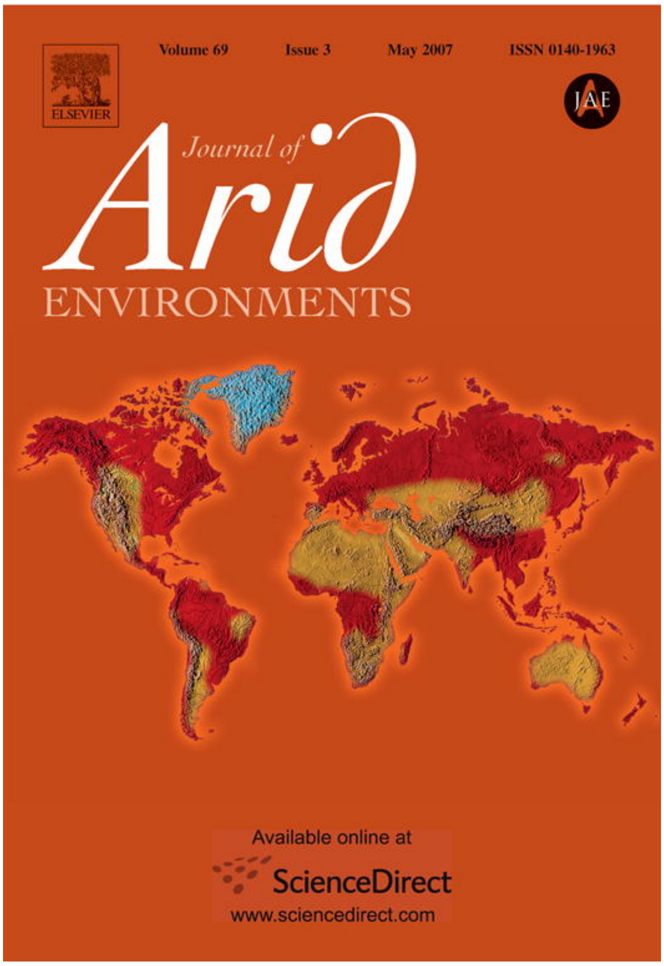


Volume 69 Issue 3 May 2007 ISSN 0140-1963

ELSEVIER

JAE

Journal of Arid ENVIRONMENTS

Available online at
ScienceDirect
www.sciencedirect.com

ELSEVIER

Journal of Arid Environments 69 (2007) 526–536

Journal of
Arid
Environments

www.elsevier.com/locate/jaridenv

Short Communication

Discriminating direct and indirect effects of exotic grazers on native plant cover in the Monte desert of Argentina

M. Tadey, A.G. Farji-Brener*

Laboratory Ecotono, CRUB-Universidad Nacional del Comahue, (8400) Bariloche, Argentina

Received 2 August 2006; received in revised form 21 September 2006; accepted 31 October 2006

Abstract

The relationship between exotic mammalian herbivores (EMH) and the native vegetation has often been focused on direct effects and viewed it as binary interactions. However, in arid environments indirect effects and the community context may also influence the effect of EMH on plants. We sampled the flora and soil nutrients (SN) in seven paddocks that differed in stocking rates, and used structural equation modeling (SEM) to partition the net effect of EMH into direct and indirect effects on the most abundant plant species of the Monte desert of Argentina. We proposed two indirect effects by which EMH can modify the cover of a focal plant species: the modification of the assemblage plant cover (APC) and alteration of SN. Indirect effects appear to be as important as direct ones. EMH did not affect the status of SN; thus indirect effects through this pathway were irrelevant. Conversely, EMH always affected the APC negatively, but the effect of APC on a focal plant varied according to their identity. Therefore, indirect effects through the APC were positive or negative depending on plant species. Several possible mechanisms explaining how changes in the cover of nearby plants can alter the cover of a focal plant species are discussed. These results emphasize the importance of indirect interactions to explain the complex relationship between EMH and native plant cover in arid ecosystems.

Keywords: Indirect interactions; Livestock; Structural equation models; Patagonia

---

*Corresponding author. Tel.: +54 2944 426368; fax: +54 2944 422111.
E-mail address: alefarji@crub.uncoma.edu.ar (A.G. Farji-Brener).

0140-1963/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2006.10.016

The use of natural habitats for production of exotic mammalian herbivores (hereafter EMH) has caused serious changes on native vegetation in arid environments (Nash et al., 1999). Most of these studies has traditionally been focused on direct effects of EMH, as browsing and trampling (Bisigato and Bertiller, 1997; Augustine and McMaughton, 1998); and treated them as binary interactions (Zamora et al., 1999). As a result, it is known that some plant species benefit from herbivory (Paige and Whitham, 1987), while others reduce their relative abundance (Milchunas and Laurenroth, 1993; Graetz, 1994; Bullock et al., 2001; Landsberg et al., 2003). However, indirect effects and the community context play an important role in EMH–plant interactions (Baraza et al., 2006). In this study, we discriminate direct and indirect effects of EMH on a broad number of native plant species in the Monte desert of Argentina.

