To the Graduate Council:

I am submitting herewith a dissertation written by Diego P. Vázquez entitled "Interactions among Introduced Ungulates, Plants, and Pollinators: A Field Study in the Temperate Forest of the Southern Andes." I have examined the final electronic copy of this dissertation for form and content and recommend that it is accepted in partial fulfillment of the requirement for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Daniel Simberloff
Major Professor

We have read this dissertation
and recommend its acceptance:

David Buehler

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Anne Mayhew
Vice Provost and
Dean of Graduate Studies

(Original signatures are on file with official student records.)

INTERACTIONS AMONG INTRODUCED UNGULATES, PLANTS, AND POLLINATORS

A FIELD STUDY IN THE TEMPERATE FOREST OF THE SOUTHERN ANDES

A Dissertation Presented for the
Doctor of Philosophy Degree

The University of Tennessee, Knoxville

Diego P. Vázquez
May 2002

A mis padres, mis primeros maestros

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ABSTRACT

Introduced mammalian herbivores can significantly affect ecosystems. I studied the effects of introduced ungulates on plant-pollinator interactions in the temperate forest of the southern Andes. Introduced mammalian herbivores, including ungulates, are a major conservation problem in this biome. I conducted field studies in eight forested sites where *Nothofagus dombeyii* was the dominant canopy tree. I described the interactions between fifteen common, insect-pollinated understory plants. I used these data to address two main questions. The first one is whether the susceptibility of plants and pollinators to disturbance by introduced ungulates is related to their degree of interaction specialization and interaction asymmetry. I found no relationship between degree of specialization and a species' response to disturbance. I also found that plant–pollinator interactions tend to be asymmetric in this system; however, asymmetry of interactions did not explain the variability in species' responses to disturbance. The second question I addressed is whether introduced ungulates can affect pollination and plant reproduction indirectly by modifying plant population density. This hypothesis is different from previous hypotheses of indirect effects of herbivores on plants, all of which concerned individual-level effects on vegetative and reproductive traits, whereas my hypothesis focuses on population-level effects. I found strong evidence of such an effect for only one of the species I studied, the herb *Alstroemeria aurea*. The general lack of evidence for indirect effects on most species may result from resistance to cattle grazing, spatial refugia, or low statistical power of my analysis. For *A. aurea*, additional evidence indicates that herbivores decrease the absolute and relative population density of this species through trampling., which in turn results in lower conspecific pollen deposition in stigmas and lower reproductive performance. Thus, my study suggests that introduced ungulates can in some circumstances affect plant-pollinator interactions significantly. However, in most cases plant-pollinator mutualisms appear resilient to the effects of introduced ungulates, and the direct effects of introduced ungulates on plants and pollinators are in general stronger than the indirect effect through mutualistic partners.

RESUMEN

Los mamíferos herbívoros introducidos pueden afectar a los ecosistemas significativamente. Estudié los efectos de los ungulados introducidos sobre las interacciones entre plantas y polinizadores en el bosque templado de los Andes australes. Los mamíferos herbívoros introducidos, incluyendo los ungulados, representan un serio problema para la conservación de este bioma. Realicé estudios de campo en ocho sitios con bosque dominado por *Nothofagus dombeyii*. Describí las interacciones entre quince plantas comunes del sotobosque polinizadas por insectos. Utilicé esos datos para responder dos preguntas principales. La primera es si la susceptibilidad de las plantas y los polinizadores a los disturbios ocasionados por el ganado está relacionada al grado de especialización y a la simetría de la especialización en las interacciones entre plantas y polinizadores. No encontré ninguna relación entre el grado de especialización y la respuesta de las especies a los disturbios. Por otro lado, observé que las interacciones entre plantas y polinizadores tienden a ser asimétricas en este sistema; sin embargo, esta asimetría no contribuyó a explicar la variabilidad en la respuesta de las especies a los disturbios. La segunda pregunta que intenté responder es si los ungulados introducidos pueden afectar la polinización y la reproducción de las plantas al modificar su densidad poblacional. Esta hipótesis es diferente de hipótesis previas sobre los efectos indirectos de los herbívoros sobre la polinización y la reproducción de las plantas, las cuales conciernen efectos a nivel individual sobre caracteres vegetativos y reproductivos, mientras que mi hipótesis está enfocada en los efectos a nivel poblacional. Encontré evidencia de la existencia de tal efecto sólo para una de las especies que estudié, la herbácea *Alstroemeria aurea*. La falta de efectos para la mayoría de las especies podría deberse a la resistencia de las plantas a la herbivoría, la existencia de refugios espaciales y la baja potencia estadística de mi análisis. Para *A. aurea*, evidencia adicional indica que los herbívoros pueden reducir la densidad poblacional absoluta y relativa de esta especie mediante el pisoteo, lo cual resulta a su vez en un menor depósito de polen en los estigmas florales y en un menor rendimiento reproductivo. De este modo, mis resultados sugieren que los ungulados introducidos pueden en algunas circunstancias afectar significativamente las interacciones entre plantas y polinizadores. Sin embargo, en la mayoría de los casos estos mutualismos parecen ser resilientes a los efectos de los ungulados introducidos, y los efectos directos de estos herbívoros son en general más fuertes que los efectos indirectos a través de los mutualistas.

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1

INTRODUCTION

Understanding the causes and consequences of species interactions has always been a central theme in ecology and evolutionary biology, for a good reason. Species can affect the short and long-term persistence of other species and influence their evolutionary pathways. However, species interact in complex ways, and whether certain kinds of interactions occur and how those interactions affect each of the interacting species is usually not obvious. For example, the role of competition in structuring ecological communities has been hotly debated (Connor and Simberloff 1979; Strong et al. 1984). Likewise, early observations of simple food webs led some theoretical ecologists to propose several generalities about food web patterns and dynamics (Cohen 1978; Pimm 1982; Cohen et al. 1990; Pimm et al. 1991); however, most of those generalities did not agree with patterns observed in more complex food webs (Paine 1988; Polis 1991; Polis and Strong 1996). There is also a current debate about whether plants and pollinators interact strongly enough to affect each other's ecologies and evolutionary pathways significantly (Herrera 1996; Ollerton 1996; Waser et al. 1996; Gómez and Zamora 1999; Johnson and Steiner 2000).

The paucity of general rules of species interactions identified by ecologists has led some to despair, claiming that we should stop devoting so much time and effort to studying species interactions (Lawton 1999). That is, they claim the time is ripe for a paradigm shift (see Kuhn 1970), from detailed study of species interactions to the study of broader, macroecological patterns and processes (Brown 1995). Others, however, argue that the search for generalities in population and community ecology are worth the effort, and that "it [is] very likely that spectacular discoveries still await us" (Ehrlich 1997, pp. 46). Many believe that a mixture of small-scale, experimental studies of species interactions with broader-scale studies is the more promising approach (Maurer 1999). I include myself among the latter.

Species introductions into new areas constitute a good opportunity to study ecological interactions. Sometimes the invader is a completely new functional group previously absent from the recipient community and can contribute to a general understanding of the role of that particular functional group. Besides being a useful tool for addressing basic ecological questions, biological invasions are one of the most serious threats to biodiversity. This makes the study of biological invasions doubly worthwhile.

Biological invasions 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 (Vitousek et al. 1997; Brown and Lomolino 1998). Many invasions have led to drastic and fundamental changes in species composition, habitat structure, and ecosystem processes (Elton 1958; Simberloff 1991; Williamson 1996), and some argue that they can affect long-term biological diversity at a global scale (Vitousek et al. 1996; but see Rosenzweig 2001; Collins et al. 2002; Rosenzweig 2002).

Although biological invasions by natural means have occurred throughout the history of life, the rate at which invasions occur has undoubtedly increased recently (Crosby 1986; Di Castri 1989; Low 1999). Humans have served as vectors of other species since prehistoric times, but the explosive increase in human population and the consequent increase in human movement at a global scale during the last five centuries have resulted in a dramatic increase in the biotic interchange among previously isolated biogeographic regions. For example, in the United States the number of introduced insect species has risen exponentially since the year 1640 (Sailer 1983). The current globalization of economy and partial homogenization of the world's cultures are also resulting in a globalization of ecology—what Lövel (1997) has called the "macdonaldization" of the world's ecology. Furthermore, invasive species are not homogeneously distributed among taxonomic groups but tend to be grouped in some "successful" taxa (Binggelli 1996; Daehler 1998; Pyšek 1998; Lockwood 1999; Cadotte and Lovett Doust 2001; Vázquez and Simberloff 2001), which exacerbates the problem of homogenization.

Some species have catastrophic effects on the native biota. For example, the introduction of the Nile perch (*Lates niloticus*) to Lake Victoria, eastern Africa, has caused the extinction of over two hundred species of endemic cyclids (Barel et al. 1985; Kaufman 1992). In North America, the introduction of the fungus *Endothia parasitica* almost exterminated a dominant tree species in the eastern deciduous forest, the American chesnut (*Castanea dentata*) (Elton 1958). And the alga *Caulerpa taxifolia*, escaped from the Musée Oceanographique in Monaco, is changing the coastal ecology of a substantial portion of the

Mediterranean (Meinesz 1997). Many introduced mammalian herbivores seem particularly able to produce drastic changes in the ecosystems they invade (de Vos et al. 1956; Ebenhard 1988).

This monograph is an attempt at understanding the effects of one particular kind of introduced mammalian herbivore (ungulates), on particular components of the community (plants and their insect pollinators), in a particular system (the temperate forest of the southern Andes [TFSA]). In chapter 2 I discuss plant-pollinator interactions in the TFSA, giving the background natural history necessary to address the questions raised in subsequent chapters. Plant-animal mutualisms are highly prevalent in the TFSA, and thus this biome seems an ideal system to study whether, and how, introduced species disrupt those interactions. Chapter 3 reviews the evidence on the effects of introduced mammalian herbivores in the TFSA. As I show, introduced mammalian herbivores appear to be affecting many components of the forest ecosystem, including forest regeneration, understory plant diversity and composition, and some animal groups. Chapter 4 is a test of a long-standing hypothesis in ecology and conservation biology—that ecological specialists are more susceptible to disturbance than are generalists. Using the data on plant pollinator interactions described in Chapter 2, I test whether the effect of disturbance by introduced cattle on plants and insect pollinators is related to the degree of interaction specialization among the latter. In Chapter 5 I take a more mechanistic approach to understanding a particular kind of effect of introduced cattle: the indirect effect on pollination and plant reproduction through pollinators. In particular, I test the hypothesis that modified population density of plants resulting from the direct effect of introduced ungulates can affect the interaction between plants and pollinators, leading in turn to modified pollination and reproductive performance. Chapter 6 is a continuation of the previous chapter, testing one hypothesis proposed to explain the lack of indirect effects on the tree *Aristotelia chilensis*—that the spatial aggregation of flowering individuals in refugia from herbivores minimizes the effect of lower population density. Finally, in the last chapter I attempt a synthesis of the findings of this work and propose directions for future research.

2

THE ECOLOGICAL THEATER: PLANT-INSECT POLLINATOR INTERACTIONS IN NAHUEL HUAPI

Summary. This chapter gives background information on the natural history of plant-pollinator interactions in the temperate forest of the southern Andes and presents descriptive results from field studies I conducted in *Nothofagus dombeyii* forest in Nahuel Huapi National Park. I show that the assemblage of insect flower visitors is more diverse than previously thought. However, relatively few species account for most of the flower visitation, suggesting that the assemblage of pollinators is functionally poorer than suggested by its diversity. I compare the patterns found in Nahuel Huapi with those of two other studies in the temperate forest in Chile, and with temperate and tropical biomes in other parts of the world.

> "For surely the purpose of theories and conceptualizations is not merely to exist in themselves, as monuments to our ingenuity and insight, but to organize the myriad details of the natural world as well."
>
> —D. J. Futuyma (Futuyma 1998, pp. 4)

INTRODUCTION

Plant-pollinator interactions have long been regarded as tightly coevolved and mutually specialized. For example, the concept of "pollination syndromes" implies adaptive specialization of particular kinds of flowers to particular kinds of pollinators (Faegri and van der Pjil 1979). In this view, floral traits reflect adaptations to one or another pollinator type roughly at the level of orders (e.g., beetles vs. butterflies vs. bees). Some evolutionary biologists have also suggested a general evolutionary trend from generalization to specialization, with increasingly tight coevolution of plants and pollinators (Armbruster and Baldwin 1998; Schluter 2000). This view of specialization and coadaptation in plant-pollinator interactions has driven most of the research traditionally done on pollination biology. This research has typically entailed detailed studies of single species of plants or pollinators, or of small groups of species.

However, pollination biologists are increasingly emphasizing a broader community-level focus, in which patterns of interaction among all the plants and pollinators in a given area, or substantial subsets, are studied simultaneously. This perspective has revealed a higher degree of generalization in pollination systems than previously anticipated (Ollerton 1996; Waser et al. 1996; but see Johnson and Steiner 2000). For example, Waser et al. (1996) used several community-wide datasets to argue that, contrary to the traditional view, pollination systems contain many generalist species of plants and pollinators, and relatively few species that specialize in one or a few interaction partners. Furthermore, plant-pollinator interactions have been observed to vary greatly across space and time (Herrera 1988; Thompson 1994; Fishbein and Venable 1996; Gómez and Zamora 1999; Aizen 2001). These observations have challenged the traditional views of specialization in plant-pollinator interactions and have stimulated renewed empirical and theoretical exploration.

One key need for the study of community-wide patterns of plant-pollinator interactions is the availability of detailed datasets. Regrettably, very few community-wide studies present such information. Furthermore, most available studies simply present data in the form of a binary matrix (i.e., with ones indicating interactions between pairs of species and zeros indicating no interaction). Although this kind of information is certainly valuable, more detailed data (e.g., frequency of interaction between pairs of species) are necessary. The same kind of binary matrices have been used for years for analyses of food web patterns (e.g., Cohen et al. 1990; Martinez 1992, 1994), although more detailed information, such as interaction strength or frequency is certainly desired (Cohen et al. 1993).

As it is suggested by the title and by the above quote by Futuyma, the purpose of this chapter is to provide the basic natural history information for the questions raised (and sometimes answered) in the subsequent chapters. Like Futuyma, I am convinced that many of our ideas about nature do not make sense in the absence of a sound knowledge of the natural world. Thus, the information presented here does not attempt to answer any question; it is simply an attempt to describe one aspect of a system in some detail. And it is the foundation for what I develop in the rest of this volume. Furthermore, I hope that this information will be a useful contribution to the database of community-wide data sets of plant-pollinator interactions.

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

The temperate forest of the southern Andes (TFSA) lies on the southwestern fringe of South America, between 39º and 55º 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 (Veblen et al. 1996; Kershaw and Wagstaff 2001). 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 (Arroyo et al. 1996; Aizen and Ezcurra 1998).

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 endemicity 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 (Willson 1991; Smith-Ramírez and Armesto 1994; Aizen and Ezcurra 1998). 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, *Sephanoides sephaniodes* (Smith-Ramírez 1993; Armesto et al. 1996; Fraga et al. 1997). A similar pattern is observed for animal-seed dispersal (Willson 1991; Armesto et al. 1996).

Figure 2.1. The temperate forest of the southern Andes (shaded area). Adapted from Cabrera and Willink (1973).

Plant phenology in the TFSA is highly seasonal. In Chiloé Island, Chile, only one plant species bears flowers during the winter, the hemiparasite *Tristerix corimbosus* (Smith-Ramírez and Armesto 1994). This species is bird-pollinated and is thought to be the only food source for the hummingbird *Sephanoides sephaniodes* during winter (Smith-Ramírez 1993). The maximum number of species in bloom has been observed to occur in December, when 65% of the plant species bear flowers. Fruiting phenology shows a similar pattern, although the proportion of plants bearing fruits during winter is higher than the proportion of plants bearing flowers (Smith-Ramírez and Armesto 1994).

Unlike bird pollination and seed dispersal, insect pollination in the TFSA is poorly known. The only published community-wide study that I am aware of was carried out by Riveros et al. (1991) in the Valdivian forest of Puyehue National Park, Chile. They studied 31 plant species and found 50 flower-visiting insect species belonging to four orders: Diptera (19 sp.), Hymenoptera (19 sp.), Coleoptera (8 sp.), and Lepidoptera (4 sp.). Regrettably, they did not publish a list of the pollinator species they found, which would have been extremely useful for more detailed comparisons with the data presented here. Another study by C. Smith-Ramírez et al. is currently ongoing on Chiloé Island (see Aizen et al. 2002). Here I present data on plant-insect pollinator interactions in eight *Nothofagus dombeyii* forest sites in Nahuel Huapi National park and adjacent areas. To my knowledge, this is the first community-wide study of an insect pollinator assemblage in the TFSA on the eastern side of the Andes.

METHODS

Study area and 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 (Dimitri 1962; Cabrera and Willink 1973).

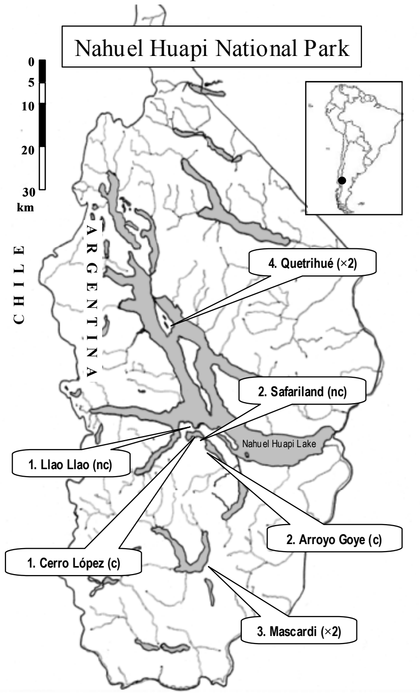

Figure 2.2. Four pairs of sites selected for the study: (1) Llao Llao (without cattle = nc) - Cerro López (with cattle = c); (2) Safariland (nc) - Arroyo Goye (c); (3) Lago Mascardi (nc) - Lago Mascardi (c); and (4) Península Quetrihué (nc) - Península Quetrihué (c). Paired sites in pairs 1 and 2 were separated by a few kilometers; sites in pairs 3 and 4 were contiguous (indicated as "× 2" in the graph).

Because the objective of this dissertation was to evaluate the effects of introduced ungulates, I 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 dombeyii*), 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 Mascardi (nc) – Lago Mascardi (c); and (4) Quetrihué (nc) – Quetrihué (c). The paired sites are contiguous in two sets (i.e., Mascardi and Quetrihué) 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.

Plant and pollinator species included

I included 15 species of plants growing in the understory and groundcover of my sites. These 15 species constituted all animal-pollinated species abundant enough in at least one site to allow replication for statistical analyses. All species were insect-pollinated, although one of them (*Tristerix corymbosus*) is pollinated mainly by the hummingbird *Sephanoides sephaniodes*. Pollinator species were not selected a priori; rather, all pollinator species visiting flowers of the study plant species were included. Lists of the plant and pollinator species included in the study are in Appendix 3.

Pollinator sampling

I observed pollinator visitation to flowers in two consecutive flowering seasons, 1999-2000 and 2000-2001, between early October to late February. However, whereas in the first year I sampled the whole community as comprehensively as possible, the second year I concentrated on a few plant species to address more specific questions. Therefore, the analysis presented in this chapter is based on data collected during 1999-2000.

A total of 2710 10 min. observation periods were conducted for all sites and plant species in 1999-2000. The numbers of sampling periods per site and plant species are given in Table 4.3; these numbers varied across species and sites, because species differed in their abundance, duration of the flowering period, and flowering time overlap with other species. For each visiting pollinator I recorded species name, number of flowers visited, and whether it contacted flower reproductive parts (anthers or stigmas). For unknown pollinator species, I collected the specimen and identified it in the laboratory. A reference collection has been deposited in the Laboratorio Ecotono at the Universidad Nacional del Comahue in Bariloche, Río Negro, Argentina (some bee specimens were also placed in the Museo Argentino de Ciencias Naturales in Buenos Aires).

RESULTS

A total of 129 morphospecies of flower visitors were recorded in the 1999-2000 flowering season in the eight study sites. Later identifications found that some of these morphospecies contained more than one species, so the number of flower visitors recorded is greater than 129. A complete list of the pollinator species recorded is given in Appendix 3, and the complete interaction matrices per site (i.e., which pollinator species visited which plant species) are given in Appendix 5. The taxonomic affiliation of flower visitors included at least one species of crab spider (Thomisidae), 24 morphospecies of coleopterans, 35 dipterans, 1 heteropteran, 2 homopterans, 60 hymenopterans, 3 lepidopterans, 1 dragonfly (Odonata), 1 unidentified insect order, and 1 hummingbird. When only individuals that contacted floral reproductive parts are considered (see Appendix 4), the number of recorded morphospecies drops to 95.

Phenology of flower visitors appears to be highly seasonal. Both species richness of flower visitors and number of individuals of all species recorded per week had two peaks, one in late October–early November (spring) and the second in late December–early January (summer) (Fig. 2.3a,b). These peaks partly coincided with those of the number of plant species bearing flowers (Fig. 2.3c). However, notice that, although during the summer the number of plants in bloom is lower than in the spring, both richness and number of individual visitors are higher. This is because one of the species flowering in the

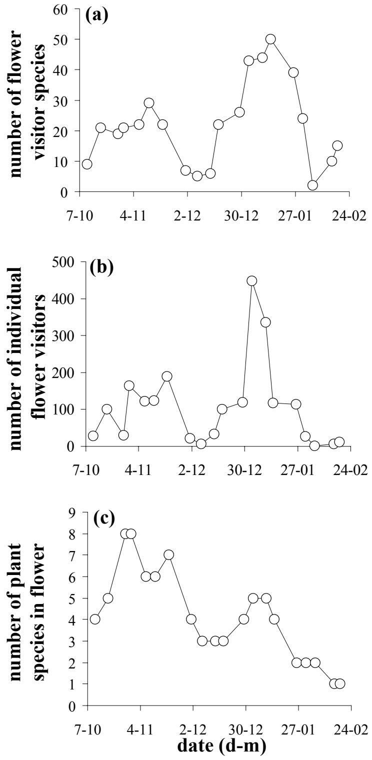

Figure 2.3. Phenology of insect flower visitors during the 1999-2000 flowering period. Data for the eight sites were pooled. (a) Number of species of flower visitors recorded per week; only those species contacting the floral reproductive parts were included. (b) Number of individual flower visitors recorded visiting flowers per week. (c) Number of plant species bearing flowers in each week.

summer is *Alstroemeria aurea*, which had the highest number of flower visitor species recorded for any plant species (Fig. 2.4).

However, this relatively diverse pollinator fauna appears to be poorer from a functional perspective. On the one hand, a high proportion of plant species interact with a low number of flower visitors (Fig. 2.4). Similarly, most flower visitors interact with a relatively low number of plants, and only a few species of insects account for a high proportion of all the visits recorded during 1999-2000 (Fig. 2.5). On the other hand, even for those plant species that interact with a relatively high number of pollinator species, the number of functionally important species of flower visitors (at least in terms of visitation frequency) is probably much lower than one would imagine by looking only at the number of species. For example, although 53 species of potential pollinators (i.e., flower visitors that contacted reproductive parts) were recorded visiting flowers of *Alstroemeria aurea*, only 6 species accounted for 80% of the visits. Similary, Aizen (2001) recorded, in three subsequent years in *Nothofagus pumilio* forest in Nahuel Huapi, over 90% of the visits to this species were by the bumblebee *Bombus dahlbomii* (Apidae: Bombini), the only native bumblebee in the TFSA.

Bombus dahlbomii is in turn an extremely generalized pollinator; it was recorded visiting 10 of the 15 plant species (Fig. 2.5), and was the most frequent flower visitor in 5 of them. Another frequent pollinator was the colletid bee *Cadeguala albopilosa*, accounting for 85% of the recorded visits to *Aristotelia chilensis* and more than 50% of the visits to *Schinus patagonicus*. *C. albopilosa* was also recorded occasionally visiting flowers of the orchid *Gavilea odoratissima* and the michay *Berberis darwinii* during the 2000-2001 flowering season. Although less abundant than *B. dahlbomii* and *C. albopilosa*, several other bee species were recorded. The oil-collecting bee *Chalepogenus caeruleus* (Apidae) was responsible for 73.4% of the visits to *Calceolaria crenatiflora* (Scrophulariaceae). *C. caeruleus* also visits occasionally flowers of other species (Roig Alsina 1999; Aizen 2001). Several apid, megachilid, colletid, and halictid bees are also relatively frequent (Fig. 2.5).

Two exotic bees were recorded, the European bumblebee *Bombus ruderatus* and the Eurasian honeybee *Apis mellifera*. *Bombus ruderatus* invaded the Argentine side of the TFSA a few years ago from Chile (Roig Alsina and Aizen 1996) and is now common in the Nahuel Huapi area. Conversely, *Apis mellifera*, although widespread throughout the region, does not appear to penetrate under the canopy of *Nothofagus dombeyii* forest, as it was only occasionally recorded in my study sites. It is interesting that, although *B. ruderatus* visited several of the same species as the native *B. dahlbomii*, the phenology of these two species differs markedly: whereas queens of *B. dahlbomii* are active from the early spring, *B. ruderatus* queens are not seen until the late spring (Fig. 2.6). This partially non-overlapping phenology has an important consequence: *B. dahlbomii* visits several early flowering species that are not visited by *B. ruderatus*, whereas late flowering species are visited by both bumblebee species. Thus, a replacement of the native *B. dahlbomii* by the exotic *B. ruderatus* could have important consequences on early flowering species.

Several species of "atypical" hymenopteran flower visitors were also recorded. For example, an ant species and parasitoids of the families Braconidae and Torymidae were frequently recorded visiting flowers of the milkweed *Cynanchum diemii*. The introduced German yellowjacket (*Vespula germanica*) was occasionally recorded in flowers of *Alstroemeria aurea*.

The dipteran flower visitors were also diverse. Two species of nemestrinid flies were observed. *Trichophthalma amoena* was the most frequent visitor of two early flowering species, *Ribes magellanicum* and *Berberis buxifolia*, and the second most frequent visitor of *B. darwinii*. The other nemestrinid, *T. jaffueli*, was a frequent visitor of *Alstroemeria aurea* in the summer. At least six species of syrphid flies were also common, representing 48% and 9% of the visits received by the exotic rose *Rosa eglanteria* and the understory tree *Schinus patagonicus*, respectively. Finally, at least two bombilid flies (*Phthiria* spp.) and species in the families Acroceridae, Lauxaniidae, Tabanidae and Phoridae were also frequently seen visiting flowers, although it is uncertain how much these species contribute to pollination.

Several coleopteran species were common. The buprestid beetle *Anthaxia* spp. accounted for 19% of the visits to the late-flowering vine *Mutisia decurrens* and also visited flowers of *Alstroemeria aurea* in one site (Mascardi). Several species in the families Mordellidae, Nitidulidae, Salpingidae, and Staphilinidae were also occasionally recorded.

Lepidopterans were generally rare in my study sites, both in terms of number of species and visitation frequency (<0.01% of total recorded visits). However, some individuals of moth species were repeatedly found trapped dead in flowers of the milkweed *Cynanchum diemii*.

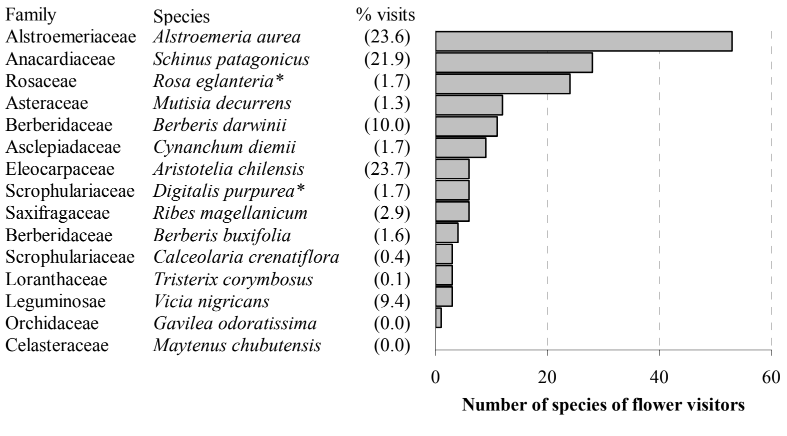

Figure 2.4. Plant species included in the study and the number of flower visitors recorded on them. Only flower visitors that contacted reproductive parts were included. Numbers between parenthesis represent the percentage of all pollinator visits received by each plant species (a measure of their total interaction frequency). Asterisks indicate exotic species.

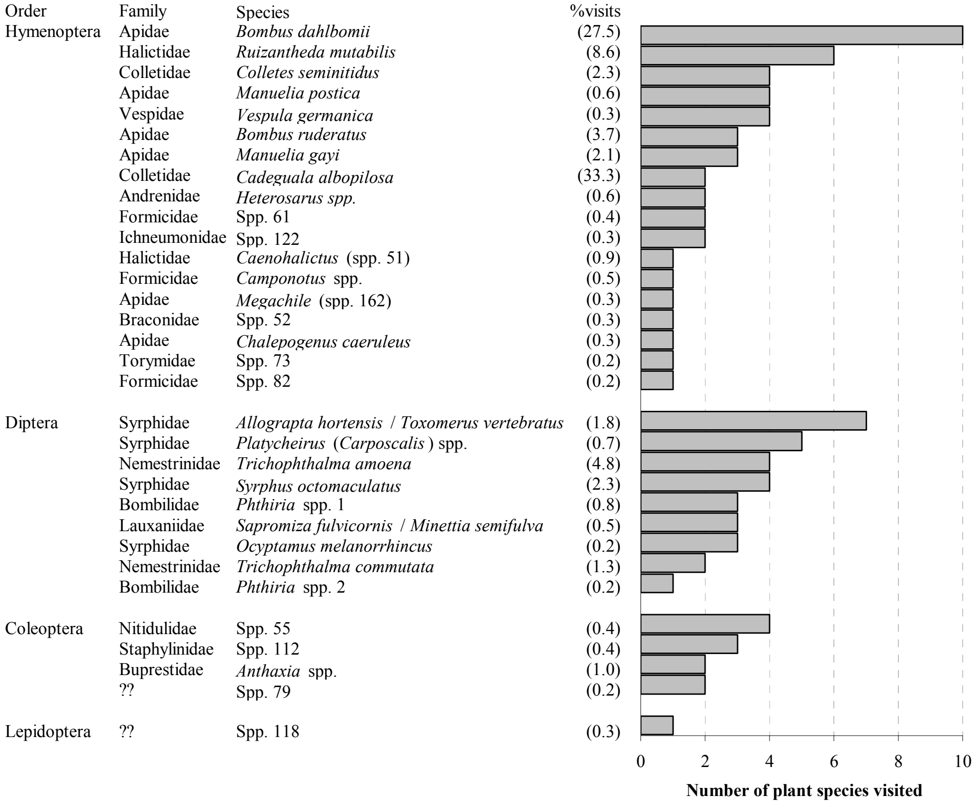

Figure 2.5. Most commonly recorded pollinator species in the eight study sites. Numbers between parenthesis represent percentage of all visits made by each pollinator species.

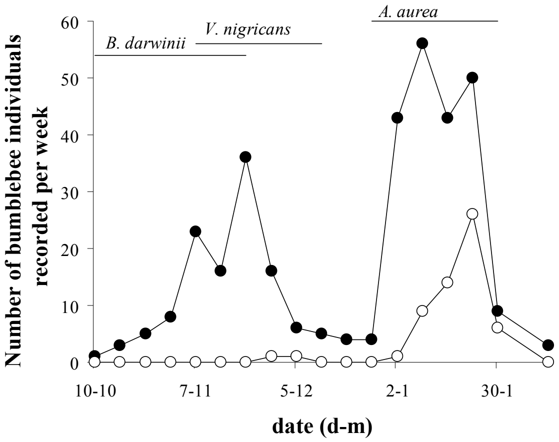

Fig. 2.6. Mean number of visits per week recorded in the eight study sites for the two bumblebee species present in the TFSA. Black circles: *Bombus dahlbomii*; white circles: *B. ruderatus*. Horizontal lines in upper part of graph indicate flowering periods of the three plant species most visited by bumblebees.

DISCUSSION

The results of my study, together with those of Riveros et al. (1991) and C. Smith-Ramírez et al. (see Aizen et al. 2002) in Chile, indicate that the diversity of insect pollinators in the TFSA is greater than previously thought (e.g., Aizen and Ezcurra 1998). This fact differentiates insect-pollination mutualisms from bird-pollination mutualisms in the TFSA: whereas only one hummingbird species is responsible for the pollination of many bird-pollinated plant species, many insect species visit flowers insect-pollinated plants of the TFSA.

It is noteworthy that the number of insect species recorded in the present study (95) was substantially greater than the 50 recorded by Riveros et al. (1991). The lower species richness of flower visitors in Riveros et al.'s study might be explained by the lower sampling effort by those authors compared to the present study (175 h of observation by Riveros et al. *vs*. 452 h in the present study). However, this is not the case: the expected number of species in Nahuel Huapi after rarefying[1] to 175 h of observation is 69 (95% confidence interval 62.99–75.79), substantially greater than the 50 species observed by Riveros et al. in Puyehue.

The prevalence of insect pollination in the TFSA appears higher than in other temperate regions of the world and may be comparable to that in some tropical forests. In Chiloé Island 75% of woody species and 65% of woody genera have insect pollination syndromes. At least at the generic level, this proportion increases towards the east: 77% of woody genera have insect pollination syndromes in Nahuel Huapi (Aizen and Ezcurra 1998). In contrast, biotic pollination in general is believed to decrease with increasing latitudes in the northern hemisphere, reaching 80-100% of wind pollination at the northernmost latitudes (Regal 1982). On the other hand, incidence of insect pollination in the TFSA appears lower than in some tropical forests; for example, 82.6% of plant species in La Selva, Costa Rica, are insect-pollinated, and Bawa (1990) has estimated that 76-94% of trees in lowland tropical forests have insect-pollination syndromes. The biogeographic history of the TFSA is believed to have generated these unusual "tropical" characteristics in a temperate forest (Arroyo et al. 1996; Aizen and Ezcurra 1998). However, the TFSA differs from tropical forests in its seasonality: flowering occurs in the spring and summer, with a peak in the late spring (this study; Smith-Ramírez and Armesto 1994), whereas flowering and pollinator activity occur year-round in moist tropical forests (Bawa 1990).

Despite the high diversity of flower visitor species, only a fraction of the insect flower visitors are responsible for most of the pollination of plants, at least in terms of visitation frequency. This pattern agrees with that observed in other systems in other parts of the world: only a few extremely generalized and abundant species account for a large proportion of the visits to many plant species (e.g., Clements and Long 1923; Motten 1982, 1986; Memmott 1999). This observation makes sense in light of general abundance patterns identified by ecologists long ago: in most communities a few species are highly abundant and many are rare (e.g., Fisher et al. 1943; Preston 1962a, b; May 1975; Hubbell 1979).

The fact that a relatively small proportion of flower visitors apparently do most of the pollination should not be overstated. There is a conflict between the conservation of biodiversity in its different levels of organization *vs*. the conservation of the functioning of ecosystems (Kunin and Lawton 1996; Nott and Pimm 1997; Vázquez and Gittleman 1998; Kinzig et al. 2002). In the TFSA, the majority of flower visitors appear to be of little importance from a functional perspective (either owing to their low abundance or to their low effectiveness as pollinators). However, as occurs in many other groups, the insect fauna of the TFSA is characterized by a high degree of endemism. For example, the bee fauna of the TFSA lacks many widespread neotropical groups, such as the Meliponinae or the Euglossinae, but has several endemic groups such as the Xeromelissinae and the Diphaglossinae (Michener 1979). A similar situation occurs with some dipteran groups, like the Nemestrinidae (Edwards 1930; Bernardi 1973) or the Syrphidae (Thompson 1999). Too much emphasis on the conservation of the functional aspects of plant-pollinator interactions could have disastrous consequences for the many groups with little functional importance but that contribute disproportionately to the phylogenetic diversity of the TFSA.

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[1] Rarefaction was done using EcoSim software (Gotelli and Entsminger 2000), as described in Chapters 3 and 4.

3

MULTIPLE EFFECTS OF INTRODUCED MAMMALIAN HERBIVORES IN THE TEMPERATE FOREST OF SOUTHERN SOUTH AMERICA: A REVIEW OF THE EVIDENCE[1]

Summary. Introduced mammalian herbivores can significantly affect ecosystems. Here, I review evidence on effects of introduced mammalian herbivores in the temperate forest of the southern Andes. Available data suggest that introduced herbivores decrease the abundance of seedling and saplings of dominant tree species in some forest types, which could impair forest regeneration. They also affect understory species composition. The mechanisms of the effects of introduced herbivores are probably complex, and include direct effects of browsing or trampling and more complex interactions such as indirect effects through other species. Very little is known about the effect of introduced herbivores on native animals. Some native mammalian and avian predators may benefit from increased food availability resulting from high densities of some introduced mammalian herbivores. In turn, enhanced populations of predators may have resulted in increased predation on native prey. Competition for resources and disease transmission have also been proposed as possible negative effects of introduced herbivores on native herbivores, but little evidence supports this claim. Little is known about effects on invertebrates.

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 (Vitousek et al. 1997; Brown and Lomolino 1998). 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 (Tansley and Adamson 1925; Hope-Simpson 1940). 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 (Mack 1989; Hobbs and Huenneke 1992; Hobbs 2001; Chaneton et al. 2002).

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

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[1] A slightly modified version of this chapter is in press as: Vázquez, D. P. 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. Biological Invasions 4.

and frugivores. Sheep grazing in California is believed to affect native pollinators of *Astragalus monoensis* through food removal (Sudgen 1985).

Alternatively, by enhancing predator populations, introduced herbivores can indirectly affect native prey species (i.e., apparent competition; Holt 1977). For example, introduced rabbit populations on many oceanic islands are believed to affect native birds indirectly by enhancing predator populations (Courchamp et al. 2000). A similar indirect effect of introduced mammalian herbivores on native animals, especially closely related species, can occur through disease transmission (Combes 2001). Many animal species can also be affected by habitat modifications induced by introduced herbivores (Simberloff 1991). In New Zealand forests, trampling by introduced deer and goats affects the composition of litter-dwelling mesofauna and macrofauna (Wardle 2001).

Finally, sometimes introduced mammalian herbivores affect fundamental ecosystem-level processes, such as nutrient cycles, primary production, and disturbance regimes (Williamson 1996; Mack and D'Antonio 1998). A good example is feral pigs (*Sus scrofa*), which have modified entire communities and ecosystems around the world through their digging and rooting activities (Mack and D'Antonio 1998). Introduced goats have contributed to soil disturbance and erosion in many island ecosystems (Coblentz 1978), and introduced ungulates can reduce above-ground biomass production, thus altering fire regimes in fire-prone ecosystems (Mack and D'Antonio 1998).

An important point to consider when analyzing effects of introduced herbivores is the evolutionary history of herbivory in the invaded system. Systems that evolved in the absence of mammalian herbivores are expected to be more susceptible to introduced herbivores than systems with a long evolutionary history of mammalian herbivory (Milchunas et al. 1988). However, Hobbs and Huenneke (1992) argue that it is not only the absence of native herbivores that determines the potential effect of introduced herbivores, but also the imposition of a new type or level of herbivory. Thus, introduced herbivores are likely to affect the invaded ecosystem if they are functionally different from, or if they can attain higher densities than, native herbivores.

In this paper I review the ecological effects of introduced mammalian herbivores in the temperate forest of the southern Andes (TFSA). I discuss effects on forest regeneration, plant community diversity and composition, vertebrate and invertebrate species, and ecosystem processes. Although little is known, available data suggest that introduced herbivores have important impacts on many components of the forest ecosystem.

NATURAL HISTORY OF MAMMALIAN HERBIVORY IN THE TEMPERATE FOREST OF THE SOUTHERN ANDES

The natives

Native mammalian herbivores in Andean Patagonia include the guanaco (*Lama guanicoe*) and two species of deer, the huemul (*Hippocamelus bisulcus*) and the pudu (*Pudu pudu*) (Olrog and Lucero 1980; Redford and Eisenberg 1992). The guanaco uses mainly open dry areas throughout its range, although it does get into the TFSA in some areas. In Tierra del Fuego, guanacos feed on dominant *Nothofagus* trees (Bonino and Pelliza-Sbriller 1991); however, in Torres del Paine National Park, Chile, guanacos rarely use available forest habitats (Ortega and Franklin 1988). Although available data suggest that they impede forest regeneration, this effect is apparently restricted to steppe-forest ecotones (Rebertus et al. 1997; Martínez-Pastur et al. 1999).

The huemul was widespread in the southern Andes of Chile and Argentina before European colonization, occupying open areas above and below the tree line (Díaz 1993; Smith-Flueck and Flueck 1995; Povilitis 1998). Its distribution has been drastically reduced, and it is currently rare and geographically restricted (Díaz 1993; Povilitis 1998).

The pudu is found in a wide variety of habitats but typically occurs in thick forests from sea level to 1,000 m (Redford and Eisenberg 1992). Pudu populations are believed to have declined owing to human activities (Redford and Eisenberg 1992).

Thus, it is possible that the impact of guanacos and huemul on forest ecosystem has always been limited to ecotones. In contrast, pudus may have had greater effects in the past, when population densities were higher.

The invaders

Twelve herbivorous mammals have been successfully introduced to the TFSA. I include both domestic and wild introduced mammalian herbivores found in natural forest areas but exclude failed introductions (e.g., reindeer, *Rangifer tarandus*) and species mainly restricted to human dwellings (Norway and black rats [*Rattus norvegicus* and *R. rattus*], and house mouse [*Mus musculus*]), because their potential effects on the forest ecosystem are limited. General overviews of the history of the introduction and current distribution of these species are in Daciuk (1978), Navas (1987), Bonino (1995), Jaksic (1998), and Jaksic et al. (2002).

- Domestic cattle (*Bos taurus*) and horses (*Equus caballus*) were probably the first introduced herbivores in the TFSA. They escaped from ranches in the Chilean Pacific coast or in the Argentinean pampas, spreading to the TFSA (see Veblen et al. 1996). For example, cattle and horses were present in the Nahuel Huapi area in Argentina in the early eighteenth century (Biedma 1997). Cattle occupy many natural areas, including 56% of the land area in Nahuel Huapi National Park in Argentina (Lauría Sorge and Romero 1999).
- Sheep (*Ovis aries*) and goats (*Capra hircus*) are mainly restricted to dry grasslands, although they do occur in some forest areas, especially in the dry eastern forest types (Relva and Veblen 1998; Lauría Sorge and Romero 1999).
- Red deer (*Cervus elaphus*) were originally introduced in central Argentina around 1904 and were later introduced in several areas in Chile and Argentina in the TFSA (Jaksic et al. 2002). 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; Jaksic et al. 2002).
- Fallow deer (*Dama dama*) and axis deer (*Axis axis*) were introduced in the 1930s in Nahuel Huapi National Park in Argentina (Navas 1987; Bonino 1995). Fallow deer are now apparently restricted to Isla Victoria, in Nahuel Huapi Lake (Navas 1987) and are not found in the wild in Chile (Jaksic 1998); axis deer was always restricted to Isla Victoria, and are presumed extinct (Navas 1987).
- Wild boar (*Sus scrofa*) were introduced into central Argentina around 1906 and were translocated to Neuquén between 1917 and 1922 (Daciuk 1978), spreading south and west. They are currently found in a large area of the TFSA, between Neuquén and northern Santa Cruz provinces in Argentina (Daciuk 1978; Navas 1987) and in regions X and XI in Chile (Jaksic 1998; Jaksic et al. 2002).
- The European hare (*Lepus capensis*) was first introduced in Cañada de Gómez, Santa Fe, Argentina, in 1888 and was later introduced in southern Chilean Patagonia in 1896 (Grigera and Rapoport 1983). It is currently common and widespread, occupying most of Argentina, Chile, Paraguay, Uruguay, and southern Brazil and Bolivia (Grigera and Rapoport 1983; Jaksic et al. 2002).
- The European rabbit (*Oryctolagus cuniculus*) was introduced in two separate locations in Chile: in Tierra del Fuego around 1880, and in central Chile in 1884; from there it later expanded to Neuquén province, Argentina (Jaksic and Yáñez 1983; Bonino and Amaya 1985; Bonino and Gader 1987; Jaksic et al. 2002). The northern population is spreading south in Neuquén, but it apparently has not reached the TFSA region (Bonino and Gader 1987; Jaksic et al. 2002). The southern population is widespread in Tierra del Fuego, occupying a large area of the TFSA (Bonino and Amaya 1985; Jaksic et al. 2002).
- The Canadian beaver (*Castor canadensis*) was introduced in Tierra del Fuego in 1946. It has spread to most streams in Argentine Tierra del Fuego and is currently spreading to Chilean Tierra del Fuego; it is also found in several islands of the Magellanic archipelago (Lizarralde 1993; Jaksic et al. 2002).
- The muskrat (*Ondatra zibethicus*) was introduced to Argentine Tierra del Fuego in 1948 and is now widespread throughout a large part of the island (Jaksic et al. 2002).

