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Indirect effects of exotic grazers: livestock decreases the nutrient content of refuse dumps of leaf-cutting ants through vegetation impoverishment

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Abstract

1. We present evidence of how exotic grazers can indirectly change the nutrient availability on the soil surface by affecting the quality of refuse dumps of leaf-cutting ants through changes in vegetation. Understanding the mechanisms involved in this process is vital to propose proper control and restoration practices.

2. In the Monte Desert of Argentina, we sampled seven paddocks with similar environmental conditions but different stocking rates (individuals ha^{-1}). In each paddock we measured grazing intensity, plant species number and cover, leaf-cutting ant nest density, leaf-cutting ant diet and the nutrient content of the external ant refuse dumps and of the adjacent non-nest soils. We found higher content of N, C and P in refuse dumps than in non-nest soils, but the strength of this effect decreased with an increase in stocking rates. As stocking rate increased, plant richness and cover, the number of plant species harvested by ants and the nutrient content of their refuse dumps all decreased. Nest density was not affected by stocking rates.

3. These results suggests that livestock reduce plant richness and cover through grazing, affecting ant diet with the subsequent alteration of the nutrient content of their external refuse dumps. A decrease in the nutrient quality of the refuse dumps may affect plants that establish and grow on this substrate and the rate of nutrient cycling.

4. *Synthesis and applications*. We have shown that negative effects of exotic grazers on plants may spread throughout native insect herbivores to affect soil nutrient availability. These results can provide useful information to prevent soil impoverishment and restore the nutrient content of soils in this managed system. A slight reduction in stocking rates can restore the contribution of ants to soil fertility. Additionally, refuse dumps from paddocks with low grazing levels should be employed as fertilizer to restore soil quality in paddocks with high grazing intensities.

Key-words: *Acromyrmex lobicornis*, ant debris, exotic mammals, grazing, indirect interactions, Patagonia, soil nutrients.

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Introduction

Besides the well-known direct effects on the native plant species, introduced mammalian herbivores indirectly generate substantial changes in other structural and functional components of ecosystems (Milchunas *et al.* 1998). Grazing-induced structural changes of plant assemblages generate concomitant changes in the structure of other animal assemblages (Whitford 1997). For example, the modification of vegetation by mammalian herbivores changed the structure of bird communities in oak forests (DeGraf *et al.* 1991), lizards in deserts (Jones 1981), arthropods in woodlands (Abensperg-Traun *et al.* 1996), web spiders in forests (Miyashita *et al.* 2004) and ants in subtropical savannas and cool temperate deserts (Bestelmeyer & Wiens 2001; Nash *et al.* 2001). In addition, mammalian herbivores, through their effects on plants, can indirectly alter the quality

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and quantity of nutrients in the soil surface, a primary component of nutrient cycling (Pastor & Cohen 1997; Abril & Bucher 2001; Bardgett & Wardle 2003; Feely & Terborgh 2005). However, these effects on structural and functional components of ecosystems have been usually studied separately.

Recent studies (Sirotnak & Huntly 2000; Bardgett & Wardle 2003; Olofsson *et al.* 2004; Semmartín *et al.* 2004) showed that direct changes in structural components of ecosystems caused by grazing may indirectly alter ecosystem processes (e.g. nutrient cycling). Nevertheless, the direct impact of introduced herbivores on plants may cascade up through other native organisms that use plants as food resources and whose activities also affect nutrient cycling. To our knowledge, the role of this indirect interaction between exotic grazers and native insect herbivores and its effect on nutrient availability had never been investigated. Here we present evidence of how livestock can indirectly change the availability of nutrients on the soil surface by affecting the quality of refuse dumps of leaf-cutting ants through changes in vegetation.

Mammalian herbivores often enhance, but sometimes retard the rate of nutrient cycling, and the factors that determine whether this net effect is positive or negative are not clear (Pastor & Cohen 1997; Bardgett & Wardle 2003). In general, the short-term effect of browsing may accelerate the rate of litter decomposition and improve litter quality by increasing nutrient availability through waste products (Ruess & McNaughton 1987; Frank & Evans 1997). Conversely, the long-term effect of browsing may reduce litter decomposition because selective foraging on plants that produce high-quality litter may shift plant assemblages toward species with low-quality litter (Pastor *et al.* 1993; Sirotnak & Huntly 2000). Therefore, the quality and quantity of nutrients on the soil surface as direct or indirect consequences of browsing are key factors determining the effect of exotic grazers on nutrient cycling (Singer & Shoenecker 2003; Semmartín *et al.* 2004; Feely & Terborgh 2005).

Browsing may indirectly affect other organisms that feed on plants and also affect soil fertility and nutrient cycling, including some insect species (Chapman *et al.* 2003). Due to their abundance and rapid turnover (short life span), insect herbivores may strongly influence soil nutrient availability and accelerate nutrient cycling in several ways (Schowalter 1981). For example, grasshoppers can speed up nitrogen cycling by changing the abundance and decomposition rate of plant litter (Belovsky & Slade 2000). Wastes from larvae of the gypsy moth *Lymantria dispar* increased microbial growth and N mineralization in soils (Lovett & Ruesink 1995). Harvester ants alter soil chemistry and soil biota by accumulation of organic debris (Wagner *et al.* 1997; Boulton *et al.* 2003). However, leaf-cutting ants are probably the most remarkable example among all invertebrate herbivores in terms of their capacity to alter soil fertility and nutrient cycling.

Leaf-cutting ant activities generate microsites of high soil nutrient content wherever they occur (Farji-Brener & Illes 2000). They selectively collect large quantities of fresh vegetation from a large area and carry it to their nest chambers, where the plant material is degraded by a mutualistic fungus. The waste material from the fungal decomposition, dead ants and other debris are removed from the fungus gardens to specific external or internal disposal areas (hereafter, refuse dumps). These refuse dumps are several times richer in organic carbon and nutrients than the adjacent soils, generating nutritive hot spots around the nest area (Farji-Brener & Illes 2000). For example, soils surrounding leaf-cutting ant nests have three to 80 times higher concentrations of C, N, P, Ca, Mg and K than non-nest soils in tropical rainforests (Haines 1978; Moutinho *et al.* 2003; Wirth *et al.* 2003), tropical savannas (Farji-Brener & Silva 1995a) and temperate semideserts (Farji-Brener & Ghermandi 2000). Moreover, this high availability of nutrients generally increases plant abundance, diversity, productivity and accelerates nutrient cycling around the nest area (Lugo *et al.* 1973; Haines 1978; Jonkman 1978; Farji-Brener & Silva 1995b; Farji-Brener & Illes 2000; Moutinho *et al.* 2003; Wirth *et al.* 2003; Farji-Brener & Ghermandi 2004). The amount and/or the quality of this important source of soil nutrients may be affected by the activities of introduced livestock in several ways. Livestock may reduce the number of ant nests directly by trampling, or indirectly deplete the diet of leaf-cutting ants through grazing which, in turn, may affect the quality of refuse dumps.

