Arroyo Goye (c); (3) Lago Mascaridi (nc) - Lago Mascaridi (c); and (4) Península Quettrihué (nc) - Península Quettrihué (c). Paired sites in pairs 1 and 2 were separated by a few kilometers; sites in pairs 3 and 4 were contiguous (indicated as “x 2” in the graph).

Because objective of these studies was to evaluate the effects of introduced ungulates, we chose comparable sites that were similar in everything except presence of ungulates. I selected four pairs of forested sites for the study, each pair consisting of one site with cattle and one without them. No comparable sites with and without deer could be found. Site area ranged between 6 and 12 ha. All sites were dominated by coihue (*Nothofagus dombeyi*), usually accompanied by Patagonian cypress (*Austrocedrus chilensis*); these two tree species are wind-pollinated. In contrast, many understory and groundcover species are insect-pollinated. The four pairs of sites (Fig. 2.2) are: (1) Llao Llao (withouth cattle = nc) – Cerro López (with cattle = c); (2) Safariland (nc) – Arroyo Goye (c); (3) Lago Mascaridi (nc) – Lago Mascaridi (c); and (4) Quettrihué (nc) – Quettrihué (c). The paired sites are contiguous in two sets (i.e., Mascaridi and Quettrihué) and separated by a few kilometers in the other two. I worked with pairs of sites rather than unmatched replicates because of the strong longitudinal humidity gradient that characterizes the area. To be comparable, all sites should be located at the same longitude; since it was impossible to find a set of sites that met this criterion, I used paired sites differing only in the presence of cattle.

Question 1: Changes in interaction biodiversity induced by introduced ungulates

Many studies documenting anthropogenic changes, and most conservation efforts designed to mitigate them, are concerned with maintaining biodiversity at multiple levels of organization, mainly species diversity and the genetic diversity of populations (Caughley 1994; Pickett et al. 1997). However, the long term conservation of biodiversity may depend not only on maintaining the “parts” that compose such diversity but also on the way these parts are assembled—what Thompson (1997) has termed “the conservation of interaction biodiversity.” Previous studies of anthropogenic effects on plant–pollinator interactions have considered interactions among subsets of species within a community and the fitness consequences of such interactions, particularly for plants (Aizen and Feinsinger 1994; Kearns et al. 1998; Kremen et al. 2002; Renner 1998; Sugden 1985; Vázquez and Simberloff 2002; Vázquez and Simberloff 2004). However, to our knowledge, no previous study had considered the effect of introduced species on properties of whole networks of interacting species. Here we discuss results from a previously published study (Vázquez and Simberloff 2003) that strongly suggest that cattle introduced in a native temperate forest of the southern Andes have modified the structure of an interaction network of plants and pollinators.

Methods

Field methods

We studied plant–pollinator interactions in four grazed and four ungrazed sites in native *Nothofagus dombeyi* forest in and around Nahuel Huapi National Park. Of 15 plant species originally included in the study, 14 received visits by presumed pollinators (i.e., flower visitors that contacted floral reproductive parts and thus have the potential to be effective pollinators) and were thus included in the analysis; a total of 90 presumed pollinator species were recorded.

Quantification of plant–pollinator interactions

With the above data we constructed a plant–pollinator interaction network for each of the eight sites (Fig. 1). These networks can also be represented as two-dimensional matrices (see Supplementary Material) in which each column represents a plant and each row a pollinator species, and cells represent the number of times each interaction was observed (Vázquez and Aizen 2003; Vázquez and Aizen 2004).

We used the proportion of visits in which a particular pollinator species contacted the reproductive parts as a rough estimate of its effectiveness (Vázquez and Simberloff 2002). We then calculated the effective number of visits for plants as $e = pt$, where p is the proportion of visits in which the pollinator contacted the reproductive parts of the flower, t is the total number of visits of the particular pollinator species, and e is the estimated number of effective visits. We used e values corresponding to each combination of plant and pollinator species as entries in the interaction matrix. Interaction matrices were standardized by sampling effort by dividing the entries of each matrix by the number of observation periods in the corresponding site. We conducted all analyses using both the standardized and the unstandardized (“raw”) matrices; because results with the two data formats were similar, only results for standardized data are reported.

Results

Fig. 1 shows the plant–pollinator interaction networks webs for the eight sites. Statistical analyses reveal ungrazed sites are distinctly separated from grazed sites in the two-dimensional space defined by the first two coordinates resulting from multivariate ordination (Fig. 2). These results suggest that the structure of the plant–pollinator interaction network in

each site is not independent of the presence of cattle. Furthermore, results of a permutation test strongly suggest that the association between grazing and network structure is highly significant.