EFFECTS OF INTRODUCED MAMMALIAN HERBIVORES IN THE TFSA

Effects on forest regeneration

The effects of introduced mammalian herbivores on forest regeneration have been quantitatively analyzed in four published studies (Ramírez et al. 1981; Veblen et al. 1989; Veblen et al. 1992b; Relva and Veblen 1998), all of which dealt with introduced ungulates (cattle and deer). Results from these four studies are summarized in Table 3.1. Although the magnitude of the effect varies, in most cases introduced ungulates decrease the abundance and height of seedlings and saplings of dominant canopy trees.

Table 3.1. Summary of results of studies of the effects of introduced ungulates on forest regeneration. Studies compared sites with contrasting levels of ungulate browsing and grazing, except study (4), where the comparison was made between two and six years after deer introduction in the same island site (Islote Rupanco, Osorno, Chile). For each comparison, the mean effect in grazed and ungrazed sites, the number of statistical replicates (*n*), and the effect size (*lr*) are given. *lr*, the log response ratio statistic, is a conventional measure of effect size in meta-analysis (Gurevitch and Hedges 2001). The response ratio is calculated for study *i* as $lr_i = \ln\left(\overline{X}_i^G / \overline{X}_i^U\right)$, where $\overline{X}_i^G$ is the mean effect in the experimental (i.e., grazed) sites, and $\overline{X}_i^U$ is the mean effect in control (i.e., ungrazed) sites.

			grazed		ungrazed			
Canopy species	Variable	stand age	mean	*n**	mean	*n**	*lr*	Source
Nothofagus dombeyii	seedling frequency (5-200 cm tier)	young (80-100 yr)	32.7	1	61.2	1	-0.63	2
		young (80-100 yr)	30.6	1	32.7	1	-0.07	1
		mature (~200 yr)	18.4	(2)	24.5	1	-0.29	1
		forest gap	62.7	(10)	15.6	(6)	1.39	1
	seedling mean max. height (cm)	forest gap	28.0	1	117.0	1	-1.43	1
		young (80-100 yr)	10.7	(10)	56.0	(6)	-1.66	2
Austrocedrus chilensis	seedling frequency (5-200 cm tier)	young (80-100 yr)	20.4	1	0.0	1	7.62	2
		young (80-100 yr)	2.0	1	6.1	1	-1.12	1
		mature (~200 yr)	1.0	(2)	14.3	1	-2.66	1
		forest gap	1.3	1	2.2	1	-0.53	1
	seedling-sapling abundance per ha	...[a]	3250.0	14	6320.5	13	-0.67	3
	seedling mean max. height (cm)	...[a]	10.3	1	101.0	1	-2.28	1
Nothofagus antarctica	seedling frequency (5-200 cm tier)	>80 yr	14.3	1	16.3	1	-0.13	2
	seedling mean max. height (cm)	>80 yr	19.4	1	97.9	1	-1.62	2
Aexotoxicon punctatum	no. of individuals / ha (0-20 cm tier)	...[a]	1484.9[b]	1	1409.1[b]	1	0.05	4

	no. of individuals / ha (0-20 cm tier)	...[a]	1121.2[b]	1	1727.3[b]	1	-0.43	4
Laurelia philippiana	no. of individuals / ha (0-20 cm tier)	...[a]	2225.6[b]	1	1829.3[b]	1	0.20	4
	no. of individuals / ha (0-20 cm tier)	...[a]	7012.2[b]	1	8963.4[b]	1	-0.25	4
Eucrypia cordifolia	no. of individuals / ha (0-20 cm tier)	...[a]	176.9[b]	1	289.2[b]	1	-0.49	4
	no. of individuals / ha (0-20 cm tier)	...[a]	506.2[b]	1	715.4[b]	1	-0.35	4

[a] Not specified in the original study.

[b] Approximate estimates obtained from Fig. 7 in study (4).

Study sources: (1) Veblen et al. (1989); (2) Veblen et al. (1992b); (3) Relva and Veblen (1998); (4) Ramírez et al. (1981).

* Numbers between brackets indicate replicates included in the study that cannot be considered true statistical replicates owing to lack of spatial interspersion (see Hurlbert 1984). In these cases, the number of statistical replicates was taken as 1.

Veblen and colleagues (Veblen et al. 1989; Veblen et al. 1992b) suggest that introduced ungulates can decrease seedling and sapling abundance and height of coihue, *Nothofagus dombeyi* (Table 3.1). Notice, however, that seedlings (5-200 cm tall) of coihue, *Nothofagus dombeyi*, were more abundant in the grazed than in the ungrazed site in forest gaps in Veblen et al.'s (1989) study, although these authors mention that saplings (i.e., >200 cm tall) were absent from canopy gaps in the grazed site but present in the ungrazed site. Furthermore, it is also noteworthy that the magnitude of the effect is higher for seedling height than for seedling abundance (Table 3.1). Thus, even though shorter size classes are more abundant in grazed gaps, it appears that they do not reach taller size classes.

De Pietri (1992b) argues that the combined effect of fire and heavy grazing by cattle can transform *N. dombeyi* forest into grasslands. However, in many post-fire *N. dombeyi* forests in northern ArgentinePatagonia established during the 1930s and 1940s (when livestock pressure was highest), even the heaviest grazing seems to have failed to impede regeneration of *N. dombeyi* forests (Veblen et al. 1992a). Thus, although introduced ungulates appear to decrease abundance and growth of *N. dombeyi* seedlings and saplings, it is unclear whether this effect can inhibit forest regeneration.

Seedling abundance of the Patagonian cypress, *Austrocedrus chilensis*, was higher in the grazed than in the ungrazed site in Veblen et al.'s (1992b) study. In contrast, the well-replicated study by Relva and Veblen (1998) shows that abundance of seedlings/saplings of *A. chilensis* is lower in grazed than in ungrazed sites (Table 3.1). The apparent contradiction between these two studies could be due to the fact that the former included only seedlings (i.e., 5-200 cm tall), whereas the latter included both seedlings and saplings (i.e., >5 cm tall and <4 cm dbh). Furthermore, both in Veblen et al.'s (1992b) and in Relva and Veblen's (1998) studies, seedling/sapling height is lower in grazed than in ungrazed sites; as for *N. dombeyi*, the magnitude of this effect is higher than for seedling/sapling abundance (Table 3.1). This evidence agrees with experimental results showing that even low levels of browsing can inhibit the growth of this species (Relva and Sancholuz 2000) and strongly suggests that regeneration of *A. chilensis* forest can be inhibited by introduced ungulates. In fact, retrospective studies of forest dynamics indicate that introduced ungulates appear to have inhibited post-fire regeneration of *A. chilensis* forest in the past (Veblen et al. 1992a).

The only published study addressing the effect of ungulates on the regeneration of ñire, *Nothofagus antarctica*, suggests that regeneration of this species can also be inhibited by introduced ungulates: both seedling abundance and height were lower in the grazed than in the ungrazed site in Veblen et al.'s (1992b) study. As for *N. dombeyi* and *A. chilensis*, the magnitude of the effect on seedling height is higher than on seedling abundance (Table 3.1).

Finally, Ramírez et al.'s (1981) study shows that the abundance of seedlings and saplings of three dominant tree species was higher with early grazing (i.e., two years after deer introduction in Islote Rupanco) than with late grazing (i.e., six years after deer introduction; Table 3.1). This result holds for all seedling/sapling height classes except the shortest (0-20 cm), which had higher abundance after deer introduction for two of the tree species (Table 3.1).

Little evidence is available on the effects of introduced herbivorous mammals on the regeneration of other forest types besides those discussed above. Roig et al. (1985) noted that cattle do not forage in the forest interior of deciduous forest dominated by lenga, *Nothofagus pumilio*, but they do use forest gaps, where they browse on *N. pumilio* seedlings and saplings. Since regeneration of *N. pumilio* is gap-dependent (see Rebertus and Veblen 1993), Roig et al. (1985) suggest that cattle can impede forest regeneration. Bava and Rechene (1998) note that *N. pumilio* saplings of approximately 30 years of age growing inside exclosures or among fallen trees typically reach 7-10 m height, whereas saplings of the same age exposed to continuous guanaco or cattle browsing do not grow above 30 cm. To my knowledge, there has been no quantitative evaluation of the impact of ungulate grazing on this species.

I know of no quantitative studies in this region addressing impacts of introduced mammalian herbivores other than ungulates on forest regeneration. Rebertus and Veblen (1993) studied forest regeneration in treefall gaps in Tierra del Fuego, in six sites with different composition of dominant trees, of which one was dominated by *N. pumilio*. They observed that current sapling abundance was lower than in other forest types. They also observed some rabbit browsing on saplings. Based on this observation, they suggest that rabbits prevent regeneration of *N. pumilio*. However, it is important to consider other possible causes for this pattern, such as differences among sites not related to rabbit browsing.

Table 3.2. Summary of results of effects of grazing by introduced ungulates on species richness of understory plants. Studies compared sites with contrasting levels of ungulate browsing and grazing, except study (4), where the comparison was made between two and six years after deer introduction in the same island site (Islote Rupanco, Osorno, Chile). For each comparison, the mean effect in grazed and ungrazed sites, the number of statistical replicates (*n*), and the effect size on mean richness (*lr*) are given. (See Table 3.1 for details on the calculation of *lr*.)

		grazed			ungrazed				
Canopy species	Forest characteristic	mean richness	% exotic	*n**	mean richness	% exotic	*n**	*lr*	Source
Nothofagus dombeyi	forest gap	44	11.4	(10)	21	0.0	(6)	0.74	(1)
	young stand (80-100 yr)	12	0.0	1	17	0.0	1	-0.35	(1)
	young stand (80-100 yr)	9	0.0	1	10	0.0	1	-0.11	(2)
	mature stand (~200 yr)	22	2.9	(2)	24	0.0	1	-0.09	(1)
Austrocedrus chilensis	post-fire matorral	5.6	0.0	5	8.5	0.0	5	-0.42	(3)
Nothofagus antarctica	>80 yr	17	29.4	1	12	0.0	1	0.35	(2)
Aexotoxicon punctatum	not specified	47	?	1	52	?	1	-0.10	(4)

Study sources: (1) Veblen et al. (1989); (2) Veblen et al. (1992b); (3) Raffaele and Veblen (2001); (4) Ramírez et al. (1981).

* Numbers between brackets indicate replicates included in the study that cannot be considered true statistical replicates owing to lack of spatial interspersion (see Hurlbert 1984). In these cases, the number of statistical replicates was taken as 1.

Introduced beavers can devastate *Nothofagus* forests in Tierra del Fuego. They cut and kill the dominant tree species—*N. pumilio*, *N. betuloides*, *N. antarctica* and *Drymis winteri*—for dam construction. However, the flooding associated with the dams probably causes the greatest damage (Daciuk 1978; Lizarralde 1993). In Argentine Tierra del Fuego, beavers have apparently colonized all streams in the Andean and extra-Andean areas in the island, and about 91% of all streams if adjacent islands of the Magellanic Archipelago are included. They cause complete destruction of the flooded forest and can clear surrounding areas for dam construction (Lizarralde 1993).

In conclusion, available evidence suggests that introduced herbivorous mammals can negatively affect the establishment and growth of seedlings and saplings of several dominant canopy trees. Effects are apparently stronger on seedling/sapling growth than on their abundance.

Effect on understory species richness and invasion by exotic plants

A few studies have analyzed the effect of introduced herbivores on species richness of understory plants (summarized in Table 3.2). As for forest regeneration, all these studies dealt with introduced ungulates. Grazing by introduced ungulates seems to result in increased species richness in some cases, while the opposite effect is observed in other instances. In the only published study in which experimental exclosures have been used to study the effect of introduced herbivores in the TFSA, Raffaele and Veblen (2001) reported increased richness in ungrazed (fenced) plots in a post-fire mixed *Austrocedrus chilensis–Maytenus boaria* matorral, compared with control (unfenced) plots with low levels of cattle grazing. Similarly, Veblen et al. (1989) reported that ungrazed young and mature *Nothofagus dombeyi* forest sites had higher understory species richness compared to grazed sites of similar ages, and Veblen et al. (1992b) found a similar pattern in another pair of grazed and ungrazed young *N. dombeyi* forest sites (Table 3.2). On Islote Rupanco, Ramírez et al. (1981) also found higher species richness in 1977 (2 years after deer introduction) compared to 1981 (6 years after introduction). In all these cases, all species were native except in the grazed mature forest of Veblen et al. (1989), where foxglove (*Digitalis purpurea*) was recorded. Thus, decreased plant species richness in grazed sites in these studies is due to a reduction in the richness of native species.

Conversely, Veblen et al. (1989) reported higher richness in grazed forest gaps in *N. dombeyi* forest on Isla Victoria compared to ungrazed gaps on the Quetrihué Peninsula. Likewise, Veblen et al. (1992b) reported higher richness in a grazed *N. antarctica* forest site compared to an ungrazed site of the same forest type. In both cases, increased total richness was partly due to increased richness of herbaceous exotic species (Table 3.2).

It is noteworthy that in Veblen et al.'s (1989; 1992b) studies the only cases where substantial invasion by exotic plants occurred were in an open forest type (*N. antarctica*) and in gaps in a closed-canopy forest type (*N. dombeyi–A. chilensis*). This fact suggests an interaction between forest cover and grazing, so that introduced mammalian herbivores favor invasion by exotic plants only when canopy cover is low. Below I discuss additional evidence that can help to answer this question.

Simberloff et al. (2002) studied invasion by exotic woody plants in Isla Victoria, in Nahuel Huapi National Park. Over 100 introduced woody species were planted between 1910 and 1940 as part of an experimental plantation near the center of the island. Two species of introduced deer (*Cervus elaphus* and *Dama dama*) have heavily impacted the understory of *Nothofagus dombeyi – Austrocedrus chilensis* forest. Yet very little invasion by exotic species into the forest has occurred. Invasion by woody plants does occur on the island (particularly by highly invasive shrubs *Rosa eglanteria* and *Cytisus scoparius*, and a few tree species, mainly conifers), but it is largely restricted to areas cleared for use as cattle pastures.

In *Nothofagus dombeyi – Austrocedrus chilensis* forests in and near Los Alerces National Park, De Pietri (1992a) found livestock burden and soil compaction positively correlated with relative cover of exotic plant species. However, in De Pietri's study, designed for identifying ecological indicators of cattle ranching, it is not possible to separate the effect of introduced herbivores *per se* from the effect of associated ranching activities—such as forest clearing or burning—used to create pastures. Therefore, the increased cover of exotic plant species cannot be solely attributed to livestock. A more plausible explanation of De Pietri's finding is that both livestock and the reduction of forest cover favor invasion by introduced plants.

In conclusion, available data suggest that, when introduced ungulates lead to decreased plant species richness, this is because of a loss of native species in grazed sites, whereas increased plant species richness with grazing results, at least in part, from increased richness of exotic species. However, the latter effect might be possible only when canopy cover is low.

Effect on understory plant composition: patterns and mechanisms

Browsing by introduced herbivores can decrease abundance of palatable, browsing-susceptible understory trees, shrubs and herbs. Probably the best-documented case is that of maqui, *Aristotelia chilensis*, a small tree that dominates the understory of ungrazed *Nothofagus dombeyi* forests but almost disappears from grazed forests (see Chapter 5, and Dimitri 1962; Veblen et al. 1989; Veblen et al. 1992b). Interestingly, a similar pattern is observed for *Aristotelia serrata* in New Zealand, where it is affected by introduced red and sika deer (Allen et al. 1984). Other understory species that tend to decrease with grazing in *Nothofagus dombeyi–Austrocedrus chilensis* forests are the herb *Alstroemeria aurea*, the shrub *Ribes magellanicum*, the milkweed vine *Cynanchum diemii*, the mistletoe *Tristerix corymbosus*, and the bamboo *Chusquea culeou* (see Chapter 5, and Veblen et al. 1989; Veblen et al. 1992b). Likewise, several palatable shrub and vine species become less abundant with grazing in post-fire *Austrocedrus chilensis–Maytenus boaria* matorrals (Raffaele and Veblen 2001).

Although all these species show a similar response to grazing by introduced herbivores, the underlying mechanism probably differs among species. For some species, the direct effect of browsing is the most likely explanation. For example, *Aristotelia chilensis*, *Ribes magellanicum* and *Chusquea culeou* are preferred food items for both cattle and deer and are highly susceptible to ungulate browsing (Dimitri 1962; Veblen et al. 1989; Veblen et al. 1992b; Relva and Caldiz 1998). Thus, it seems likely that the decline of these species in areas with introduced herbivores is due to the direct, negative effect of browsing.

The mechanisms underlying the observed effect of introduced herbivores on other understory species are probably more complex and may involve indirect effects through one or more other species. An indirect effect occurs when one species affects another through a third species (Strauss 1991; Wooton 1994). In part because the possibilities for indirect effects are probably unlimited, their documentation is usually difficult. Below I discuss a few examples for which evidence suggests that indirect effects could be occurring.

Besides the direct effect on individual plant survivorship, herbivores can affect plant fitness, both directly by consuming flowers or seeds (Louda 1982; Herrera 1993; Gómez and Zamora 2000; Herrera 2000) and indirectly by affecting the interaction with pollinators through a modification of floral traits (Strauss et al. 1996; Strauss 1997; Mothershead and Marquis 2000). The amancay, *Alstroemeria aurea*, is an abundant insect-pollinated herb flowering during the summer in the TFSA. As I show in Chapter 5, the decreased abundance of *A. aurea* resulting from cattle trampling alters the interaction between this species and its pollinators, which in turn results in lower reproductive performance. Although lower population density of *A. aurea* does not necessarily mean lower visitation frequency by its main pollinators (*Bombus* bumblebees; see Chapter 2, and Aizen 2001; Aizen et al. 2002), pollination quantity (number of conspecific pollen grains) and quality (as determined by contamination with heterospecific pollen grains) dramatically decrease with grazing; decreased pollination performance in turn results in lower reproductive performance.

Another possible indirect effect is on the mistletoe *Tristerix corymbosus*. The main host of this parasitic shrub in *N. dombeyi* forests is *Aristotelia chilensis*; and although *T. corymbosus* does grow occasionally on other host species in *N. dombeyi* forests (such as *Azara* sp. and *Maytenus boaria*), no individual of *Tristerix corymbosus* growing on other species besides *Aristotelia chilensis* was recorded in my study sites in Nahuel Huapi. As I mentioned above, *Aristotelia* drastically decreases in abundance in grazed sites. Abundance of *T. corymbosus* also decreases in grazed sites (see Chapter 5). Thus, the decreased abundance of *T. corymbosus* is better explained by a decreased availability of its host plant than by a direct effect of cattle.

It has been suggested that grazing by introduced ungulates results in an overall increase in the abundance of spiny shrubs (e.g., De Pietri 1992b; Veblen and Alaback 1996). *Berberis buxifolia* is probably the most conspicuous example in the TFSA. Several studies have documented increased abundance of this species with ungulate grazing, despite heavy browsing pressure by ungulates (see Chapter 5, and Veblen et al. 1989; De Pietri 1992b; Veblen et al. 1992b; Relva and Veblen 1998). However, Raffaele and Veblen (2001) found, in a post-fire *Austrocedrus chilensis – Maytenus boaria* matorral, that *B. buxifolia* was less abundant in grazed than in ungrazed plots. Another *Berberis* species, *B. darwinii*, has also been cited as increasing with introduced herbivores (Ramírez et al. 1981; Veblen et al. 1989; Veblen et al. 1992b), although I failed to find such an increase (see Chapter 5). Thus, although introduced mammalian herbivores may in some cases increase the abundance of some spiny shrubs, that effect is not universal. Furthermore, it is important to bear in mind that many areas subject to grazing (especially by domestic animals) have partially or totally lost forest cover, a loss that cannot always be attributed to grazing; other anthropogenic disturbances, such as fire or logging, may be causal. In such cases, the increased abundance of spiny shrubs cannot be unambiguously attributed to the presence of introduced herbivores.

Could the increased abundance of browse-resistant, shade-intolerant shrubs influence forest dynamics and forest regeneration? Several studies show that grazing-resistant shrubs can have nurse effects on seedlings of many plant species (De Pietri 1992a; Raffaele and Veblen 1998; Kitzberger et al. 2000). Raffaele and Veblen (2001) suggested that nurse plants could play a double facilitative role: protection from moisture stress and from large herbivores. Along the same lines, De Pietri (1992a) suggested that bushes of the exotic eglantine rose, *Rosa eglanteria*, could help the regeneration of the forest under heavy grazing conditions.

In conclusion, introduced mammalian herbivores are able to affect understory community structure and composition strongly through a variety of mechanisms, involving both direct effects of browsing and trampling and several kinds of indirect effects.

Effects on vertebrates

One way in which introduced mammalian herbivores could affect native vertebrate herbivores is through competition for resources and habitat modification. The recent abrupt decline in the distribution of huemul (Díaz 1993; Povilitis 1998) has been attributed partly to competition for resources and habitat modification caused by exotic herbivorous mammals (Flueck et al. 1995; Smith-Flueck and Flueck 1995; Povilitis 1998). Many areas formerly occupied by huemul have now been colonized by red deer (Flueck et al. 1995). Similarly, Lever (1985) argues that red deer could be competing with pudu populations in Neuquén, Argentina. Competition for food has also been presumed to occur between sheep and guanacos in Torres del Paine National Park, Chile (Sarno and Franklin 1999), and dietary overlap between red deer and guanacos was reported in Neuquén, Argentina (Bahamonde et al. 1986). However, diet overlap does not necessarily imply competition. Thus, although it is possible that introduced herbivores are indeed negatively affecting native species through competition for food or habitat modification, no hard evidence exists demonstrating such effect.

Exotic herbivores may benefit native predators by increased food availability. There is ample evidence that native predators feed on exotic prey. Pumas (*Felis concolor*) and grey and culpeo foxes (*Pseudalopex griseus* and *P. culpaeus*) are the main large mammalian predators throughout Andean Patagonia. They are feeding generalists; their feeding habits usually reflect the availability of prey. They have been repeatedly reported to prey on exotic herbivores in areas where the latter are abundant; in many cases exotic prey comprise the bulk of the predator's diet (pumas, Courtin et al. 1980; Jaksic et al. 1983; Yáñez et al. 1986; Iriarte et al. 1991; Rau et al. 1991; Franklin et al. 1999; Novaro et al. 2000). Avian predators also prey on introduced herbivores. European hare and rabbit account for 55% of the prey biomass of great horned owl (*Bubo virginianus*), and 58% of frequency of the diet of grey buzzard-eagle (*Geranoaetus melanoleucus*) in arid Patagonia in Neuquén (Hiraldo et al. 1995; Donázar et al. 1997). In the same region, six species of avian scavengers feed on carcases of European hare (Travaini et al. 1997). Although these studies on the feeding habits of avian predators and scavengers were conducted in the Patagonian steppe, similar effects could occur in the temperate forest. On Isla Victoria (Nahuel Huapi, Argentina), black vulture (*Coragyps atratus*) feeds on carcasses of introduced red deer (D.P. Vázquez, personal observation), which might explain their high local density.

Enhanced predator abundances could be detrimental for native prey. One way exotic herbivores could affect native animals is through "apparent competition" (Holt 1977). Apparent competition occurs when "the presence of multiple noncompeting prey species elevates predator abundance above levels maintained by single prey species, which increases predation pressure on multiprey assemblages" (Morin 1999). Predation by native predators on native prey is well-documented (Courtin et al. 1980; Jaksic et al. 1983; Yáñez et al. 1986; Iriarte et al. 1991; Rau et al. 1991; Hiraldo et al. 1995; Smith-Flueck and Flueck 1995; Donázar et al. 1997; Franklin et al. 1999; Novaro et al. 2000). Populations of introduced herbivores are known to fluctuate (Novaro 1997), and in some areas current densities of native predators are probably

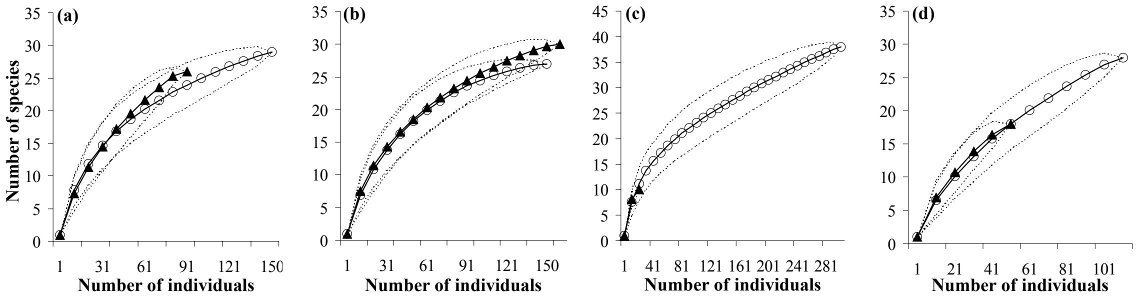

Figure 3.1. Rarefaction curves for the species richness of insects recorded visiting flowers of *Alstroemeria aurea*. Rarefaction calculations were performed using EcoSim software (Gotelli and Entsminger 2000). Continuous lines indicate expected richness; dashed lines are 95% confidence limits calculated over 1000 iterations of the simulation. ▲: grazed sites; ○: ungrazed sites. Actual species richness corresponds to upper-right end of the lines. Rarefaction curves given separately for each of four pairs of sites. Paired sites are: (a): Llao Llao (no cattle = nc), Cerro López (cattle = c); (b): Safariland (nc), Arroyo Goye (c); (c): Mascardi (nc and c); (d): Quetrihué (nc and c).

higher than in the past (Crespo 1975). This fact could result in increased predation on native prey species during periods of low abundance of introduced herbivores (Novaro et al. 2000).

Another way in which introduced herbivores could affect native mammals indirectly is through parasites, in many cases also introduced. For example, parasites have the potential to affect the competitive relationships among species, so that competitively superior species become weaker competitors when parasitized (Combes 2001). Huemul are known to be susceptible to several parasitic diseases carried by livestock or introduced deer (see Smith-Flueck and Flueck 1995; Povilitis 1998). However, it is not known how much these diseases affect populations of huemul in the wild, and whether disease played a role in the distributional reduction of the species.

The decreased abundance of some plant species resulting from introduced herbivores could in turn be affecting pollinators and seed dispersers. The decreased abundance of the mistletoe *Tristerix corymbosus* with grazing described above could affect two vertebrate species. *T. corymbosus* is the only ornithophilous plant flowering in the winter in many areas and is the only food source for the hummingbird *Sephanoides sephaniodes* during this period (Fraga et al. 1997). Its fruits are also the main food source for the endemic marsupial *Dromiciops gliroides* (Amico and Aizen 2000). It is possible that the decreased abundance of *T. corymbosus* resulting from grazing also indirectly affects the hummingbird and the marsupial. Thus, introduced herbivores could affect these vertebrate species through a doubly-indirect effect (introduced ungulates → *Aristotelia chilensis* → *Tristerix corymbosus* → *Sephanoides* and *Dromiciops*).

Effects on invertebrates

Large introduced herbivores have the potential to affect invertebrates in several ways. They could affect them directly through trampling on nests or indirectly through their effects on habitat characteristics or on food sources (Siemann et al. 1998; Rambo and Faeth 1999). If introduced herbivores affect invertebrates through their food sources, species that depend on fewer food resource types (i.e., specialists) could be more affected by introduced herbivores than species that depend on many resources types (i.e., generalists). I tested this hypothesis using data on plant pollinator interactions in four pairs of grazed and ungrazed sites in *Nothofagus dombeyi* forest (see Chapter 4). I found no relationship between degree of pollinator feeding specialization on flowers and their response to cattle grazing. Although the reasons for this lack of relationship between specialization and response to cattle disturbance are unclear, one possible explanation is that the direct effect of cattle on the pollinators (e.g., trampling on nests) is strong enough to override any indirect effect through resource availability. On the other hand, the fact that the response of pollinators to cattle is not related to their degree of specialization on floral resources need not mean there is no response. Some insect pollinator species tend to become rarer in the presence of cattle, whereas others tend to increase. A conspicuous "decreaser" in Chapter 4 is the bumblebee *Bombus dahlbomii*, a pollinator of many plant species in the TFSA (see Chapter 2, and Aizen et al. 2002). Conspicuous "increasers" are the syrphid flies *Allograpta hortensis* and *Toxomerus vertebratus* and the bees *Colletes seminitidus* and *Heterosarus* sp.

Another interesting question is whether the species diversity of entire invertebrate guilds is affected by introduced herbivores. Here, I analyze part of the data presented in Chapter 2 to address this question. As I mentioned above, *Alstroemeria aurea* is an herbaceous plant flowering in the summer in the forest understory. In *Nothofagus dombeyi* forests it is virtually the only insect-pollinated plant flowering during the summer, and it receives visits from a broad assemblage of flower visitors—twice as many as any other insect-pollinated plant in this forest type (see Chapters 2 and 4). Because abundance of *A. aurea* decreases with grazing (see above), one could hypothesize that this will in turn affect flower visitors.

Total species richness of flower visitors to *A. aurea* was lower in grazed than in ungrazed sites in 3 of the 4 pairs of sites described in Chapter 2, and slightly higher in the remaining pair (Fig. 3.1). However, in comparisons of species richness it is important to account for differences in the number of individuals in the different samples. Owing to random sampling, a sample of, say, 100 individuals is likely to contain more species than a sample of 10 individuals. Rarefaction (Simberloff 1978; Gotelli and Graves 1996) can account for this effect. After rarefaction, species richnesses of flower visitors of *A. aurea* in grazed and ungrazed sites are virtually identical in three of the four pairs of sites (Fig. 3.1a, c, d) and slightly higher in the grazed site of the remaining pair (Fig. 3.1b). Therefore, no effect of grazing on the diversity of insects visiting flowers of *A. aurea* is detected after adjusting for differences in total abundance of flower visitors.

Effects on ecosystem processes

Mammalian herbivores are known to have important effects on ecosystem processes in many biomes, including temperate forests. For example, ungulates can influence the nitrogen cycle by changing litter quality (and thus affect conditions for nitrogen mineralization), and by adding readily available nitrogen to upper levels of the soil in urine and feces, which can result in drastic changes in plant community composition (Hobbs 1996).

Not much is known about nutrient cycling in Patagonian forest ecosystems in general (Mazzarino et al. 1998), much less about how it is affected by introduced herbivores. Deforestation by beaver in Tierra del Fuego leads to increased erosion and increased accumulation of organic material in water courses, which can in turn affect nutrient cycling, altering the biochemical composition of waters, sediments, soils and adjacent riparian areas (Lizarralde 1993; Lizarralde et al. 1996). Decreased plant cover and trampling resulting from ungulate activity can significantly affect soil properties, including litter quality and mineralization processes, and can lead to soil erosion (De Pietri 1992b).

DISCUSSION AND CONCLUSIONS

It appears that introduced mammalian herbivores have multiple ecological effects in the temperate forest of the southern Andes. Evidence at hand suggests they can affect forest regeneration, understory plant community structure and composition, vertebrate and invertebrates species, and ecosystem processes. The mechanisms generating these impacts are complex and apparently involve many simultaneous direct and indirect effects.

Not all canopy tree species seem equally susceptible to introduced mammalian herbivores. In particular, even though juveniles of *Nothofagus dombeyi* are less abundant and attain lower heights in grazed than in ungrazed sites, this species appears to have been able to regenerate under heavy grazing in post-fire stands (Veblen et al. 1992a). In contrast, regeneration of *Austrocedrus chilensis* seems more susceptible to introduced herbivores. This differential susceptibility has been attributed to the life history traits of these species. *N. dombeyi* can establish at higher densities and grow at faster rates than *A. chilensis*, making the former less susceptible to browsing by introduced ungulates than the latter (Veblen et al. 1992a).

The observed effects of introduced mammalian herbivores on forest regeneration in the TFSA are consistent with what has been observed in other regions. In New Zealand, deer seem not to impede regeneration of *Nothofagus* species, and a long-term effect on forest regeneration seems unlikely (Veblen and Stewart 1982; Nugent et al. 2001). However, deer do impede the regeneration of several tree species accompanying *Nothofagus* (Allen et al. 1984), which could result in a switch in tree species relative abundances, favoring the most browse-resistant species (Nugent et al. 2001). In Australia, rabbits prevent regeneration of trees and shrubs, especially *Acacia* sp. (Myers et al. 1994), and in continental Europe high densities of introduced deer impede regeneration by several dominant tree species (Ebenhard 1988; Gill 1992).

Available data also suggest that, when introduced ungulates lead to decreased plant species richness, this decrease is due to a loss of native species in grazed sites, whereas increased plant species richness with grazing results, at least in part, from increased richness of exotic species. Similar effects have been observed in North American temperate forests, where livestock grazing increases richness of native and exotic ruderal species and causes a loss of woodland-restricted native species (Dennis 1997). Likewise, in many grassland ecosystems, grazing by introduced ungulates results in increased plant species richness, which is frequently accompanied by an increased proportion of unpalatable, exotic species (Mack 1989; Hobbs and Huenneke 1992; Hobbs 2001; Chaneton et al. 2002). However, it seems that low canopy cover could be a necessary condition for introduced herbivores to favor invasion by exotic plants, a situation that can happen both naturally (e.g., in some open forest types or in treefall gaps) and anthropogenically (e.g., though forest logging or burning). An interaction between canopy cover and plant invasions has been observed in many forest ecosystems worldwide, so that exotic plant richness increases with decreasing canopy cover (Von Holle et al. 2002). Thus, it is possible that an interaction between grazing and decreased forest cover, rather than grazing alone, favors invasion by exotic plants.

Although the mechanisms accounting for effects of introduced mammalian herbivores on some plant species can be accounted for by the direct effects of trampling and browsing, several kinds of indirect effects are also possible. For example, introduced ungulates appear to affect the reproductive success of *Alstroemeria aurea*, and decreased abundance of the mistletoe *Tristerix corymbosus* is apparently caused by lower availability of its main host, *Aristotelia chilensis*. Likewise, increased abundance of browsing-resistant species in sites with introduced ungulates (including some spiny shrubs and herbaceous exotic species) may be attributed to an indirect effect of lowered light competition from palatable, shade-tolerant species. Although indirect effects are usually weaker in communities than direct effects, they are usually strong enough to make their study worthwhile (Schoener 1993; Menge 1995; Abrams et al. 1996).

Introduced mammalian herbivores may be affecting native animals through a variety of mechanisms, although little evidence currently exists. Competition with introduced ungulates has been suggested as a possible cause of the decline of the huemul and the pudu. Similar effects of introduced herbivorous mammals have been suggested in other regions, but in very few cases have those effects been demonstrated (see Introduction, and Ebenhard 1988). Disease transmission from introduced herbivores has also been invoked as a possible cause of the decline of huemul, although, again, no hard evidence exists. There are several well-documented cases of indirect effects between mammalian herbivores through disease transmission. In North America, white-tailed deer (*Odocoileus virginianus*) exclude moose (*Alces alces*) through their common parasite, the meningeal worm (*Parelaphostrongylus tenuis*) (Schmitz and Nudds 1994). Meningeal worm infection is clinically benign in white-tailed deer but almost always fatal in moose (Anderson 1972). Introduced herbivores could also be affecting native herbivores by enhancing predator populations. Other effects are likely (such as a doubly indirect effects of herbivores on a hummingbird and an endemic marsupial), although, again, no hard evidence exists.

Virtually no data are available about the effects of introduced mammalian herbivores on invertebrates. The only available study suggests that some functionally important insect pollinators could be negatively affected by cattle grazing; however, the mechanism accounting for this effect is not known. In other regions, there are several documented cases of negative effects of introduced mammalian herbivores on invertebrates. Sheep negatively affect the abundance and biomass of most invertebrate groups in New South Wales, Australia (Hutchinson and King 1980). And there are several documented cases of pollinator declines caused by grazing by domestic animals (Kearns 1997); for example, sheep grazing in California is believed to affect native pollinators of *Astragalus monoensis* through trampling and food removal (Sudgen 1985).

Little is known about effects on ecosystem processes. Beavers in Tierra del Fuego can affect nutrient cycling, and ungulates may affect soil properties and increase erosion processes. Effects of introduced mammalian herbivores on ecosystem processes have been observed in other systems. Feral pigs (*Sus scrofa*) have modified entire communities and ecosystems through their digging and "rooting" activities. In Great Smoky Mountains National Park in the southeastern United States, feral pigs have greatly modified soil characteristics by thinning the forest litter, mixing organic and mineral layers, and creating bare ground. These effects have in turn led to increased concentrations of nitrogen and potassium in soil solution and accelerated leaching of many minerals from the soil and litter (Singer et al. 1984). Similar effects of feral pigs have been observed in many other regions (Mack and D'Antonio 1998). Introduced goats have contributed to soil disturbance and loss in many island ecosystems (Coblentz 1978). And introduced ungulates can cause a decline in aboveground biomass production, altering fire-regimes in fire-prone ecosystems (Mack and D'Antonio 1998).

Evidence for the effects of introduced mammalian herbivores comes from a few studies, most of which are observational and with low replication. The importance of manipulation and appropriate replication in ecological studies cannot be overemphasized. The establishment of a network of well-planned, long-term exclosures stands out as a research priority in the TFSA. Similar systems of exclosures have proven extremely useful to understanding the ecological impacts of introduced mammalian herbivores in North America (Dennis 1997; Milchunas et al. 1998; Proulx 1998), New Zealand (Fitzgerald and Gibb 2001; Wardle 2001), and Europe (Hester et al. 2000). Furthermore, this kind of manipulative approach is necessary to understand the effects of introduced herbivores at relevant spatial and temporal scales. However, many ecological processes operate at broad spatial and temporal scales, and experimental removals or introductions of large herbivores at such scales are not feasible in many situations. In those cases, the comparison of areas where introduced herbivores were already present or absent is a more feasible option. And in some cases it may simply be too late to document some effects. For example, although it is possible to hypothesize about the possible causes of the decline of the huemul throughout its range, it is probably not possible to test whether that decline was caused by introduced ungulates through some of the mechanisms discussed above.

I have not stressed the different ways in which different introduced mammalian herbivores can affect the invaded ecosystems. Obvious differences are between species that differ greatly in their ecologies, such as beaver and deer. Beaver affect the invaded ecosystems through browsing on leaves for feeding, by deforestation resulting from dam construction, and by the flooding of large tracts of forest. Deer, on the other hand, can exert their effects through browsing, trampling and rubbing or “horning.” But even species that are more ecologically similar, such as deer and cattle, may differ in their effects, sometimes in subtle ways. Deer are more selective than cattle in their feeding preferences (Veblen et al. 1992b); because other kinds of interactions besides herbivory are probably involved, such as competitive interactions among plants, differences in feeding preferences can result in very different effects of species of introduced herbivores on plant community structure and dynamics (Ebenhard 1988; Huntly 1991). The scarce available information on the impacts of different herbivorous species does not allow a comparison of their impacts. Furthermore, most of the studies of the effects of introduced ungulates come from a few locations and forest types. Although it is tempting to extrapolate these effects to the entire TFSA and to other forest types, it would be risky to do so. Clearly, more research is needed.

More than anything, this review will contribute to the realization of how little we know about how introduced mammalian herbivores are affecting the biota of the TFSA. Virtually all aspects of the ecological impacts of introduced mammalian herbivores reviewed here need further research. Several research needs stand out as especially important. First, we need data on the effects of introduced mammalian herbivores on the regeneration of forest types not included in previous studies. Furthermore, even those forest types included in previous studies need further research, with higher replication and at broader spatial and temporal scales. Second, it is important to understand the effects on plant community structure and composition, including effects on rare and endemic plants, effects on exotic plant invasions, how these effects vary across space and time, and what mechanisms cause these effects. Third, the interaction between effects of introduced mammalian herbivores and other anthropogenic changes (especially fire and logging) needs to be understood. Fourth, it is important to understand the effects of introduced mammalian herbivores on other biotic components of the ecosystem besides plants. We know very little about the potential effects of introduced herbivores on other vertebrates, virtually nothing about the potential effects on insects, and absolutely nothing about effects on other organisms (e.g., other invertebrates, fungi). Given the drastic habitat changes introduced mammalian herbivores can induce, an equally drastic effect on the organisms using that habitat can be expected. Fifth, it is important to understand how habitat changes induced by introduced herbivores affect ecosystem processes. Finally, the effects of introduced herbivores must be understood in the context of climatic variability. A sound scientific understanding of the multiple effects of introduced mammalian herbivores is crucial for the long-term conservation of the unique biota of the TFSA.

4

ECOLOGICAL SPECIALIZATION AND SUSCEPTIBILITY TO DISTURBANCE: CONJECTURES AND REFUTATIONS[1]

Summary. Niche breadth of species has been hypothesized to be associated with their response to disturbance. Disturbance is usually believed to affect specialists negatively, while generalists are believed to benefit from disturbance; I call this the "specialization–disturbance" hypothesis. I also propose an associated hypothesis (the "specialization–asymmetry–disturbance" hypothesis), under which both specialization and asymmetry of interactions would explain species' responses to disturbance. I test these hypotheses using data from a plant–pollinator system that has been grazed by cattle (i.e., a biological disturbance) in southern Argentina. I quantified specialization in species interactions, specialization of interaction partners, and species' responses to disturbance. I found no relationship between degree of specialization and a species' response to disturbance. I also found that plant–pollinator interactions tend to be asymmetric in this system: there was no relationship between the degree of specialization of a given species and the degree of specialization of its interaction partners. However, asymmetry of interactions did not explain the variability in species' responses to disturbance. Thus, both hypotheses are rejected by my data. Possible reasons include failure to assess crucial resources, substantial direct effects of disturbance, inaccurate measures of specialization, difficulty detecting highly non-linear relationships, and limitations of a non-experimental approach. Or, in fact, there may be no relationship between specialization and response to disturbance.

> *La especialización, hijos, es cosa de insectos.*
> —F.L. Vázquez (1998, pp. 74)

> *In fact, specialization is arguably the most*
> *fundamental concept in the history of thought*
> *on extinction risk.*
> —M.L. McKinney (1997, pp. 500)

> *it may not always be so*
> —E.E. Cummings (1923)

INTRODUCTION

Understanding what factors are important for species persistence when ecosystems are subject to change is of paramount importance for ecology. Why are some species negatively affected by disturbance, while others respond positively or are not affected at all? Can any ecological characteristics of species help to predict how they will respond to disturbance?

One possible answer to the above questions is that the niche breadth of a species is related to its response to disturbance. It is usually believed that specialists are negatively affected by disturbance, while generalists benefit from it (e.g., Baker 1955; Preston 1962; Wilson and Willis 1975; Parrish and Bazzaz 1979; McKinney 1997; Hobbs 2000); throughout this chapter, I will call this the "specialization–disturbance hypothesis." This is what Den Boer (1968) called "spreading the risk". Den Boer hypothesized that species can "spread the risk" of extinction in at least four different ways: (i) phenotypically, by having high phenotypic variation among individuals; (ii) temporally, by having low synchronization of developmental times among individuals; (iii) spatially, by using different kinds of habitats; and (iv) in terms of the interactions with other species, for example by being polyphagous as opposed to monophagous. It is this last way of spreading the risk that I analyze here.

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[1] A slightly modified version of this chapter has been published as: Vázquez, D.P., and D. Simberloff. 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. American Naturalist 159: 606-623.

Specialization in interspecific interactions has been hypothesized to affect species in several ways. First, populations of specialists might be more temporally variable than generalists, as originally hypothesized by MacArthur (1955). Population variability (one of many possible measures of stability, see Pimm 1984, 1991) is usually believed to be positively correlated with probability of extinction (Pimm et al. 1988; Pimm 1991; but see Tracy and George 1992). However, the evidence for MacArthur's hypothesis has been ambiguous. Redfearn and Pimm (1988) and Morin and Lawler (1996) found niche breadth and population stability to be *positively* correlated, while Watt (1964; 1965) and Rejmánek and Spitzer (1982) found them to be *negatively* correlated. All these studies dealt with predation; none of them analyzed specialization in terms of other kinds of interactions (e.g., mutualism), nor in terms of other "niche axes."

Second, specialists might have more restricted distributions than generalists (1984) and thus be at a higher risk of extinction. The probability of extinction of a population is believed to be related to its geographic range, range-restricted populations being more prone to extinction than wide-ranging populations (e.g., Manne et al. 1999; Chown and Gaston 2000)(e.g., Manne et al. 1999; Chown and Gaston 2000). Thus, specialists could be more prone to extinction than generalists because they tend to have more restricted distributions. However, the study of the relationship between niche breadth and geographic range is methodologically problematic; because geographically widespread and locally abundant species tend to be represented more in samples, a positive correlation between niche breadth and these two variables is expected simply as a by-product of sampling. The few studies that have controlled for this sampling effect have failed to find a positive correlation between niche breadth and geographic range size (Burgman 1989; Kouki and Häyrinen 1991; Gaston et al. 1997).

Regardless of the mechanism, according to the specialization–disturbance hypothesis specialists should be more vulnerable to disturbance than generalists. Below, I point out some conceptual problems with the specialization–disturbance hypothesis and propose an alternative hypothesis. To our knowledge, there have been only two attempted tests of this hypothesis, which I also briefly discuss below. Finally, I test these hypotheses with data from our work on plant–pollinator interactions in the temperate forests of the southern Argentine Andes.