There are two major non-mutually excluding ways by which EMH can alter the abundance of a focal plant species indirectly; by (1) changing the neighboring plant assemblage, and/or (2) altering the soil quality. Selective browsing on preferred species may indirectly affect the relative abundance of less or no preferred plant species as well. Spatial distribution of palatable and unpalatable plants can influence the foraging behavior of herbivores, changing plant-damage probability (Baraza et al., 2006). Moreover, changes in the relative assemblage composition may affect other non-trophic interactions between plants, such as competition or facilitation (Callaway and Walker 1997). Overall, changes of the surrounding plant matrix via browsing can potentially have either positive or negative indirect effects on a target plant species, depending on its identity and on the ecological context. On the other hand, EMH may indirectly alter the status of soil nutrients (hereafter SN) (Sirotnak and Huntly, 2000; Semmartín et al., 2004). In the short term, browsing may improve soil quality by increasing nutrient availability through waste products (Ruess and McMaughton, 1987; Frank and Evans, 1997). Conversely, at the long term EMH may deplete soil quality. Selective foraging on plants that produce high-quality litter may shift plant assemblages toward species with low-quality litter (Pastor et al., 1993; Sirotnak and Huntly, 2000). Plant species may differ in their demographic responses to these changes in soil fertility, changing their relative abundances. In sum, EMH may indirectly modify the abundance of a plant species through the alteration of the abundance of the surrounding plant assemblage and/or the status of SN.

In the semi-arid regions of Patagonia, EMH often reduces plant cover (Ares et al., 1990; Bertiller, 1996; Bisigato and Bertiller, 1997; Perelman et al., 1997). This effect is especially important in the Monte desert, where grasses are scarce and livestock has to feed upon less nutritional plant species (Golluscio et al., 1998; Guevara et al., 1996; Tadey, 2006). Yet there is little knowledge in this region whether the influence of EMH on plants is a consequence of direct or indirect effects.

The goal of our study is to discriminate the direct and indirect effect of EMH on a broad number of native plant species of the Monte desert. To do this, we sampled the flora and SN in seven paddocks that differed in stocking rates and used structural equation modeling (hereafter SEM) to identify direct and indirect effects of EMH on the most abundant native plant species.

The study area is located in NW Patagonia, 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. The vegetation of this region 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*, *Bougainvillea spinosa, Chuquiraga erinacea*, *Prosopis alpataco*, and *Atriplex lampa* (Correa, 1969–1998).

During the spring of 2001, we selected seven paddocks with different grazing intensities (i.e., livestock ha^{-1}) but with similar climatic and plant physiognomic characteristics (Del Valle, 1998; León et al., 1998, Tadey, 2006). Livestock composition of the paddocks is a mixture of goats, cattle, and horses. The paddocks varied in size from 4000 to 25,000 ha, are adjacent to one other, have the same orientation (NW), and had been grazed for 20 ± 5 years (mean$\pm$1 SD). Stocking densities were standardized using animal unit equivalents and expressed as livestock ha^{-1} (Vallentine, 2001). Sampling was done in spring of 2002. In each paddock, we sampled the flora and soils within an area of ~4 ha located at 300 m from the road and >3 km away from the stockpots. To estimate the effect of EMH on plant species cover, in each paddock we randomly located 20 circular plots 3 m in diameter. Within each plot, we visually quantified plant species cover as the area (in %) occupied by each individual plant species. We selected the most abundant plant species ($n = 9$, see Table 1) to discriminate direct and indirect effects of EMH.

To determine the chemical properties of soils along a gradient of grazing intensity, we analysed organic carbon (C), total nitrogen (N), and extractable phosphorus (P) contents. In each paddock, we randomly selected five points of bare soil. Each soil sample was composed by four sub-samples collected from a depth of 20 cm within an area of 9 m^2. Soil samples (total $n = 35$; five per paddock) were air-dried and analyzed in the laboratory. Organic carbon was obtained by the Walkley–Black method, total N determined by the Kjeldahl method, and extractable P by an extraction with buffered alkaline solution (see Bigham, 1996).