Although the above results suggest the existence of strong effects of cattle on the structure of the plant–pollinator interaction networks of Nahuel Huapi, the analysis is silent about the details of such effects. In particular, we ask whether all pairwise interactions contribute equally to the observed pattern in inter-site dissimilarity and, if not, which interactions contribute most. Permutation tests indicate that only a handful of pairwise interactions drive the observed dissimilarity pattern, while the influence of the remaining interactions is minimal (Table 1).

All influential interactions identified by the above test are among pairs of relatively abundant species whose abundances tend to covary, either negatively or positively, with the presence of cattle (Vázquez and Simberloff 2002; Vázquez and Simberloff 2004). For example, the herb *Alstroemeria aurea* interacts very frequently with the bumblebee *Bombus dahlbomii* in ungrazed sites, but it does so less frequently in grazed sites, where both species are relatively rare; conversely, the interaction between the understory tree *Schinus patagonicus* and the halictid bee *Ruizantheda mutabilis* is frequent in grazed sites but virtually absent from ungrazed ones (Fig. 1, Table 2). Thus, the observed effect of cattle on site dissimilarity is brought about by the change in the frequency of a few “dominant” interactions.

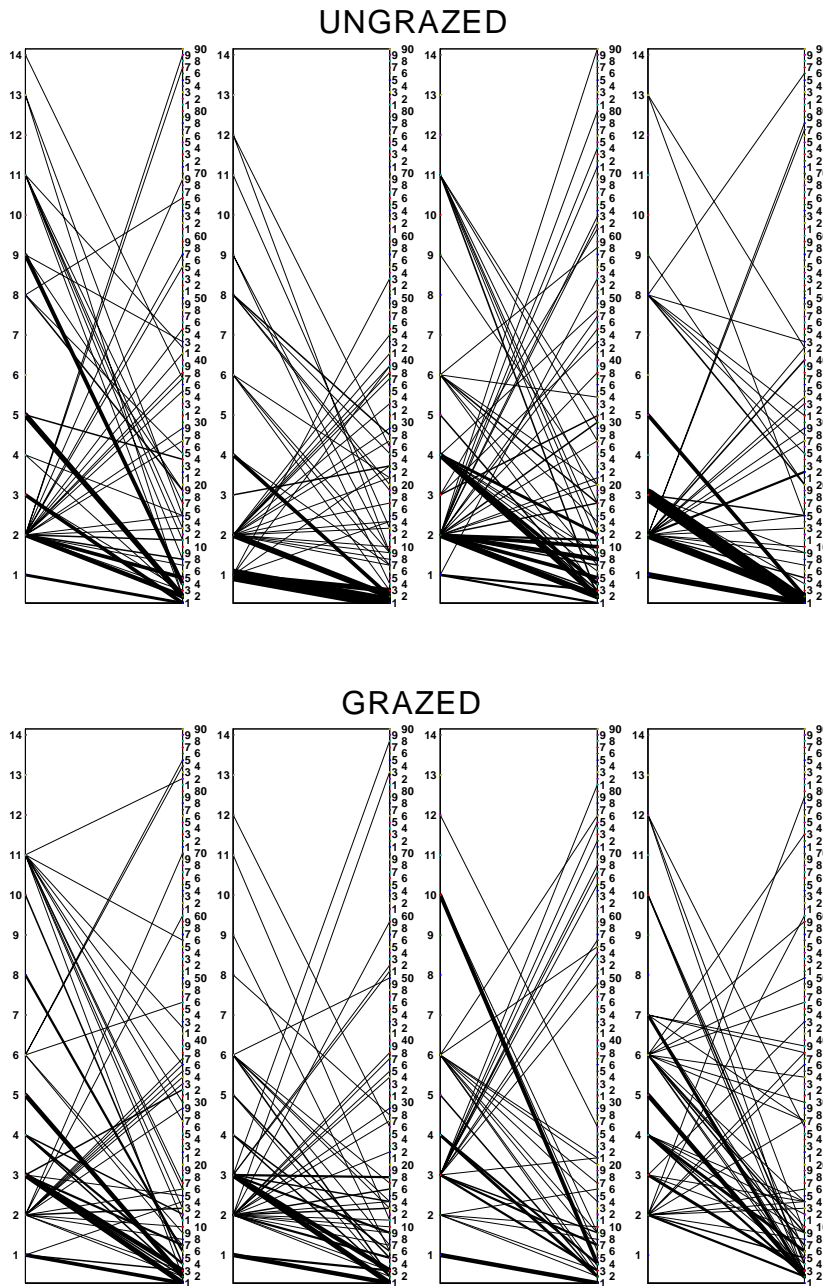


Figure 1. Plant–pollinator interaction networks in the eight sites. In each network, lines indicate pairs of interacting species; end points of lines represent plant (left) and pollinator (right) species. Species identities are indicated by numbers (see Supplementary Material for names; notice that only first digit