The hypotheses

The specialization–disturbance (S-D) hypothesis can be described mathematically as

$$A_i = b_0 + b_1 s_i^f \qquad [1]$$

where A_i is an index of abundance change of species i with disturbance, with range $A_i = [-1,1]$ (negative values of A_i mean negative effects of disturbance, while positive values mean positive effects); s_i is the niche breadth of species i (low values of s_i mean narrow niche breadth, i.e., high specialization); f is a constant, with range $f = [0,1]$; b_0 is a constant that can take any negative value; and b_1 is a constant that can take any positive value. When $f = 1$, A_i is a linear function of s_i; however, when $f < 1$, the relationship is nonlinear. This relationship is shown in Fig. 4.1a.

The constant f can be thought of as representing the degree of redundancy of plant-pollinator interactions. When $f = 1$ there is no redundancy, and each new mutualist species adds a little, resulting in a linear relationship between s_i and A_i. Thus, when $f = 1$ it will always be beneficial to be a generalist when disturbance occurs, and a broad generalist has a substantial advantage over a moderate generalist. However, when $f << 1$ plant-pollinator interactions are highly redundant, and the relationship between s_i and A_i is strongly nonlinear; then the only strong negative effect of disturbance will be on those species with extremely narrow niches, and having an extremely broad niche will not be much more advantageous than having a moderately broad one.

One implicit assumption of the S-D hypothesis is that disturbance does not affect species directly by increasing their mortality, but indirectly by changing the resource availability, as shown in Fig. 4.2a. Therefore, because specialists depend more on specific resources than generalists, they should on average be more likely to be affected by disturbance. However, this assumption may be unrealistic in many cases; disturbance may affect species not only indirectly through their resources, but also directly through an effect on mortality, as shown in Fig. 4.2b. The relative importance of direct vs. indirect effects of disturbance will determine whether a relationship between specialization and disturbance is actually observed. Thus, if disturbance does affect species directly, then a main assumption of the S-D hypothesis will be false, and a true effect of specialization on response to disturbance may be "hidden" by the direct effect of disturbance on mortality. The importance of the violation of this assumption will depend on the relative importance of the direct effect of disturbance on mortality and the indirect effect through the modification of resource availability.

In the particular case of plant–pollinator mutualisms analyzed here, species are at the same time "focal species" for the analysis (i.e., the species for which specialization and response to disturbance are being studied) and resources for their interaction partners. The S-D hypothesis also assumes that the chain of effects is unidirectional, so that disturbance affects resources, which in turn affect species; I have just mentioned that disturbance can affect species directly. However, when resources are also "focal species," it is likely that there will be a reciprocal effect from species to the resource (Fig. 4.2 c); in this case, the flow of effects is no longer unidirectional, because species can affect their resources. This means that an effect of disturbance on the resource (e.g., plants) will affect species (pollinators), but this effect on pollinators will also affect plants, since pollinators are a resource from the plants' perspective.

This reciprocal effect is expected if the degree of specialization of species is also reciprocal (i.e., if there is a correlation between the degree of specialization of species and that of their partners, so that specialists tend to interact with specialists, and generalists with generalists). However, reciprocity is not expected if specialization is not symmetrical (i.e., if specialists tend to interact with generalists, and vice-versa). Thus, a combination of both specialization of a given species and that of its interaction partners would determine its response to disturbance. I call this new, modified hypothesis the "specialization–asymmetry–disturbance hypothesis" (or S-A-D hypothesis). This hypothesis can be described mathematically as

$$A_i = \varphi(s_i, p_i) \qquad [2]$$

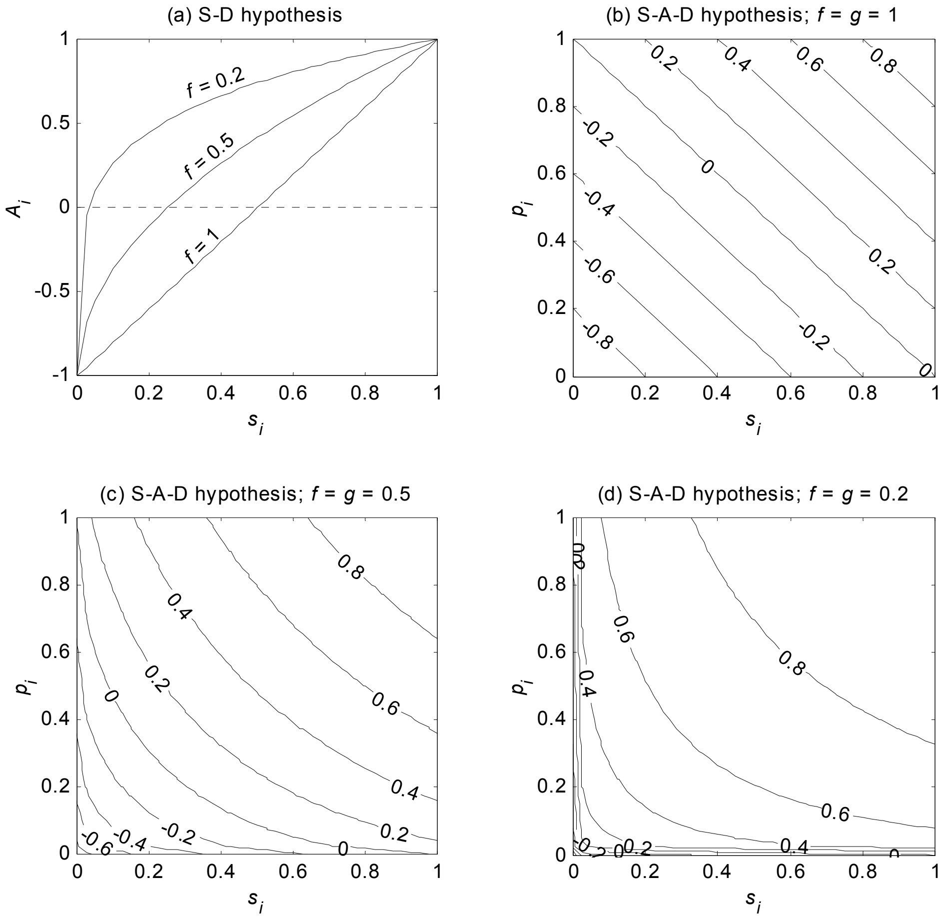
where A_i and s_i are defined as above, p_i is degree of specialization of interaction partners, and $\varphi(s_i, p_i)$ is some function of s_i and p_i. One possible explicit form of equation [2] is an additive model such as

$$A_i = b_0 + b_1 s_i^f + b_2 p_i^g \qquad [3]$$

where b_0 is a constant that can take any negative value, b_1 and b_2 are constants that can take any positive value, and f and g are constants with range f = range g = [0,1] (Fig. 1b-d). As for s_i, low values of p_i mean high specialization of interaction partners. When both f and g are large (i.e., equal or close to 1; Fig. 1b), negative values of the response to disturbance A_i are expected when both s_i and p_i are moderately to extremely low, as with the S-D hypothesis (A_i values are represented by transverse straight isolines in Fig. 1b and by concave isolines in Figs. 4.1c and d); however, even if s_i is relatively large (i.e., species have relatively broad niches), negative values of A_i are still possible so long as p_i is low enough. As f and g decrease, the A_i isolines become increasingly concave. As a result of this concavity, negative values of A_i are clumped in the neighbourhood of the figure axes; the lower the values of f and g, the higher the degree of clumpiness of the isolines in the neighborhood of the axes. Clearly, a strongly non-linear relationship between s_i, p_i, and A_i greatly restricts the range of possible values of s_i and p_i necessary to obtain a negative response to disturbance—only extremely specialized species whose interaction partners are also extremely specialized will be negatively affected by disturbance when this relationship is highly non-linear.

Previous tests of the specialization–disturbance hypothesis

Kitahara and Fujii (1994) and Kitahara et al. (2000) tested the S-D hypothesis with data from lepidopteran communities in central Japan. Kitahara and Fujii (1994) studied communities of lepidopteran larvae feeding on plants in nine sites in three forested areas of varying degrees of human disturbance in or around Tsukuba City; they surveyed lepidopteran larvae along transects in each site to estimate their abundance. Kitahara et al. (2000) censused adult butterflies along transects in five grassland sites of increasing human disturbance on the Asagiri Plateau at the western foot of Mt. Fuji. In both cases, using literature reports, they also assigned species to one of two specialization categories—specialist or generalist—according to two different niche axes—time and food. They considered uni- or bivoltine species to be temporal specialists and multivoltine species to be temporal generalists. They considered lepidopteran species whose larvae were known to feed on 10 or fewer plant species belonging to the same family as trophic specialists and species feeding on more than 10 plant species of the same family, or on plants belonging to different families, as trophic generalists. Finally, they considered those species that were both time and food specialists as specialists, and those that were both time and food generalists as generalists; they did not analyze the remaining species. In both cases, they found that the number of specialist species increased with decreasing disturbance, while the number of generalist species did not change significantly. Thus, their results support the specialization–disturbance hypothesis.



(a) S-D hypothesis

(b) S-A-D hypothesis; *f* = *g* = 1

(c) S-A-D hypothesis; *f* = *g* = 0.5

(d) S-A-D hypothesis; *f* = *g* = 0.2

Figure 4.1. Hypothesized relationships between interaction specialization and susceptibility to disturbance. (a) The specialization–disturbance hypothesis. According to this hypothesis, response to disturbance should go from negative to positive as niche breadth increases, as described by the following model: $A_i = b_0 + b_1 s_i^f$, where A_i is some measure of the response of species *i* to disturbance; s_i is interaction specialization of species *i*; *f* is a constant with range $f = [0,1]$; and b_0 and b_1 are constants that can take any value (see text for details). (b-d) The specialization–asymmetry–disturbance hypothesis. Here, for a given species, species response to disturbance is expected to go from negative to positive as both its degree of specialization and some measure of the specialization of its interaction partners increase, as described by the following model: $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$, where A_i and s_i are defined as above, p_i is the specialization of interaction partners, b_0, b_1 and b_2 are constants that can take any value, and *f* and *g* are constants with range $f = [0,1]$ and $g = [0,1]$. Therefore, a decreasing susceptibility to disturbance is expected as one goes away from the lower left corner of the graph. A_i values are represented by transverse straight isolines in (b), and by concave isolines in (c) and (d).

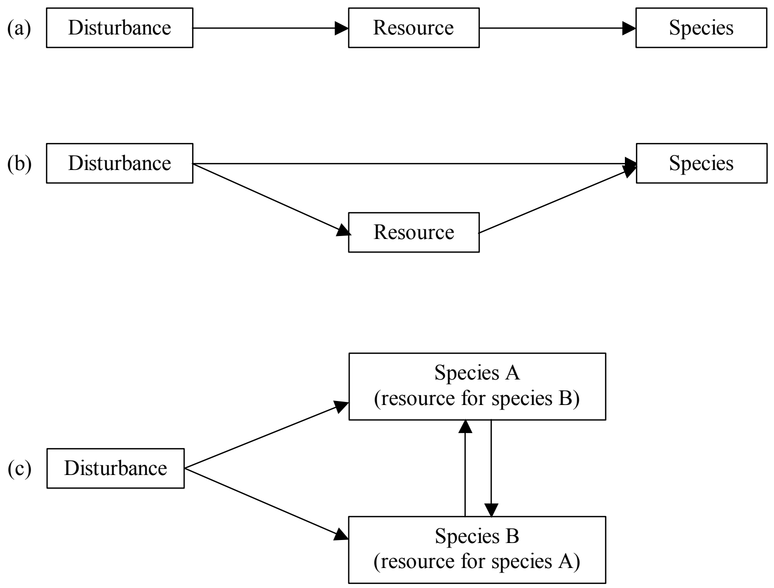


Figure 2. Three possible ways in which species can be affected by disturbance. (a) According to the specialization–disturbance hypothesis, disturbance affects species only indirectly through their resources. (b) More realistically, disturbance could affect species not only indirectly through their resources, but also directly through an effect on mortality. (c) When resources are also "focal species," it is likely that there will be a reciprocal effect between species and their resource.

A possible problem with Kitahara and Fujii's, and Kitahara et al.'s analyses (as with most other analyses of specialization) is how they measured specialization. First, their measure of food specialization seems too coarse: for example, they put in the same "specialist" category a species feeding on as many as ten plant species, as long as they were in the same family, and a species feeding on only one plant species, while they considered to be "generalist" a lepidopteran species feeding on just two plant species, as long as they belonged to different families. Second, they did not consider relative frequency of use of resources; thus, a lepidopteran species found 95% of the time on a single plant species, but with records on two other plant species of different families, would be considered a generalist. It would be interesting to see whether their results hold when these conventions are changed.

In the present paper I propose a different measure of specialization, which I think is more reliable than that of Kitahara and Fujii (1994) and Kitahara et al. (2000). Using this measure, I test whether the degree of specialization in plant–pollinator interactions is related to the response of species to the presence of cattle—a biological disturbance (Huntly 1991). I also develop a simple measure of specialization of interaction partners (p_i, the weighted average of specialization of interaction partners) and use it to test whether the degree of symmetry in interactions can help explain the variability in species' responses to disturbance.

METHODS

Study area and sites

Study area and sites were the same as described for Chapter 2 (see Fig. 2.2).

Study organisms

I included all animal-pollinated plants growing in the understory and groundcover that were abundant enough to allow replication; these totalled 15 species, of which 12 had enough visits by pollinators to allow statistical treatment of the data. Plant species are listed in Table 4.1.

Because of the sampling methods, I could not select *a priori* the insect species to study. Rather, I included all species visiting any of the plant species studied. However, because most pollinator species were too rare to allow statistical analysis of their specialization and abundance (see below), I analyzed only

Table 4.1. Plant species included in the study.

Plant species	Family	Common name	Life form	Origin	A_i	F_i	s_i	p_i
Alstroemeria aurea	Alstroemeriaceae	Amancay	Herb	Native	-0.64	-0.16	7.56	2.58
Aristotelia chilensis	Eleocarpaceae	Maqui	Understory tree	Native	-0.46	-0.22	2.10	2.16
Berberis buxifolia	Berberidaceae	Calafate	Shrub	Native	0.74	1.00	2.50	3.03
Berberis darwinii	Berberidaceae	Michai	Shrub	Native	0.01	0.15	4.88	3.14
Calceolaria crenatiflora	Scrophulariaceae	Topa-topa	Herb	Native	0.00	0.36	3.00	1.71
Cynanchum diemii	Asclepiadaceae	—	Vine	Native	-0.41	-0.34	5.52	2.59
Digitalis purpurea	Scrophulariaceae	Dedalera	Herb	Exotic	0.25	…[b]	3.62	3.20
Gavilea odoratissima	Ochidaceae	Orquídea	Herb	Native	0.20	0.52	…[a]	…[a]
Maytenus chubutensis	Celastraceae	Chaurilla	Shrub	Native	0.00	…[b]	…[a]	…[a]
Mutisia decurrens	Asteraceae	Mutisia	Vine	Native	0.56	…[b]	8.05	2.33
Rosa eglanteria	Rosaceae	Rosa mosqueta	Shrub	Exotic	-0.24	…[b]	9.71	2.97
Ribes magellanicum	Saxifragaceae	Parrilla	Shrub	Native	-0.70	-0.10	3.80	3.07
Schinus patagonicus	Anacardiaceae	Laura	Understory tree	Native	0.03	-0.21	5.24	2.35
Tristerix corymbosus	Loranthaceae	Quintral	Parasitic shrub	Native	-0.50	-0.50	…[a]	…[a]
Vicia nigricans	Leguminosae	Arvejilla	Vine	Native	0.08	0.03	1.80	3.45

Note: Variables A_i, F_i, s_i and p_i defined in text.

[a] Species did not have enough visits to allow calculation of specialization and were therefore excluded from the analyses.

[b] Fruit set could not be measured for species.

31 of the 129 recorded species. Most bee and syrphid fly species and all bombilid and nemestrinid fly species were identified to species or genus. Species in other groups were usually identified to family and assigned to "morphospecies" categories. Insect species are listed in Table 4.2. Late in the flowering season I realized that one syrphid fly morphospecies actually contained two species (see *Allograpta hortensis*, *Toxomerus vertebratus* in Table 4.2). I am confident that the rest of the morphospecies included in this study represent single taxonomic species.

Abundance estimation

To estimate plant abundance, I examined 30 rectangular quadrats of 20 m^2 separated by a fixed distance along transects in each site, counting the number of individuals of each species per quadrat. Because the density of understory vegetation was too high to permit walking through it in some cases (especially in sites without cattle), forest walking paths served as transects in all sites. Transect length varied between ~300 m (Quetrihué nc) to ~700 m (Llao Llao); therefore, inter-quadrat distance also varied (~10–23 m). Because I used pre-existing forest trails as transects, transect shape also varied among sites, ranging from one single nearly-linear transect to irregular, "s" shaped transects.

I took the number of insect individuals visiting any plant species at any time during the flowering season as an estimate of insect pollinator abundance in each site. Thus, the abundance estimates depend partly on the abundance of the plant species sampled. However, because I sampled virtually all animal-pollinated plants growing in our sites throughout the entire flowering season and sampled with similar effort in paired sites, I believe this is a reliable estimate of abundance. (I also used Malaise traps to sample the insect fauna. However, for most pollinator species the catch was too low for statistical analysis.) Pollinators visiting flowers of each species were sampled in 10 min. periods. Paired sites were always simultaneously sampled by different observers. A total of 2710 10 min. observation periods were conducted for all sites and plant species. The numbers of sampling periods per site and plant species are given in Table 4.3; these numbers varied across species and sites, because species differed in their abundance, duration of the flowering period, and flowering time overlap with other species. For each visiting pollinator I recorded species name, number of flowers visited, and whether it contacted flower reproductive parts (anthers or stigmas). When the pollinator species was unknown, I collected the specimen and identified it in the laboratory. A reference collection from the collected material has been deposited in the Laboratorio Ecotono at the Universidad Nacional del Comahue in Bariloche, Río Negro, Argentina (some bee specimens were also placed in the Museo Argentino de Ciencias Naturales in Buenos Aires).

Fruit set

Fruit set was calculated as the proportion of flowers that set fruit. I marked individuals of most plant species in all sites where they were present, recording the number of flowers per individual (herbs) or per branch (shrubs, trees and vines). I then counted the number of fruits produced. Fruit set could not be measured for four species (*Maytenus chubutensis*, *Mutisia decurrens*, *Rosa eglanteria*, and *Digitalis purpurea*).

Table 4.2. Insect species included in the study. A_i, s_i, and p_i defined in text. Numbers in the species column indicate the catalog number in the collection deposited in the Ecology Department of the Universidad del Comahue, in Bariloche, Río Negro, Argentina. A question mark in the "Origin" column indicates species that were presumably native but whose origin could not be confirmed because of incomplete identification.

Order	Family	Species	Origin	A_i	s_i	p_i
Hymenoptera	Andrenidae	*Heterosarus* sp.	Native (?)	1.00	1.82	7.63
	Apidae	*Bombus dahlbomii*	Native	-0.42	3.57	5.13
		Bombus ruderatus	Exotic	-0.09	1.84	7.07
		Chalepogenus caeruleus	Native	0.55	1.00	5.52
		Manuelia gayi	Native	-0.46	1.36	7.56
		Manuelia postica	Native	-0.46	3.82	6.60
	Colletidae	*Colletes seminitidus*	Native	0.79	2.80	4.19
		Policana albopilosa	Native	-0.27	2.00	3.33
	Halictidae	*Caenohalictus* sp. 2	Native (?)	0.16	1.57	4.78
		Ruizantheda mutabilis	Native	0.28	3.12	4.32
	Megachilidae	*Megachile* sp. 1	Native (?)	0.00	1.00	7.56
	Braconidae	Sp. 052	Native (?)	-0.75	1.87	3.26
	Formicidae	Sp. 061	Native (?)	-0.25	2.69	3.14
	Sphecidae	Sp. 078	Native (?)	-0.43	1.77	7.59
	Torymidae	Sp. 073	Native (?)	-0.13	2.61	3.27
	Vespidae	*Vespula germanica*	Exotic	-0.23	4.08	7.53
Diptera	Bombilidae	*Phthiria* sp. 1	Native (?)	-0.21	1.60	7.61
		Phthiria sp. 2	Native (?)	0.08	1.40	7.58
	Lauxaniidae	*Sapromyza fulvicornis*	Native	-0.37	2.85	8.31
	Nemestrinidae	*Trichophthalma amoena*	Native	0.04	3.03	3.89
		Trichophthalma jaffueli	Native	0.07	1.09	7.58
	Syrphidae	*Allographta hortensis*, *Toxomerus vertebratus*	Native	0.66	3.62	6.49
		Platycherius (*Carposcalis*) sp.	Native	0.40	4.77	6.11
		Syrphus octomaculatus	Native	0.00	3.04	6.89
		Sp. 120	Native (?)	-0.16	2.92	7.95
	Tabanidae	Sp. 109	Native (?)	0.50	2.07	2.52
	Phoridae	Sp. 210	Native (?)	-0.42	1.36	7.58
Coleoptera	Buprestidae	*Anthaxia* sp.	Native (?)	-0.31	1.79	7.62
	Nitidulidae	Sp. 055	Native (?)	-0.62	3.88	5.49
	Staphylinidae	Sp. 112	Native (?)	-0.44	2.23	7.95
	Melyridae	Sp. 011	Native (?)	0.25	1.83	7.74

Table 4.3. Number of 10 min. sampling periods performed per site and plant species. Taxonomic affiliations and other species' characteristics are given in the appendices. Paired sites without (nc) and with (c) cattle are listed contiguous.

Plant species	LL (nc)	CL (c)	S (nc)	AG (c)	M (nc)	M (c)	Q (nc)	Q (c)	Total
Alstroemeria aurea	147	83	151	129	140	57	103	83	893
Aristotelia chilensis	17	23	34	14	23	11	28	0	150
Berberis buxifolia	0	6	0	3	0	10	0	11	30
Berberis darwinii	10	23	19	24	17	23	1	44	161
Calceolaria crenatiflora	28	12	13	24	11	31	8	49	176
Cynanchum diemii	30	41	51	6	0	0	29	7	164
Digitalis purpurea	0	0	0	0	0	0	0	56	56
Gavilea odoratissima	61	31	26	1	17	18	0	14	168
Maytenus chubutensis	4	0	3	0	13	15	0	0	35
Mutisia decurrens	45	89	29	49	35	16	8	19	290
Rosa eglanteria	0	8	2	3	19	17	1	19	69
Ribes magellanicum	42	7	31	10	11	5	12	2	120
Schinus patagonicus	5	18	10	29	6	23	7	5	103
Tristerix corymbosus	15	0	0	0	0	0	16	0	31
Vicia nigricans	66	35	21	42	21	35	20	24	264
Total	470	376	390	334	313	261	233	333	2710

Response variables

I evaluated the response of plants to the presence of cattle by comparing species abundance between grazed and ungrazed sites. However, because abundance in plants may take a long time to change, and because the resource I considered is expected to affect abundance only through an effect on reproduction, I also used fruit set as a more direct measure of plants' response to cattle.

To quantify species responses to cattle, I developed a normalized index that measures the change of species abundance in response to disturbance:

$$A_i = \frac{1}{n}\left(\sum_{j=1}^{n} \frac{\delta_{ij}^{a}}{\sigma_{ij}^{a}}\right) \qquad [4]$$

where A_i is the differential abundance index of species i, with range $A_i = [-1,1]$; δ_{ij}^{a} is the difference in abundance of species i between ungrazed and grazed sites of pair j; σ_{ij}^{a} is the sum of abundances of species i in ungrazed and grazed sites of pair j; and n is the number of pairs of sites ($n = 4$ in all cases). The absolute value of A_i will be maximized when species responses across pairs of sites are consistent and of high relative magnitudes (i.e., the δ_{ij}^{a} values have the same signs and are high relative to the σ_{ij}^{a} values). An important point here is whether n should always equal 4 (the total number of replicates), or rather equal the number of pairs in which a given species was present; I judged the former to be more appropriate, because this convention prevents A_i from being inflated for species found in fewer than four pairs.

In a similar way, I defined

$$F_i = \frac{1}{n}\left(\sum_{j=1}^{n} \frac{\delta_{ij}^{f}}{\sigma_{ij}^{f}}\right) \qquad [5]$$

where F_i is the differential fruit production index, with similar properties as A_i; in this case, δ_{ij}^{f} is the difference in mean fruit set of species i between ungrazed and grazed sites of pair j; σ_{ij}^{f} is the sum of mean fruit set of species i in ungrazed and grazed sites of pair j; and n is the number of pairs of sites as defined above.

Specialization

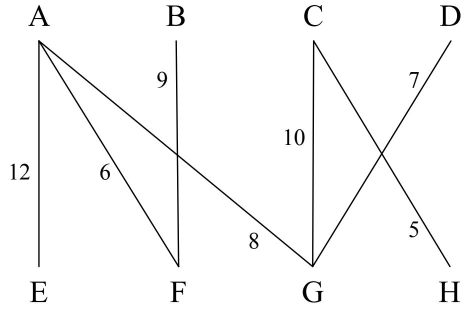
Flower visitors differ widely in terms of their effectiveness as pollinators (Lindsey 1984; Schemske and Horwitz 1984), a fact that must be borne in mind when one assesses specialization. The best way to study pollination effectiveness is through experiments. However, in community-wide studies such as this one involving many species of plants and pollinators, the number of experiments necessary to assess specialization would be prohibitive. I thus estimated pollinator effectiveness differently. Each time a pollinator visited a flower, I recorded whether it touched the anthers or the stigma. I used the proportion of visits in which a particular pollinator species contacted the reproductive parts as an estimate of its effectiveness; I 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. I used e to calculate plant specialization, but t for the calculation of insect specialization (from an insect's perspective, it does not really matter whether it is an effective pollinator).

The measurement of niche breadth is analogous to the measurement of species diversity. Two main components have to be taken into account for the quantification of species diversity: species richness (i.e., the number of species) and species evenness (i.e., the relative abundance of species). When measuring niche breadth, "richness" is the number of different resource items used by a given species (e.g., the number of pollinators "used" by a given plant species, or the number of plants visited by a given pollinator species), and "evenness" is the relative frequency of use of the different resource types (e.g., the frequency of interaction between plants and pollinators). A third attribute of niche breadth can be taken into account—the relative abundance of resources. Many measures of species diversity and niche breadth have been proposed (see Gotelli and Graves 1996; Krebs 1998). Two major problems with many of the measures of species diversity and niche breadth is that they are biologically difficult to interpret, and they are sensitive to sample size (Gotelli and Graves 1996). One alternative is to use the rarefaction technique. Rarefaction allows the comparison of species richness between samples of different sizes, standardizing by sample size (Gotelli and Graves 1996). Furthermore, the shape of the rarefaction curve reflects the evenness of the sample: for any two samples of equal size and richness but differing in evenness, the value of the rarefaction function is lower for the less even sample throughout the entire function domain (Gotelli and Graves 1996). Thus, it is important to note that, although I used species richness as a measure of specialization, the evenness component of diversity is also accounted for by rarefaction: the rarefied expected richness is a function of both the observed number of species and the observed abundance distribution.

To quantify specialization in species interactions, I defined s_i, the interaction specialization of species i, as the "rarefied" species richness of its interaction partners. Thus, the richness of pollinators visiting a given plant species served as a measure of plant interaction specialization, and I used the number of plant species visited by a given pollinator species as a measure of insect specialization. I used EcoSim software (Gotelli and Entsminger 2000) to perform the rarefaction calculations.

Of the 15 plants originally included in the study, three had e values too low to be used for rarefaction (*Gavilea odoratissima*: 1; *Maytenus chubutensis*: 0; *Tristerix corymbosus*: 6); therefore, these plant species were not analyzed. For the remaining species, I used the lowest e recorded (i.e., that corresponding to *Calceolaria crenatiflora*) as the rarefaction sample size; this choice allowed us to compare the expected richness each species would have had if it had received 19 visits. To test whether results depended on the sample size chosen for rarefaction, I also used a rarefaction sample size of 67, the e value for *Mutisia decurrens*, the species with the next lowest number of visits after *Calceolaria crenatiflora*; I then re-rarefied for 11 species only, excluding *C. crenatiflora*.

As mentioned above, of the total of 129 species of insects, most were recorded rarely. I included in the analyses only species that had abundances (i.e., number of individuals recorded visiting flowers) of at least 10; thus, I could include only 31 of the 129 species of flower visitors. As I did for plants, I performed the rarefaction simulations for insects using two different sample sizes, 10 and 20; all 31 species were included when simulations were run using a sample size of 10, while only 20 species where included with a sample size of 20.



Plants	Pollinators						
	A	B	C	D	n	s_i	p_i
E	12	0	0	0	12	1.00	2.61
F	6	9	0	0	15	1.95	1.64
G	8	0	10	7	25	2.67	1.88
H	0	0	5	0	5	1.00	1.91
n	26	9	15	7			
s_i	2.61	1.00	1.91	1.00			
p_i	1.73	1.95	2.11	2.67			

Figure 4.3. A hypothetical community of plants and pollinators to illustrate how the specialization of interaction partners, p_i, is calculated. In the example, four pollinator species, A–D, visit four plant species, E–H, in different frequencies; lines uniting species represent interactions, and numbers besides the lines represent frequencies of interaction. For simplicity, assume that all pollinators are 100% efficient (i.e., $e = t$). The s_i values for each species have been calculated using a rarefaction sample size of 5 (see text for an explanation).

Symmetry of interactions

I also quantified the degree of interaction symmetry, or reciprocity in the degree of specialization between a species and its interaction partners. To quantify the specialization of interaction partners I calculated the weighted mean specialization of interaction partners; I used the weighted instead of unweighted mean because species differ in their frequencies of interaction. Therefore, the weighted mean specialization of interaction partners, p_i, is

$$p_i = \frac{1}{n}\sum_{j=1}^{m} s_j v_j \qquad [6]$$

where s_j is the specialization of interaction partner species j, v_j is the frequency of interaction between species j and species i ($v_j = e_j$ for plants, and $v_j = t_j$ for insects), and $n = \sum v_j$.

As an example of how the p_i index works, consider a community with four species of plants and four species of pollinators, as shown in Fig. 4.3. For simplicity, assume all pollinators are 100% effective (i.e., $e = t$). Using the frequency of visits of pollinators shown in the graph, I have calculated the expected species richness of interaction partners, s_i, for each species, using a rarefaction sample size of 5, then using equation [6] to calculate p_i. Thus, for example, plant species E has an s_i of 1, which means it is highly specialized in its pollinator (A); however, its p_i value is 2.61, so its pollinator partner is highly generalized.

Statistical analyses

I tested the fit of our data to the following five nested models:

Model 1: $A_i = b_0$ [7]

Model 2: $A_i = b_0 + b_1 s_i$ [8]

Model 3: $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$ [9]

Model 4: $A_i = b_0 + b_1 s_i + b_2 p_i$ [10]

Model 5: $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$ [11]

Model 1 is the null model of no relationship between A_i, s_i, and p_i, and models 2-5 are possible forms of this relationship. Because regression analyses of linear models are more straightforward and easier to interpret than equivalent analyses of non-linear models, I included models 2 and 4 as special cases of models 3 and 5, respectively.

To study the fit of our linear models 2 and 4 to the data I used procedure REG in SAS (SAS Institute 1999).

As a more comprehensive confrontation between all models and the data, I used the method of sum of squares (Hilborn and Mangel 1997). I used a computer algorithm written in Matlab to conduct numerical searches of parameter values within a range of parameters that I judged reasonable. For each combination of parameter values I calculated the sum of squared deviations between the predicted and the observed values of the dependent variable (A_i); I selected the combination of parameters that minimized the sum of squares as the best fit for the model. However, because increasing numbers of parameters will tend to decrease the sum of squares, I used a criterion that penalizes the addition of new parameters to compare among models:

$$C = \mathrm{SSQ}/(n-2m) \qquad [12]$$

where C is the model selection criterion, SSQ is the sum of squares, n is the sample size (i.e., the number of observations), and m is the number of parameters in the model (Efron and Tibshirani 1993; Hilborn and Mangel 1997). (Note that this criterion will be meaningful only if $n > 2m$.) The model with the lowest C value is judged "best." Thus, C rewards increasing sample size and penalizes adding parameters.

RESULTS

Effect of rarefaction sample size on the estimation of specialization

The rarefied species richness of interaction partners (i.e., our measure of specialization, s_i) was, as expected, higher for the largest rarefaction sample sizes. However, these values are highly correlated between the two rarefaction sample sizes used (Fig. 4.4). Thus, using different sample sizes for rarefaction should not affect the results, so I used the smallest sample size below.

Symmetry of interactions

As discussed above, the response of plants and pollinators to disturbance by cattle might be determined not only by specialization (s_i) but also by specialization of interaction partners (p_i) (see the S-A-D hypothesis above); this would be particularly true if interactions were not symmetrical—i.e., if there were no positive correlation between s_i and p_i.

There is, in fact, no correlation (plants) or a slightly negative correlation (all insects and bees) between the s_i and p_i (Fig. 4.5), which indicates a high degree of asymmetry in plant–pollinator interactions in the *Nothofagus dombeyi* forests: specialists do not necessarily interact with specialists, nor generalists with generalists. Furthermore, for insects, there seems to be a slightly negative correlation between s_i and p_i, which means that specialists tend to interact with generalists and generalists with specialists. Finally, for insects, no species combine extremely low values of both s_i and p_i: species with the lowest s_i values have moderate values of p_i, while species with the lowest p_i have only moderate values of s_i; thus, those species that, according to the S-A-D hypothesis, should be most affected by disturbance are not represented in our dataset.

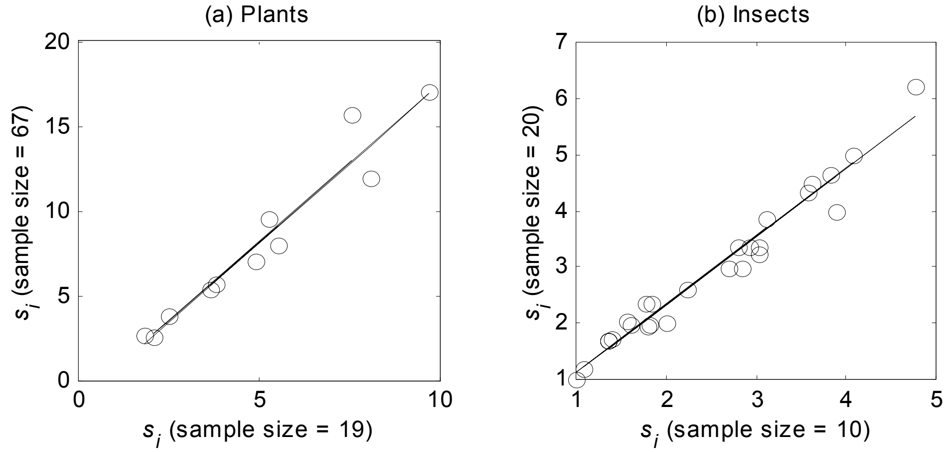


Figure 4.4. Relationship between s_i values obtained for the two rarefaction sample sizes used. (a) Plants: $P < 0.0001$; $r^2 = 0.9418$. (b) Insects: $P < 0.0001$; $r^2 = 0.9617$.

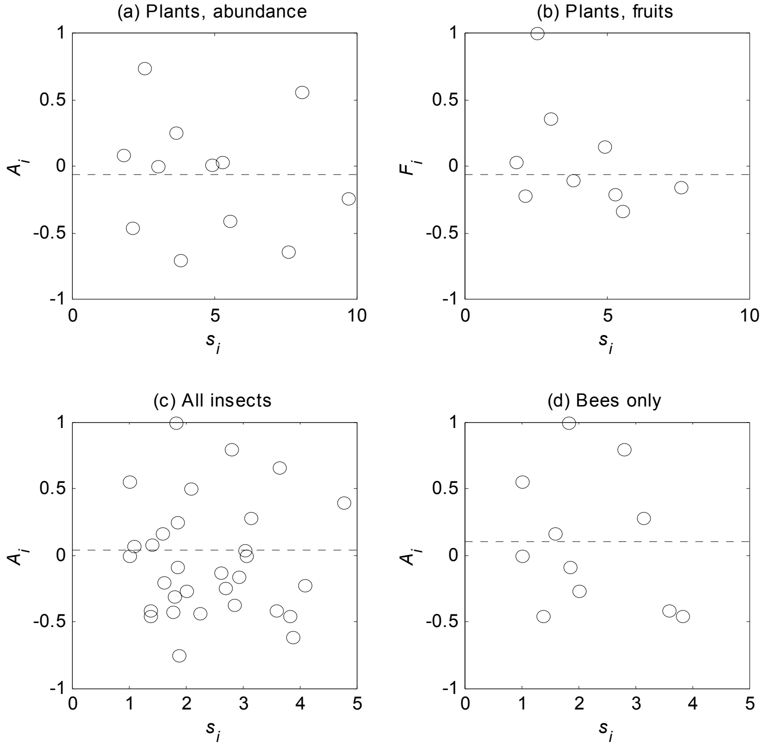


Figure 4.5. Relationship between the abundance index, A_i, and the specialization index, s_i. (a) Plants, abundance. (b) Plants, fruits. (c) All insects. (d) Bees only. See Tables 4.2 and 4.3 for statistics. In all cases, the dotted line represents the best fit for model 1 (i.e., the b_0 value that minimized the sum of squares).

Table 4.4. Linear regressions using specialization (s_i) and specialization of partners (p_i) as predictors of the abundance (A_i) or the fruit set (F_i) indices.

Taxon	Model	n	F	P	R^2
Plants (abundance)	$A_i = b_0 + b_1 s_i$	12	0.19	0.6758	0.0182
	$A_i = b_0 + b_1 s_i + b_2 p_i$	12	0.13	0.8803	0.0279
Plants (fruits)	$F_i = b_0 + b_1 s_i$	9	1.61	0.2448	0.1871
	$F_i = b_0 + b_1 s_i + b_2 p_i$	9	0.75	0.5113	0.2004
All insects	$A_i = b_0 + b_1 s_i$	31	0.00	0.9988	0.0000
	$A_i = b_0 + b_1 s_i + b_2 p_i$	31	0.25	0.7769	0.0132
Bees only	$A_i = b_0 + b_1 s_i$	11	0.56	0.4752	0.0581
	$A_i = b_0 + b_1 s_i + b_2 p_i$	11	0.35	0.7122	0.0813

Note: b_0, b_1, and b_2 are regression parameters. Regressions were performed using SAS procedure REG (SAS Institute 1999).

Testing the hypotheses

If the S-D hypothesis were correct, model 3 (eq. 9 above), or its special case, model 2 (eq. 8), should provide the best fit to the data; alternatively, if the S-A-D hypothesis were correct, models 4 or 5 (eqs. 10 and 11) should fit the data best. The plots of specialization (s_i) and response to disturbance (A_i) (Fig. 4.5) show that there is no relationship between these variables; our data do not follow the S-D hypothesis. Similarly, a plot of s_i, p_i (specialization of interaction partners), and A_i also seems to show that our data do not agree with the S-A-D hypothesis (Fig. 4.6). If this hypothesis were supported by our data, I should see in Fig. 4.6 a gradual change from dark diamonds (A_i values close to –1) in the lower left corner of the graph to white diamonds, triangles, or circles (A_i values close to 0), to dark circles (A_i values close to 1) in the upper right corner. However, there seems to be no functional relationship of A_i with s_i and p_i. Furthermore, the results of the linear regressions testing the fit of linear models 2 and 4 are compelling: both models are rejected (Table 4.4); the null hypothesis (model 1) provides the best fit to the data. These linear regressions formally tell us what I already see in Figs. 4.5 and 4.6: there is no relationship between specialization, specialization of interaction partners, and response to disturbance in our data. This conclusion applies to the two different response variables analyzed for plants (i.e., abundance and fruit set), as well as to insects; even if I consider only bees (which, unlike other pollinators, depend exclusively on flowers as their food source throughout their entire life cycles, Michener 2000), the pattern is still the same (Fig. 4.5d, 4.6d).

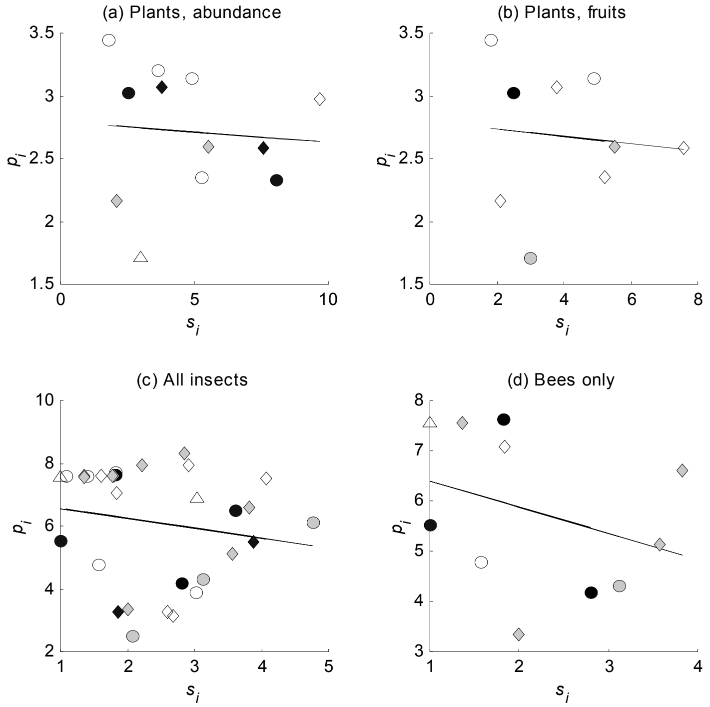


Figure 4.6. Relationship between the specialization index, s_i, the specialization of interaction partners index, p_i, and the response of species to disturbance, A_i. Symbol shape and shading indicate A_i values: circles represent species which showed a positive response to the presence of cattle (i.e., $A_i > 0$), while diamonds represent species which showed a negative response to the presence of cattle (i.e., $A_i < 0$); species with an A_i value of exactly zero are represented by triangles; darker colours respresent $|A_i|$ values closer to 1, while clearer colors represent $|A_i|$ values closer to 0. Black lines are the linear regression curves of p_i vs. s_i, with the following statistics: Plants (a) abundance, and (b) fruits: regression of p_i vs. s_i, $P = 0.8036$; $r = –0.0806$. (c) All insects: $P = 0.3525$; $r = –0.1729$. (d) Bees only: $P = 0.3141$; $r = –0.3348$.

Table 4.5. Sum of squares and selection criteria used for confrontation among models.

Taxon	Model	m	n	SSQ	C
Plants (abundance)	1: $A_i = b_0$	1	12	2.2176	**0.2218**
	2: $A_i = b_0 + b_1 s_i$	2	12	2.1778	0.2722
	3: $A_i = b_0 + b_1 s_i^f$	3	12	2.1629	0.3605
	4: $A_i = b_0 + b_1 s_i + b_2 p_i$	3	12	2.1560	0.3593
	5: $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	12	2.2669	1.1334
Plants (fruits)	1: $F_i = b_0$	1	9	1.3679	**.1954**
	2: $F_i = b_0 + b_1 s_i$	2	9	1.1123	.2225
	3: $F_i = b_0 + b_1 s_i^f$	3	9	1.1875	.3958
	4: $F_i = b_0 + b_1 s_i + b_2 p_i$	3	9	1.4524	.4841
	5: $F_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	9	1.2592	…
All insects	1: $A_i = b_0$	1	41	5.5194	**0.1903**
	2: $A_i = b_0 + b_1 s_i$	2	41	5.5171	0.2043
	3: $A_i = b_0 + b_1 s_i^f$	3	41	5.5690	0.2228
	4: $A_i = b_0 + b_1 s_i + b_2 p_i$	3	41	5.5690	0.2228
	5: $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	41	5.5614	0.2648
Bees only	1: $A_i = b_0$	1	11	2.6052	**0.2895**
	2: $A_i = b_0 + b_1 s_i$	2	11	2.4545	0.3506
	3: $A_i = b_0 + b_1 s_i^f$	3	11	2.7112	0.5422
	4: $A_i = b_0 + b_1 s_i + b_2 p_i$	3	11	2.3936	0.4787
	5: $A_i = b_0 + b_1 s_i^f + b_2 p_i^g$	5	11	2.7110	2.7110

Note: Indices of species abundance (A_i) or fruit set (F_i) were used as response variables, and interaction specialization (s_i) and specialization of interaction partners (p_i) were used as predictors. b_0, b_1, b_2, f, and g are parameters. A computer algorithm written in Matlab was used to conduct numerical searches of parameter values that minimized the sums of squares. The number of parameters in the model (m), the sample size (n), the sum of squares (SSQ), and the selection criterion (C) are given for each model and data set. Best values of the selection criterion are highlighted in bold type. Ellipses indicate value cannot be calculated because $n < 2k$.