The total co-variation between two variables (i.e., their correlation value) is often a composite measure of direct and indirect effects (Legendre and Legendre, 2004). To identify these components of the net effect of EMH on the cover of our selected plant species, we used SEM (Shipley, 2000). This methodology was originally developed as path analysis as a way to partition the variation from observational data into causal and non-causal components (Mitchell, 2001). We constructed a general model in which we could partition the net effect of EMH on a focal plant species into direct and indirect effects. We proposed two indirect effects: the modification of the assemblage plant cover (hereafter

Table 1
Principal characteristics of the nine focal plant species used in this study

Plant species	Family	Life form	Mean height (cm)	Spines	Browse intensity
Acantholippia seriphioides (AS)	Verbenaceae	E	50	None	Very high
Atriplex lampa (AL)	Chenopodiaceae	E	100	None	High
Bougainvillea spinosa (BS)	Nyctaginaceae	D	200	Yes	Moderate
Chuquiraga erinacea (ChE)	Asteraceae	E	150	Yes	Very high
Gutierrezia solbrigii (GS)	Asteraceae	E	50	None	Very high
Larrea cuneifolia (LC)	Zygophyllaceae	E	200	None	High
Larrea divaricata (LD)	Zygophyllaceae	E	200	None	High
Monttea aphylla (MA)	Scrophulariaceae	A	200	Yes	Very high
Prosopis alpataco (PA)	Leguminosae	D	150	Yes	Moderate

Life form: (E = evergreen, D = Deciduous, A = Aphyllous). Browse intensity was estimated as the % of branches grazed/plant in the paddocks with the highest stocking rates (Very high: >90%; High: ~70%, Moderate: ~50%).

APC) and the alteration of SN (Fig. 1). The APC was calculated, in each case, as the cover of all the plant species measured minus the focal plant species cover (hereafter FPC). To estimate a single value of soil quality per paddock, we first performed a principal component analysis (PCA) to order the 35 soil samples according to their content of C, N and P. The PCA extracted only one factor that explained 92% of the variance of SN samples. This axis was positively correlated with all the elements analyzed ($r = 0.97$ for C and N, $r = 0.94$ for P, $P < 0.001$ in each case), and was interpreted as a gradient of soil fertility. Therefore, in the path analysis we used the mean of soil samples axis scores per paddock of the PCA as an estimation of soil fertility. The adequacy of the model with the data was evaluated via SEM using χ^2 and associated probabilities (Shipley, 2000), and pathways were evaluated by their t-values and associated probabilities. Path coefficients were computed using standardized variables. We calculated total co-variation (TC) as Pearson's correlation coefficients (r), and estimate non-causal co-variation as TC minus the sum of direct and indirect effects (Legendre and Legendre, 2004). The values of indirect effects were obtained multiplying the respective path coefficients from the pathway proposed (Fig. 1). For example, the indirect effect of EMH (measured as stocking rates, SR) on a FPC through APC was estimated as the multiplication between the SR–APC and APC–FPC path coefficients.

In order to avoid pseudoreplication (Hulbert, 1984), we used mean values per paddock for all the variables (APC, FPC and SN, $n = 7$ each one) in the SEM analysis instead of using plots as independent data. This approach offers more reliable 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). Therefore, we predetermined a $P < 0.10$ as our statistical significant level. This procedure is commonly employed when, as here, the degrees of freedom for the

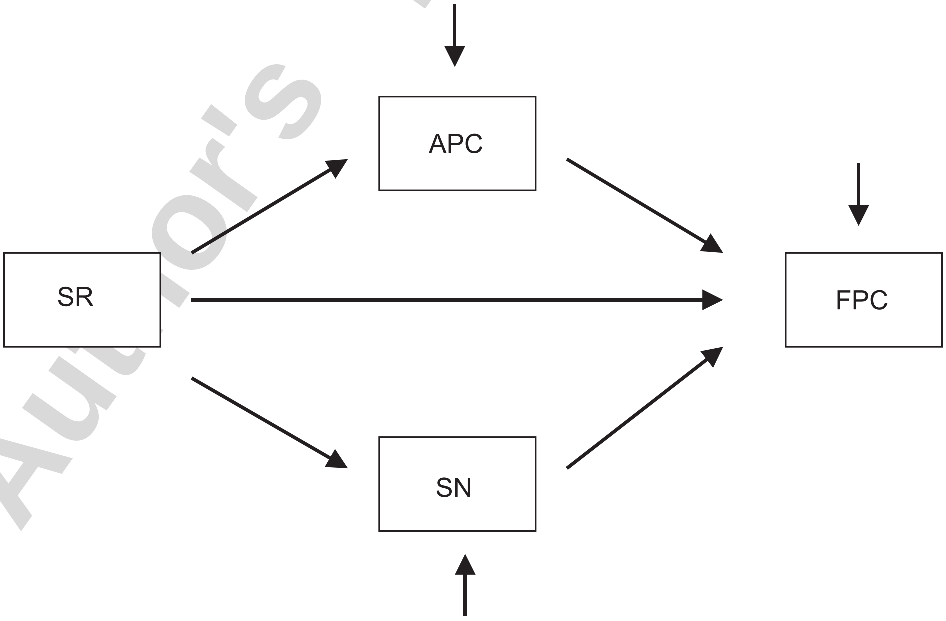


Fig. 1. Causal model used to determine direct and indirect effects of stocking rates on the cover of each of the focal 9 plant species. One-headed arrows represent directional effects. Variables included are stocking rates (SR), assemblage plant cover (APC), focal plant cover (FPC), and soil nutrients (SN). Unexplained variability is indicated with vertical arrows.

analyses are limited (Belovsky and Slade, 2000; Sankaran and Augustine, 2004; Vázquez and Simberloff, 2004).

