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Biological interactions at different spatial scales in the Monte desert of Argentina

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ABSTRACT

In this review, we compiled published results on biological interactions at different spatial scales in the Monte desert of Argentina and identified gaps in current knowledge. We presented evidence of competitive and facilitative plant–plant conspecific and heterospecific interactions, and plant–soil–microbes interactions in relation to the abiotic environment at the fine patch-scale. We also showed evidence of animal–animal interactions and plant–animal interactions at the community scale through study cases involving both native and introduced herbivores. Moreover, we identified bottom-up and top-down forces governing the interactions between granivores (birds, ants, and small mammals) and seed availability/production at the community scale. At the landscape scale, we discussed feedbacks between domestic grazers and the spatial patterns of resources and their interrelationships with processes occurring at other scales. We concluded that research has steadily increased during the last 6 years but knowledge on biological interactions in the Monte desert is still scarce, particularly at a landscape scale.

1. Introduction

Arid ecosystems are characterized by a patchy spatial structure and highly stochastic water inputs. These abiotic drivers do exert strong control over ecosystem dynamics but not necessarily reduce the importance of biological interactions in structuring communities and landscapes (Chesson et al., 2004). We analysed biological interactions in the Monte desert of Argentina (Fig. 1) by compiling published results at spatial scales from patch to landscape, and integrated this knowledge within and across scales.

2. Biological interactions at the patch scale

2.1. Plant–plant interactions

Plant–plant interactions vary from positive to negative effects on the performance of neighbours (Armas and Pugnaire, 2005). Vegetation in the Monte desert of Argentina is characterized by a spotted two-phase mosaic formed by areas with high plant cover dominated by shrubs alternating with areas of scattered vegetation or bare soil (Bertiller et al., 2002c; Bisigato and Bertiller, 1997; Rossi and Villagra, 2003). As in other ecosystems (Montaña et al., 2001), shrub canopies create spatial heterogeneity in soil water and nutrient availability affecting plant processes (Bertiller et al., 2002a; Bisigato and Bertiller 2004a, b; Kröpfl et al., 2002; Mazzarino et al., 1998).

Studies on plant–plant conspecific interactions in the Monte desert of Argentina are extremely scarce. Several of them refer to *Poa ligularis*, a dioecious anemophilus grass highly preferred by herbivores (Pelliza Sbriller et al., 1997), with a wide distribution in this region. Bertiller et al. (2000, 2002a, b) analysed the spatial distribution of sexes of *P. ligularis* at three sites of the southern Monte with variable shrub-patch structure. They reported that as patch size and their area of influence increased, the density and the spatial segregation of the sexes of *P. ligularis* also increased, resulting in biased habitat-specific sex ratios. Females were more frequent at more protected and nitrogen/water-rich areas, and tolerated higher levels of intra/inter-sexual conspecific competition than males. In contrast, males tolerated low nitrogen concentration in soil and less shelter from wind at open areas, probably gaining advantage in pollen dispersal. However, with reduced shrub patch size and/or cover males and females concentrated at the borders of shrub patches leading to high intra/inter-sexual competition, and

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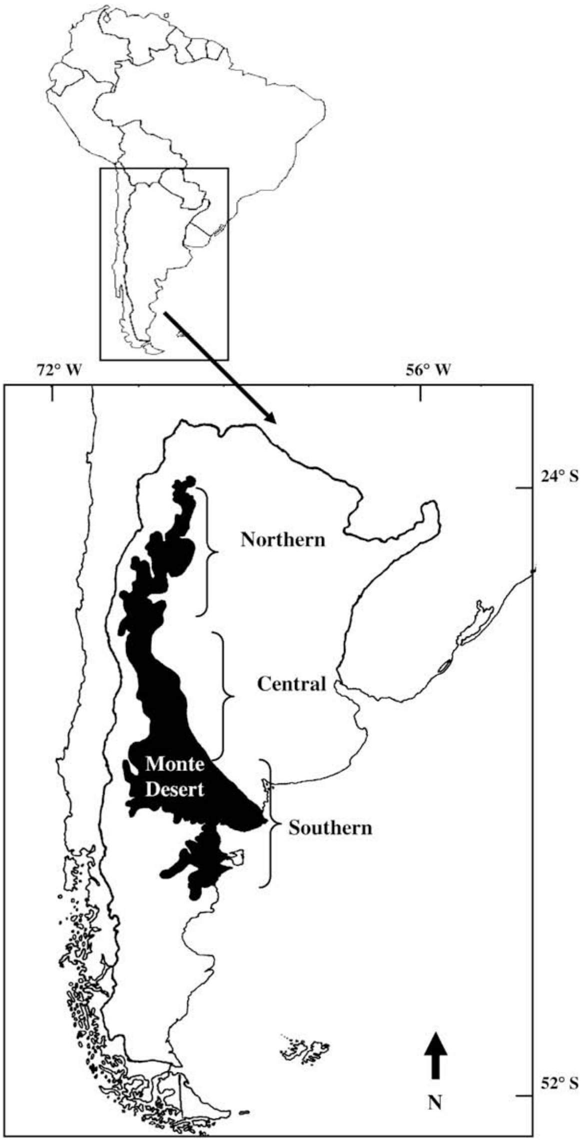

Fig. 1. Location of Monte desert of Argentina (black area) indicating the northern, central, and southern portion. Redrawn from Marone et al. (2000a).

the reduction of male and female populations. These studies set out evidence on morphological/functional sex dimorphism and spatial sex segregation in *P. ligularis* at different microenvironments induced by plant canopy resulting in avoidance of inter-sexual competition (Bertiller et al., 2000, 2002a, b). These findings suggest that both higher costs of female versus male reproduction and differences in competitive abilities between the sexes could be main causes of sex spatial segregation of *P. ligularis* as recently reported for other dioecious plant species (Eppley, 2006).

Several studies addressed plant–plant heterospecific interactions in the Monte desert of Argentina, particularly those between the woody matrix and herbaceous plants. Rossi and Villagra (2003) reported that the tree *Prosopis flexuosa* in the central Monte induced different microhabitats under its canopy by modification of the soil chemical properties and also probably by reduced incidence of sunlight and passive facilitation by providing perches for seed dispersing birds. In agreement with results in other ecosystems (Moro et al., 1997), trees, shrubs and grasses were differentially distributed across these microhabitats indicating different facilitation/competition balances at the microenvironments created by woody canopies. Woody life-forms were more abundant than most of the C_4 grasses at woody-canopy that at inter-canopy microhabitats and at northern than at southern canopy-microhabitats (Fig. 2a).These difference were associated with different ability of life forms to colonize contrasting microenvironments. C_4 grasses would benefit from high temperature, high radiation, and limited nutrient and water supply at inter-canopy microhabitats. In contrast, woody species would benefit from hot and dry microenvironments with high organic matter content and nutrient concentrations at the northern canopy sides. Bisigato and Bertiller (2004a) compared the temporal and microspatial patterning of seedling emergence and establishment of two cohorts of C_3 perennial grasses and shrubs at the southern Monte. Seedlings of perennial grasses were concentrated at the periphery of shrub patches. The emergence of perennial grasses was more frequent at the southern/western patch-periphery (more wet and cold) than at other patch-periphery locations. Established seedlings of perennial grasses, however, were homogeneously distributed along the patch periphery (Fig. 2b). The emergence of shrubs was more frequent at the centre and periphery of patches than at inter-patch microhabitats. In contrast, established seedlings of shrubs were homogeneously distributed among microhabitats (Fig. 2c). Only perennial grasses differed in seedling emergence between cohorts probably due to differences in the amount of precipitation in the year previous to the emergence. Bisigato and Bertiller (2004b) also showed that the recruitment of perennial grass seedlings is more affected by limiting seeds and water shortage than by the nurse plant (Fig. 2d). Accordingly, the establishment of C_3 perennial grasses was benefited from sheltered and water/nutrient rich microhabitats at the patch periphery but also by high seed concentration at these microhabitats (Bertiller, 1998).

In conclusion, plant establishment in the Monte of Argentina is strongly affected by the spatial variation in abiotic factors induced by the heterogeneity of the shrub matrix as reported for other arid ecosystems (Armas and Pugnaire, 2005). However, responses of perennial grasses to the spatial environmental heterogeneity created by woody canopies vary between the central and southern Monte probably in relation to different environmental requirements of the dominant C_4 and C_3 perennial grasses, respectively. Because of the ability to establish both at inter-patch and patch microhabitats, shrubs could be identified as colonizers or initiators of small plant patches in bare soil. Accordingly, as in other arid environments (Montaña et al., 2001), woody vegetation appear to have an important role in the origin, dynamics, and maintenance of spotted vegetation of the Monte desert. Further research should be oriented to identify the consequences of changes in the balance of positive and negative plant–plant interactions induced by abiotic factors at different scales for the structure and dynamics of plant community.