is given for pollinator species, except for multiples of ten). Line thickness is proportional to the square root of the standardized frequency of interaction between the plant–pollinator species pair. Upper row, ungrazed sites (from left to right: Llaol Llaol, Safariland, Lago Mascardi, Península Quetrichué); lower row, grazed sites (from left to right: Cerro López, Arroyo Goye, Lago Mascardi, Península Quetrichué). Grazed and ungrazed sites in the same geographical location are vertically aligned. Source: Vázquez and Simberloff (2003).

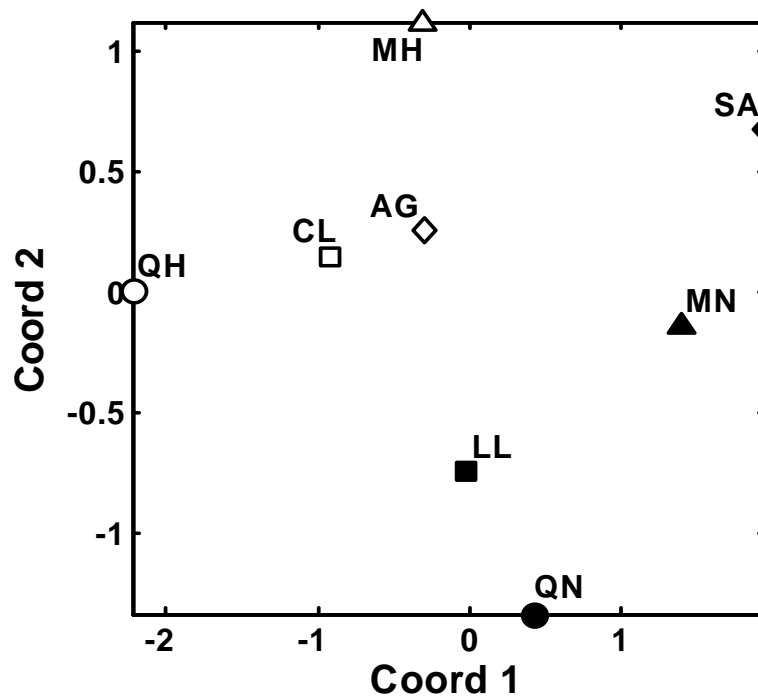


Figure 2. Reduced-space plot of first two coordinates resulting from nonmetric multidimensional scaling (MDS). White symbols: grazed sites (CL, Cerro López; AG, Arroyo Goye; MH, Mascardi; QH, Quetrihué); black symbols: ungrazed sites (LL, Llao Llao; SA, Safariland; MN, Mascardi; QN, Quetrihué). Paired sites are represented by the same symbol. The good fit of the linear regression of the distance among original descriptors (x) vs. those obtained after reduction with MDS (y) suggests that reduced-space scaling is a good representation of the data ($y = 0.2236 + 0.9037 x$; $P < 0.0001$; $R^2 = 0.89$; (Legendre and Legendre 1998). Source: Vázquez and Simberloff (2003).

Table 1. Influence of particular interactions between pairs of species on results of Mantel permutation test. Listed below are pairs of interacting species whose removal caused the Mantel statistic to become non-significant at the 95% (**) or 99% (*) significance level (numbers to the left of species names match those of Fig. 1 and Supplementary Material). Also given is resulting value of Mantel's statistic after removal of the selected interaction (r_m). Source: Vázquez and Simberloff (2003).