The paddocks sampled showed great variation in stocking rates and plant species cover, but were relatively similar in soil nutrient content. Stocking rates varied between 0.002 up to 0.038 livestock Ha^{-1}, mean plant assemblage cover varied between 15% and 70%, and the individual cover of the nine species studied varied between 2% and 10% (range 0–18%). Conversely, the soil content of C, N and P varied only between 0.2–0.4%, 0.02–0.04% and 3–6 mg/K, respectively.

The data fit well with the proposed model for all the focal species studied (χ^2 values between 0.002 and 2.2, $0.14 < P < 0.99$, Fig. 2), supporting our hypothesized causal scheme to explain the effect of EMH on plant species cover (Fig. 1). The model explained very well the cover of MA, LC, ChE, GS and LD (>50%), relatively well the cover of BS and AS (30–45%) and only a small proportion of the variation in the cover of AL and PA (10–25%). Direct effects of EMH were often negatives but their strength depends on plant species. In three cases, these direct effects were strong and statistically significant (LD, MA and AL), in five cases were negative but statistically non-significant (GS, LC, PA. BS. ChE), and in one case was near zero (AS).

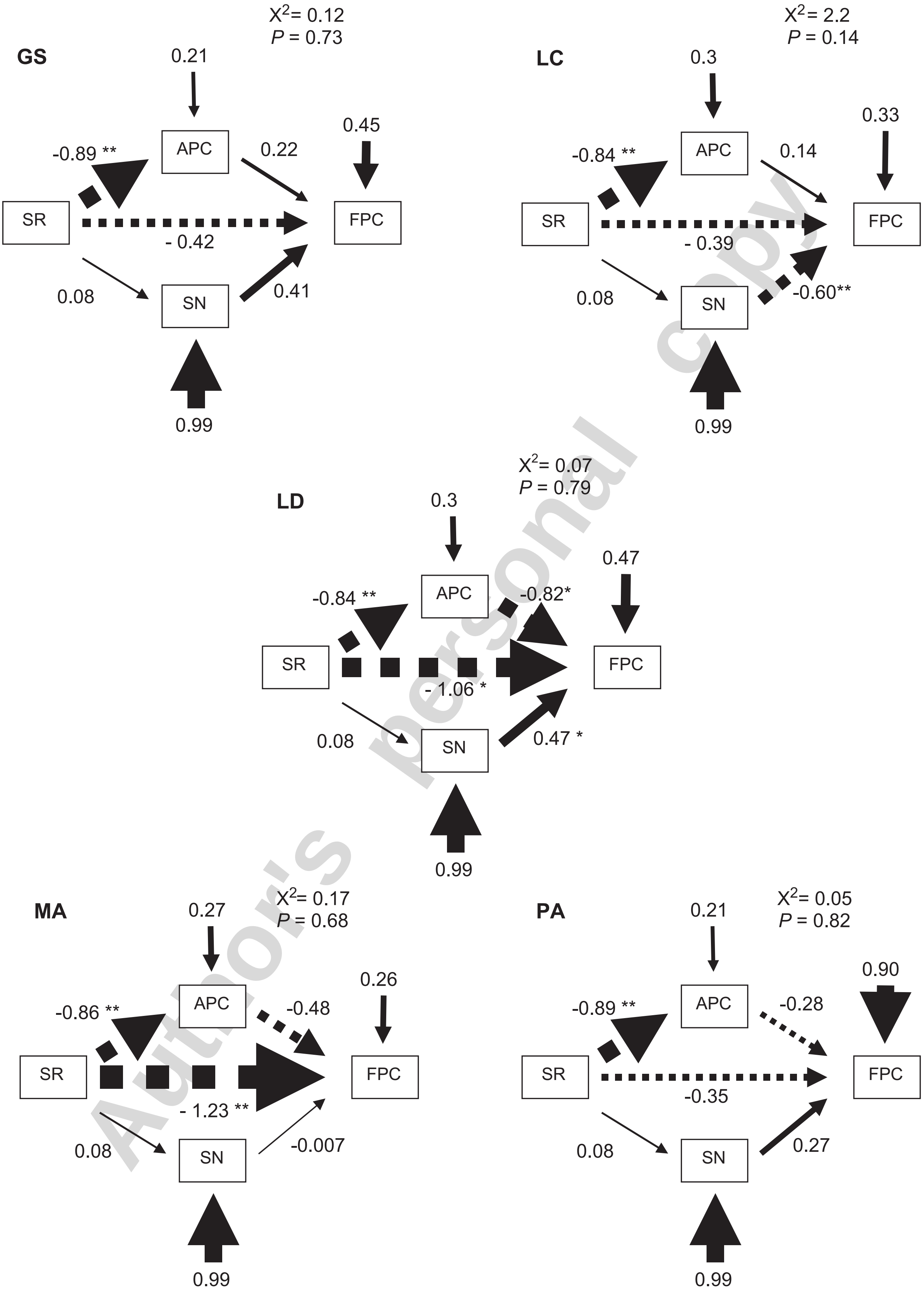
The strength and sign of indirect effects was different among plant species. Although the effect of EMH on the APC was negative and statistically significant in all the cases analyzed, changes on the APC affected differentially the focal plant species (Fig. 2). For example, the APC negatively affected the cover of LD, slightly positive the cover of BS, and showed a null effect on the cover of ChE (Fig. 2). Therefore, the indirect effect of EMH on a target plant species through changes on APC varied in strength and sign depending on their identity (Fig. 2).