2.2. *Plant–soil–microbe interactions*

Carrera et al. (2003) reported that N-concentration in green leaves increased in perennial grasses and decreased in evergreen shrubs during wet years. A possible explanation for different inter-annual responses between both life forms is that fast-growing perennial grasses are more sensitive and can react more quickly to changing water inputs and N availability than slow-growing evergreen shrubs (Bertiller et al., 1991). Mazzarino et al. (1998) found that soil-N availability increased during wet years. This may result in fast growth of perennial grasses that would outcompete evergreen shrubs in capturing N from soil (Bertiller et al., 1991). Such negative interaction of perennial grasses with evergreen shrubs would be reflected in the reduction of N-concentration in green leaves of evergreen shrubs and in the lack of "luxury uptake" in this plant group, contrasting with results reported for other slow-growing species (Crawley, 1998). However, the microbial-N flush

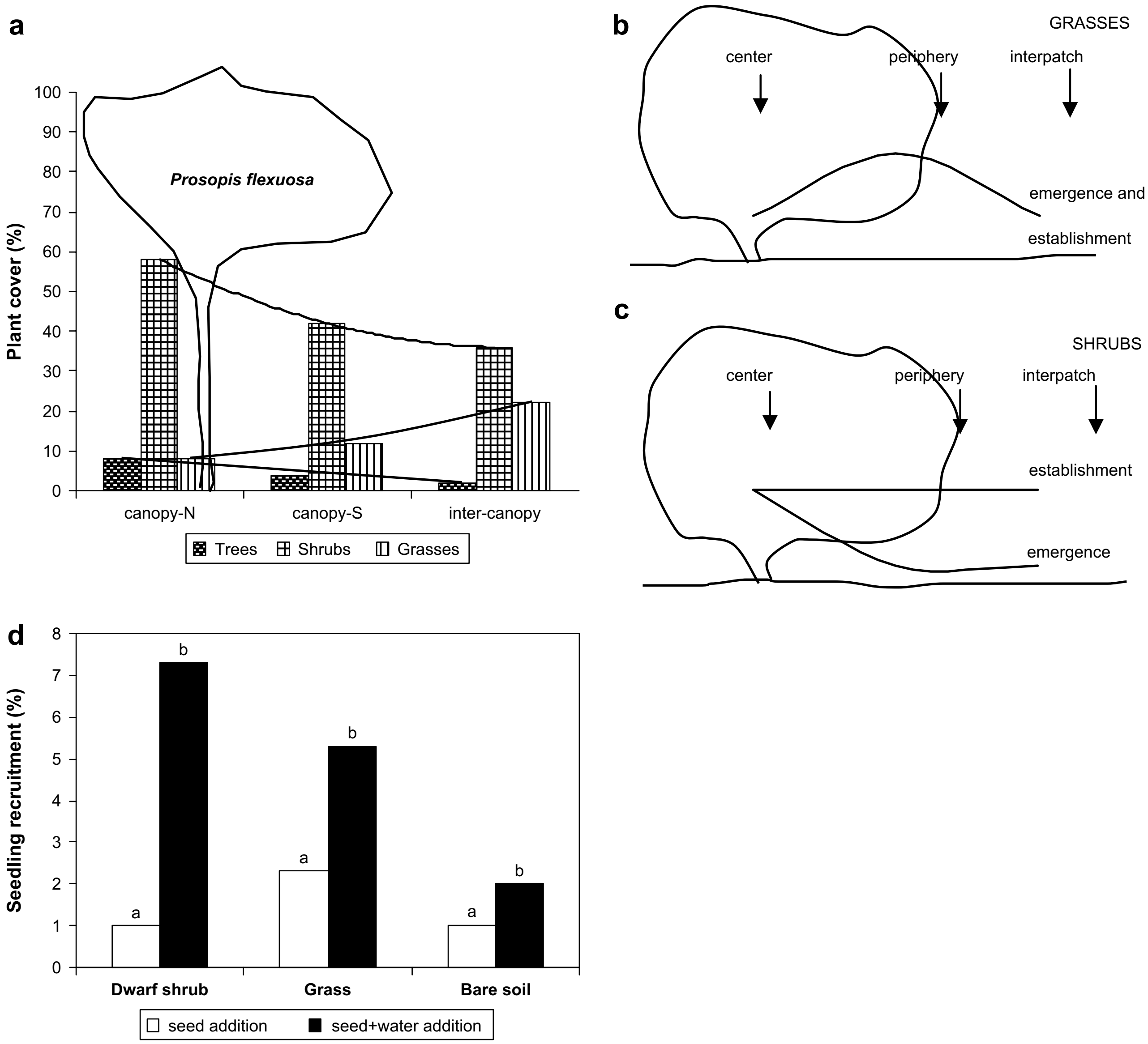

Fig. 2. Life form cover (trees, shrubs, grasses) at different microhabitats with respect to *P. flexuosa* canopy (north and south beneath canopy, inter-canopy) at the central Monte (a). Redrawn from Rossi and Villagra (2003). Emergence and establishment of grasses (b) and shrubs (c) with respect to shrub patches at the southern Monte. Redrawn from Bisigato and Bertiller (2004a). Seedling recruitment at different microsites (grass, dwarf shrub, bare soil) with addition of water and water plus seeds at the southern Monte (d). Redrawn from Bisigato and Bertiller (2004b).

was reduced in wet years indicating that roots of perennial grasses would outcompete both microorganisms and evergreen shrubs in capturing mineralized N (Aerts and Chapin, 2000). This evidence should be further explored since soil microorganisms are generally thought to be more competitive than plants for nutrients (Dunn et al., 2006).

3. Biological interactions at the community scale

3.1. Granivory

Seed predation may be an important plant–animal interaction in arid and semiarid ecosystems, where several plant species depend on seeds for recruitment. Under such conditions the soil seed bank uses to be abundant, a major guild of post-dispersal seed predators develops (Chambers and MacMahon, 1994), and granivory (i.e., the consumption of mostly herbaceous seeds, frequently weighting <1 mg, by ants, birds and small mammals) may be an important ecological force.

Mares and Rosenzweig (1978) measured seed removal rates through bait experiments in the northern Monte, and established the foundational base of this kind of studies in South America. Their main conclusions, however, appeared to be an obituary for such studies: "… total granivory is much depressed … granivorous mammals are rare and illadapted, ants are depauperate and not usually granivorous, and birds are unimportant seed consumers …". We herein assess the results of several bait removal experiments performed 25 years later, and discuss their extent and limitations. Our thesis is that knowledge on granivory in the Monte goes far from removal experiments, and that it only developed when natural history was seriously considered.

What did we learn from bait removal experiments?

López de Casenave et al. (1998) carried out a year-round experiment in open woodland of the central Monte. They found that seed removal rates vary seasonally and spatially, that ants are the most important granivores in spring-summer and birds in autumn-winter. The average rate of seed removal (all granivores) was 3.6 g tray^{-1} day^{-1}. In a similar trial, Saba and Toyos (2003) reported that birds were the main and most constant seedeaters during all seasons in the southern Monte. Average removal rate was about 1.0 g tray^{-1} day^{-1}. High seed removal by birds was also found in experiments carried out in semiarid habitats of central (Vásquez et al., 1995) and northern Chile (Kelt et al., 2004), which have some abundant bird species in common with the Monte (e.g., *Diuca diuca* and *Zonotrichia capensis*). Overall results imply that total seed removal was still low in the Monte compared to the 21.0 g tray^{-1} day^{-1} of Sonora (Mares and Rosenzweig, 1978), but higher than previous measurements (0.5 g tray^{-1} day^{-1}; Mares and Rosenzweig, 1978).

A last experiment carried out over three habitat types of the central Monte (Sassi et al., 2004) confirmed the high variance of seed removal rates among seasons and habitats together with a high level of granivory compared with the northern Monte. This study showed, however, some unexpected results: overall as well as rodent seed removal rates were often an order of magnitude greater than previous measures. A careful assessment of these results offers some keys to understand them. Firstly, Sassi et al. (2004) baited 50% of every tray with big sunflower seeds. Several Monte's rodent species are very efficient in removing and hoarding sunflower seeds (Giannoni et al., 2001) as well as other big seeds of native scrubs (Giannoni et al., 2005). By contrast, most previous experiments were baited with small grass seeds of *Phalaris, Setaria* or *Panicum* (Kelt et al., 2004; López de Casenave et al., 1998; Mares and Rosenzweig, 1978; Saba and Toyos, 2003; Vásquez et al., 1995). Higher removal of sunflower than smaller seeds can explain differences in overall seed removal rates. Second, there is a clear explanation for the prevalence of rodents as seed removers. Bird enclosures used by Sassi et al. (2004) were wire screen-wall cages (40×40×7 cm) with two 5-cm openings on each of the four walls "…to allow only murid rodents to enter…", according to author's words. Natural history suggests strongly that trays in this enclosure were visited by rodents as well as birds and, therefore, seed removal should be adjudicated to both taxa instead of rodents alone. Classical bait experiments distinguish bird from mammal removal by considering that all diurnal removal is caused by birds and all nocturnal removal by mammals. Although this assumption is only approximately true, the standardized procedure appears, however, much more appropriate that the cages used by Sassi et al. (2004) to exclude birds. But this is not the only trouble with seed bait experiments.