In some dry areas of Argentina, the combined effects of insufficient rainfall, poor soils and overgrazing have produced important changes in vegetation and soil fertility (Bucher 1987; Abril & Bucher 2001; Tadey 2006) which, in turn, may affect the activity of leaf-cutting ants as foragers and soil-nutrient improvers. Patagonian semideserts have some characteristics that may enhance the effects of interactions between introduced herbivores and leaf-cutting ants on the availability of soil nutrients. First, soil nutrients, together with water availability, are limiting factors for plant establishment, growth and reproduction (Satti *et al.* 2003); thus any factor that changes the size of the soil nutrient pool should have important ecological consequences. Secondly, the low plant abundance and the scarcity of palatable species in this region force livestock to feed upon unpalatable or less nutritional plant species (Golluscio *et al.* 1998); thus high grazing intensity may decrease the availability of plants for other native herbivores. Thirdly, both types of herbivores, livestock and leaf-cutting ants inhabit the same areas and share preferences for some plant species (Robinson & Fowler 1982; Pilatti *et al.* 1997); therefore, changes in plant biomass caused by high grazing intensity can potentially affect the composition of the leaf-cutting ant diet with negative consequences on nest abundance and/or the nutrient content of their refuse dumps. Finally, given that the debris of the only leaf-cutting ant species of the Monte Desert (*Acromyrmex*

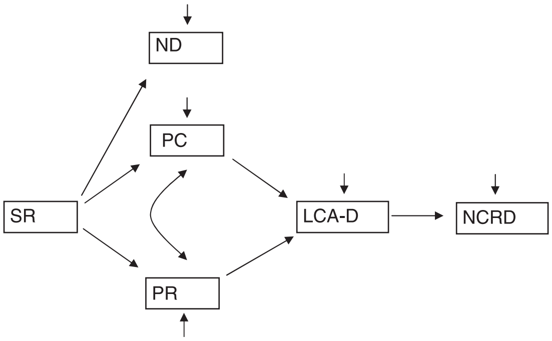

Fig. 1. Causal model used to relate stocking rates with the quantity (nest density) and quality (nutrient content of refuse dumps) of nutrients available on the soil surface generated by leaf-cutting ants. One-headed arrows represent directional effects; two-headed arrows represent correlations between pair of variables. Variables included are stocking rates (SR), plant cover (PC), plant richness (PR), the number of plant species in the leaf-cutting ants diet (LCA-D), ant nest density (ND) and the nutrient content of the ant refuse dumps (NCRD). Unexplained variability is indicated with vertical arrows.

lobicornis Emery) has been characterized as nutrient-rich in other similar habitats (Farji-Brener & Ghermandi 2000), changes in nest abundance and/or the nutrient content of refuse dumps could affect the quantity and/or quality of nutrients generated by leafcutters in the study area.

We evaluated whether exotic livestock affect the amount and/or the quality of refuse dumps of leaf-cutting ants, an important source of soil fertility in NW Patagonia (Farji-Brener & Ghermandi 2000). We hypothesize that livestock may affect the abundance of refuse dumps directly, by trampling (i.e. reducing nest density), or their quality indirectly by grazing. High grazing intensity may reduce plant availability for leaf-cutting ants, depleting their diet and hence affecting the nutrient content of their refuse dumps (Fig. 1). To study this possible sequence of effects we used a correlative approach (see Feely & Terborgh 2005), analysing the effect of different stocking rates on plant species richness and cover, leaf-cutting ant diets, ant nest density and nutrient content of refuse dumps.

Methods

STUDY SITE

The study area is located in NW Patagonia, in Neuquén province (39°17′S, 68°55′W), Argentina. This is a temperate arid region with a mean annual precipitation between 80 and 300 mm. The mean annual temperature is 15 °C, with a minimum temperature of –13 °C in winter and a maximum of 43 °C in summer (El Chocón meteorological station).

The vegetation of this region belongs to the phytogeographical province of Monte (Cabrera 1953). It is characterized by a xerophytic shrubland dominated by *Larrea cuneifolia* (Cavanilles) and *L. divaricata* (Cavanilles) associated with other xerophytic or aphyllous shrubs such as *Monttea aphylla* (Miers) Berthan et Hooker, *Bougainvillea spinosa* (Cavanilles) Heimerl, *Chuquiraga erinacea* (Don), *Prosopis alpataco* (Philippi) and *Atriplex lampa* (Gillies ex Moquin) D. Dietrich (Correa 1969, 98). Grasses are scarce in this region (< 6% of cover) and are represented mainly by *Stipa* species.

Acromyrmex lobicornis Emery is the only leaf-cutting ant species that inhabits arid regions of Patagonia (Farji-Brener & Ruggiero 1994), and its nests are important components of this ecosystem. *A. lobicornis* nests reach depths of 1 m, and on the soil surface the ants construct a mound of twigs, soil and dry plant material, which may reach a height of 0·5 m and width of 1 m. Inside this mound, ants tend the fungus on which ant larvae feed. Refuse material is removed from the internal fungus garden and dumped onto the soil surface. This refuse dump is deposited in a flat pile on the soil surface near the mound, which makes it accessible to nearby plants and seeds (Farji-Brener & Ghermandi 2000, 2004).

During the spring of 2001, paddocks with different stocking rates and similar climatic, edaphic and physiognomic characteristics were chosen to carry out our study. Given the previous restrictions we found only seven paddocks that satisfied all those requisites. Although these paddocks showed discontinuous changes in stocking rates (e.g. do not represent a continuous gradient of individuals ha^{-1}), they characterize well the stocking rates of the region in general and were the best possible scenario to achieve the objective of this work (Tadey 2006). Livestock composition of the paddocks is a mixture of goats (~ 50%), cattle (~ 40%) and horses (~10%). Sampling was performed between October 2002 and March 2004. The maximum distance between paddocks was 42 km. The paddocks varied in size from 4000 to 25000 ha, were adjacent one to another, and had been grazed for 20 ± 5 years (mean ± 1 SE). This information was obtained by interviewing the owners of each paddock and was verified in the Sanitary Commission of Neuquén province. In each paddock, we sampled plants and ant nests within an area of approximately 4 ha located at 300 m from the road and far away (> 3 km) from the stockpots. Within a paddock, livestock grazed freely throughout the year and, because paddocks lacked water points, grazing intensity was similar within each paddock.