In contrast, the indirect effect of EMH through the alteration of soil quality did not affect the cover of any species studied. This was a consequence of the lack of effect by EMH on soil quality. Therefore, independently of the importance of soil quality on plant cover (variable in strength and sign depending on the species, Fig. 2), indirect effects of EMH through this pathway were always irrelevant and less important than indirect effects through APC (Table 2).

The net effects of EMH on the cover of focal plant species (total co-variation estimated by Pearson coefficients) were always negative, varying between −0.08 and −0.82. Only two focal species (AL and PA) showed a total co-variation with EMH near to zero (−0.15 and −0.08, respectively). However, this absence of net effect was in both cases due to the fact that direct and indirect effects were relatively similar in magnitude but opposite in sign (Table 2). The sum of direct an indirect effects was very similar to the total co-variation values of each focal species, suggesting the absence of non-causal co-variation effects. The relative importance of indirect effects compared to the direct effects was larger for AS (1.5), similar for LD, PA, AL and BS (~0.8), and smaller for GS, LC, MA and ChE (<0.6) (Table 2).

There were two major findings in this study: indirect effects had almost the same importance than direct effects for explaining the net effect of EMH on plant species cover; and indirect effects of EMH through changes in the cover of nearby plants were stronger than indirect effects through changes in soil quality.

Our data fitted the model, suggesting that the pathways proposed explain relatively well the variation of the plant species cover. Both direct and indirect effects were important to understand the net effect of EMH on plant cover. While direct effects were more important


GS
X2= 0.12
P = 0.73
0.21
APC
0.22
0.45
-0.89 **
SR
- 0.42
FPC
0.08
SN
0.41
0.99
LC
X2= 2.2
P = 0.14
0.3
APC
0.14
0.33
-0.84 **
SR
- 0.39
FPC
0.08
SN
-0.60**
0.99
LD
X2= 0.07
P = 0.79
0.3
APC
-0.82*
0.47
-0.84 **
SR
- 1.06 *
FPC
0.08
SN
0.47 *
0.99
MA
X2= 0.17
P = 0.68
0.27
APC
-0.48
0.26
-0.86 **
SR
- 1.23 **
FPC
0.08
SN
-0.007
0.99
PA
X2= 0.05
P = 0.82
0.21
APC
-0.28
0.90
-0.89 **
SR
-0.35
FPC
0.08
SN
0.27
0.99