Overall seed removal rate in the Sonoran desert (Mares and Rosenzweig, 1978) was 42, 6 and 21 times higher than in the northern (Mares and Rosenzweig, 1978), central (López de Casenave et al., 1998) and southern Monte (Saba and Toyos 2003), respectively. The absolute value of seed removal in trays is artificial—in particular, artificially high—but the relative variation of such rate among sites should reflect true differences in nature. As a consequence, it seems reasonable to think that six times superior removal rates in Sonora than in the central Monte could not exist without concurrent huge differences in the number of available seeds. How much seeds should have Sonora's soils to make calculations realistic? Though linear and simplistic, we can attempt some general estimate. Given that seed production of edible seeds is about 6000 seeds m^{-2} in the Monte (Marone et al., 1998a), and that seed removal rate is six times lower than in Sonora, we would expect about 36,000 edible seeds m^{-2} (or 130 kg ha^{-1}) produced in Sonora. On the other hand, there is an average of 3000 edible seeds m^{-2} in the spring soil seed bank in the Monte (Marone et al., 2000b). Then, making a raw extrapolation, spring soil reserves in Sonora should be 18,000 edible seeds m^{-2}. This figure is unrealistic since average reserves of *total* seeds in Sonora are near 3000 seeds m^{-2} (range 400–7700 seeds m^{-2}; Kemp, 1989). Indeed, soil seed banks (Gutiérrez and Meserve, 2003; Marone and Horno, 1997; Marone et al., 2000a) as well as grass seed production are very similar in several South and North American desert sites at several scales (Marone and Horno, 1997; Marone et al., 2004). In sum, seed removal experiments alone do not allow to quantify correctly the ecological consequences of seed–consumer interactions. Only a research programme that uses multiple approaches including the assessment of animal diets and seed selection-preference patterns along with realistic enclosure and bait removal experiments and energetics can do that (Marone et al., 2000a).

What have we learnt from the research programme on granivory?

The diet of Emberizidae bird species is mostly composed by seeds during the dry autumn-winter season in the central Monte (López de Casenave et al., 2007), and these birds consume (Lopez de Casenave, 2001; Marone et al., 1998b) and prefer (Cueto et al., 2001, 2006) several grass seed species. Ants of the genus *Pogonoyrmex* consume almost exclusively grass seeds in the full wet season (Pirk and Lopez de Casenave, 2006; Pirk et al., 2004). Though rodents are not strictly granivorous in the Monte, at least one of them (*Calomys musculinus*) eats up to 30% grass seeds in the dry season (Giannoni et al., 2005). Which is the impact of granivory on grass seed populations? Marone et al. (1998a) measured >50% of post-dispersal grass-seed losses in autumn and winter 1995. Given that a minor fraction of grass seeds germinates or buries deeply in the soil, grass seed loss was adjudicated to predation, mainly by birds (Marone et al., 2000b). During dry periods, winter seed reserves of grasses may decay up to 80% of previous reserves (from 7233 seeds m^{-2} to 1370 seeds m^{-2}; Marone et al., 2000b) and seeds of some grass species may almost disappear from the soil (L. Marone unpublished). Under such scenario, top-down control over seed numbers, the amount of germinated seeds and, ultimately, grass seedling recruitment is plausible. Next step, however, is to corroborate and quantify experimentally seed losses under natural conditions, and to evaluate likely bottom-up effects by measuring the seed-to-seedling transition in grass species.

Another goal of granivory studies is to know whether fluctuations in seed resources can cause numerical or behavioural responses in animal consumers. Little is known about this kind of response in Monte's rodents and ants, although the great ability to sequester ephemeral resources by rodents (Giannoni et al., 2001, 2005) as well as ants (Pirk and Lopez de Casenave, 2006; Pol and Lopez de Casenave, 2004) may well be an adaptive consequence of bottom-up forces through evolutionary time. At the ecological time, bottom-up effects of seeds on birds have received more attention (Blendinger and Ojeda, 2001; Blendinger, 2005; Gonnet, 2001; Lopez de Casenave, 2001; López de Casenave et al., 2007; Marone, 1992; Marone et al., 1997; Milesi et al., 2002). According to Marone (1992) seed-eating birds of the central Monte are limited only occasionally by unusual periods of seed shortage. In a comparison over several sites across continents, including one in the northern Monte, Schluter and Repasky (1991) reported that overall seed reserves positively correlate with bird abundance and inferred continuous seed limitation and competition. Over three sites within the northern Monte, Blendinger and Ojeda (2001) found the same positive correlation during winter, and suggested that birds are limited by their seed resources. Nevertheless, they pointed out properly that owing that the most mobile bird species track patches of high seed availability in an opportunistic fashion, the association found does not necessarily imply changes in bird abundance at a regional scale nor seed limitation on bird populations *per se*. Finally, Lopez de Casenave (2001) thoroughly studied bottom-up effects on bird populations in the central Monte. He assessed medium and long-term annual variation in bird populations as well as seed and bird morphology, and used bioenergetic models to test the hypothesis of constant seed limitation and competition during winter months. His results show that such birds are not usually limited by food and could only be occasionally limited during unusual periods of seed shortage. In sum, the evidence is not easy to conciliate since some studies show continuous but others just occasional (and unusual) bottom-up control. The discrepancy—at least in the ecological time—may be mostly due to the fact that seeds and bird assemblages are open systems whose dynamics is difficult to study through mere correlations. Ecologists usually include very contrasting conditions in spatial comparisons (e.g., sites with a lot of seed resources together with sites with a few seed resources) which can overestimate the positive association between seeds and consumers. By contrast, temporal comparisons in undisturbed habitats (e.g., a year-to-year study in a reserve) use to be dominated by several intermediate conditions that can underscore true associations. Although these studies have apparently fixed the boundaries of likely bottom-up forces in the Monte, the ecological context that might promote the release of such forces should deserve more attention.

Granivory studies have gone far from the often inconclusive results of bait experiments. Once the research programme incorporated sound natural history, planned observation and careful field and laboratory experimentation, it revealed the plausibility of top-down as well as bottom-up forces in the Monte. The next step is to unveil how far they can go through the chain of ecological interactions.

3.2. *Interactions between plants and herbivores*

Although studies on plant–herbivore interactions in the Monte desert have been mainly focused on mammals, herbivorous insects are very diverse (Rundel et al., 2007) and play an important role in ecosystem function. For example, *Schistocerca americana* (Orthoptera) have a major impact on native and cultivated vegetation (Claver and Kufner, 1989). Among the ants, the leaf-cutting *Acromyrmex lobicornis* consumes as much green biomass as cattle in the central Monte of Mendoza (Claver, 2000). The dominant *Larrea* shrubs are under strong pressure by specialized, monophagous insects; and communities of phytophagous insects differ among the Zygophyllaceae of the central Monte (Debandi, 1999). Like in other deserts, solitary bees are the most important pollinators in the Monte (Rundel et al., 2007). Bee species visiting *Larrea* shrubs were found to vary across sites, microhabitats, seasons and even time of the day (Debandi et al., 2002; Rossi et al., 1999).

Nutritional properties of plants and the spatial and temporal availability of forage interact with the nutritional requirements of the animals to shape the feeding strategies (Gordon and Illius, 1996). For mammalian herbivores, body size and its morphological correlates play an important role in diet selection (Jarman, 1974; Robbins et al., 1995) as well as the type of digestive system (ruminants or hindgut fermenters) and adaptations to tolerate particular plant attributes (i.e. the presence of secondary compounds, lignin, dry matter, etc.; Hofmann and Stewart, 1972). Mammal species with larger body size tend to be predominantly herbivores rather than granivores or omnivores as smaller-sized species. In the Monte desert, while the small sigmodontine rodents are either omnivorous or tend to be granivorous, the largest sized rodents such as the hystricognaths, comprising the mara (*Dolichotis patagonum*), vizcacha (*Lagostomus maximus*) and two cavy species (*Microcavia australis* and *Galea musteloides*) are all herbivores (Campos et al., 2001a). Diet selection by the hystricognath rodents includes both mono and dicotyledoneous plants (Branch et al., 1994; Kufner and Pelliza Sbriller, 1987), as well as the diets of the introduced lagomorph European hare *Lepus europaeus* (Bonino et al., 1997), and the largest mammalian herbivores like the native guanaco (*Lama guanicoe*) and the introduced domestic sheep (Baldi et al., 2004; Pelliza Sbriller et al., 1997; Puig et al., 1997).

In the Monte Desert, the importance of herbivory by large rodents contrasts with the North American or African deserts where the native ungulate guild is more diverse than in South America (Bucher, 1987; Kerley, 1992; Ojeda et al., 2000). Although most mammals feed on a wide range of grass and shrub species, they do not consume the dominant creosote bush of the Monte (*Larrea* spp.), due to the secondary compounds that these plants produce (Rhoades, 1977). However, *Larrea* shrubs are heavily grazed by tuco-tucos and cavies (Borruel et al., 1998; Monge et al., 1994). These species reduce the cover of *Larrea* shrubs and several herb species (Campos et al., 2001b), as well as the survival of woody plants by gnawing (Campos et al., 2006).