CHEMICAL ANALYSES OF REFUSE DUMPS AND NON-NEST SOILS

To determine the chemical properties of refuse dumps of leaf-cutting ants and non-nest soils along a gradient of grazing intensity, we analysed organic carbon (C), total nitrogen (N) and extractable phosphorus (P) contents for samples collected from refuse dumps from a total of 35 nests and adjacent non-nest soil. For each paddock, we selected randomly five adult nests of *A. lobicornis* (mound of ~1 m of diameter) and samples of the refuse dump and adjacent non-nest soil. Samples from each substrate consisted of four subsamples collected between 0 and 20 cm at both the refuse dump and non-nest soil surfaces (~ 300 g each one). Non-nest soils were sampled randomly ~ 3 m away from the nests on bare soils. In total, we analysed 70 samples, 35 from ant refuse dumps and 35 from non-nest soils, from the seven paddocks. Refuse and soil samples were air-dried and analysed in the laboratory. Organic carbon (C) was obtained by the Walkley–Black method, total nitrogen (N) determined by the Kjeldahl method using block digester, and extractable phosphorus (P) by an extraction with buffered alkaline solution (0·5 $NaHCO_3$; see Bigham 1996 for methodological details).

GRAZING INTENSITY, PLANT COVER, SPECIES NUMBER AND ABUNDANCE OF ANT NESTS

To estimate the level of herbivory by livestock in each paddock we located randomly 20 circular plots of 3 m diameter (~ 7 m^2). In each plot we identified each plant to species level and quantified the percentage of grazing intensity per plant as the number of browsed branches/total number of branches. We also determined plant cover (in percentage) and the number of plant species (i.e. plant richness). In addition, to have an independent estimate of grazing pressure, we located randomly in each paddock ~ 45 plots of 6 m diameter (~ 28 m^2) and recorded the abundance of dung of different mammalian species. These plots were also used to estimate the density of *A. lobicornis* nests per paddock.

COMPOSITION OF LEAF-CUTTING ANT DIETS

To determine the plant species harvested by leaf-cutting ants, we sampled a total of 40 *A lobicornis* nests along the seven paddocks. In each paddock we selected randomly four to seven adult nests, and determined the identity of all the plant species that were carried by the ants to their nest. This methodology is employed widely to determine the diet composition of leaf-cutting ants (Farji-Brener 2001 and references therein). We observed each nest a for total of 3–5 h for several periods of 15 min throughout the season of maximum foraging activity, between November (spring) and March (autumn) of 2002–03 and 2003–04. To estimate the total number of plant species consumed by the leafcutters in each paddock, we compiled the diet composition data for all nests sampled in each paddock.

STATISTICAL ANALYSES

The chemical properties of refuse dumps and non-nest soil samples were analysed using two-way factorial analyses of variance (ANOVAS). Response variables were C, N and P contents; substrate (refuse dumps and non-nest soils) and paddock were considered fixed and random factors, respectively. Paddock was considered a random rather a fixed factor because our interest was to test for the effect of ant nests on soil properties among a grazing intensity in general, rather than answering the more restricted question of whether ant nests had an effect in these particular seven paddocks. Duncan *post-hoc* comparisons of means were employed when ANOVA results were statistically significant ($P < 0{\cdot}05$). In addition, principal component analysis was used to order refuse and soil samples according to their chemical characteristics. We also calculated the net contribution of C, N and P in the soil surface generated by refuse dumps as the difference, for each nutrient, between the values of each refuse dump minus the values of the adjacent non-nest soils sample. On the other hand, nest densities were analysed by one-way ANOVA considering paddocks as a random factor.

We used a regression approach to determine the relationships between stocking rates, nest density, plant cover and richness, the number of plant species consumed by leaf-cutting ants and the net input of N, C, and P generated from the refuse dumps. Dependent and independent variables were selected, in each case, following the relationships proposed in our hypothesis (Fig. 1). First, we explored the pattern: the existence of the relationship between stocking rates (independent variable), nest density and the net input of nutrients generated by the ants (dependent variables). Secondly, we tested the following potential mechanisms or cause–consequence relationships: (a) the effect of stocking rates on plant species cover and richness; (b) the effect of plant species richness and plant cover on plant species richness consumed by leafcutters; and (c) the effect of plant species richness consumed by leafcutters on the net input of N, C and P of refuse dumps. In addition, to determine the effect of plant cover on the number of plant species consumed by the ants after controlling for the effect of plant richness (and vice versa), we performed partial correlations. Although other causal relationships may be possible (e.g. leaf-cutting ants theoretically could affect the number of plant species consumed by livestock), we believe that the relationships proposed here and their sequence are the most biologically plausible alternative to explain the relationship between stocking rates and the nutrient content of the ant refuse found in this system.

In order to avoid pseudoreplication (Hulbert 1984) we used mean values per paddock ($n = 7$) for plant cover and richness, and for the net input of nutrients in the regression analyses instead of using each individual sample as an independent datum (e.g. $n = 140$ for plant cover and richness). This approach offers more interpretable biological information because statistically independent experimental units (i.e. paddocks) are used as replicates; however, this may increase the probability of a type II error (i.e. failure to detect a real treatment effect, or false negative results). Therefore, we predetermined a $P < 0{\cdot}10$ as our statistically significant level for the regression analyses. This procedure is employed commonly when, as here, the degrees of freedom for the analyses are limited (see Belovsky & Slade 2000; Sankaran & Augustine 2004; Vázquez & Simberloff 2004). Similarly, we show the precise P-values in all the cases. We performed linear, quadratic and exponential regressions, but we present here only the best-fitting model for each response variable. In all analyses, inspection of residuals was conducted to check for normality and homoscedasticity. When residuals did not follow the expected parametric pattern, data were log-, square root- or arcsine–square root-transformed.

We also carried out a path analysis as a way to summarize the relationships among the variables studied. Therefore, we constructed a path model that matched the hypothesized causal relationships presented in Fig. 1. The small number of experimental units (seven paddocks) prevented the use of structural equation modelling (SEM) procedures because most of the model selection criteria become unreliable at low samples sizes (Shipley 2000). However, path coefficients can also be calculated as standardized regression coefficients with conventional regression procedures (Mitchell 2001). Although this technique does not allow evaluation of the overall goodness-of-fit of the model to the data, it is useful to summarize relationships among a set of variables in a logical way (e.g. Vázquez & Simberloff 2004). The statistical significance of the path coefficients was tested by the *t*-test for the parameter estimates in the regression analysis. To avoid multiple tests with the same purpose and to simplify the path diagram, we tested the effect of the number of plant species in ant diets on refuse nutrient content using the refuse axis scores of the PCA analysis instead of estimating the standardized regression coefficients for each nutrient individually. The magnitude of unanalysed causes for each dependent variable was estimated as $(1 - R^2)^{1/2}$ (Mitchell 2001).

Results

STOCKING RATES AND GRAZING INTENSITY

Both the percentage of grazed branches and the presence of faeces reflected well the gradient of stocking rates. The percentage of browsed branches and the number of faeces increased linearly with stocking rates ($R^2 = 0{\cdot}98$; $F_{1,5} = 272$; $P < 0{\cdot}001$, $R^2 = 0{\cdot}86$, $F_{1,5} = 30{\cdot}6$; $P = 0{\cdot}003$, respectively). Therefore, stocking rate was selected as the estimator of grazing intensity and employed as the independent variable in all regression analyses.