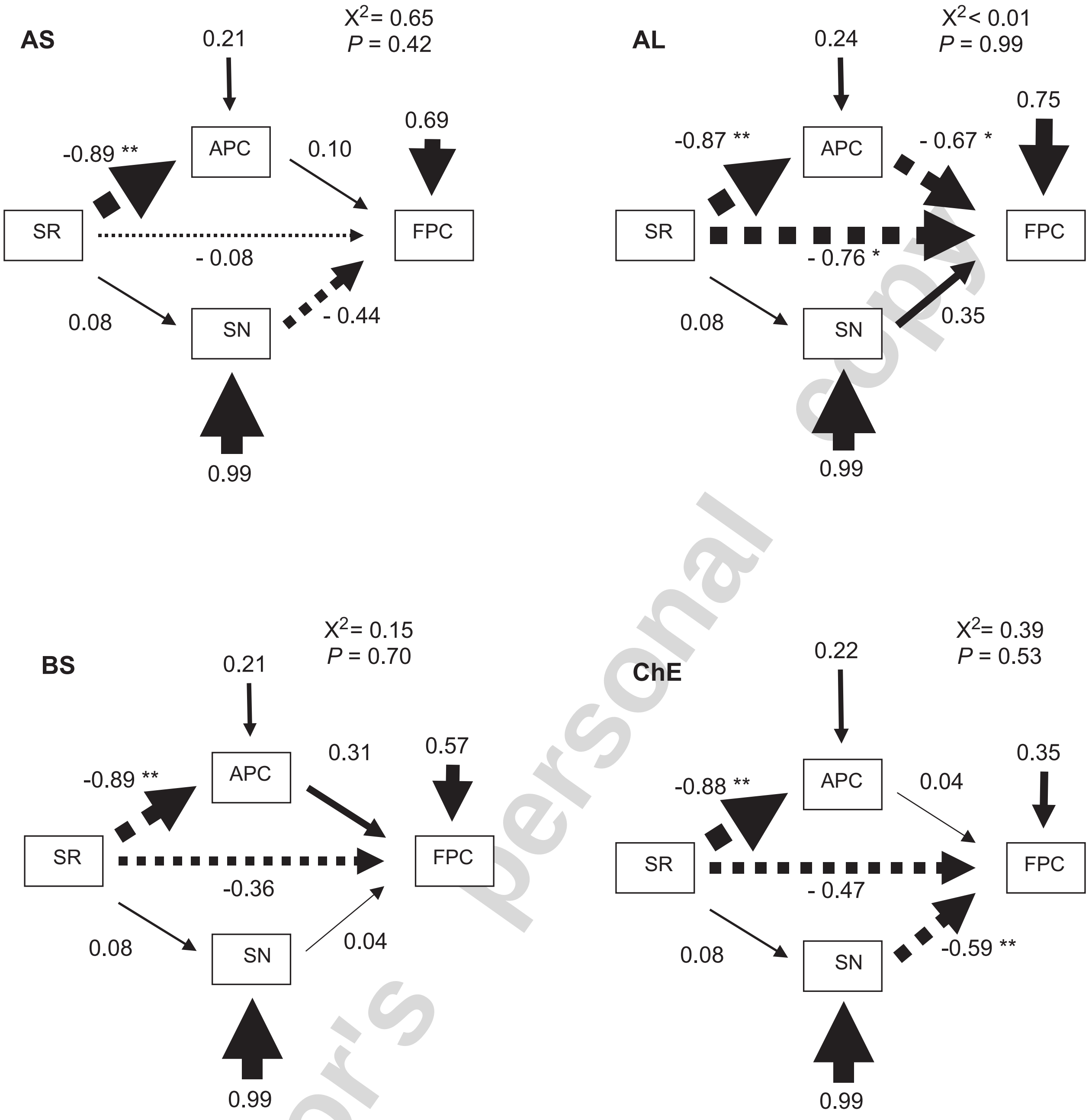


Fig. 2. (*Continued*)

than indirect effects for ChE, GS, LC, LD and MA; indirect effects were stronger or similar than direct effects for AS, AL, BS and PA (Table 2). Direct and indirect effects also differ in sign and complexity.

Fig. 2. Path analysis of causal relationship among variables hypothesized to be involved in direct and indirect effects of stocking rates on the cover of nine focal plant species. One-headed arrows represent direct causal effects. For each effect path, coefficients are given and are also represented by arrow line-thickness. Continuous lines indicate positive effects; dashes lines indicate negative effects. Significance of the path coefficients is indicated as follows: $*P<0.10$, $**P<0.05$. Variables included in the model are: stocking rates (SR), assemblage plant cover (APC), focal plant cover (FPC), and soil nutrients (SN). Unexplained variability is indicated with vertical arrows. The adequacy of models was evaluated based on χ^2 and associated *P*-values (higher *P*-value, means a better fit of the data with the model). Symbols of plant species are described in Table 1.

Table 2
Direct and indirect effects of exotic grazers on the cover of the plant species studied

Bivariate relationships	TC (A)	Direct (B)	CC—Indirect via APC (C)	CC—Indirect via SN (D)	Total (E = B+C+D)	NC (A–E)	RIIE
SR-AS	−0.21	−0.08	−0.09	−0.03	−0.20	−0.01	1.5
SR-AL	−0.15	−0.76	0.58	0.03	−0.15	0	0.8
SR-BS	−0.64	−0.36	−0.28	0.00	−0.64	0	0.8
SR-ChE	−0.55	−0.47	−0.03	−0.05	−0.55	0	0.2
SR-GS	−0.59	−0.42	−0.20	0.03	−0.59	0	0.6
SR-LC	−0.57	−0.39	−0.12	−0.05	−0.56	−0.01	0.4
SR-LD	−0.33	−1.06	0.69	0.04	−0.33	0	0.7
SR-MA	−0.82	−1.23	0.41	0.00	−0.82	0	0.3
SR-PA	−0.08	−0.35	0.25	0.02	−0.08	0	0.8

TC represents the total co-variation between stocking rates (SR) and each of the plant species studied estimated as correlation coefficients. The symbols of the plant species are given in the Table 1. Direct effects (Direct) and indirect effects (causal co-variation, CC) were estimated using the path values of the SEM. Non-causal co-variation (NC) was estimated as indicated in the table. The relative importance of indirect effects (RIIE) was estimated as $|(C+D)/B|$. Values larger than one represent a relatively more importance of indirect effects, similar than one represent similar relative importance, and smaller than one represent that direct effects are relatively more important than indirect effects.