However, the above linear analyses do not reject the non-linear models 3 and 5 described above; i.e., I cannot reject the more general forms of the S-D and S-A-D hypotheses. To make the analysis more general I can refer to the sum of squares method of confrontation described above. The confrontation of the five models using this method gives us the same answer: in all four data sets the model chosen using C, our selection criterion, is model 1, the null model (Table 4.5). (Note, however, that for the fruits data set the selection criterion could not be calculated for model 5, because $n < 2m$; nevertheless, model 5 had a higher sum of squares than model 4, which selects against it.) This result agrees with those obtained in the analysis of the linear models described in the previous paragraph.

DISCUSSION

Contrary to the specialization–disturbance hypothesis, the prevailing view in the ecological and conservation literature, I found no relationship between the degree of specialization of species in plant–

pollinator interactions and their response to a biological disturbance—the presence of cattle. This result casts doubt on the generality of the S-D hypothesis.

I also found that, in this system, plant–pollinator interactions tend to be asymmetric (or, at least, they are not symmetric). This is apparently the second time that symmetry of interactions in plant–pollinator systems is quantified (the first one being the study by Petanidou and Ellis 1996). Thus, it is impossible to know how general this pattern is. Nevertheless, it is important to mention two related pieces of work here: Jordano's (1987) observation that plant–seed disperser systems tend to be highly asymmetric in terms of the dependence of species on this mutualism, and Fonseca and Ganade's (1996) finding of high asymmetry in the dependence of ant–plant mutualists in an Amazonian forest. What Jordano on the one hand and Fonseca and Ganade on the other call "dependence" is actually a measure of interaction specialization. They calculate the proportion of all interactions of a given species that involves each of the species' interaction partners, high proportions meaning high specialization on a given interaction partner, and low proportions meaning low specialization. In this respect, their work is more similar to ours than it might seem. On the other hand, what they call asymmetry has a somewhat different meaning from ours: they are more interested in a mean value of "dependence" (or specialization), whereas I am interested in the correspondence of the degree of specialization of a given species with that of its interaction partners. Thus, I believe that the findings of Jordano and Fonseca and Ganade on symmetry are not comparable to the finding of our work, simply because they have different meanings.

The existence of asymmetry in interaction specialization did not, however, explain the variability in species' responses to disturbance. These results therefore do not support the specialization–asymmetry–disturbance hypothesis: our conjecture was not supported by our data. It is noteworthy that the lower left corner of Fig. 4.5 is empty for the insects. Species having a combination of low s_i and p_i (presumably those more likely to be affected by disturbance, according to the specialization–asymmetry–disturbance hypothesis) are lacking.

Faced with these overwhelmingly negative results, I need to ask why specialists are not more affected by disturbance than generalists, as expected according to the S-D and the S-A-D hypotheses. I briefly discuss several possible explanations below.

The resource axes measured are not important ones (or the *most important ones) in this case*. The "niche axes" considered in this analysis were a reproductive resource for plants (i.e., the service of pollinators) and a food resource for pollinators (the rewards obtained in flowers); these resources might not be the key resources for some of our species. For example, Bond (1995) suggested that it is possible that plants compensate for negative effects of pollination specialization by being highly self-compatible or by having a low dependence on pollinators or seeds for reproduction. A similar reasoning could apply to insect pollinators: many species of flower visitors (e.g., flies and lepidopterans) depend on flowers during only one part of their life cycles (typically the adult phase). However, for bees, for which flowers are indeed a key resource, the pattern (or lack of) is still the same. So at least for bees, this explanation is not satisfactory, and I believe that I am considering a crucial resource for them.

Direct vs. indirect effect of disturbance. As I discussed above (see Fig. 4.2), disturbance can affect species not only indirectly through the resource but also directly through an impact on mortality rates. It is possible that in our system direct effects of cattle on mortality were more important than indirect effects transmitted through plant–pollinator interactions. I know that several of our plant species are, to some extent, affected by browsing or trampling; this might in part explain the results obtained for this group. And, although I cannot evaluate this possibility for insects, the direct effect of disturbance by cattle on mortality could be important. However, our data do not allow us to ascertain the relative importance of direct and indirect effects of cattle.

Specialization was not appropriately measured. It could be that insects used other floral resources (other plant species) flowering outside the study sites, especially those flowering in other forest types not included in the study. This possibility is particularly relevant for species with wide home-ranges, such as bumblebees. However, I believe our sites were large enough (typically 6-15 ha.) for this problem to be greatly minimized. In any event, our knowledge of the behavioral ecology of the insect species present at our sites is too poor to allow us to evaluate this possibility.

Another caveat in how specialization was measured is that I used only a measure of "regional" specialization (i.e., using the pooled data for all the sites to quantify specialization). Some species use a wide range of resources over large spatial scales but are relatively specialized locally, while others are both locally and geographically specialized (Fox and Morrow 1981; Hughes 2000). I could not evaluate specialization for each site separately, because the rarefaction sample sizes were in most cases too small; thus, our measure of specialization did not discriminate between these different kinds of specialization.

Difficulty of detecting highly non-linear relationships. Highly non-linear relationships are usually more difficult to detect than linear ones. First, the number of parameters in non-linear models is usually higher than that in equivalent linear models (compare model 2 with 3, and model 4 with 5); this higher number of parameters decreases statistical power, as is evident in our selection criterion. Second, in our case detecting of a highly non-linear relationship (i.e., low values of f and g) depends on the existence of species with very low values of s_i and p_i (note, for example, that all negative values of A_i in Fig. 1d are clumped in the neighborhood of the axes). When the species pool is not too large (as in our dataset), missing one species will make a big difference. As I pointed out above, it is clear from Fig. 4.6 that, at least for insects, species with a combination of low s_i and p_i are missing from our dataset. Thus, even if there were a relationship between s_i, p_i, and A_i, the absence of species with low s_i and p_i would make detection of this pattern difficult. It might well be that those species were present in the area in the past but were the first ones extirpated by earlier human disturbance in the region. This would mean that, even if the S-D and S-A-D hypotheses were true, the relationship would not be detected because these species were absent. Although this is a possible explanation, I have no way of testing it with our data.

Limitations of non-manipulative approach. Manipulative experiments are a powerful tool that allows direct tests of hypothesized causal relationships between variables. However, manipulation is not feasible in many cases, and other approaches are called for. I chose to take advantage of the pre-existing distribution of introduced cattle in our study area. A problem is the possible existence of hidden variables that covary with the presence of cattle. For example, natural differences in the pre-cattle vegetation between paired sites could have led to the introduction of cattle in some areas but not others. Although not the most parsimonious explanation, it is possible that these hidden variables could be obscuring real relationships between degree of specialization and response to disturbance.

There is, in fact, no relationship. Since I cannot be sure that the five possible explanations discussed above do not apply in our case, I cannot definitively falsify the S-D hypothesis or its modified version, the S-A-D hypothesis. Furthermore, our test applies only to this particular system, type of specialization, and type of disturbance; thus, it does not universally refute these hypotheses, only invalidates them for this particular case. Therefore, I believe that both hypotheses deserve further attention (and, particularly, further careful, rigorous tests) in other ecological settings before we can discard them.

However, it is possible that such a relationship does not exist, that our hypotheses are indeed false. As Popper (1968, pp. 49) put it: "Our propensity to look out for regularities, and to impose laws upon nature, leads to the psychological phenomenon of *dogmatic thinking* or, more generally, dogmatic behavior: we expect regularities everywhere and attempt to find them even where there are none; events which do not yield to these attempts we are inclined to treat as a kind of 'background noise'; and we stick to our expectations even when they are inadequate and we ought to accept defeat." Only careful studies attempting to tease apart the different factors discussed above will let us assess the real importance of ecological specialization for species response to disturbance.

5

INDIRECT EFFECTS OF INTRODUCED UNGULATES ON POLLINATION AND PLANT REPRODUCTION

Abstract. Herbivores can affect plants not only directly through browsing and trampling, but also indirectly through other species. For example, herbivores could affect the interaction between plants and their pollinators. Because plant population density affects plant-pollinator interactions and plant reproductive success, I hypothesized that herbivores could affect pollination and plant reproduction indirectly by modifying plant population density. This hypothesis differs from previous hypotheses of indirect effects of herbivores on plants; previous hypotheses concerned individual-level effects on vegetative and reproductive traits, whereas my hypothesis focuses on population-level effects. To test this hypothesis, I conducted field studies in the temperate forest of the southern Andes, where introduced ungulates are a major source of anthropogenic alteration. For thirteen animal-pollinated understory plants, I compared population density, pollinator visitation, pollen deposition in stigmas, and reproduction in four pairs of grazed and ungrazed sites. I found evidence of indirect effects of ungulates on pollination and reproduction for only one of the thirteen species, the herb *Alstroemeria aurea* (Alstroemeriaceae). The general lack of evidence for indirect effects on most of the species may result from resistance to cattle grazing, spatial refugia, or low statistical power. For *A. aurea*, I present additional evidence from trampling experiments, path analyses of the effect of density across and within sites, and hand-pollination experiments showing that: (i) cattle decrease the absolute and relative population density of this species through trampling; (ii) floral neighborhood density affects conspecific pollen deposition, and (iii) conspecific pollen deposition affects reproduction. Thus, my results indicate that, by directly reducing the population density of *A. aurea*, introduced ungulates are indirectly affecting its reproduction. I argue that the demonstrated indirect effect has important conservation implications for both plants and pollinators.

> "Given the ubiquitous presence of herbivores and their ability to utilize all the different plant tissues available, it is surprising that herbivory has not always been recognized as having a significant impact on the reproductive ecology of plants."
>
> —S.D. Hendrix (1988, pp. 246)

INTRODUCTION

Herbivores affect plants in different ways, sometimes with dramatic ecological and evolutionary consequences on 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 algae communities by the snail *Littorina littorea* (Lubchenco 1978). The most obvious effect of herbivores on plants is increased mortality from browsing and trampling. The seedling stage is usually the most vulnerable to increased herbivore-induced mortality. 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 (e.g., Gómez and Zamora 2000; Herrera 2000) or by preying on seeds (e.g., Louda 1982; Herrera 1993).

Herbivores also affect plants in subtler ways, for example through an indirect effect mediated by one or more other species. An indirect effect occurs when one species affects another through a third one (Strauss 1991; Wooton 1994). 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 visitation frequency and, ultimately, male and female reproductive success (e.g., Hendrix 1988; Strauss et al. 1996; Strauss 1997; Strauss and Agrawal 1999; Mothershead and Marquis 2000).

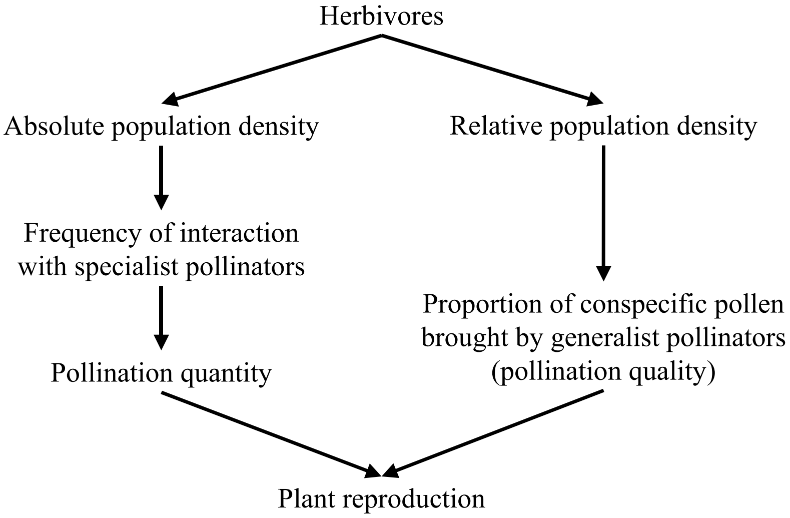


Figure 5.1. Hypothetical effects of herbivores on plant reproduction through plant-pollinator interactions. Herbivores can reduce absolute population density (i.e., density of flowering conspecifics) directly through browsing or trampling. Decreased population density may result in lower pollinator visitation rates, especially by specialist pollinators that do not visit flowers of other plant species. Lower visitation can in turn result in lower conspecific pollen deposition in flower stigmas (pollination quantity). Alternatively, herbivores can decrease relative population density, leading to lower pollination quality (i.e., lower deposition of conspecific pollen and higher deposition of heterospecific pollen in stigmas per pollinator visit). This effect of relative density on pollination quality is expected if pollinators are relatively generalized, visiting flowers of other plant species in the community. Both low pollination quantity and quality can result in low reproductive success.

Modification of floral traits is not the only way herbivores can indirectly affect plant-pollinator interactions, however. Plant population density strongly influences plant-pollinator interactions, pollination and plant reproductive success (Rathcke 1983; House 1992; Kunin 1993, 1997b, a; Bosch and Waser 2001). 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.

This density-mediated indirect effect of herbivores on plant reproduction can be brought about through at least two different chains of events (Fig. 5.1). First, herbivore-induced decreased density of flowering conspecifics can result in lower pollinator visitation rates, leading in turn to lower conspecific pollen deposition in flower stigmas (pollination quantity). Absolute density of conspecifics is expected to affect visitation rates more strongly when pollinators are specialists and do not visit other plant species in the community (Rathcke 1983; Kunin 1993, 1997b, a). Conversely, absolute density of conspecifics will have little effect on visitation frequency when pollinators behave as generalists (Rathcke 1983; Kunin 1993; Kunin and Iwasa 1996; Kunin 1997a). Decreased visitation frequency at lower densities can occur in spite of increased proportion of flowers visited in small patches, given that a pollinator visits the patch (see Goulson 2000).

Second, reduced relative population density (i.e., density of conspecifics relative to density of all species visited by pollinators) can lead to decreased conspecific and increased heterospecific pollen deposition in stigmas per pollinator visit (i.e., pollination “quality;” Rathcke 1983; Herrera 1987; Kunin 1993). This effect of relative population density is expected when pollinators are generalists, visiting flowers of other plant species in the community (Rathcke 1983; Feinsinger 1991; Kunin 1993). Thus, even if visitation rates do not change, pollination success can be affected because pollinators bring fewer conspecific and more heterospecific pollen grains per visit. Conversely, when pollinators are specialists, relative population density is not expected to affect pollination quality (Rathcke 1983; Feinsinger 1991; Kunin 1993).

Reduced pollination quantity and quality can both translate into lower reproductive success. The lower pollination level resulting from herbivore-induced reduction in population density may lead to lower reproductive success if reproduction is pollen-limited (Burd 1994), self-compatibility is low, and dependence on pollinators for reproduction is high (Feinsinger 1991; Kunin 1993; Bond 1995; Kunin 1997b, a). In addition, reproductive success can suffer from high deposition of heterospecific pollen because of competition with conspecific pollen (Galen and Gregory 1989; Fishman and Wyatt 1999). Thus, by directly affecting population density, herbivores can also indirectly affect plant fitness through a modification of the interaction with pollinators.

The hypothesis I am proposing for the effects of ungulates on plant reproduction differs from previous models. To my knowledge, all previous models of indirect effects of herbivores on plant reproduction involved a direct effect of herbivores on individual plants by affecting their flowering phenology (Brody 1997), flower number (Karban and Strauss 1993; Quesada et al. 1995; Mothershead and Marquis 2000), or flower size and pollinator rewards (Strauss et al. 1996; Strauss 1997; Mothershead and Marquis 2000). In contrast, my hypothesis does not require any effect at the individual level on the plant's vegetative or reproductive traits. Rather, it involves an effect at the population level through a direct effect on mortality: browsing or trampling kills some individuals, and those that escape this direct effect suffer the indirect effect.

Objectives of the study

I tested the hypothesis that introduced ungulates affect pollination and plant reproduction by affecting plant population density and that this effect operates through the mechanisms described above (Fig. 5.1). I took advantage of the presence of cattle introduced into the native forest of Nahuel Huapi National Park (Río Negro, Argentina). Introduced ungulates (both cattle and deer) are widespread throughout the region and are a major problem for the conservation of the temperate forest ecosystem in the southern Andes (see Chapter 3). I compared population density, plant-pollinator interactions, pollination, and reproduction for thirteen plant species growing in the understory of eight paired grazed and ungrazed sites in *Nothofagus dombeyii* forest. Specifically, I asked the following questions: (i) Do cattle affect plant population density? (ii) If cattle affect plant population density, does this in turn affect pollinator visitation rates, pollination quantity, and quality? (iii) If pollination quantity or quality is affected, does this affect plant reproductive success? Because of the limitations of my non-manipulative approach, for the only species for which I found evidence of indirect effects of herbivores on its pollination and reproduction, I looked for additional, independent evidence for the hypothesized mechanisms.

METHODS

Field and laboratory methods

Study area and sites.—I used the same study area and sites used in previous chapters (see Fig. 2.2).

Study organisms.—I selected 13 animal-pollinated plants growing in the understory and groundcover of my sites. These constituted all animal-pollinated species abundant enough to allow replication and on which I could measure interaction with pollinators and fruit or seed set. Plant species are listed in Table 5.1.

Estimation of plant population density.—To estimate plant abundance, I examined 30 rectangular quadrats of 2 m × 10 m separated by a fixed distance along transects in each site, counting the number of individuals of each species per quadrat. Because understory vegetation was too dense to permit walking through it at times (especially in sites without cattle), I used forest walking paths as transects. Each quadrat was divided in two halves (2×5 m^2), and each half was placed at the sides of a walking path, at a distance of 1-2 m from the edge of the trail. Transect length varied according to site size, ranging between ~300 m (Quetrihué nc) and ~700 m (Llao Llao); therefore, inter-quadrat distance also varied (~10-23 m). Because I used pre-existing forest trails as transects, transect shape also varied among sites, ranging from one nearly linear transect to irregular, "s" shaped transects. Since all my plant species were perennials, I assumed their population abundance would not change significantly from year to year. Thus, although I studied pollinator visitation, pollination, and reproduction in two consecutive flowering seasons (1999-2000 and 2000-2001), I estimated plant abundances only in the first field season (1999-2000).

Table 5.1. Plant species included in the study and their life form, origin, and reproductive characteristics.

Scientific name	Family	Common name	Life form	Origin	Breeding system	Dependence on pollinators for reproduction	Ref.
Alstroemeria aurea	Alstroemeriaceae	Amancay	Herb	Native	self compatible, protandrous*	high	1
Aristotelia chilensis	Eleocarpaceae	Maqui	Small tree	Native	dioecious	high	2
Berberis buxifolia	Berberidaceae	Calafate	Shrub	Native	self incompatible	high	2
Berberis darwinii	Berberidaceae	Michai	Shrub	Native	self incompatible	high	2,3
Calceolaria crenatiflora	Scrophulariaceae	Topa-topa	Herb	Native	self compatible	possibly low	2
Cynanchum diemii	Asclepiadaceae	—	Vine	Native	unknown	possibly high	—
Digitalis purpurea	Scrophulariaceae	Dedalera, digital	Herb	Introduced	self compatible, protandrous	high	4
Gavilea odoratissima	Ochidaceae	Orquídea	Herb	Native	self compatible	high	3
Rosa eglanteria	Rosaceae	Rosa mosqueta	Shrub	Introduced	self compatible	low	6
Ribes magellanicum	Saxifragaceae	Parrilla	Shrub	Native	unknown	unknown	—
Schinus patagonicus	Anacardiaceae	Laura	Small tree	Native	dioecious	high	3
Tristerix corymbosus	Loranthaceae	Quintral	Parasitic shrub	Native	self compatible	high	7
Vicia nigricans	Leguminosae	Arvejilla	Vine	Native	self compatible	high	3

References for breeding systems and dependence on pollinators: (1) Aizen and Basilio (1995); (2) Riveros et al. (1996); (3) this study (see Appendix 2); (4) Stead and Moore (1979); (6) Hansen (1985); (7) M.A. Aizen (unpublished manuscript).

* Flowers of this species are synchronized within ramets and among neighboring ramets, which makes opportunity for selfing virtually nil (Aizen and Basilio 1995).

Pollinator visitation.—Pollinators visiting flowers of each species were sampled in 10 minute periods. Paired sites were always simultaneously sampled. A total of 2710 observation periods were conducted for all sites and plant species in 1999-2000, and 1039 observation periods were conducted for 6 plant species in 2000-2001. These numbers varied across species and sites, because species differed in their abundance, duration of flowering period, and flowering time overlap with other species. For each visiting pollinator I recorded species name, number of flowers visited, and whether it contacted flower reproductive parts (anthers or stigmas). When the pollinator species was unknown, I collected the specimen and identified it in the laboratory. A reference collection from the collected material has been deposited in the Laboratorio Ecotono at the Universidad Nacional del Comahue in Bariloche, Río Negro, Argentina (some bee specimens were also placed in the Museo Argentino de Ciencias Naturales in Buenos Aires).

The number of flowers observed per observation period varied across periods, depending on the species, the total number of flowers on the plant, and their spatial arrangement. In each sampling period, I recorded the number of flowers visited by each individual pollinator. Following the methods described in Chapter 4, I estimated the number of flowers of plant species *j* effectively visited by each individual pollinator of species *i* as

$$e_{ij} = p_{ij} t_{ij} \,, \qquad [1]$$

where t_{ij} is the total (uncorrected) number of visits made by an individual pollinator of species *i* to plant species *j* during a given observation period, and p_{ij} is the overall proportion of visits (across all observation periods) in which pollinators of species *i* contacted flower reproductive parts of plant species *j* (my estimate of pollinator effectiveness). I assume p_{ij} to be constant for each combination of plant and flower visitor species. I used the 1999-2000 data for the calculation of e_{ij} and assumed p_{ij} values to be the same in 2000-2001. Since it was impossible to calculate p_{ij} for unidentified insects that could not be captured, I assumed p_{ij} based on what was known for similar species in the same family or order. However, these unidentified species were usually rare and poorly represented in my samples, and thus overall results are unlikely to be affected by the latter assumption.

Because my statistical unit was each sampling period, I summed *e* values obtained for each individual visitor within each sampling period to calculate *V*, the total number of visits per flower of plant species *j* observed in a given observation period, as

$$V_j = \sum_{i=1}^{n} e_{ij} \big/ o \,, \qquad [2]$$

where *n* is the number of individual flower visitors recorded in the sampling period and *o* is the number of flowers observed. Thus V_j estimates all the effective visits made by flower visitors of any species per flower in 10 minutes.

Pollination.—I studied pollination performance of plants by estimating the number of conspecific and heterospecific pollen grains deposited in flower stigmas. Flower pistils of most species were collected and immediately placed in vials with 70% ethanol. Stigmas were excised, placed in microscope slides and stained with Alexander's stain (Kearns and Inouye 1993); the number of conspecific and heterospecific pollen grains was counted under a compound microscope. I usually collected five pistils per individual and used the average number of conspecific and heterospecific pollen grains per individual for statistical analyses. For the orchid *Gavilea odoratissima* I counted the number of pollinia inserted in flower stigmas. For the asclepiad *Cynanchum diemii* I observed virtually no pollinia inserted in the flower stigmatic surfaces; therefore, I used number of pollinia removed as a surrogate for pollination success. For *Alstroemeria aurea*, only primary flowers were considered for the analysis, because secondary flowers usually do not contribute significantly to reproduction (Ladio and Aizen 1999).

To evaluate pollen limitation in the only species for which I found evidence of indirect effects of cattle on pollination and reproduction, *Alstroemeria aurea*, I performed hand-pollination in the grazed sites. *A. aurea* is clonal, and it is usually difficult to determine in situ which ramets belong to the same genet without destroying the plants. Since it has been shown that the degree of genetic relatedness falls sharply after 10 m (Souto et al. 2002), I took pollen from individual ramets that were >20 m apart from the individual to be hand-pollinated to ensure cross-pollination, usually mixing pollen from anthers collected from individuals at different locations within each site. To compare the reproductive performance between hand-pollinated and naturally pollinated ramets I selected unmanipulated ramets that were close to and at the same floral phase as the hand-pollinated ramets.

Plant breeding systems.—Because the degree of self-compatibility and of dependence on pollinators for reproduction may be important for determining the indirect effects of herbivores on plant reproduction, I compiled the available information on breeding systems for the species included in the study. For those species for which I could not find published studies on breeding systems, I conducted hand-pollination experiments to study their degree of self-compatibility and of dependence on pollinators for reproduction. A description of the methods and results of these experiments is given in Appendix 2. A summary of self-compatibility and dependence on pollinators for the thirteen species is given in Table 5.1.

Plant reproduction.—I 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). I estimated three reproductive variables: fruit set (proportion of tagged flowers that set fruit), seeds per fruit, and seeds per flower (mean number of seeds produced per tagged flower).

Evaluation of browsing and trampling by cattle.—I calculated browsing indices for each plant species as

$$B_i = \left(\sum_{j=1}^{n} b_{ij}\right)\Big/ n , \qquad [3]$$

where B_i is the browsing index for species i, b_{ij} is the proportion of individuals of species i browsed in quadrat j, and n is the number of quadrats sampled ($n = 30$ in all cases).

I used soil compaction as an indirect measure of the intensity of trampling by cattle. I took 30 soil samples per site using a 442 cm^3 corer. Sample locations were separated by a fixed distance along transects, as I did for the estimation of plant population density. Soil samples were dried at 105º C for 24 hr and weighed immediately afterwards.

I studied the effect of trampling on survival of *Alstroemeria aurea*, which I suspected to be highly susceptible to trampling. For this purpose, I selected a high-density patch of *A. aurea* in an ungrazed area in Quetrihué. I set up 4 pairs of 1 m^2 plots, to which I assigned one of two treatments: trampled and control (not trampled). In the "trampled" plots, the same person walked once over the entire surface of the plot; the control plots were left untouched. I counted the number of live ramets of *A. aurea* before trampling and three weeks later.

Spatial analysis of floral neighborhood density effects on the pollination and reproduction of A. aurea.—To study the effect of floral neighborhood density on pollinator visitation, pollination, and reproduction of *A. aurea* (the only species for which I found evidence of indirect effects in the comparison between paired sites), I mapped all flowering ramets of *A. aurea* in the four grazed sites. Maps were drawn by taking the linear distance with a measuring tape and the angular deviation from the north with a hand compass from known points taken from a previously drawn topographic map. Density of floral neighborhood was calculated as described in Appendix 1. Because I included all flowering ramets in each of the four grazed sites, sample sizes for the path analysis (see below) varied among sites. The total numbers of individual ramets mapped at the sites were: Cerro López, $n = 139$; Arroyo Goye, $n = 220$; Mascardi (c), $n = 34$; Quetrihué (c), $n = 228$.

The sex ratio of floral phases of *A. aurea* populations varies from male-skewed to female-skewed throughout the flowering season, strongly affecting pollination and reproductive success (Aizen 2001). To account for this effect I included the date of female phase as an exogenous (i.e., explanatory) variable in my path analysis (see below). I assumed perfect synchronization among flowers within a ramet, which is a realistic assumption (see Aizen and Basilio 1995). Because it was impossible to follow each ramet in each of the four populations on a daily basis, I estimated the half-time date of female phase (that is, the mid point between the start and the end of the female phase). For this estimation I calculated the average time elapsed between the half-time of one floral phase to the half-time of the next phase for each floral phase separately for each of the four sites, and then added or subtracted this average to the date of the closest known phase. For example, for a ramet that had a known date in male phase, I added the average time from half-time male phase to half-time neutral phase, and from half-time neutral phase to half-time female phase, to obtain the estimated half-time female phase for the ramet.

I estimated pollinator visitation frequency as described above. Because visitation frequency is affected by environmental variables (Herrera 1995b, a), I recorded irradiance and ambient temperature in each observation period. Irradiance was measured in lux with a hand light-meter held over the flowers being observed. Temperature was recorded with a digital thermometer placed within 15 cm of the flowers being observed. Both environmental variables were used as exogenous variables in the path analysis (see below). Pollen deposition and fruit and seed set were estimated as described above.

Statistical analyses and inference

I used a mixed ANOVA model to test for effect of herbivory on each of the independent variables. The model was:

$$y_{ijk} = \mu_{...} + G_{i..} + P_{.j.} + G \times P_{ij.} + \varepsilon_{ijk}\ , \qquad [4]$$

where y_{ijk} is the response of the dependent variable to the factors and their interaction, $\mu_{...}$ is the overall mean, $G_{i..}$ is the difference in the mean caused by presence of cattle (fixed factor with two levels, grazed and ungrazed), $P_{.j.}$ is the difference in the mean due to the effect of "pair" (a random factor with four levels), $G{\times}P_{ij.}$ is the interaction between grazing and site, and ε_{ijk} is an independent error term drawn from a normal distribution with mean 0 and variance σ^2. I performed the tests with the MIXED procedure in SAS (SAS Institute 1999). A mixed linear model is a generalization of standard linear models, the generalization being that the data are permitted to exhibit correlation and nonconstant variability. The parameters of the mean model are referred to as fixed-effects parameters, and the parameters of the variance-covariance model are referred to as covariance parameters. The fixed-effects parameters are associated with known explanatory variables, as in the standard linear model. However, the covariance parameters distinguish the mixed linear model from the standard linear model. One common situation in which the need for covariance parameters arises is when the experimental units can be grouped into clusters, and data from a common cluster are correlated (Littell et al. 1996). In my design, data were clustered in sites, and each pair of sites represented a level of the random factor, pair. Because in most cases data did not meet the assumption of normality, I performed non-parametric tests using ranks in the mixed procedure described above, as recommended by Conover and Iman (1981).

Because of the low number of replicates (i.e., four pairs of sites), the statistical power of my analyses was rather low. Therefore, I used a critical probability level of $\alpha = 0.1$ for all ANOVAs to avoid an excessive probability of committing type II error (i.e., accepting a false null hypothesis). However, in order to accept the observed effects as evidence of indirect effects of cattle on pollination and plant reproduction, I also used a "congruence criterion." That is, I required that significant effects be detected for all the variables hypothesized in the chain of effects leading to the indirect effects (Fig. 5.1) in at least one of the two study years. The probability of getting significant results in all variables by chance is $\theta = \alpha^n$, where n is the number of variables and θ is the overall probability value. For example, if I set $\alpha = 0.1$ and $n = 3$ (e.g., population density, conspecific pollen deposition, and fruit set), the overall probability of getting significant results in the three variables by chance is $\theta = 0.001$. Thus, although my α value is rather high compared to the conventional $\alpha = 0.05$, my congruence criterion makes my test very conservative. A caveat in my analysis is that I performed multiple tests for each of 13 plant species. By doing so, I increased the probability of getting congruent effects by chance in at least one of the 13 species. A procedure frequently used to correct α to account for multiple tests is the sequential Bonferroni correction (Rice 1989). Using this correction, for $\alpha = 0.05$ the overall significance level for the lowest P-value becomes $\theta = 0.05/13 = 0.0038$, a value still higher than the 0.001 I got by fixing α at the 0.1 level.

For the only species that met the congruence criterion, *Alstroemeria aurea*, I looked for additional evidence for the hypothesized mechanisms. I conducted trampling experiments to test for the effects of trampling on the survival of ramets; data from these experiments were analyzed by a two-sample *t*-test with the TTEST procedure in SAS. To check whether lower reproductive performance was due to pollen limitation, I also performed hand-pollinations in three of the grazed sites. Differences in the means of the three reproductive variables for hand- and naturally-pollinated plants were tested with a *t*-test, with the TTEST procedure in SAS.

I also used path analysis to test for causal relationships among the variables hypothesized to be involved in the chain of effects leading to the indirect effects of cattle on pollination and reproduction. I performed this analysis at two different scales: (i) among sites, using the mean in each of the 8 sites for each of the variables, and (ii) within-site, using a detailed spatial analysis of floral neighborhood density. The idea behind the path analysis among site means was that the variability in the means should be explained, at least in part, by the hypothesized causal scheme imposed by my hypothesis. I used the REG procedure in SAS to calculate path coefficients, which can be obtained in the REG procedure as standardized regression coefficients, using the *stb* option in the *model* statement. The statistical significance of the path coefficients can be tested using the *t*-tests for the parameter estimates in the regression analysis. Owing to the low sample size of the comparison among site means ($n = 8$ sites), I could not apply a model selection procedure to test the fit of alternative causal models to the data (as I did for the within-site comparison, where the sample sizes were much larger; see below). Most model selection criteria used in structural equations modeling are sensitive to sample size, becoming unreliable at low sample sizes (Shipley 2000).

For the within-site analysis of the effect of floral neighborhood density on pollination and reproduction of *A. aurea*, I used a series of 13 nested models that were compared by the CALIS procedure in SAS software (SAS Institute 1999). In the most general model (see Fig. 5.11) all paths are free to vary. The specific variables excluded from each nested model are given in Table 5.9. I first computed the covariance matrix for the variables using the CORR procedure in SAS and then used the covariance matrix as input in CALIS. Since I could not measure all the variables for all flowering ramets in the population, I dealt with missing observations by applying "pairwise deletion" to my dataset, which is the default option in SAS; that is, I calculated the covariances between pairs of variables with all the available observations. I used Akaike's Information Criterion (AIC; see Hilborn and Mangel 1997; Bozdogan 2000) for model selection. AIC is based on maximum likelihood and can be used to compare nested models with different degrees of freedom. In the CALIS procedure it is calculated as AIC = $\chi^2 - 2\,df$, where χ^2 is the maximum likelihood chi-square statistic, and *df* is the degrees of freedom of the model. The model with the lowest AIC value is selected as the model that best fits the data. Once a specific model was selected, I used the REG procedure in SAS to test the significance of individual paths, as described above for the among-site path analysis.

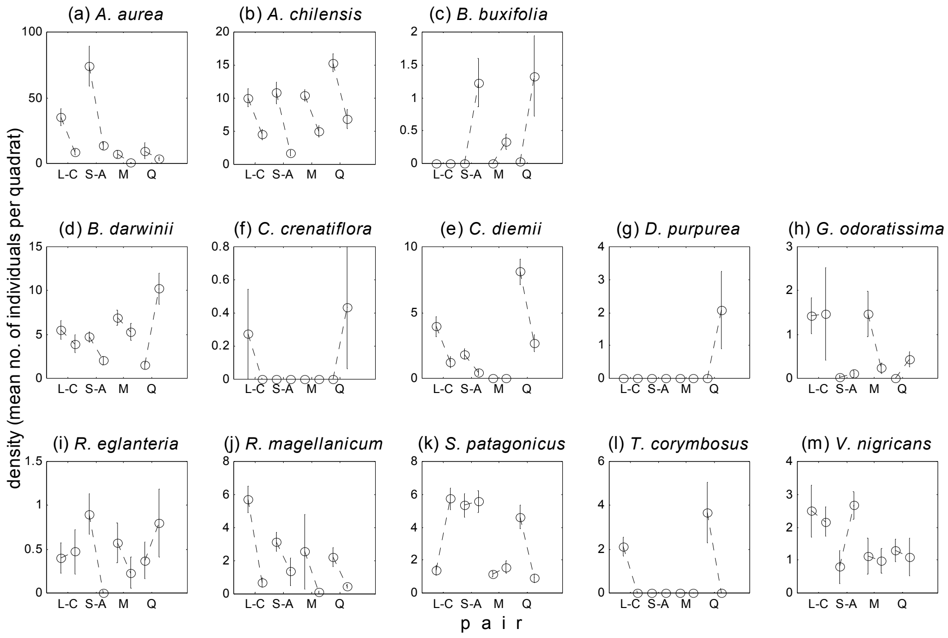


Figure 5.2. Plant species density per site. Circles represent mean density per quadrat per site, averaged over 30 quadrats. Error bars represent standard error of mean. Paired sites are joined by lines, ungrazed site on the left and grazed site on the right. Letters on x-axis indicate paired sites, as follows: L-C, Llao Llao–Cerro López; S-A, Safariland–Arroyo Goye; M, Mascardi (nc)–Mascardi (c); Q, Quetrihué (nc)–Quetrihué (c). Species for which fixed (grazing) effect was significant (at $p < 0.1$) in mixed model ANOVA are indicated by asterisks (see Table 5.2 for complete statistics).

RESULTS

Testing the hypothesis for the thirteen species: comparison between grazed and ungrazed sites

Plant population density.—Four species (*Alstroemeria aurea*, *Aristotelia chilensis*, *Cynanchum diemii* and *Ribes magellanicum*) were significantly less abundant in grazed sites (Fig. 5.2, Table 5.2). A fifth species (*Tristerix corymbosus*) showed a similar pattern, but one that was not statistically significant (probably owing to the absence of this species from two of the four pairs of sites; Fig. 5.2, Table 5.2). Flower abundance was also significantly lower in grazed sites for three of these species (*A. aurea*, *A. chilensis* and *R. magellanicum*; Table 5.2). On the other hand, one species (*Berberis buxifolia*) showed significantly higher total abundance in grazed sites (Fig. 5.2, Table 5.2); although there was also a trend towards higher flower abundance in grazed sites, this pattern was not statistically significant (Table 5.2).

It is important to note that some species were absent from some pairs of sites. For example, *Cynanchum diemii* was absent from Lago Mascardi; likewise, *Tristerix corymbosus* was absent from Lago Mascardi and extremely rare in the Arroyo Goye-Safariland pair (I saw only one individual in Safariland); *Berberis buxifolia* was scarce and spatially restricted in Cerro López, and no individual was observed in my quadrats; finally, *Digitalis purpurea* was present only in the grazed site at Península Quetrihué. The absence of these species from some of the sites is probably explained by distributional constraints rather than by the effects of cattle; the lack of significance in my tests for *D. purpurea* and *T. corymbosus* is thus probably due, at least in part, to the confounding effect of the absence of these species from some pairs rather than to a lack of effect of cattle on the abundance of these species.

Table 5.2. Anova results for total population density and density of flowering individuals. Results of mixed model analysis of variance for the fixed effect (grazing) are given. *P*-values <0.1 are highlighted in bold.

Species	Response variable	d.f.	F	P
Alstroemeria aurea	Total abundance	3	8.40	**0.0626**
	Flower abundance	3	8.51	**0.0617**
Aristotelia chilensis	Total abundance	3	60.37	**0.0044**
	Flower abundance	3	69.15	**0.0036**
Berberis buxifolia	Total abundance	3	7.05	**0.0767**
	Flower abundance	3	2.82	0.1916
Berberis darwinii	Total abundance	3	0.00	0.9819
	Flower abundance	3	2.71	0.1983
Calceolaria crenatiflora	Total abundance	3	0.20	0.6850
	Flower abundance	3	0.19	0.6894
Cynanchum diemii	Total abundance	3	7.80	**0.0683**
	Flower abundance	3	2.78	0.1938
Digitalis purpurea	Total abundance	3	1.00	0.3910
	Flower abundance	3	1.00	0.3910
Gavilea odoratissima	Total abundance	3	0.42	0.5628
	Flower abundance	3	1.57	0.2995
Rosa eglanteria	Total abundance	3	2.95	0.1841
	Flower abundance	3	1.00	0.3910
Ribes magellanicum	Total abundance	3	7.55	**0.0708**
	Flower abundance	3	8.29	**0.0635**
Schinus patagonicus	Total abundance	3	0.01	0.9221
	Flower abundance	3	0.15	0.7285
Tristerix corymbosus	Total abundance	3	3.00	0.1819
	Flower abundance	3	2.99	0.1820
Vicia nigricans	Total abundance	3	0.83	0.4297
	Flower abundance	3	4.04	0.1380

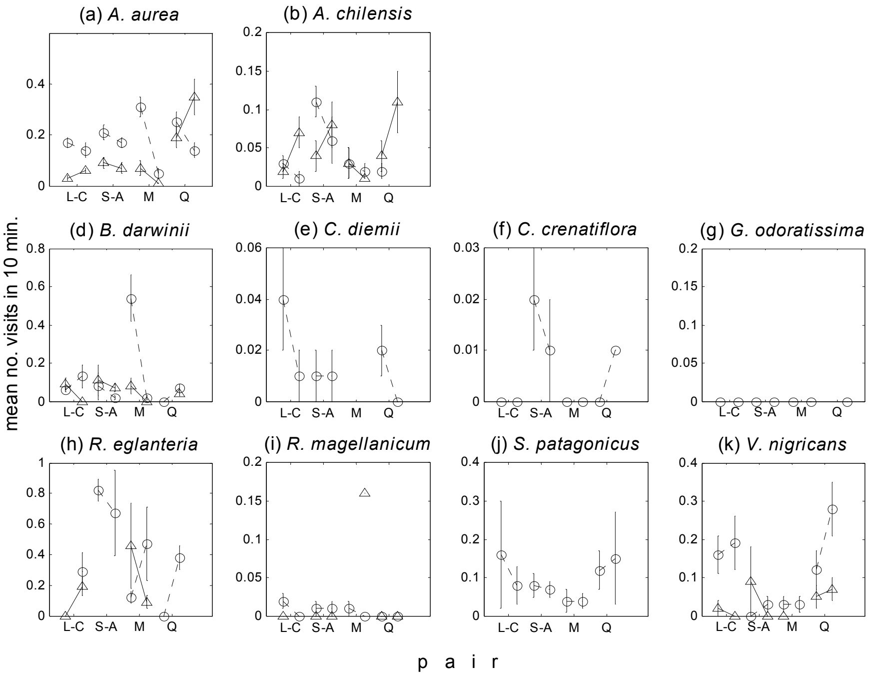


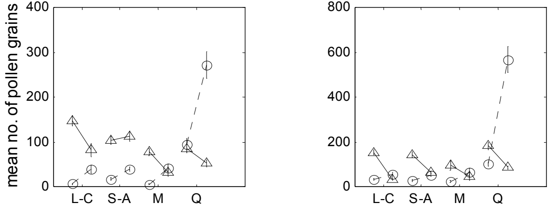
Figure 5.3. Mean visit frequency per 10 min. sampling period. Circles correspond to 1999-2000 data; triangles correspond to 2000-2001 data. Error bars represent standard error of mean. Paired sites are joined by lines, ungrazed site on left and grazed site on right. Letters on *x*-axis indicate paired sites (see Fig. 5.2). Sites with no marker indicate that no observation periods were conducted owing to scarcity of flowering individuals. Effects of grazing on visit frequency were statistically insignificant in all cases (see Table 5.3 for complete statistics). No comparisons were possible for *Berberis buxifolia* and *Digitalis purpurea* because no flowering individuals were found in ungrazed sites. No observations were made for *Tristerix corymbosus* because species flowers mainly during winter, when I was unable to sample.

Table 5.3. Anova table for analysis of visitation frequency. Results of mixed model analysis of variance for the fixed effect (grazing) are given.

Species	Response variable	Year	d.f.	F	P
Alstroemeria aurea	Visitation frequency	1999-2000	3	4.46	0.1252
	Visitation frequency	2000-2001	3	0.06	0.8280
Aristotelia chilensis	Visitation frequency	1999-2000	3	1.73	0.3185
	Visitation frequency	2000-2001	3	2.64	0.2029
Berberis darwinii	Visitation frequency	1999-2000	3	0.80	0.4365
	Visitation frequency	2000-2001	2	0.70	0.4918
Calceolaria crenatiflora	Visitation frequency	1999-2000	3	0.05	0.8382
Cynanchum diemii	Visitation frequency	1999-2000	2	3.40	0.2064
Gavilea odoratissima	Visitation frequency	1999-2000	2	0.53	0.5425
Rosa eglanteria	Visitation frequency	1999-2000	2	1.72	0.3196
	Visitation frequency	2000-2001	1	0.37	0.6505
Ribes magellanicum	Visitation frequency	1999-2000	3	0.68	0.4711
	Visitation frequency	2000-2001	1	0.99	0.5018
Schinus patagonicus	Visitation frequency	1999-2000	3	0.17	0.7080
Vicia nigricans	Visitation frequency	1999-2000	3	1.16	0.3604
	Visitation frequency	2000-2001	2	0.01	0.9414

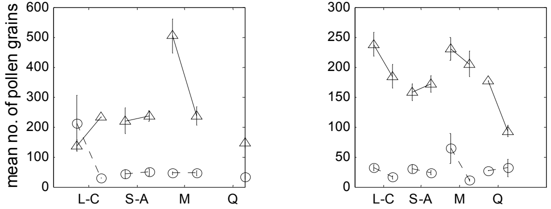
Pollinator visitation.—Although some species show trends towards lower or higher visitation frequency with cattle (e.g., *A. aurea* in the first sampling season), none of those trends were statistically significant (Fig. 5.3; Table 5.3). Thus, the presence of cattle does not result in any detectable effect on pollinator visitation frequency for any of thirteen species.

Pollination.—Deposition of conspecific pollen was significantly lower in grazed sites for only one species, *A. aurea*, in the second year of study; a similar pattern of conspecific pollen deposition in the first sampling season was not statistically significant (Fig. 5.4; Table 5.4). *A. aurea* also showed a higher heterospecific pollen deposition in grazed sites (Fig. 5.4); this pattern was statistically significant for the first sampling season only (Table 5.4). The number of heterospecific pollen grains, particularly in the second sampling season, was comparable to the number of conspecific pollen grains, which increases the potential for competition for pollination. Furthermore, the proportion of conspecific pollen over total pollen received (i.e., a measure of pollination quality) was significantly lower in grazed than in grazed sites in both years (Table 5.4). Two other species showed statistically significant patterns of heterospecific pollen deposition: *R. magellanicum* showed higher heterospecific pollen deposition in grazed sites, whereas *B. darwinii* showed lower heterospecific pollen deposition in grazed sites (Fig. 5.4, Table 5.4). However, for these two species the number of heterospecific pollen grains deposited in flower stigmas was much lower than the number of conspecific pollen grains, which minimizes the chances of competition for pollination. Furthermore, there was no significant effect on the proportion of conspecific pollen for these species (Table 5.4).