STOCKING RATES, SOIL PARAMETERS AND NEST DENSITIES

We found statistically significant differences among paddocks, substrate type (refuse dumps and non-nest soils) and in the interactions between them for all the nutrients analysed (Table 1). Organic carbon (C), nitrogen (N) and extractable phosphorous (P) concentrations were higher in refuse dumps than in non-nest soils, and these differences were stronger in paddocks with lower stocking rates (Fig. 2, Table 1). Despite some variability within paddocks, samples from refuse dumps were

Table 1. ANOVA results testing the effects of substrate (refuse dumps and non-nest soils) and paddock on organic carbon (C), nitrogen (N) and extractable phosphorous (P) contents

	Source	d.f.	MS	*F*	*P*
C	Substrate	1	2560·0	412·4	<0·0001
	Paddock	6	42·0	6·8	<0·0001
	S × P	6	42·3	6·8	<0·0001
	Error	56	6·2		
N	Substrate	1	8·2	232·5	<0·0001
	Paddock	6	0·09	2·5	0·032
	S × P	6	0·09	2·6	0·027
	Error	56	0·03		
P	Substrate	11	141 461	121·9	<0·0001
	Paddock	6	42 640	4·5	0·008
	S × P	6	42 686	4·6	0·008
	Error	56	9365·05		

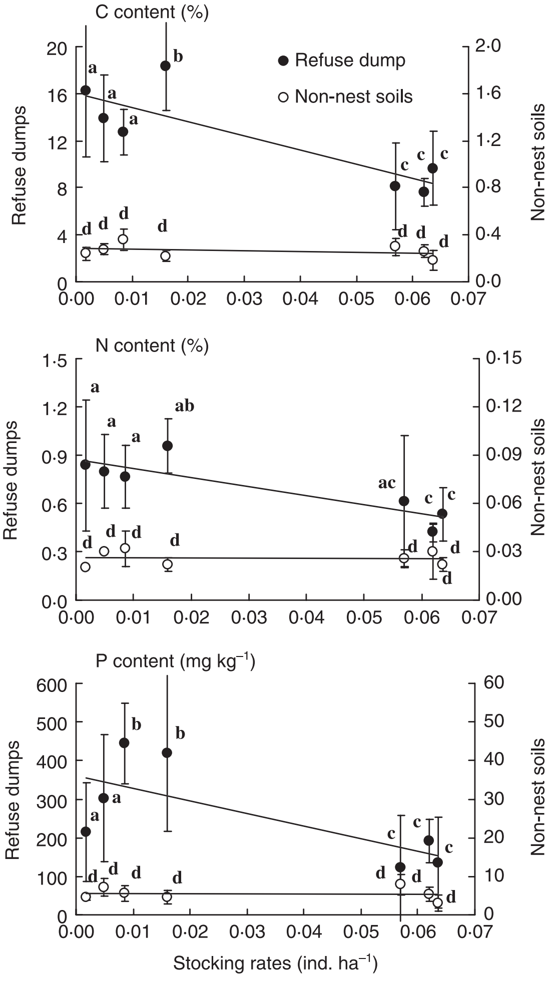

Fig. 2. Content of organic carbon (C), nitrogen (N) and phosphorous (P) in refuse dumps (left axis) and non-nest soils (right axis) in paddocks with different stocking rates (*x*-axis). Note that each axis has different scaling. Error bars represent ± 1 SD. The same superscripts mean statistical homogeneous groups (Duncan *post-hoc* comparisons). Trend lines are shown to illustrate the significant interaction between substrate × paddock (i.e. that refuse dumps are less nutrient-rich in paddocks with high stocking rates). ANOVA results associated with this figure are presented in Table 1.

always 1–2 orders of magnitude higher than non-nest soil samples in all nutrients (C: 0·8–4·8 vs. 28–240 g kg^{-1}; N: 0·2–0·3 vs. 1·4–14·8 g kg^{-1}; and P: 0·7–11·7 vs. 24–571 mg kg^{-1}, respectively, ranges considering all samples, Fig. 2). Consequently, the PCA extracted only one factor (axis) that explained 92% of the variance in the nutrient content of samples from refuse dumps and non-nest soils. This axis was correlated highly and positively with all the elements analysed ($r = 0{\cdot}97$ for C and N, $r = 0{\cdot}94$ for P, $P < 0{\cdot}001$ in each case), and clearly segregated non-soil samples (factor scores around –0·85) from refuse dump samples (factor scores around 0·95). Consistent with these results, the contribution of nutrients from refuse dumps to the soil system was always positive, with a net increment of 121 ± 16 g kg^{-1} for C, 7 ± 2 g kg^{-1} for N and 256 ± 49 mg kg^{-1} for P (mean ± 1 SE). However, these increments decreased as stocking rates increased for all the nutrients (see statistical homogeneous groups in Fig. 2). An increase in stocking rates explained most of the decrease in the net input of C (linear regression, $F_{1,5} = 11{\cdot}8$, $P = 0{\cdot}01$, $\beta = -0{\cdot}84$, $R^2 = 0{\cdot}71$), the decrease in the net input of N (linear regression, $F_{1,5} = 14{\cdot}6$, $P = 0{\cdot}01$, $\beta = -0{\cdot}86$, $R^2 = 0{\cdot}74$), and the variance in the net input of P (quadratic regression, $F_{1,5} = 5{\cdot}8$, $P = 0{\cdot}06$, $R^2 = 0{\cdot}74$). The net increments in all nutrients were the consequence of an increased nutrient content in refuse dumps, and not the result of nutrient decline in non-nest soil samples; none of the nutrients in non-nest soil samples showed a significant relationship with stocking rates (linear regression for stocking rates vs. C, N and P; $F_{1,5} = 0{\cdot}54$, $F_{1,5} = 0{\cdot}0008$, $F_{1,5} = 0{\cdot}04$, respectively, $P > 0{\cdot}50$ all cases, Fig. 2).

On the other hand, the density of *A. lobicornis* nests showed differences among paddocks ($F_{6,312} = 2{\cdot}9$, $P = 0{\cdot}008$). However, this difference was not related to the stocking rates (linear regression, $F_{1,5} = 0{\cdot}04$, $P = 0{\cdot}85$). The mean number of nests ranged between 0·17 and 0·50 per 28 m^2, and only a paddock with an intermediate stocking rate showed a high density of nests.