Although variable in magnitude, direct effects were always negative (Fig. 2). This result did not come out as a surprise. Browsing and trampling, the two possible direct effects of EMH on plants, often have negative consequences on plant cover (Huntly, 1991; Marquis, 1992; Hunt, 2001). Accordingly, most of the plant species with stronger direct effects (e.g., MA, AL and LD) were frequently observed as very browsed (Table 1). On the other hand, indirect effects varied in importance and sign.

Among the two indirect pathways proposed that could affect the cover of a plant species, the effect of EMH through soil quality (SN) was always negligible and less important than the effect through changes in APC (Table 2). Conversely, indirect effects through APC were more important and complex. While EMH always affected the APC negatively; changes in the sign of indirect effects through APC depended exclusively on the effect of nearby plants on a given plant species.

An increase in the APC affected strong and negatively the cover of AL and LD, and subtly and negatively the cover of PA and MA (Fig. 2). There are, at least, two causes by which the cover of a particular species may be negatively affected by the cover of nearby plants: competition for resources and/or an increase in their chance to be eaten. In arid regions, water and nutrients availability largely determine plant vigor (Fowler, 1986). It is reasonable to expect that a target plant species suffer more competition for those resources as the cover of the surrounding plants increases. On the other hand, the probability of being browsed of a species often depends on the attractiveness of the context (Karban, 1997). In the study area, large generalist herbivores make foraging choices in relation to the distribution and abundance of the palatable plants (Guevara et al., 1996). Independently of its absolute palatability, a plant species may increase its chance to be eaten if the cover of nearby vegetation increases (Rousset and Lepart, 2002). Plant species with high probabilities to reduce their vigor through these two processes will benefit from the cover reduction of nearby plants by the EMH. Therefore, EMH should affect positively these plant species through indirect effects.

On the other hand, an increase in the cover of nearby plants affected positively BS and slightly positively GS and LC (Fig. 2). There are several ways by which a plant species may be benefited from an increase in the cover of the neighboring vegetation. For example, the accumulation of nutrients, provision of shade, amelioration of disturbance, or the protection from herbivores with the surrounding vegetation can enhance the vigor of a given plant species (Callaway et al., 2002; Booker et al., 2006; Baraza et al., 2006). Species highly dependent on these positive interactions will be negatively affected by the reduction in the cover of adjacent vegetation by EMH. Therefore, EMH affected negatively these species through indirect effects.

This work showed that the relationship between EMH and plant cover is often composed by direct and indirect effects. Moreover, we showed that the lack of statistical association (e.g., $r \sim 0$) not necessarily implies the absence of a biological relationship. Direct and indirect effects may be equal in magnitude but with different signs, producing a null net effect. This suggests that measures of net effects such as a simple correlation between EMH and plant traits, although it may be informative in some circumstances, it depicts an incomplete picture of the effects of EMH on plant cover. For example, it is inexactly that EMH did not affect the cover of AL; the strong and direct negative effect was moderately compensated by a positive indirect effect (Table 2). One possibility is that the negative impact of browsing on AL was compensated with a release in competitive pressure as a consequence of browsing on neighboring plants. This example illustrates well one of the main merit of this work: hypothesis like the one described above can be better formulated only if the relative importance of direct and indirect effects for each plant species is previously known.

The relative importance of direct versus indirect effects; and positive versus negative indirect effects was not related to any of the plants' traits analyzed (Table 1). With these results we cannot identify exactly which mechanisms among those proposed are modeling the cover of the plant species studied. However, this work offer good information about which plant species are more susceptible to indirect interactions and should be understood as the first step to understand the complex EMH–plant relationship in this arid ecosystem.

This work was partially supported by the CONICET, Argentina. We thank M. A. Aizen and two anonymous referees for their comments.

References

Ares, J., Beeskow, A., Bertiller, M., Rostagno, C., Irisarri, M., Anchorena, J., Defossé, G., Meroni, C., 1990. Structural and dynamics characteristics of overgrazed lands of Northern Patagonia, Argentina. In: Bremeyer, A. (Ed.), Managed Grasslands: Regional Studies. Elsevier Science Publishers, Amsterdam, pp. 149–175.