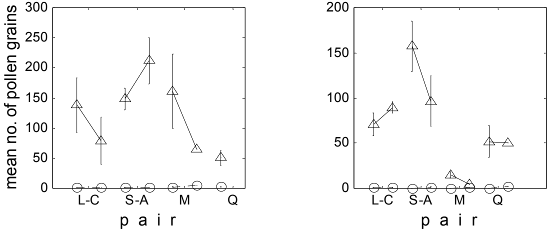
(a) *A. aurea*: 99-00

(b) *A. aurea*: 00-01



(c) *B. darwinii*: 99-00

(d) *B. darwinii*: 00-01



(e) *R. magellanicum*: 99-00

(f) *R. magellanicum*: 00-01

Figure 5.4. Pollen deposition in flower stigmas. Circles represent mean conspecific pollen grains, and triangles represent heterospecific pollen grains deposited in flower stigmas; error bars represent standard error of mean. Paired sites are joined by lines, ungrazed site on left and grazed site on right. Letters on *x*-axis indicate paired sites (see Fig. 5.2). Sites with no marker indicate cases where no observation periods were conducted. Only species that had at least some significant effects are shown (see Table 5.4 for complete statistics).

Table 5.4. Anova table for analysis of pollen deposition. Results of mixed model analysis of variance for the fixed effect (grazing) are given. *P*-values <0.1 are highlighted in bold.

Species	Response variable	Year	d.f.	F	P
Alstroemeria aurea	Conspecific pollen	1999-2000	3	5.23	0.1062
		2000-2001	3	17.79	**0.0243**
	Heterospecific pollen	1999-2000	3	16.18	**0.0276**
		2000-2001	3	3.76	0.1478
	Proportion conspecific pollen	1999-2001	3	9.27	**0.0557**
		2000-2002	3	213.71	**0.0007**
Aristotelia chilensis	Conspecific pollen	2000-2001	3	0.58	0.5018
	Heterospecific pollen	2000-2001	3	4.69	0.1191
	Proportion conspecific pollen	2000-2002	3	1.31	0.3361
Berberis darwinii	Conspecific pollen	1999-2000	2	0.11	0.7726
		2000-2001	3	4.04	0.1380
	Heterospecific pollen	1999-2000	2	2.91	0.2299
		2000-2001	3	15.83	**0.0284**
	Proportion conspecific pollen	1999-2001	2	0.28	0.6505
		2000-2002	3	5.28	0.1052
Calceolaria crenatiflora	Conspecific pollen	2000-2001	1	0.85	0.5256
	Heterospecific pollen	2000-2001	1	0.11	0.7927
	Proportion conspecific pollen	2000-2002	1	0.65	0.5685
Cynanchum diemii	Pollinia remaining	1999-2000	2	1.48	0.3483
Rosa eglanteria	Conspecific pollen	2000-2001	1	3.77	0.3029
	Heterospecific pollen	2000-2001	1	0.40	0.6419
Ribes magellanicum	Conspecific pollen	1999-2000	2	0.00	0.9673
		2000-2001	3	0.21	0.6811
	Heterospecific pollen	1999-2000	2	0.81	0.4641
		2000-2001	3	6.65	**0.0818**
	Proportion conspecific pollen	1999-2001	2	0.22	0.6800
		2000-2002	3	3.83	0.3006
Tristerix corymbosus	Conspecific pollen	2000-2001	1	2.47	0.3608
	Heterospecific pollen	2000-2001	1	2.67	0.3495
Vicia nigricans	Conspecific pollen	1999-2000	3	0.04	0.8478
		2000-2001	2	1.76	0.3776
	Heterospecific pollen	1999-2000	3	3.46	0.1598
		2000-2001	2	0.38	0.6009
	Proportion conspecific pollen	1999-2001	3	2.97	0.1833
		2000-2002	2	4.78	0.1167

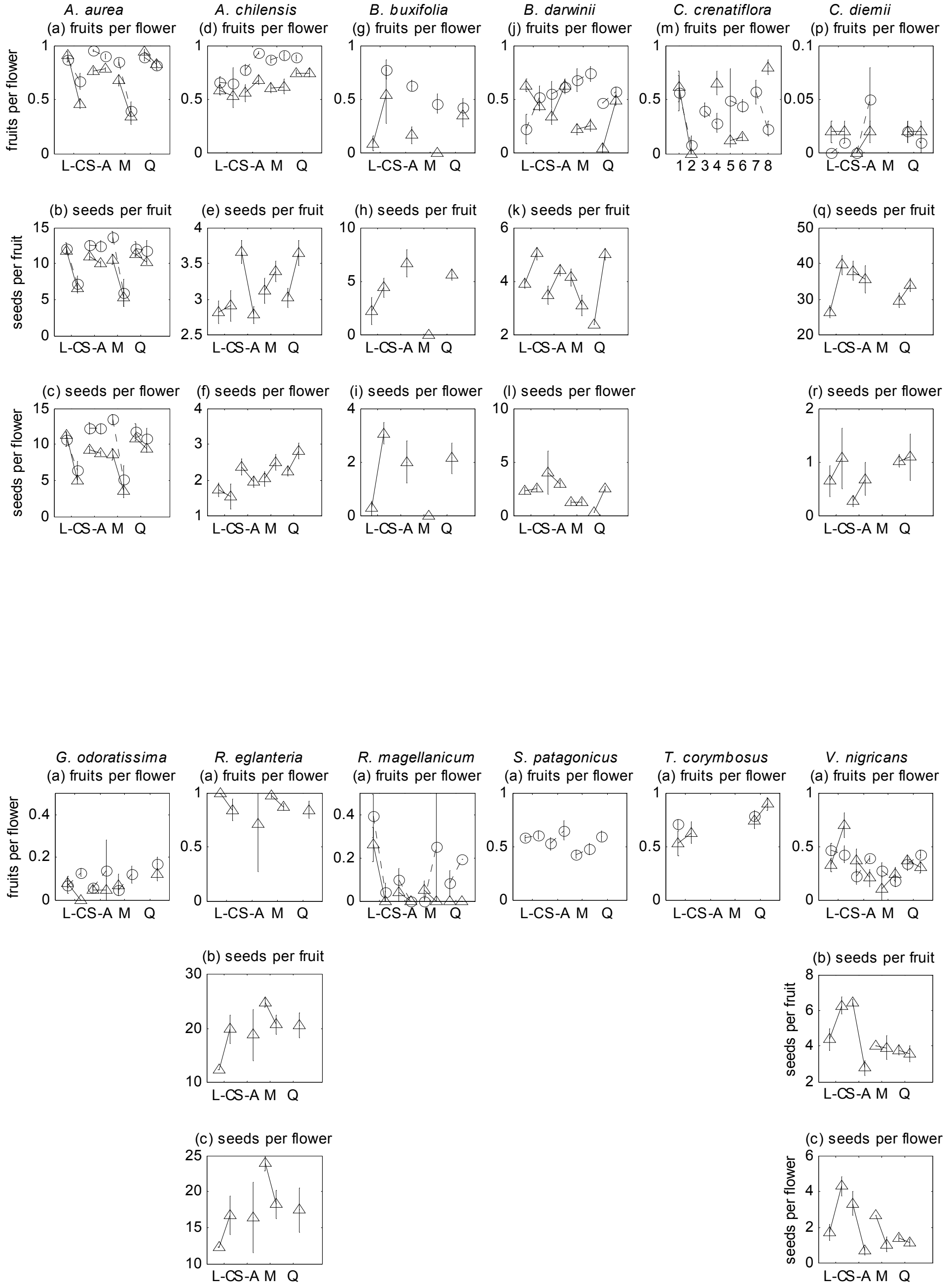


Figure 5.5. Mean fruit set (upper row in each of two panels), number of seeds per fruit (middle row), and number of seeds per flower (lower row) in each species (data for *D. purpurea* not shown because it was present only at one site). Circles correspond to 1999-2000 data; triangles correspond to 2000-2001 data. Error bars represent standard error of mean. Paired sites are joined by lines, ungrazed site on left and grazed site on right. Letters on *x*-axis indicate paired sites (see Fig. 5.2). Sites with no marker indicate that no observation periods were conducted. See Table 5.5 for statistics.

Table 5.5. Anova table for analysis of fruit and seed set. Results of mixed model analysis of variance for the fixed effect (grazing) are given. *P*-values <0.1 are highlighted in bold.

Species	Response variable	Year	d.f.	F	P
Alstroemeria aurea	Fruits per flower	1999-2000	3	5.73	**0.0965**
		2000-2001	3	3.57	0.1554
	Seeds per fruit	1999-2000	3	3.62	0.1534
		2000-2001	3	9.92	**0.0513**
	Seeds per flower	1999-2000	3	3.48	0.1590
		2000-2001	3	6.32	**0.0866**
Aristotelia chilensis	Fruits per flower	1999-2000	2	3.70	0.1942
		2000-2001	3	1.08	0.3747
	Seeds per fruit	2000-2001	3	0.02	0.8995
	Seeds per flower	2000-2001	3	1.20	0.3539
Berberis darwinii	Fruits per flower	1999-2000	3	1.91	0.2604
		2000-2001	3	1.05	0.3806
	Seeds per fruit	2000-2001	3	2.13	0.2409
	Seeds per flower	2000-2001	3	1.84	0.2678
Calceolaria crenatiflora	Fruits per flower	1999-2000	3	3.66	0.1517
		2000-2001	1	0.00	0.9780
Cynanchum diemii	Fruits per flower	1999-2000	2	4.57	0.1660
		2000-2001	2	0.33	0.6240
	Seeds per fruit	2000-2001	2	1.43	0.3542
	Seeds per flower	2000-2001	2	0.00	0.9784
Gavilea odoratissima	Fruits per flower	1999-2000	2	21.55	**0.0434**
		2000-2001	1	0.07	0.8348
Rosa eglanteria	Fruits per flower	2000-2001	1	2.54	0.3568
	Seeds per fruit	2000-2001	1	1.13	0.4803
	Seeds per flower	2000-2001	1	2.79	0.3435
Ribes magellanicum	Fruits per flower	1999-2000	3	0.00	0.9533
		2000-2001	3	1.32	0.3335
Schinus patagonicus	Fruits per flower	1999-2000	2	1.05	0.4129
Tristerix corymbosus	Fruits per flower	2000-2001	1	1.09	0.4865
Vicia nigricans	Fruits per flower	1999-2000	3	0.31	0.6168
		2000-2001	3	0.12	0.7548
	Seeds per fruit	2000-2001	3	0.64	0.4832
	Seeds per flower	2000-2001	3	0.95	0.4014

Table 5.6. Summary of results of mixed model ANOVAs on the different dependent variables. Significant effects ($P < 0.1$) are highlighted in gray, with direction of effect indicated by sign (+: positive effect; –: negative effect); "n.s." are statistically unsignificant results. Empty cells indicate unmeasured effects.

	Dependent variable															
	Tot. dens.	Fl. dens.	Poll. visitation		Pollination[†]						Reproduction[‡]					
					consp.		heterosp		prop. consp.		fr/fl		s/fr		s/fl	
Plant species	99-00	99-00	99-00	00-01	99-00	00-01	99-00	00-01	99-00	00-01	99-00	00-01	99-00	00-01	99-00	00-01
Alstroemeria aurea	–	–	n.s.	n.s.	n.s.	–	+	n.s.	–	–	–	n.s.	n.s.	–	n.s.	–
Aristotelia chilensis	–	–	n.s.	n.s.		n.s.		n.s.		n.s.	n.s.	n.s.		n.s.		n.s.
Berberis buxifolia[§]	+	n.s.														
Berberis darwinii	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.	n.s.	n.s.		n.s.		n.s.
Calceolaria crenatiflora	n.s.	n.s.	n.s.			n.s.		n.s.		n.s.	n.s.	n.s.				
Cynanchum diemii	–	n.s.	n.s.			n.s.*					n.s.	n.s.		n.s.		n.s.
Digitalis purpurea[§]	n.s.	n.s.														
Gavilea odoratissima	n.s.	n.s.	n.s.			n.s.					+	n.s.				
Rosa eglanteria	n.s.	n.s.	n.s.	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.
Ribes magellanicum	–	–	n.s.	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.				
Schinus patagonicus	n.s.	n.s.	n.s.								n.s.					
Tristerix corymbosus	n.s.	n.s.				n.s.		n.s.		n.s.		n.s.				
Vicia nigricans	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		n.s.		n.s.

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

[‡] Reproductive variables are: fruits per flower (fr/fl), seeds per fruit (s/fr), and seeds per flower (s/fl).

*Proportion of pollinia remaining in flower was used for this species.

[§] No comparisons were possible for these species for reproductive variables because they flowered only in grazed sites.

Fruit and seed set.—The final step in my hypothesis assumes that an effect of density on pollination (either quantity or quality) affects reproduction (Fig. 5.1). Of four species that were sparser in grazed sites, only *Alstroemeria aurea* showed decreased reproductive performance there; this effect was statistically significant for fruits per flower in 1999-2000 and for seeds per fruit and seeds per flower for 2000-2001 (Fig. 5.5; Table 5.5). For the only species that was significantly denser in grazed sites (*Berberis buxifolia*) I was unable to compare reproduction between grazed and ungrazed sites, because virtually no individuals flowered in ungrazed sites (only one individual was found in 2000-2001 in Llao Llao). Finally, one species whose density and pollination showed no clear pattern in relation to the presence of cattle, *Gavilea odoratissima*, produced significantly more fruits in grazed sites in 1999-2000 but not in 2000-2001 (Fig. 5.5; Table 5).

Summary of comparisons for the 13 species.—The results of the comparisons between grazed and ungrazed sites for the 13 plant species are summarized in Table 5.6. For most species I found no density-mediated indirect effects of cattle on pollination and reproduction. In eight cases, there were no significant effects of grazing on density, which precludes further analysis of effects on plant-pollinator interactions, pollination, and reproduction. For the five species for which I found significant effects on density, only *Alstroemeria aurea* showed effects on pollination and reproduction that were consistent with the hypothesis in both years of the study, although the effects were statistically significant in only one of the two years. Notice that, although no statistically significant effect on pollinator visitation frequency was found, such an effect is not necessary in my hypothesis: an effect through decreased pollination quality is possible even if pollinator visitation is not affected (see Fig. 5.1). Thus, my congruence criterion is met for *A. aurea*: I found significant effects for all the variables involved in my hypothesis in at least one of the two years, with the exception of pollinator visitation, for which I found no significant effects in either year. Therefore, I take these results as evidence for indirect effects of cattle on the pollination and reproduction of *A. aurea*.

A closer look at Alstroemeria aurea

Are these effects on *A. aurea* really due to the mechanisms hypothesized in Fig. 5.1? Is there truly an effect of cattle on the population density of *A. aurea*, and does population density affect pollination and reproductive success? I conducted further studies to test the hypothesized mechanisms involved in the indirect effect of cattle on pollination and reproduction of *A. aurea*.

Table 5.7. Browsing indices. Numbers are mean percentage of browsed individuals per quadrat for each site and species. Empty cells indicate that browsing index could not be estimated because species was rare in site. Species are indicated in first row by initials of genus and species names (see Table 5.1 for full names).

Site	A.a.	A.c.	B.b.	B.d.	C.d.	C.c.	D.p.	G.l.	R.e.	R.m.	S.p.	T.c.	V.n.	Total
Llao Llao	0.0	0.0		0.0	0.0	0.0		0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cerro López	0.0	85.7		94.0	0.0			0.0	0.0	45.0	98.3	0.0	0.0	32.3
Safariland	0.0	9.9		3.5	0.0			0.0	0.0	2.2	17.5		0.0	3.7
Arroyo Goye	0.0	96.0	73.0	70.5	23.1			33.3		92.5	98.2		3.8	54.5
Mascardi (nh)	0.0	0.0		1.9				2.3	0.0	11.8	17.1		0.0	4.1
Mascardi (h)	0.0	100.0	100.0	100.0				57.1	0.0	66.7	100.0		0.0	58.2
Quetrihué (nh)	0.0	27.7	0.0	50.0	9.9				0.0	27.3	46.8	17.3	0.0	17.9
Quetrihué (h)	1.1	88.8	70.0	93.5	38.8	0.0	0.0	0.0	0.0	84.6	88.9	0.0	0.0	35.8
Average (nc)	0.0	9.4	0.0	13.9	3.3	0.0		0.8	0.0	10.3	20.4	8.6	0.0	5.6
Average (c)	0.3	92.6	81.0	89.5	20.6	0.0	0.0	22.6	0.0	72.2	96.3	0.0	0.9	36.6

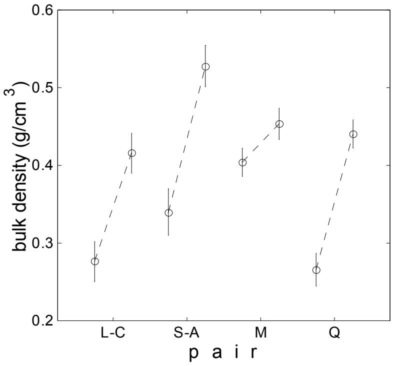


Figure 5.6. Soil dry weight in grazed and ungrazed sites. Circles represent mean dry weight (g.) of 30 samples taken at each site; error bars represent standard error of mean. Paired sites are joined by lines, ungrazed site on left and grazed site on right. Letters on *x*-axis indicate paired sites (see Fig. 5.2). Fixed effect test for mixed model ANOVA: d.f. = 3; $F_{1,3} = 19.0$; $P =$

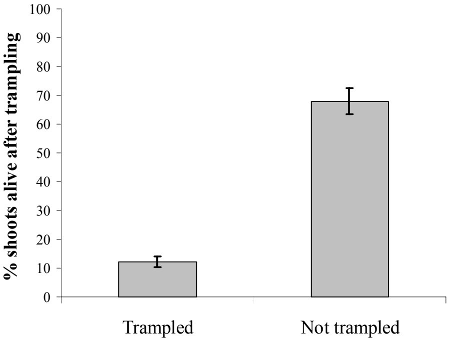


Figure 5.7. Effect of trampling on *A. aurea*. Bars represent mean percent of ramets alive after trampling in four experimental and four control (not trampled) plots (see Methods section). $t_{0.05(2),3} = 5.58$; $P < 0.002$.

Direct effect of cattle on the population density of A. aurea.—A requirement of my hypothesis is that cattle directly reduce the population density of *A. aurea*. *A. aurea* is indeed consistently sparser in grazed sites. How does the effect of cattle on *A. aurea* arise? *A. aurea* is virtually unbrowsed by cattle (Table 5.7). However, observational evidence indicated that *A. aurea* is highly susceptible to trampling (D.P. Vázquez, personal observation). Furthermore, soil dry weight per unit volume (an indirect measure of trampling intensity) is significantly higher in grazed than in ungrazed sites (Fig. 5.6). This fact led me to formulate the following prediction: if trampling leads to decreased density of *A. aurea*, then simulating this effect should also lead to decreased density owing to increased ramet mortality. To test this prediction, I simulated trampling by walking once on selected 1×1 m plots (see Methods). There is a significant decrease in ramet survivorship in trampled plots compared to control (untrampled) plots (Fig. 5.7). Taken together, this evidence supports the hypothesis that cattle trampling can directly decrease the population density of *A. aurea*.

Effect of density on pollination and reproduction: among-site path analysis.—If the hypothesized causal relationships among population density, pollination and reproduction are true, variability in site means of these variables should be explained by this causal scheme. If so, population density should positively affect conspecific pollen deposition and negatively affect heterospecific pollen position. I used path analysis to test for these causal relationships.

An effect of density on pollination was observed both years (Fig. 5.8 and Table 5.8). However, the effect of density was not significant for conspecific pollen deposition in 00-01, nor for heterospecific pollen deposition in either year. This lack of statistical effect may be partly due to the low power of my analysis resulting from the low sample size, rather than to a real lack of effect. The relationship between density and conspecific pollen deposition is linear because both variables were log-transformed; when an arithmetic density scale for density is used instead, a plateau in the number of conspecific pollen grains is reached at intermediate densities (Fig. 5.9).

Finally, conspecific pollen deposition positively affected the reproductive variables, as expected; however, this effect was not statistically significant for seeds per fruit and seeds per flower in 99-00. The effect of heterospecific pollen deposition on reproduction was weaker and never staticsally significant.

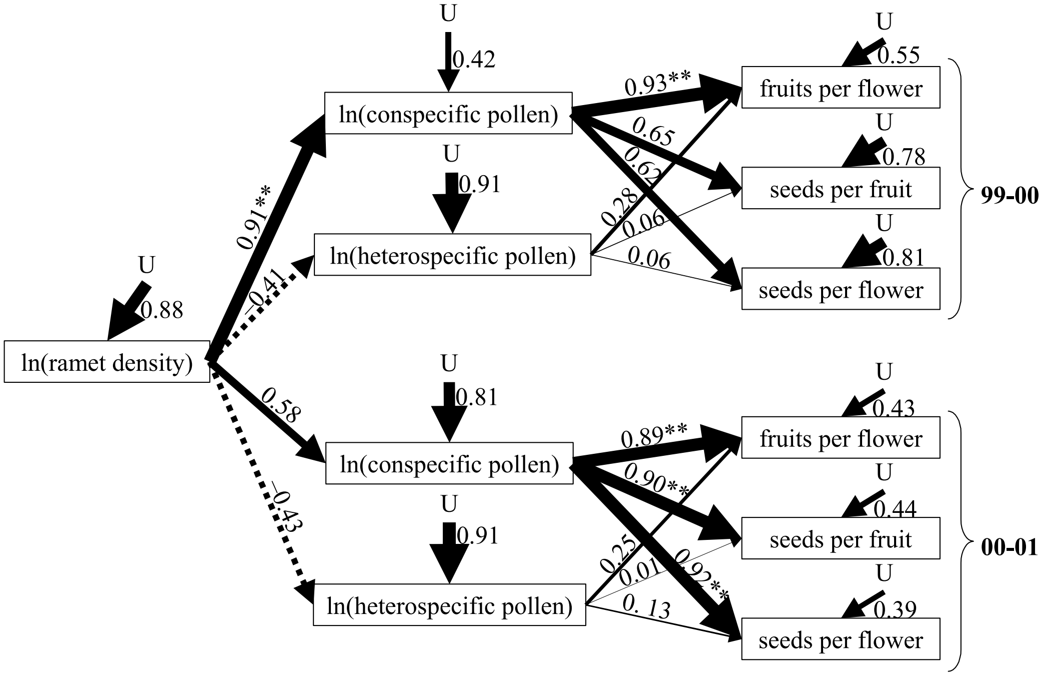


Figure 5.8. Results of among-site path analysis of causal relationship among different variables hypothesized to be involved in indirect effects of cattle on pollination and reproduction of *Alstroemeria aurea*. Arrows represent directional effects. For each effect path coefficients are given and are also represented by arrow line-thickness. Continuous lines indicate positive effects; dashed lines indicate negative effects. All flowering ramets within each site were included in analysis. (*: $P < 0.05$; **: $P < 0.01$.)

Table 5.8. Direct, indirect and total effects for path analysis of variables across sites.

		Effect on														
		ln(pc)			ln(ph)			fruits per flower			seeds per fruit			seeds per flower		
Year	Variable	DE	IE	TE	DE	IE	TE	DE	IE	TE	DE	IE	TE	DE	IE	TE
99-00	ln(density)*	0.91	—	0.91	-0.41	—	-0.41	—	0.73	0.73	—	0.57	0.57	—	0.54	0.54
	ln(pc)	—	—	—	—	—	—	0.93	—	0.93	0.65	—	0.65	0.62	—	0.62
	ln(ph)	—	—	—	—	—	—	0.28	—	0.28	0.06	—	0.06	0.06	—	0.06
	R2			0.83			0.18			0.70			0.39			0.35
00-01	ln(density)*	0.58	—	0.58	-0.43	—	-0.43	—	0.41	0.41	—	0.52	0.52	—	0.48	0.48
	ln(pc)	—	—	—	—	—	—	0.89	—	0.89	0.90	—	0.90	0.92	—	0.92
	ln(ph)	—	—	—	—	—	—	0.25	—	0.25	0.01	—	0.01	0.13	—	0.13
	R2			0.33			0.18			0.82			0.81			0.85

* Density was measured only in 1999-2000, assuming no change in density between the two years.

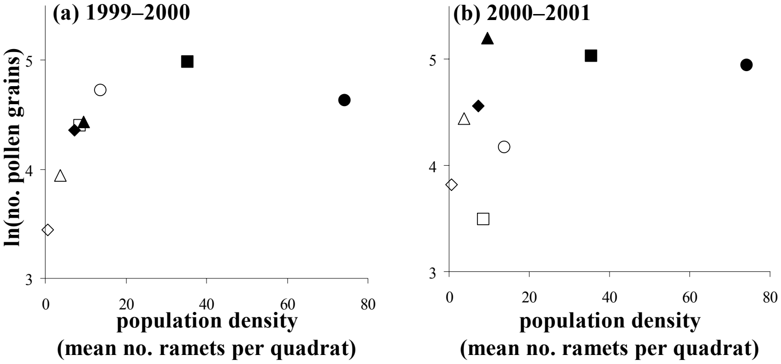


Figure 5.9. Logarithm of mean number of conspecific pollen grains deposited in stigmas of *A. aurea* per site as function of population density. White symbols: grazed sites; black symbols: ungrazed sites. Paired sites are indicated with same symbol shape: squares, Llao Llao–Cerro López; circles, Safariland–Arroyo Goye; diamonds, Mascardi; triangles, Quetrihué.

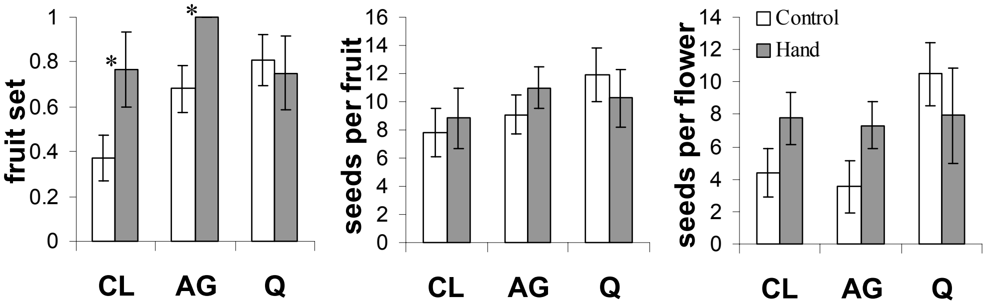


Figure 5.10. Results of hand-pollination experiments in *Alstroemeria aurea*. Asterisks indicate statistically significant differences between means of reproductive variables of natural- and hand-pollinated flowers. Letters on *x*-axis represent sites: CL, Cerro López; AG, Arroyo Goye; Q, Quetrihué. (*: $P < 0.05$.)

Pollen limitation.—Receiving fewer pollen grains can lead to lower reproductive success if reproduction is pollen-limited. Thus, increasing pollen loads in *A. aurea* populations in grazed sites should lead to higher reproductive success. My hand-pollination experiments provide some support for this condition. In two of the three grazed sites in which I performed hand-pollination experiments (Cerro López and Arroyo Goye), hand-pollination resulted in higher reproductive success compared to open-pollinated ramets, although this effect was significant only for fruit set (Fig. 5.10). In Quetrihué, hand-pollinated ramets reproduced slightly worse than open-pollinated ramets, but this effect was not significant (Fig. 5.10).

Effect of floral neighborhood density on pollination and reproduction: within-site path analysis.—As a final test of the effect of population density on the pollination and reproduction of *A. aurea*, I conducted detailed spatial analyses of the effect of floral neighborhood on pollinator visitation, pollination, and reproduction. I used the model in Fig. 5.11 as a general hypothesis of the causal relationships among these variables (see also Table 5.9). Besides the variables originally posited (see Fig. 5.1), I included others that I believed could directly or indirectly affect reproduction (see Methods).

Although the specific causal models selected vary among sites and reproductive variables (Table 5.10), the square root of floral neighborhood density positively affects conspecific pollen deposition. This effect, albeit weak, is statistically significant in all cases except for seeds per fruit in Arroyo Goye. In turn, conspecific pollen deposition positively affects each reproductive variable, although it is significant only in three sites (Fig. 5.12; Table 5.11). The exception is the grazed site in Mascardi, where path coefficients between conspecific pollen and the reproductive variables were not statistically significant, in spite of their relatively high magnitude (Fig. 5.12; Table 5.11). Because the sample size in Mascardi was considerably lower than in other sites, this lack of significance is probably due to a lack of statistical power rather than lack of effect. Nevertheless, the amount of unexplained variation in conspecific pollen deposition and reproduction was generally high, as indicated by the thickness of the "U" arrows in Fig. 5.12 and the generally low R^2 values in Table 5.11. The total effect of density on reproduction (sum of the direct and indirect effects) is generally weaker than the direct effect of density on pollination, ranging from 0.06 (fruits per flower in Arroyo Goye) to 0.35 (seeds per fruit in Mascardi; Table 5.11).

Seven selected models did not contain heterospecific pollen deposition. Even in the five that did, heterospecific pollen had no significant effect in four of them (the exception was the model for fruit set in Arroyo Goye, Fig. 5.12d). Other variables included in the general model (Fig. 5.11) were not retained in the best-fitting models in most cases. When they were retained, in most cases their effects were not significant. However, there is a significant effect of number of flowers per ramet on seeds per fruit and seeds per flower in Cerro López (Fig. 5.12c), and there are significant effects of date of female phase and heterospecific pollen deposition on fruit set in Arroyo Goye (Fig. 5.12d).

I conclude that there is a significant effect of plant population density on pollination success and that this effect is due to lower pollination quality rather than quantity. I also have presented evidence that conspecific pollen deposition—but not heterospecific pollen deposition—affects the reproductive success of *A. aurea*. My ultimate goal is to determine whether the ungulate-induced decrease in the population density of *A. aurea* results in a negative effect on the reproductive success of *A. aurea*. To this end, I examine the direct, indirect and total effects of density on the reproductive variables (Table 5.11). The total effect of density is always positive. However, the magnitude of this effect is highly variable and never strong. In the simplest model (13), the effect of density on reproduction is only indirect through conspecific pollen deposition. In other, more complex models, there are also indirect effects through other variables (i.e., pollinator visitation rate and heterospecific pollen deposition) and a direct effect of density. Thus, population density positively affects, either directly, indirectly, or both, the reproductive success of *A. aurea*. However, other variables (either explicitly included in the my models or implicitly included as "unexplained variability") also have important effects on reproduction.

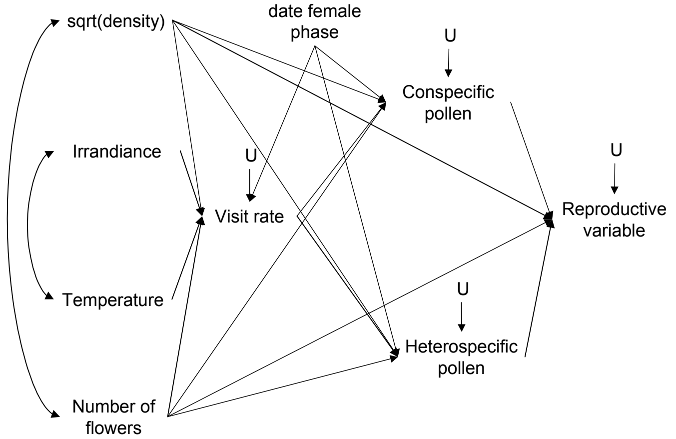


Figure 5.11. Full causal model used to study relationship between floral neighborhood density, pollinator visitation, pollination and reproduction of *Alstroemeria aurea*. One-headed arrows represent directional effects; two-headed arrows represent correlations between pairs of variables. Conspecific and heterospecific pollen deposition were log-transformed. Variables included in full model are: the sum of square root of flowering ramet density per band (see Appendix 1); number of flowers per ramet; irradiance and temperature recorded per pollinator sampling period; pollinator visitation rate; date of half-time female phase; number of conspecific and heterospecific pollen grains deposited in flower stigmas; and one of the three reproductive variables (fruits per flower, seeds per fruit, or seeds per flower). Unexplained variability in endogenous (dependent) variables is indicated as "U."

Table 5.9. Variables included in each of the nested structural equation models used to study effect of floral neighborhood density on pollination and reproduction of *Alstroemeria aurea* in four grazed sites. See Fig. 5.11 for explanation of variable names.

Model	Model description (paths constrained to zero)
1	all paths free to vary (full model; Fig. 5.11)
2	light and temperature to visits
3	light and temperature to visits; all paths from date female phase
4	light and temperature to visits; number of flowers to reproductive variable
5	light and temperature to visits; number of flowers to reproductive variable; all paths from date female phase
6	light and temperature to visits; number of flowers and density to reproductive variable; all paths from date female phase
7	light and temperature to visits; all paths from visits; all paths from date female phase
8	all paths constrained to zero in model 7; number of flowers to reproductive variable
9	all paths constrained to zero in model 8; density to reproductive variable
10	all paths constrained to zero, except: density to conspecific pollen; density to heterospecific pollen; conspecific pollen to reproductive variable; heterospecific pollen to reproductive variable
11	all paths contrained to zero, except: density to conspecific pollen; density to visits; conspecific pollen to reproductive variable; visits to conspecific pollen
12	all paths constrained to zero in model 11; density to conspecific pollen
13	all paths constrained to zero in model 11; density to visits; visits to conspecific pollen

Table 5.10. Results of model selection procedure for nested structural equation models used to study relationship between floral neighborhood density, pollinator visitation, pollination and reproduction of *Alstroemeria aurea* in the four grazed sites. Numbers are Akaike's Information Criterion (AIC) calculated for each combination of model, reproductive variable, and site. AIC values for best-fitting models are highlighted in bold. AIC was calculated with CALIS procedure in SAS.

model	Cerro López			Arroyo Goye			Mascardi (c)			Quetrihué (c)		
	fr/fl	s/fr	s/fl	fr/fl	s/fr	s/fl	fr/fl	s/fr	s/fl	fr/fl	s/fr	s/fl
1	21.01	16.13	18.27	26.80	24.54	23.98	—	—	—	55.52	84.15	66.93
2	9.96	8.11	9.38	2.73	**-2.85**	-0.43	—	—	—	29.61	19.62	19.82
3	11.28	10.93	11.09	-0.52	0.65	2.02	—	—	—	29.55	21.46	21.26
4	7.64	7.08	7.39	8.91	0.79	5.13	—	—	—	28.17	19.62	18.08
5	9.34	9.90	9.11	5.67	4.29	7.57	—	—	—	28.11	21.46	19.53
6	8.04	24.30	20.83	3.70	7.04	15.53	—	—	—	27.57	21.21	17.88
7	5.46	5.27	5.21	-0.77	-0.86	**-0.86**	28.49	28.49	28.49	20.63	19.27	19.27
8	3.52	**4.24**	**3.22**	5.42	2.79	4.70	37.22	22.31	28.91	19.19	19.27	17.53
9	2.23	18.63	14.94	3.45	5.54	12.66	35.22	24.82	29.47	18.65	19.02	15.88
10	3.46	18.98	16.25	**-3.32**	1.35	6.56	0.79	0.79	3.34	17.44	16.52	15.12
11	0.47	16.32	13.53	-0.74	3.37	10.21	9.44	5.45	5.50	7.45	**-2.00**	**-3.62**
12	-1.26	14.59	11.80	-1.88	2.16	9.01	7.44	3.45	3.50	15.12	5.09	3.46
13	**-1.41**	12.42	10.95	-1.53	1.19	8.49	**-2.00**	**-2.00**	**0.54**	**0.24**	-0.39	-1.68

Note: The most complex models (1-6) could not be tested in Mascardi because of low sample size.

Table 5.11. Direct, indirect, and total effects for best structural equation models used to study relationship between floral neighborhood density, pollinator visitation, pollination and reproduction of *Alstroemeria aurea* in four grazed sites.

				Effect on											
				visit rate			ln(pc)			ln(ph)			reproduction		
Site	Reproductive var.	Model	Variable	DE	IE	TE	DE	IE	TE	DE	IE	TE	DE	IE	TE
Cerro López	fruits per flower	13	sqrt(dens)				0.29	—	0.29				—	0.18	0.18
			ln(pc)				—	—	—				0.63	—	0.63
			R2						0.08						0.40
	seeds per fruit	8	sqrt(dens)				0.24	—	0.24	-0.16	—	-0.16	0.19	0.13	0.32
			no. flowers				0.26	—	0.26	0.00	—	0.00	—	0.13	0.13
			ln(pc)				—	—	—	—	—	—	0.50	—	0.50
			ln(ph)				—	—	—	—	—	—	-0.05	—	-0.05
			R2						0.15			0.03			0.35
	seeds per flower	8	sqrt(dens)				0.24	—	0.24	-0.16	—	-0.16	0.21	0.12	0.33
			no. flowers				0.26	—	0.26	0.00	—	0.00	—	0.13	0.13
			ln(pc)				—	—	—	—	—	—	0.49	—	0.49
			ln(ph)				—	—	—	—	—	—	-0.03	—	-0.03
			R2						0.15			0.03			0.37
Arroyo Goye	fruits per flower	10	sqrt(dens)				0.17	0.00	0.17	-0.16	0.00	-0.16	—	0.06	0.06
			ln(pc)				—	—	—	—	—	—	0.57	—	0.57
			ln(ph)				—	—	—	—	—	—	0.21	—	0.21
			R2						0.03			0.02			0.38
	seeds per fruit	2	sqrt(dens)	0.03	—	0.03	0.15	0.00	0.15	-0.37	0.00	-0.37	0.08	0.13	0.21
			no. flowers	0.02	—	0.02	0.25	0.00	0.25	0.03	0.00	0.03	0.07	0.11	0.18
			date female	0.19	—	0.19	0.49	-0.03	0.46	0.42	0.03	0.45	—	0.14	0.14
			visit rate	—	—	—	-0.16	—	-0.16	0.15	—	0.15	—	-0.10	-0.10
			ln(pc)	—	—	—	—	—	—	—	—	—	0.47	—	0.47
			ln(ph)	—	—	—	—	—	—	—	—	—	-0.16	—	-0.16
			R2			0.03			0.23			0.47			0.29
	seeds per flower	7	sqrt(dens)				0.17	—	0.17	-0.15	—	-0.15	0.09	0.08	0.17

			no. flowers	0.09	—	0.09	-0.18	—	-0.18	0.09	0.04	0.13
			ln(pc)	—	—	—	—	—	—	0.51	—	0.51
			ln(ph)	—	—	—	—	—	—	0.04	—	0.04
			R2			0.04			0.05			0.30
Mascardi (c)	fruits per flower	13	sqrt(dens)	0.75	—	0.75				—	0.18	0.18
			ln(pc)	—	—	—				0.24	—	0.24
			R2			0.56						0.06
	seeds per fruit	13	sqrt(dens)	0.75	—	0.75				—	0.35	0.35
			ln(pc)	—	—	—				0.46	—	0.46
			R2			0.56						0.21
	seeds per flower	13	sqrt(dens)	0.75	—	0.75				—	0.29	0.29
			ln(pc)	—	—	—				0.39	—	0.39
			R2			0.56						0.15
Quetrihué (c)	fruits per flower	13	sqrt(dens)	0.45	—	0.45				—	0.21	0.21
			ln(pc)	—	—	—				0.46	—	0.46
			R2			0.20						0.21
	seeds per fruit	13	sqrt(dens)	0.45	—	0.45				—	0.17	0.17
			ln(pc)	—	—	—				0.37	—	0.37
			R2			0.20						0.14
	seeds per flower	13	sqrt(dens)	0.45	—	0.45				—	0.19	0.19
			ln(pc)	—	—	—				0.42	—	0.42
			R2			0.20						0.18

Abbreviations: DE, direct effect; IE, indirect effect; TE, total effect; sqrt(dens), the sum of the square root of the density in concentric bands used to estimate floral neighborhood density (see methods and Appendix 1); ln(p_c) and ln(p_h), natural logarithm of the number of conspecific and heterospecific pollen grains deposited in stigmas, respectively.

[a] Direct effects are path coefficients, obtained using *stb* option in *model* statement in SAS PROC REG.

[b] Indirect effects are obtained by multiplying path coefficients between pairs of variables along an indirect pathway.

[c] Total effects are sums of direct and indirect effects.

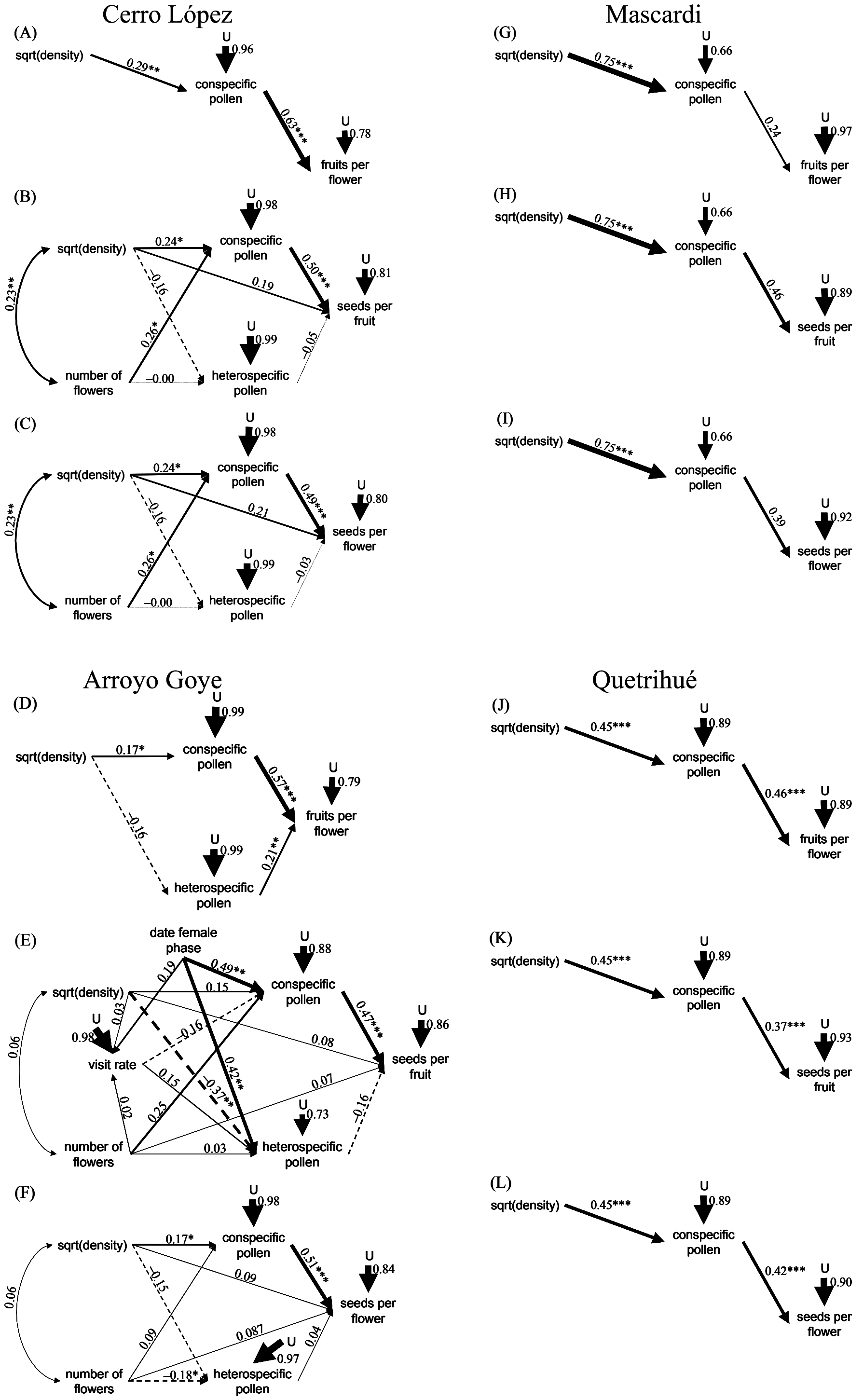


Figure 5.12. Path analysis of best-fitting structural equations models for three reproductive variables. (A-C) Cerro López; (D-F) Arroyo Goye; (G-I) Mascardi; (J-L) Quetrihué. See Table 5.9 for results of model selection procedure, and Fig. 5.11 for explanation of variables. One-headed arrows represent directional effects; two-headed arrows represent correlations between pairs of variables. For each effect path coefficients are given and also represented by arrow line-thickness. Continuous lines indicate positive effects; dashed lines indicate negative effects. All flowering ramets within each site were included in analysis. (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.)