3.3. *Herbivores and plant regeneration processes*

Several field studies indicated that more than 75% of the seeds are predated after dispersal (Crawley, 1998). However, many plants with hard and heavy seeds may profit from seed and fruit dispersal by animals (Gutterman, 1993). In the central Monte, mammals had different effects on dispersal and germination of *P. flexuosa.* Cattle and native rodents increased seed germination of this species after seed passage through the gut but at the expense of viability. Seed passage through horse's and grey fox's gut did not affect viability but it did not increase germination. In contrast, the European wild boar damaged all the seeds that it consumed (Campos and Ojeda, 1997). Herbivores affected the size of the soil seed bank, seedling emergence and establishment of perennial grasses but did not affect or eventually promote regeneration process of shrubs in the southern Monte (Bertiller, 1998; Bisigato and Bertiller, 2004a). These results, although scarce, set evidence of negative and positive interactions between herbivores and plant regeneration processes that should be further investigated in relation to the structure and dynamics of plant communities in the Monte desert of Argentina.

3.4. *Domestic herbivore–cryptogamic crust interactions*

Grazing by domestic herbivores reduced the overall richness of lichen species and the number of species per cryptogamic crust in the Monte of Argentina (Scutari et al., 2004). Both saxicolous (*Rinodina bischoffii*, *Caloplaca holocarpa*, *Catillaria lenticularis*, *Acarospora heppii*) and terricolous (*Lecanora dispersa, Psora decipiens, Rinodina mucronatula*) lichen species were the most sensitive to grazing disturbance. Among them, saxicolous lichens colonizing calcareous gravels were the most sensitive to heavy grazing probably due to animal trampling directly on lichens with large areoles such as *P. decipiens* or indirectly on calcareous gravels colonized by lichens as reported for other rangelands (Belnap and Lange, 2003). Species of terricolous lichens with dark, foliose thallus (*Collema coccophorum*), and lichens growing on siliceous gravels (*Aspicilia contorta*) were identified as the most resistant to grazing disturbance as in the case of Australian rangelands (Belnap and Lange, 2003). These results suggest that the knowledge on the structure and functioning of cryptogamic crusts is extremely scarce in the Monte of Argentina and more research is needed to identify how grazing effects on cryptogamic crusts affect patch, community, and ecosystem processes.

3.5. *Animal competition*

In addition to forage availability, inter-specific competition affects community structure (Putman, 1996). Potentially competing species should have similar preferences for food resources, they must overlap in habitat use, and food availability must be limited (Belovsky, 1986; de Boer and Prins, 1990; Putman, 1996). Competition is expected to result in the exclusion of a species or a change in the pattern of resource use in the presence of another species (Schoener, 1974). In contrast, coexistence results from a fundamental difference in resources preferred by two or more species

(Putman 1996), or when food is not limiting to herbivore populations (Belovsky, 1986).

Although studies on herbivore inter-specific competition are usually scarce, Baldi et al. (2001) showed evidence that competition between guanacos and the introduced sheep occurred and was probably a major force in structuring guanaco spatial and temporal distribution and abundance. Guanacos were the only large herbivores across the Monte and Patagonian deserts, until the massive introduction of sheep in the late 19th century. Both herbivore species largely overlap in their diets, especially during summer when forage plants are scarcer (Baldi et al., 2004). Guanacos and sheep preferred the same plant species, especially the grasses *Poa* spp. and *Stipa* spp. However, while sheep abundance was directly related to the environmental availability of *Poa* and *Stipa*, guanaco abundance was inversely related to them and to sheep abundance both in space and time (Baldi et al., 2001). Furthermore, sheep abundance was up to 40 times higher than guanacos in sympatric sites across the Monte and Patagonian steppe (Baldi et al., 1997, 2001). In fact, sheep abundance and its correlates accounted for most of the variation in guanaco abundance in space and time. While sheep ranching monopolized the most productive lands, guanacos were pushed to marginal habitats where the availability of the most important plant species in their diet were lower (Baldi, 1999; Baldi et al., 2001).

Other studies looking at dietary similarities between native and introduced herbivores have found that guanacos in sympatry with the introduced red deer (*Cervus elaphus*) overlap in the seasonal use of shrubs (Bahamonde et al., 1986). Likewise, European hares showed a high dietary overlap with maras in the Southern Monte of Rio Negro (Bonino et al., 1997), although specific studies to test competitive interactions have not yet been conducted.

3.6. Herbivore habitat selection

Plants are important not only in the composition of herbivore diets. Vegetation structure is often influential of the patterns of habitat use by bird and mammal species. For example small, less than 100 g mammals, were more abundant and diverse with increased vegetation density in the Andean foothills of Mendoza (Gonnet and Ojeda, 1998). However, at the microhabitat scale, while *Graomys griseoflavus* preferred closed habitats dominated by taller shrubs (Mares, 1977; Ojeda, 1989), *C. musculinus* occupied open, grass-dominated sites (Gonnet and Ojeda, 1998).

Habitat use is expected to result from the interaction of multiple factors such as food distribution, thermoregulation, social structure, the presence of competitors and predation risk among others. In the southern Monte, guanaco home range size is influenced both by group size, vegetation community structure within the home range and the occurrence of the breeding season (Burgi, 2005). Pioneering work by Taber (1987) and Taber and MacDonald (1992a, b) has shown that maras tend to build their breeding warrens in open habitats either in denudated or herbaceous clearings, while adults use both grass and shrub communities within a 40–60 ha drifting home-range around the breeding warren. More recently, Baldi (2007) found that mara pups born in warrens located in open habitats survived significantly better than those born at warrens in the shrubby sites, consistent with hypotheses on early detection of predators.

3.7. Predation on native and exotic herbivores

Selection of habitat types by animals interacts with predator avoidance strategies resulting of living in groups. Dilution effects and collective vigilance have been recently described for guanacos in the southern Monte, where hunting pressure by pumas (*Puma concolor*) is high (Baldi, unpublished data; Marino, 2005). Predators in the Monte and Patagonian Steppe include the puma, the culpeo (*Pseudalopex culpaeus*) and chilla fox (*Pseudalopex chilla*) among others. For these three species, Novaro et al. (2000) have found that native prey is less represented in their diets where exotic, introduced herbivores are abundant. It is likely that the introduction of exotic herbivores in large numbers have kept the numbers of native predators relatively high even after the decline of native herbivores (Novaro and Walker, 2005). In fact, puma predation may be limiting some guanaco populations at low densities even after sheep were removed or substantially reduced in numbers.

3.8. Human effects on biological interactions

We have shown that variation in food availability, the presence of potential competitors and predators will affect the way the animals use the resources and hence the way they are distributed in the environment. Thus, biological interactions known to occur in the Monte desert play a major role in community structure. But biological interactions are also influenced by human actions, which have dramatic effects on native communities. It is well known that habitat degradation following overgrazing by introduced domestic herbivores affects severely the native plant composition. Total plant cover can be drastically reduced by overgrazing, and changes in plant community structure from highly to less palatable plant species cannot be reverted in many cases even after reducing the grazing pressure (Beeskow et al., 1995; Bisigato and Bertiller, 1997).

As mentioned above, sheep ranching activities brought interspecific competition with the native guanaco (Baldi et al., 2001), and wildlife hunting is still widespread across the region (Baldi et al., 1997; Ojeda and Mares, 1982). In addition, management decisions often affected community structure in unexpected ways. For example, bounty hunting of pumas and culpeo fox implemented by provincial Governments apparently resulted in the reduction of carnivore densities across the region (Bellati and von Thungen, 1990). But at the same time predator populations have been subsidized by the maintenance of large numbers of introduced herbivores, and today the culpeo fox has expanded its range while pumas recolonized part of their former range (Novaro and Walker, 2005). As a result, native prey species occurring at low densities are more likely to be limited by predators, as it can be the case of the lesser rhea or choique (*Pterocnemia pennata*) which nest communally on the ground (Funes et al., 2000).

Habitat perturbation resulted in changes in abundance and species richness of small and medium sized mammals. While the loss of habitat complexity may favour some species like maras and the introduced European hare, smaller mammals were reported to decrease at grazed sites (Tabeni and Ojeda, 2003). At larger, landscape and regional scales, habitat loss due to human activities resulted in the spatial fragmentation and loss of functionality of guanaco populations, today occupying only 40% of their original distribution range (Cunazza et al., 1995; Puig, 1995).

The decline of wildlife species can be also associated with human activities in other ways than habitat modification and poaching. Introduced herbivores such as the sheep and hare may interact with native species through disease transmission. Evidence is showing than guanacos are exposed to sheep disease and parasites (Beldoménico et al., 2003; Karesh et al., 1998) and maras share Johne's disease and toxoplasmosis with the sheep and European hare (Marull et al., 2004). As human associated activities are widespread and have consequences at different spatial and temporal scales, it is a priority to understand the ecological processes affecting wild species population dynamics and interactions in order to predict how wildlife communities in the Monte can react to disturbance.