STOCKING RATES AND PLANT SPECIES COVER, PLANT RICHNESS AND LEAF-CUTTING ANTS DIET

As stocking rates increase, plant cover and plant richness/plot decrease strongly (both exponential fit, $R^2 = 0{\cdot}95$, $P < 0{\cdot}05$, $t_{(4)} = 2{\cdot}8$; $R^2 = 0{\cdot}92$, $P = 0{\cdot}036$, $t_{(4)} = 3{\cdot}1$, respectively, Fig. 3). The number of plant species harvested by ants decreased linearly as stocking rate increased. The increase in stocking rates explained most of the decrease in the number of plant species harvested by the leafcutters ($R^2 = 0{\cdot}82$, $F_{1,} = 22{\cdot}6$, $P = 0{\cdot}004$, Fig. 4). This decrease in the number of plant species harvested was explained by both the decrease of plant cover ($R^2 = 0{\cdot}87$, $F_{1,5} = 33{\cdot}5$, $P = 0{\cdot}002$) and plant richness ($R^2 = 0{\cdot}84$, $F_{1,5} = 23{\cdot}1$, $P = 0{\cdot}004$) (Fig. 4). However, partial correlation analyses suggested that the effect of plant species richness on the number of plant species consumed by ants was mainly a consequence of plant cover. After controlling for plant richness, plant cover and plant species consumed by the ants were still correlated ($r = 0{\cdot}93$–$0{\cdot}58$), but after controlling for plant cover the relationship between plant species richness and plant species consumed by ants was diminished substantially ($r = 0{\cdot}91$–$0{\cdot}16$).

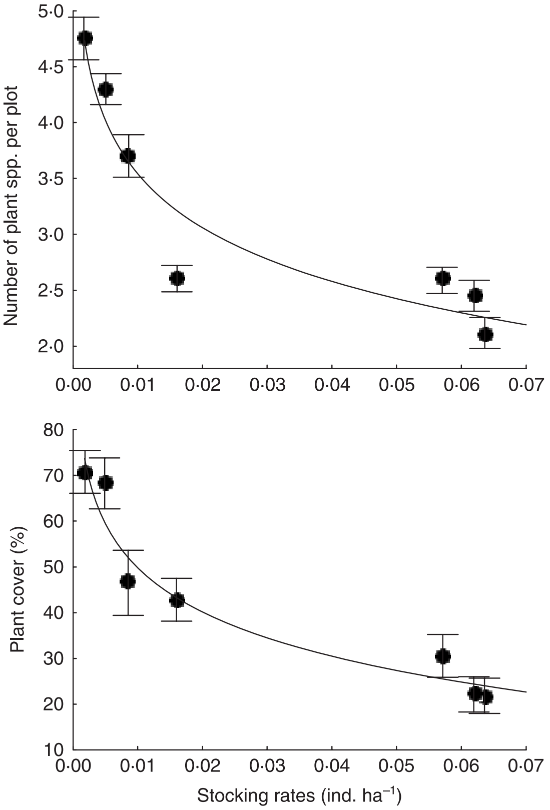

Fig. 3. Both the number of plant species per plot and plant cover decrease exponentially as stocking rate increases. Each point represents a different paddock. Error bars represent ± 1 SE. See text for regression statistics.

LEAF-CUTTING ANT DIET AND NET INPUTS OF NUTRIENTS FROM REFUSE DUMPS

The levels of nutrients in the refuse dumps were associated positively with the number of species harvested by the leaf-cutting ants (Fig. 5). An increase in the number of species consumed by the ants explained 57% and 47% of the net increase in C and N, respectively (for C: $R^2 = 0{\cdot}57$, $F_{1,5} = 6{\cdot}7$, $P = 0{\cdot}04$; for N: $R^2 = 0{\cdot}47$, $F_{1,5} = 4{\cdot}6$, $P = 0{\cdot}08$, both linear fit). In addition, the net input of P showed a quadratic relationship with the number of plant species consumed by the ants, with a peak in eight plant species, which corresponded to the paddocks with moderate stocking rates ($R^2 = 0{\cdot}74$, $F_{1,5} = 5{\cdot}8$, $P = 0{\cdot}06$).

Path analysis summarized well the relationships among the variables studied (Fig. 6). Livestock did not affect the number of refuse dumps (i.e. nest density), but reduced their quality. As stocking rate increased, plant availability decreased which, in turn, depleted the number of plant species harvested by ants. This diet reduction decreased the nutrient quality of ant refuse dumps.

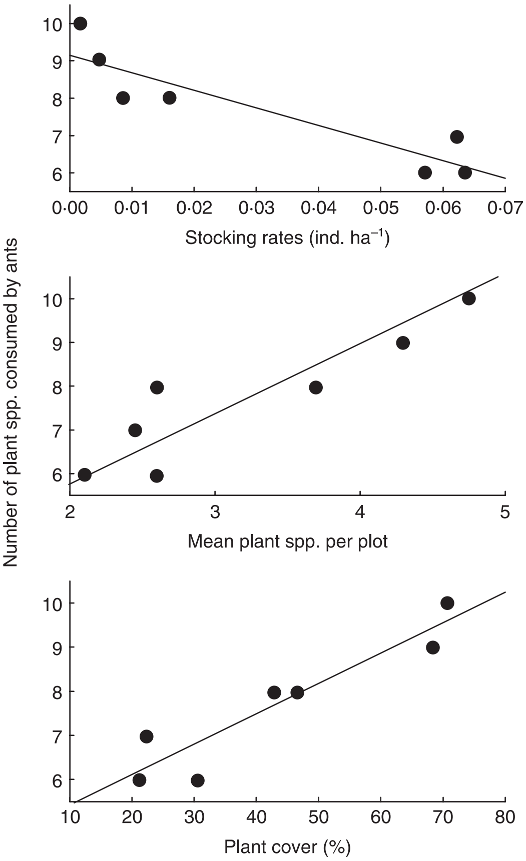

Fig. 4. The number of plant species harvested by leaf-cutting ants decreases linearly as stocking rate increases, and increases when the number of plant species per plot and plant cover increase. Each point represents a different paddock. See text for regression statistics.

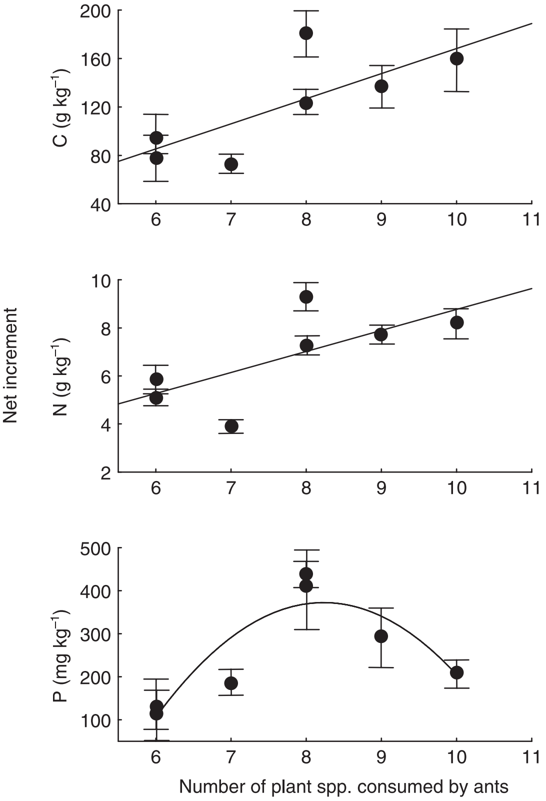

Fig. 5. Relationship between the net increment of organic carbon (C), nitrogen (N) and phosphorous (P) generated by the refuse dumps and the number of plant species harvested by the ants. Each point represents a different paddock. Error bars represent ± 1 SE. See text for regression statistics.