DISCUSSION

Effects of cattle on plant population density

My hypothesis (see Fig. 5.1) requires that cattle affect (either negatively or positively) plant population density. The population density of eight of the thirteen species showed no association with the presence of cattle. Thus, the first part of the mechanism hypothesized to link cattle with plant pollination and reproduction indirectly is not observed. For only five species did I find significant effects of cattle on population density; cattle seem also to affect two other species, *T. corymbosus* and *D. purpurea* (negatively and positively, respectively), although their absence from some pairs of sites makes it impossible to evaluate whether this pattern is truly due to cattle. For two of these seven species I could not study effects of cattle on their reproduction because they were virtually absent from grazed sites. For only one of the five species whose population density was significantly lower in grazed than in ungrazed sites did I find evidence of indirect effects of cattle on pollination and reproduction.

By what means do cattle affect population density of these species? Two species, *A. chilensis* and *R. magellanicum*, were heavily browsed (Table 5.7), and this direct effect is the more parsimonious explanation for their decreased abundance in grazed sites. Heavy browsing on these species has previously been observed (Dimitri 1962; Veblen et al. 1989; Veblen et al. 1992; Relva and Caldiz 1998). Interestingly, a similar pattern to that observed here for *A. chilensis* is observed for its congener *A. serrata* in New Zealand, where it is affected by introduced red and sika deer (Allen et al. 1984). Similarly, sheep and rabbit grazing prevent the spread of *Ribes sanguineum* in New Zealand pasturelands (Williams 1984).

The situation for *C. diemii* is less clear-cut; browsing seems not as strong as for *A. chilensis* and *R. magellanicum*, and there was no browsing in one grazed site, even though density was lower in grazed sites. *A. aurea* is not heavily browsed by cattle but, as my experiments demonstrate, trampling by cattle negatively affects ramet survival. It is surprising that no previous study had noted an effect of introduced herbivores on this species. However, my data do not allow me to assess the relative importance of direct vs. indirect effects in causing the decline of this species. The simplest explanation is that trampling causes a decline in density, which is followed by an indirect effect on pollination and reproduction. At low population densities (i.e., very high trampling intensity), this effect could be important enough to decrease abundance of *A. aurea* further. Finally, *T. corymbosus* also is little browsed by cattle. A mistletoe, this species is unlikely to be affected by trampling, since it usually grows on branches of trees and shrubs at > 1 m height from the ground (D.P. Vázquez, personal observation). Further, I found little browsing on this species. One possible reason for its decline in grazed sites is low host availability. In my study sites, the main host of *T. corymbosus* is *A. chilensis* (I found all individuals on this host species), although it occasionally grows on other hosts (such as *Azara* sp. and *Maytenus boaria*; M.A. Relva, personal communication). Given the drastic decrease of *A. chilensis* in grazed sites, it is possible that cattle are indirectly affecting *T. corymbosus* by decreasing host availability in grazed sites.

The only species with higher density in grazed than in ungrazed sites was *Berberis buxifolia*. The abundance of this species can increase despite heavy browsing. Although low browsing levels increase growth rates for some species (Belsky 1986; Agrawal 2000), it is also possible that a more complex, indirect effect is occurring in this case, involving increased light availability in the understory. Light availability is lower in the understory of ungrazed sites (Fig. 5.13). *B. buxifolia* is usually found in forest gaps and seems unable to reproduce in the shady understory of ungrazed *N. dombeyii* forests: virtually no *B. buxifolia* individuals produced flowers in ungrazed sites, and those that did had extremely low fruit and seed set, whereas flowering individuals were present in all grazed sites, and most reproduced successfully. A similar effect of ungulates on *B. buxifolia* has been observed in other studies. Both in *Nothofagus dombeyii* and their *N. antarctica* sites, Veblen et al. (1989, 1992b) found increased abundance of *Berberis buxifolia* with grazing. Relva and Veblen (1998) mention a trend towards increased abundance of *Berberis* spp. (which included both *B. buxifolia* and *B. darwinii*; M.A. Relva, personal communication) with heavy grazing. De Pietri (1992) also mentions this species as increasing with heavy grazing. However, Raffaele and Veblen (2001) found that, in post-fire *Austrocedrus chilensis – Maytenus boaria* matorral, *B. buxifolia* was *more* abundant in fenced than in unfenced plots. This surprising result might be due to an interaction between fire and grazing. It is possible that grazing can inhibit the recolonization by *B. buxifolia* after fire.

Contrary to expectations, I found no positive effect of cattle on the abundance of *Berberis darwinii*. Veblen et al. (1989, 1992b) found that *B. darwinii* tended to be more abundant with increased grazing pressure, a pattern similar to that shown by *B. buxifolia*. In Islote Rupanco, Chile, Ramírez et al. (1981) found *B. darwinii* absent from their study plots in 1977 (two years after deer introduction), whereas it was

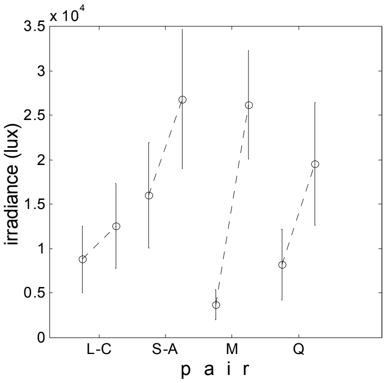


Figure 5.13. Average irradiance reaching ground in understory of each of eight sites. Mixed model ANOVA for fixed effect (grazing): *d.f.* = 3; *F* = 9.78; *P* = 0.0521.

present in 1981 (six years after introduction). In my study sites, *B. darwinii* showed no such pattern: *B. darwinii* was actually more abundant in the ungrazed sites of three of the four pairs, but the overall difference was not significant. *B. darwinii* reproduces successfully under the canopy, and, although it showed a trend to decreased density of flowering individuals and decreased reproductive performance in ungrazed sites, that trend was not significant. Studies of *B. darwinii* in its introduced range in New Zealand—where it escaped 1946 from a garden—also suggest this species is highly shade-tolerant (Allen 1991).

Also surprising was the lack of invasion by *Rosa eglanteria* in grazed sites. This spiny shrub commonly invades open areas (Damascos and Gallopin 1992), where it usually forms large thickets virtually unbrowsed by cattle (see Table 5.7). However, I found no significant effect of cattle on the abundance of *R. eglanteria*. This result is probably explained by the fact that I worked under a tree canopy (to avoid the confounding effect of tree cover with that of cattle). In fact, thickets of this species were more common in open areas of grazed sites than in similar areas of ungrazed sites (D.P. Vázquez, personal observation). Thus, once the canopy is removed, grazing may indeed enhance invasion by this species.

Indirect effects of cattle on pollination and plant reproduction

Lack of effect in most species: possible explanations.—Cattle seem to have no indirect effects on pollination and reproduction of most plant species in my study. Only for the herb *Alstroemeria aurea* did I find evidence for such effects. Several reasons may explain the lack of effect in most species.

Density of eight species showed no association with cattle. Thus, the first part of the hypothesized mechanism (see Fig. 5.1) is not met. For only five species were there significant effects of cattle on density, and, as discussed above, two other species (*T. corymbosus* and *D. purpurea*) might also be affected. For two of these seven species (*B. buxifolia* and *D. purpurea*) I could not study effects of cattle on reproduction because they were virtually absent from grazed sites. This left five species whose population density was lower in grazed than in ungrazed sites.

The most striking lack of indirect effects involves *Aristotelia chilensis*. This species showed the strongest decline in response to cattle. *A. chilensis* is a preferred food item for both introduced deer (Veblen et al. 1989; Veblen et al. 1992; Relva and Caldiz 1998) and cattle (Table 5.7; see also Veblen et al. 1992), and thus its decreased abundance in grazed sites is probably explained by the direct effect of browsing. Furthermore, this species is dioecious, which should exacerbate Allee effects resulting from low population density (House 1992, 1993; Kunin 1997a). Another characteristic that can make this species more vulnerable to low population densities is that in my sites it is pollinated almost exclusively by a single bee species, the colletid *Cadeguala albopilosa*. However, this bee is not restricted to *A. chilensis*: only about 60% of visits in my sites were to *A. chilensis*, while the remaining 40% were to *Schinus patagonicus* (see Chapter 6). *C. albopilosa* was also recorded visiting flowers of seven species in Chiloé Island, Chile (Aizen et al. 2002). Specialization on a generalist pollinator may be beneficial at low densities, because it increases the likelihood of receiving visits if other, coflowering species can support the population of the pollinator (although it can also be problematic at low population densities because of increased probability of improper pollen transfer; Rathcke 1983; Kunin 1993; Kunin and Iwasa 1996). It is thus surprising that I detected no effects of cattle on pollination and reproduction of this species. Furthermore, *C. albopilosa* behaved as a specialist during the second year of study, because *S. patagonicus* failed to flower that year; the change from generalist to specialist behavior of *A. chilensis*' main pollinator did not make a difference for its reproductive success. As I show elsewhere (see Chapter 6), this lack of negative effect at low densities may be partly due to the aggregated distribution of this species in grazed sites. *A. chilensis* individuals in grazed sites are mostly found in "refugia"—habitat patches not accessible to ungulates (e.g., steep slopes, spring beds, areas with many fallen trees). A detailed spatial analysis of the effects of floral neighborhood density on pollination and reproduction showed that the few isolated individuals of *A. chilensis* tend to receive fewer pollen grains and reproduce more poorly than individuals in refugia. Since most individuals in grazed sites are in these refugia, it is not surprising that I saw no significant difference between the mean reproductive performance in grazed and ungrazed sites.

Also striking is the apparent lack of indirect effects on the pollination and reproduction of *Cynanchum diemii* and *Ribes magellanicum*, in spite of their decreased density in grazed sites. There is no obvious explanation. A possibility for *C. diemii* is that the natural low reproductive output of this species (a characteristic of most species in the Alsclepiadaceae; Wyatt and Broyles [1994]) makes it harder to detect differences between grazed and ungrazed sites. Another factor may have been the low power of my analysis owing to the low number of replicates (four pairs). Finally, it was also surprising that the few individuals of *Tristerix corymbosus* that I found in grazed sites reproduced successfully. This species is pollinated mainly by the hummingbird *Sephanoides sephaniodes*, a generalist pollinator visiting other ornithophilous plants in the forest (Smith-Ramírez 1993; Fraga et al. 1997). As discussed above, rare plants pollinated by generalist pollinators are not expected to suffer from low visitation frequency (Rathcke 1983; Kunin 1993). It seems possible that *T. corymbosus* received enough visits even at low densities.

Indirect effects of cattle on the pollination and reproduction of A. aurea.—My results suggest that cattle decrease the population density of *A. aurea* through trampling and that this decreased abundance leads to decreased pollination and reproductive performance.

What is the specific mechanism leading to this apparent indirect effect? Neither in my paired comparisons between grazed and ungrazed sites, nor in my path analysis of the effect of floral neighborhood density on pollination and reproduction, did I find an effect on pollinator visitation. In my paired comparisons between grazed and ungrazed sites, the lack of effect could be attributed to the low power of my analyses (especially in the first year of study, when all grazed sites had lower visitation rates than their paired ungrazed sites). However, it is noteworthy that even when visitation rates were higher in the grazed than in the ungrazed site within a pair (i.e., Llao Llao–Cerro López and Quetrihué in 2000-2001; see Fig. 5.3) pollination performance was still poorer in grazed sites. Thus, the lower number of pollen grains deposited in stigmas may be attributed to lower pollination quality (i.e., fewer conspecific pollen grains brought by pollinators per visit) rather than lower quantity (i.e., fewer visits). In my path analysis of the effect of floral neighborhood density on pollination and reproduction, visitation rate was retained in only one of the 12 best-fitting models. Thus, density appears not to affect pollinator visitation rates, nor do pollination visitation appear to affect pollination. However, according to my hypothesis (see Fig. 5.1), an effect on pollinator visitation rates is not necessary for an indirect effect of cattle on plant reproduction. Cattle can also affect plant reproduction through an effect on pollination quality, which can occur without an effect on pollinator visitation. Was pollination quality actually affected?

Pollination quality is expected to decrease with decreasing relative population density, and this effect is expected to be greater when pollinators are generalists (Rathcke 1983; Kunin 1993). It is possible to estimate relative population density by dividing the mean density of *A. aurea* per site by the sum of the mean abundances whose flowering period overlapped with that of *A. aurea*. Five insect-pollinated species partially overlapped with *A. aurea* in their flower periods in my study sites (Fig. 5.14). Of these, all but *C. crenatiflora* were visited by the main pollinators of *A. aurea*, the native bumblebee *Bombus dahlbomii* and the introduced bumblebee *B. ruderatus*. As shown in Fig. 5.15, mean relative density of *A. aurea* is consistently lower in grazed than in ungrazed sites. Furthermore, the main pollinators of *A. aurea* are in fact extreme generalists (see Chapter 4). In my study sites, *B. dahlbomii* visited more plant species than any other pollinator species; and although the spectrum of plant species visited by *B. ruderatus* is somewhat narrower, this is mainly due to its shorter activity period (see Fig. 2.6). Thus, it is likely that the mechanism responsible is indeed decreased pollination quality.

It is important to note that heterospecific pollen deposition does not appear to affect the reproduction of *A. aurea*, as suggested by the lack of significant effects of heterospecific pollen on the reproductive variables in both my among-site and within-site path analyses (in the only structural equation model for which heterospecific pollen affected reproduction, that effect was positive; Fig. 5.12d). Therefore, the effect of lower pollination quality is the lower deposition of conspecific pollen grains per pollinator visit rather than the "improper transfer" (Rathcke 1983) of heterospecific pollen. For this depiction to be true, pollinators must bring fewer conspecific pollen grains per visit. Although I have indirect evidence that this may be occurring (i.e., lower conspecific pollen deposition in grazed sites in spite of higher visitation by pollinators in some cases), I am unable to demonstrate it conclusively. Such demonstration would require measuring the amount of conspecific pollen brought by individual pollinators. Regrettably, I could not capture enough pollinators in each of the eight sites to test this mechanism.

Another necessary condition for the hypothesized mechanism is that *A. aurea* be pollen-limited. If it is, then lower pollen receipt should result in lower reproductive success. However, if pollen is not limiting (e.g., because reproduction is resource-limited), then lower pollen receipt of plants at low densities should not result in lower reproductive success. As I showed in my among-site path analysis (Fig. 5.8), there was a positive effect of the logarithm of the mean number of conspecific pollen grains received per site on the mean reproductive output for the three reproductive variables in both years, although this effect was not significant for seeds per fruit and seeds per flower in 1999-2000. The same positive effect of conspecific pollen deposition on reproduction is observed in my within-site path analysis in three of the four grazed sites. However, although pollen deposition positively affected the reproductive variables in Mascardi, these effects were not statistically significant. As I discussed above (see Results), a possible explanation for this lack of effect is the lower sample size at Mascardi compared to the other sites (see Methods). Thus, rather than a true lack of effect, the lack of statistical significance could be a problem of statistical power.

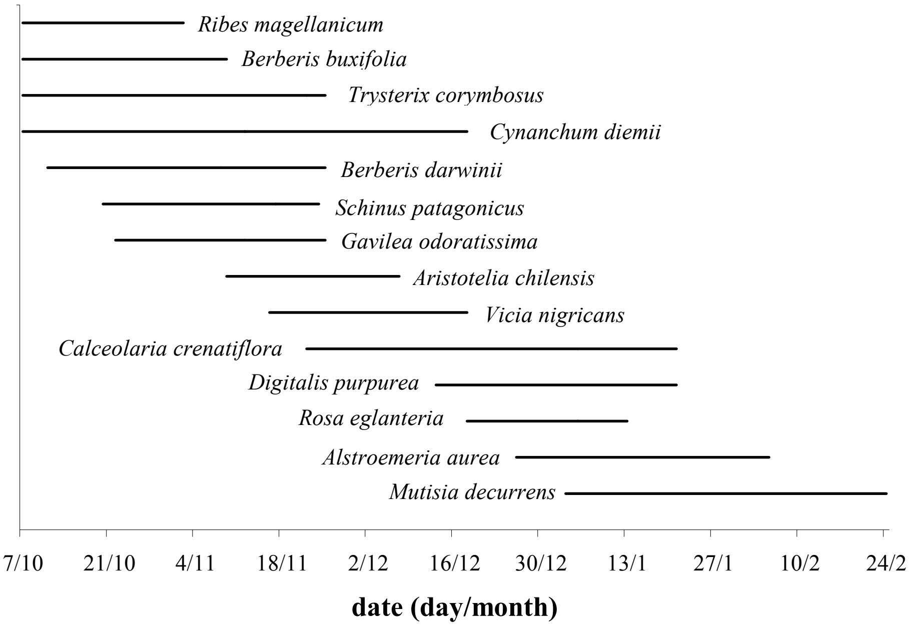


Figure 5.14. Phenology of insect-pollinated plants in study sites. Horizontal bars represent period during which plants were recorded bearing flowers at any study site during 1999-2000 field season. A fourteenth species, *Mutisia decurrens*, not included in the study, was included in graph because it was abundant at study sites and was visited by some of the pollinator species visiting some of the species included in the study.

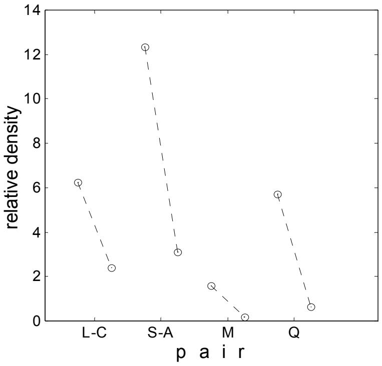


Figure 5.15. Relative density of *A. aurea*. Relative density was calculated by dividing mean density of *A. aurea* per site by sum of densities of species whose flowering period overlapped with that of *A. aurea* (see Fig. 5.14).

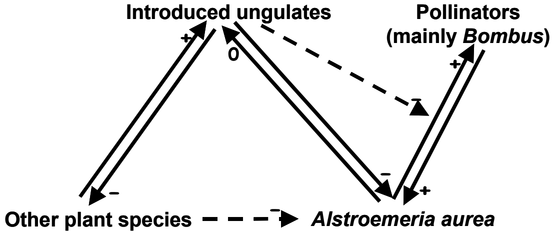


Figure 5.16. A conceptual model of effects of introduced herbivores on *Alstroemeria aurea*. Continuous lines indicate direct effects; dashed lines indicate indirect effects. Symbols indicate direction of effect: +, positive effect; 0, no effect; –, negative effect. (See text for explanation.)

The hand-pollination results suggest that pollen limitation could be occurring in at least two of the three experimental sites, Arroyo Goye and Cerro López. In these sites, hand-pollinated plants had a higher reproductive output than naturally pollinated plants, although this effect was significant for only one reproductive variable (fruits per flower). In the third site (Quetrihué), however, hand-pollinated plants had *lower* reproductive performance than naturally pollinated plants, although this difference was not significant for any reproductive variable. It must be borne in mind that in Quetrihué several hand-pollinated plants were lost, presumably to cattle trampling; this loss resulted in a low sample size for hand-pollinated plants (n = 4).

The results for *A. aurea* make sense in light of the reproductive biology of the species. Although *A. aurea* is self-compatible, flowers are protandrous, and the development of the different sexual phases is highly synchronized among flowers within a ramet and among flowers of neighboring ramets (Aizen and Basilio 1995). Thus, this species is functionally unable to self-pollinate. Furthermore, pollinator visitation is necessary for reproduction to occur (Aizen and Basilio 1995). The effects of density on pollination are expected to be stronger for self-incompatible species that depend on pollinators for reproduction. In fact, experiments support this expectation (Kunin 1993, 1997b, a).

My finding that population density affects pollination and reproductive success of *A. aurea* contrasts with the results of another study by Aizen (1997) in the same region. Aizen analyzed the impact of local floral neighborhood density on pollination and reproduction of *A. aurea* in three populations in Nahuel Huapi National Park. My study involved analyses of the effect of density at two different geographic scales: comparisons between means per site (a scale of 5-12 hectares), and studies of floral neighborhood at smaller scales (meters). The latter scale is comparable to that of Aizen's study. Yet my results are strikingly different: whereas Aizen failed to find significant effects of density on pollination and reproduction, I found significant effects of density on conspecific pollen deposition and of conspecific pollen deposition on reproduction. I offer two possible explanations for this apparent contradiction. First, Aizen's measure of floral neighborhood differed from mine. Aizen used nearest neighbor distances (distance to the nearest neighbor, distance to the fifth nearest neighbor, and the geometric mean of the distances to the five nearest neighbors), whereas I used the square roots of the actual densities in concentric bands around the focal ramet. As I show in Appendix 1, my measure is more likely to detect contrasting densities, especially for populations with clumped spatial distribution. Thus, it is possible that the contradiction between Aizen's and my results is explained by the different methods used to quantify local floral neighborhood densities.

My second explanation has to do with the scale at which pollinators respond to variations in floral neighborhood density. Some pollinators respond to large-scale variations in floral density, but not variation at smaller scales. For example, Thomson (1981) found that bumblebees respond to variation in floral density in patches of >500 m^2 but not in smaller patches. As noted above, bumblebees are the main pollinators of *A. aurea*. Can this scale variance in bumblebee perception of floral density explain the contradiction between Aizen's and my results? The overall densities at each of Aizen's (1997) sites seem to be higher than the densities at my grazed sites, as can be inferred from the range of nearest neighbor distances observed by this author. In Aizen's study, distance to the nearest neighbor varied between 0.1 to 1.1 in the site with the highest density (Challhuaco in 1993) and 0.1 to 15 m in the site with the lowest density (Cerro Otto). In contrast, distance to the nearest neighbor varied between 0.05 and 18.94 m in Arroyo Goye and 0.01 to 52.97 m in Quetrihué. I found a saturation of the effect of density on pollen deposition (Fig. 5.9). Only sites at relatively low densities suffer from low pollination levels, whereas the relationship between density and pollen deposition reaches a plateau at higher densities. Thus, I expect to find a stronger effect of local neighborhood density when overall (site) density is low. In fact, it is in the grazed site with the lowest mean density (Mascardi) that the relationship between neighborhood density and conspecific pollen deposition is strongest, and it is in the grazed site with the highest mean density (Arroyo Goye) that this relationship is weakest. I propose that the effect of local floral density on pollination and reproduction depends on the larger-scale density at entire sites and that it will be only at low overall densities that floral neighborhood density will affect pollination and reproduction.

The path analyses at two different scales provide insights about effects of plant population density on pollination and reproduction. The among-site path analysis indicates that density has a strong, direct effect on pollen deposition and a strong indirect effect of density on reproduction. Magnitudes of these effects are surprisingly high, given the small sample size of this analysis. As I pointed out above, the lack of statistical significance in some of these effects is probably due to the low power of the analysis resulting from this sample size rather than to a true lack of effect. Conversely, the within-site path analysis also suggests that density directly affects conspecific pollen deposition and that it indirectly affects reproduction, although the magnitudes of these effects are smaller than for the among-site analysis. Density seems to have strong effects at the contrasting densities observed among the eight sites, but it seems less important within each of the sites, where the local variation in density is smaller. Thus, this difference between the magnitudes of the path coefficients at the two scales suggests that density effects on pollination and reproduction may be scale-dependent.

Synthesis: a model of the indirect effect of cattle on the pollination and reproduction of A. aurea

Fig. 5.16 depicts a graphical model summarizing the effects found in my study. In this model, cattle negatively affect *A. aurea* directly through trampling (continuous arrow going from "introduced ungulates" to "*Alstroemeria aurea*" in Fig. 5.16). This negative effect on *A. aurea* does not result in a positive effect for ungulates (ungulates do not benefit from trampling on *A. aurea*). Cattle do feed on other plants in the same community (Table 5.7). Since these other species are supporting the cattle population, they have a negative indirect effect on *A. aurea* (represented by a dashed arrow going from other plant species to *A. aurea*). The decreased density of *A. aurea* negatively affects its interaction with pollinators; by this I mean a negative effect on the quality of the interaction (i.e., how much pollen individual pollinators deposit on flower stigmas), but not necessarily on the quantity (i.e., pollinator visitation frequency). This is because pollinators bring less conspecific pollen and more heterospecific pollen than at higher densities. Thus, by directly decreasing the population density of *A. aurea*, cattle indirectly affect the interaction between *A. aurea* and its pollinators (represented in Fig. 5.16 by a dashed arrow going from cattle to the arrows between *A. aurea* and its pollinators). Finally, this decreased pollination quality results in lower reproductive performance in *A. aurea*.

As I pointed out in the introduction, the model I am proposing for the effects of ungulates on *A. aurea* differs from previous models of indirect effects of herbivores on plant reproduction. To my knowledge, all previous models involved herbivores directly affecting individual plants by affecting their floral traits. In contrast, my model does not require any effect at the individual level on the plant's vegetative or reproductive traits. Rather, it involves an effect at the population level through a direct effect on mortality: some individuals in the population are killed by trampling, and those that escape this effect are the ones that suffer from the indirect effect, even though they are not affected by herbivores.

Paraphrasing the quote by Hendrix (1988) cited at the outset of this paper, I conclude that, given the ubiquitous presence of herbivores and their ability to decrease plant population density, it is surprising that herbivore-induced decreased population density has not been previously recognized as having a significant impact on the reproductive ecology of plants.

Conservation implications

The temperate forest of the southern Andes is rich in endemism. For example, 34% of the plant genera and three plant families present in this biogeographic region are endemic (Arroyo et al. 1996). This high degree of endemicity is also observed in other groups, such as amphibians (Duellman 1999), bees (Michener 1979) and coleopterans (Morrone and Roig-Juñent 1995). The temperate forest also has one of the highest incidences of animal pollination and seed dispersal known for any temperate ecosystem (Armesto and Rozzi 1989; Aizen and Ezcurra 1998; Aizen et al. 2002). In Chile, the temperate forest has undergone alarming rates of deforestation (Armesto et al. 1998). Although in Argentina the magnitude of deforestation has been lower, introduced species and anthropogenic fires constitute a major conservation threat (see Chapter 3, and Veblen and Alaback 1996; Veblen et al. 1999; Aizen et al. 2002).

Previous studies of the effects of introduced ungulates have dealt mainly with the 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 (see Chapter 3). My study is the first to demonstrate that subtler indirect effects can also occur, although this effect was manifested in only one of thirteen species.

The observed effects on *A. aurea* could be occurring beyond the limited geographic range of this study. In Nahuel Huapi National Park, cattle occupy 56% of the area suitable for them (Lauría Sorge and Romero 1999); although no similar estimates exist for the area occupied by introduced deer, the combined area occupied by deer and cattle is surely larger than 56%. Furthermore, this problem is not restricted to the Nahuel Huapi region: introduced ungulates occupy extensive areas in both Argentina and Chile (Navas 1987; Bonino 1995; Jaksic 1998; Jaksic et al. 2002). Although my study dealt only with the impact of cattle, it is likely that other introduced ungulates (e.g., 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, personal observation).

Effects of introduced ungulates could cascade to other species in the system. For example, animal pollinators could be affected by the decreased abundance of their floral resources. Some of the plant species negatively affected by introduced ungulates are likely to be important resources for the guild of flower-visiting insects. *A. aurea* seems particularly important: it is the species in my study with the highest number of flower visitors (see Chapter 2). *A. aurea* is virtually the only insect-pollinated plant flowering in the summer in the *Nothofagus dombeyii* forest, and many of the insect species recorded visiting *A. aurea* seem not to visit other species. Thus, the decreased abundance of *A. aurea* in grazed sites could negatively affect the assemblage of flower visitors.

6

HIDING FROM HERBIVORES: THE ROLE OF SPATIAL REFUGES AND FLORAL NEIGHBORHOOD DENSITY ON POLLINATION AND REPRODUCTION OF *ARISTOTELIA CHILENSIS*

Abstract. Introduced herbivores can drastically reduce plant abundance through trampling and browsing. For animal-pollinated plants, this decreased abundance can in turn affect reproductive performance through a decreased frequency of interaction with pollinators—a density-mediated indirect effect. However, the existence of "refuges" where plants avoid herbivores can minimize this effect if these refuges house groups of individuals dense enough to attract pollinators. I studied this problem in the understory tree *Aristotelia chilensis* (Eleocarpaceae). *A. chilensis* is dioecious and depends on its almost-exclusive pollinator *Cadeguala albopilosa* (Hymenoptera: Colletidae) for reproduction. The population density of *A. chilensis* drastically declines in sites with cattle, yet there is no detectable effect on its reproductive performance. I hypothesized that this lack of effect was due to spatial aggregation of flowering individuals in refuges where individuals can escape herbivores, attaining local densities high enough to attract pollinators and reproduce successfully. To test this hypothesis I studied spatial distribution, floral neighborhood density, pollination levels and fruit set of *A. chilensis* in four grazed sites. I found an association between the density of flowering neighbors and female reproductive performance. The relationship between density of neighbors and reproductive performance was positive in two sites, negative in another, and unsignificant in the remaining site. Furthermore, when data for all sites were pooled, a significant second-order polynomial relationship between density and reproduction was found, so that individuals at intermediate densities tended to attain higher reproductive performance than individuals at low and high densities. The mechanisms leading to this effect of density on reproduction are unclear and may include resource competition and pollination limitation. Further studies are needed to understand whether either of these factors, or both, are responsible for the observed effect.

INTRODUCTION

In the preceding chapter I hypothesized that, under some conditions, herbivores affect pollination and plant reproduction indirectly by decreasing plant population abundance. I presented evidence that this kind of indirect effect occurs in the herb *Alstroemeria aurea*. The population density of the herb *Alstroemeria aurea* decreases in the presence of cattle, and this decreased density leads to decreased pollination and reproductive performance. However, I failed to find such an effect in other species whose population density was also strongly affected by cattle.

Probably the most striking lack of indirect effects of cattle on reproduction is in the understory tree *Aristotelia chilensis* (Eleocarpaceae). This species showed the strongest decline in response to cattle, yet there was no effect on pollinator visitation, pollination, or reproduction. *A. chilensis* is a preferred food item for both introduced deer (Veblen et al. 1989; Veblen et al. 1992; Relva and Caldiz 1998) and cattle (see Table 7 in previous chapter; see also Veblen et al. [1992b]), and thus its decreased abundance in grazed sites is probably explained by the direct effect of browsing. Furthermore, this species is dioecious, which should exacerbate Allee effects resulting from low population density (see Fig. 5.1; see also House 1992, 1993; Kunin 1997). Another characteristic that can make this species more vulnerable to low population density is the fact that, at least in my sites, it is pollinated almost exclusively by one bee species, the colletid *Cadeguala albopilosa*. Here I present a hypothesis to explain that lack of effect and test it using spatial data on pollination and reproduction of *Aristotelia chilensis*.

It has been long recognized that spatial refuges can play an important role in determining the outcome of species interactions. Host refuges can stabilize host-parasitoid systems (Hassell and May 1974), and many examples of such stabilization exist in the biological control literature (e.g., Udayagiri and Welter 2000). Similarly, spatial refuges where plants can avoid herbivores favor their coexistence. In many cases, refuges are physical features of the environement. For example, pocket gophers (*Thomomys bottae*) strongly affect the distribution of aspen (*Populus tremuloides*) in northern Arizona. In the presence of pocket gophers, aspen are restricted to rock outcrops, a habitat not used by pocket gophers (Cantor and

Whitham 1989). And in deciduous forests in the eastern United States, individuals of the herb *Maianthemum canadense* growing on large boulder tops can escape the effects on morphology and shoot demography produced by white-tailed deer (*Odocoileus virginianus*; Rooney 1997). In other cases, herbivory-resistant species may act as a refuge for herbivory-susceptible species. For example, the small cacti *Mammillaria microcarpa* and *Echinocereus englemannii* growing under larger tree-like cacti escape the negative effects of mammalian herbivores in North American Sonoran desert (McAuliffe 1984).

The hypothesis presented in the previous chapter implicitly assumed a "mean field" population density, homogeneous across the landscape. However, the existence of refuges where plants can escape herbivores may generate heterogeneity in the spatial distribution of density. This spatial heterogeneity may have important consequences for the hypothesis presented in the previous chapter. Specifically, if refuges harbor local densities of flowering individuals high enough to attract pollinators, the detrimental effect of decreased population density could be minimized. I hypothesize that the lack of an indirect effect of cattle on the reproduction of *Aristotelia chilensis* results from the high spatial aggregation of flowering individuals in refuges where they can attain high local densities, thus attracting enough pollinators to reproduce succesfully. For this hypothesis to be true, a relationship between local density of flowering individuals and reproductive success must exist, so that female individuals growing at high local densities reproduce more successfully than females at low local densities.

Here I show that individuals of *A. chilensis* are aggregated in spatial refuges and test the prediction that reproductive success of *A. chilensis* is positively related to density of flowering individuals.

METHODS

Plant species and its pollinators

Aristotelia chilensis (Eleocarpaceae) is an evergreen understory tree in the temperate forest of the southern Andes, extending north to central Chile. It flowers profusely during the late spring (see Fig. 5.14). Its main pollinator in the study area is the bee *Cadeguala albopilosa* (Hymenoptera, Colletidae), although it is also visited by other bee species, especially *Ruizantheda mutabilis* (Hymenoptera, Halictidae). *C. albopilosa* is not restricted to *A. chilensis*. In my study sites *C. albopilosa* also visits flowers of another understory tree, *Schinus patagonicus* (of the total number of visits by *Cadeguala albopilosa* recorded in 1999, 60% were to *A. chilensis* and 40% to *S. patagonicus*). *S. patagonicus* failed to flower in the spring of 2000, when I conducted the field study reported here. Therefore, *C. albopilosa* behaved as a specialist pollinator.

Field methods

The study was conducted in the four grazed sites described in previous chapters (Cerro López, Arroyo Goye, Lago Mascardi, and Península Quetrihué). All flowering individuals in each population were mapped (Fig. 6.1) by taking linear distance with a measuring tape and the angular deviation from the north with a hand compass from known points taken from a previous topographic map. Density of flowering neighbors was calculated as described in the Appendix 1. Both male and total (i.e., male and female) densities of flowering neighbors were calculated.

Pollinator visitation, pollen deposition in flower stigmas, and reproduction were studied as described in the previous chapter. I collected 5 pistils per plant at a given time. Because unpollinated senescent flowers fall rapidly from branches, and because pollinated senescent flowers rapidly lose the pistil, I collected fresh female flowers for quantifying pollen deposition in stigmas. Since it was not possible to determine flower age, my pollen counts may not accurately represent total pollen receipt throughout the entire receptive phase of the flower. Only conspecific pollen grains were considered for the analysis, because the number of heterospecific pollen grains deposited in stigmas was extremely low (see previous chapter). Three reproductive variables were measured: fruit set (proportion of tagged flowers that set fruit), seeds per fruit, and seeds per flower (mean number of seeds produced per tagged flower).

Statistical methods

I used randomization techniques to test whether the spatial arrangement of flowering individuals in each population differed from the random distribution. To this end I wrote a computer algorithm in Matlab (MathWorks 1999) that calculated the density of flowering neighbors around each individual in the population (as described in Appendix 1) and then calculated the mean and the standard error of the density in each 1 m band between 1 and 50 m from the focal individual. The algorithm then randomized 100 times

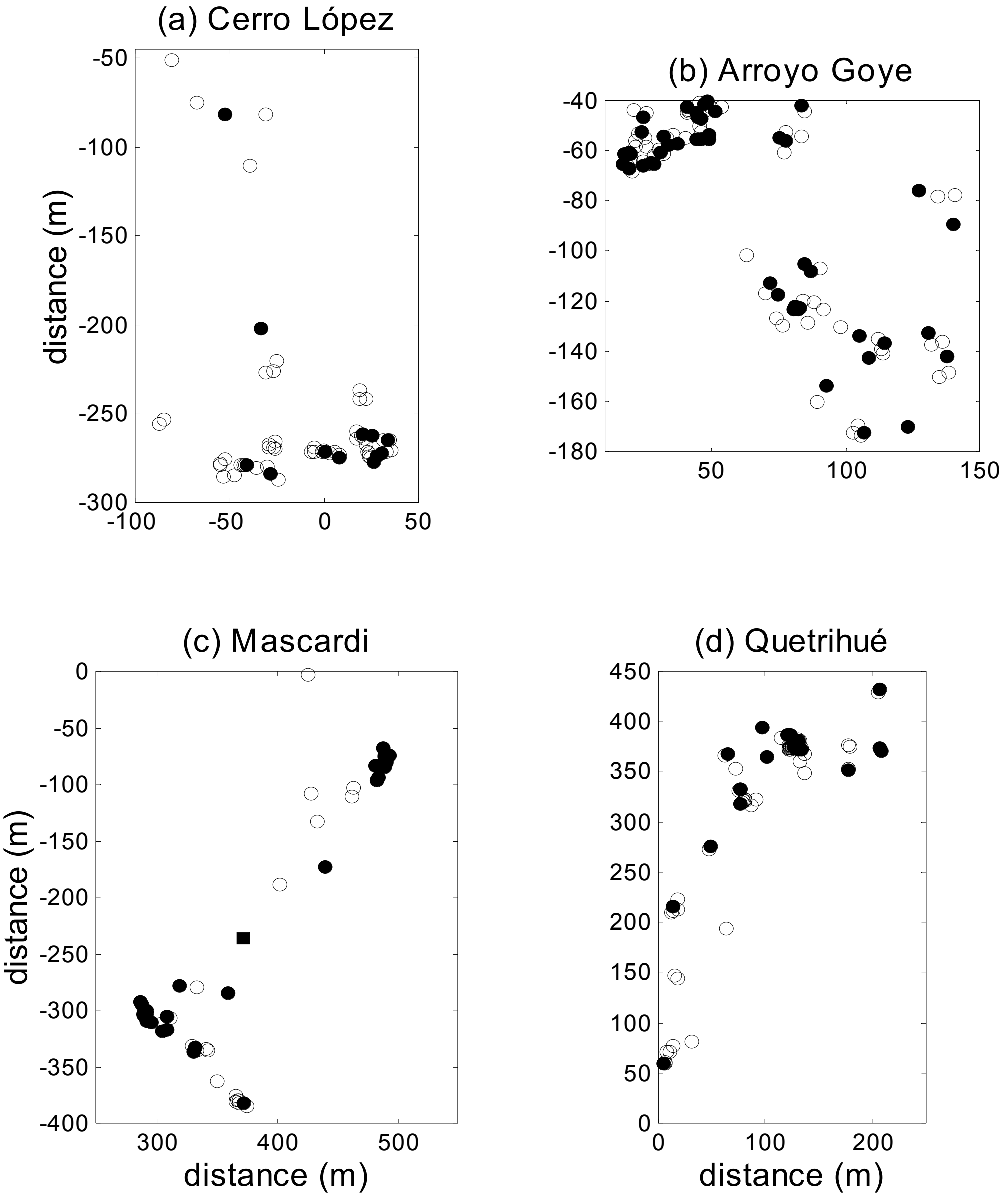


Figure 6.1. Maps showing distribution of individuals of *A. chilensis* in four study sites. Black circles represent females, white circles males. The black square in Mascardi represents a group of 9 unsexed individuals that could not be approached because they were in the middle of a large patch of the spiny shrub *Rosa eglanteria*.

the location of the flowering individuals and then calculated the mean and confidence intervals of the density per band for the 100 iterations. In a randomly distributed population, density of neighbors is expected to remain constant as distance increases. However, because the area of the concentric bands increases with increasing distance from the focal individual, the confidence intervals around that mean are expected to be broader at shorter distances owing to sampling effects. In contrast, in an aggregated distribution, density of neighbors at short distances is expected to be high, and density should decrease with increasing distance. However, with real, discrete objects, there is a minimum separation distance between any two objects (e.g., two plants cannot be in *exactly* the same spot), so density of neighbors should increase rapidly at extremely short distances and then show a monotonic decrease as distance increases.

To test whether the mean number of pollinator visits per flower and the mean number of flowers per individual differed between males and females, I used *t*-tests run in the TTEST procedure in SAS (SAS Institute 1999). Because of unequality of variances, I used Statterthwaite's *t* for unequal variances given by the TTEST procedure.

The low overall population density in the four sites resulted in few female individuals available to conduct the study. This low sample size precluded the use of formal structural equation selection procedures to compare alternative causal models. Most model selection criteria used in structural equation modeling are sensitive to sample size, becoming unreliable at low sample sizes (Shipley 2000). Instead, I used correlation analysis to explore the degree of association among variables hypothesized to be causally linked and then used regression analysis to test whether the hypothesized predictor variables accurately predicted the hypothesized response variable. I used simple linear regression to study the effect of total and male neighborhood density on the three reproductive variables in each site, and second-order polynomial regression (i.e., $y = \beta_0 + \beta_1 x + \beta_2 x^2$) to test for a humpback-shaped relationship between density and reproduction with pooled data for all sites. The CORR and REG procedures in SAS (SAS Institute 1999) were used to perform correlation and regression analysis, respectively.

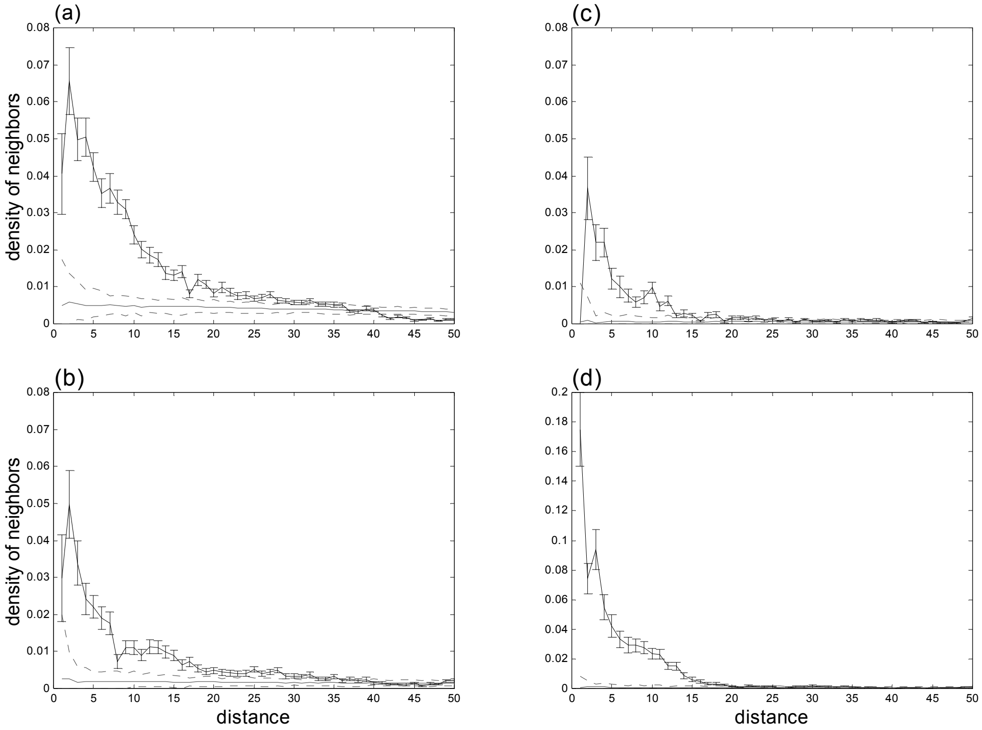


Figure 6.2. Results from randomness test. In each graph, the upper, continuous line represents mean distance of neighbors per site at increasing distances from focal individual. Error bars represent standard deviations of mean. The three dashed lines correspond to mean (central line) and confidence interval of mean (upper and lower lines) of 100 randomizations of the data. (a) Arroyo Goye. (b) Cerro López. (c) Mascardi. (d) Quetrihué.

RESULTS

Hiding from herbivores?—spatial distribution of flowering individuals

Neighborhood density around each flowering individual exceeded the random expectation at short distances for the four sites (15-35 m, depending on the site; Fig. 6.2). The mean density for the observed data eventually crossed the mean for the randomized data at greater distances from the focal individual. As described in the Methods, this pattern indicates that the distribution of flowering individuals in the four populations was significantly more aggregated than the random expectation.

All aggregations of a large number of individuals were associated with places inaccessible to cattle. In Cerro López, the area with high density of flowering individuals (lower part of Fig. 6.1a) was an extremely steep slope (the piedmont of Mount López). In Arroyo Goye, high densities of flowering individuals were associated with a spring bed (lower right corner of Fig. 6.1b) and with a flat area surrounded by thick vegetation and steep slopes (upper left corner of Fig. 6.1b). In Mascardi, the two areas with high local densities of flowering individuals were spring beds surrounded by extremely steep slopes (upper right and lower left corners of Fig. 6.1c); the other high density patch (indicated with a black square in Fig. 6.1c) was in the middle of a large thicket of eglantine rose (*Rosa eglanteria*). This rose forms large, thorny thickets usually unbrowsed by cattle (see Table 5.7) and has been hypothesized to facilitate regeneration of browsing-susceptible species under high densities of introduced ungulates (De Pietri 1992). Finally, in Quetrihué, the two patches with the highest density (upper middle part of Fig. 6.1d) were surrounded by fallen trees, thick patches of juveniles of *Nothofagus dombeyii*, and a thick patch of arrayán (*Luma apiculata*), a shrub particularly abundant in Quetrihué.