4. Biological interactions at the landscape scale

4.1. Plant–plant interactions as inferred from landscape structural cues

Structural observations at the landscape scale and results with spatial explicit models of the Monte vegetation are consistent with the hypothesis that main plant life forms (shrubs and herbaceous vegetation, including perennial grasses) share common resources and exclude each other at various levels of space occupancy. Low-altitude aerial photographs of southern Monte landscapes reveal a pattern of darker spots corresponding to major vegetation patches, formed by woody perennials (Ares et al., 2003a). These are distributed on a matrix of areas of lighter grey tone occupied by herbaceous perennials and grasses alternating with bare soil (Fig. 3a). This simple optical evidence of spatial exclusion of woody and herbaceous life-forms has been confirmed through intensive field sampling. Bisigato et al. (2002) observed the aerial volumes of shrubs and perennial grasses along field transects and found that they excluded each other when present at high volumes or co-occurred when at low volumes (Fig. 3b). A spatial explicit model assuming diffusion rules for plant spread at the observed characteristic growth rates for these life forms and spatial replacements rules like in Fig. 3b could also mimic these spatial relationships. The modelled plant canopies thus obtained satisfied simple descriptors of the plant patches, like distribution of their sizes and internal cover, as well as complex parameters of their co-occurring spatial arrangement based on Fourier signatures (Ares et al., 2003b; Bisigato et al., 2002). These findings confirmed the existence of a spotted landscape in contrast to banded landscapes common to other arid ecosystems (Tongway and Ludwig, 2001).

4.2. Domestic grazer effects on plant–plant interactions

Guevara et al. (1996a) reported that grasses are more important in the diet of free ranging cattle than shrubs at the central Monte

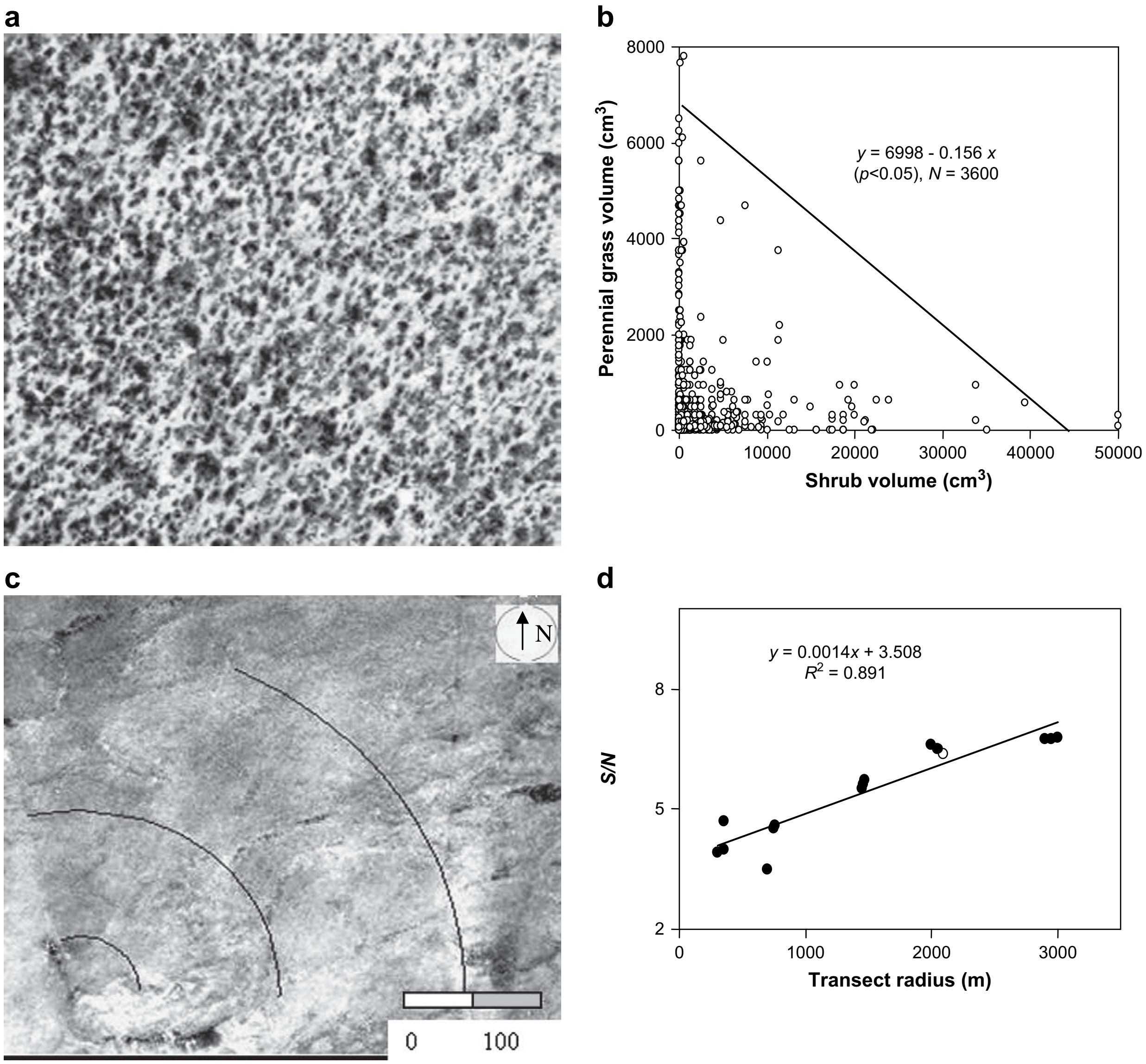

Fig. 3. A low altitude (460 m) panchromatic image of the Monte landscape. Dark spots correspond to patches dominated by woody shrubs, light grey areas to grass- and herbaceous-dominated areas and bare soil (a). Shrub and grass volumes recorded at blocks of 25×25 cm along field transects and line equation containing 95% of the observed data (b). Shrub encroachment near watering points at the Monte desert as inferred at a landscape scale from photo images of the plant canopy. The optical density of the photo image along circular transects centred at the watering point (lower left) was used to compute the *S*/*N* ratio (c). Values of the S/N ratio at varying distances (transect radii) to the watering point (d). Redrawn from Ares et al. (2003a, b, c).

during most of the year. Some grazing rotational schemes resulted in a significant decrease in total live basal cover and frequency of occurrence of the preferred grasses (Guevara et al., 1996b). Interactions of sheep flocks with the vegetation canopy are also evident through changes of shrub-grass dominance at a landscape scale in the southern Monte where sheep were introduced at the start of the last century. The magnitude of these effects has been inferred from changes in vegetation at places where sheep grazing has been discontinued during long periods (Bisigato et al., 2002) and in relatively small exclosures (1–3 ha) (Bisigato and Bertiller, 1997; Bisigato et al., 2005). Another group of evidence comes from field sampling at varying distances from constructed watering points. These define a piosphere with structural changes in the vegetation canopy at varying distances (a few metres up to 1500 m or more) around them (Beeskow et al., 1995; Bisigato et al., 2005; Guevara et al., 1996b, 2001). Asner and Heidebrecht (2003) reported shrub encroachment around watering places at the central Monte as detected through AVIRIS and Hyperion imagery and attributed it to shrub seed ingestion by cattle and further deposition near the watering places through faeces.

Other observations in the southern Monte are consistent with a mechanism of shrub encroachment through the occupation of open spaces when domestic grazers remove grass biomass. Ares et al. (2003b) developed the *S*/*N* parameter based on the Fast Fourier transform of contiguous plant cover data obtained in “ground truth” field transects. Bertiller et al. (2002c) found that this parameter is significantly positively correlated to the density of plant patches, the size of the patches, and the internal cover of the patch units. Accordingly, in the ecological sense, the *S*/*N* ratio is a meaningful indicator of patch development and patch aggregation. Ares et al. (2003b, c) calculated an *S*/*N* ratio of the optical densities in aerial photos at circular sampling transects of increasing radii around the watering points (Fig. 3c). They observed that the *S*/*N* ratio steadily increased with the distance to the watering point (Fig. 3d), an indication of shrub encroachment near the places most visited by sheep. These changes are consistent with those reported for other rangelands (Jeltsch et al., 1997).

4.3. Plant–domestic grazer interactions and feedbacks

There is also evidence that the structure of the plant canopy back-feeds into the grazing behaviour of sheep at the Monte fields. Bertiller and Ares (2006) and Ares et al. (2007) analysed paths of ewes collared with Geographic Positioning System (GPS) devices. Ewes used highly diverse paths across the range but always selected among a limited number of vegetation units. Selected vegetation units were those with structural traits allowing wide ewes’ visibility ranges and low structural anti-herbivore defences, irrespective of their local abundance, relative cover of edible plants or the distance to the watering point. Within those, ewes further selected patches offering high cover of edible plants and/or reduced structural/chemical anti-herbivore defences. In a hierarchy of decisions, the abundance of edible plants was not a sufficient condition for a high selection of vegetation units.