Plant species		Pollinator species		r_m	
2	<i>Alstromemeria aurea</i>	2	<i>Bombus dahlbomii</i>	-0.0029	**
3	<i>Schinus patagonicus</i>	3	<i>Ruizantheda mutabilis</i>	-0.4478	*
4	<i>Berberis darwinii</i>	2	<i>Bombus dahlbomii</i>	-0.4848	*
9	<i>Ribes magellanicum</i>	4	<i>Trichophthalma amoena</i>	-0.4918	*
2	<i>Alstromemeria aurea</i>	8	<i>Manuelia gayi</i>	-0.4996	*
2	<i>Alstromemeria aurea</i>	5	<i>Bombus ruderatus</i>	-0.5015	*

Discussion

Results presented here suggest that the structure of plant–pollinator interaction networks in Nahuel Huapi is strongly affected by the presence of cattle. Our work adds to a growing literature showing that introduced species can, and often do, alter the properties of communities they invade in multiple ways (Mooney and Hobbs 2000; Simberloff 1991; Williamson 1996). Together with recent reports by Vander Zanden et al. (Vander Zanden et al. 1999) and Henneman and Memmott (Henneman and Memmott 2001), our study demonstrates the potential of introduced species to modify the structure of entire networks of interacting species. Our study also adds to the long list of documented effects of introduced mammalian herbivores (de Vos et al. 1956; Dennis 1997; Ebenhard 1988; Smit et al. 2001; Vázquez 2002b; Wardle et al. 2001), thus supporting the notion that introduced consumers in general and herbivores in particular tend to have disproportionately strong impacts on the ecosystems they invade (Duffy 2003).

Of course, that the above changes in species interactions occur does not mean they are ecologically relevant. Plant–pollinator interactions are known to be, in most cases, highly resilient, and changes of the sort we have documented may have few consequences for the interacting species (Waser et al. 1996). Thus, even though the demonstration of an effect of an introduced species on the structure of the plant–pollinator interaction network is itself significant, it should be interpreted with caution.

The above caveat notwithstanding, it is very likely that the few interactions found to drive the observed patterns in network structure are in fact important for at least one of the two interaction partners involved. For example, in the highly influential interaction between the herb *Alstroemeria aurea* and the bumblebee *Bombus dahlbomii* (see Table 2), the bumblebee is in fact the most important pollinator of the herb (Aizen 2001), while the herb is in turn the most important flower resource for the bumblebee during the summer (Vázquez 2002a; Vázquez and Simberloff 2004). A similar situation occurs with other interactions listed in Table 2: they represent the most frequent interactions for the participating species. Although visitation frequency is not necessarily synonymous with interaction strength (Schemske and Horwitz 1984), it seems likely that the few statistically influential interactions are in fact also biologically important for the participating species.

The maintenance of the few dominant interactions may also be important for other species in the system. Some of the species involved in these interactions are extremely generalized, interacting with many rare specialists. Thus, the degree of specialization and of mutual dependence is likely to be highly asymmetric. For example, *B. dahlbomii* and *A. aurea* are the most generalized pollinator and plant species, respectively, in our study system (Vázquez and Simberloff 2002), interacting with a large number of species, many of them rare species that interact almost exclusively with these super-abundant, super-generalist species (Fig. 1). Although the vast majority of these interactions may be virtually irrelevant for *B. dahlbomii* and *A. aurea*, they are likely to be important for the rare specialists involved in them. Thus, these dominant interactions potentially represent “keystone interactions,” and their persistence may be important for the maintenance of a much larger set of interactions.

Although our analysis has identified clear changes in the interactions among plants and pollinators that are likely the result of the presence of cattle, it does not provide an answer to the more fundamental question of how those changes were brought about. As in most ecological studies, the complex nature of the study system requires the consideration of multiple, non-exclusive mechanisms. Some of the observed changes may be attributed to the change in the population abundance of individual species in response to cattle. For example, the abundances of two of the plant species involved in the influential interactions listed in Table 2, *A. aurea* and *R. magellanicum*, sharply decrease in grazed sites (Vázquez and Simberloff 2004); thus, the lower frequencies of some of their interactions in grazed sites may

simply reflect their increased rarity. However, the abundance of other species is not strongly affected by cattle (Vázquez and Simberloff 2002; Vázquez and Simberloff 2004), and therefore changes in their interactions probably involve more complex mechanisms, including changes in the relative visitation frequency of pollinators to the different plant species.

We have attempted to characterize the effects of an introduced species on the structure of an entire network of interacting species. We have found strong evidence of such effects and have demonstrated that they mainly result from changes in a few selected interactions. Whether these results are general or just a peculiarity of our study system is an open question; we hope our work will motivate others to seek an answer.