Therefore, individuals are highly aggregated in space, and that aggregation is associated with specific "refuges"—sites inaccessible to cattle.

Sexual differences in pollinator visitation and flower production

Mean number of pollinator visits per flower did not differ statistically between females and males, although there was a trend towards lower visitation frequency in females (Fig. 6.3a). Flower production in females was significantly lower than in males (Fig. 6.3b). This suggests that pollinator visitation frequency per individual plants (frequency of visits per flower × number of flowers per plant) is greater for males than for females.

Testing the hypothesis: effect of floral neighborhood density on the reproduction of A. chilensis

Total and male density were highly correlated in two sites, Cerro López and Arroyo Goye, but not in the other two (Table 6.1).

There were no significant correlations between total or male density and pollinator visitation frequency per flower in any of the sites (Table 6.1). In turn, pollinator visitation frequency was not significantly correlated with pollen deposition nor with fruit set (Table 6.1).

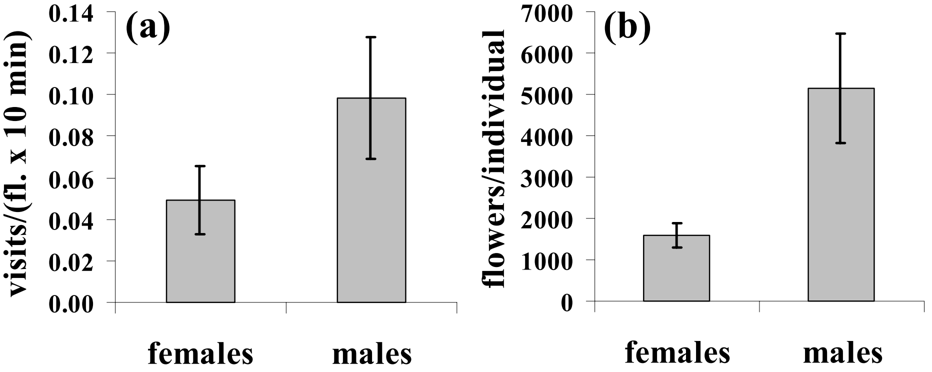


Figure 6.3. (a) Mean number of pollinator visits per flower for each sex in *Aristotelia chilensis* (d.f. = 101; *t* = 1.46; *P* = 0.1467). (b) Mean number of flowers per individual number of *A. chilensis* (d.f. = 137; *t* = 2.64; *P* = 0.0110).

Table 6.1. Correlation coefficients among total density (D_t), male density (D_m), pollinator visitation frequency per flower (visits), pollen deposition in flower stigmas (pollen), and three reproductive variables (fruit set [fr], seeds per fruit [s/fr], and seeds per flower [s/fl]). For each correlation coefficient, statistical significance (*P*-value) and sample size are given. Statistically significant correlation coefficients in bold. The lines for pollinator visitation in Mascardi indicate correlation coefficients that could not be calculated because no pollinators were observed during the observation periods.

Site	Variable	Statistic	D_m	visits	pollen	fr	s/fr	s/fl
Cerro López	D_t	*r*	**0.97**	-0.12	0.58	**0.85**	0.33	**0.72**
		P	<0.0001	0.5527	0.1016	0.0010	0.3189	0.0131
		n	12	27	9	11	11	11
	D_m	*r*		-0.41	0.44	**0.82**	0.23	**0.66**
		P		0.4958	0.2302	0.0019	0.5055	0.0283
		n		5	9	11	11	11
	visits	*r*			0.44	-0.08	-0.51	-0.23
		P			0.5590	0.8936	0.3881	0.7116
		n			4	5	5	5
	pollen	*r*				0.62	0.37	0.65
		P				0.1015	0.3720	0.0783
		n				8	8	8
	fr	*r*					0.59	**0.95**
		P					0.0588	<0.0001
		n					11	11
	s/fr	*r*						**0.80**
		P						0.0032
		n						11
Arroyo Goye	D_t	*r*	**0.91**	0.28	0.30	**0.43**	**0.50**	**0.45**
		P	<0.0001	0.2131	0.2066	0.0191	0.0041	0.0105
		n	36	21	20	29	31	31
	D_m	*r*		0.45	0.35	**0.52**	**0.50**	**0.54**
		P		0.1670	0.1307	0.0039	0.0039	0.0017
		n		11	20	29	31	31
	visits	*r*			-0.49	0.12	0.26	0.18
		P			0.2614	0.8043	0.5807	0.6975
		n			7	7	7	7
	pollen	*r*				-0.10	0.22	-0.02
		P				0.7418	0.4165	0.9456
		n				14	16	16
	fr	*r*					**0.60**	**0.90**
		P					0.0004	<0.0001
		n					31	31
	s/fr	*r*						**0.85**
		P						<0.0001
		n						31

Table 6.1, continued.

Site	Variable	Statistic	D_m	visits	pollen	fr	s/fr	s/fl
Mascardi (c)	D_t	*r*	0.35	—	-0.28	0.16	0.21	0.04
		P	0.0810	—	0.2194	0.4667	0.3854	0.8746
		n	25	17	21	23	19	21
	D_m	*r*		—	0.16	0.33	0.46	0.40
		P		—	0.4854	0.1332	0.053	0.0849
		n		10	21	22	18	20
	visits	*r*			—	—	—	—
		P			—	—	—	—
		n			9	8	9	9
	pollen	*r*				-0.04	0.23	0.08
		P				0.8603	0.3864	0.7586
		n				19	16	17
	fr	*r*					0.22	**0.93**
		P					0.3715	<0.0001
		n					19	21
	s/fr	*r*						**0.61**
		P						0.0052
		n						19
Quetrihué (c)	D_t	*r*	0.30	0.03	-0.29	-0.31	-0.20	-0.21
		P	0.1154	0.8808	0.2730	0.1954	0.4357	0.4129
		n	28	33	16	19	18	18
	D_m	*r*		-0.02	-0.12	-0.21	-0.33	-0.44
		P		0.9355	0.6697	0.3992	0.1813	0.0711
		n		15	16	19	18	18
	visits	*r*			-0.53	-0.60	0.49	0.34
		P			0.2182	0.0850	0.1515	0.3408
		n			7	9	10	10
	pollen	*r*				0.53	-0.32	-0.26
		P				0.0733	0.2874	0.3958
		n				12	13	13
	fr	*r*					**0.72**	**0.93**
		P					0.0007	<0.0001
		n					18	18
	s/fr	*r*						**0.91**
		P						<0.0001
		n						18

Table 6.2. Simple linear and polynomial regressions of pollen deposition in stigmas *vs*. total (D_t) and male (D_m) density of flowering neighbors. For each regression model, parameter values (the intercept and slopes for first and second order terms) are given, as well as fit statistics for the model. *P*-values in bold indicate statistically significant models (at $\alpha = 0.05$).

				Parameter			Model fit statistics		
Indep. var.	Site	Model	n	Int.	x	x^2	R^2	F	P
sqrt(D_m)	Cerro López	Simple linear	9	-220.66	277.67		0.21	1.9	0.2092
		Polynomial	9	-6613.09	11731.00	-5105.61	0.83	14.4	**0.0051**
	Arroyo Goye	Simple linear	20	-92.46	172.10		0.12	2.4	0.1385
		Polynomial	20	-220.15	401.37	-102.39	0.12	1.1	0.3443
	Mascardi	Simple linear	21	-139.12	174.50		0.03	0.5	0.4854
		Polynomial	21	13774.00	-26541.00	12813.00	0.12	1.2	0.3293
	Quetrihué	Simple linear	16	101.38	-27.67		0.01	0.2	0.6926
		Polynomial	16	2.83	137.50	-68.40	0.01	0.1	0.9213
	All (pooled)	Simple linear	66	-37.26	98.07		0.06	3.8	0.0543
		Polynomial	66	-1740.85	3052.37	-1266.72	0.19	7.5	**0.0012**
sqrt(D_t)	Cerro López	Simple linear	9	-288.37	334.23		0.35	3.8	0.0924
		Polynomial	9	-6316.93	11156.00	-4828.64	0.81	13.2	0.0064
	Arroyo Goye	Simple linear	20	1.51	79.73		0.07	1.7	0.2091
		Polynomial	20	-334.13	634.30	-225.76	0.10	0.9	0.4161
	Mascardi	Simple linear	21	230.51	-171.52		0.08	1.6	0.2194
		Polynomial	21	-3979.14	7540.62	-3523.89	0.18	2.0	0.1655
	Quetrihué	Simple linear	16	132.72	-47.74		0.08	1.3	0.2769
		Polynomial	16	-335.07	697.02	-288.43	0.15	1.1	0.3491
	All (pooled)	Simple linear	66	43.53	22.95		0.01	0.5	0.4875
		Polynomial	66	-603.48	1061.36	-408.13	0.07	2.2	0.1177

Pollen deposition was not significantly correlated with total or male density in any site (Table 6.1). There is, however, a significant, polynomial relationship between number of pollen grains and male density in Cerro López, and the same pattern is observed when data for all sites are pooled (Fig. 6.4; Table 6.2). In turn, pollen deposition was only weakly ($P < 0.1$) positively correlated with fruit set in Quetrihué and with seeds per flower in Cerro López (Table 6.1). Significant correlations between pollen deposition and reproduction were found in no other case (Table 6.1).

Fruit set and seeds per flower were positively correlated with total and male density in two sites, Cerro López and Arroyo Goye, but not in the other two sites (Mascardi and Quetrihué; Table 6.1). In Arroyo Goye, seeds per fruit were also significantly correlated with total and male density. Thus, in two sites, females growing at greater densities of flowering individuals reproduce more successfully than females growing at lower population densities. To test whether density of neighbors accurately predicts pollinationand reproduction, I used simple linear and polynomial regressions. Results are presented in Table 6.3 and Figs. 6.5 and 6.6. There is a significant effect of density of neighboring males on fruit set in three sites. Reproduction linearly increases with density of males in Cerro López and Arroyo Goye (Fig. 6.5a,d) and linearly decreases with density in Quetrihué (Fig. 6.5j). In the remaining site, Mascardi, there was a trend towards greater fruit set at greater densities of neighboring males, but that trend was not significant (Fig. 6.5g; Table 6.3). Seeds per fruit increased with density of neighboring males in Arroyo Goye (Fig. 6.5e), and there was a similar trend in Mascardi, although the latter trend was only marginally significant (Fig. 6.5h; Table 6.3). No significant relationship between male density and seeds per fruit was found in the other two sites (Fig. 6.5b,k). Finally, seeds per flower increased with male density in Cerro López and Arroyo Goye (Fig. 6.5c,f). There was a trend towards more fruits per flower with increasing male density in Mascardi and the opposite trend in Quetrihué, but those trends were only marginally significant (Fig. 6.5i,l).

Table 6.3. Simple linear and polynomial regressions of the three reproductive variables (fruit set [fr], seeds per fruit [s/fr], and seeds per flower [s/fl]) *vs*. total (D_t) and male (D_m) density of flowering neighbors. For each regression model, parameter values (intercept and slopes for first and second order terms) are given, as well as fit statistics for the model. *P*-values in bold indicate statistically significant models (at $\alpha = 0.05$).

					Parameter			Model fit statistics		
Dep. var.	Indep. var.	Model	Site	*n*	Int.	*x*	x^2	R^2	*F*	*P*
fr	sqrt(D_m)	Simple linear	Cerro López	11	-3.07	3.28		0.68	19.5	**0.0017**
			Arroyo Goye	31	-0.63	1.16		0.22	8.3	**0.0074**
			Mascardi	22	-3.42	3.97		0.11	2.5	0.1332
			Quetrihué	18	1.54	-0.67		0.22	4.5	**0.0494**
		Polynomial	All (pooled)	82	-8.92	16.12	-6.68	0.16	7.8	**0.0008**
	sqrt(D_t)	Simple linear	Cerro López	11	-2.94	3.13		0.72	23.0	**0.0010**
			Arroyo Goye	31	0.00	0.56		0.14	4.6	**0.0401**
			Mascardi	22	-0.35	0.90		0.03	0.6	0.4667
			Quetrihué	18	0.95	-0.17		0.04	0.7	0.4032
		Polynomial	All (pooled)	82	-3.70	6.71	-2.51	0.12	5.5	**0.0057**
s/fr	sqrt(D_m)	Simple linear	Cerro López	11	0.69	2.00		0.05	0.5	0.5055
			Arroyo Goye	31	-1.98	4.16		0.25	9.8	**0.0039**
			Mascardi	18	-6.45	9.56		0.21	4.4	0.0530
			Quetrihué	18	6.06	-2.06		0.11	2.0	0.1813
		Polynomial	All (pooled)	78	-11.35	24.05	-9.87	0.05	1.8	0.1686
	sqrt(D_t)	Simple linear	Cerro López	11	-0.17	2.74		0.11	1.1	0.3189
			Arroyo Goye	31	-0.41	2.53		0.25	0.7	**0.0041**
			Mascardi	19	5.72	-2.09		0.04	0.8	0.3854
			Quetrihué	18	4.49	-0.70		0.04	0.6	0.4357
		Polynomial	All (pooled)	79	4.74	-3.20	1.51	0.02	0.7	0.4955
s/fl	sqrt(D_m)	Simple linear	Cerro López	11	-8.82	9.54		0.43	6.8	**0.0283**
			Arroyo Goye	31	-4.19	5.44		0.29	11.9	**0.0017**
			Mascardi	18	-11.16	13.44		0.16	3.2	0.1044
			Quetrihué	18	6.74	-3.34		0.19	3.7	0.0711
		Polynomial	All (pooled)	78	-25.47	48.43	-20.16	0.11	4.8	**0.0106**
	sqrt(D_t)	Simple linear	Cerro López	11	-9.09	9.70		0.51	9.5	**0.0131**
			Arroyo Goye	31	-1.48	2.79		0.21	7.5	**0.0105**
			Mascardi	19	-1.02	3.30		0.00	0.3	0.8746
			Quetrihué	18	3.88	-0.91		0.04	0.7	0.4129
		Polynomial	All (pooled)	79	-8.87	16.93	-6.28	0.06	2.3	0.1036

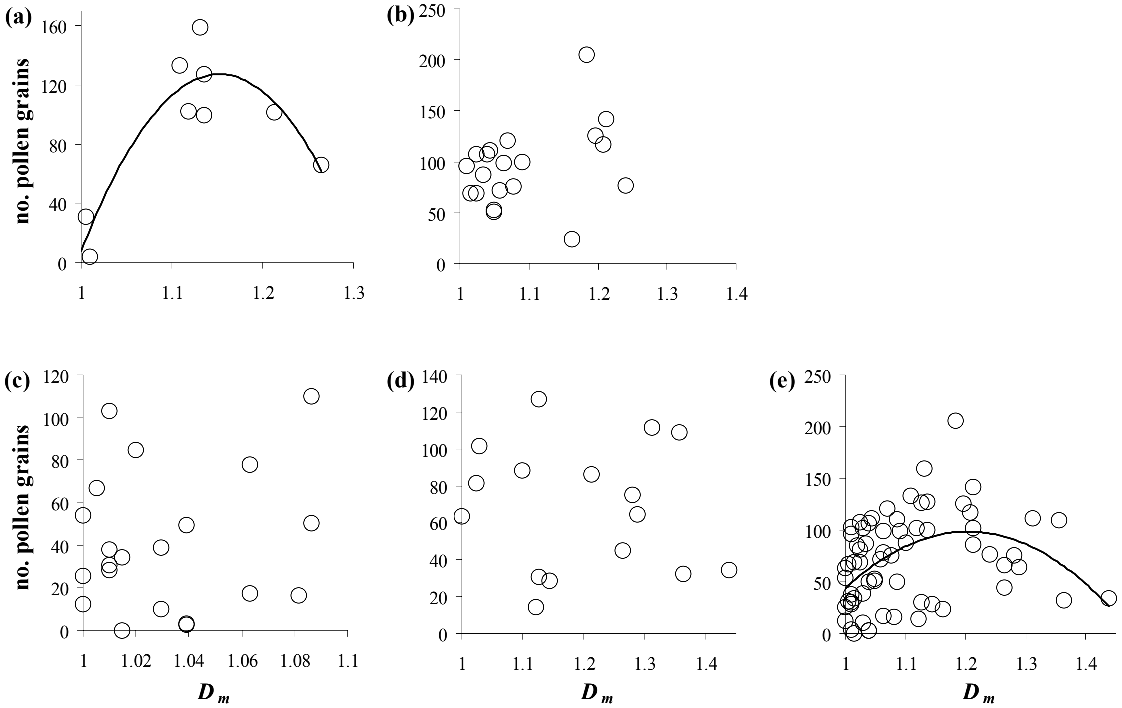


Figure 6.4. Pollen deposition in stigmas vs. D_m, estimate of neighborhood density of males (see Methods). (a) Cerro López. (b) Arroyo Goye. (c) Mascardi. (d) Quetrihué. (e) All sites (pooled data). See Table 6.2 for fit statistics. Only significant regression lines are shown.

Total density of flowering individuals had the same effect on the reproducitive variables as male density in the two sites where these two measures of population density were highly correlated (Cerro López and Arroyo Goye; Fig. 6.6a-f), although the effect of total density was generally weaker than the effect of male density (Table 6.3). In the other two sites, where both measures of population density were not highly correlated, total population density had no effect on any of the reproductive variables (Fig. 6.6g-l). Thus, density of neighboring males appears to have a stronger effect on the reproductive variables than total population density does.

The significant, negative effect of male density on fruit set and the downward trend in seeds per fruit and seeds per flower in Quetrihué suggest a decrease in reproductive performance at extremely high densities. In fact, Quetrihué is the site with the highest neighborhood densities (cf. values along the *x*-axis in Fig. 6.5j-l *vs*. Fig. 6.5a-i). As a way to test for this negative effect of high densities on reproduction, I used polynomial regression with data for all the sites pooled. With pooled data, there is a significant effect of male density on fruit set and seeds per flower (Fig. 6.7a,c) but not on seeds per fruit (Fig. 6.7b). On the other hand, total density affected fruit set (Fig. 6.8a), although this effect was weaker than for male density (Table 6.3), and total density had no effect on seeds per fruit or seeds per flower.

DISCUSSION

Results reported here suggest that spatial aggregation of flowering individuals of *A. chilensis* in refuges significantly affects reproductive success. However, the effect on reproduction was not always positive, as expected. Thus, it is unclear whether the observed lack of difference in reproductive success between grazed and ungrazed sites (chapter 5) can be explained by spatial aggregation of flowering individuals in refugia.

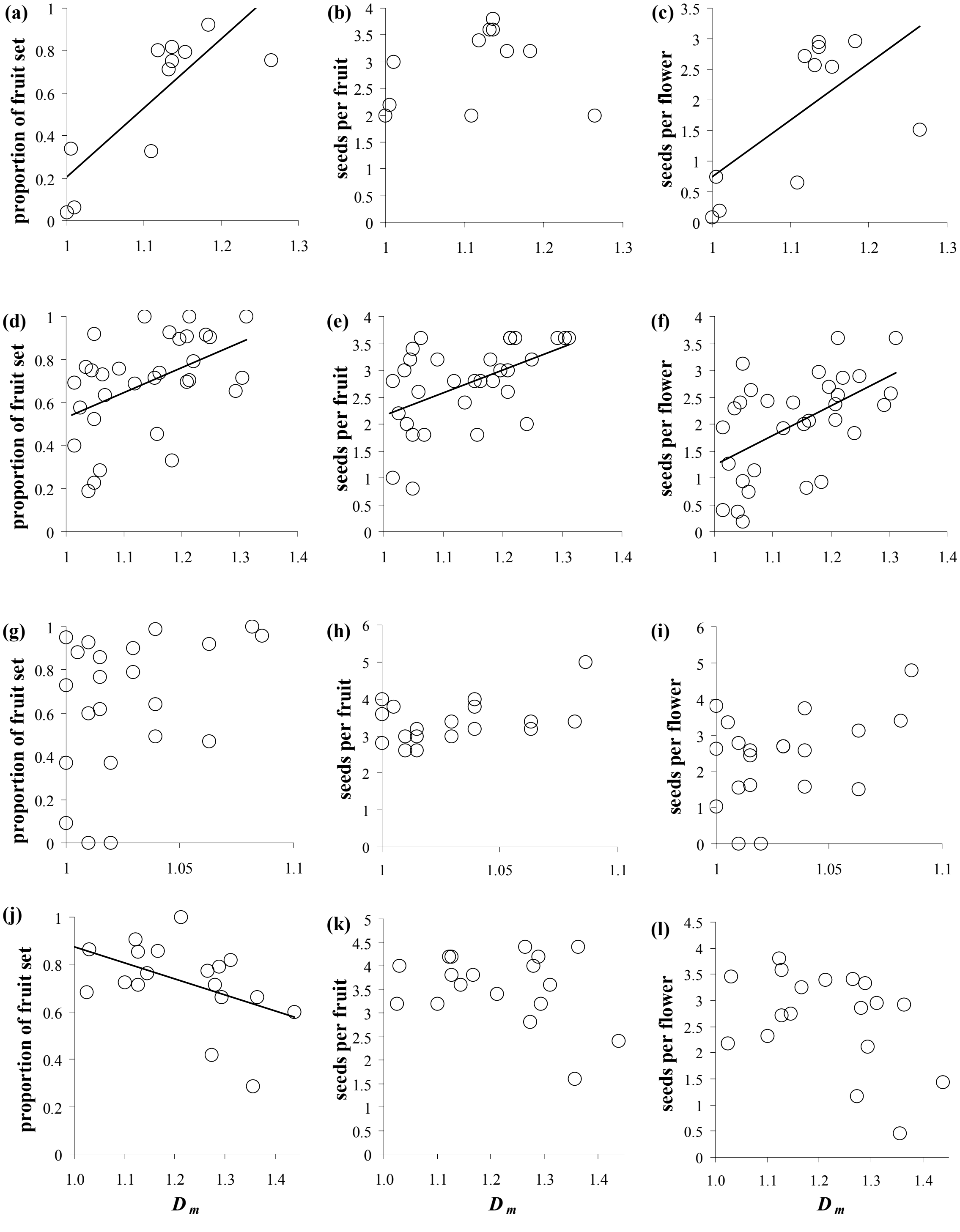


Figure 6.5. Fruit set vs. D_m, estimate of neighborhood density of males (see Methods), by site. (a) Cerro López. (b) Arroyo Goye. (c) Mascardi. (d) Quetrihué. See Table 6.3 for fit statistics. Only significant regression lines are shown.

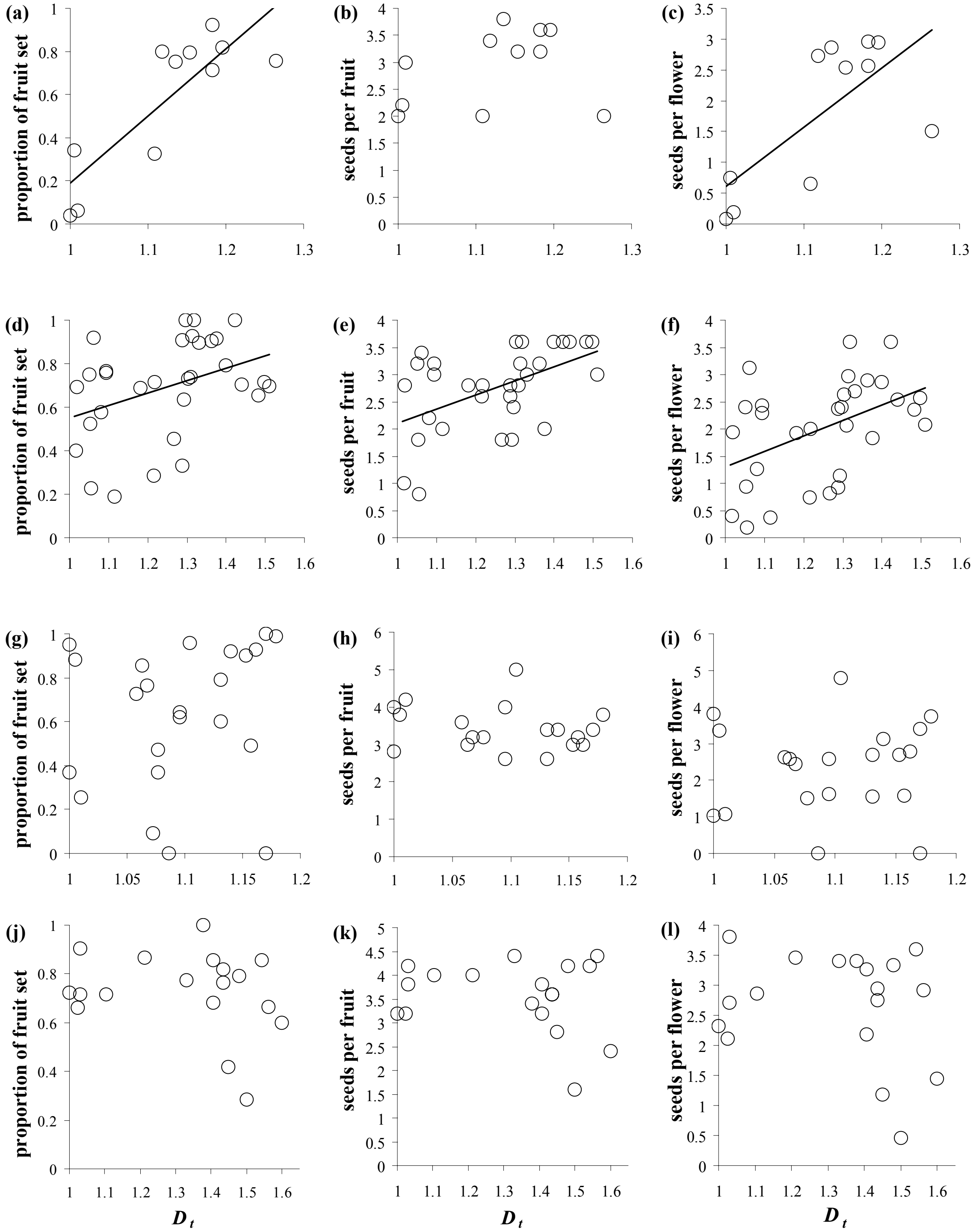


Figure 6.6. Fruit set vs. D_t, estimate of total neighborhood density (i.e., males and females; see Methods), by site. (a) Cerro López. (b) Arroyo Goye. (c) Mascardi. (d) Quetrihué. See Table 6.3 for fit statistics. Only significant regression lines are shown.

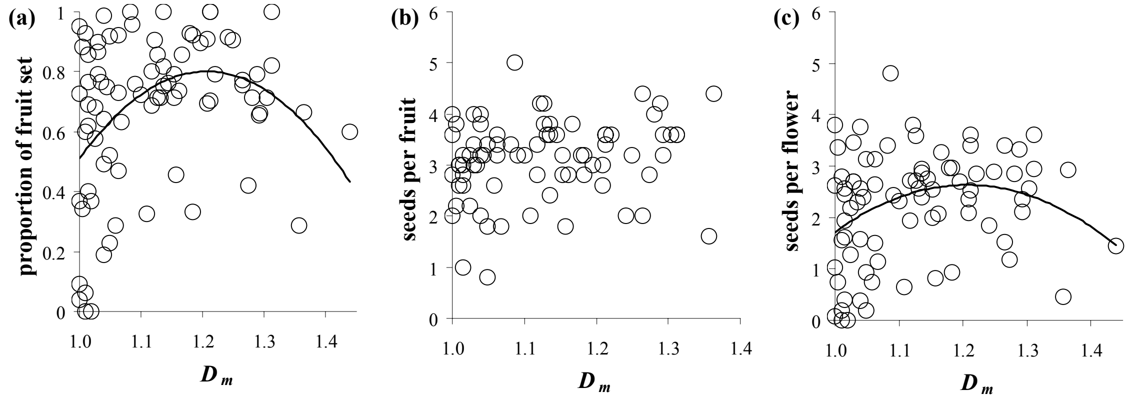


Figure 6.7. Fruit set vs. D_m, estimate of neighborhood density of males (see Methods), for data for all sites pooled. See Table 6.3 for fit statistics. Only significant regression lines are shown.

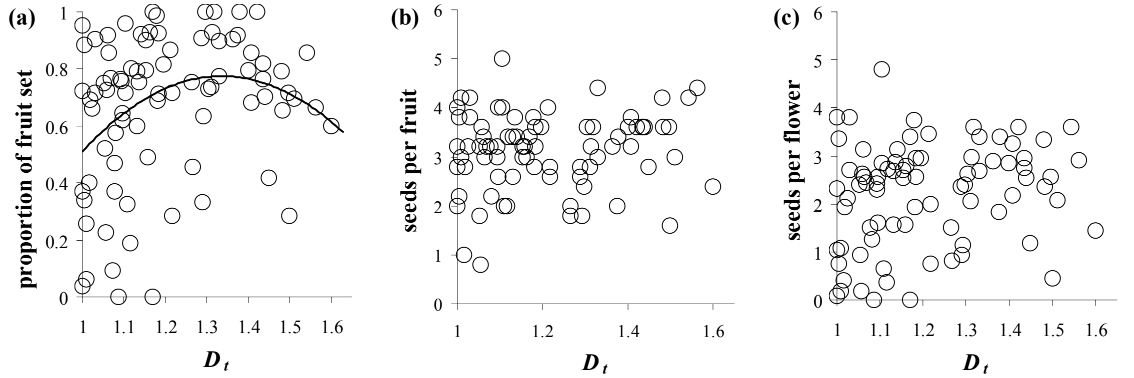


Figure 6.8. Fruit set vs. D_t, estimate of total neighborhood density (i.e., males and females; see Methods), for data for all sites pooled. See Table 6.3 for fit statistics. Only significant regression lines are shown.

It is surprising that there was no relationship between pollinator visitation frequency and density, or between pollinator visitation and pollen deposition. Even more surprising is the lack of relationship between the number of pollen grains deposited in flower stigmas and reproductive performance. This fact suggests no limitation of reproduction by pollination. However, it should be borne in mind that my quantification of pollination performance may not accurately represent pollination performance. I sampled 5 pistils per plant at one time; for a species that produces thousands of flowers maturing at different times over a month, the amount of pollen sampled in my study may simply have been too low. Furthermore, because it was impossible to determine a priori the age of flowers, my quantification of pollen receipt may not accurately represent total pollen receipt throughout the entire life of a flower. This fact may add to the natural variability of pollinator visitation, blurring any real effect of density on pollen receipt, and of pollen receipt on reproduction.

Density of flowering neighbors predicted the reproductive success of *A. chilensis*. However, this relationship was not the same in all sites. Whereas in Cerro López, Arroyo Goye and Mascardi there was at least a marginally significant effect of neighborhood density on the reproductive variables, the opposite relationship was found in Quetrihué. Furthermore, the polynomial regression on the pooled data for all sites suggests that, although there is a positive effect of neighborhood density at low and moderate densities, extremely high densities of flowering individuals may negatively affect reproduction.

The mechanisms accounting for this humped effect of density on reproduction are unclear. That male density had a stronger effect than total density on reproduction suggests that the mechanism responsible for the observed pattern has to do with pollination. Rathcke (1983) proposed that low to moderate densities of flowering neighbors would lead to increased reproductive success (i.e., facilitation), whereas extremely high densities of flowering neighbors are expected to lead to decreased reproductive success because of competition for pollinators—there are too many flowers for too few pollinators. Furthermore, many studies show that, although pollinators tend to visit more flowers and stay longer in larger floral patches, they tend to visit a smaller proportion of flowers in larger patches (see references in Goulson 2000). Thus, my finding that reproductive success decreases at greater densities is consistent with previous theory and data.

The facts that only a weak, insignificant effect of density on pollen deposition and no significant effect of pollen deposition on reproduction were found do not allow strong inference about the mechanism responsible for the observed effect on reproduction. As I discussed above, it may be that this lack of effect of density on pollination, and of pollination on reproduction, is due to the inaccuracy of my quantification of pollination rather than to a true lack of effect. However, taking for granted that reproduction is pollen-limited may lead to erroneous conclusions, since reproduction of many plants is limited by resources rather than pollen (Burd 1994). Since I did not conduct pollen supplementation experiments, it is not possible to know whether increased pollination in individuals with low reproductive performance would have led to greater reproductive success. Thus, the alternative explanation of resource limitation of reproduction cannot be excluded.

Regardless of the mechanism, density of flowering neighbors, and especially density of flowering males, appears to affect reproductive success of *A. chilensis*. We can now go back to the original question—whether the lack of indirect effects of cattle on the reproduction of *A. chilensis* can be explained by the greater reproductive success of individuals aggregated in spatial refugia. In Figs. 7a and 7c, it is clear that the few individuals with extremely low reproductive success (zero or near-zero fruit set and seeds per flower) are at very low densities. Those at extremely high densities, even though they tend to reproduce less successfully than those at moderate densities, do not reach the near-zero reproductive output observed in individuals at extremely low densities. However, the fact that a few isolated individuals fail to reproduce does not mean that all isolated individuals fail. As is clear from Figs. 7a and 7c, there is a broad spread in the reproductive output of isolated individuals, and many reproduce well. Therefore, it would be risky to conclude that my findings support the hypothesis that *A. chilensis* escapes the indirect effects of herbivory on reproduction because most remaining individuals are aggregated. All we can say is that all individuals whose reproductive success is zero or near-zero are at low floral neighborhood densities.

Even if we accept the results presented here as evidence that the negative effects of herbivory can be minimized by spatial aggregation of individuals, the long-term consequences of high spatial aggregation must be taken into account. That individuals can overcome the short-term effects of ungulate-induced decreased population density is not a panacea, however. The clumped distribution resulting from ungulate browsing could greatly increase inbreeding. For example, clumpling has been shown to decrease long-distance pollen flow in tropical, self-incompatible trees (Stacy et al. 1996). Thus, even though fitness of individuals in high-density patches may not be affected in the short term, long-term persistence could be affected if clumping is pronounced enough to prevent sufficient pollen flow.

7

SYNTHESIS

Es tan poco lo que sabemos
y tanto lo que presumimos
y tan lentamente aprendemos,
que preguntamos, y morimos.
– Pablo Neruda (1971)

In this monograph I have studied the interactions between plants and pollinators in the context of another ecological factor—herbivores. I wish now to revisit the results of the main chapters, attempting to synthesize the major findings.

I have shown in Chapter 2 that plants in Nahuel Huapi interact with a broad assemblage of pollinators. However, at least from what we can learn from patterns of frequency of interaction and from my rough estimate of pollinator effectiveness (see Chapter 4, Methods, and Appendix 4), a relatively small number of flower visitor species do most of the pollination. Likewise, a relatively small number of plant species provide a large proportion of the floral resources for the pollinators. Based on these findings, I suggested that relatively few flower visitor species are functionally important as pollinators, and, similarly, a relatively small proportion of plant species is functionally important as resources for flower visitors. This general lack of strong effects between pairs of species makes sense in light of what is known for other kinds of interactions. For example, most predator-prey interactions in food webs are weak, and only a few are strong (Paine 1992; Berlow et al. 1999).

In Chapter 4 I have shown that the details of the interactions between plants and pollinators, particularly the degree of mutual specialization, do not affect the response of species to the presence of cattle. One possible explanation I suggested for this lack of effect of interaction specialization was the relative importance of direct *vs*. indirect effects. Specifically, I suggested that, if the direct effect of disturbance (i.e., cattle) was stronger than the indirect effect through the resource, then it was likely that the direct effect would override any indirect effect, even if it existed. As the data presented in Chapter 5 suggest, cattle appear to have strong direct effects on several species through browsing or trampling. Furthermore, I also suggested that other kinds of indirect effects, involving other plant species, could also occur. For instance, the decreased abundance of *Tristerix corymbosus* in grazed sites could result from the decreased availability of its main host, *Aristotelia chilensis*. All these ecological factors could in conjunction make any real effect of plant-pollinator interactions irrelevant in determining the response of plant species to cattle.

Another possible explanation given above for the lack of effects found in Chapter 4 is that symmetrically specialized species (i.e., those with low *s* and low *p* values) were absent from the dataset, at least for the pollinators. Furthermore, I suggested that, if the relationship among specialization and response to cattle were non-linear, then symmetrically specialized species would be disproportionately more susceptible to disturbance; lacking those species from the dataset could make the detection of the relationship impossible, even if it existed. Renner (1998) suggested a similar idea when discussing the effects of forest fragmentation on plant-pollinator interactions. She argued that current arguments relating degree of specialization to extinction risk (e.g., Bond 1995) do not make sense if symmetry of interactions is not considered.

Something I did not discuss in detail in Chapter 4 was how the findings of Chapter 2 could affect my conclusions. The fact that relatively few species are functionally important could mean that my measure of specialization, even after rarefaction, is not accurately representing specialization among species. As may be exemplified by *Alstroemeria aurea*, the fact that this species interacts with dozens of flower visitors may mean very little in terms of the relative strength of each of those interactions. As my data show, and as similar data collected by Aizen (2001) also suggest, one species, the bumblebee *Bombus dahlbomii*, is by far the most frequent and most effective pollinator of *A. aurea*. Thus, it is possible that this herb is functionally specialized on *B. dahlbomii*, in spite of the many visits by other flower visitors received. Furthermore, as I mentioned in Chapter 4, the quality of my data precluded a finer-scale analysis of specialization, looking at interactions per site, instead of for the data for all sites pooled. Fox and Morrow (1981) and

Thompson (1994), among others, have suggested that species that interact with many other species over broad geographical extent could appear more generalized than their local populations really are, because local populations could be interacting with few species. Local specialization increases the chances that interacting species exert selective pressures on each other.

The analysis presented in Chapters 5 and 6 shows that, in spite of drastic changes in the population density of plants, plant-pollinator interactions do not appear greatly affected by cattle: no effects on pollinator visitation frequency were detected, and very few on pollen deposition and reproduction. Even for the one case for which I found strong evidence for indirect effects of cattle on reproduction, *A. aurea*, this effect was a by-product of the direct effect of trampling (i.e., trampling is necessary to produce a decline in population density, which in turn leads to decreased pollination and reproductive performance). It is noteworthy that this species is the most generalized plant species in my dataset, in terms of the number of species with which it interacts. Here, however, the same caveat discussed above should be mentioned: *A. aurea* may be more specialized on its main pollinator than appears from the diverse assemblage of pollinators that visit its flowers.

Several studies have suggested that, when plant-pollinator interactions are considered in the context of other ecological factors, such as herbivory, the effect of pollinators on plant firness may become virtually irrelevant. For example, Herrera (1993) studied selection on floral morphology in a hawk moth-pollinated violet, *Viola cazorlensis*. Herrera found selection by pollinators to be highly variable and overridden by other ecological factors, including direct flower and fruit predation by herbivores; the latter were much more important determinants of plant reproductive success. In another study on the perennial herb *Paeonia broteroi*, Herrera (2000) found an interaction between herbivory by invertebrate and vertebrate herbivores and pollination, so that pollination produced a significant effect on plant reproductive success in the absence of herbivores but not in their presence. Similarly, Gómez and Zamora (2000) found that the effect of pollinators on the fitness of the shrub *Hormathophylla spinosa* depended on ungulate pressure. Ungulates feed on inflorescences of *H. spinosa*, thus directly affecting fitness. Under high ungulate pressure, the effect of pollinators on the reproduction of *H. spinosa* was virtually nil. Conversely, when ungulate pressure was low, pollinators positively affected reproductive success. In all these examples, the importance of pollinators as selective agents for plants was contingent on herbivory; when herbivores are present, the benefit of pollination on fitness is overridden by herbivory. These findings, together with recent studies showing that plant-pollinator interactions tend to be moderately to extremely generalized (see, e.g., Struck 1994; Fishbein and Venable 1996; Herrera 1996; Waser et al. 1996; Gómez and Zamora 1999; Memmott 1999), suggest that the conditions for pollinators to have strong effects on plants are unlikely to be met in many ecological circumstances. This apparent generalization of pollination systems conflicts with the view that pollinators can be important selective agents on plants. Ollerton (1996) and Gómez (2002) pointed out to the apparent paradox between the observed generalized nature of plant-pollinator interactions and the many studies demonstrating that pollinators can in fact act as selective agents for plants. However, both Ollerton and Gómez suggest that even apparently generalized pollinators can pose a selective pressure on plants under some circumstances. Such circumstances include geographic and temporal variation in the abundance of pollinators (see also Thompson 1994), variation in the effectiveness of flower visitors as pollinators, and functional similarity of different taxa of flower visitors in pollination.

It is important to consider that the above studies, as well as most ecological studies, were done in small spatial and temporal extents compared to the scales at which evolutionary processes usually operate. Thus, conclusions from spatially and temporally restricted studies may not hold for evolutionary relevant scales. For example, my within-site path analyses (Chapter 5) showed that floral neighborhood density significantly affected pollination and reproduction, but that effect was weak in some cases and left unexplained a large amount of variability. Conversely, the among-site path analysis revealed comparatively stronger effects of density on pollination, and of pollination on reproduction. Thus, the conclusions that I would have reached by looking only at the within-site path analyses would have been different, had I not made among-site comparisons as well.

The above discussion is from the plants' perspective. Similar arguments can be made for pollinators. If the direct effects of herbivores are stronger than the indirect effects through the plants, then not to have found an effect of interaction specialization on pollinators' response to cattle disturbance is not surprising. Regrettably, I could not analyze the contribution of different plant species to pollinator fitness (doing so could be the subject of an entire dissertation!), and time constraints prevented a more in-depth analysis of the direct effects of cattle on the pollinators.

Where should we go from here? I think my study raises several interesting questions. One concerns the existence of asymmetric specialization in pollination systems. Does the apparent lack of species with low *s* and low *p* in the insect dataset in Nahuel Huapi differ from what we would expect with a random assemblage of species? I have recently started to explore this avenue using null models. My preliminary results suggest an unusually low number of species (of both plants and pollinators) with low values of *s* and *p*, compared to the random expectation. If this result holds, it will have important implications for our understanding of the ecology and evolution of plant-pollinator interactions.

Another issue that deserves further attention is the methodological aspects of the quantification of interaction specialization between plants and pollinators. Although I have made an effort to provide an objective quantification of specialization, I am convinced that this picture is incomplete. I have discussed above a few factors that should be included in a more realistic measure of interaction specialization; I could add many more.

The conditions under which introduced ungulates (and herbivores in general) will indirectly affect plant pollination and reproduction also need more careful evaluation. The mechanism proposed in Chapter 5 for indirect effects of large herbivores on pollination and plant reproduction is likely to occur in many ecological settings. I think the reason why there are no more examples is because we have not looked. If my conjecture is correct, then it will be important to refine our models, so we can predict in what circumstances this kind of effect will occur. In Chapter 5 I have identified several important factors. Yet, I was unable to provide good explanations for the lack of indirect effects in some species. Although in some instances this inability is due to the lack of appropriate data to evaluate the question, I am convinced that part of the reason is that my understanding of the complexity of these interactions is too poor to make full sense of my observations.

From the standpoint of conservation, the research priorities outlined in Chapter 3 should serve as a starting point. Particularly important is the establishment of long-term herbivore exclosures in a variety of forest types throughout the TFSA. Another important conservation research need is to address the effects of introduced ungulates on flower-visiting insects, even if they are not functionally important. To enable this evaluation, however, basic natural history studies are desperately needed. We know virtually nothing about plant-insect pollinator interactions in the TFSA.

Nature is exceedingly complex. The more we look, the more we realize the vastness of this complexity. Asking questions about nature always means a high risk of not getting the right answer. However, we can learn a lot in the process. I hope to have provided some answers to the many questions I may have raised. But even if I have not, I hope my effort will lead others in the right direction to a better understanding of our complex world.

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APPENDICES

APPENDIX 1. CALCULATION OF FLORAL NEIGHBORHOOD DENSITY

I used a computer program written in Matlab to calculate the density of the floral neighborhood around each ramet in a given population from maps of flowering ramets of *Alstroemeria aurea*. For each flowering ramet, my algorithm added the square root of the density of flowering neighbors in concentric bands of 1 m width at increasing distances of 1 m from the ramet, according to the following equation:

$$D = \sum_{i=1}^{x} \sqrt{r_i / a_i} \ , \qquad \text{[A1.1]}$$

where D is the total density of flowering neighbors within radius x from the ramet, r_i is the number of ramets in band i, and a_i is the area of band i. I chose $x = 20$ m, because densities at greater distances from the focal ramet were extremely low and did not change the value of D significantly. To avoid underestimating density of neighbors in the edges of the distribution of individual ramets, I used a "buffer zone" in my distributional maps. Individuals in the buffer zones were used to estimate densities but not as focal individuals for the analysis (see Dale 1999).

My method for the estimation of neighborhood density resembles that of Galiano (1982). My method has the disadvantage of being rather computationally intensive and requiring detailed maps of the location of each flowering individual in the population. However, it has an advantage over more traditional nearest-neighbor distance methods in that it allows a finer resolution at high and moderate densities, especially for clumpled species. Under a highly clumped distribution, most individuals will have a close neighbor, yet the neighborhood density may markedly differ. Thus, the use of nearest-neighbor estimates will probably not detect this density difference. An example is provided in Fig. A1.1. I plotted D (obtained from eq. A1.1) vs. the distance to nearest neighbor for each flowering ramet of *A. aurea* in the Cerro López population. Most ramets in this population have their nearest neighbor at short distances (2-3 m); however, the density of their floral neighborhood, as estimated by D, shows a great spread. Thus, using nearest neighbor distance as a surrogate of density would have led to assuming wrongly that very different densities were similar.