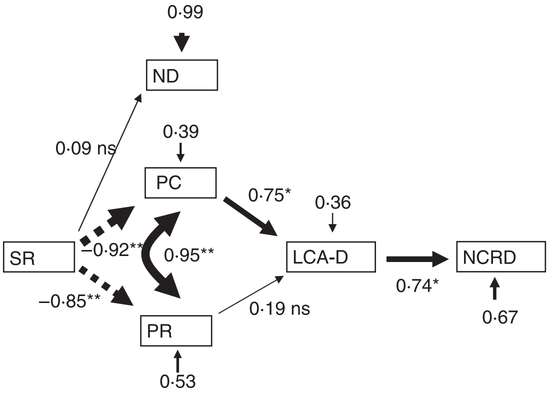

Fig. 6. Path analysis of causal relationship among variables hypothesized to be involved in indirect effects of stocking rates on the quantity (nest density) and quality (nutrient content of refuse dumps) of nutrients available on the soil surface generated by leaf-cutting ants. One-headed arrows represent direct causal effects; two-headed arrows correlative 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. Significance of the path coefficients is indicated as follows: *$P < 0.05$, **$P < 0.001$. Variables included in the model are: stocking rates (SR), plant cover (PC), plant richness (PR), the number of plant species in leaf-cutting ants diet (LCA-D), nest density (ND) and the nutrient content of the ant refuse dumps (NCRD). Unexplained variability is indicated with vertical arrows.

Discussion

There are three major findings in this study: (1) external refuse dumps of *A. lobicornis* are an important source of soil nutrients in the Monte Desert; (2) the strength of this soil-enrichment is influenced greatly by grazing pressure of introduced mammalian herbivores; and (3) the mechanisms responsible for this effect appear to be unrelated to a direct effect of livestock on ant nest density (e.g. by trampling), but related to a reduction in plant cover induced by livestock through grazing, which affects leaf-cutting ant diet, and this alters the nutrient content of external refuse dumps.

In the Monte Desert of Argentina, refuse dumps of *A. lobicornis* may be considered as soil nutrient hot spots. The concentration of N, C and P in refuse dumps was one to two orders of magnitude higher than adjacent non-nest soils. Both the poor soil fertility of non-nest soils and the high nutrient content of refuse dumps were responsible for this effect. The non-nests soils showed values of C, N and P lower than bare soils of other semi-arid systems of Argentina (Farji-Brener & Ghermandi 2000; Abril & Bucher 2001). In contrast, refuse dumps of *A. lobiornis* showed nutrient contents similar to or higher than those reported for debris of other ant species, including leaf-cutting ants (Haines

1978; Farji-Brener & Silva 1995a; Wagner *et al.* 1997; Boulton *et al.* 2003; Moutinho *et al.* 2003; Wirth *et al.* 2003). Although the extent of differences between sites on and off ant nests may be somewhat magnified because nutrient levels are typically quite low in unvegetated patches, the net nutrient input caused by *A. lobicornis* in the Monte Desert can be considered one of the most important contributions to soil fertility of leaf-cutting ants.

Although water availability clearly influences the structure and dynamics of arid regions, soil nutrients have also been recognized as an important determinant of plant growth and reproduction in these habitats (Ritchie 2000; Augustine *et al.* 2003). Therefore, any disturbances that enhance nutrient availability may be considered a key ecological factor for these systems. In the Monte Desert of Argentina, the nutrient-rich debris of *A. lobicornis* nests may positively affect plant establishment and growth, soil water retention and the rate of nutrient cycling. Although we did not measure these effects, a large number of other studies showed that refuse dumps of leaf-cutting ants decompose rapidly and release nutrients for plant uptake, thereby having a net positive effect on plant abundance, diversity and productivity in habitats ranging from temperate deserts to tropical rainforests (Lugo *et al.* 1973; Haines 1978; Jonkman 1978; Farji-Brener & Silva 1995b,a; Moutinho *et al.* 2003; Wirth *et al.* 2003; Farji-Brener & Ghermandi 2004). Moreover, in recent studies in a Patagonian steppe, field and experimental evidence showed that the external refuse of *A. lobicornis* improve the establishment, growth and fitness of several plant species promoting the existence of a more diverse plant community (Farji-Brener & Ghermandi 2000, 2004). It is likely that the nutrient-rich refuse dump of *A. lobicornis* positively affects plants and/or nutrient cycling also in this study area. Research on these topics is currently in progress.

Although refuse dumps increased the nutrient availability on soil surface in all the paddocks studied, the strength of this effect depended on the stocking rates. The net level of nutrients generated by refuse dumps showed a strong decrease with an increment of grazing intensity. An increment in the grazing intensity of only 0·06 individuals ha^{-1} determined a mean net decrease of 80 g kg^{-1} of C, 3 g kg^{-1} of N and a 250 mg kg^{-1} of P in the refuse dumps (see Fig. 2). The results of this work offer a strong correlative evidence to understand the mechanism responsible for this effect: livestock reduce plant cover, affecting leaf-cutting ant diets which, in turn, alter the nutrient content of their external refuse dumps.

The direct negative effect of introduced herbivores on plant richness and cover is well known. Although some plant species can eventually benefit from mammalian herbivory (Paige & Whitham 1987), there is strong evidence that heavy grazing by livestock often reduces plant fitness, abundance and richness worldwide (Milchunas & Lauenroth 1993). In the semi-arid regions of Patagonia, grazing by exotic livestock causes an overall reduction of plant cover through the decrease in abundance, or eventually the extinction, of palatable species (Bertiller 1996; Bisigato & Bertiller 1997; Tadey 2006). We found the same pattern in the Monte Desert: a subtle increase in grazing intensity was associated with a decrease of ~ 50% on plant cover and a reduction of two plant species per plot (Tadey 2006). This impoverishment of plant availability was not associated with the density of leaf-cutting ant nests, precipitation, soil fertility or other natural environmental variation. Therefore, livestock appear to be the major cause of the reduction on plant species richness and cover in the study area.

We found that as plant cover and richness decreased, the number of plant species harvested by *A. lobicornis* also decreased. The drastic decrease in plant cover (70% to 20%), concomitant with the increment in grazing intensity, seems to deplete the leaf-cutting ant diet by reducing the chance of encounter between scout ants and palatable plant species. Supporting this idea, plant species that disappeared from the ant diet as stocking rate increased were the same species that decreased in cover with grazing intensity (e.g. *Grindelia chiloensis*, *Gutierrezia solbrigii*, *Junellia aspera*, *Schinus johnstonii* and *Stipa* sp.). In semi-arid areas of South America, livestock and leaf-cutting ants both forage on the most nutritive species and may interact indirectly by exploitative competition (Robinson & Fowler 1982; Bucher 1987). Consequently, high grazing intensity may deprive leafcutters access to the most palatable species (Robinson & Fowler 1982; Bucher 1987; Pilatti *et al.* 1997).