The emerging picture of plant effects on sheep behaviour at a landscape scale combines plant–plant interactions and feedback effects of changes occurring at the plant canopy over the sheep. Removal of preferred perennial species by sheep would alter the competition balance between these and the shrub components of the plant canopy. Tall woody components of this latter group would reduce horizontal visibility, causing avoidance by sheep. Eventually, the grass components would partially recover high values of aerial biomass, and extensive patches with high offer of these preferred species would remain unexplored by sheep because of reduced visibility and high anti-herbivore defences. The piosphere around watering points grows in extension as areas turn non-accessible to sheep. Structural evidence of plant–domestic grazer interactions and feedbacks at the landscape scale are thus consistent with plant–plant–grazer interactions observed at lower spatial scales in the southern Monte. Accordingly future research should be focussed to explore these interactions at the northern and central Monte.

5. Final remarks

Research on biological interactions in the Monte desert of Argentina has steadily increased in the last 6 years but there are still many aspects to be addressed in order to adequately assess the importance of biological interactions at the patch, community, and landscape scales and across them. This revision sets out evidence of (1) the importance of biological interactions at all spatial scales (from patch to landscape) as drivers of ecosystem dynamics, (2) top-down and bottom-up forces modelling biological interactions, and (3) the importance of man induced disturbance on the fate and outcome of biological interactions. The generalization of this evidence needs further research but a main knowledge gap is how biological interactions occurring at one spatial scale affect those at the other scales.

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References

Aerts, R., Chapin, F.S., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Advances in Ecological Research 30, 1–67.

Ares, J., Bertiller, M.B., Bisigato, A., 2003a. Modeling and measurement of structural changes at a landscape scale in dryland areas. Environmental Modeling and Assessment 8, 1–13.

Ares, J., Bertiller, M.B., Bisigato, A., 2003b. Estimates of dryland degradation in Argentina with Fourier signatures from low-altitude monochromatic images with high spatial resolution. Landscape Ecology 18, 51–63.

Ares, J., del Valle, H., Bisigato, A., 2003c. Detection of process-related changes in plant patterns at extended spatial scales during early dryland desertification. Global Change Biology 9, 1643–1659.

Ares, J.O., Dignani, J., Bertiller, M.B., 2007. Cost analysis of remotely sensed foraging paths in patchy 4 landscapes with plant anti-herbivore defenses (Patagonia, Argentina). Landscape Ecology, in press, doi:10.1007/s10980-007-9107-5.

Armas, C., Pugnaire, F.I., 2005. Plant interactions govern population dynamics in a semi-arid plant community. Journal of Ecology 93, 978–989.

Asner, G.P., Heidebrecht, K.B., 2003. Imaging spectroscopy for desertification studies: comparing AVIRIS and EO-1 Hyperion in Argentina Drylands. IEEE Transactions on Geoscience and Remote Sensing 41, 1283–1296.

Bahamonde, N., Martin, S., Pelliza Sbriller, A., 1986. Diet of guanaco and red deer in Neuquen Province, Argentina. Journal of Range Management 39, 22–24.

Baldi, R., 1999. The distribution and feeding strategy of guanacos in the Argentine Patagonia: a sheep dependent scenario. Ph.D. Dissertation, University of London, London, 167 pp.

Baldi, R., 2007. Breeding success of the endemic mara *Dolichotis patagonum* in relation to habitat selection: conservation implications. Journal of Arid Environments 68, 9–19.

Baldi, R., Campagna, C., Saba, S., 1997. Abundancia y distribución del guanaco (*Lama guanicoe*) en el NE del Chubut, Patagonia Argentina. Mastozoología Neotropical 4, 5–15.

Baldi, R., Albon, S.D., Elston, D.A., 2001. Guanacos and sheep: evidence for continuing competition in arid Patagonia. Oecologia 129, 561–570.

Baldi, R., Pelliza-Sbriller, A., Elston, D., Albon, S.D., 2004. High potential for competition between guanacos and sheep in Patagonia. Journal of Wildlife Management 68, 924–938.

Beeskow, A.M., Elissalde, N.O., Rostagno, C.M., 1995. Ecosystem changes associated with grazing intensity on the Punta Ninfas rangelands of Patagonia, Argentina. Journal of Range Management 48, 517–522.

Beldoménico, P.M., Uhart, M., Bono, M.F., Marull, C., Baldi, R., Peralta, J.L., 2003. Internal parasites of free-ranging guanacos from Patagonia. Veterinary Parasitology 118, 71–77.

Bellati, J., von Thungen, J., 1990. Lamb predation in Patagonian ranches. In: Davis, L.R., Marsh, R.E. (Eds.), Proceedings of the 14th Vertebrate Pest Conference. University of California, Davis, CA, USA, pp. 263–268.

Belnap, J., Lange, O.L., 2003. Biological Soil Crusts: Structure, Function, and Management. Ecological Studies, vol. 150. Springer, Berlin, Heildelberg. 503 pp.

Belovsky, G.E., 1986. Generalist herbivore foraging and its role in competitive interactions. American Zoologist 26, 51–59.

Bertiller, M.B., 1998. Spatial patterns of the germinable soil seed bank in northern Patagonia. Seed Science Research 8, 39–45.

Bertiller, M.B., Ares, J., 2006. Patrones espaciales de uso ovino de la vegetación del Monte Patagónico. In: Proceedings of the XXII Reunión Argentina de Ecología, Córdoba, Argentina, 22–25 August 2006, p. 282.

Bertiller, M.B., Beeskow, A.M., Coronato, F., 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). Journal of Arid Environments 21, 1–11.

Bertiller, M.B., Ares, J.O., Graff, B.P., Baldi, R., 2000. Sex-related patterns of *Poa ligularis* in relation to shrub patch occurrence in northern Patagonia. Journal of Vegetation Science 11, 9–14.

Bertiller, M.B., Sain, C.L., Bisigato, A.J., Coronato, F.R., Ares, J.O., Graff, P., 2002a. Spatial sex segregation in the dioecious grass *Poa ligularis* in northern Patagonia: the role of environmental patchiness. Biodiversity and Conservation 11, 69–84.

Bertiller, M.B., Sain, C.L., Carrera, A.L., 2002b. Effect of fine-scale spatial variation of soil nitrogen on the performance of the sexes of *Poa ligularis* in patchy ecosystems of northern Patagonia. International Journal of Plant Sciences 163, 419–425.

Bertiller, M.B., Ares, J., Bisigato, A., 2002c. Multiscale indicators of land degradation in the Patagonian Monte, Argentina. Environmental Management 30, 704–715.

Bisigato, A., Bertiller, M.B., 1997. Grazing effects on patchy dryland vegetation in northern Patagonia. Journal of Arid Environments 36, 639–653.

Bisigato, A.J., Bertiller, M.B., 2004a. Temporal and micro-spatial patterning of seedling establishment. Consequences for patch dynamics in the southern Monte, Argentina. Plant Ecology 174, 235–246.

Bisigato, A., Bertiller, M.B., 2004b. Seedling recruitment of perennial grasses in degraded areas of the Patagonian Monte. Journal of Range Management 57, 191–196.

Bisigato, A., Ares, J., Bertiller, M.B., 2002. Assessment of pristine vegetation structure in semiarid shrublands based on spatial explicit modeling. Phytocoenologia 32, 581–596.

Bisigato, A., Bertiller, M.B., Ares, J., Pazos, G., 2005. Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. Ecography 28, 561–572.

Blendinger, P.G., 2005. Abundance and diversity of small-bird assemblages in the Monte desert, Argentina. Journal of Arid Environment 61, 567–587.

Blendinger, P.G., Ojeda, R.A., 2001. Seed supply as a limiting factor for granivorous bird assemblages in the Monte Desert, Argentina. Austral Ecology 26, 413–422.

Bonino, N., Sbriller, A., Manacorda, M.M., Larosa, F., 1997. Food Partitioning between the mara (*Dolichotis patagonum*) and the introduced hare (*Lepus europaeus*) in the Monte desert, Argentina. Studies on Neotropical Fauna and Environment 32, 129–134.

Borruel, N., Campos, C., Gioanonni, S.M., Borghi, C.E., 1998. Effect of herbivorous rodents (cavies and tuco-tucos) on a shrub community in the Monte Desert, Argentina. Journal of Arid Environments 39, 33–37.

Branch, L.C., Villarreal, D., Pelliza Sbriller, A., Sosa, R.A., 1994. Diet selection of the plains vizcacha (*Lagostomus maximus,* family Chinchillidae) in relation to resource abundance in semi-arid scrub. Canadian Journal of Zoology 72, 2210–2216.

Bucher, E.H., 1987. Herbivory in arid and semi-arid regions of Argentina. Revista Chilena de Historia Natural 60, 265–273.

Burgi, M.V., 2005. Radio de acción y uso de hábitat en hembras de guanaco (*Lama guanicoe*) en el NE de Chubut. Tesis de Lincenciatura en Ciencias Biológicas. Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia.