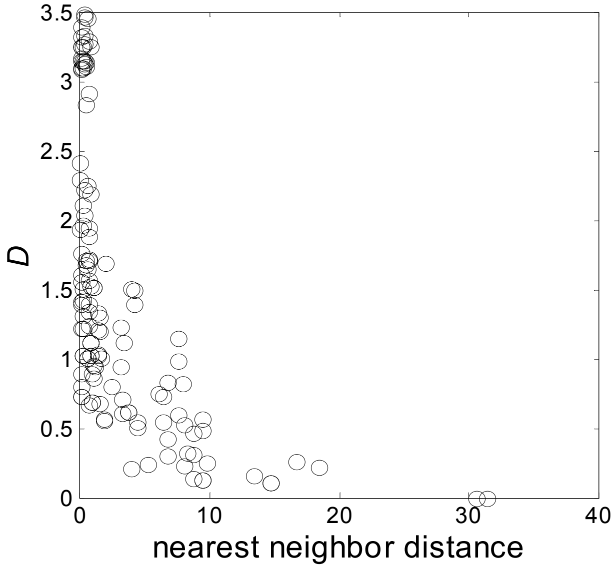

Figure A1. D, my estimate of floral neighborhood density, vs. distance to the nearest neighbor, for *A. aurea* in Cerro López.

APPENDIX 2. STUDY OF SELF-COMPATIBILITY AND DEPENDENCE ON POLLINATORS FOR REPRODUCTION

Self-compatibility and dependence were studied for the following five species: *Berberis darwinii*, *Gavilea odoratissima*, *Ribes magellanicum*, *Schinus patagonicus* and *Vicia nigricans*. Because *S. patagonicus* is dioecious, no pollen additions were made to study self-compatibility. I could not study self-compatibility and dependence on pollinators for *C. diemii* because I was unable to insert pollinia in the stigmatic surfaces.

Plants selected for the experiments were tagged, and the following treatments were applied: (i) unbagged flowers with no pollen addition (natural); (ii) bagged flowers with no pollen addition (bagged, no pollen); (iii) bagged flowers with self hand-pollination (bag, self); and (iv) bagged flowers with cross hand-pollination (bag, cross). For *Schinus patagonicus*, no hand-pollinations were applied to the bagged flowers. Bags were removed after flower senescence to minimize the negative effect of bagging on fruit development. Proportion of fruit set was the reproductive variable used for comparisons. Treatments were always applied to branches in different individuals to minimize the effect of resource re-allocation between branches.

Means, standard errors, and sample sizes are given for each treatment (Table A2.1). *B. darwinii* had the same proportion of fruits per tagged flower in the natural and cross-pollinated treatments. The proportion of fruit set by self-pollinated flowers was lower than for natural- and cross-pollinated flowers but still higher than for bagged flowers with no pollen addition. Thus, my results agree with those of Riveros (1996), indicating a relatively high degree of self-incompatibility and dependence on pollinators for reproduction in this species.

G. odoratissima had low fruit set in the naturally pollinated flowers. However, the fruit set for these flowers was still over four times higher than for bagged flowers with no pollen addition. Conversely, bagged flowers with either self- or crossed-hand-pollination had high fruit sets. The fruit set for self-pollinated flowers was higher than for cross-pollinated flowers. Thus, my results indicate a high dependence on pollinators for reproduction and a high degree of self-compatibility.

All the flowers in the three bagged treatments for *R. magellanicum* produced no fruits. This result indicates a negative effect of bagging on reproduction. These results cannot be used to interpret the degree of self-compatibility and the degree of dependence on pollinators of this species. Riveros (1996) mentions this species as being dioecious. This observation is incorrect, since flowers of this species develop hermaphroditic flowers with functional gynoecia and androecia.

Bagged flowers in *S. patagonicus* produced almost three times fewer fruits than naturally pollinated flowers. This species is dioecious, and thus this result suggests dependence on pollinators (i.e., absence of agamospermy). However, this lower fruit production in bagged flowers could also be in part due to an effect of bagging, as described in *R. magellanicum*. Thus, my results for this species should be interpreted with caution.

Finally, self- and cross-pollinated bagged flowers of *Vicia nigricans* had similar fruit sets, produced a higher fruit set than bagged flowers with no pollen addition but still lower than the naturally-pollinated flowers. Thus, my results indicate a high degree of self-compatibility, high degree of dependence on pollinators for reproduction, and a negative effect of bagging on reproduction in this species.

Table A2.1. Results of hand-pollination experiments to study the self compatibility of some of the species included in the study. Treatments were: unbagged flowers with no pollen addition (natural); bagged flowers with no pollen addition (bagged, no pollen); bagged flowers with self-hand-pollination (bag, self); and bagged flowers crossed-hand-pollination (bag, cross). Means, standard errors, and sample sizes are given for each treatment. For *Schinus patagonicus*, no hand-pollinations were applied to bagged flowers.

	natural			bag, no pollen			bag, self			bag, cross		
species	mean	s.e.	*n*	mean	s.e.	*n*	mean	s.e.	*n*	mean	s.e.	*n*
Berberis darwinii	0.59	0.05	51	0.15	0.04	27	0.24	0.06	19	0.59	0.05	27
Gavilea odoratissima	0.09	0.02	72	0.02	0.02	18	0.84	0.06	15	0.67	0.10	15
Ribes patagonicus	0.10	0.05	26	0.00	0.00	5	0.00	0.00	4	0.00	0.00	4
Schinus patagonicus	0.59	0.04	56	0.21	0.04	11						
Vicia nigricans	0.35	0.02	108	0.01	0.01	25	0.14	0.04	15	0.15	0.09	10

Appendix 3: Plant and Pollinator Species

Table A3.1 Plant species included in the study.

Species no.	Family	Plant species	Common name	Life form	Origin
1	Alstroemeriaceae	*Alstroemeria aurea*	Amancay	Herb	Native
2	Eleocarpaceae	*Aristotelia chilensis*	Maqui	Understory tree	Native
3	Berberidaceae	*Berberis buxifolia*	Calafate	Shrub	Native
4	Berberidaceae	*Berberis darwinii*	Michai	Shrub	Native
5	Scrophulariaceae	*Calceolaria crenatiflora*	Topa-topa	Herb	Native
6	Asclepiadaceae	*Cynanchum diemii*	-	Vine	Native
7	Scrophulariaceae	*Digitalis purpurea*	Dedalera	Herb	Exotic
8	Ochidaceae	*Gavilea odoratissima*	Orquídea	Herb	Native
9	Celastraceae	*Maytenus chubutensis*	Chaurilla	Shrub	Native
10	Asteraceae	*Mutisia decurrens*	Mutisia	Vine	Native
11	Rosaceae	*Rosa eglanteria*	Rosa mosqueta	Shrub	Exotic
12	Saxifragaceae	*Ribes magellanicum*	Parrilla	Shrub	Native
13	Anacardiaceae	*Schinus patagonicus*	Laura	Understory tree	Native
14	Loranthaceae	*Tristerix corymbosus*	Quintral	Parasitic shrub	Native
15	Leguminosae	*Vicia nigricans*	Arvejilla	Vine	Native

Table A3.2 Pollinator species recorded visiting flowers of plants in Table A3.1.

Species no.	Order	Family	Species name	Catalog number
1	Araneae	Thomisidae	All species (pooled)	—
2	Coleoptera	Salpingidae	—	63
3	Coleoptera	Buprestidae	*Anthaxia* sp.	39
4	Coleoptera	Cantharidae	—	121
5	Coleoptera	Coccinellidae	—	—
6	Coleoptera	Coccinellidae	—	45
7	Coleoptera	Curculionidae	—	69
8	Coleoptera	Curculionidae	—	213
9	Coleoptera	Nitidulidae	—	55
10	Coleoptera	Mordellidae	—	157, 159
11	Coleoptera	Staphilinidae	—	112
12	Coleoptera	Melyridae	—	11
13	Coleoptera	Curculionidae	—	69
14	Coleoptera	Unknown	—	79
15	Coleoptera	Torymidae	—	94
16	Coleoptera	Unknown	—	105
17	Coleoptera	Unknown	—	106
18	Coleoptera	Unknown	—	107
19	Coleoptera	Pedilidae	—	115
20	Coleoptera	Unknown	—	—
21	Coleoptera	Melyridae	—	165
22	Coleoptera	Unknown	—	176
23	Coleoptera	Unknown	—	192
24	Coleoptera	Unknown	—	201
25	Coleoptera	Unknown	—	206
26	Diptera	Acroceridae	—	159
27	Diptera	Asilidae	—	125
28	Diptera	Bombilidae	*Phthiria* sp.	29
29	Diptera	Bombilidae	*Phthiria* sp.	43
30	Diptera	Bombilidae	—	174
31	Diptera	Lauxaniidae	*Sapromyza fulvicornis*, *Minettia semifulva*	149
32	Diptera	Nemestrinidae	*Trichophthalma amoena*	54
33	Diptera	Nemestrinidae	*Trichophthalma jaffueli*	16
34	Diptera	Phoridae	—	114
35	Diptera	Phoridae	—	116
36	Diptera	Sciaridae	—	129
37	Diptera	Syrphidae	*Syrphus poecilogaster*	2
38	Diptera	Syrphidae	*Platycherius* (*Carposcalis*) *fenestratus*	13
39	Diptera	Syrphidae	*Scaeva melanostoma*	14
40	Diptera	Syrphidae	*Allograpta hortensis*, *Toxomerus vertebratus*	15, 56
41	Diptera	Syrphidae	*Platycheirus* (*Carposcalis*) sp.	87
42	Diptera	Syrphidae	*Ocyptamus melanorrhinus*	110
43	Diptera	Syrphidae	*Syrphus octomaculatus*	104, 120
44	Diptera	Syrphidae	*Allograpta exotica*	164
45	Diptera	Tabanidae	—	109
46	Diptera	Tachinidae	—	103
47	Diptera	Unknown	—	67
48	Diptera	Unknown	—	68
49	Diptera	Unknown	—	97
50	Diptera	Unknown	—	100
51	Diptera	Unknown	—	169
52	Diptera	Unknown	—	183
53	Diptera	Unknown	—	186
54	Diptera	Unknown	—	187
55	Diptera	Unknown	—	193
56	Diptera	Unknown	—	199

Species no.	Order	Family	Species name	Catalog number
57	Diptera	Unknown	—	207
58	Diptera	Unknown	—	208
59	Diptera	Unknown	Phoridae	210
60	Diptera	Unknown	—	215
61	Heteroptera	Unknown	All species (pooled)	75, 189, 190
62	Homoptera	Unknown	—	70
63	Homoptera	Unknown	—	123
64	Hymenoptera	Andrenidae	*Heterosarus* sp.	178
65	Hymenoptera	Apidae	*Bombus dahlbomii*	4, 5
66	Hymenoptera	Apidae	*Bombus ruderatus*	3
67	Hymenoptera	Apidae	*Chalepogenus caeruleus*	141
68	Hymenoptera	Apidae	*Manuelia gayi*	37
69	Hymenoptera	Apidae	*Manuelia postica*	19
70	Hymenoptera	Apidae	*Svastrides melanura*	34
71	Hymenoptera	Braconidae	—	52
72	Hymenoptera	Braconidae	—	124
73	Hymenoptera	Braconidae	—	205
74	Hymenoptera	Chalcicoidea	—	90
75	Hymenoptera	Chalcicoidea	—	188
76	Hymenoptera	Colletidae	*Colletes seminitidus*	62
77	Hymenoptera	Colletidae	*Diphaglosa gayi*	184
78	Hymenoptera	Colletidae	*Policana albopilosa*	65
79	Hymenoptera	Diapriidae	—	117
80	Hymenoptera	Eumenidae	*Hydrodynerus* sp.	144
81	Hymenoptera	Formicidae	*Camponotus* sp.	185
82	Hymenoptera	Formicidae	—	61
83	Hymenoptera	Formicidae	—	80
84	Hymenoptera	Formicidae	—	82
85	Hymenoptera	Halictidae	*Caenohalictus* sp.	190
86	Hymenoptera	Halictidae	*Caenohalictus* sp.	49
87	Hymenoptera	Halictidae	*Caenohalictus* sp.	51
88	Hymenoptera	Halictidae	*Chilicola* sp.	175
89	Hymenoptera	Halictidae	*Chilicola* sp.	179
90	Hymenoptera	Halictidae	*Chilicola* sp.	191
91	Hymenoptera	Halictidae	*Corynura prothysteres*	48
92	Hymenoptera	Halictidae	*Corynura* sp.	153
93	Hymenoptera	Halictidae	*Evylaeus* (=*Dialictus*) sp.	168
94	Hymenoptera	Halictidae	*Ruizantheda mutabilis*	9
95	Hymenoptera	Halictidae	*Ruizantheda nigrocaerulea*	161
96	Hymenoptera	Halictidae	*Ruizantheda proxima*	180
97	Hymenoptera	Halictidae	—	—
98	Hymenoptera	Ichneumonidae	—	25
99	Hymenoptera	Ichneumonidae	—	95
100	Hymenoptera	Ichneumonidae	—	98
101	Hymenoptera	Ichneumonidae	—	122
102	Hymenoptera	Ichneumonidae	—	132
103	Hymenoptera	Ichneumonidae	—	203
104	Hymenoptera	Ichneumonidae	—	211
105	Hymenoptera	Megachilidae	*Megachile* sp.	162, 163
106	Hymenoptera	Megachilidae	*Megachile* sp.	194
107	Hymenoptera	Sphecidae	—	78
108	Hymenoptera	Tinnidae	—	93
109	Hymenoptera	Torymidae	—	73
110	Hymenoptera	Torymidae	—	94
111	Hymenoptera	Vespidae	—	113
112	Hymenoptera	Vespidae	*Vespula germanica*	50
113	Hymenoptera	Unknown	—	32
114	Hymenoptera	Unknown	—	64
115	Hymenoptera	Unknown	—	71
116	Hymenoptera	Unknown	—	93
117	Hymenoptera	Unknown	—	130
118	Hymenoptera	Unknown	—	166
119	Hymenoptera	Unknown	—	173
120	Hymenoptera	Unknown	—	195
121	Hymenoptera	Unknown	—	204
122	Hymenoptera	Unknown	—	212
123	Hymenoptera	Unknown	—	214
124	Lepidoptera	Unknown	—	74
125	Lepidoptera	Unknown	—	118
126	Lepidoptera	Hesperiidae	—	160
127	Odonata	Unknown	—	—
128	Trochiliformes	Trochilidae	*Sephanoides galeritus*	—
129	Unknown	Unknown	—	108

APPENDIX 4: EFFECTIVENESS MATRIX

This matrix was calculated by taking the proportion of visits each pollinator species contacted reproductive parts (anthers or stigmatic surfaces) of each plant species. Numbers for pollinator (rows) and plant (columns) species correspond to those given in Appendix 3.

Table A4.1. Effectiveness matrix.

Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0.22					0.00	0.50								
2			0.00			1.00						1.00	0.50		
3	0.34									0.76					
4	0.25	0.00						0.00			1.00				
5	0.25														
6										0.00					
7													0.50		
8	0.00														
9	0.25					1.00					0.50	1.00			
10											1.00				
11	0.43										1.00		1.00		
12	0.25										0.00				
13				1.00											
14						1.00							1.00		
15						1.00									
16	0.00									1.00			0.50		
17													0.50		
18													0.50		
19								0.00							
20	0.50														
21	0.34										0.75				
22	0.50														
23	1.00														
24	0.50														
25	0.00														
26	0.17						0.00				1.00				
27	1.00														
28	0.33									0.53	1.00				
29	0.27									0.00					
30	1.00														
31	0.45									0.71	0.71				0.00
32			1.00	1.00								1.00	1.00		
33	0.69										1.00				
34													1.00		
35													1.00		
36															0.00
37	0.00														
38											1.00		1.00		
39													1.00		
40	0.25		1.00	1.00	0.50						0.91	1.00	0.50		
41	0.19	1.00		1.00	0.00		0.00				0.78		0.67		0.00
42	0.75									1.00	0.50				
43	0.44			1.00			0.00				0.93		1.00		
44											0.50				
45	1.00										0.00				0.00
46													1.00		
47			0.00												
48				0.00											
49													1.00		
50													1.00		
51											0.50				
52	0.00														
53	0.00														
54	0.00														
55	1.00														
56	0.00														
57	1.00														
58	1.00														
59	0.00									0.00					
60	0.00														
61	0.25									0.00					
62									0.00						
63		0.00													
64	0.41									0.88					
65	0.91		1.00	1.00	0.90		1.00			1.00	1.00		1.00	1.00	1.00
66	0.86						1.00								1.00
67					0.90										
68	0.63			1.00						1.00					
69	0.44			1.00				0.00					1.00	0.67	
70	0.63														
71						1.00							0.00		
72		1.00													

Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
73										0.00					
74												0.00			
75	0.00														
76			1.00	1.00		1.00						1.00			
77	0.00														
78		1.00											1.00		
79													1.00		
80												1.00			
81	0.00												1.00		
82						1.00	0.00	0.00				0.67			
83								0.00							
84													1.00		
85	0.00														
86										1.00					
87			0.00	1.00				0.00							
88	0.50														
89	1.00														
90	0.20														
91	0.75	0.50					1.00								
92											1.00				
93	0.83									0.50					
94	0.53	1.00		1.00			0.67				0.94		1.00		
95	0.42										0.83				
96	1.00														
97											1.00				
98						1.00									
99								0.00							
100								0.00							
101		1.00											1.00		
102		1.00													
103	0.50														
104	1.00														
105	0.76														
106	0.83														
107	0.17							1.00		0.00					
108	1.00			0.00											
109			0.00			1.00							0.00		
110								0.00							
111	0.00												1.00		
112	0.75						1.00			1.00	0.75		0.00		
113	0.00														
114				0.00											
115			0.00									0.00			
116	0.00														
117															0.00
118	0.50														
119	0.00														
120	0.00														
121	1.00														
122	0.00														
123	0.00														
124			0.00												
125															1.00
126	0.40									0.00					
127							0.00								
128	1.00									1.00				1.00	
129													1.00		

APPENDIX 5: INTERACTION MATRICES

This appendix contains matrices of plant pollinator interactions recorded during the 1999-2000 Austral spring-summer for the eight sites (Tables a-h), plus a matrix for aggregated data for all sites (Table i). Two types of matrices are given: (i) "frequency matrix," containing the visitation frequency of each pollinator species to each plant species; and (ii) "individuals matrix," containing the number of individual pollinators visiting flowers of each plant species. Numbers for pollinator (rows) and plant (columns) species correspond to those given in Appendix 3.

Table A5.1. Llao Llao.

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	5					1										6	5					1										6
2												1				1												1				1
3	40									1						41	16									1						17
4	3	1						1								5	3	1						1								5
5																0																0
6																0																0
7																0																0
8	1															1	1															1
9																0																0
10																0																0
11																0																0
12																0																0
13																0																0
14																0																0
15						1										1						1										1
16																0																0
17																0																0
18																0																0
19																0																0
20	3															3	2															2
21																0																0
22																0																0
23	1															1	1															1
24																0																0
25	1															1	1															1
26																0																0
27																0																0
28	10									1						11	9									1						10
29	8															8	8															8
30																0																0
31										1						1										1						1
32												68				68												3				3
33																0																0
34																0																0
35																0																0
36																0																0
37																0																0
38																0																0
39																0																0
40																0																0
41					1											1					1											1
42																0																0
43	4															4	4															4
44																0																0
45																0																0
46																0																0
47																0																0
48																0																0
49																0																0
50																0																0
51																0																0
52	1															1	1															1
53																0																0
54																0																0
55																0																0
56																0																0
57																0																0
58																0																0
59	6															6	4															4
60																0																0
61																0																0
62																0																0
63																0																0
64																0																0
65	126			1						4				1	146	278	21			1						2				1	21	46
66	78															78	17															17
67																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
68	36									1						37	20									1						21
69	22			5				3						3		33	11			4				3						3		21
70																0																0
71						8							2			10						6							2			8
72																0																0
73																0																0
74																0																0
75																0																0
76																0																0
77																0																0
78		64											82			146		8											6			14
79																0																0
80																0																0
81																0																0
82						11						4				15						4						3				7
83																0																0
84																0																0
85																0																0
86																0																0
87								1								1								1								1
88																0																0
89	2															2	2															2
90	2															2	2															2
91																0																0
92																0																0
93																0																0
94	10												2			12	4												1			5
95																0																0
96																0																0
97																0																0
98																0																0
99								1								1								1								1
100																0																0
101																0																0
102																0																0
103	2															2	2															2
104	1															1	1															1
105																0																0
106																0																0
107	3							1								4	2							1								3
108																0																0
109																0																0
110																0																0
111																0																0
112	1															1	1															1
113																0																0
114																0																0
115																0																0
116																0																0
117																0																0
118	1															1	1															1
119																0																0
120																0																0
121																0																0
122																0																0
123																0																0
124																0																0
125															16	16															2	2
126	7									1						8	6									1						7
127																0																0
128										1						1										1						1
129																0																0
Total	374	65	0	6	1	21	0	7	0	10	0	73	86	4	162	809	145	9	0	5	1	12	0	7	0	8	0	7	9	4	23	230

Table A5.2. Cerro López.

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	1															1	1															1
2																0																0
3	1									11						12	1									9						10
4																0																0
5																0																0
6																0																0
7																0																0
8																0																0
9																0																0
10											2					2											2					2
11																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
12	1															1	1															1
13																0																0
14																0																0
15																0																0
16	1									1						2	1									1						2
17																0																0
18																0																0
19																0																0
20																0																0
21																0																0
22																0																0
23																0																0
24	1															1	1															1
25																0																0
26																0																0
27																0																0
28	26									6						32	23									6						29
29	14									2						16	12									1						13
30	1															1	1															1
31										5						5										5						5
32			15	32												47			6	6												12
33	7															7	6															6
34																0																0
35																0																0
36																0																0
37																0																0
38																0																0
39																0																0
40											2					2											2					2
41		2			1											3		1			1											2
42										1						1										1						1
43											7		24			31											5		3			8
44										2						2										1						1
45															10	10															4	4
46																0																0
47																0																0
48																0																0
49																0																0
50																0																0
51																0																0
52																0																0
53																0																0
54																0																0
55																0																0
56																0																0
57																0																0
58																0																0
59																0																0
60																0																0
61																0																0
62																0																0
63																0																0
64	19									9						28	9									9						18
65	4			11						1			16		100	132	1			4						1			2		13	21
66																0																0
67																0																0
68	2															2	1															1
69													2			2													2			2
70	2															2	1															1
71																0																0
72																0																0
73										1						1										1						1
74																0																0
75																0																0
76						32										32						2										2
77																0																0
78		59											110			169		4											16			20
79																0																0
80											4					4											1					1
81	2															2	2															2
82																0																0
83								2								2								2								2
84													10			10													5			5
85	2															2	2															2
86										1						1										1						1
87			1	11												12			1	2												3
88																0																0
89	3															3	2															2
90	1															1	1															1
91																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
92											1					1											1					1
93	6									1						7	5									1						6
94	3	17											81			101	2	3											12			17
95	8															8	3															3
96																0																0
97											1					1											1					1
98																0																0
99																0																0
100																0																0
101																0																0
102																0																0
103																0																0
104																0																0
105																0																0
106																0																0
107	3															3	3															3
108				2												2				2												2
109																0																0
110								1								1								1								1
111																0																0
112										1						1										1						1
113	2															2	2															2
114																0																0
115																0																0
116																0																0
117																0																0
118																0																0
119																0																0
120																0																0
121																0																0
122																0																0
123	1															1	1															1
124																0																0
125																0																0
126																0																0
127																0																0
128										2						2										1						1
129																0																0
Total	111	78	16	56	1	32	0	3	0	44	17	0	243	0	110	711	82	8	7	14	1	2	0	3	0	39	12	0	40	0	17	225

Table A5.3. Safariland.

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	4					1										5	4					1										5
2																0																0
3																0																0
4	1															1	1															1
5																0																0
6																0																0
7																0																0
8																0																0
9						1										1						1										1
10																0																0
11	10										3					13	6										3					9
12																0																0
13																0																0
14																0																0
15																0																0
16																0																0
17																0																0
18																0																0
19																0																0
20																0																0
21																0																0
22																0																0
23																0																0
24																0																0
25																0																0
26																0																0
27																0																0
28	23									1						24	20									1						21
29	3															3	2															2
30																0																0
31	3															3	2															2
32												2				2												1				1
33	5															5	2															2
34																0																0
35																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
36																0																0
37	1															1	1															1
38																0																0
39																0																0
40	3				2						2	3				10	3				1						2	1				7
41	3	4														7	2	1														3
42																0																0
43	12			5							4					21	7			1							3					11
44																0																0
45																0																0
46																0																0
47																0																0
48																0																0
49																0																0
50																0																0
51																0																0
52																0																0
53																0																0
54																0																0
55																0																0
56																0																0
57																0																0
58																0																0
59	3															3	2															2
60																0																0
61																0																0
62																0																0
63		1														1		1														1
64																0																0
65	169			67												236	50			2												52
66																0																0
67					3											3					2											2
68	11															11	8															8
69																0																0
70	9															9	7															7
71						2										2						1										1
72		1														1		1														1
73																0																0
74																0																0
75	1															1	1															1
76																0																0
77																0																0
78		673														673		80														80
79																0																0
80																0																0
81																0																0
82						8										8						2										2
83																0																0
84																0																0
85																0																0
86																0																0
87																0																0
88																0																0
89																0																0
90																0																0
91	4	1														5	2	1														3
92																0																0
93																0																0
94		110									6					116		18									3					21
95																0																0
96	4															4	2															2
97																0																0
98																0																0
99																0																0
100																0																0
101		1											15			16		1											1			2
102																0																0
103	7															7	4															4
104																0																0
105																0																0
106																0																0
107	8															8	7															7
108																0																0
109						9										9						6										6
110																0																0
111																0																0
112	5												2			7	3												1			4
113																0																0
114																0																0
115																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
116																0																0
117																0																0
118																0																0
119																0																0
120	1															1	1															1
121																0																0
122																0																0
123																0																0
124																0																0
125																0																0
126																0																0
127																0																0
128																0																0
129																0																0
Total	290	790	0	72	5	21	0	0	0	1	15	5	17	0	0	1216	137	103	0	3	3	11	0	0	0	1	11	2	2	0	0	273

Table A5.4. Arroyo Goye.

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	3															3	2															2
2																0																0
3	5									3						8	2									2						4
4																0																0
5																0																0
6										1						1										1						1
7																0																0
8																0																0
9																0																0
10																0																0
11																0																0
12																0																0
13																0																0
14																0																0
15																0																0
16																0																0
17																0																0
18																0																0
19																0																0
20																0																0
21																0																0
22																0																0
23																0																0
24																0																0
25																0																0
26	5															5	2															2
27																0																0
28	46										1					47	40										1					41
29	11															11	10															10
30																0																0
31											1					1											1					1
32																0																0
33	6															6	3															3
34																0																0
35																0																0
36																0																0
37																0																0
38											1					1											1					1
39													3			3													2			2
40	15												45			60	14												13			27
41	5										1		13			19	3										1		4			8
42																0																0
43	5									1	1					7	3									1	1					5
44																0																0
45											1					1											1					1
46																0																0
47																0																0
48																0																0
49																0																0
50													3			3													3			3
51																0																0
52																0																0
53																0																0
54																0																0
55																0																0
56																0																0
57																0																0
58																0																0
59	4															4	3															3

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
60	1														1	1														1
61																0																0
62																0																0
63																0																0
64	30														30	17														17
65	4			15							8				7	34	2			5							1				2	10
66	35													10	45	11													1	12
67					6										6					3										3
68																0																0
69																0																0
70																0																0
71																0																0
72																0																0
73																0																0
74																0																0
75																0																0
76				13							5				18				2							1				3
77																0																0
78		85											94			179		10											21			31
79																0																0
80																0																0
81													27			27													2			2
82																0																0
83																0																0
84																0																0
85																0																0
86																0																0
87																0																0
88																0																0
89	2														2	2														2
90	3														3	3														3
91																0																0
92																0																0
93																0																0
94	1	26											79			106	1	10											22			33
95	2														2	1														1
96																0																0
97																0																0
98																0																0
99																0																0
100																0																0
101																0																0
102																0																0
103																0																0
104																0																0
105	7														7	4														4
106																0																0
107	17										2						19	11										2						13
108																0																0
109						2									2						2									2
110																0																0
111	1												1			2	1												1			2
112	1														1	1														1
113	2														2	1														1
114																0																0
115																0																0
116																0																0
117																0																0
118																0																0
119																0																0
120																0																0
121																0																0
122																0																0
123																0																0
124																0																0
125																0																0
126																0																0
127																0																0
128																0																0
129																0																0
Total	211	111	0	28	6	2	0	0	0	7	14	5	265	0	17	666	138	20	0	7	3	2	0	0	0	6	7	1	68	0	3	255

Table A5.5. Mascardi (nc).

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	3														3	3														3
2													3			3													1			1
3	71										2						73	33										1						34

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
4																0																0
5	1															1	1															1
6																0																0
7																0																0
8																0																0
9	6										1	4				11	6										1	4				11
10																0																0
11	15															15	15															15
12	10															10	10															10
13				3												3				1												1
14													9			9													5			5
15																0																0
16																0																0
17																0																0
18																0																0
19																0																0
20																0																0
21											2					2											2					2
22											2					2											1					1
23																0																0
24																0																0
25																0																0
26	1															1	1															1
27	1															1	1															1
28	1									1						2	1									1						2
29																0																0
30																0																0
31	21									2	11					34	19									2	8					29
32				48												48				13												13
33	79															79	28															28
34																0																0
35																0																0
36																0																0
37																0																0
38																0																0
39																0																0
40	2			6												8	1			2												3
41	2										2					4	2										1					3
42	10									1						11	6									1						7
43	33										1					34	26										1					27
44																0																0
45	1														2	3	1														1	2
46																0																0
47																0																0
48				6												6				2												2
49													2			2													1			1
50																0																0
51																0																0
52																0																0
53	1															1	1															1
54	1															1	1															1
55																0																0
56																0																0
57																0																0
58																0																0
59	2															2	2															2
60																0																0
61	2															2	2															2
62									1							1									1							1
63																0																0
64																0																0
65	135			111						14					15	275	43			14						6					4	67
66	56															56	14															14
67																0																0
68	103			1						5						109	55			1						3						59
69																0																0
70																0																0
71																0																0
72		2														2		2														2
73										1						1										1						1
74																0																0
75	1															1	1															1
76				7												7				3												3
77	2															2	1															1
78		26														26		7														7
79																0																0
80																0																0
81																0																0
82																0																0
83																0																0

	Matrix 1: visitation frequency															Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
84																0																0
85																0																0
86																0																0
87				34												34				12												12
88	3															3	1															1
89																0																0
90																0																0
91																0																0
92																0																0
93																0																0
94	17	19		9							2					47	11	8		3							2					24
95											2					2											1					1
96																0																0
97																0																0
98																0																0
99																0																0
100								1								1								1								1
101																0																0
102																0																0
103																0																0
104																0																0
105																0																0
106																0																0
107	1															1	1															1
108	2															2	2															2
109																0																0
110																0																0
111																0																0
112	1									2						3	1									2						3
113																0																0
114																0																0
115																0																0
116	1															1	1															1
117																0																0
118																0																0
119	1															1	1															1
120																0																0
121	1															1	1															1
122																0																0
123																0																0
124																0																0
125																0																0
126	2															2	1															1
127																0																0
128																0																0
129																0																0
Total	589	47	0	225	0	0	0	1	1	28	23	4	14	0	17	948	294	17	0	51	0	0	0	1	1	17	17	4	7	0	5	414

Table A5.6. Mascardi (c).

	Matrix 1: visitation frequency															Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	1															1	1															1
2																0																0
3																0																0
4											1					1											1					1
5																0																0
6																0																0
7													1			1													1			1
8																0																0
9											4					4											4					4
10																0																0
11											4		1			5											1		1			2
12																0																0
13																0																0
14																0																0
15																0																0
16													1			1													1			1
17													1			1													1			1
18													1			1													1			1
19																0																0
20																0																0
21																0																0
22																0																0
23																0																0
24																0																0
25																0																0
26																0																0
27																0																0

	Matrix 1: visitation frequency															Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
28																0																0
29																0																0
30																0																0
31											3					3											3					3
32			43	19												62			6	2												8
33	1															1	1															1
34													1			1													1			1
35													3			3													2			2
36																0																0
37																0																0
38																0																0
39																0																0
40	1		1								2		26			30	1		1								1		5			8
41											2					2											2					2
42																0																0
43											3		25			28											1		4			5
44																0																0
45																0																0
46													1			1													1			1
47			1													1			1													1
48																0																0
49																0																0
50																0																0
51											1					1											1					1
52																0																0
53																0																0
54																0																0
55																0																0
56																0																0
57																0																0
58																0																0
59	1															1	1															1
60																0																0
61	1									1						2	1									1						2
62																0																0
63																0																0
64	2															2	1															1
65	7			26							5				14	52	4			5							2				4	15
66																0																0
67					1											1					1											1
68	6															6	2															2
69																0																0
70																0																0
71																0																0
72																0																0
73																0																0
74																0																0
75																0																0
76			6													6			4													4
77																0																0
78		73														73		10														10
79													1			1													1			1
80																0																0
81																0																0
82																0																0
83																0																0
84																0																0
85																0																0
86																0																0
87			1													1			1													1
88																0																0
89																0																0
90																0																0
91																0																0
92																0																0
93																0																0
94	1										1		15			17	1										1		3			5
95																0																0
96																0																0
97																0																0
98																0																0
99																0																0
100																0																0
101																0																0
102													2			2													1			1
103																0																0
104																0																0
105																0																0
106																0																0
107																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
108																0																0
109			1										2			3			1										2			3
110																0																0
111																0																0
112																0																0
113																0																0
114																0																0
115			4									1				5			3									1				4
116																0																0
117																0																0
118																0																0
119																0																0
120																0																0
121																0																0
122	1															1	1															1
123																0																0
124																0																0
125																0																0
126																0																0
127																0																0
128																0																0
129													3			3													1			1
Total	22	73	57	45	1	0	0	0	0	1	26	1	84	0	14	324	14	10	17	7	1	0	0	0	0	1	17	1	26	0	4	98

Table A5.7. Quetrihué (nc).

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	1															1	1															1
2						1										1						1										1
3	1															1	1															1
4																0																0
5	1															1	1															1
6																0																0
7																0																0
8																0																0
9						7						4				11						4						4				8
10																0																0
11																0																0
12																0																0
13																0																0
14						1										1						1										1
15																0																0
16																0																0
17																0																0
18																0																0
19																0																0
20																0																0
21																0																0
22																0																0
23																0																0
24																0																0
25																0																0
26	1															1	1															1
27																0																0
28	10															10	9															9
29	4															4	4															4
30																0																0
31	1															1	1															1
32													3			3													1			1
33	2															2	1															1
34																0																0
35																0																0
36															2	2															2	2
37																0																0
38																0																0
39																0																0
40	5												9			14	3												1			4
41																0																0
42																0																0
43	10															10	4															4
44																0																0
45																0																0
46																0																0
47																0																0
48																0																0
49																0																0
50																0																0
51																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
52																0																0
53																0																0
54																0																0
55	1															1	1															1
56	1															1	1															1
57	1															1	1															1
58																0																0
59	10															10	7															7
60																0																0
61	1															1	1															1
62																0																0
63																0																0
64																0																0
65	162														37	199	43														8	51
66	8															8	3															3
67																0																0
68																0																0
69	4												10	3		17	3												1	2		6
70	2															2	1															1
71						5										5						2										2
72																0																0
73																0																0
74												1				1												1				1
75																0																0
76																0																0
77																0																0
78		89											404			493		19											25			44
79																0																0
80																0																0
81																0																0
82																0																0
83																0																0
84																0																0
85																0																0
86																0																0
87																0																0
88																0																0
89																0																0
90																0																0
91																0																0
92																0																0
93																0																0
94																0																0
95	2															2	2															2
96																0																0
97																0																0
98						1										1						1										1
99																0																0
100																0																0
101																0																0
102																0																0
103																0																0
104																0																0
105	16															16	11															11
106	7															7	1															1
107	1															1	1															1
108																0																0
109						1										1						1										1
110																0																0
111																0																0
112	1															1	1															1
113																0																0
114																0																0
115																0																0
116																0																0
117															1	1															1	1
118																0																0
119																0																0
120																0																0
121																0																0
122																0																0
123																0																0
124																0																0
125																0																0
126																0																0
127																0																0
128	1													1		2	1													1		2
129																0																0
Total	254	89	0	0	0	16	0	0	0	0	0	5	426	4	40	834	104	19	0	0	0	10	0	0	0	0	0	5	28	3	11	180

Table A5.8. Quetrihué (c).

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	3						1									4	3						1									4
2			1										1			2			1										1			2
3																0																0
4	1															1	1															1
5																0																0
6																0																0
7																0																0
8																0																0
9																0																0
10											1					1											1					1
11																0																0
12											1					1											1					1
13																0																0
14																0																0
15																0																0
16																0																0
17																0																0
18																0																0
19								1								1								1								1
20																0																0
21																0																0
22																0																0
23																0																0
24																0																0
25																0																0
26							1				1					2							1				1					2
27																0																0
28	2															2	2															2
29	1															1	1															1
30	1															1	1															1
31																0																0
32			17	9												26			7	2												9
33											1					1											1					1
34																0																0
35																0																0
36																0																0
37																0																0
38				2							2					4				1							1					2
39																0																0
40	2			3	1						31		5			42	2			2	1						24		1			30
41	3			1	1	1	4				8		11		1	30	2			1	1	1	3				5		4		1	18
42											2					2											1					1
43	1						2				21					24	1						2				16					19
44											2					2											2					2
45															5	5															3	3
46																0																0
47																0																0
48																0																0
49																0																0
50																0																0
51																0																0
52																0																0
53																0																0
54																0																0
55																0																0
56																0																0
57																0																0
58	1															1	1															1
59	1									1						2	1									1						2
60																0																0
61																0																0
62																0																0
63																0																0
64	2															2	1															1
65	34		2	34	4		66				11				150	301	15		1	7	1		21				4				2	51
66	24						13									37	9						4									13
67					5											5					4											4
68	3															3	1															1
69																0																0
70																0																0
71																0																0
72																0																0
73																0																0
74																0																0
75																0																0
76			2	57												59			2	8												10
77																0																0

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
78																0																0
79																0																0
80																0																0
81																0																0
82								3								3								1								1
83																0																0
84																0																0
85																0																0
86																0																0
87				2												2				1												1
88																0																0
89																0																0
90																0																0
91							2									2							1									1
92																0																0
93	1															1	1															1
94							12				2		63			77							8				2		11			21
95											2					2											2					2
96																0																0
97																0																0
98																0																0
99																0																0
100																0																0
101																0																0
102																0																0
103																0																0
104																0																0
105																0																0
106																0																0
107																0																0
108																0																0
109																0																0
110																0																0
111																0																0
112	2						1				3					6	2						1				2					5
113																0																0
114				1												1				1												1
115																0																0
116																0																0
117																0																0
118																0																0
119																0																0
120																0																0
121																0																0
122																0																0
123																0																0
124			4													4			2													2
125																0																0
126																0																0
127							8									8							3									3
128																0																0
129																0																0
Total	82	0	26	109	11	1	110	4	0	1	88	0	80	0	156	668	44	0	13	23	7	1	45	2	0	1	63	0	17	0	6	222

Table A5.9. Total.

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
1	21					2	1									24	20					2	1									23
2			1			1						1	4			7			1			1						1	2			5
3	118									17						135	53									13						66
4	5	1						1			1					8	5	1						1			1					8
5	2															2	2															2
6										1						1										1						1
7													1			1													1			1
8	1															1	1															1
9	6					8					5	8				27	6					5					5	8				24
10											3					3											3					3
11	25										7		1			33	21										4		1			26
12	11										1					12	11										1					12
13				3												3				1												1
14						1							9			10						1							5			6
15						1										1						1										1
16	1									1			1			3	1									1			1			3
17													1			1													1			1
18													1			1													1			1
19								1								1								1								1
20	3															3	2															2
21											2					2											2					2

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
22											2					2											1					1
23	1															1	1															1
24	1															1	1															1
25	1															1	1															1
26	7						1				1					9	4						1				1					6
27	1															1	1															1
28	118									9	1					128	104									9	1					114
29	41									2						43	37									1						38
30	2															2	2															2
31	25									8	15					48	22									8	12					42
32			75	108								70	3			256			19	23								4	1			47
33	100										1					101	41										1					42
34													1			1													1			1
35													3			3													2			2
36															2	2															2	2
37	1															1	1															1
38				2							3					5				1							2					3
39													3			3													2			2
40	28		1	9	3						37	3	86			167	24		1	4	2						29	1	20			81
41	13	6		1	3	1	4				13		24		1	66	9	2		1	3	1	3				9		8		1	37
42	10									2	2					14	6									2	1					9
43	65			5			2			1	37		49			159	45			1			2			1	27		7			83
44										2	2					4										1	2					3
45	1										1				17	19	1										1				8	10
46													1			1													1			1
47			1													1			1													1
48				6												6				2												2
49													2			2													1			1
50													3			3													3			3
51											1					1											1					1
52	1															1	1															1
53	1															1	1															1
54	1															1	1															1
55	1															1	1															1
56	1															1	1															1
57	1															1	1															1
58	1															1	1															1
59	27									1						28	20									1						21
60	1															1	1															1
61	4									1						5	4									1						5
62									1							1									1							1
63		1														1		1														1
64	53									9						62	28									9						37
65	641		2	265	4		66			19	24		16	1	469	1507	179		1	38	1		21			9	7		2	1	54	313
66	201						13								10	224	54						4								1	59
67					15											15					10											10
68	161			1						6						168	87			1						4						92
69	26			5				3					12	6		52	14			4				3					3	5		29
70	13															13	9															9
71						15							2			17						9							2			11
72		3														3		3														3
73										2						2										2						2
74												1				1												1				1
75	2															2	2															2
76			8	77		32						5				122			6	13		2						1				22
77	2															2	1															1
78		1069											690			1759		138											68			206
79													1			1													1			1
80											4					4											1					1
81	2												27			29	2												2			4
82						19		3				4				26						6		1				3				10
83								2								2								2								2
84													10			10													5			5
85	2															2	2															2
86										1						1										1						1
87			2	48				1								51			2	15				1								18
88	3															3	1															1
89	7															7	6															6
90	6															6	6															6
91	4	1					2									7	2	1					1									4
92											1					1											1					1
93	7									1						8	6									1						7
94	32	172		9			12				11		240			476	19	39		3			8				8		49			126
95	12										4					16	6										3					9
96	4															4	2															2
97											1					1											1					1
98						1										1						1										1
99								1								1								1								1
100								1								1								1								1
101		1											15			16		1											1			2

	Matrix 1: visitation frequency																Matrix 2: individual flower visitors															
Pol\Pla	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Tot
102													2			2													1			1
103	9															9	6															6
104	1															1	1															1
105	23															23	15															15
106	7															7	1															1
107	33							1		2						36	25							1		2						28
108	2			2												4	2			2												4
109			1			12							2			15			1			9							2			12
110								1								1								1								1
111	1												1			2	1												1			2
112	11						1			3	3		2			20	9						1			3	2		1			16
113	4															4	3															3
114				1												1				1												1
115			4									1				5			3									1				4
116	1															1	1															1
117															1	1															1	1
118	1															1	1															1
119	1															1	1															1
120	1															1	1															1
121	1															1	1															1
122	1															1	1															1
123	1															1	1															1
124			4													4			2													2
125															16	16															2	2
126	9									1						10	7									1						8
127							8									8							3									3
128	1									3				1		5	1									2				1		4
129													3			3													1			1
Total	1933	1253	99	541	25	93	110	15	1	92	183	93	1216	8	516	6179	958	186	37	110	16	38	45	13	1	73	127	20	197	7	69	1897

VITA

Diego Pedro Vázquez was born on December 7th, 1970, in San Fernando, Buenos Aires, Argentina. As a young man, Diego attended the Jardín de Infantes Número 1 of San Fernando, and later the Escuela Nacional Normal Mixta "José Gervasio Artigas,"also in San Fernando, where he received his elementary school diploma in 1982 and his highschool diploma in 1988. He entered the University of Buenos Aires in 1989, where got his Licence diploma (Licenciatura) in Biology in 1995. He started a Ph.D. in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville, in August 1997, graduating in August 2002 with a dissertation on the interactions between herbivores, plants, and pollinators. He will join the National Center for Ecological Analysis and Synthesis in Santa Barbara, California, as a postdoctoral fellow in October 2002. He plans to return to Argentina and work as a researcher and university teacher.