Question 2: Indirect effects of introduced ungulates on pollination and plant reproduction

Herbivores affect plants in different ways, sometimes with dramatic ecological and evolutionary consequences for plant populations. For example, grazing animals can determine the relative abundance of different plant species in a community (Harper 1977; Huntly 1991). Classic examples are the control of the diversity of herbaceous species in British chalk grasslands by rabbits (Tansley and Adamson 1925) and the control of species diversity in intertidal algal communities by the snail *Littorina littorea* (Lubchenco 1978). The most obvious effect of herbivores on plants is increased mortality from browsing and trampling. On the other hand, loss of vegetative tissues and resulting decreased growth may reduce plant fitness (Hendrix 1988). Furthermore, herbivores sometimes decrease plant fitness by directly consuming reproductive tissues (Gómez and Zamora 2000; Herrera 2000) or by preying on seeds (Herrera 1993; Louda 1982).

Herbivores also affect plants in subtler ways, for example through indirect effects mediated by one or more other species. An indirect effect occurs when one species affects another through a third one (Strauss 1991; Wootton 1994; Wootton 2002). One way herbivores can affect plants indirectly is by modifying interactions with animal mutualists such as pollinators and seed dispersers. Several studies have demonstrated that folivores and florivores indirectly affect both male and female fitness of plants. Folivory and florivory can affect floral morphology and physiological traits, which can in turn affect pollinator visit frequency and, ultimately, male and female reproductive success (Hendrix 1988; Mothershead and Marquis 2000; Strauss 1997; Strauss and Agrawal 1999; Strauss et al. 1996).

Modification of floral traits is not the only way herbivores can indirectly affect plant-pollinator interactions, however. Plant population density may strongly influence plant-pollinator interactions, pollination, and plant reproductive success (Bosch and Waser 2001; House 1992; Kunin 1993; Kunin 1997a; Kunin 1997b; Rathcke 1983). Thus, if herbivores modify plant population density directly (e.g., through browsing and trampling), this modification can in turn indirectly affect pollination and reproduction of individuals that have escaped herbivores, via a modified interaction with pollinators.

Below I discuss results of a published study (Vázquez and Simberloff 2004) aimed at evaluating whether introduced ungulates affect pollination and plant reproduction by modifying plant population density. The study compared population density, plant-pollinator interactions, pollination, and reproduction for eleven plant species growing in the understory of pairs of sites with and without cattle in a forest dominated by *Nothofagus dombeyi*. Specifically, we asked: (i) Do cattle affect absolute and relative plant population density? (ii) If absolute population density is affected, does this in turn result in further effects in the same direction on pollinator visitation, and on conspecific and heterospecific deposition? (iii) If relative population density is affected, does this result in further effects in the same direction on conspecific pollen deposition, and in the opposite direction on

heterospecific pollen deposition? (iv) If pollen deposition is affected, does this affect plant reproductive success? Because of the limitations of our non-manipulative approach, for the only species for which we found evidence of indirect effects of herbivores on its pollination and reproduction, we looked for additional, independent evidence for the hypothesized mechanisms.

Study sites and organisms

The study was conducted on the four pairs of sites described above for question 1. It included 11 animal-pollinated plants growing in the understory and groundcover of our sites. These constituted all animal-pollinated species abundant enough in at least three pairs of sites to allow replication and on which we could measure interaction with pollinators and fruit or seed set.

Field methods: comparison between grazed and ungrazed sites

Here we give a brief overview of field and laboratory methods used in the study. Details can be found in Vázquez and Simberlof (2004). Plant population density was estimated by examining 30 rectangular quadrats of $2\text{ m} \times 10\text{ m}$ separated by a fixed distance along transects in each site, counting the number of individuals of each species per quadrat. Pollinator visitation observations were conducted on individual plants flowering throughout each of the eight sites. Individual plants to be sampled were selected haphazardly; we tried to sample as many individuals in as many locations within each site as possible, so as to minimize spatial autocorrelation among samples. Pollinators visiting flowers of each species were sampled in 10 minute periods. Pollination performance of plants was studied by estimating the number of conspecific and heterospecific pollen grains deposited on flower stigmas. To study plant reproduction, we tagged individuals of all plant species in all sites where they were present, recording the number of flowers per individual (herbs) or per branch (shrubs, trees and vines).

To evaluate browsing intensity on plants, we checked all individuals of all species within each quadrat used to estimate density for signs of browsing and then calculated a browsing index. We also measured the impact of cattle on soil compaction (bulk density) as a measure of the intensity of trampling by cattle by taking 30 soil samples per site with a corer.