Campos, C.M., Ojeda, R., 1997. Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. Journal of Arid Environments 35, 707–714.

Campos, C., Ojeda, R., Monge, S., Dacar, M., 2001. Utilization of food resources by small and medium-sized mammals in the Monte Desert biome, Argentina. Austral Ecology 26, 142–149.

Campos, C., Giannoni, S.M., Borghi, C.E., 2001. Changes in Monte Desert plant communities induced by a subterranean mammal. Journal of Arid Environments 47, 339–345.

Campos, C.M., Borghi, C.E., Giannoni, S.M., Mangeaud, A., Tognelli, M.F., 2006. Bark consumption of cerosote bush (*Larrea cuneifolia*) by cuises (*Microcavia australis*): effect on branch survival and reproduction. Ecología Austral 16, 1–6.

Carrera, A.L., Bertiller, M.B., Sain, C.L., Mazzarino, M.J., 2003. Relationship between plant nitrogen conservation and the dynamics of soil nitrogen in the arid patagonian Monte, Argentina. Plant and Soil 255, 595–604.

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25, 263–292.

Chesson, P., Gebauer, R.I., Schiwinning, S., Huntly, S., Wiegand, K., Ernst, M., Sher, A., Novoplansky, A., Weltzin, J., 2004. Resource pulses, species interactions, and diversity maintainance in arid and semiarid environments. Oecologia 141, 236–253.

Claver, S., 2000. Ecología de *Acromyrmex lobicornis* (E.) (Hymenoptera: Formicidae) en la Reserva de Biosfera de Ñacuñán, Provincia Biogeográfica del Monte. Preferencia de hábitat, abundancia de colonias y patrones de actividad. Tesis Doctoral, Universidad Nacional de La Plata.La Plata.

Claver, S., Kufner, M.B., 1989. La fauna de invertebrados de zonas áridas y sus relaciones con el sobrepastoreo y la desertificación. In: IADIZA, Detección y control de la Desertificación. UNEP, Mendoza, pp. 287–293.

Crawley, M.J., 1998. Life history and environment. In: Crawley, M.J. (Ed.), Plant Ecology. Blackwell Science, Oxford, pp. 73–131.

Cueto, V.R., Marone, L., Lopez de Casenave, J., 2001. Seed preferences by birds: effects of the design of feeding-preference experiments. Journal of Avian Biology 32, 275–278.

Cueto, V.R., Marone, L., Lopez de Casenave, J., 2006. Seed preferences in sparrow species of the Monte desert: implications for seed–granivore interactions. Auk 123, 358–367.

Cunazza, C., Puig, S., Villalba, L., 1995. Situación actual del guanaco y su ambiente. In: Puig, S. (Ed.), Técnicas para el manejo del guanaco. UICN, Gland, Switzerland, pp. 27–53.

Debandi, G., 1999. Dinámica de la comunidad de artrópodos asociados a Larrea (Zygophyllaceae). Tesis Doctoral, Universidad Nacional de La Plata.

Debandi, G., Rossi, B.E., Araníbar, J., Ambrosetti, J.A., Peralta, I., 2002. Breeding system of *Bulnesia retama* (Gill. ex Hook.) Gris. (Zygophyllaceae) in the central Monte Desert (Mendoza, Argentina). Journal of Arid Environments 51, 141–152.

de Boer, W.F., Prins, H.H.T., 1990. Large herbivores that strive mightily but eat and drink as friends. Oecologia 82, 264–274.

Dunn, R.M., Mikola, J., Bol, R., Bardgett, R.D., 2006. Influence of microbial activity on plant–microbial competition for organic and inorganic nitrogen. Plant and Soil 289, 321–334.

Eppley, S.M., 2006. Females make tough neighbors: sex-specific competitive effects in seedlings of a dioecious grass. Oecologia 146, 549–554.

Funes, M.C., Rosauer, M.M., Sanchez Aldao, G., Monsalvo, O.B., Novaro, A.J., 2000. Manejo y conservación del choique en la Patagonia. Informe 2da etapa: Análisis de los relevamientos poblacionales. Report to Centro de Ecología Aplicada del Neuquén, Argentina. 27 pp.

Giannoni, S.M., Dacar, M., Taraborelli, P., Borghi, C.E., 2001. Seed hoarding by rodents of the Monte Desert, Argentina. Austral Ecology 26, 259–263.

Giannoni, S.M., Borghi, C.E., Dacar, M., Campos, C.M., 2005. Main food categories in diets of sigmodontine rodents in the Monte (Argentina). Mastozoología Neotropical 12, 181–187.

Gonnet, J.M., 2001. Influence of cattle grazing on population density and species richness of granivorous birds (Emberizidae) in the arid plain of the Monte, Argentina. Journal of Arid Environments 48, 569–579.

Gonnet, J.M., Ojeda, R.A., 1998. Habitat use by small mammals in the arid Andean foothills in the Monte Desert of Mendoza, Argentina. Journal of Arid Environments 38, 349–357.

Gordon, I.J., Illius, A.W., 1996. The nutritional ecology of African ruminants: a reinterpretation. Journal of Animal Ecology 65, 18–28.

Guevara, J.C., Stasi, C.R., Estevez, O.R., 1996a. Seasonal specific selectivity by cattle on rangeland in the Monte Desert, Mendoza, Argentina. Journal Arid Environments 34, 125–132.

Guevara, J.C., Stasi, C.R., Estevez, O.R., 1996b. Effect of cattle grazing on range perennial grasses in the Mendoza plain, Argentina. Journal Arid Environments 34, 205–213.

Guevara, J.C., Gonnet, J.M., Estevez, O.R., 2001. Impact of cattle grazing on native perennial grasses in the arid rangelands of the Mendoza plain, Argentina. In: Prakash, I. (Ed.), Ecology of Desert Environments. Scientific Publisher, Jodhpur.

Gutiérrez, J.R., Meserve, P.L., 2003. El Niño effects on the soil seed bank dynamics in north-central Chile. Oecologia 134, 511–517.

Gutterman, Y., 1993. Seed germination in desert plants. In: Cloudsley Thompson, J.L. (Ed.), Adaptations of Desert Organisms Series. Springer, Berlin.

Hofmann, R.R., Stewart, D.R.M., 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36, 226–240.

Jarman, P.J., 1974. The social organisation of antelope in relation to their ecology. Behaviour 48, 215–267.

Jeltsch, F., Milton, S.J., Dean, D.R.J., van Rooyen, N., 1997. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. Journal of Vegetation Science 8, 177–188.

Karesh, W.B., Uhart, M.M., Dierenfeld, E.S., 1998. Health evaluation of free-ranging guanaco (*Lama guanicoe*). Journal of Zoo and Wildlife Medicine 29 (2), 134–141.

Kelt, D.A., Meserve, P.L., Gutiérrez, J.R., 2004. Seed removal by small mammals, birds and ants in semi-arid Chile, and comparison with other systems. Journal of Biogeography 31, 931–942.

Kemp, P.R., 1989. Seed bank and vegetation processes in deserts. In: Allessio-Leck, M., Parker, V.T., Simpson, R.L. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 257–281.

Kerley, G.I.H., 1992. Trophic status of small mammals in the semi-arid Karoo, South Africa. Journal of Zoology 226, 563–572.

Kröpfl, A.I., Cecchi, G.A., Villasuso, N.M., Distel, R., 2002. The influence of *Larrea divaricata* on soil moisture and on water status and growth of *Stipa tenuis* in southern Argentina. Journal Arid Environments 52, 29–35.

Kufner, M., Pelliza Sbriller, A., 1987. Composición botánica de la dieta del mara (*Dolichotis patagonum*) y del ganado bovino en el monte mendocino. Revista Argentina de Producción Animal 7, 255–264.

Lopez de Casenave, J., 2001. Estructura gremial y organicación de un ensamble de aves del desierto del Monte. Doctoral Thesis, Universidad de Buenos Aires, Buenos Aires.

López de Casenave, J., Cueto, V.R., Marone, L., 1998. Granivory in the Monte desert: is it less intense than in other arid zones of the world? Global Ecology and Biogeography Letters 7, 197–204.

López de Casenave, J., Cueto, V.R., Marone, L., 2007. Seasonal dynamics of guild structure in a bird assemblage of the central Monte desert. Basic and Applied Ecology, in press, doi:10.1016/j.baae.2006.08.006.

Mares, M., 1977. Water balance and other ecological observations on three species of *Phyllotis* in northwestern Argentina. Journal of Mammalogy 4, 514–520.

Mares, M.A., Rosenzweig, M.L., 1978. Granivory in North and South American deserts: rodents, birds, and ants. Ecology 59, 235–241.

Marino, A., 2005. Efecto del tamaño de grupo sobre los presupuestos de actividad del guanaco (*Lama guanicoe*) en el NE de Chubut. Tesis de Lincenciatura en Ciencias Biológicas. Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia.