Previous studies have demonstrated that changes in the composition and abundance of plant assemblages significantly affect the composition of the diet of leaf-cutting ants, including the ant species studied here (Vasconçelos 1997; Franzel & Farji-Brener 2000). On the other hand, the decrease of plant cover increased the proportion of bare soil where extreme soil temperatures may limit ant foraging activity (Whitford & Ettershank 1975). Temperature affects foraging activities through (1) its effects on oxygen consumption, water loss and transport cost (Lighton & Feener 1989), which reduces daily and seasonally leaf-cutting ants foraging (Mintzer 1979); and (2) by increasing the desiccation rate of the leaf fragments, as well-hydrated leaves are important for fungal growth (Bowers & Porter 1981). Therefore, a reduction of plant availability due to grazing and the associated increment of bare soil are probable candidates to explain the reduction on plant species harvested by this leaf-cutting ant species.

We found that changes in the number of plant species harvested by ants greatly affected the nutrient content of their refuse dumps (Figs 5 and 6). The nutrient content of refuse dumps made by leaf-cutting ants often depends on the richness (i.e. different plant species) of the plant material harvested (Wirth *et al.* 2003; Bucher *et al.* 2004). In semi-arid regions of Patagonia exotic livestock often prefer to forage on nutrient-rich plant species (Bisigato & Bertiller 1997; Bertiller & Bisigato 1998).Therefore, the overall reduction in the more palatable plants may cause leafcutters to forage on the relatively more abundant, but less nutrient-rich remaining species. This shift toward less nutritive plant species may impoverish the nutrient content of refuse dumps (Wirth *et al*. 2003; Bucher *et al*. 2004). It is well known that introduced herbivores affect directly and indirectly the quantity and quality of soil nutrients (McNaughton *et al*. 1988; Pastor *et al*. 1993; Pastor & Cohen 1997; Sirotnak & Huntly 2000; Singer & Shoenecker 2003; Olofsson *et al*. 2004; Sankaran & Augustine 2004; Semmartín *et al*. 2004; Feely & Terborgh 2005). However, and to the best of our knowledge, this is the first study that shows an indirect effect of exotic grazers on nutrient availability that involves interactions with native insect herbivores.

Overall, our results have both theoretical and applied implications. First, they show how the negative impact of exotics grazers on plants affect native insects and how these effects spread along the trophic chain by indirect interactions, impacting ecosystem attributes and functioning. Secondly, they provide useful information to prevent further soil impoverishment and to restore the nutrient content of soils in this managed system. Management to prevent soil impoverishment should include the reduction of stocking rates. A slight reduction in stocking rates (only 0·03 individuals ha^{-1}) may improve 100% the contribution of ants to soil fertility (see Fig. 2). Additionally, refuse dumps could be employed as a cheap and renewable fertilizer for plants already established and damaged by livestock, and to restore soil quality. In particular, the high nutrient level of ant debris from paddocks with lower grazing intensities can be utilized to improve the soil fertility of paddocks with higher stocking rates.

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References

Abensperg-Traun, M., Smith, G., Arnold, G. & Steven, D. (1996) The effects of habitat fragmentation and livestock-grazing on animal communities in remnant of gimlet *Eucalyptus salubris* woodland in the Western Australian wheat belt. I. Arthropods. *Journal of Applied Ecology*, **33**, 1281–1301.

Abril, A. & Bucher, E. (2001) Overgrazing and soil carbon dynamics in the western Chaco of Argentina. *Applied Soil Ecology*, **16**, 243–249.

Augustine, D., McMaughton, S. & Frank, D. (2003) Feedbacks between soil nutrient and large herbivores in a managed savanna ecosystem. *Ecological Applications*, **13**, 1325–1337.

Bardgett, R. & Wardle, D. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, **84**, 2258–2268.

Belovsky, G. & Slade, J. (2000) Insect herbivory accelerates nutrient cycling and increase plant production. *Proceedings of the National Academy of Sciences USA*, **97**, 14412–14417.

Bertiller, M. (1996) Grazing effects on sustainable semi-arid rangelands in Patagonia: the state and dynamics of the soil seed bank. *Environmental Management*, **20**, 123–132.

Bertiller, M. & Bisigato, A. (1998) Vegetation dynamics under grazing disturbance. The state-and-transition model for the Patagonian steppes. *Ecología Austral*, **8**, 191–199.

Bestelmeyer, B. & Wiens, J. (2001) Ant biodiversity in semi-arid landscape mosaics: the consequence of grazing vs. natural heterogeneity. *Ecological Applications*, **11**, 1123–1140.

Bigham, J. (1996) *Methods of Soil Analysis*. Soil Society of America, Wisconsin, USA.

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

Boulton, A., Jaffe, B. & Scow, K. (2003) Effects of a common harvester ant (*Messor andrei*) on richness and abundance of soil biota. *Applied Soil Ecology*, **23**, 257–265.

Bowers, M. & Porter, S. (1981) Effect on foraging distance on water content of substrates harvested by *Atta colombica*. *Ecology*, **62**, 273–275.

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

Bucher, E., Marchesini, V. & Abril, A. (2004) Herbivory by leaf-cutting ants: nutrient balance between harvested and refuse material. *Biotropica*, **36**, 327–332.

Cabrera, A. (1953) Esquema fitogeográfico de la República Argentina (Phytogeographic map of Argentina). *Revista del Museo de La Plata Botánica*, **8**, 87–168.

Chapman, S., Hart, S., Cobb, N., Whitham, T. & Koch, G. (2003) Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology*, **84**, 2867–2876.

Correa, M. (1969–98) *Flora Patagónica (Siete Volúmenes)*. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires.

DeGraf, R., Healy, W. & Brooks, R. (1991) Effects of thinning and deer browsing on breeding birds in New England oak woodlands. *Forest Ecology and Management*, **41**, 179–192.

Farji-Brener, A.G. (2001) Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos*, **92**, 169–177.

Farji-Brener, A.G. & Ghermandi, L. (2000) The influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. *Journal of Vegetation Science*, **11**, 453–460.

Farji-Brener, A.G. & Ghermandi, L. (2004) Seedling recruitment in a semi-arid Patagonian steppe: facilitative effects of refuse dumps of leaf-cutting ants. *Journal of Vegetation Science*, **15**, 823–830.

Farji-Brener, A.G. & Illes, A. (2000) Do leaf-cutting ant nests make ‘bottom up’ gaps in neotropical rain forests? A critical review of the evidence. *Ecology Letters*, **3**, 219–227.

Farji-Brener, A.G. & Ruggiero, A. (1994) Leaf-cutting ants (*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical range sizes. *Journal of Biogeography*, **21**, 391–399.