Field and laboratory methods: further studies on *Alstroemeria aurea*

For *Alstroemeria aurea*, the only species for which we found evidence of indirect effects of cattle on pollination and reproduction in the comparisons between grazed and ungrazed sites, we sought additional evidence for the hypothesized mechanisms. To this end, we conducted trampling and hand-pollination experiments and a spatial analysis of the effect of floral neighborhood density on pollinator visitation, pollination, and reproduction. Again, details of these methods can be found in Vázquez and Simberlof (2004).

Results

Results of the comparisons between grazed and ungrazed sites for the 11 plant species are summarized in Table 2. For most species we found no density-mediated indirect effects of cattle on pollination and reproduction. In six cases, there were no significant effects of grazing on either absolute or relative population density, which precludes further analysis of effects on plant-pollinator interactions, pollination, and reproduction; a seventh species for which we detected positive effects of grazing on density, *B. buxifolia*, failed to produce flowers in ungrazed sites, which precluded further analyses of other dependent variables. Of the remaining four species, for which we found at least partial evidence of negative effects of grazing on absolute or relative population density, only *A. aurea* showed effects on

pollination and reproduction that were consistent with the hypothesis. Thus, for *A. aurea* we found significant effects for all the variables examined in at least one of the two years.

Further studies on *A. aurea*, including detailed studies of the effect of floral neighborhood on pollinator and reproduction and experiments to evaluate susceptibility to trampling and pollen limitation further suggest that cattle indeed affect the pollination and reproduction of *A. aurea* indirectly by decreasing its population density.

Conservation implications

Previous studies of the effects of introduced ungulates in the southern Andean temperate forest have dealt mainly with direct effects on forest dynamics and understory vegetation. These studies, along with the results presented here, have shown that introduced ungulates have important effects on some understory species (Vázquez 2002b). Our study demonstrates that subtler indirect impacts can also occur.

Although our study dealt only with the impact of cattle, it is likely that other introduced ungulates (particularly deer) have similar effects. For example, on Isla Victoria, where introduced deer have important impacts on the forest understory vegetation (Veblen et al. 1989), *A. aurea* is also extremely rare, restricted to areas relatively inaccessible to deer (e.g., among fallen trees, D.P. Vázquez and D. Simberloff, personal observation). Likewise, the observed effects on *A. aurea* could be occurring beyond the limited geographic range of this study, as introduced ungulates are widespread in the region (Bonino 1995; Jaksic 1998; Jaksic et al. 2002; Navas 1987).

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Table 2. Summary of results of comparisons between grazed and ungrazed sites for the eleven species. Shaded cells indicate at least partial evidence for effects of grazing on a particular species, dependent variable, and season; symbols in shaded cells indicate the following: +, –: significant main effect of grazing with no significant interaction, or significant interaction with all contrasts significant, thus providing strong evidence of positive or negative effects, respectively; (+), (–): significant interaction with at least half of contrasts significant and with effects in the same direction, thus providing weak evidence of positive or negative effects, respectively. Unshaded cells with “n.s.” are statistically insignificant results. Empty cells indicate unmeasured or unreported effects. Source: Vázquez and Simberloff (2004).

Plant species \ season:*		Dependent variable															
		Abs. dens.	Rel. dens.	Poll. visitation		Pollination [†]						Reproduction [‡]					
						consp.		heterosp		pr. consp.		fr/fl		s/fr		s/fl	
						1	2	1	2	1	2	1	2	1	2	1	2
<i>Alstroemeria aurea</i>	(−)	−	ns	ns	(−)	−	+	(+)	−	−	(−)	(−)	(−)	(−)	(−)	(−)	
<i>Aristotelia chilensis</i>	−	ns	ns	ns	ns		ns		ns		+	ns	ns		ns		
<i>Berberis buxifolia</i> [§]	(+)	+															
<i>Berberis darwinii</i>	ns	ns															
<i>Calceolaria crenatiflora</i>	ns	ns															
<i>Cynanchum diemii</i>	(−)	ns	ns	ns								ns	ns	ns		ns	
<i>Gavilea odoratissima</i>	ns	ns															
<i>Rosa eglanteria</i>	ns	ns															
<i>Ribes magellanicum</i>	(−)	−	ns	ns		ns	ns	ns	+	ns	(−)	ns	ns	ns		ns	
<i>Schinus patagonicus</i>	ns	ns															
<i>Vicia nigricans</i>	ns	ns															

[†]Results summarized for deposition of conspecific pollen (consp.), heterospecific pollen (heterosp.), and proportion of conspecific pollen (% consp).

*Fieldwork seasons are indicated as follows: 1, 1999-2000; 2, 2000-2001.