Marone, L., 1992. Seasonal and year-to-year fluctuations of bird populations and guilds in the Monte desert, Argentina. Journal of Field Ornithology 63, 294–308.

Marone, L., Horno, M.E., 1997. Seed abundance in the central Monte desert, Argentina: implications for granivory. Journal of Arid Environments 36, 661–670.

Marone, L., Lopez de Casenave, J., Cueto, V.R., 1997. Patterns of habitat selection by wintering and breeding granivorous birds in the central Monte desert, Argentina. Revista Chilena de Historia Natural 70, 73–81.

Marone, L., Rossi, B.E., Horno, M.E., 1998. Timing and spatial patterning of seed dispersal and redistribution in a South American warm desert. Plant Ecology 137, 143–150.

Marone, L., Rossi, B.E., López de Casenave, J., 1998. Granivore impact on soil-seed reserves in the Monte desert, Argentina. Functional Ecology 12, 640–645.

Marone, L., López de Casenave, J., Cueto, V.R., 2000. Granivory in the southern South American deserts: conceptual issues and current evidence. BioScience 50, 123–132.

Marone, L., Horno, M.E., González del Solar, R., 2000. Post-dispersal fate of seeds in the Monte desert of Argentina: patterns of germination in successive wet and dry years. Journal of Ecology 88, 940–949.

Marone, L., Cueto, V.R., Milesi, F.A., Lopez de Casenave, J., 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. Canadian Journal of Botany 82, 1809–1816.

Marull, C., Marticorena, D., Baldoménico, P., Baldi, R., Uhart, M., 2004. Interacción epidemiológica entre la mara *Dolichotis patagonum* y especies introducidas en la Patagonia Argentina. Abstracts of the 2nd Argentine-Chilean Ecology Meeting. Mendoza, Argentina, p. 263.

Mazzarino, M.J., Bertiller, M.B., Sain, C., Satti, P., Coronato, F., 1998. Soil nitrogen dynamics in northeastern Patagonia steppe under different precipitation regimes. Plant and Soil 202, 125–131.

Milesi, F.A., Marone, L., Lopez de Casenave, J., Cueto, V., Mezquida, E.T., 2002. Gremios de manejo como indicadores de las condiciones del ambiente: un estudio de caso con aves y perturbaciones del hábitat en el Monte central, Argentina. Ecología Austral 12, 149–161.

Monge, S., Dacar, M., Roig, V.G., 1994. Comparación de dietas de cuises en la Reserva de la Biosfera de Ñacuñán (Santa Rosa, Mendoza, Argentina). Vida Silvestre Neotropical 3, 115–117.

Montaña, C., Seghieri, J., Cornet, A., 2001. Vegetation dynamics: recruitment and regeneration in two-phase mosaics. In: Tongway, D.J., Valentin, C., Seghieri, J. (Eds.), 2001. Banded Vegetation Patterning in Arid and Semiarid Environments. Ecological Processes and Consequences for Management. Ecological Studies, vol. 149. Springer, Berlin, pp. 132–145.

Moro, M.J., Pugnaire, F.I., Haase, P., Puigdefabregas, J., 1997. Effect of the canopy of *Retama spaherocarpa* on its understorey in a semiarid environment. Fuctional Ecology 11, 425–431.

Novaro, A.J., Walker, R.S., 2005. Human-induced changes in the effect of top carnivores on biodiversity in Patagonia. In: Ray, J.C., Berger, J., Redford, K.H., Steneck, R. (Eds.), Large Carnivores and the Conservation of Biodiversity. Island Press, pp. 267–287.

Novaro, A.J., Funes, M.C., Walker, R.S., 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. Biological Conservation 92, 25–33.

Ojeda, R.A., 1989. Small mamad responses to fire in the Monte desert, Argentina. Journal of Mammalogy 70, 416–420.

Ojeda, R.A., Mares, M.A., 1982. Conservation of South American mammals: Argentina as a paradigm. In: Mares, M.A., Genoways, H.H. (Eds.), Mammalian Biology in South America. Special Publication Series. Pymatuning Laboratory of Ecology. University of Pittsburg, Pennsylvania, pp. 505–521.

Ojeda, R.A., Blendinger, P.G., Brandl, R., 2000. Mammals in South American drylands: faunal similarity and trophic structure. Global Ecology and Biogeography 9, 115–124.

Pelliza Sbriller, A., Willems, P., Nakamatsu, V., Manero, A., 1997. Atlas dietario de herbívoros Patagónicos. In: Somlo, R. (Ed.), PRODESAR-INTA-GTZ. Bariloche, Argentina.

Pirk, G.I., Lopez de Casenave, J., 2006. Diet and seed removal rates by the harvester ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the central Monte desert, Argentina. Insectes Sociaux 53, 119–125.

Pirk, G.I., Lopez de Casenave, J., Pol, R.G., 2004. Asociación de las hormigas granívoras *Pogonomyrmex pronotalis*, *P. rastratus* y *P. inermis* con caminos en el Monte central. Ecología Austral 14, 65–76.

Pol, R.G., Lopez de Casenave, J., 2004. Activity patterns of harvester ants *Pogonomyrmex pronotalis* and *Pogonomyrmex rastratus* in the central Monte desert, Argentina. Journal of Insect Behaviour 17, 647–661.

Puig, S., 1995. Uso de los recursos ambientales por el guanaco. In: Puig, S. (Ed.), Técnicas para el manejo del guanaco. UICN, Gland, Switzerland, pp. 119–134.

Puig, S., Videla, F., Cona, M.I., 1997. Diet and abundance of the guanaco (Lama guanicoe Muller 1776) in four habitats of northern Patagonia, Argentina. Journal of Arid Environments 36, 343–357.

Putman, R.J., 1996. Competition and Resource Partitioning in Temperate Ungulate Assemblies. Chapman & Hall, London.

Rhoades, D.F., 1977. The antiherbivore chemistry of *Larrea*. In: Mabry, T.J., Hunziker, J.H., DiFeo, D.R.J. (Eds.), Creosote Bush: Biology and Chemistry of Larrea in New World Deserts. Dowden, Hutchinson and Ross, Inc., Pennsylvania, pp. 135–175.

Robbins, C.T., Spalinger, D.E., van Hoven, W., 1995. Adaptations of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? Oecologia 103, 208–213.

Rossi, B.E., Villagra, P.E., 2003. Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understorey species in arid Argentina. Journal of Vegetation Science 14, 543–550.

Rossi, B.E., Debandi, G.O., Peralta, I.E., Martinez, E., 1999. Comparative phenology and floral patterns in Larrea species (Zygophyllaceae) in the Monte desert (Mendoza, Argentina). Journal of Arid Environments 43, 213–226.

Rundel, P., Villagra, P.E., Dillon, M.O., Roig-Juñent, S.A., Debandi, G., 2007. Arid and semi-arid ecosystems. In: Veblen, T.T., Young, K., Orme, A.e. (Eds.), The Physical Geography of South America. Oxford University Press, Oxford, pp. 158–183, in press.

Saba, S.L., Toyos, A., 2003. Seed removal by birds, rodents and ants in the Austral portion of the Monte Desert, Argentina. Journal of Arid Environments 53, 115–124.

Sassi, P.L., Tort, J., Borghi, C.E., 2004. Effect of spatial and temporal heterogeneity on granivory in the Monte Desert, Argentina. Austral Ecology 29, 661–666.

Schluter, D., Repasky, R.R., 1991. Worldwide limitation of finch densities by food and other factors. Ecology 72, 1763–1774.

Schoener, T.W., 1974. Competition and the form of habitat shift. Journal of Theoretical Population Biology 6, 265–307.

Scutari, N., Bertiller, M.B., Carrera, A., 2004. Soil-associated lichens in rangelands of north-eastern Patagonia. Their potential as bioindicators of conservation and grazing disturbance. The Lichenologist 36, 405–412.

Tabeni, S., Ojeda, R.A., 2003. Assessing mammal responses to perturbations in temperate aridlands of Argentina. Journal of Arid Environments 55, 715–726.

Taber, A.W., 1987. The behavioural ecology of the mara *Dolichotis patagonum*. Ph.D. Dissertation, University of Oxford, Oxford.

Taber, A.W., MacDonald, D.W., 1992. Communal breeding in the mara, *Dolichotis patagonum*. Journal of Zoology (London) 227, 439–452.

Taber, A.W., MacDonald, D.W., 1992. Spatial organization and monogamy in the mara *Dolichotis patagonum*. Journal of Zoology (London) 227, 417–438.

Tongway, D.J., Ludwig, J.A., 2001. Theories on the origins, maintenance, dynamics, and functioning of banded landscapes. In: Tongway, D.J., Valentin, C., Seghieri, J. (Eds.), 2001. Banded Vegetation Patterning in Arid and Semiarid Environments. Ecological Processes and Consequences for Management. Ecological Studies, vol. 149. Springer, Berlin, pp. 20–31.

Vásquez, R.A., Bustamante, R.O., Simonetti, J.A., 1995. Granivory in the Chilean matorral: extending the information on arid zones of South America. Ecography 18, 403–409.