Farji-Brener, A.G. & Silva, J. (1995a) Leaf-cutting ant nests and soil fertility in a well-drained savanna in western Venezuela. *Biotropica*, **27**, 250–253.

Farji-Brener, A.G. & Silva, J. (1995b) Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession? *Journal of Tropical Ecology*, **11**, 651–669.

Feely, K. & Terborgh, J. (2005) The effects of herbivory density on soil nutrients and tree growth in tropical forest fragments. *Ecology*, **86**, 116–124.

Frank, D. & Evans, R. (1997) Effects of native grazers on grasslands N cycling in Yellowstone National Park. *Ecology*, **79**, 2229–2241.

Franzel, C. & Farji-Brener, A.G. (2000) ¿Oportunistas o selectivas? Plasticidad en la dieta de la hormiga cortadora de hojas *Acromyrmex lobicornis* en el N-O de la Patagonia (Selective or oportunistic? Diet plasticity of the leaf-cutting ant Acromyrmex lobicornis in NW Patagonia). *Ecología Austral*, **10**, 159–168.

Golluscio, R., Deregibus, V. & Paruelo, J. (1998) Sustainability and range management in the Patagonian steppes. *Ecología Austral*, **8**, 265–284.

Haines, B. (1978) Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica*, **10**, 270–277.

Hulbert, S. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Jones, K. (1981) Effects of grazing on lizard abundance and diversity in western Arizona. *South Western Naturalist*, **26**, 107–115.

Jonkman, J. (1978) Nests of the leaf-cutting ant *Atta vollenweideri* as accelerators of succession in pastures. *Zeitschrift für Angewandte Entomolgie*, **86**, 25–34.

Lighton, J. & Feener, D. (1989) Water-loss rate and cuticular permeability in foragers of the desert ant *Pogonomyrmex rugosus*. *Physiological Zoology*, **62**, 1232–1256.

Lovett, G. & Ruesink, A. (1995) Carbon and nitrogen mineralization from decomposing gypsy moth frass. *Oecologia*, **104**, 133–138.

Lugo, A., Farnworth, E., Pool, D., Jerez, P. & Kaufman, G. (1973) The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology*, **54**, 1292–1301.

McNaughton, S., Ruess, R. & Seagle, S. (1988) Large mammals and process dynamics in African ecosystems. *Bioscience*, **38**, 794–800.

Milchunas, D. & Lauenroth, W. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, **63**, 327–366.

Milchunas, D., Lauenroth, W. & Burke, C. (1998) Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos*, **83**, 65–74.

Mintzer, A. (1979) Foraging activity of the Mexican leaf-cutting ant, *Atta Mexicana,* in a Sonoran desert habitat. *Insects Sociaux*, **26**, 364–372.

Mitchell, R. (2001) Path analysis. *Design and Analysis of Ecological Experiments* (eds S. Scheiner & J. Gurevitch), pp. 217–234. Oxford University Press, Oxford.

Miyashita, T., Takada, M. & Shimazaki, A. (2004) Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. *Ecoscience*, **11**, 74–79.

Moutinho, P., Nepstad, D. & Davidson, E. (2003) Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. *Ecology*, **84**, 1265–1276.

Nash, M., Whitford, W., Breadford, D., Franson, S., Neale, A. & Heggem, D. (2001) Ant communities and livestock grazing in the great Basin, USA. *Journal of Arid Environments*, **49**, 695–710.

Olofsson, J., Tark, S. & Oksanen, L. (2004) Reindeer influence on ecosystem processes in the tundra. *Oikos*, **105**, 386–396.

Paige, K. & Whitham, T. (1987) Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist*, **129**, 407–416.

Pastor, J. & Cohen, Y. (1997) Herbivores, the functional diversity of plants species, and the cycling of nutrient in ecosystems. *Theoretical Population Biology*, **51**, 165–179.

Pastor, J., Dewey, B., Naiman, R., McInnes, P. & Cohen, Y. (1993) Moose browsing and soil fertility in the boreal forests of Isle Royal National Park. *Ecology*, **74**, 467–480.

Pilatti, A., Quirán, E. & Esterlich, H. (1997) Actividad forrajera de *Acromyrmex lobicornis* en un pastizal natural semiárido de la provincia de La Pampa (Argentina). (Foraging activity of Acromyrmex lobicornis in a natural semiardi grassland of La Pampa province (Argentina)). *Ecología Austral*, **7**, 49–56.

Ritchie, M. (2000) Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology*, **81**, 1601–1612.

Robinson, S. & Fowler, H. (1982) Foraging and pest potential of Paraguayan grass-cutting ants (*Atta* and *Acromyrmex*) to the cattle industry. *Zeitschrift für Angewandte Entomolgie*, **93**, 42–54.

Ruess, R. & McNaughton, S. (1987) Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. *Oikos*, **49**, 101–110.

Sankaran, M. & Augustine, D. (2004) Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. *Ecology*, **85**, 1052–1061.

Satti, P., Mazzarino, M., Gobbi, M., Funes, F. & Roselli, L. (2003) Soil N dynamics in relation to leaf-litter quality and soil fertility in north-western Patagonian forests. *Journal of Ecology*, **91**, 173–181.

Schowalter, T. (1981) Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession. *Oikos*, **37**, 126–130.

Semmartín, M., Aguiar, M., Distel, R., Moretto, A. & Ghersa, C. (2004) Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient. *Oikos*, **107**, 148–160.

Shipley, B. (2000) *Cause and Correlation in Biology: a User Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge University Press, Cambridge.

Singer, F. & Shoenecker, K. (2003) Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management*, **181**, 189–204.

Sirotnak, J. & Huntly, N. (2000) Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology*, **81**, 78–87.

Tadey, M. (2006) Grazing without grasses: effects of introduced livestock on plant community of an arid ecosystem in northern Patagonia. *Applied Vegetation Science*, **9**, 109–116.

Vasconçelos, H. (1997) Foraging activity of an Amazonian leaf-cutting ant: responses to changes in the availability of woody plants and to previous damage. *Oecologia*, **112**, 370–378.

Vázquez, D. & Simberloff, D. (2004) Indirect effects of an introduced ungulate on pollination and plant reproduction. *Ecological Monographs*, **74**, 281–308.

Wagner, D., Brown, M. & Gordon, D. (1997) Harvester ant nests, soil biota and soil chemistry. *Oecologia*, **112**, 232–236.

Whitford, W. (1997) Desertification and animal biodiversity in the desert grasslands of North America. *Journal of Arid Environments*, **37**, 709–720.

Whitford, W. & Ettershank, G. (1975) Factors affecting foraging activity in Chihuahuan desert harvester ants. *Environmental Entomology*, **4**, 689–696.

Wirth, R., Herz, H., Ryel, R., Beyschlag, W. & Hölldobler, B. (2003) *Herbivory of Leaf-Cutting Ants. A Case Study on Atta Colombica in the Tropical Rainforest of Panama*. Springer, Berlin.

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