Augustine, D., McMaughton, S., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wild Life Management 62, 1165–1183.

Baraza, E., Zamora, R., Hodar, J., 2006. Conditional outcomes in plant–herbivore interactions: neighbors matter. Oikos 113, 148–156.

Belovsky, G., Slade, J., 2000. Insect herbivory accelerates nutrient cycling and increase plant production. Proc. Natt. Acad. Sci. 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.

Bigham, J.M., 1996. Methods of Soil Analysis. Soil Society of America, INC., Madison, Wisconsin, USA.

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

Booker, R., Scott, D., Palmer, S., Swaine, E., 2006. Transient facilitative effects of heather on Scots pine along a grazing disturbance gradient in Scottish moorland. Journal of Ecology 94, 637–645.

Bullock, J.M., Franklin, J., Stevenson, J., Silvertown, J., Coulson, S., Gregory, S., Tofts, R., 2001. A plant trait analysis of responses to grazing in a long-term experiment. Journal of Applied Ecolology 38, 253–267.

Callaway, R., Brooker, R., Chler, P., Kikvidez, Z., Lortie, C., Michalet, R., Paolini, L., Pugnaire, F., Newingham, B., Aschehough, E., Armas, C., Kikodze, D., Cook, B., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–847.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965.

Correa, M., 1969–1998. Flora Patagónica (siete volúmenes). Instituto Nacional de Tecnología Agropecuaria, Buenos Aires.

Del Valle, H., 1998. Patagonian soils: a regional synthesis. Ecología Austral 8, 103–123.

Fowler, N.L., 1986. The role of competition in plant communities in arid and semi-arid regions. Annu. Rev. Ecol. Syst. 17, 89–110.

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

Golluscio, R.A., Deregibus, V.A., Paruelo, J.M., 1998. Sustainability and range management in the Patagonian steppes. Ecología Austral 8, 265–284.

Graetz, D., 1994. Grasslands. In: Meyer, W., Turner, B. (Eds.), Changes in Land Use and Land Cover: A Global Perspective. Cambridge University Press, Cambridge, pp. 125–147.

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

Hulbert, S., 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monog. 54, 187–211.

Hunt, L.P., 2001. Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. Journal of Appl. Ecolology 38, 238–252.

Huntly, N., 1991. Herbivores and the dynamics of communities and ecosystems. Ann. Rev. Ecol. Syst. 22, 477–503.

Karban, R., 1997. Neighborhood effects plant's risk of herbivory and subsequent success. Ecol. Entomology 22, 433–439.

Landsberg, J., James, C.D., Morton, S.R., Müller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. Journal of Applied Ecolology 40, 1008–1024.

Legendre, P., Legendre, L., 2004. Numerical Ecology, second ed. Elsevier Scientific Publishing Company, Amsterdam.

León, R., Brand, D., Collantes, M., Paruelo, J., Soriano, A., 1998. Grandes unidades de vegetación de la Patagonia extra andina. Ecología Austral 8, 125–144.

Marquis, R.J., 1992. The selective impact of herbivores. In: Fritz, R., Simms, E. (Eds.), Plant Resistance to Herbivores and Pathogens: Ecology, Evolution and Genetics. University of Chicago Press, Chicago, Illinois, USA, pp. 301–325.

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

Mitchell, R., 2001. Path Analysis. In: Scheiner, S., Gurevitch, J. (Eds.), Design and Analysis of Ecological Experiments. Oxford University Press, Oxford, pp. 217–234.

Nash, M.S., Whitford, W.G., Soyza, A.G., Van Zee, J.W., Havstad, K.M., 1999. Livestock activity and Chihuahuan Desert annual-plant communities: boundary analysis of disturbance gradients. Ecological Applications 9, 814–823.

Paige, K., Whitham, T., 1987. Overcompesation in response to mammalian herbivory: the advantage of being eaten. Am. Nat. 129, 407–416.

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

Perelman, S., León, R., Bussacca, J., 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. Ecography 20, 400–406.

Rousset, O., Lepart, J., 2002. Neighborhood effects on the risk of an unpalatable being grazed. Plant Ecology 165, 197–206.

Ruess, R.W., McMaughton, 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.

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.

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 composition in an arid environment in northern Patagonia. Applied Vegitation. Science 9, 109–116.

Vallentine, J.F., 2001. Grazing Management. Academic Press, San Diego.

Vázquez, D.P., Simberloff, D., 2004. Indirect effects of an introduced ungulate on pollination and plant reproduction. Ecol. Monog. 74, 281–308.

Zamora, R., Hódar, J., Gómez., J.M., 1999. Plant–herbivore interaction: beyond a binary vision. In: Puignaire, F.I., Valldares, F. (Eds.), Handbook of Functional Plant Ecology. Marcel Dekker Inc, New York, pp. 677–718.